

CHAPTER 2-1

MEET THE BRYOPHYTES

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CHAPTER 2-1

MEET THE BRYOPHYTES



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

Definition of Bryophyte

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

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



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



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



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

Nomenclature

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

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

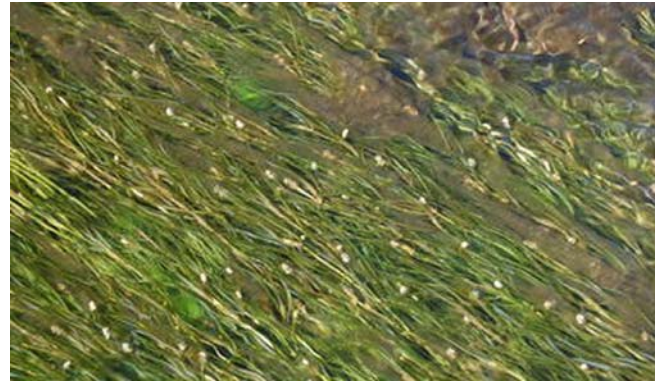


Figure 4. *Potamogeton turionifer*, in a genus that was originally included in the moss genus *Fontinalis*. Photo by C. B. Hellquist, through Creative Commons.



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

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

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

What Makes Bryophytes Unique?

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

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

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



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



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



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

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



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

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

to retention of zygotes on the parent, resulting in embryos. The plant subkingdom **Bryobiotina** (bryophytes) is separated from the Kingdom Protista by the presence of **multicellular sexual reproductive structures** protected by a **jacket layer** (antheridia for sperm and archegonia for

eggs), as opposed to unicellular antheridia and oogonia in the algae, and the presence of an **embryo** (Figure 15), the forerunners of which can be found in the charophytes (Kingdom Protista; Graham *et al.* 1991; Mishler 1991).

