

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, they 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, 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** (=division), the **Anthocerotophyta**. Most bryologists also now agree that the liverworts should occupy a separate phylum, the **Marchantiophyta** (also known as Hepatophyta, Hepaticophyta, and class Hepaticae), leaving the mosses as the only members of **Bryophyta** (also known as the class Musci). Together, the mosses, liverworts, and hornworts are still considered by the English name of **bryophytes**, a term to be used in its broad sense in this book and having no taxonomic status, and some have suggested for them the subkingdom name **Bryobiotina**.

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



Figure 1. *Buxbaumia aphylla*, a moss dependent upon its protonema for support of the sporophyte and sporting a thick stalk and robust capsule. Photo by Michael Lüth.

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* and *Viridivellus pulchellum* (Crum 2001). The more common *Buxbaumia* has a large capsule on a

thick stalk (Figure 1), 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* is only 0.5-2 mm in diameter. At the other end of the scale, the moss *Polytrichum commune* (Figure 2) can attain more than half

a meter height in the center of a hummock and *Dawsonia superba* (Figure 2) can be up to 70 cm tall with leaves of 35 mm length (Crum 2001) and be self-supporting. *Fontinalis* species (Figure 2), supported by their water habitat, can be 2 m in length.

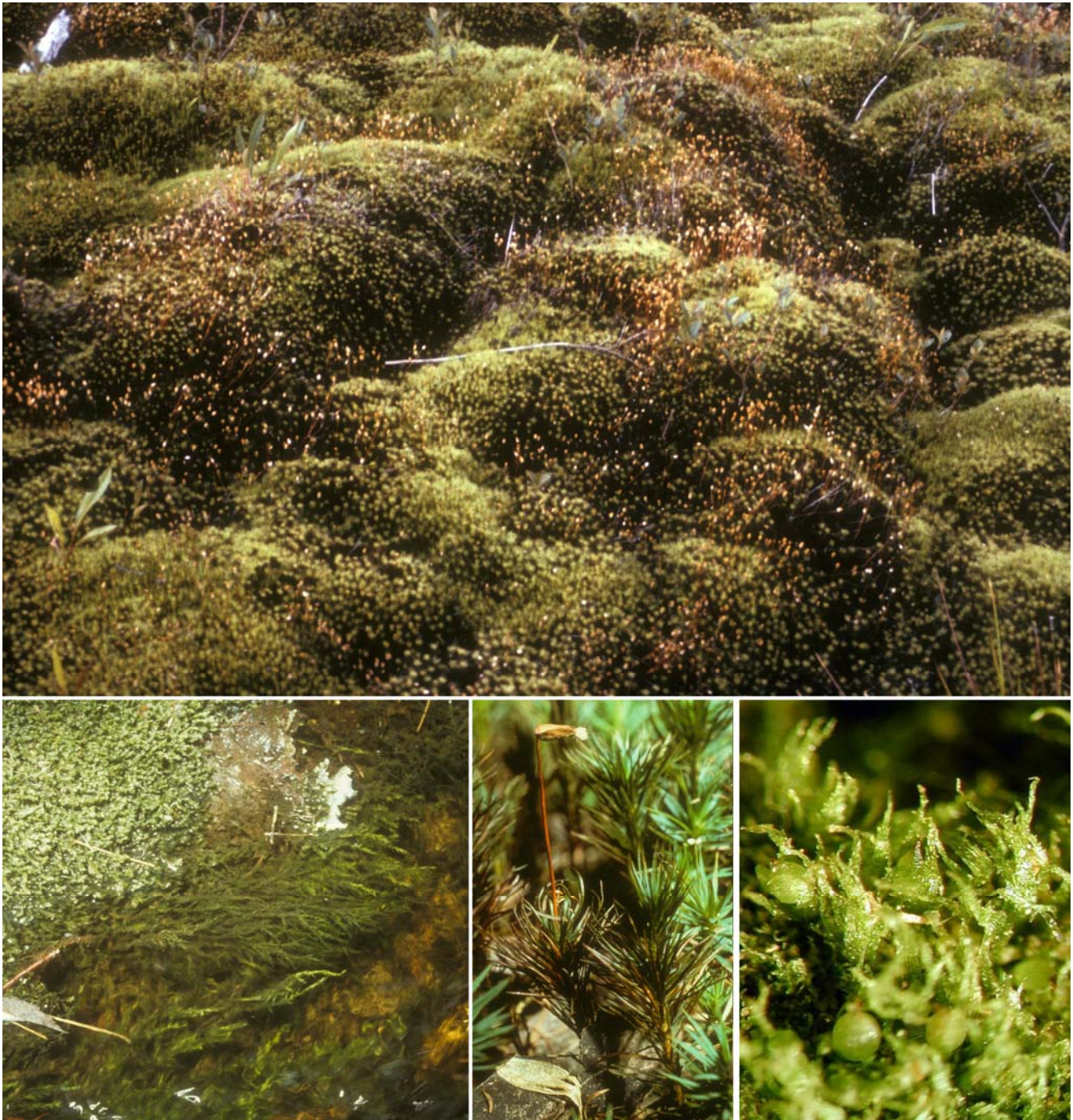


