CHAPTER 2-1
MEET THE BRYOPHYTES

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"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** (=division), the **Anthocerotophyta** (Shaw & Renzaglia 2004). Most bryologists also now agree that the liverworts should occupy a separate phylum, the **Marchantiophyta** (also 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 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**.

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 has 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.
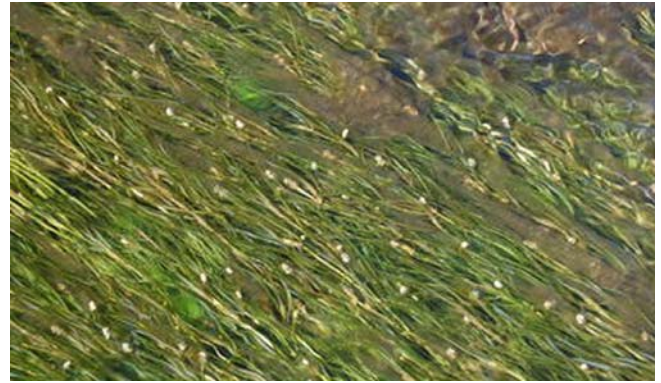

Figure 4. *Potamogeton turionifer*, in a genus that was originally included in the moss genus *Fontinalis*. Photo by C. B. Hellquist, through Creative Commons.

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**, **Hepaticae**, 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; Séneca & 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. Its lack of leaves caused scientists originally to consider it to be a fungus. Photo by Michael Lüth, with permission.

Figure 8.   *Monocarpus sphaerocarpus*. 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 **1*n*** (**gametophyte**) generation, having just one set of chromosomes to dictate their appearance and function. By contrast, the analogous structures are **sporophytic** (**2*n***) 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 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 parasitic on 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).
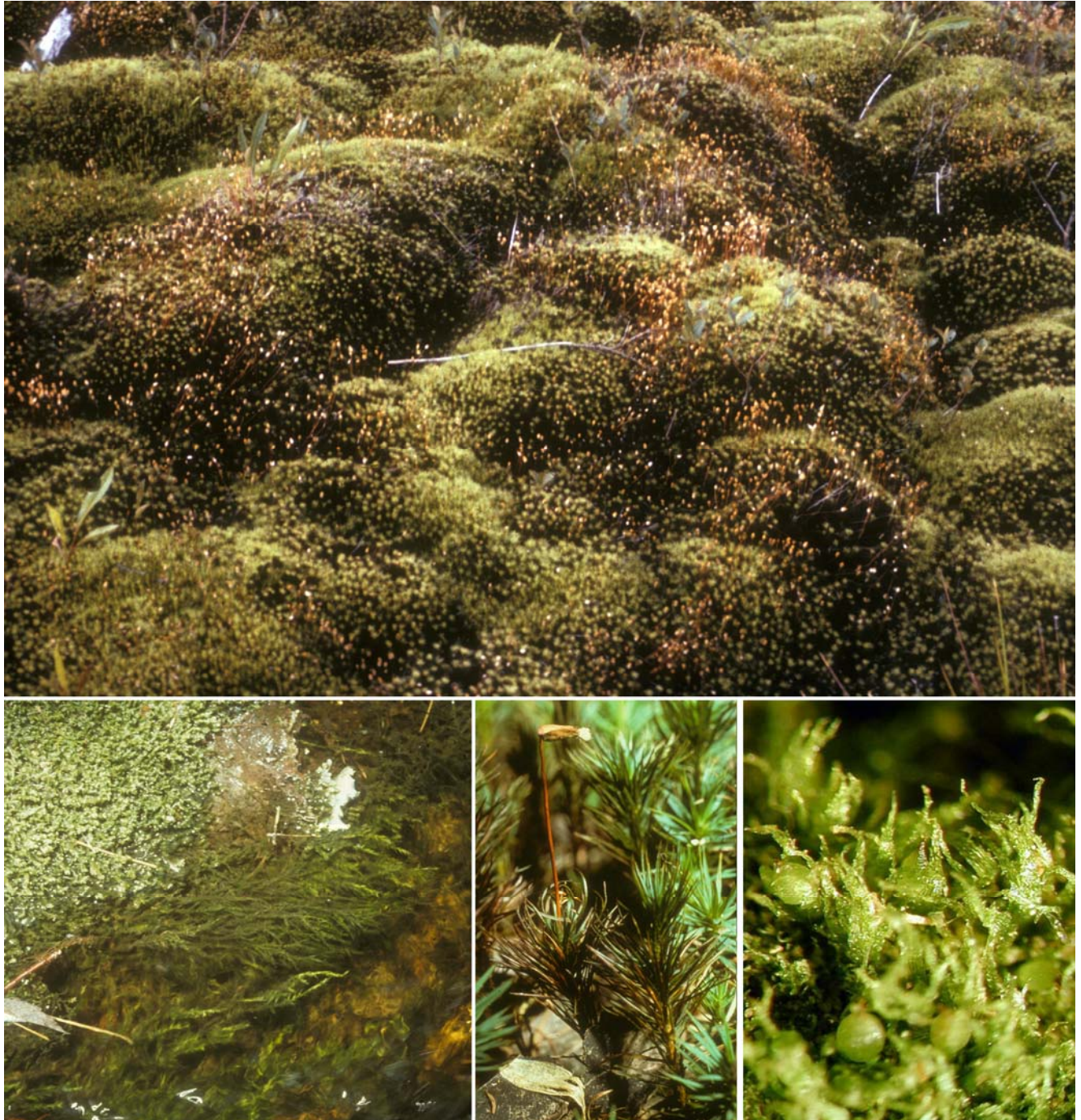

Figure 10. Bryophytes vary in size from the large *Polytrichum commune* (**upper**), *Fontinalis novae-angliae* (**left**), and *Dawsonia superba* (**middle**) to the minute *Ephemerum minutissimum* (**right**). Photos by Janice Glime; *Ephemerum* by Michael Lüth, with permission.

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.
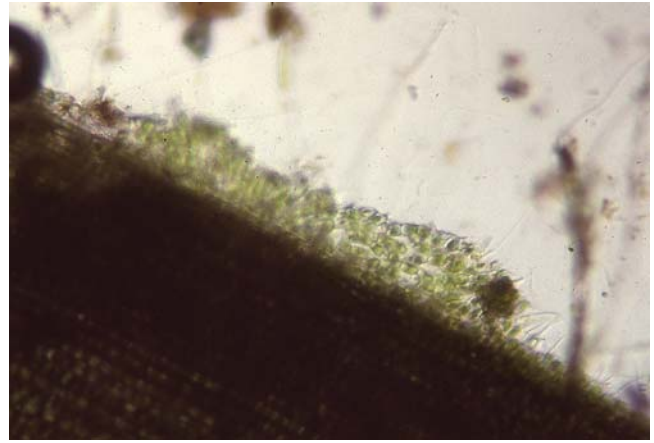

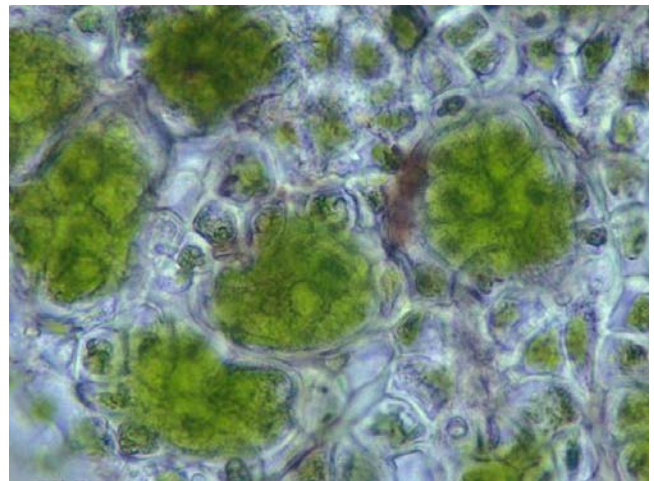Figure 13. *Coleochaete* thallus from a side view on a vascular plant. Photo by Janice Glime.

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

Figure 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.

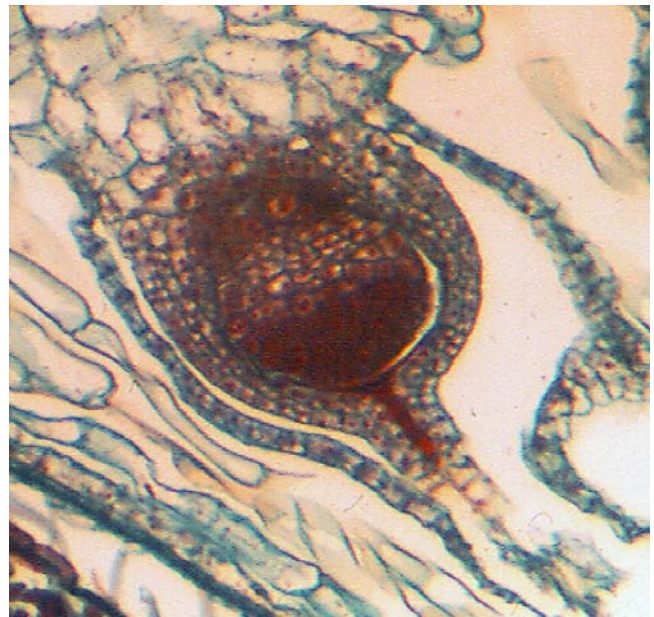Figure 12. *Coleochaete* thallus. Photo by Yuuji Tsukii, with permission.

Figure 15. *Marchantia* (Phylum **Marchantiophyta**, Class **Marchantiopsida**) archegonium with embryo attached to parent gametophyte tissue. Photo by Janice Glime.
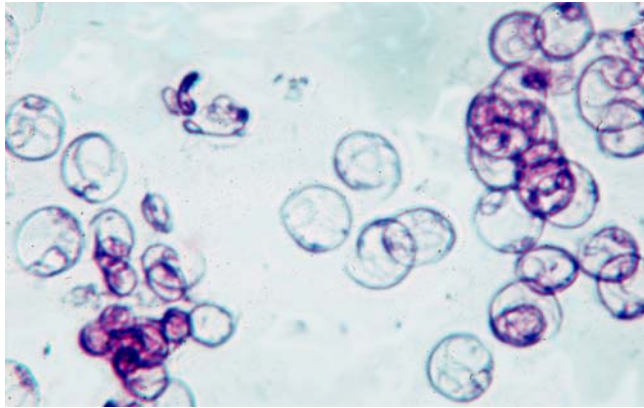
Figure 16. Stained sperm of Bryophyta, having spiral body and two flagella. Photo by Janice Glime.

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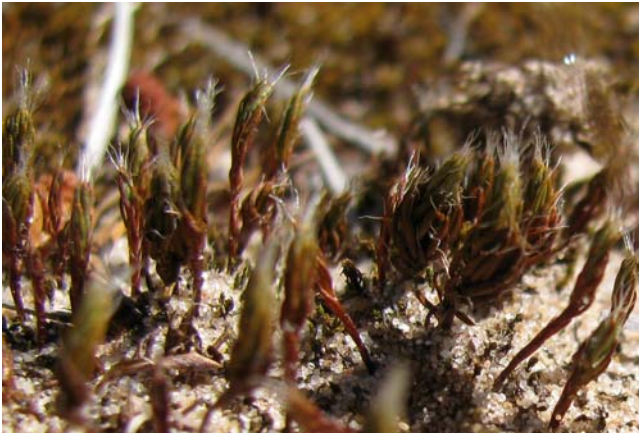
Figure 21. *Polytrichum piliferum* in a dry state. Water is slow to penetrate these leaves with a thin waxy coating. Photo by Janice Glime.

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) 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** (Figure 23), a covering of **sporopollenin** on their spores, and the presence of **flavonoids**.
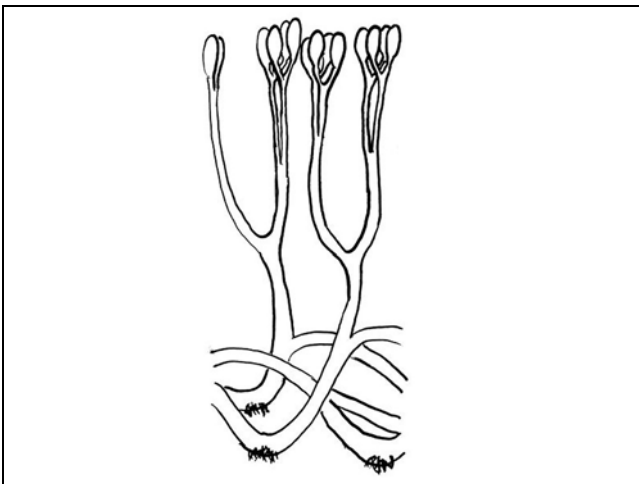

Figure 22. *Aglaophyton* reconstruction. Drawing by Griensteidl, through Creative Commons.

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** (Hébant 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 Hébant (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. Many bryophytes possess phenolic compounds similar to lignin. The problem, at least in part, is 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 phenylpropenols 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.
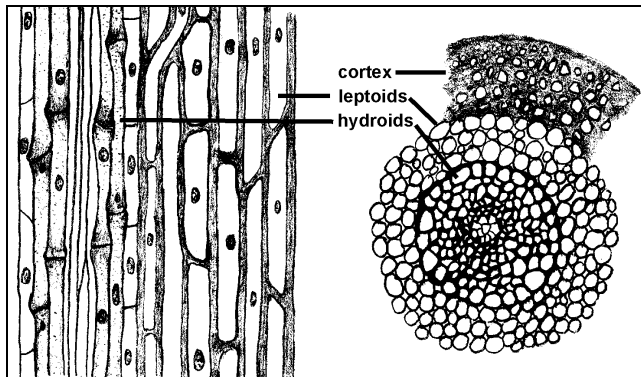

Figure 24. Longitudinal and cross sections of a stem with hydroids and leptoids, typical of taxa such as the Polytrichaceae. Drawings by Margaret Minahan, with permission.

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.
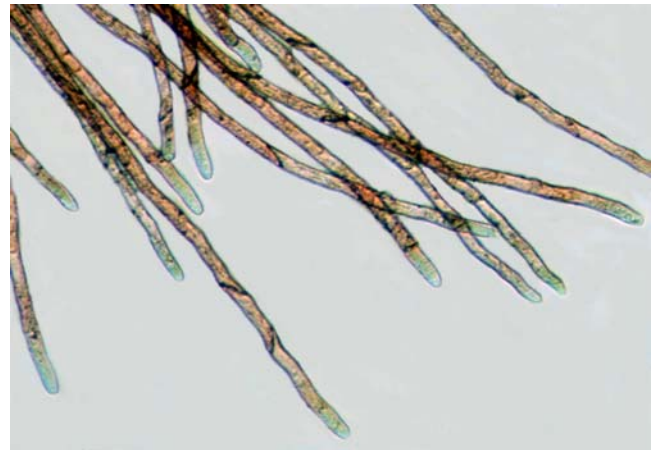

Figure 27. Microscopic view of rhizoids of the brook moss, *Fontinalis*, showing multicellular structure and diagonal crosswalls. Photo by Janice Glime.

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 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 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.
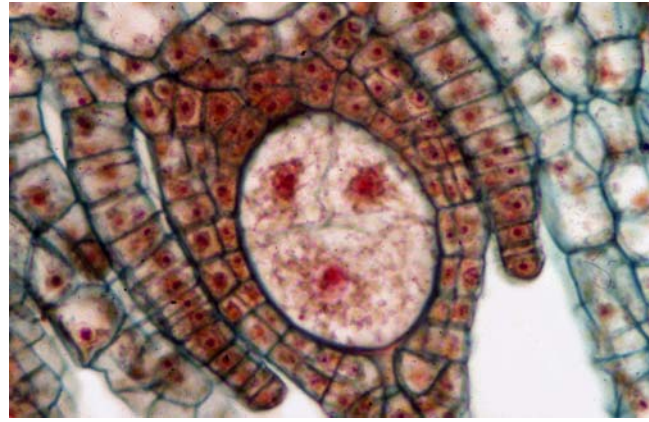

Figure 28. Young embryo of the liverwort **Marchantia polymorpha** showing early multicellular stage enclosed within the archegonium. Photo modified from Triarch by Janice Glime.

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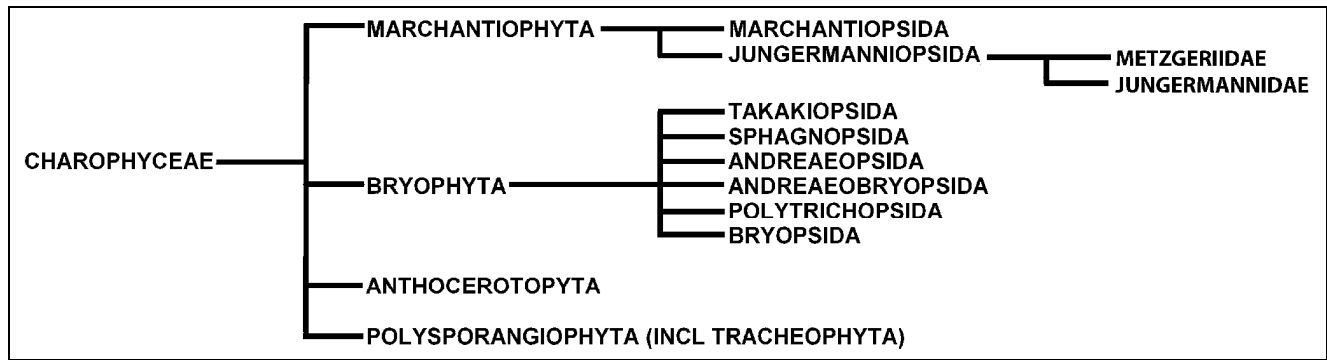
Figure 29.   Schematic representation of the **Bryobiotina** phyla and classes related to other members of the Plant Kingdom (**Polysporangiophyta**), based on Shaw & Goffinet 2000.

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 *Phylonyms: 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 *Phylonyms* 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)
                    Hepaticae
                    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 *Phylonyms* chose to "apply the traditional names **Hepaticae**, **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 not room for it in formal cladistic classification.

But not all bryologists are enamored with cladistics. I am still wary of them because I don't 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 acetylization 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** (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 (Hébant 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 CO_2 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 CO_2 present in the late Lower Palaeozoic.

Infraspecific Taxa

Bryologists recognize several types of infraspecific taxa. These include **sub-species**, **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 s**ubspecies** 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 Malesia, 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 also are 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 bar coding 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 bar coded 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 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.