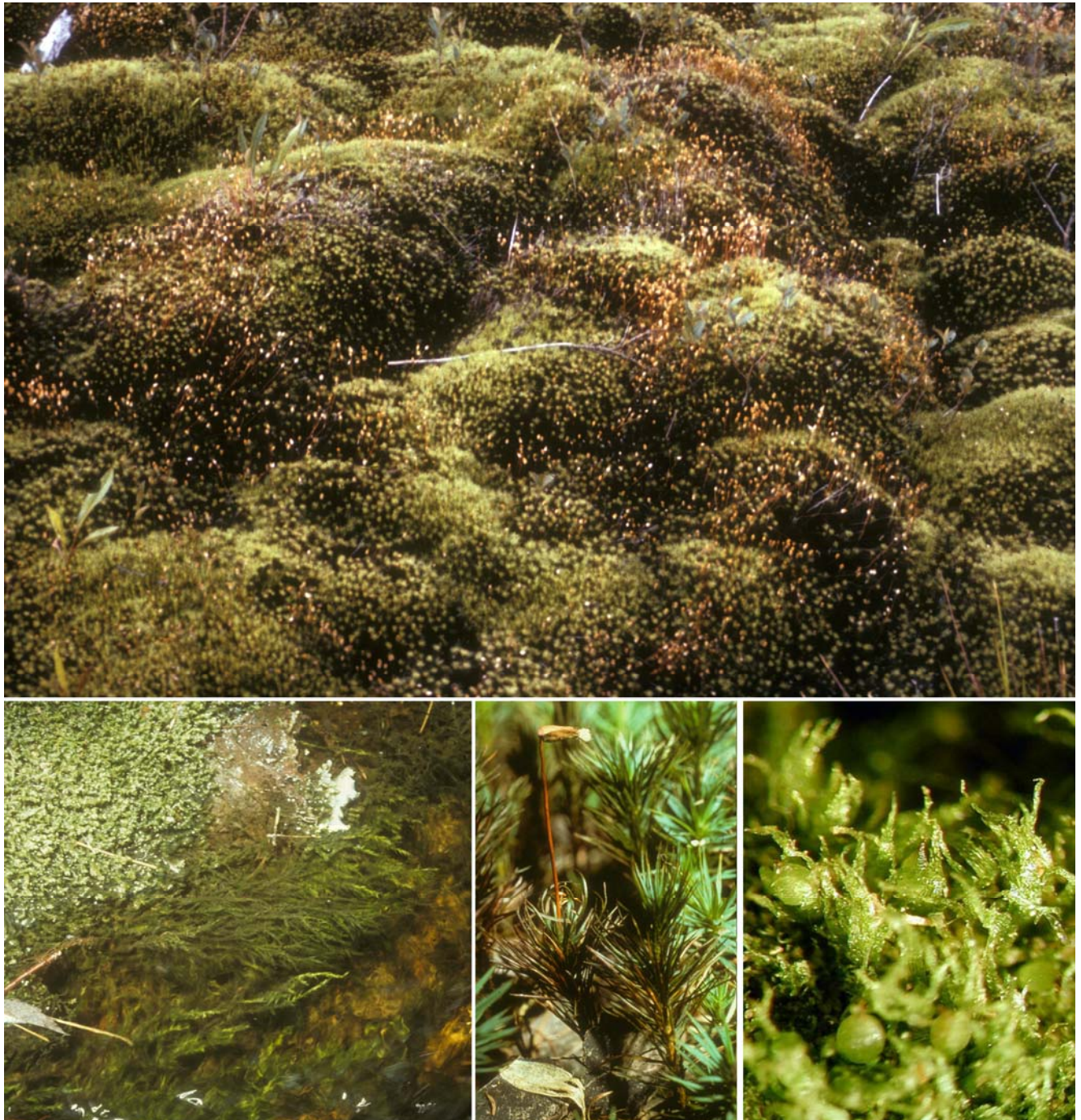


Figure 10. Bryophytes vary in size from the large *Polytrichum commune* (upper), *Fontinalis novae-angliae* (left), and *Dawsonia superba* (middle) to the minute *Ephemenum minutissimum* (right). Photos by Janice Glime; *Ephemenum* by Michael Lüth, with permission.

Who are the Relatives?

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



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



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

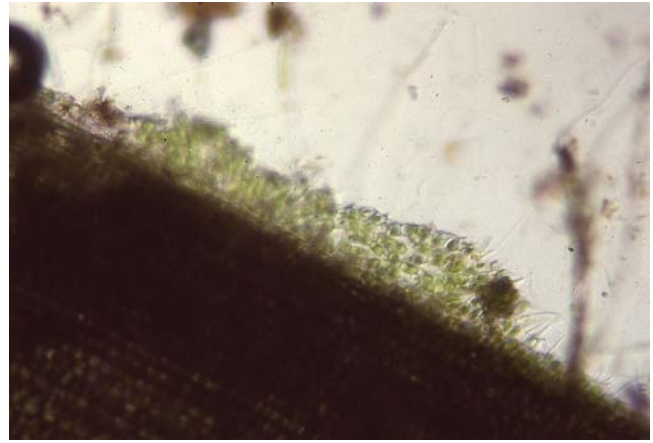


Figure 13. *Coleochaete* thallus from a side view on a vascular plant. Photo by Janice Glime.

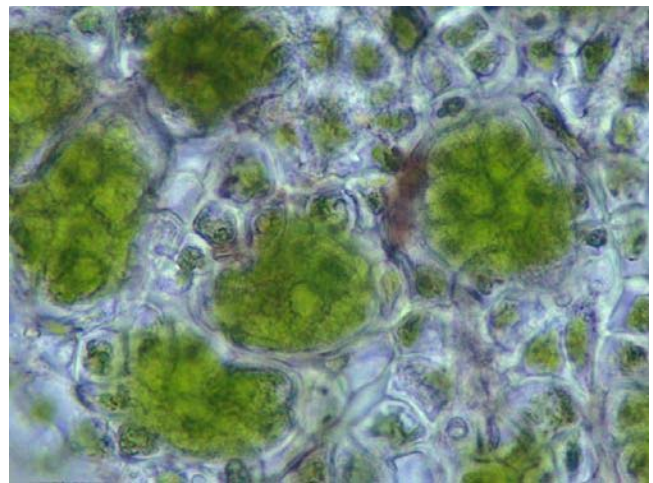


Figure 14. *Coleochaete conchata* with dividing zygotes. Photo by Charles F. Delwiche. Permission pending.