Figure 2. Bryophytes vary in size from the large *Polytrichum commune* (**upper**), *Fontinalis novae-angliae* (**left**), and *Dawsonia superba* (**middle**) to the minute *Ephemerum minutissimum* (**right**). Photos by Janice Glime; *Ephemerum* by Michael Lüth.

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 **parasitic** on the gametophyte (Figure 3)! The gametophyte **lacks secondary growth** and **meristematic tissues**, growing new tissue instead from a **single apical cell** (Crum 1991).



Figure 3. *Physcomitrium pyriforme* showing leafy gametophyte with parasitic sporophyte stalk and capsule. Photo by Michael Lüth.

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 4), the

forerunners of which can be found in the charophytes (Kingdom Protista; Graham *et al.* 1991; Mishler 1991).

Their nearest algal relatives appear to be members of the Charophyta. Although the charophyte reproductive structure is still only a single cell, that cell is surrounded by corticating cells that give the egg and **zygote** multicellular protection. Nevertheless, the zygote fails to develop further until leaving its parent. In the green alga *Coleochaete*, however, the female reproductive organ becomes surrounded by overgrowths of cells from the thallus following fertilization, and the zygote divides, becoming multicellular. Recognition of these similarities to 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 5), 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.

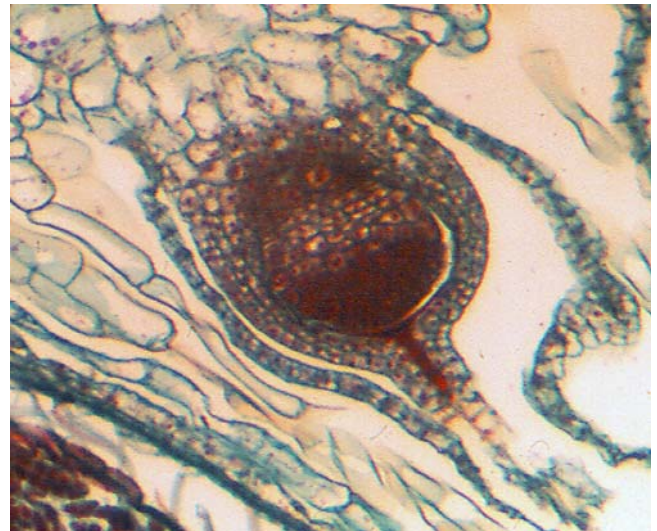


Figure 4. *Marchantia* (Phylum Marchantiophyta, Class Marchantiopsida) archegonium with embryo attached to parent gametophyte tissue. Photo by Janice Glime.