Infraspecific 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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CHAPTER 2-2
LIFE CYCLES: SURVIVING CHANGE

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CHAPTER 2-2

LIFE CYCLES: SURVIVING CHANGE

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

The General Bryobiotina Life Cycle

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

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

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

Dominant Generation

One of the ways that plants manage to survive as "immobile" organisms, yet are able to survive the severe changes of seasons, is by having different life cycle stages that are adapted to different conditions. As we progress through the protist and plant kingdoms, we see that most green algae (Chlorophyta), especially in freshwater, spend most of their time in the water and most of them have only one set of chromosomes (**1n**). Although there is much disagreement about evolutionary pathways among photosynthetic organisms, all evolutionary biologists seem to agree that this **life strategy** was first, with invasion of land and dominant **2n** organisms both coming later. (The **dominant generation** refers to the most conspicuous and generally the most long-lived generation.) This 1n stage is termed the **gametophyte generation** (1n or **haploid** generation that reproduces by gametes in plants) because the generation ends when it produces **gametes** (sexual reproductive structures that have one set of chromosomes and must unite with another of the same species but opposite strain to continue the life cycle) that join to form the 2n **zygote** (2n cell resulting from fusion of male and female gametes, *i.e.* from fertilization; Figure 2). Hence, the zygote is the first structure of the 2n stage or **sporophyte generation** [**diploid** (2n) generation that reproduces by **meiospores** in plants; Figure 2]. The **meiospores** in many bryophytes are able to survive many years in a dry state, thus permitting at least some taxa to live in habitats that only occasionally get moisture.
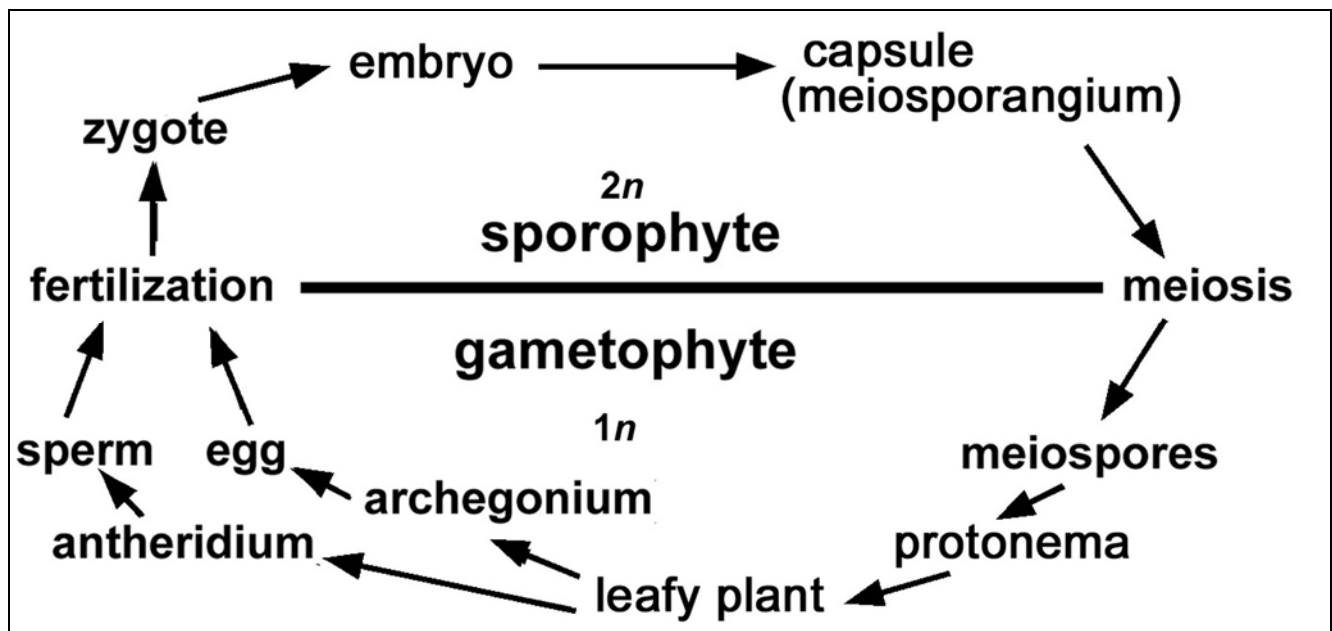
Figure 2. Basic sexual life cycle of a bryophyte. Gemmae or other propagules, not shown here, can occur on the leafy plant or on the protonema (pl. **protonemata:** alga-like, usually filamentous, stage that develops from spores of bryophytes), giving rise to the same generation as its origin. Diagram by Janice Glime.

The Life Cycle

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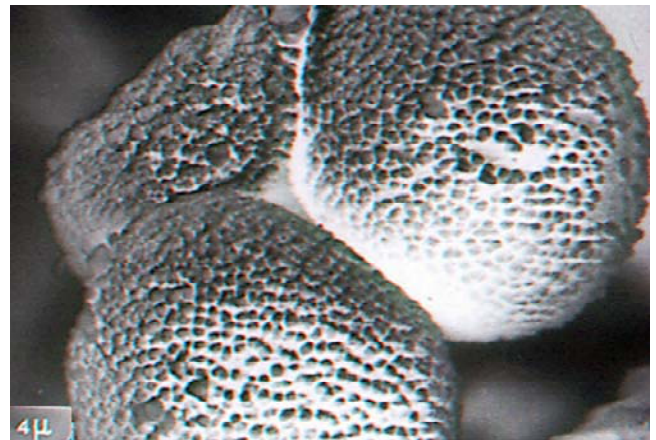

Figure 3. SEM of tetrad of meiospores of aquatic moss *Fontinalis squamosa*, with fourth spore hidden beneath. Photo by Janice Glime

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

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

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

Figure 6. Thalloid protonema of liverwort *Sphaerocarpus texanus*. Photo from Plant Actions through Eugenia Ron and Tom Sobota, with permission.
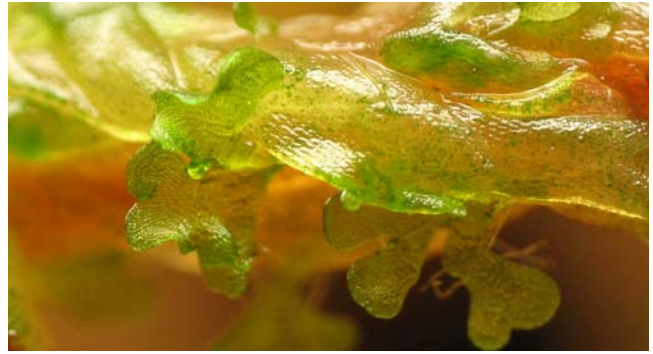
Figure 7.   *Sphagnum* protonemata on a branch of *Sphagnum*. Photo by Andras Keszei, with permission.

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

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

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

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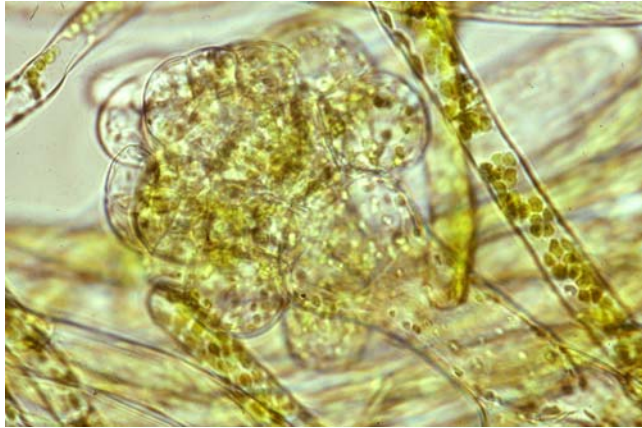
Figure 11. Moss ***Funaria hygrometrica*** protonemal bud. Photo by Janice Glime.

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

The mature gametophytes are the leafy plants you see (Figure 13-Figure 19), and they produce **antheridia** (sing. **antheridium**; male gamete containers; sperm-containers; Figure 20-Figure 27) and **archegonia** (sing. **archegonium**; multicellular egg-containing structures that later house embryo; Figure 30-Figure 35) on the same or different plants, depending on the species. Antheridia can number

up to several hundred in ***Philonotis***, but a much smaller number is typical (Watson 1964). Archegonia are generally few, but reach as many as 20-30 in ***Bryum***.

Figure 13. Leafy liverwort ***Porella navicularis*** male branches. Photo from botany website at the University of British Columbia, with permission.
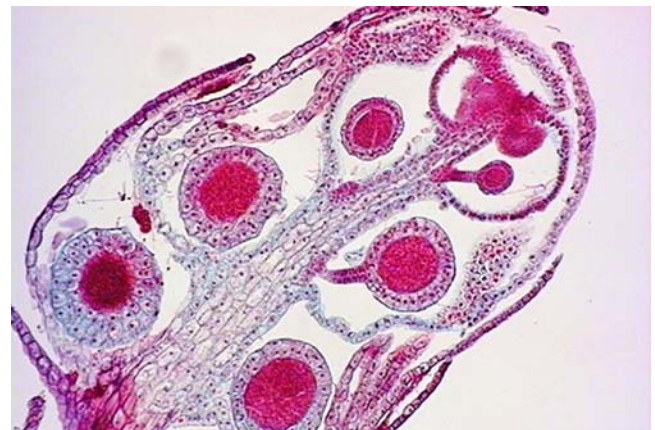
Figure 14. Leafy liverwort ***Porella*** antheridia in antheridial branch. Photo by Paul Davison, with permission.

Figure 15. ***Porella navicularis*** female with arrow indicating perianth. Photo from botany website at the University of British Columbia, with permission.
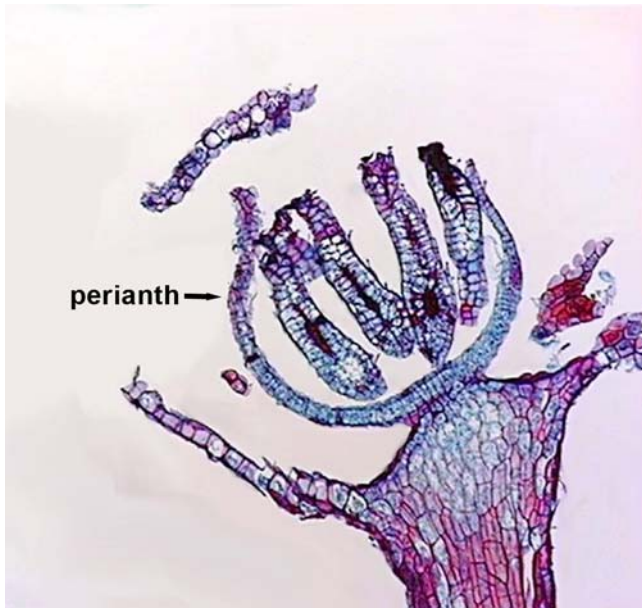
Figure 16. *Porella* archegonia in perianth. Photo by Paul Davison, with permission.

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

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

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

The **antheridium** consists of a layer of cells, the **sterile jacket**, surrounding the **spermatogenous** cells (Figure 21), *i.e.*, those that divide to form the **spermatocytes** (sperm-containing cells). If you remember that this is the gametophyte generation, and therefore already in the haploid state, you will realize that the **sperm** (Figure 28-Figure 29), produced in large numbers within an antheridium, and the **egg** (non-motile female gamete that is larger than motile sperm), produced singly within an archegonium, must be produced by **mitosis** (ordinary cell division).
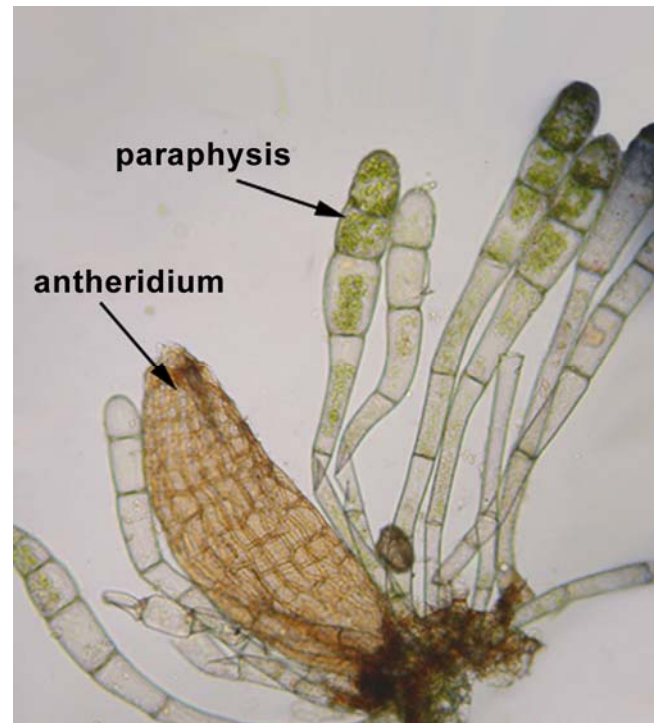
Figure 20. *Plagiomnium insigne* antheridia and paraphyses. Photo from Botany 321 website at the University of British Columbia, with permission.
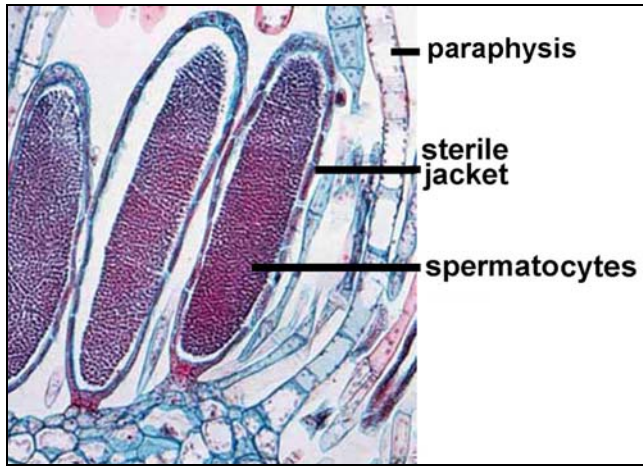
Figure 21. Moss **antheridia** showing **spermatocytes** that have been formed by the **spermatogenous tissue**. Photo by Janice Glime.

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

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

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

Figure 25. ***Fissidens bryoides*** **antheridia** on a special branch. Photo by Dick Haaksma, with permission.
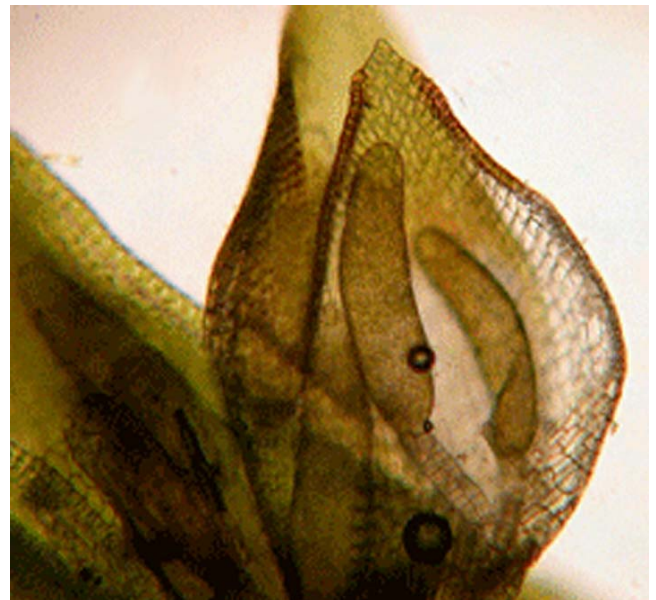
Figure 26. ***Orthotrichum pusillum*** **antheridia** nestled among leaves. Photo by Bob Klips, with permission.
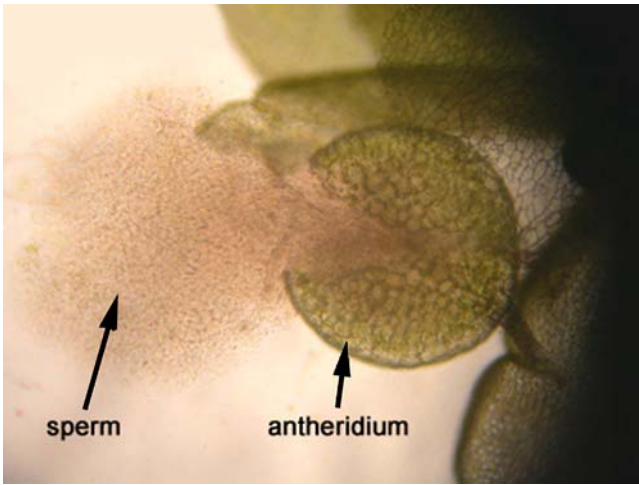
Figure 27. *Porella navicularis* **antheridium** releasing **sperm**. Photo by Jonathan Choi from Botany 321 website at the University of British Columbia, with permission.
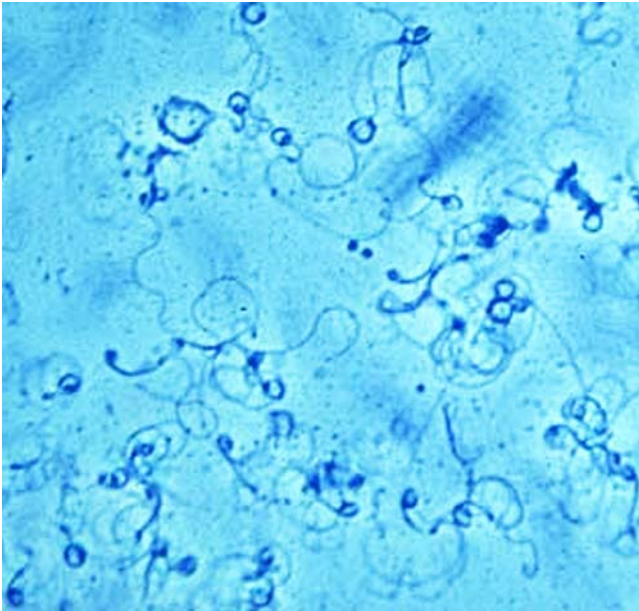
Figure 28. *Marchantia polymorpha* **sperm**. Photo from Botany 321 website at the University of British Columbia.
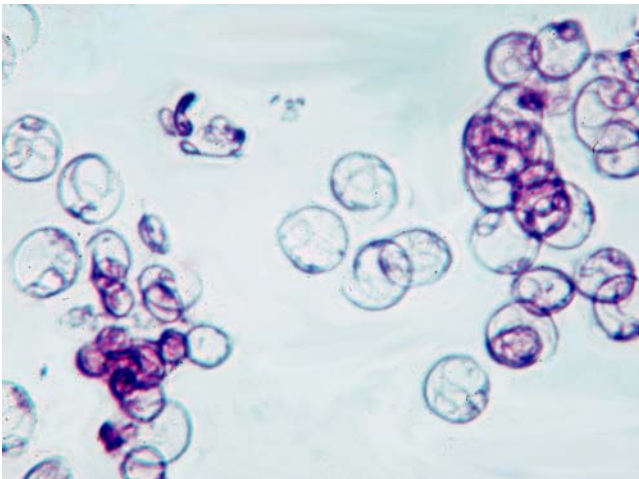
Figure 29. Stained bryophyte **sperm**. Photo by Janice Glime.