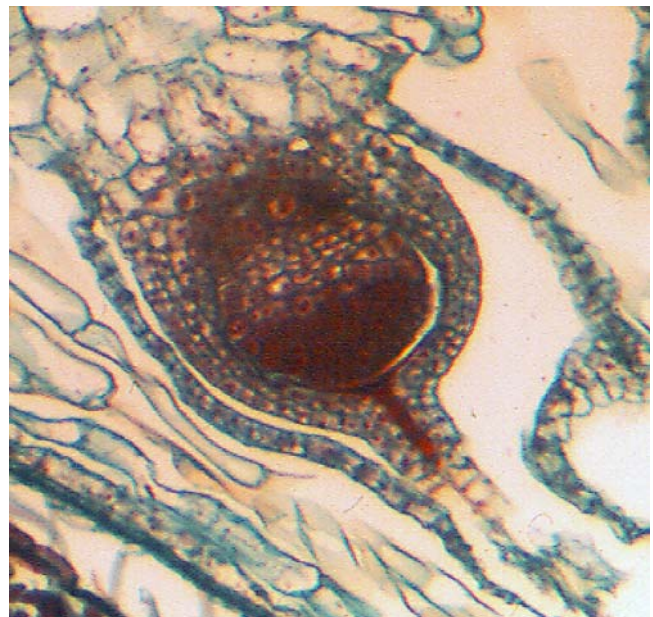


Figure 15. *Marchantia* (Phylum **Marchantiophyta**, Class **Marchantiopsida**) archegonium with embryo attached to parent gametophyte tissue. Photo by Janice Glime.

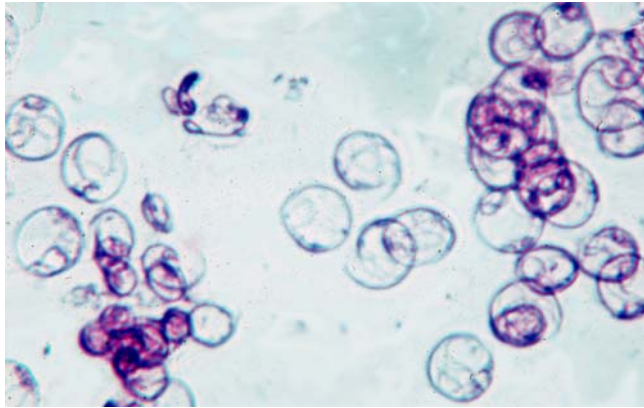


Figure 16. Stained sperm of Bryophyta, having spiral body and two flagella. Photo by Janice Glime.

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



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



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



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



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

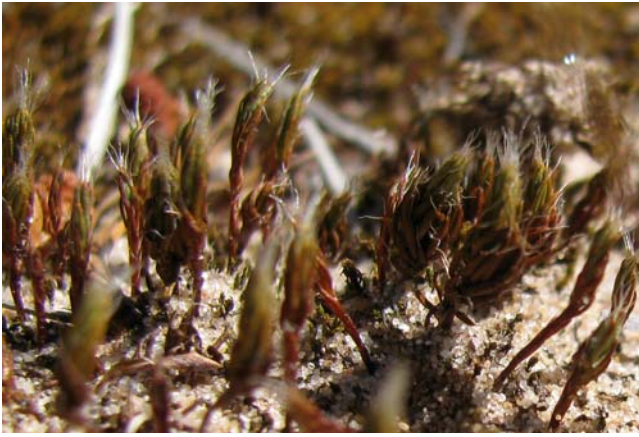


Figure 21. *Polytrichum piliferum* in a dry state. Water is slow to penetrate these leaves with a thin waxy coating. Photo by Janice Glime.

