

# CHAPTER 1-1

# INTRODUCTION

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# CHAPTER 1: INTRODUCTION

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



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

## Thinking on a New Scale

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

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

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

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

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

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

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

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

## Adaptations to Land

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



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

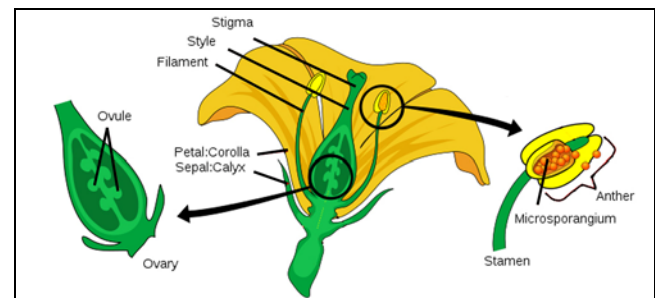


Figure 3. Flower diagram showing locations of sporophyte reproductive parts. Modified from drawing by Mariana Ruiz, through public domain.

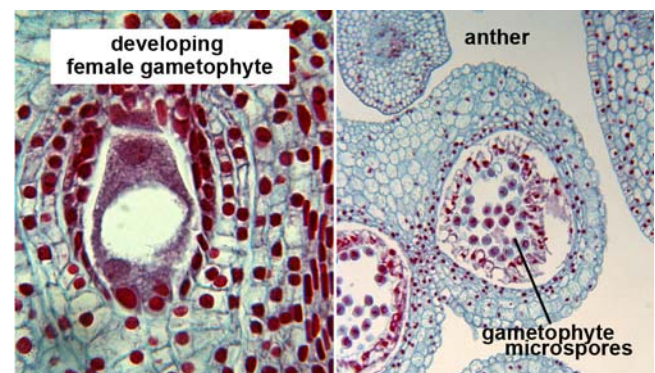


Figure 4. *Lilium* gametophytes showing developing female gametophyte inside ovule on left and developing male gametophytes (microspores) in anther on right. Photos by D. L. Nickrent, through fair use license for educational use.

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



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



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

Proctor (2007) points out that minimizing water loss in bryophytes is regulated by boundary-layer resistances and energy budgets (see also Gates 1980; Proctor *et al.* 2007; Monteith & Unsworth 2013). For these small plants, the "intricacy of form" lies within this laminar boundary layer, a space where water vapor and CO<sub>2</sub> are able to move, albeit slowly, by molecular diffusion. This degree of intricacy may affect capillary storage, water movement, gas exchange, and CO<sub>2</sub> uptake.

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

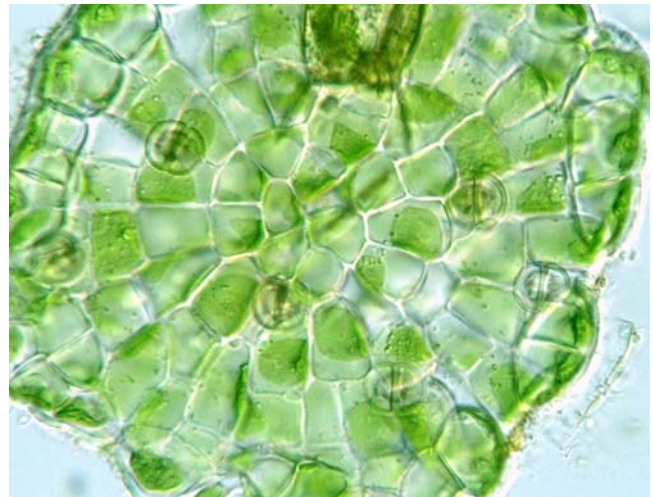


Figure 7. *Coleochaete*, a likely ancestor of bryophytes. Photo by Yuuji Tsukii, with permission.