It is then the task of the **sperm**, with its two **flagella**, to find a film of water within which to swim to the awaiting egg in the **archegonium** (Figure 30-Figure 35). This is facilitated, most likely in all cases, by the presence of a chemical gradient produced by the archegonium and serving as an attractant. The archegonium is shaped like a flask with a **neck** (Figure 30), albeit a short one in some taxa. This neck has an outer layer of cells and a middle layer, the **neck canal cells** that disintegrate prior to fertilization, leaving this area as the **neck canal** (Figure 30). It is this disintegration that releases the chemicals that attract the sperm, and the cellular remains provide a fluid medium in which the sperm can swim. Yet it appears that the ability of the sperm to advance any great distance by means of its flagella may be unlikely, if *Riccardia pinguis* is at all representative. Showalter (1926) found that when sperm of that species were placed at one end of a 1 x 0.5 cm pool, the majority still remained at that end of the pool an hour later.
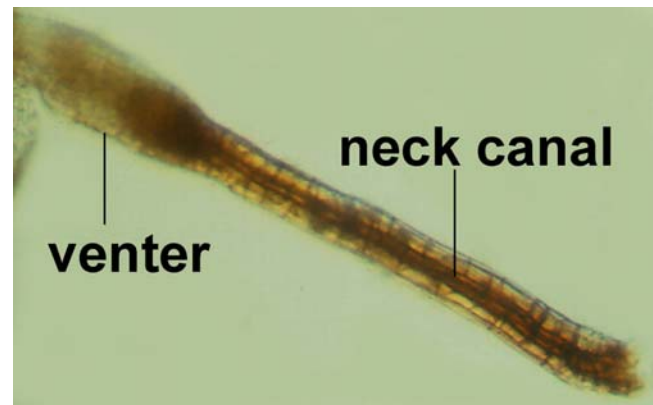
Figure 30. **Archegonium** of *Fontinalis dalecarlica* showing entry pathway (**neck canal**) for the sperm. Photo by Janice Glime.
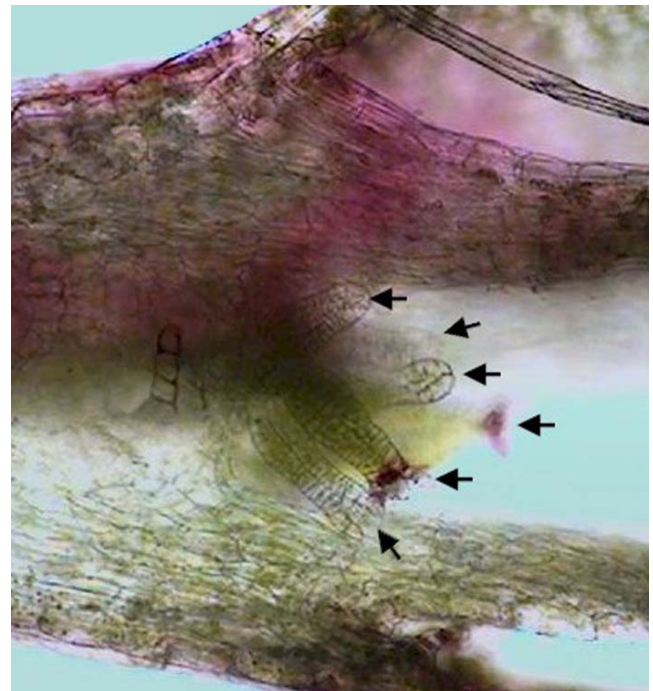
Figure 31. Terminal **archegonia** (arrows) of leafy liverwort *Jungermannia evansii*. Photo by Paul Davison, with permission.

Figure 32. *Pleurozium schreberi* archegonia on short side branch. Photo by Janice Glime.
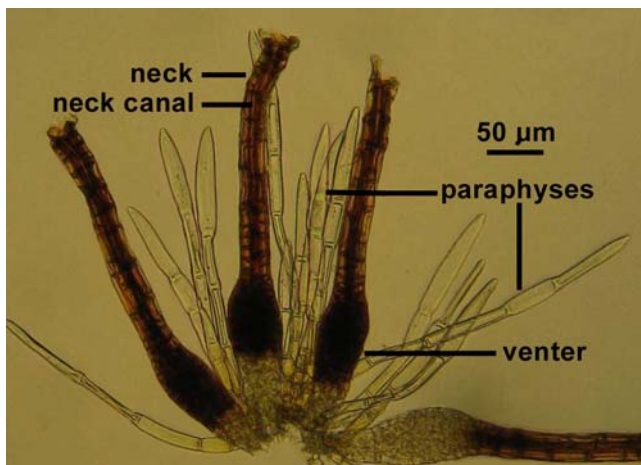

Figure 33. Moss *Zygodon intermedius* archegonia with paraphyses. Photo by Tom Thekathyil, with permission.

Figure 34. Archegonia of leafy liverwort *Lophocolea cuspidata*. Photo from Botany 321 website at the University of British Columbia, with permission.
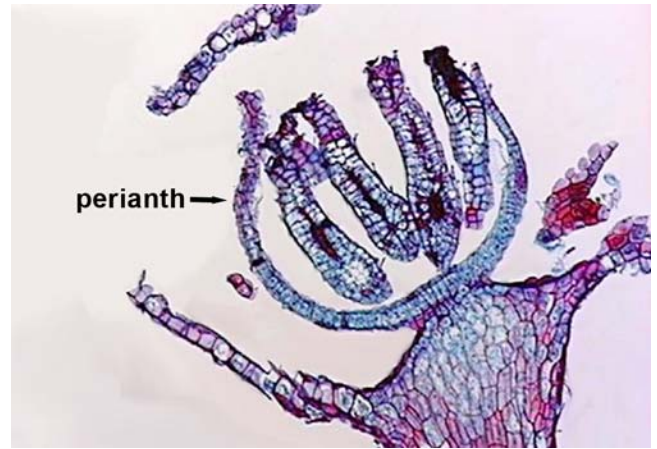

Figure 35. *Porella* archegonia in perianth. Photo by Paul Davison, with permission.

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

In 2009, Rosenstiel and Eppley reported the first study on the longevity of bryophyte sperm. They selected *Pohlia nutans* (Figure 36), a widespread moss that tolerates the high temperatures of geothermal areas and the extremes of the Antarctic. In their study population, 20% of the sperm survived 100 hours in DI or rainwater and their lifespan was unaffected by temperatures between 22 and 60°C. Temperatures above 75°C were lethal, and dilution reduced viability. This longevity is much longer than anticipated, but may not be representative of bryophytes with more narrow ecological distributions.

Figure 36. *Pohlia nutans* with capsules, a widespread moss from geothermal areas to the Arctic. Photo by Michael Lüth, with permission.

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

We know little about the ability of this archegonial fluid to attract the sperm, but it appears that **sucrose** may be one of the factors, perhaps the only one, involved (Kaiser *et al.* 1985; Ziegler *et al*. 1988). These researchers found that in the moss **Bryum capillare** (Figure 37), once the neck canal cells of the archegonium had disintegrated, the leaves and the archegonia contained less than 20% of the sucrose found in the intact neck region. There was virtually no fructose in the intact archegonium, but the glucose concentration rose after the receptive period ended.

Figure 37. **Bryum capillare** with capsules. Photo by David Holyoak, with permission.

Once the sperm reaches the **venter** of the archegonium (the bulbous base of the flask; Figure 38), it penetrates the egg and together they form the **zygote** (Figure 39), that first 2*n* cell of the sporophyte. Unlike an alga, the bryophyte retains its zygote in the female **gametangium** (archegonium) and when conditions are right the zygote divides, forming the **embryo** (young plant still contained in archegonium). This embryo continues dividing (Figure 40) and then specializing, forming eventually a **foot**, **stalk**, and **capsule** (sporangium; spore-container of mosses and liverworts; Figure 40) with a **cuticle** (water-protective layer; Crum 2001), the **mature sporophyte** (Figure 41-Figure 51). Because the base of this sporophyte is still firmly anchored in the gametophyte tissue, the sporophyte is necessarily a parasite on the gametophyte, gaining its nutrition through a joining tissue called the **haustorium**. As a parasite on the gametophyte, the zygote necessarily competes for energy, as well as space, with other zygotes

or embryos, and thus it is not surprising that multiple capsules are rare. Notable exceptions occur in the mosses **Dicranum** (Figure 1), **Plagiomnium** (Figure 52), **Rhodobryum** (Figure 53), and **Mittenia plumula**, with as many as nine capsules in **Plagiomnium insigne** (Figure 52) (Crum 2001).

Figure 38. Moss **Polytrichum** archegonia. The archegonium on the right has an egg in the bottom of the venter and a biflagellate sperm near the neck. Two more sperm are in the neck canal. Photo from botany teaching collection, Michigan State University, with permission.
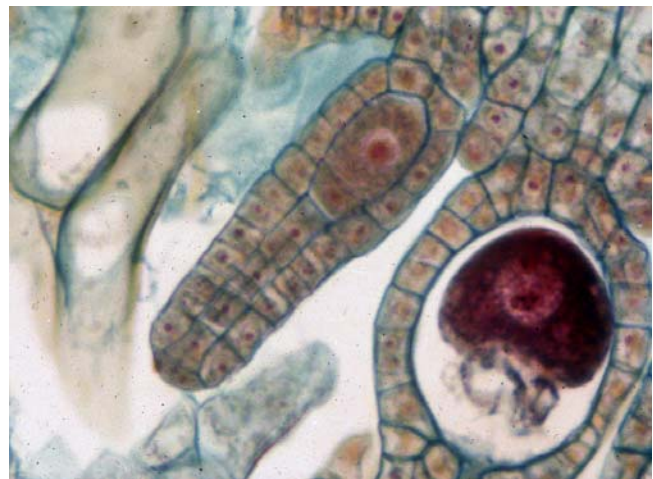

Figure 39.   Thallose liverwort **Marchantia polymorpha** fertilization. Archegonium on left is young and neck canal cells have not broken down yet. The egg cell is in the swollen venter. On the right is an egg that is fusing with the sperm during fertilization. Photo from botany teaching collection at Michigan State University, with permission.
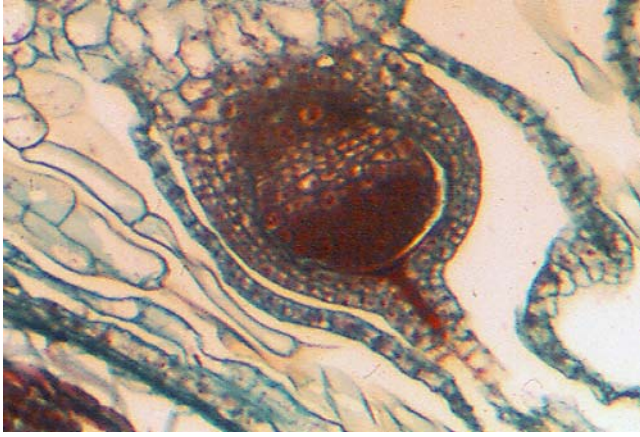
Figure 40. Thallose liverwort *Marchantia polymorpha* embryo in archegonium, showing development of the **foot**, **seta**, and **sporogonium**. Note the red-stained **neck canal** of the archegonium. Photo by Janice Glime.

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

Figure 41. Liverwort *Blasia pusilla* capsule and stalk. Photo by Walter Obermayer, with permission.
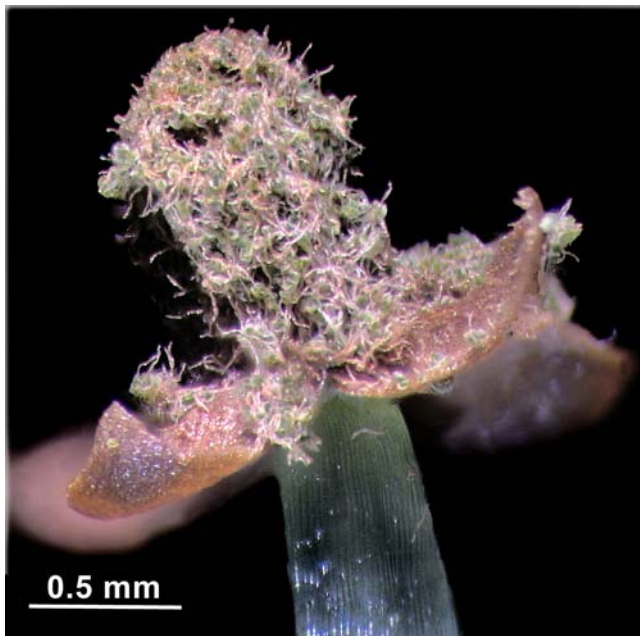
Figure 42. Liverwort *Blasia pusilla* open capsule showing spores and elaters. Photo by Walter Obermayer, with permission.

Figure 43. Liverwort *Lophocolea cuspidata* capsule with elongated seta. Photo from Botany 321 website at the University of British Columbia, with permission.

Figure 44. Moss *Orthotrichum stramineum* capsule with calyptra. Photo by Des Callaghan, with permission.
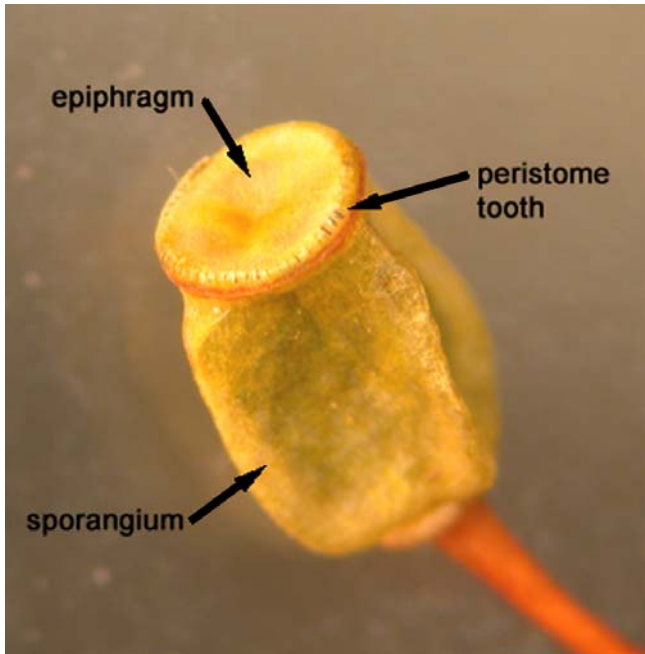
Figure 45. *Polytrichum commune* capsule. Photo from Botany 321 website at the University of British Columbia, with permission.
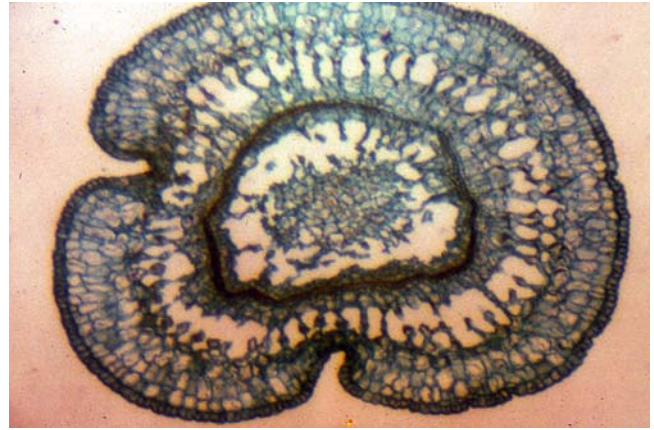

Figure 47. *Polytrichum* capsule cross section. The blue center is the columella. The dark circle around it is the developing sporogenous tissue. Photo by Janice Glime.

Figure 46. *Polytrichum commune* capsule longitudinal section. Photo from Botany 321 website at the University of British Columbia, with permission.

Figure 48. *Bartramia pomiformis* showing leafy gametophytes and sporophyte capsules. Photo by Janice Glime.

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

The details of the foregoing structures differ among the phyla of **Bryobiotina** and in many cases form the basis for separating the phyla. These are best understood by examining each phylum and class in greater detail.
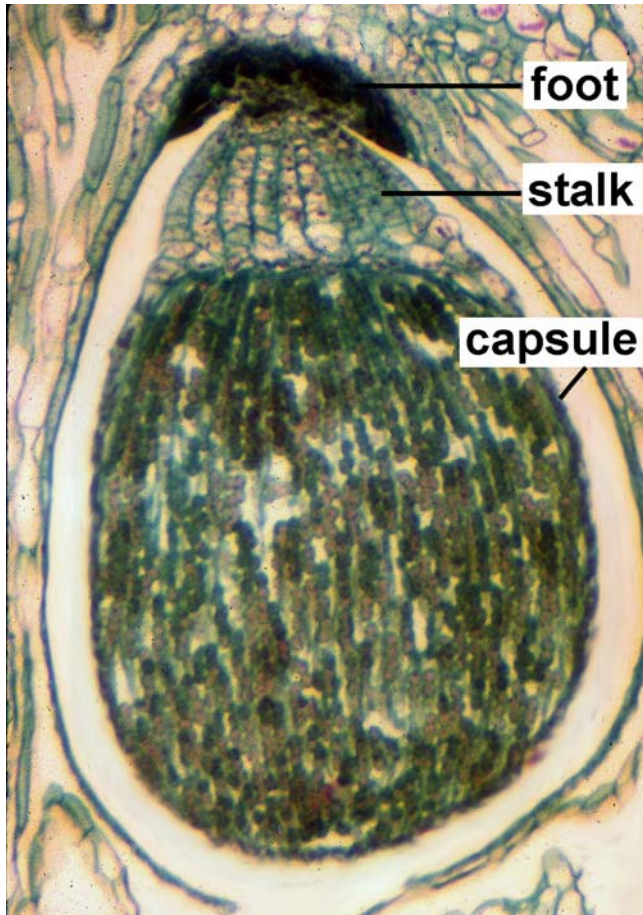
Figure 49. Mature sporophyte of thallose liverwort *Marchantia polymorpha* showing **foot**, **stalk**, and **capsule**. Photo modified from botany teaching collection, Michigan State University, with permission.

Figure 50. *Gigaspermum repens* capsule showing spores. Photo by David Tng, with permission.

Figure 51. Longitudinal section through mature *Fontinalis squamosa* capsule, showing green spores. Photo by Janice Glime.

Figure 52. *Plagiomnium insigne* **sporophytes**, illustrating multiple sporophytes on one shoot. Photo from Botany 321 website at the University of British Columbia, with permission.

Figure 53. *Rhodobryum roseum* with multiple capsules from one shoot. Photo by Michael Lüth, with permission.

Life Cycle Controls

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

For example, in *Mnium hornum* (Figure 54) there is an endogenous rhythm that coincides approximately with the seasonal cycle (Newton 1972). Short days delay gametangial production, but when 7.25-hour days are maintained, neither 10 nor 20°C is capable of completely suppressing the gametangia. Newton interpreted this to mean that the short days of winter maintained coordination with the seasons. In *Plagiomnium undulatum* (Figure 55), archegonial induction responds to long days (7.25-12 hours at 10°C). Males are also long-day plants, but in addition they require a diurnal temperature fluctuation.
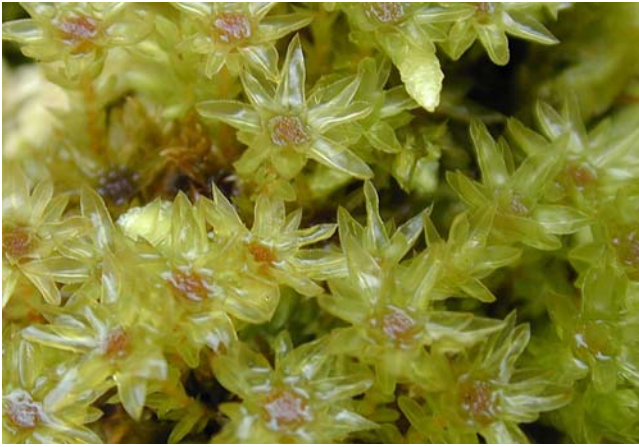
Figure 54. ***Mnium hornum*** showing antheridia that cease production in response to short days. Photo by Michael Lüth, with permission.

Figure 56. ***Aloina ambigua***, a moss with a short life cycle of only 5-6 months. Photo by Hermann Schachner, through Creative Commons.

But do we have information for many, or even any, bryophytes on time required from spore or fragment germination to spore production? This is easy for annual bryophytes, but for perennials, few have been grown from spore to mature capsule and our field observations will be based mostly on colonists. But some bryophytes further complicate this by often never producing capsules, forcing us to guess based on gametangial maturation time. However, once fertilization occurs, sporophyte maturation can proceed rapidly as in the annuals, or take 15 months as in some ***Polytrichum*** (Figure 57) species.

Figure 55. ***Plagiomnium undulatum*** with **antheridia** that respond to long days and diurnal temperature fluctuations. Photo by Jan-Peter Frahm, with permission.