Two Branches

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

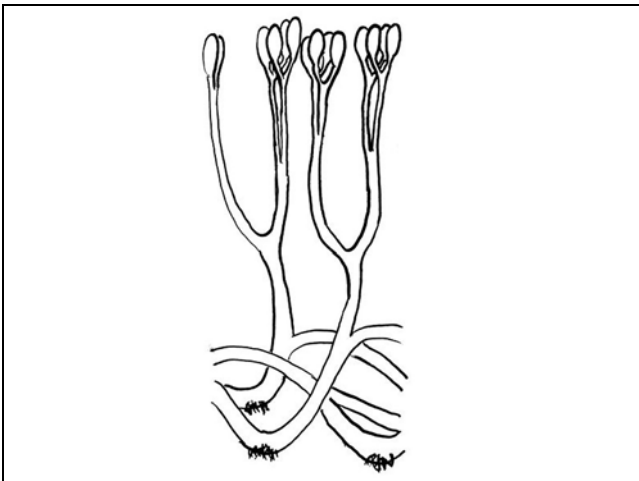


Figure 22. *Aglaophyton* reconstruction. Drawing by Griensteidl, through Creative Commons.



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

Limitations of Scale

Limited by Scale – and No Lignin

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

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

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

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

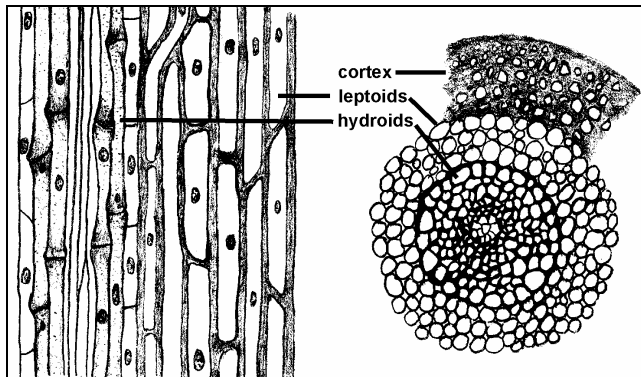


Figure 24. Longitudinal and cross sections of a stem with hydroids and leptoids, typical of taxa such as the Polytrichaceae. Drawings by Margaret Minahan, with permission.

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

Limited by Scale – Forced to Be Simple

Niklas (1997) suggests that maintaining hydration necessarily imposes a small size on bryophytes. But this could be a question of the chicken or the egg. Being small

prevents bryophytes from having a complex conducting system, and lacking a complex conducting system keeps them from attaining great size. Bonner (2004) demonstrates that in general larger entities, whether they are organisms or societies, have a greater division of labor. In plants, this is manifest in a greater variety of cell types. Thus, smaller organisms are necessarily simpler.

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



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



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

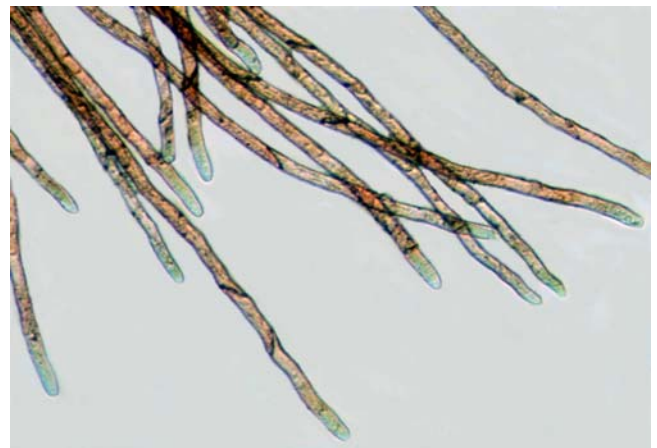


Figure 27. Microscopic view of rhizoids of the brook moss, *Fontinalis*, showing multicellular structure and diagonal crosswalls. Photo by Janice Glime.