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

#### Bryo-ontogeny

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

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

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

Contributed by Wim Meijer, Bryonet 3 September 1999

## Minimum Size

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

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

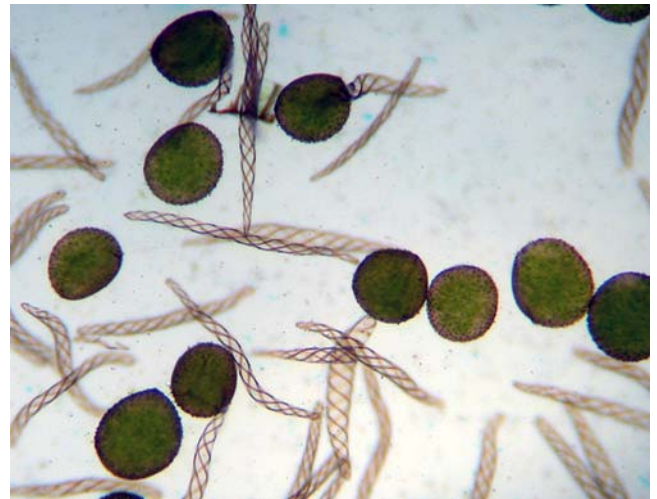


Figure 8. *Conocephalum conicum* spores & elaters, an example of **homosporous** in liverworts. Photo by UBC Botany Website, with permission.



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

Proctor (2010) considers it infeasible for evolution and natural selection to produce a tracheophyte *de novo*. Rather, these must have evolved from a poikilohydric strategy. The drive toward tracheophytes could very likely have arisen from the limitations of two essential resources, water and CO<sub>2</sub>. Whereas having air spaces within the leaves is common among tracheophytes, it is rare among bryophytes. Nevertheless, we find that a number of modern bryophytes also have such adaptations: **Marchantiales** (thallose liverworts; Figure 10), **Polytrichaceae** (haircap mosses; Figure 11), and sporophytes of **Bryophyta** (mosses; Figure 12) and **Anthocerotophyta** (hornworts; Figure 13) in particular.



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



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



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



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

Although the early atmosphere most likely provided higher levels of CO<sub>2</sub> (~10X; Berner 1998 in Proctor 2010) than our present-day environment, an epidermis, seen in many thallose liverworts, would protect against both mechanical damage and water loss. The development of the epidermis, followed by increasing cuticle development on both epidermal and non-epidermal plants, most likely marked the beginnings for a greater need for CO<sub>2</sub>.

The complexity required to maintain a tree simply would not work to maintain a plant that is 100 times smaller and has a volume one millionth that of a tree (Proctor 2010). This smaller size necessarily means that the bryophyte as a plant has less interaction with the atmosphere, although its surface to volume ratio is greater, creating more area for interaction per unit volume. The non-linear nature of the bryophyte surface can create eddy diffusion that permits exchange between the bryophyte and its surroundings, but this can be minimized by the tightness of the lower portions of the plant. The selection pressures of strength and movement of gases and water in a tracheophyte leaf provide no constraint on the bryophyte. Thus, slow molecular diffusion is sufficient for heat and mass transfer in bryophytes. The one-cell-thick leaves of most bryophytes present two surfaces for diffusion of CO<sub>2</sub> into the leaf and directly to the cells that need it. Thus, being small has its advantages, albeit requiring quite different strategies.

## Do Bryophytes Lack Diversity?

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

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

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

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

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

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

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

## The "Moss"



The term "moss" has a multitude of meanings in English, and even in other languages, the term referring to this group of plants likewise has multiple meanings. In Japanese, the word is "koke" (left) and means not

only members of the Bryophyta, but also any of the small plants. Thus plants suitable for plantings under a bonsai tree are *koke*.

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



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



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

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

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

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

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

## What's in a Name?

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

'What sort of insects do you rejoice in, where YOU come from?' the Gnat inquired.

'I don't REJOICE in insects at all,' Alice explained, 'because I'm rather afraid of them — at least the large kinds. But I can tell you the names of some of them.'