Generation Time

The concept of generation time is well known even to the layperson. We know that in humans it means the time from birth to becoming a parent, and for the population we average the data from everybody. I like the Wikipedia definition: The average difference in age between parents and offspring when the population is at the stable age distribution. For plants, it seems the best definition is one complete life cycle. Lloyd Stark (Bryonet 20 February 2014) agrees with this implied spore-to-spore definition, but he suggests expanding it to include shoot fragment or fragment of a protonema as the starting point instead of a spore. For example, he and John Brinda have found that it takes only 5-6 months for a shoot fragment of ***Aloina ambigua*** (Figure 56) to produce viable spores. In this rapid cycle, only 40 days are required for the sporophyte to develop.   On the other hand, Stenøien (Bryonet 21 February 2014) suggests that the average length of time required to replace an individual is a workable definition of generation time. But Lars Hedenäs (Bryonet 21 February 2014) cautions us that we rarely know what this means in a specific case.

Figure 57. ***Polytrichum commune*** sporophytes, in 4 cases covered by the gametophyte calyptra. Photo by Michael Lüth, with permission.

Even "annuals" might cause problems. For example, ***Buxbaumia*** (Figure 58-Figure 59) is usually considered an annual because the sporophyte lasts only one year and there is no leafy gametophore.   But Hancock and Brassard (1974) found that despite the annual disappearance of the sporophyte, the protonema remained for several years.

Figure 58. ***Buxbaumia aphylla*** with capsule wall peeled back and interior exposed. The greenish ground cover is caused by protonemata that will survive the winter and form new plants. Photo by Janice Glime.

Let us take an example first given by Hans Stenøien and carried further by Lars Hedenäs (Bryonet 21 February 2014). If a moose walks across a bog and kills a ***Sphagnum*** (Figure 60) shoot, the empty space created will most likely be filled by an expanding neighboring shoot. The probability is high that the neighbor originated by branching from the now dead shoot. This means the same individual survives despite the death of one of its shoots. Do we know anything about the frequency of this happening?

Figure 60. ***Sphagnum capillifolium***, a moss that spreads by branches. Photo by David Holyoak, with permission.

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

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

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

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

Figure 59. ***Buxbaumia aphylla*** with mature capsules. Photo by Jan-Peter Frahm, with permission.

Importance

So why is it important to understand generation time of a bryophyte? The question about the length of a generation was raised by Jon Shaw who wanted to know the generation time in *Sphagnum* (Figure 60). As Hans Stenøien and Richard Zander summarized on Bryonet (21 February 2014), understanding generation times (and population sizes) enables us to use population genetic models to infer the action of evolutionary processes. Likewise, phylogenetic models enable us to infer evolutionary relationships. From these, we can infer migration rates and divergence time between lineages.

Longevity and Totipotency

Bryophyte longevity can be difficult to define because unlike most other plants, they die at the bottom and continue growing at the tip. Furthermore, they may seem dead and still be capable of life. For example, I have boiled *Fontinalis* (Figure 61) for two weeks, replaced it in its native stream, and found a few new leaves on one stem tip a year later, whereas all the original leaves were brown or gone.

Figure 61. *Fontinalis dalecarlica*, a species that can survive two weeks of boiling because of its totipotency. Photo by J. C. Schou, through Creative Commons.

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

We know that *Sphagnum* (Figure 60) continues growing for hundreds of years, but only the recent few years of growth seem to be alive. But is that really true?

Recent studies in polar regions suggest that bryophytes can retain life for 1500 years under ice (LaFarge *et al*. 2013; Roads *et al*. 2014). Working in the Arctic, LaFarge *et al*. (2013) were able to grow new gametophytes from two species of buried bryophytes: *Aulacomnium turgidum* (Figure 62) ~400 years old and *Bartramia ithyphylla* (Figure 63) ~460 years old.

Figure 62. *Aulacomnium turgidum*, a species found buried in Arctic ice cores. Photo by Michael Lüth, with permission.

Figure 63. *Bartramia ithyphylla*, a moss found in ice cores from the Arctic. Photo by Michael Lüth, with permission.

Then Roads *et al*. (2014) found new growth of *Chorisodontium aciphyllum* (Figure 64-Figure 65) in Antarctic cores at 138 cm, a layer they interpreted to be ~1500 years old! They found that after 55 days the *Chorisodontium aciphyllum* grew *in situ* at the base of their ice core at 110 cm. Protonemata developed on the rhizoids at the base in 22 days. (See also Miller 2014; Zimmer 2014).

Figure 64. *Chorisodontium aciphyllum* showing the extensiveness of a mat. Photo through Creative Commons.

Figure 65. *Chorisodontium aciphyllum* showing upper live green parts and lower dead or dormant parts. Photo through Creative Commons.

Summary

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

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

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

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CHAPTER 2-3
MARCHANTIOPHYTA

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MARCHANTIOPHYTA

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

Distinguishing Marchantiophyta

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

Because of the long tradition of considering these to be bryophytes, liverworts (and hornworts) are still lumped into that group for a vernacular name instead of creating a new name that is unfamiliar to everyone. As a phylum, **Marchantiophyta** are distinguished from the phylum **Bryophyta** by their **dorsi-ventral orientation** (Figure 1, Figure 12), **unicellular rhizoids** (Figure 2), **inoperculate capsules** [*i.e.* lacking a lid (Figure 3), although there are a few exceptions], **absence of a columella** in the center of the capsule (Figure 4), and **no stomata** in the capsule. They possess a **seta** (stalk on the capsule), as do mosses, but it elongates **after** development of the capsule (Figure 11-Figure 12), whereas in mosses it elongates first, then develops the capsule. The spores, as in mosses, are all produced simultaneously by **meiosis** (Figure 5). The

capsule, unlike that of most mosses, dehisces typically by **splitting into four valves** (Figure 6), but not in the class Marchantiopsida, revealing spores mixed with **elaters** (thickened elongate cells with spiral wall thickenings that twist in response to drying; Figure 6-Figure 7).

Figure 2. *Fossombronia* rhizoids. Note that these rhizoids are unicellular, and the ones in this genus are purple by nature. Photo by Paul Davison, with permission.
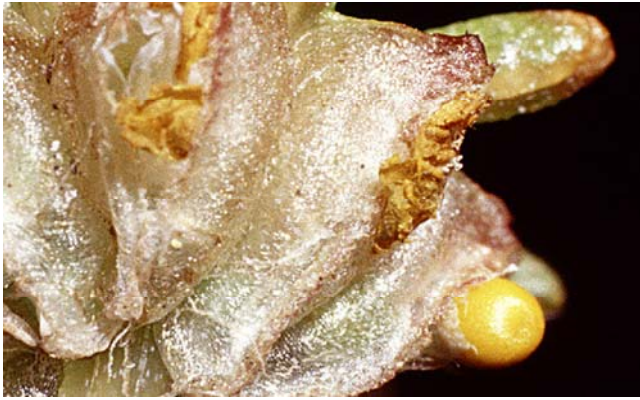
Figure 3. *Marchantia polymorpha* archegonial head showing inoperculate capsule in lower right. Photo by George Shepherd through Creative Commons.

Elaters

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

Figure 4. Capsule, lacking cell wall, of *Marchantia polymorpha*. Photo from Michigan State University Botany Department teaching collection, with permission.
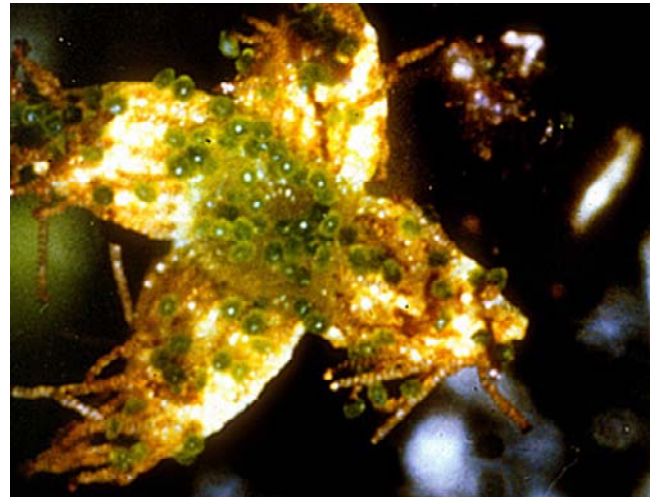
Figure 6. Open valvate capsule of the leafy liverwort *Frullania kagoshimensis* (Class **Jungermanniopsida**) showing spores and elaters and no columella. Photo by Zen Iwatsuki, with permission.

Figure 5. *Marchantia polymorpha* spore tetrads and one elater (upper) before spiral thickenings form. Photo from botany teaching collection at Michigan State University, with permission.
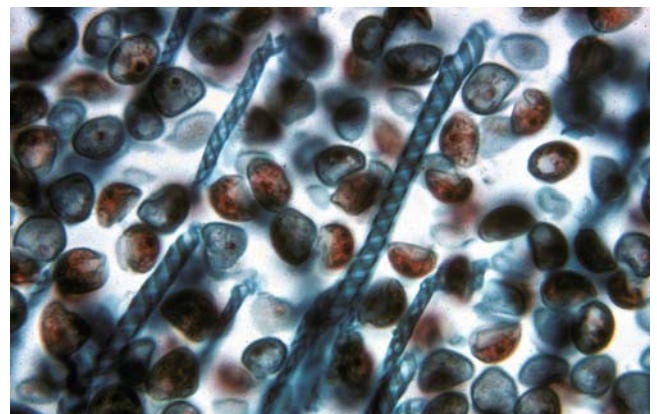
Figure 7. Spores and elaters with spiral thickenings from *Marchantia polymorpha* (**Marchantiopsida**). Photo from botany teaching collection at Michigan State University, with permission.

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

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

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

In *Marchantia* (Figure 10), elaters twist and untwist, based on moisture changes. The capsules do not open along four distinct lines of dehiscence (compare Figure 10 to Figure 14), but rather open irregularly into short lobes that bend back. Elaters twist as they dry and become entangled (Figure 10). When an elater becomes free of the others, it does so with a sudden movement that throws spores from the capsule, although the elater generally remains (Ingold 1939 in Schuster 1966). In other liverworts, such as *Pellia* (Figure 11-Figure 13), the spiral thickenings are not so thick and the movements are too

subtle to accomplish much dispersal (Schuster 1966). Rather, release of pressure at the time of dehiscence seems to be responsible for at least some dispersal. However, even the subtle movement of elaters may serve to loosen spores from each other, making dispersal easier when something disturbs the stalk and capsule (Figure 14). (See chapter on dispersal.)

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

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

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

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

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

Leafy or Thallose?

The Marchantiophyta can be divided into two classes (Figure 40), the **Marchantiopsida** (thallose liverworts; Figure 15 & Figure 18) and **Jungermanniopsida**, the latter with two subclasses, the **Metzgeriidae** (mostly thallose liverworts; Figure 41), and the **Jungermanniidae** (mostly leafy liverworts; Figure 47 & Figure 48). One could argue that these two classes should actually be separate phyla (Bopp & Capesius 1996), but most modern systematists disagree (Crandall-Stotler & Stotler 2000). Based on 18S rRNA genes for all bryophytes tested, the **Marchantiopsida** are clearly separated from the **Jungermanniopsida**, but the latter are in the same clade as the **Bryophyta**! Furthermore, the orders **Metzgeriales** and **Jungermanniales** are indicated on the same branch. I will

leave these arguments for the future and describe the two classes of **Marchantiopsida** and **Jungermanniopsida** as comprising the **Marchantiophyta**.

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

Class Marchantiopsida
Thallus Construction

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

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

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

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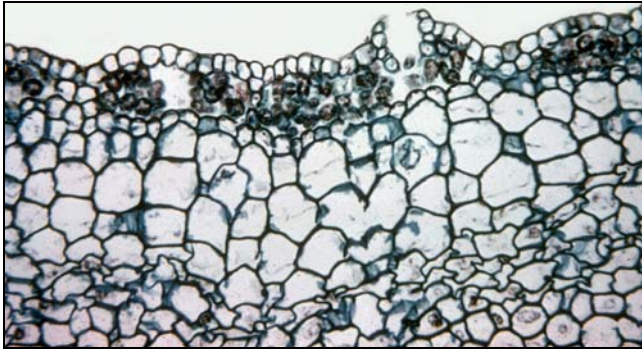
Figure 18. Cross section of thallose liverwort *Marchantia polymorpha* (**Marchantiopsida**) showing the internal air chambers, pores, and fragments of rhizoids. Note stacks of cells in internal air chambers, somewhat resembling the spongy mesophyll of a tracheophyte leaf. Pores are surrounded with rings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

Figure 19. **Marchantiopsida** thallus showing multiple layers, rhizoids, and dorsiventral orientation. Photo by Smith through Wikimedia Commons.
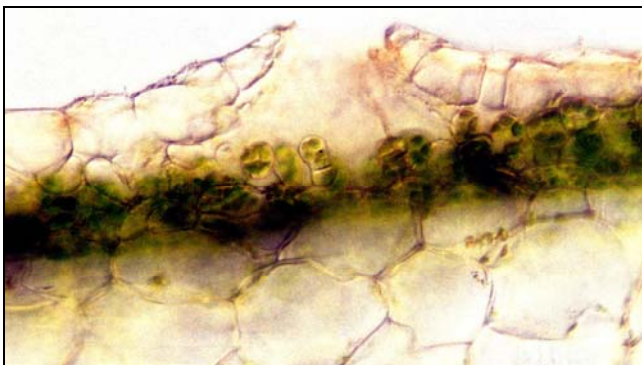
Figure 20. *Marchantia polymorpha* thallus pore. Photo by George Shepherd through Creative Commons.
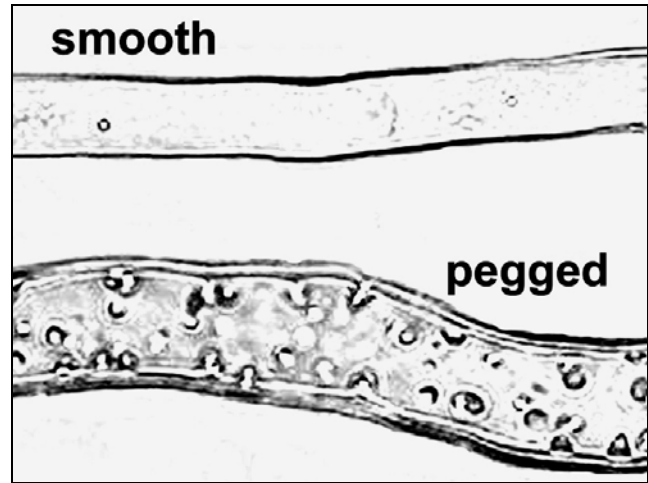
Figure 21. Smooth and pegged rhizoids of *Conocephalum conicum* in the Class **Marchantiopsida**. Photo with permission, modified from web site of Paul Davison, <www2.una.edu/pdavis/bryophytes.htm>, with permission.
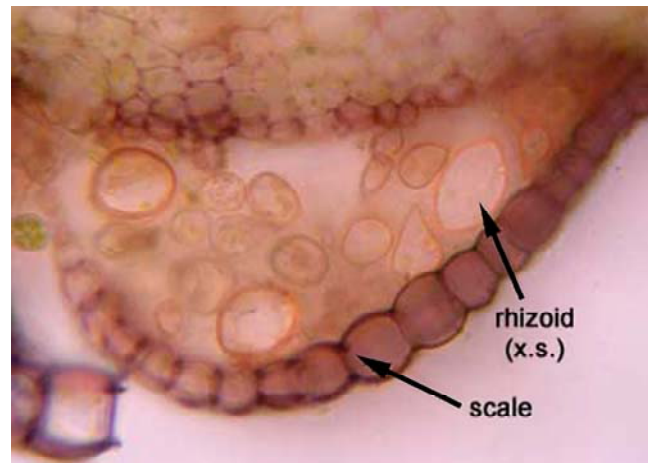
Figure 22. *Marchantia polymorpha* cross section showing ventral surface with scale and rhizoids. Photo from University of British Columbia website, with permission.

Sexual Structures

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

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

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

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

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

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

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

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

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

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

Sperm Dispersal

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

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

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

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

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

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

Shimamura *et al*. (2008) have successfully filmed <http://www.youtube.com/watch?v=ALGDLzWcvnU> the remarkable dispersal of **sperm** from the antheridia (Figure 32) of *Conocephalum conicum* (Figure 32). In *Conocephalum*, there is no splash platform, and instead the sperm are ejected from the antheridium in a cloud that rises into the air several centimeters (Shimamura 2008), a phenomenon originally described by Cavers (1903), and again by Muggoch & Walton (1942) and Benson-Evans (1950). In Hiroshima, Japan, these sperm are typically dispersed in April to May. Shimamura (pers. comm. 2008) relayed to me that they were able to detect many airborne sperm on a sunny day after a rain shower. After a week of dry, sunny conditions, sperm were dispersed following a rainy day, resulting in most of the mature antheridiophores being empty. In the lab, antheridia can be persuaded to release their sperm by misting them. The intense lighting for photography also seemed to help. Initially, the sperm in these droplets are non-motile. Touching the droplets causes them to swim (Masaki Shimamura, Bryonet 3 January 2008), suggesting that these might be packets that must be broken for the sperm to begin swimming (Muggoch & Walton 1942) (see Figure 79).

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

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

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

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

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

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

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

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

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

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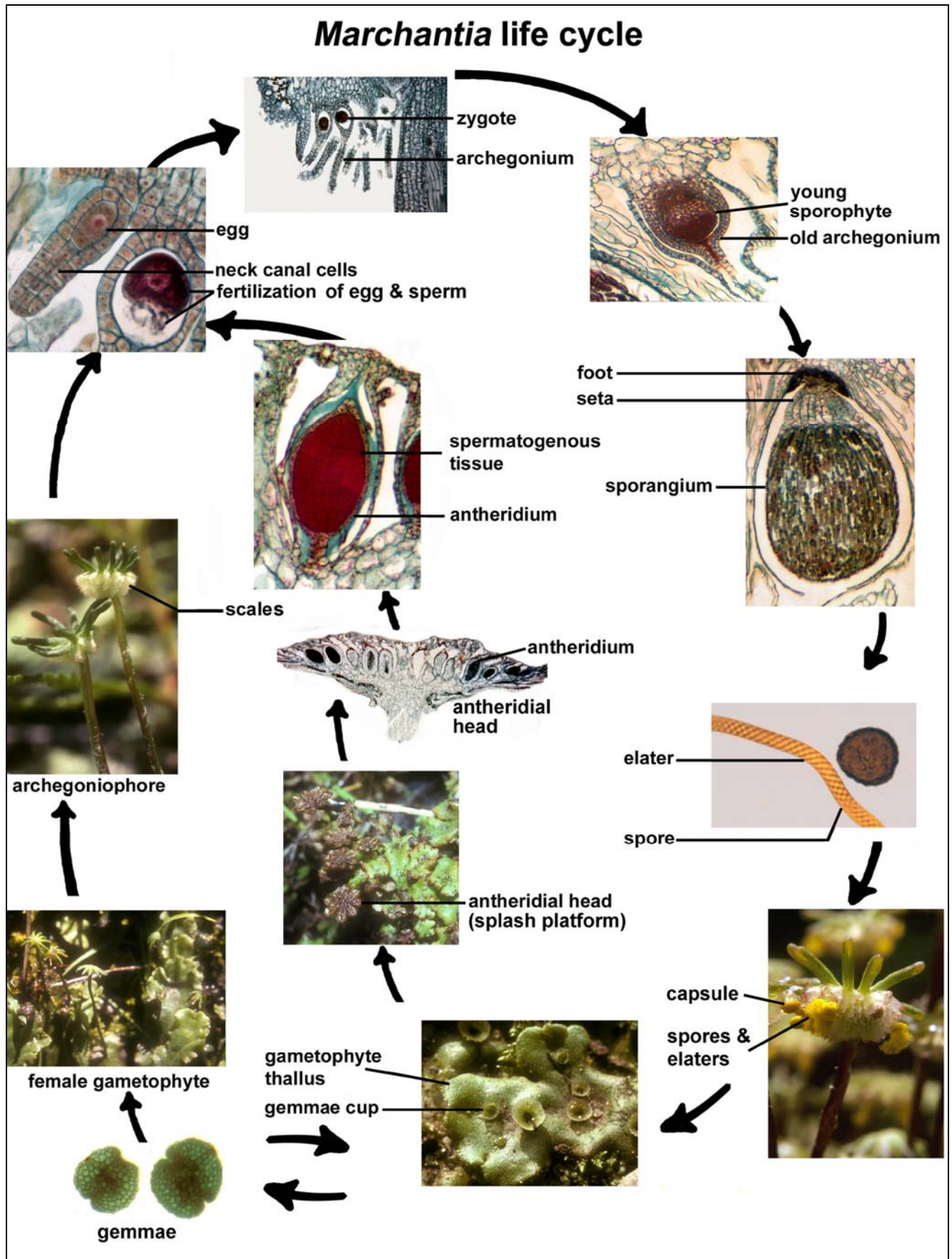
Figure 39. Life cycle of *Marchantia polymorpha*, showing dominance of the gametophyte generation. Photos by Janice Glime, photomicrographs from botany teaching collection of Michigan State University, and spore and elater modified from photo by Noris Salazar Allen.