Limited by Scale – Needing to Swim

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

Limited by Scale – and Housing an Embryo

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

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



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

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

Higher Classifications and New Meanings

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

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

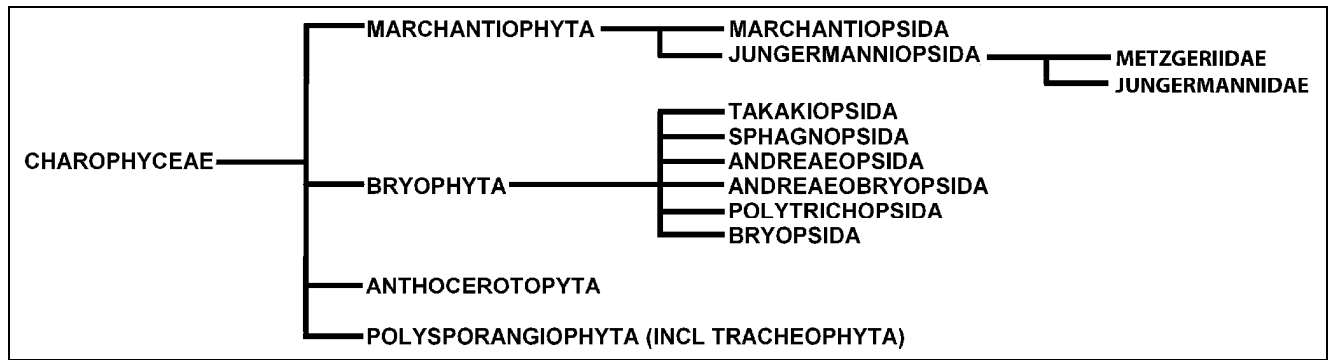


Figure 29. Schematic representation of the **Bryobiotina** phyla and classes related to other members of the Plant Kingdom (**Polysporangiophyta**), based on Shaw & Goffinet 2000.

New Meanings for the Term Bryophyte

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

Viridiplantae

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

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

This brings us back to our earlier discussion of the term "bryophyte." Mishler states that he does agree with Jon Shaw that "bryophyte" (small "b") is a useful term for talking about plants with a somewhat similar biology, like

"prokaryote," "invertebrate," or "algae," but there is no room for it in formal cladistic classification.

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

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

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

Differences within Bryobiotina

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

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

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

Perhaps the bigger question that remains to be answered is whether the bryophytes are truly the first and most primitive land plants, or if they are instead derived from other land plant embryophytes by reduction. In any case, it appears that they were derived independently from the tracheophytes as we know them (Héban 1965). Their absence of lignin to protect them from UV light and other aspects of their simple structure suggests they would have been unable to survive on land until the development of larger plants to provide shade and maintain moisture. Raven (2000) suggests that such protective compounds, common throughout the rest of the plant kingdom, may have been lost by reduction. Rather, based on their CO₂ affinities through use of **RUBISCO** (enzyme that catalyzes carbon fixation in plants), it would appear that all the **embryophytes** (*i.e.* all members of plant kingdom) may have evolved under the influence of the high levels of atmospheric CO₂ present in the late Lower Palaeozoic.

Intraspecific Taxa

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

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

While generally a **species** is a group of potentially interbreeding organisms, isolated reproductively from other units considered to be species, that is not a practical

definition because we do not have the resources to determine it each time we find an organism. On the other hand, genetic variation and founder populations may look different from their parent populations. In attempting to indicate differences among our study locations, we are forced to apply one of the above terms to distinguish our organisms.

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

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



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

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

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

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



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

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

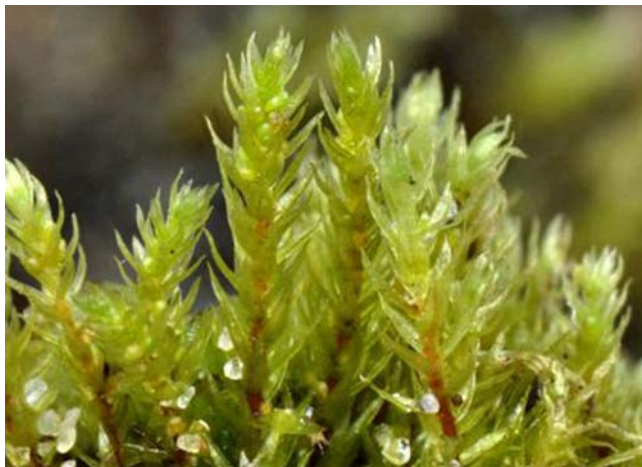


Figure 32. *Pohlia bulbifera* with bulbils in upper leaf axils. Photo by J. C. Schou, through Creative Commons.

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

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

Summary

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

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

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

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

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