'Of course they answer to their names?' the Gnat remarked carelessly.

'I never knew them do it.'

'What's the use of their having names' the Gnat said, 'if they won't answer to them?'

'No use to THEM,' said Alice; 'but it's useful to the people who name them, I suppose. If not, why do things have names at all?'

'I can't say,' the Gnat replied.

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

But the naming system is fraught with problems. As we learn more about organisms, we find they have been placed in a genus where they have no close relatives. Or their birth certificates that provide a legitimate name and

description, after being lost for a long time, resurface with an earlier name that has priority. These problems we must continue to deal with, and we have made provisions in our nomenclatural code to do so.

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

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

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

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

### Phyla/Divisions

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

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

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

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



19), **Andreaeobryopsida** (Figure 20), **Polytrichopsida** (Figure 11), and **Bryopsida** (comprising more than 95% of the species; Figure 12). **Sphagnophyta** (Figure 18): Considered by Crum (2001) to warrant a separate phylum, but still considered by most authors as a class of **Bryophyta** (**Sphagnopsida**) in the **Bryophyta**; two genera only - *Sphagnum* (Figure 18) and *Ambuchanania* (Figure 21).



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



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



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



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



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



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

## Role of Bryology

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

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

## Summary

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

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

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

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

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

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

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

## Acknowledgments

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

## Literature Cited

- Cronquist, A. A., Takhtajan, A., and Zimmermann, W. 1966. On the higher taxa of Embryobionta. *Taxon* 15: 129-134.
- Crum, H. 1976. Mosses of the Great Lakes Forest, revised edition. Vol. 10, University Herbarium, University of Michigan, Ann Arbor, pp. 1-404.
- Crum, H. A. 2001. Structural Diversity of Bryophytes. The University of Michigan Herbarium, Ann Arbor, Michigan, 379 pp.
- Edwards, S. R. 1992. Mosses in English literature. British Bryological Society special volume No 4 (48 pages, 12 figures).
- Gates, D. M. 1980. Biophysical Ecology. Springer, New York, 635 pp.
- Gerson, U. 1972. Mites of the genus *Ledermuelleria* (Prostigmata: Stigmaeidae) associated with mosses in Canada. *Acarologia* 13: 319-343.
- Graham, L. E., Arancibia-Avila, P., Taylor, W. A., Strother, P. K., and Cook, M. E. 2012. Aeroterrestrial *Coleochaete* (Streptophyta, Coleochaetales) models early plant adaptation to land. *Amer. J. Bot.* 99: 130-144.
- Lamparter, T., Brückner, G., Esch, H., Hughes, J., Meister, A., and Hartmann, E. 1998. Somatic hybridisation with aphototropic mutants of the moss *Ceratodon purpureus*: genome size, phytochrome photoreversibility, tip-cell phototropism and chlorophyll regulation. *J. Plant Physiol.* 153: 394-400.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73: 1943-1967.
- Monteith, J. L. and Unsworth, M. H. 1990. Principles of Environmental Physics. Academic Press, London, 422 pp.
- Proctor, M. C. F. 2007. Ferns, evolution, scale and intellectual impedimenta. *New Phytol.* 176: 504-506.
- Proctor, M. C. F., Oliver, M. J., Wood, A. J., Alpert, P., Stark, L. R., Cleavitt, N. L., and Mishler, B. D. 2007. Desiccation-tolerance in bryophytes: A review. *Bryologist* 110: 595-621.
- Proctor, M. C. F. 2010. Trait correlations in bryophytes: Exploring an alternative world. *New Phytol.* 185: 1-3.
- Raven, J. A. 1999. The minimum size of seeds and spores in relation to the ontogeny of homoiohydric plants. *Funct. Ecol.* 13: 5-14.
- Wyatt, R. 1994. Population genetics of bryophytes in relation to their reproductive biology. *J. Hattori Bot. Lab.* 76: 147-157.