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

Class Jungermanniopsida

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

Metzgeriidae

Plants in the subclass **Metzgeriidae** (Figure 41-Figure 45) are thalloid or ribbon-like, except that some members of *Fossombronia* (Figure 44) appear leafy, while having only one initial cell instead of 2-3 as in other members (Renzaglia 1982). But despite their thalloid nature, other features seem to place the **Metzgeriidae** within the **Jungermanniopsida**. They lack true dichotomous forking (although pseudodichotomies occur), and their tissues are solid, lacking internal air spaces. They also **lack dorsal pores** and **ventral scales**, and the **rhizoids** are all smooth, and never in clumps as in **Jungermanniidae**. Cells often have **oil bodies** (Figure 49), although these disappear upon drying.

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

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

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

Figure 44. *Fossombronia husnotii*, a "leafy" liverwort in the **Jungermanniopsida**, subclass **Metzgeriidae**. Some members of this genus appear thallose (but ruffled), and their single apical initial and developmental pattern suggest a transition between the two growth types within the **Jungermanniopsida**. Photo by Michael Lüth, with permission.
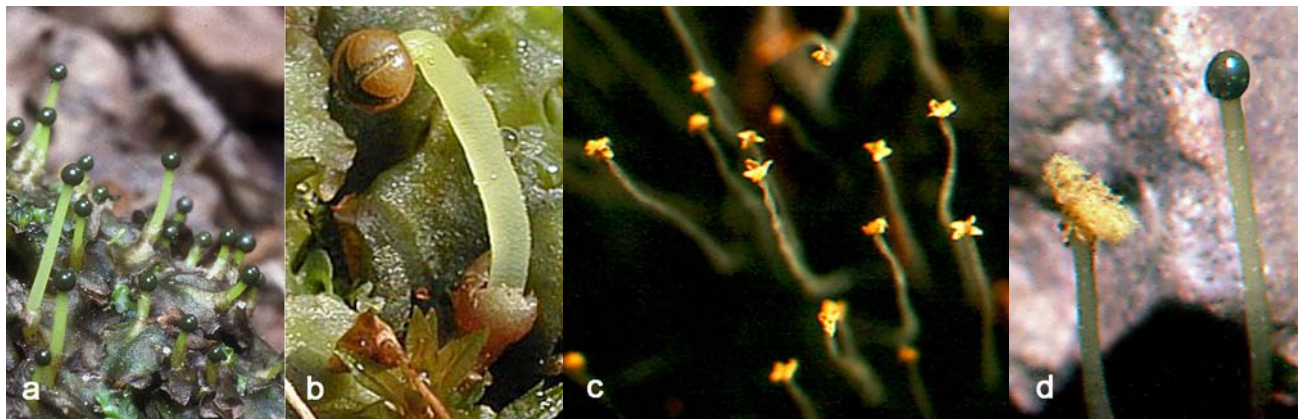
Figure 45. *Pellia*, a thalloid liverwort in the class **Jungermanniopsida**, subclass **Metzgeriidae**. Note the watery, colorless setae with the globose, inoperculate capsules. **a:** undehisced capsules and setae. **b:** capsule splitting into four valves. **c:** dehisced capsules showing four valves. **d:** dehisced capsule (left) looking fuzzy due to elaters and undehisced capsule (right). Photos a, c, & d by Janice Glime. Photo b by Michael Lüth, with permission.

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

Jungermanniidae

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

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

Figure 48. *Bazzania trilobata*, a leafy liverwort in the Class **Jungermanniopsida**. Note the two-ranked leaves and top-bottom (dorsi-ventral) orientation. Photos by Janice Glime.
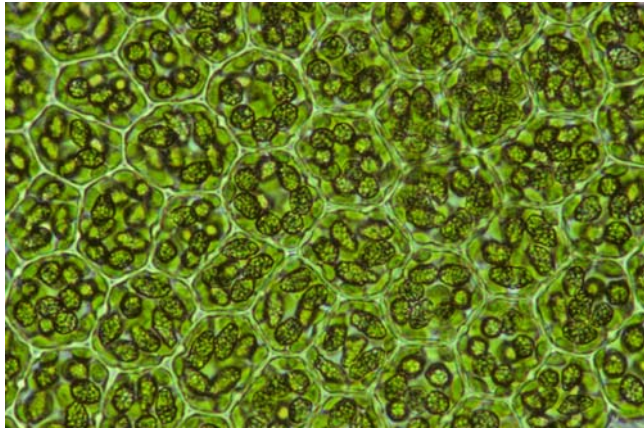
Figure 49. Leaf cells of the leafy liverwort *Frullania davarica* (**Jungermanniopsida**). Note the oil bodies resembling bunches of grapes and the numerous small chloroplasts clumped around the periphery of cells. Cell walls also have **trigones** (swellings in the walls). Photo by Zen Iwatsuki, with permission.

In the leafy liverworts, the leaf may be folded to create a pocket or pouch (**lobule**; Figure 50), usually on the lower side, but the smaller lobe may occur on the upper side in such genera as *Scapania* (Figure 51). Rhizoids, unlike those in the **Metzgeriidae**, usually occur in clumps at bases of underleaves (Figure 52).

Figure 52. *Chiloscyphus polyanthus* with a clump of rhizoids at the base of the underleaf. Photo by Paul Davison, with permission.

In all the bryophyte phyla, the spore is a **meiospore** (produced by meiosis and therefore 1*n*; Figure 53-Figure 55). These structures can be variously decorated and their size and decorations can contribute to their dispersal ability. Germination (Figure 55) in liverworts is apparently inhibited inside the capsule, thus occurring only after capsule **dehiscence** (splitting apart) and spore dispersal (Figure 56-Figure 58).

Figure 50. *Frullania dilatata* (Class **Jungermanniopsida**), a leafy liverwort showing the ventral (under) side of the stem with hood-shaped lobules under each leaf and underleaves on the stem. Photo by Michael Lüth, with permission.

Figure 51. *Scapania gracilis* showing leaves folded up to the dorsal side. Photo by Jan-Peter Frahm, with permission.
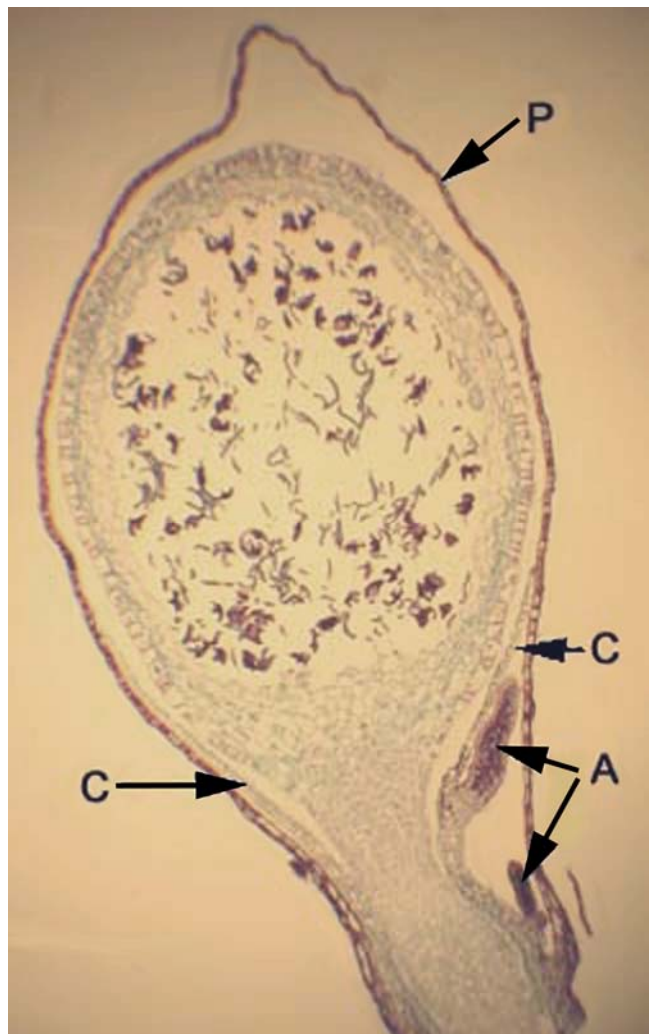
Figure 53. *Porella navicularis* capsule with meiospores and elaters. Photo from University of British Columbia website, with permission.

Figure 54. *Noteroclada confluens* (Metzgeriidae) meiospores and elaters. Photo by George Shepherd, through Creative Commons.
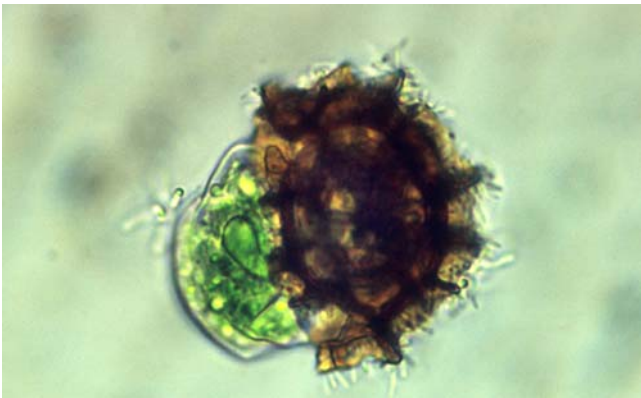
Figure 55. *Fossombronia angulosa* protonema emerging from spore. Photo by Plant Actions through Eugenia Ron Alvarez, with permission.

Figure 56. *Lophocolea* capsule. Photo by George Shepherd, through Creative Commons.
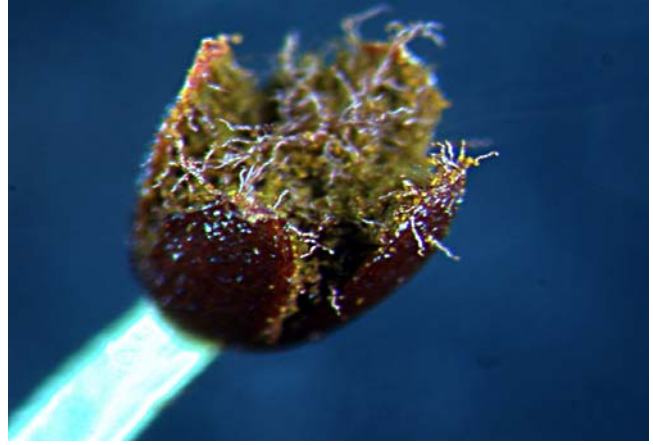
Figure 57. *Lophocolea* capsule dehiscing. Photo by George Shepherd, through Creative Commons.

Figure 58. *Lophocolea* capsule fully open into four valves. Photo by George Shepherd, through Creative Commons.

The spore, once finding a suitable condition of moisture and lighting, germinates (Figure 55-Figure 60). Here, the liverwort **sporeling** differs from that of most mosses. In liverworts the protonema is variable, even within orders, with the protonema ranging from **filamentous** to **thalloid**, but mostly forming only a few cells (Figure 63-Figure 60).

In the leafy liverworts *Frullania moniliata* and *Drepanolejeunea*, as in all **Porellales**, the protonema is formed within the spore (**endosporic**); in *Cephalozia otaruensis* it is an **ectosporic** filamentous protonema; in most of the liverworts it is **ectosporic** (developing outside the spore) and thalloid (Figure 60-Figure 64) (Nehira 1966).

Liverworts differ markedly from mosses not only in most species having a thalloid rather than filamentous protonema (exceptions in some Cephaloziaceae), but in producing only one upright plant per protonema. Furthermore, unlike many mosses, they never produce protonemal **gemmae** or other protonemal **propagules** (Schofield 1985) and rarely reproduce by fragments (Crum 2001). [See Glime (1970) for a new plant produced by a fragment in *Scapania undulata* (Figure 65)]. Nevertheless, in all bryophytes the sporeling is quite different in structure and appearance from the mature gametophyte that will develop from it.
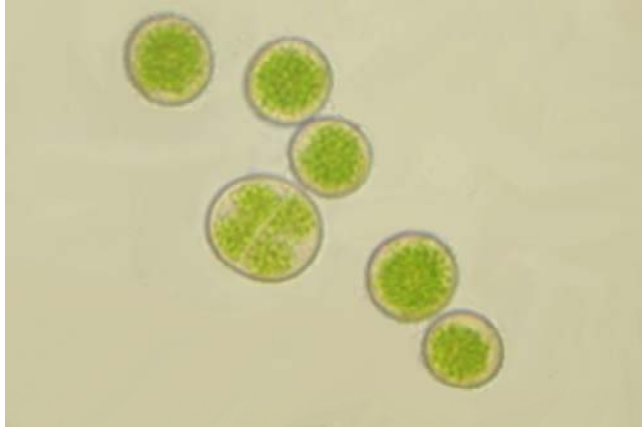
Figure 59. *Radula recubans* spores and protonema. Photo by Adaíses Simone Maciel da Silva, with permission.

Figure 60. *Radula recubans* protonema. Photo by Adaíses Simone Maciel da Silva, with permission.
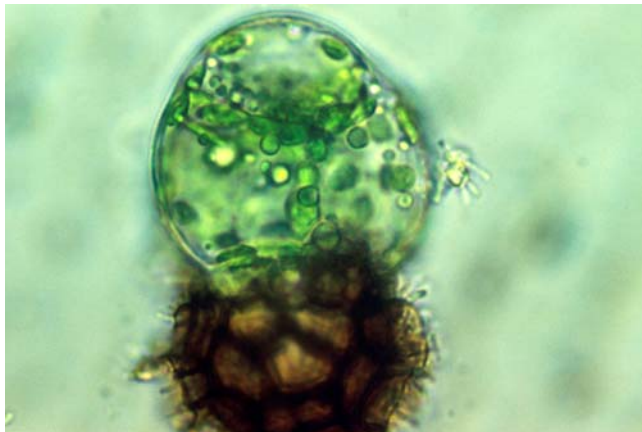
Figure 61. *Fossombronia angulosa* protonema. Photo by Plant Actions through Eugenia Ron, with permission.

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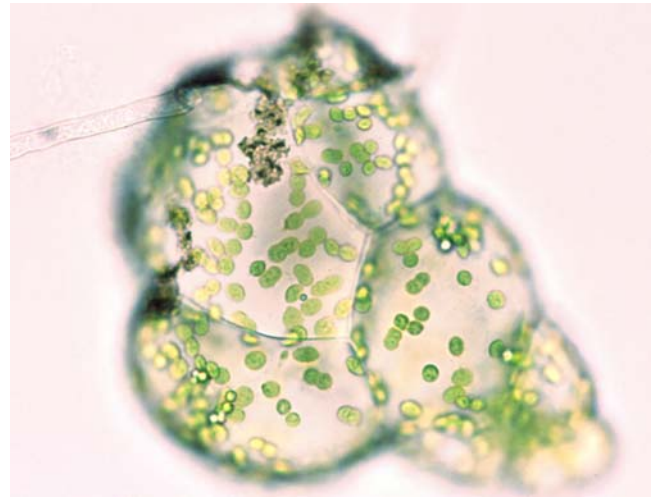

Figure 63. *Sphaerocarpus texanus* protonema. Photo by Plant Actions through Eugenia Ron, with permission.

Figure 64. Thalloid protonema of the thallose liverwort *Cyathodium foetidissimum*. Photo courtesy of Noris Salazar Allen.
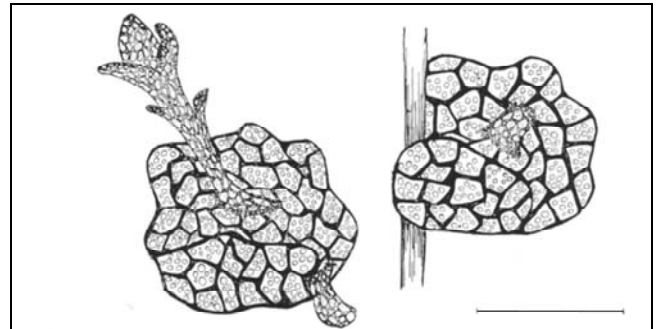
Figure 65. *Scapania undulata* showing young plant and two beginnings of plants from leaf fragments. Drawings by Flora Mace from Glime 1970.

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

Appian Way. This arrangement of leaves is reminiscent of the leaf arrangement in *Haplomitrium* (Figure 66-Figure 67). The genus *Treubia* (Figure 68) is yet another unusual liverwort (Anonymous 2010) and appears to be one of the basal groups among liverworts. This liverwort might be described as a thallus with leaves. It is intermediate between thallose and leafy liverworts and is most closely related to *Haplomitrium*.

Figure 66. *Haplomitrium gibbsiae* plants demonstrating the three-ranked leaves in this family. Photo by Jan-Peter Frahm, with permission.

Figure 67. *Haplomitrium hookeri* showing young capsules. Photo by David Holyoak, with permission.

Figure 68. *Treubia lacunosa*. Photo by Jan-Peter FFrahm, with permission.

Within the Jungermanniopsida, the **gametophore**, or mature gametophyte, can be either of two forms, depending on the family. The thalloid form has a blade-like appearance and usually produces its antheridia and archegonia within the thallus. The leafy liverworts produce their antheridia (Figure 69-Figure 72) and archegonia (Figure 73-Figure 78) along branches.

Figure 69. *Porella navicularis* antheridial branch. Photo from Botany 321 University of British Columbia website, with permission.