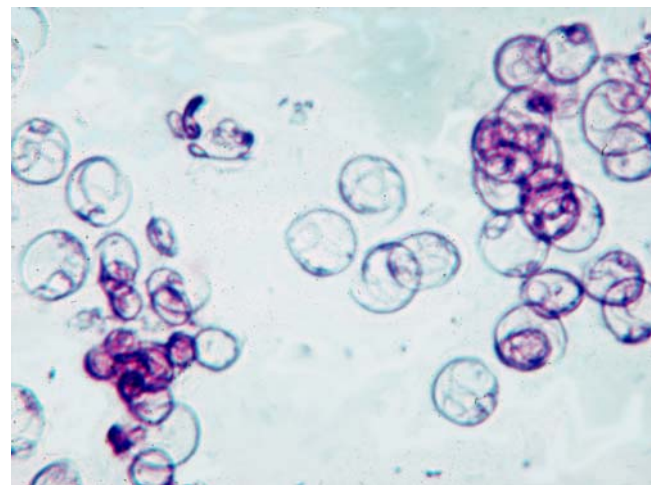


Figure 5. Stained sperm of Bryophyta, having spiral body and two flagella. Photo by Janice Glime.

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, *Notothylas orbicularis* – hornwort, and *Sphagnum fimbriatum* – peatmoss) 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**, that is having most water movement occurring within the plant, were recognized early 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 *Plagiomnium* and *Polytrichum* 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.

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*, which lacks tracheids) and those 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, and hopefully help us identify their closest relatives (Zander 2006). 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**.

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 unligified 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. Edelmann *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. Certainly many bryophytes possess phenolic compounds similar to lignin.

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 they 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 6) 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 6), 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.

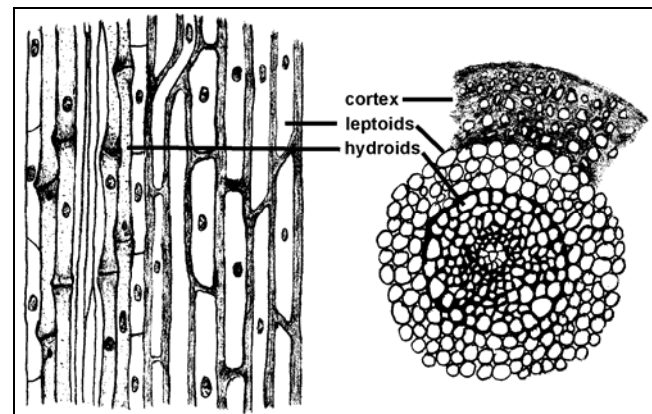


Figure 6. Longitudinal and cross sections of a stem with hydroids and leptoids, typical of taxa such as the Polytrichaceae. Drawings by Margaret Minahan.

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 7, Figure 8, Figure 9), 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.



Figure 7. *Fontinalis* showing leaves (phyllids) with a clump of rhizoids at the node. Photo by Janice Glime.



Figure 8. *Fontinalis* plant with rhizoids attached to paper towel. Photo by Janice Glime.

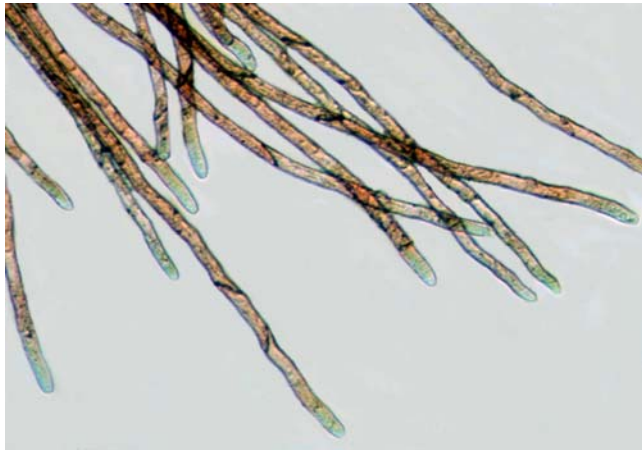


Figure 9. Microscopic view of rhizoids of the brook moss, *Fontinalis*, showing multicellular structure and diagonal crosswalls. Photo by Janice Glime.

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.

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 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 10), 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 10). 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).



Figure 10. Young embryo of *Marchantia polymorpha* showing early multicellular stage enclosed within the archegonium. Photo modified from Triarch by Janice Glime.

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 they 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.

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!

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, differing from other mosses and all liverworts, and its flavonoids 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** (chapter frontispiece). 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.

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 parasitic 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.

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