Figure 70. *Lophocolea cuspidata* male branch showing location of antheridia among leaves. Photo from Botany 321 at University of British Columbia website, with permission.
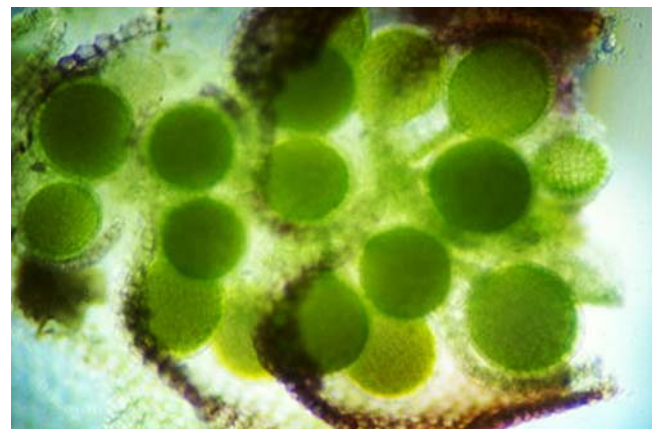
Figure 71. *Lophozia capitata* antheridia. Photo by Paul Davison, with permission.
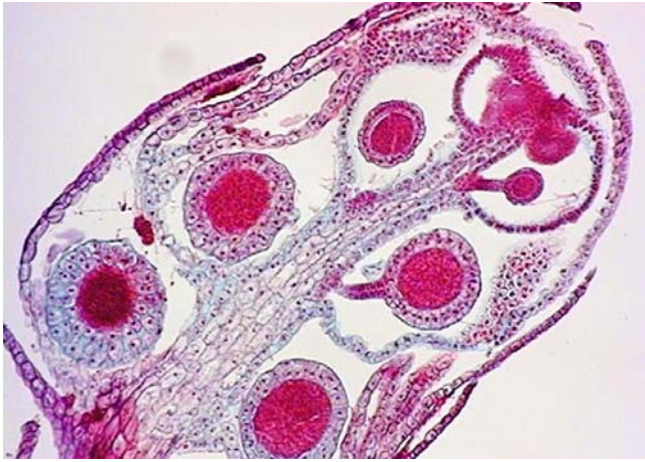
Figure 72. *Porella* sp. branch showing location of antheridia. Photo by Paul Davison, with permission.

Figure 73. *Lophocolea cuspidata* in its log habitat. Photo from Botany 321 at University of British Columbia website, with permission.
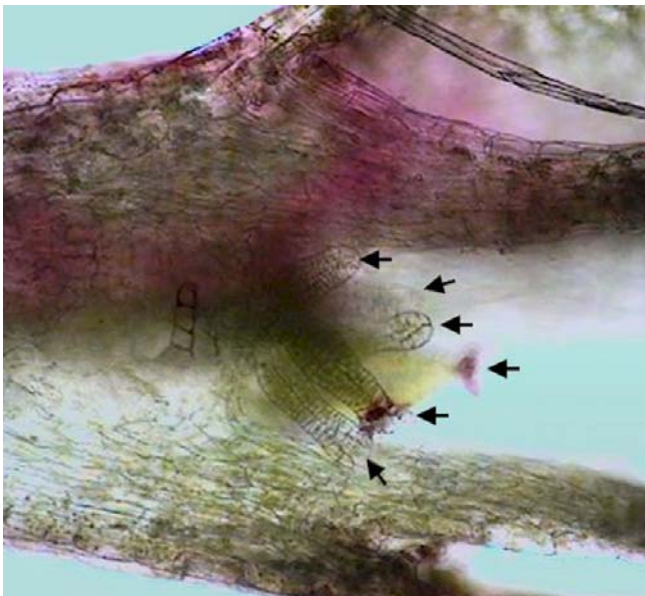
Figure 74. *Jungermannia evansii* archegonia at leaf base. Photo by Paul Davison, with permission.

Figure 75. *Lophocolea cuspidata* archegonia. Photo from Botany 321 at University of British Columbia, website, with permission.
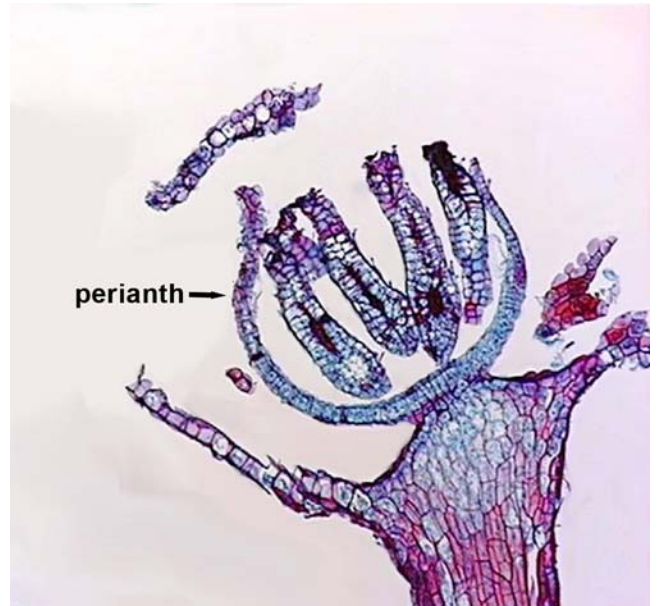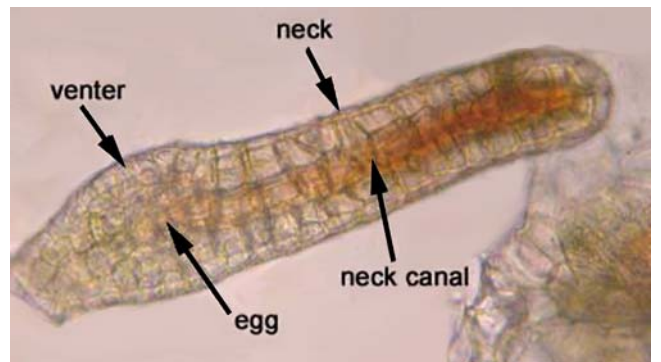

Figure 76. *Porella* archegonia in perianth. Photo by Paul Davison, with permission.

Figure 77. *Porella navicularis* archegonium. Photo by Jannah Nelson through Botany 321, University of British Columbia website, with permission.

Figure 78. *Pellia epiphylla* archegonium. Photo by Plant Actions through Eugenia Ron Alvarez, with permission.

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

Once reaching a female plant, the biflagellate sperm presumably swim, in all cases, to the archegonium. In some genera, for example the thallose *Aneura* (**Marchantiopsida**), it may take several hours for the sperm to travel a mere 10 mm (Showalter 1925 in Walton 1943). In fact, in many taxa, it is the **spermatocytes** (cells that become converted into sperm), prior to sperm release, that travel across the thallus by means of surface tension over the free water surface (Figure 79). This is at a much faster rate of 20 mm per minute (Muggoch & Walton 1942).
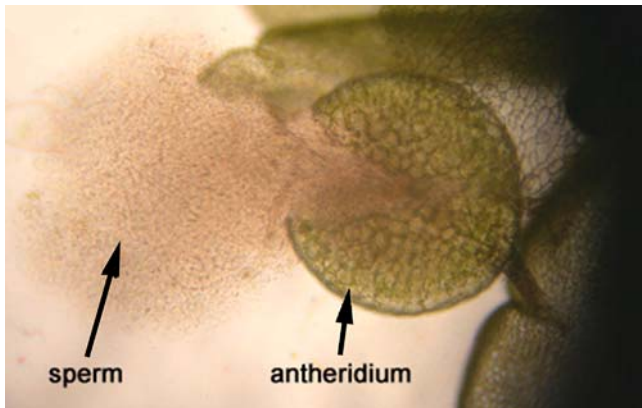
Figure 79. *Porella navicularis* (**Jungermanniopsida**) antheridium expelling sperm. Photo by Jonathan Choi, through Botany 321 University of British Columbia website, with permission.

By contrast to these earlier observations of Muggoch and Walton (1942), in *Pellia*, the emerging **spermatocytes**, in this case housing the sperm within a membrane, emerge from the dehiscing antheridium in grey masses. These masses spread rapidly across the wet surface, breaking apart as they reach the surface, with sperm emerging in about 15 seconds. It takes only 15 seconds for these spermatocytes to reach the archegonial **involucre** (protective sheath of tissue of thallus origin surrounding single antheridium, archegonium, or sporophyte; Figure 80). Another 15 minutes is required for the free sperm to emerge from the spermatocyte. Thus, the sperm disperse and are ready to enter the archegonia in little more than 15

minutes from the time of antheridial dehiscence. Such rapid movement could not be achieved by the slow-swimming sperm, which would require hours to achieve the same distance, often failing to reach their destination before the necessary water was gone.

Figure 80. *Pallavicinia lyellii* (**Metzgeriidae**) showing filamentous fringe of the involucre where archegonia are located on the thallus. **F** denotes female gametophyte; **M** denotes male gametophyte. Photo by Noris Salazar Allen, with permission.

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

In **Jungermanniidae**, the antheridia are not imbedded, but occur at the bases of leaves, whereas the archegonia are at the ends of stems or branches, surrounded by a **perianth** (Figure 81), and that is again surrounded by an **involucre** of two **bracts** and often a **bracteole**, all of which are often joined. The capsule develops inside the **perichaetium** (modified leaves that surround the archegonia), but ultimately sits atop an elongate, **hyaline** (colorless), delicate **seta** (stalk; Figure 82-Figure 84) that soon withers away. The capsule itself opens by four valves and usually contains **elaters**.

Figure 81. *Frullania* sp. perianth. Photo by George Shepherd, through Creative Commons.

Figure 82. *Porella navicularis* with young sporophyte emerging, through Botany 321 University of British Columbia website, with permission.

Figure 84. *Lophocolea heterophylla* with mature sporophytes. Photo by David Holyoak, with permission.

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

Liverworts frequently produce **gemmae** that occur on leaves of leafy liverworts (Figure 85-Figure 90) or on the thallus of thallose taxa (Figure 91). These permit the plants to reproduce asexually in places where sexual reproduction is unsuccessful. As will be discussed in a later chapter, this is especially important when the sexes are on separate plants. These gemmae are often useful for taxonomic purposes because they have a variety of shapes and colors.

Figure 85. *Tritomaria exsecta* (**Jungermanniidae**) showing gemmae on leaf tips. Photo by Michael Lüth, with permission.

Figure 83. *Lophocolea cuspidata* perianth and developing sporophyte. Photo through Botany 321 University of British Columbia website, with permission.

By contrast to the mosses, liverworts lack a split-off **calyptra** (covering of capsule formed from upper part of torn archegonial wall) and the capsule matures while it is still immersed among the protecting leaves. As the capsule (sporangium) expands, the archegonial wall is ruptured and remains at the base of the sporangial stalk. In contrast to the **Marchantiopsida** taxa that may have thalloid stalks supporting the archegonia and ultimately the capsules (*e.g. Marchantia*), and the sporophyte stalk remains small and is typically not visible among elevated scales and thallus, in the Jungermanniopsida the sporophyte stalk is conspicuous. In leafy taxa (**Jungermanniidae**) and other thalloid taxa this sporangial stalk elongates only after the capsule matures. The stalk elongates (in leafy liverworts) by rapid (3-4 days) elongation of the watery stalk (**seta**) cells (Bold *et al.* 1987) and extends the capsule away from the plant (Figure 84), using turgor pressure within the delicate cells to maintain this position. This **seta** supports and extends the capsule of most mosses and liverworts.
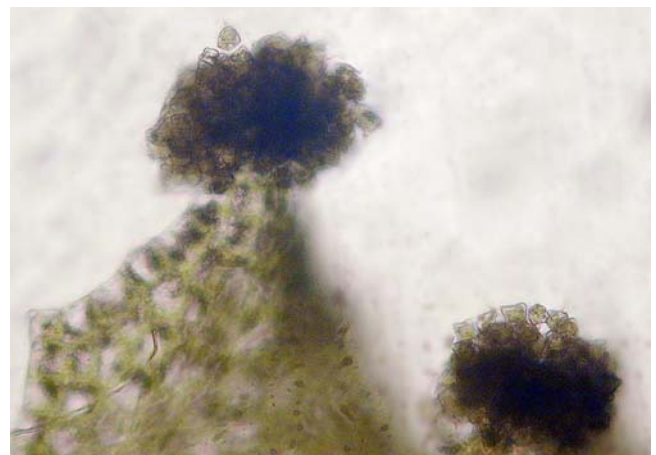

Figure 86. Microscopic view of *Tritomaria exsectiformis* leaf tips with gemmae. Photo by Michael Lüth, with permission.
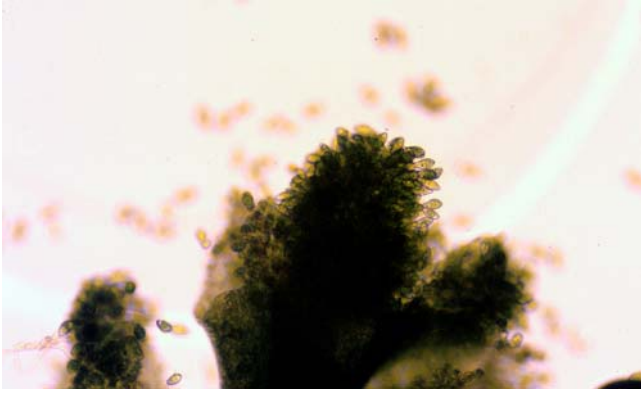
Figure 87. *Scapania aspera* gemmae on leaf tips. Photo from PlantActions through Eugenia Ron Alvarez, with permission.

Figure 88. *Anastrophyllum hellerianum* with terminal leaf gemmae. Photo by Des Callaghan, with permission.
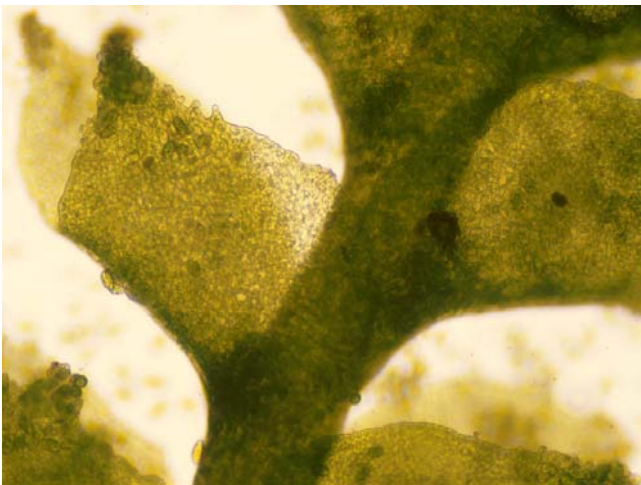

Figure 89. *Scapania aspera* with gemmae on leaves. See Figure 90. Photo from PlantActions through Eugenia Ron Alvarez, with permission.
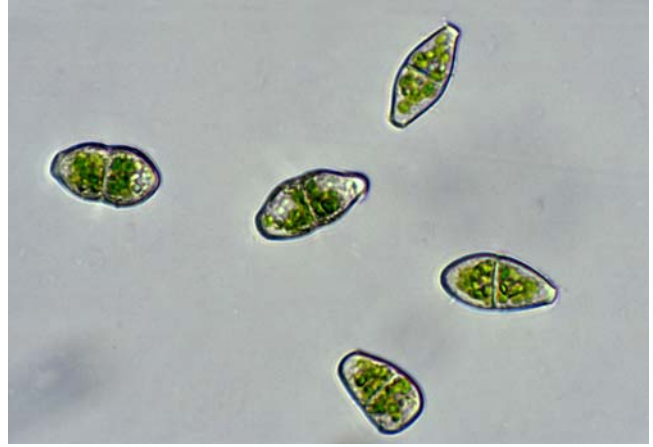

Figure 90. Gemmae of *Scapania aspera*. Photo from PlantActions through Eugenia Ron Alvarez, with permission.

Figure 91. Arrow indicates gemmae on the thallus of *Blasia pusilla* (Metzgeriidae). Photo by Michael Lüth, with permission.

Summary

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

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

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

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

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CHAPTER 2-4
BRYOPHYTA – TAKAKIOPSIDA

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CHAPTER 2-4
BRYOPHYTA – TAKAKIOPSIDA

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

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

Phylum Bryophyta

Bryophyta, *sensu stricto* (in their narrowest sense), are the mosses. These comprise, roughly, 13,000 species worldwide (Crum 2001), but with many tropical taxa likely to be as yet undiscovered, the number could be much higher. Three classes have been recognized traditionally,

the **Bryopsida**, **Andreaeopsida**, and **Sphagnopsida** (Crum 1991). However, as more evidence from genetic and biochemical relationships have become available, and the interesting genus ***Takakia*** has produced sporophytes in our presence, further division seems justified. Buck and Goffinet (2000) define six classes: **Takakiopsida**, **Sphagnopsida**, **Andreaeopsida**, **Andreaeobryopsida**, **Polytrichopsida**, and **Bryopsida**. Recent cladistic analyses using morphological, developmental, anatomical, ultrastructural, and nucleotide sequencing data supports placement of these classes into a single phylum (Newton *et al.* 2000).

Class Takakiopsida

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

liverworts. Although its 3-dimensional structure seemed a bit out of place, it seemed most like a liverwort, and there it stayed for several decades (Hattori & Inoue 1998; Hattori & Mizutani 1958). But eventually, its **slime papillae** (Figure 4), its **leaves in 3 rows** (Figure 5), its **simple oil bodies** – not granular as in liverworts, its **archegonia** (Figure 3) sometimes on a **pedestal**, and its archegonial **neck cells** in **6 vertical rows** began to raise questions. Its chromosome number was 4 or 5, unlike the typical 10 in liverworts and even higher numbers in most mosses.
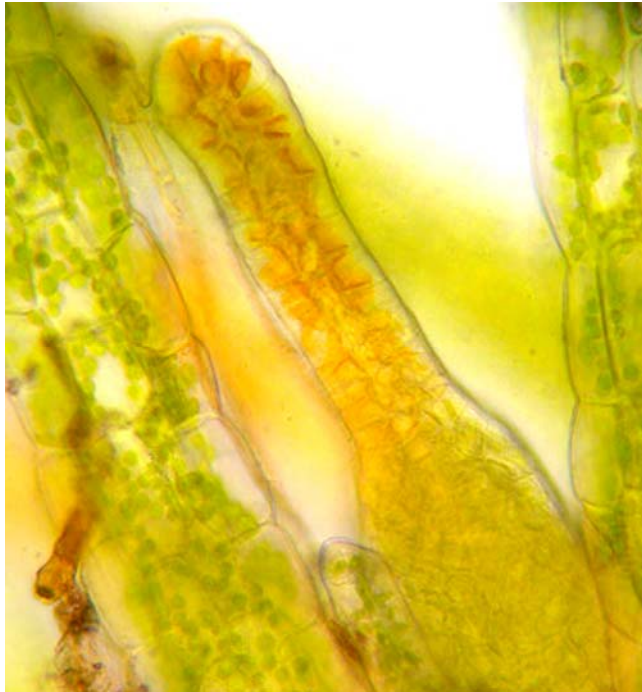
Figure 3. Archegonium of *Takakia lepidozioides*. Photo with permission from <www.botany.ubc.ca/ bryophyte/LAB8.htm.>.

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

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

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

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

Some of its characters are unlike both mosses and liverworts. The antheridia lack perigonia and the archegonia lack perichaetial leaves.

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

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

Figure 8. *Takakia ceratophylla* stem stripped of leaves to reveal the antheridia. Photo by Karen Renzaglia, with permission.
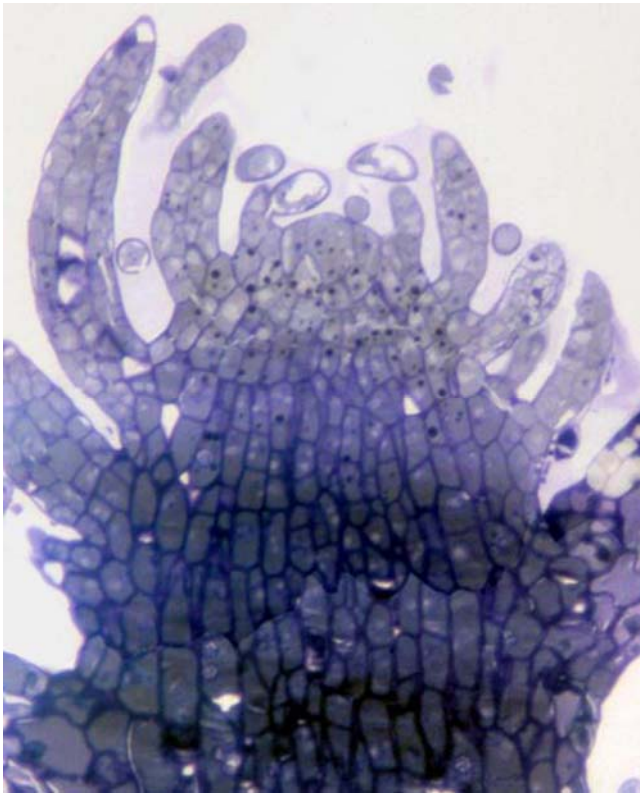
Figure 6. *Takakia ceratophylla* longitudinal section of stem tip. Photo by Karen Renzaglia, with permission.
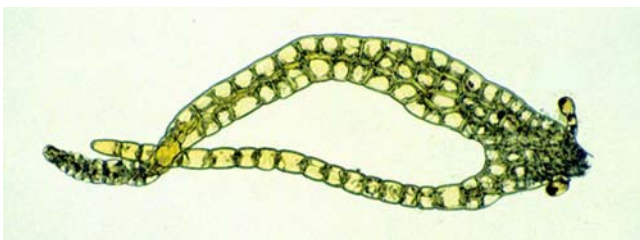
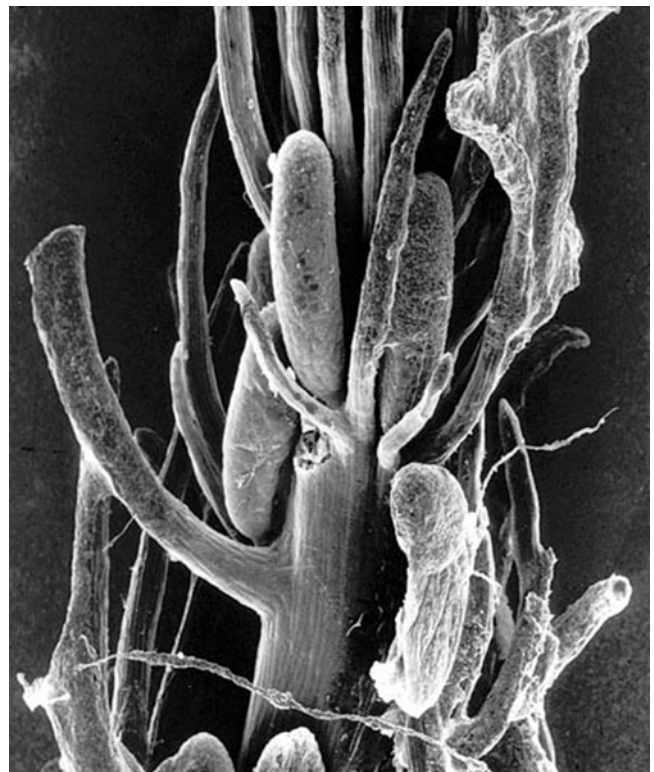Figure 7. *Takakia ceratophylla* leaf. Photo by Karen Renzaglia, with permission.

Figure 9. SEM of *Takakia ceratophylla* stem stripped of leaves to reveal the antheridia. Photo by Karen Renzaglia, with permission.
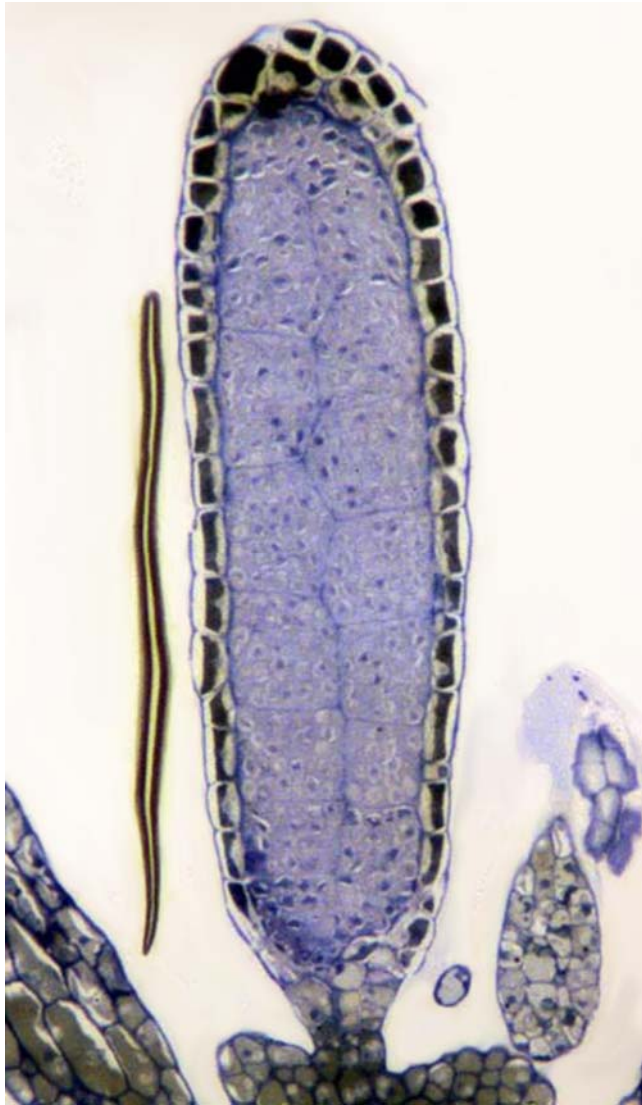
Figure 10. *Takakia ceratophylla* antheridium. Photo by Karen Renzaglia, with permission, and modified by Janice Glime.

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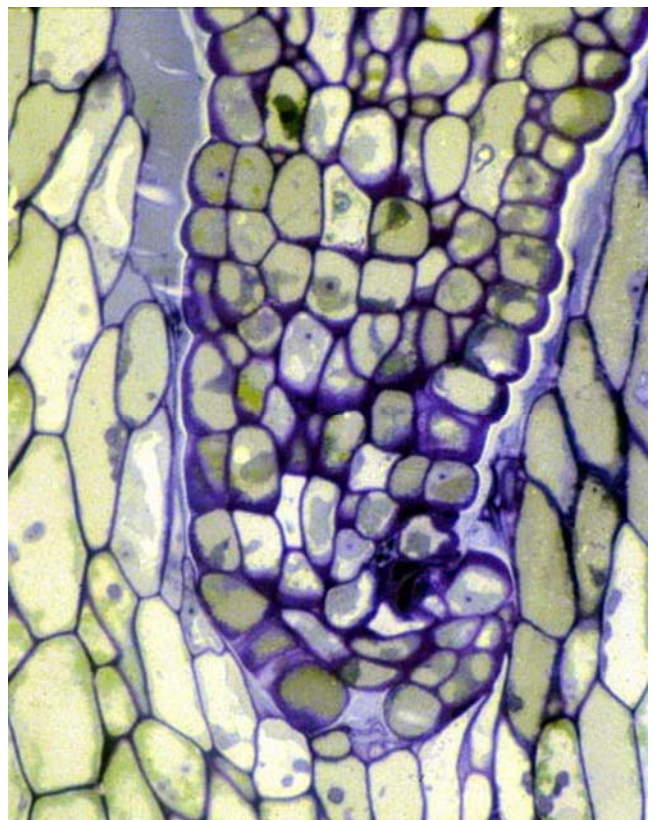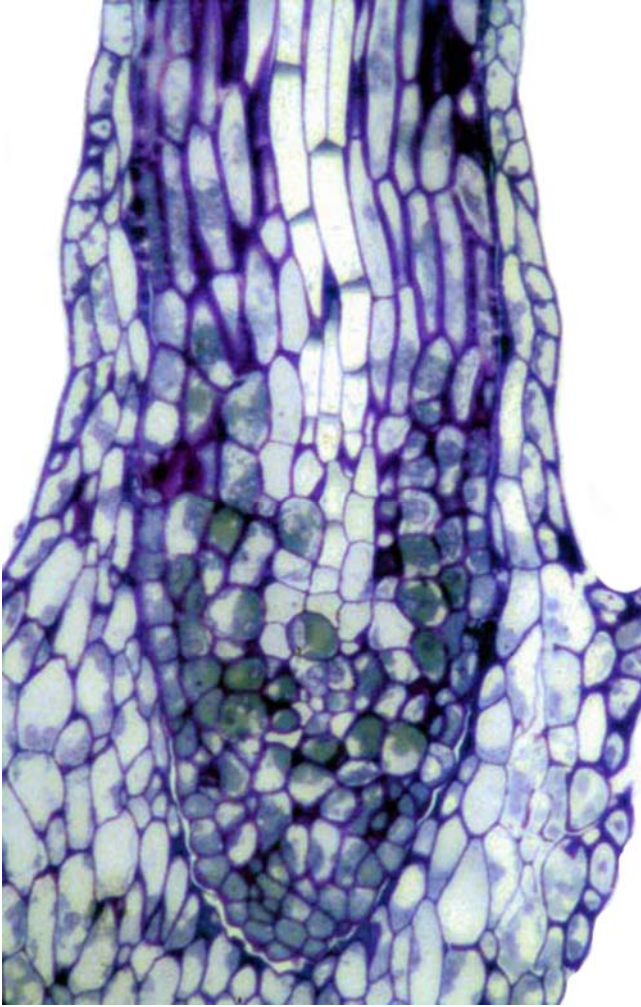

Figure 11. *Takakia ceratophylla* seta and aborted archegonia. Photo by Karen Renzaglia, with permission.

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

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

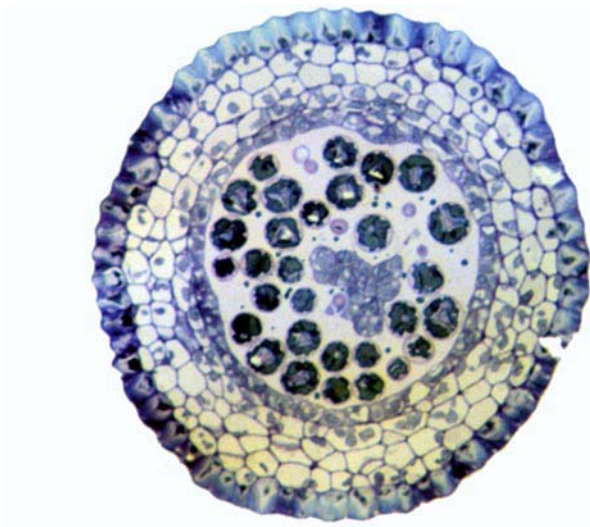Figure 14. *Takakia ceratophylla* sporophyte foot. Photo by Karen Renzaglia, with permission.

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

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

Figure 18. *Takakia ceratophylla* sporophyte cross section showing columella and tetrads of spores. Photo by Karen Renzaglia, with permission.
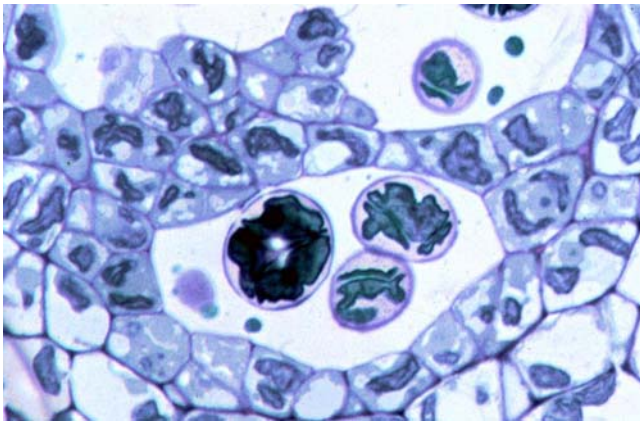
Figure 19. *Takakia ceratophylla* sporophyte cross section showing chambers with tetrads of spores. Photo by Karen Renzaglia, with permission, and modified by Janice Glime.
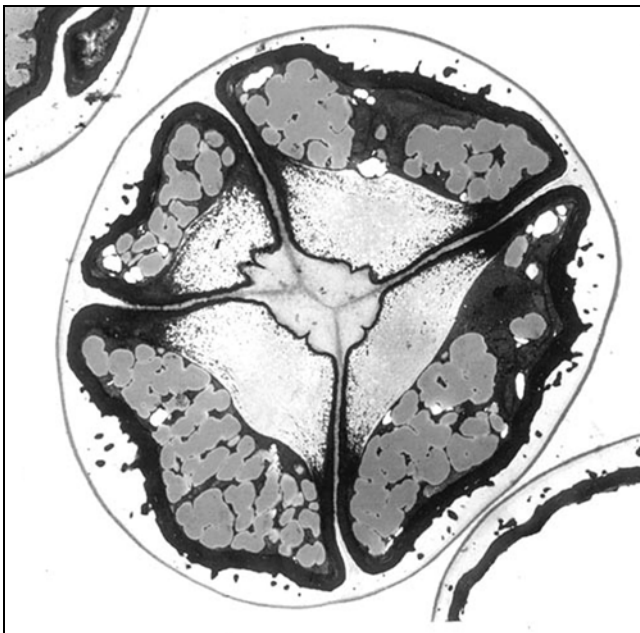

Figure 20. *Takakia ceratophylla* TEM of tetrad of spores. Photo by Karen Renzaglia, with permission.
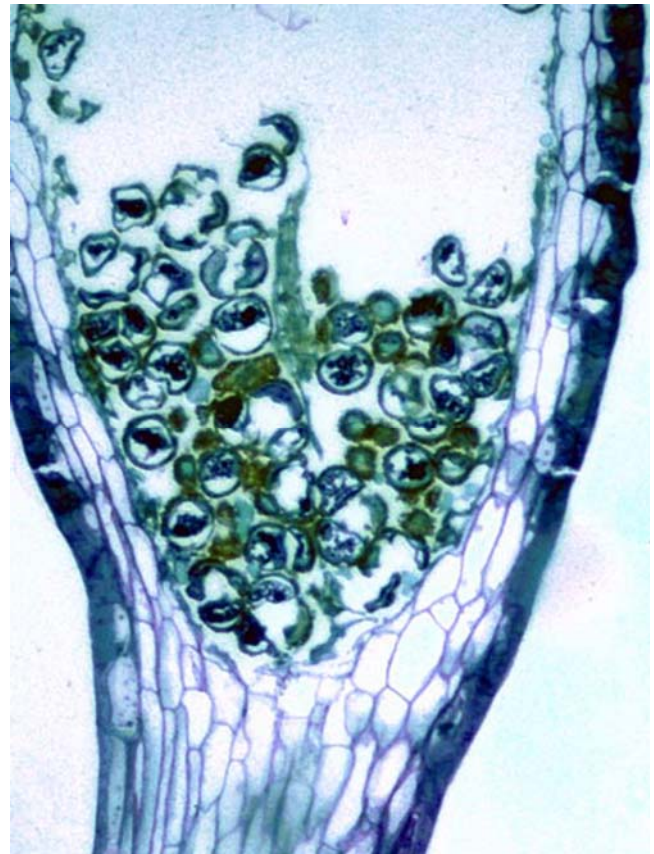

Figure 21. *Takakia ceratophylla* sporophyte longitudinal section showing spores. Photo by Karen Renzaglia, with permission.

Figure 22. *Takakia ceratophylla* with dehisced capsules. Photo by Karen Renzaglia, with permission.
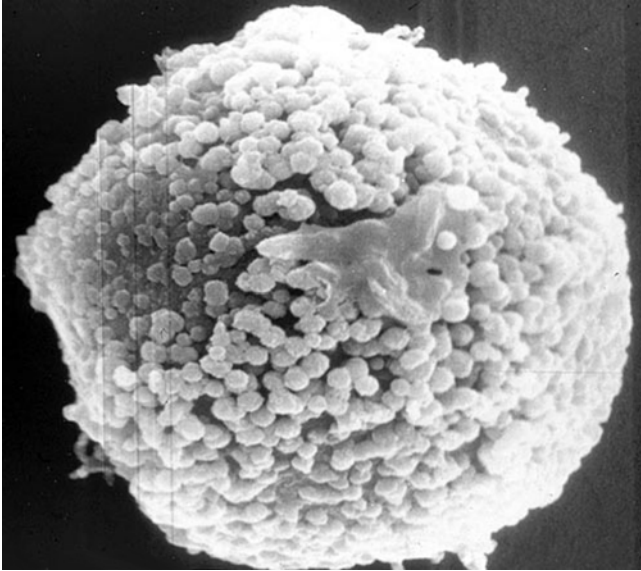
Figure 23. *Takakia ceratophylla* spore SEM. Photo by Karen Renzaglia, with permission.

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

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

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

Figure 27. *Takakia lepidozioides* showing connecting rhizomes. Photo from the Herbarium of Hiroshima University, with permission.
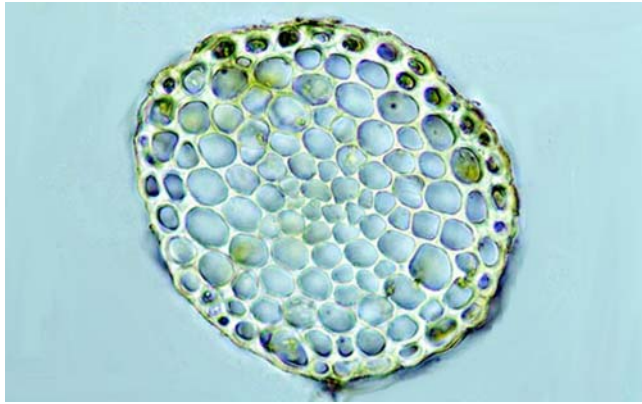
Figure 28. *Takakia lepidozioides* stem cross section. Photo from the website of the Herbarium of Hiroshima University, with permission.
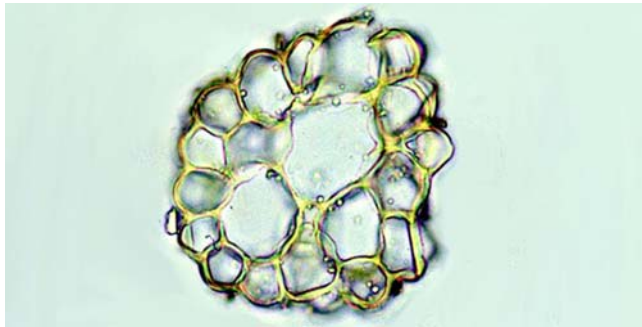

Figure 29. *Takakia lepidozioides* leaf cross section. Photo from the website of the Herbarium of Hiroshima University, with permission.

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

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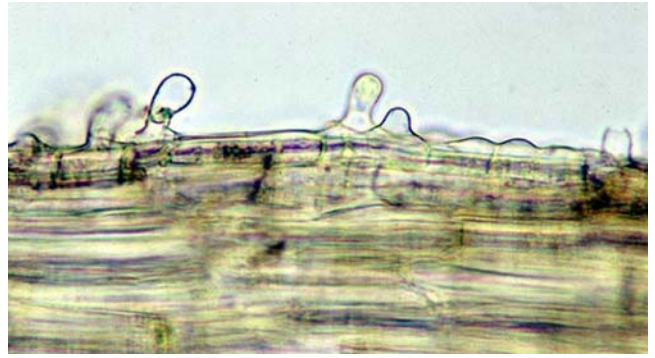

Figure 32. *Takakia lepidozioides* mucous cells on stem. Photo from the website of the Herbarium of Hiroshima University, with permission.
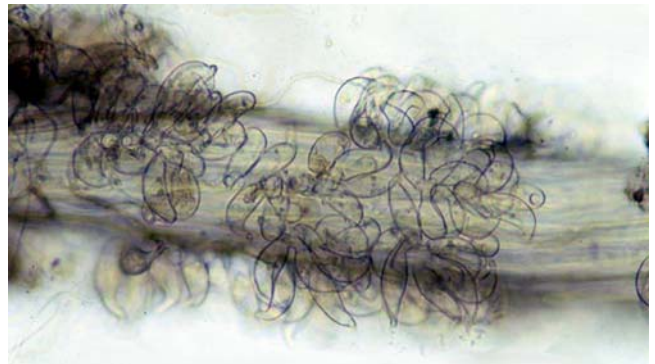

Figure 33. *Takakia lepidozioides* slime papillae. Photo from the website of the Herbarium of Hiroshima University, with permission.
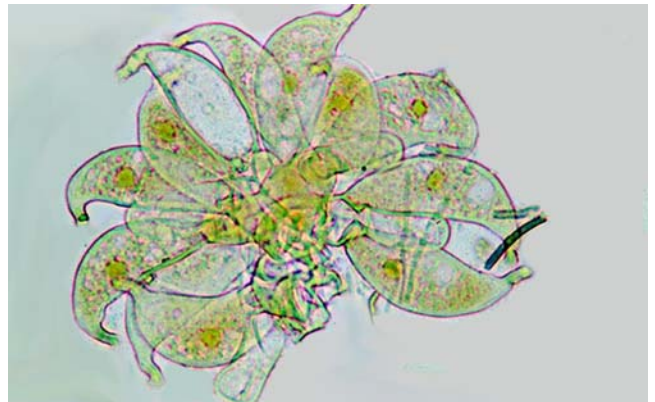

Figure 34. *Takakia lepidozioides* mucous cells on stem. Photo from the website of the Herbarium of Hiroshima University, with permission.

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

Summary

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

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

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CHAPTER 2-5
BRYOPHYTA – SPHAGNOPSIDA

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BRYOPHYTA - SPHAGNOPSIDA

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

Class Sphagnopsida – the peat mosses

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

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

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

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

Sphagnaceae

Of all the Bryobiotina, *Sphagnum* is best known to the layperson because of its formation of peat and use in horticulture. The class Sphagnopsida is distinguished by **leaves** that are **one cell thick** and mostly possessing two types of cells – **photosynthetic cells** that possess chloroplasts and that form a network arrangement, and **hyaline** (colorless) **cells** that are dead at maturity, have one or more **pores** (giving access to the environment), and hold water (Figure 45). These hyaline cells form transparent patches among the network formed by the photosynthetic cells and may be equal in height to those cells or may surround them on the top (inner leaf surface) or on both surfaces. This arrangement seems to correlate well with the ability to avoid desiccation because the hyaline cells provide a reservoir of water to the photosynthetic cells. Those species typically occupying drier habitats generally have more of the hyaline cell surrounding the photosynthetic cell. These hyaline cells are usually strengthened by bar-like thickenings (**fibrillae**, Figure 45) in the cell walls, making them look superficially like many cells instead of the single long cell that they are. These leaves never possess a **costa** (moss version of a midrib).

The branches in Sphagnopsida occur in **fascicles** (bunches) along the stem, usually with some descending branches close to the stem (helping in capillary movement

of water) and some extending outward. The stems have a wood-like cylinder that may be brittle or soft. The most readily distinctive feature is the arrangement of young branches in a tight **capitulum** (Figure 46), the result of branch production and elongation without the elongation of the stem. As older portions of the stem elongate, new branches form and the capitulum is maintained. This gametophyte can reproduce by fragmentation, often bifurcating at the apex to produce two capitula.

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

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

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

Subgenus *Cuspidata* has a pronounced difference between hanging branches and spreading branches, usually with hanging branches longer and more slender than spreading branches; stem leaves are much smaller than branch leaves and usually hang downward on the stem; colors vary but are never red; they are typical in wet mineral-rich depressions, submerged or near the water level (Figure 15-Figure 25).

Subgenus *Subsecunda* has flexuose hanging and spreading branches that are very similar, about the same length, or with few no branches; stem leaves are much smaller than branch leaves and usually hang downward on stems; plants are various colors but never red (branches and stems sometimes pinkish) (Figure 26-Figure 30).

Subgenus *Squarrosa* has distinctly squarrose branch leaves and large (1-1.5 mm long) lingulate stem leaves (Figure 31-Figure 32).

Subgenus *Acutifolia*

Section *Acutifolia*, like Subgenus *Cuspidata*, has a pronounced difference between hanging branches and spreading branches, usually with hanging branches longer and more slender than spreading branches; they differ from *Cuspidata* in having stem leaves nearly the same size as branch leaves or larger and usually upright on stems; plants are various shades of green, brown, or red (Figure 33-Figure 42).

Section *Polyclada* is monotypic and lacks the cucullate leaf structure, being distinguished by having six or more branches per fascicle and a dense, rounded capitulum (Figure 43).

Section *Insulosa* has toothed branch leaves and pores in hyaline cell ends (Figure 44).

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

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

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

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

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

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Figure 15. *Sphagnum riparium* (Subgenus *Cuspidata*). Photo by Des Callaghan, with permission.

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Figure 25. *Sphagnum torreyanum* (Subgenus *Cuspidata*). Photo by Janice Glime.
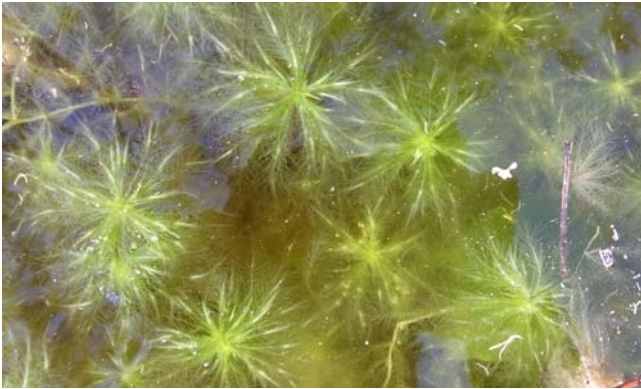

Figure 22. *Sphagnum trinitense* (Subgenus *Cuspidata*). Photo by Blanka Shaw, with permission.

Figure 26. *Sphagnum pylaisii* (Subgenus *Subsecunda*). Photo by Jan-Peter Frahm, with permission.

Figure 23. *Sphagnum mendocinum* (Subgenus *Cuspidata*). Photo by Adolf Ceska, with permission.
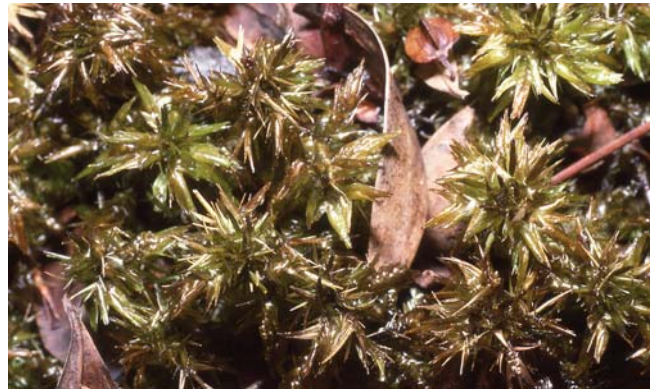

Figure 27. *Sphagnum macrophyllum* (Subgenus *Subsecunda*). Photo by Janice Glime.

Figure 24. *Sphagnum cuspidatum* (Subgenus *Cuspidata*). Photo by Michael Lüth, with permission.

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

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

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

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Figure 31. *Sphagnum squarrosum* (Subgenus *Squarrosa*). Photo by Dick Haaksma, with permission.

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Figure 38.   *Sphagnum meridense* (Subgenus *Acutifolia*, Section *Acutifolia*). Photo by Jan-Peter Frahm, with permission.

Figure 42.   *Sphagnum capillifolium* (Subgenus *Acutifolia*, Section *Acutifolia*). Photo by David Holyoak, with permission.

Figure 39.   *Sphagnum warnstorfii* (Subgenus *Acutifolia*, Section *Acutifolia*). This species can turn blue in a basic *p*H. Photo by Michael Lüth, with permission.

Figure 43.   *Sphagnum wulfianum* (Subgenus *Acutifolia*, Section *Polyclada*). Photo by Jan-Peter Frahm, with permission.

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

Figure 44.   *Sphagnum aongstroemia* (Section *Insulosa*). Photo by Dale Vitt, with permission.
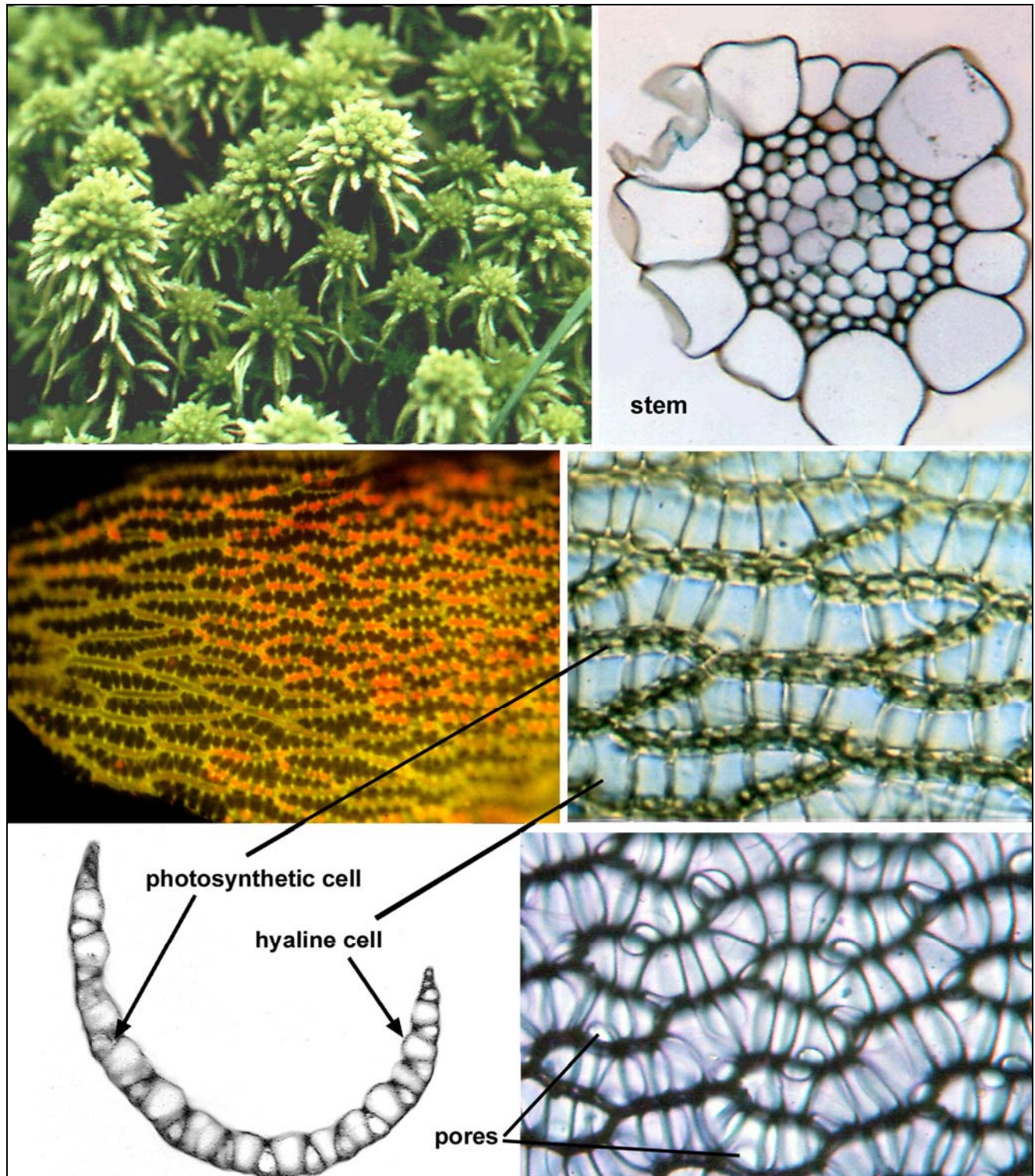
Figure 45. Vegetative characters of *Sphagnum*, Class Sphagnopsida. **upper left:** *Sphagnum wulfianum* capitula; **upper right:** cross section of stem showing hyaline cells and "woody strand;" **middle left:** leaf showing pattern of hyaline and photosynthetic cells illuminated by UV light; red areas indicate chlorophyll fluorescence; **middle right:** portion of leaf showing photosynthetic and hyaline cells (note fibrillae on hyaline cells); **lower left:** cross section of leaf showing hyaline cells that nearly enclose the photosynthetic cells; **lower right:** methylene-blue-stained portion of leaf showing pores in hyaline cells. Photos by Janice Glime.

Figure 46. *Sphagnum fimbriatum* showing capitulum where archegonia will arise. Photo by Janice Glime.

The **antheridia** are nearly globose (Figure 47) and are nestled among the leaves near the tips of the capitulum branches, usually endowing those tips with a reddish color (Figure 48). The **archegonia** are terminal on short branches near the center of the capitulum.
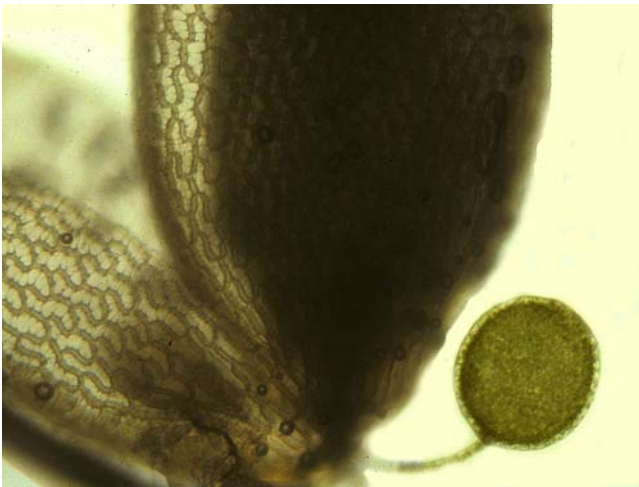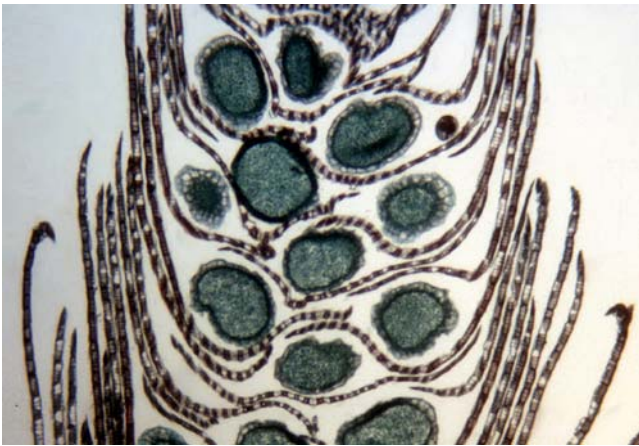

Figure 47. Globose *Sphagnum* antheridia nestled among the leaves of a capitulum branch. Photos by Janice Glime (**top**) and Yenhung Li (**bottom**), with permission.

Jennings (1915) and Bryan (1915 in Jennings 1915) recognized the unique character of *Sphagnum*. They described a globose antheridial head that began development in August, before the September initiation of the archegonia. They discovered that some of the oldest archegonia matured by 25 October, whereas others did not mature until spring. But the uniqueness was the structures.

The archegonia have a stalk, thick venter, and a narrow, twisted neck, all characteristic of mosses. But their inactive cover cell, intercalary growth of the archegonia, and the small number of canal cells (8-9) are characteristic of liverworts.

Figure 48. Antheridial branches in the capitulum of *Sphagnum*. Red coloration is from the antheridia. Photo by Janice Glime.

Sphagnum **capsules** (Figure 49), or sporangia, are rarely seen in many of the species, but some fruit abundantly. Nevertheless, one must be lucky to see them because they, like the liverwort sporophytes, are **short-lived**. They develop from fertilized eggs (**zygotes**) in the capitulum (Figure 46). As these develop embryos, they likewise form a **foot**, **stalk**, and **capsule** (Figure 49), but the stalk does not elongate. Instead, it remains with its foot, embedded in gametophyte tissue. *Sphagnum* is much like the liverworts in that its stalk matures after the capsule is mature, but in *Sphagnum*, this watery stalk (**pseudopodium**, pl. **pseudopodia**) is part of the gametophyte generation, not the sporophyte (Figure 49). It soon disintegrates, as do the liverwort stalks.

The capsule does not split as in liverworts and the **Takakiopsida**, **Andreaeopsida**, and **Andreaeobryopsida** in the **Bryophyta**, but instead possesses an **operculum** (lid; top part of capsule of mosses that comes off for spore dispersal) that is shed prior to spore dispersal (Figure 49), as in the **Bryophyta** classes **Bryopsida** and **Polytrichopsida**. However, unlike most members of the latter two classes, it lacks a **peristome** (set of teeth-like appendages around the opening of capsule; Figure 49). The **columella** (Figure 49), that central mass of sterile tissue that is like a column in **Bryopsida** and **Polytrichopsida**, is globose in *Sphagnum*, protruding like a knob into the center of the capsule without reaching its top. **Elaters are lacking**, a characteristic shared with all other **Bryophyta** (*sensu stricto*).

Within the capsule, meiosis occurs, producing the spores. When the spores are mature, the **operculum** (Figure 49) is shed explosively when the capsule shrinks and compresses the gases, dispersing nearly all the spores in one blast of 4-6 atmospheres of pressure (Crum 2004; see Chapter 4-9). In fact, bryological folklore claims that

one can hear the explosions when the sun and moisture are just right to cause the capsules to explode. No extant sphagnologist seems to have actually heard this, but following a *Sphagnum* field trip at an international meeting in Great Britain, one of the bryologists was startled to hear ping...ping-ping...ping-ping-ping while he was sitting in bed reading. He had put his *Sphagnum* with capsules under the bed lamp to dry, and so it had, with capsules shrinking and exploding. The pings were opercula hitting the metal shade on the lamp!

It appears that *Sphagnum* is prolific in its spore production, ranging 8-90 million among six species examined by Sundberg (2005). And these spores seem to disperse quite well, with only 2-14% of those dispersed remaining within the parent colony. Being large helps. The larger capsules dispersed a greater percentage of spores, had a smaller percentage trapped within the parent colony, and thus dispersed more spores to greater distances.

In the presence of moisture and light, the spores germinate to form a short thread. This thread soon, however, divides in more than one direction to form a **thalloid protonema** (Figure 49), as in most liverworts. A similar thalloid protonema is present also in other bryophytes such as *Andreaea* (Bryophyta class Andreaeopsida) and would be more appropriately called a **sporeling**. Like the liverworts, and unlike the other mosses, each protonema produces **only one bud**, thus only one mature gametophyte.
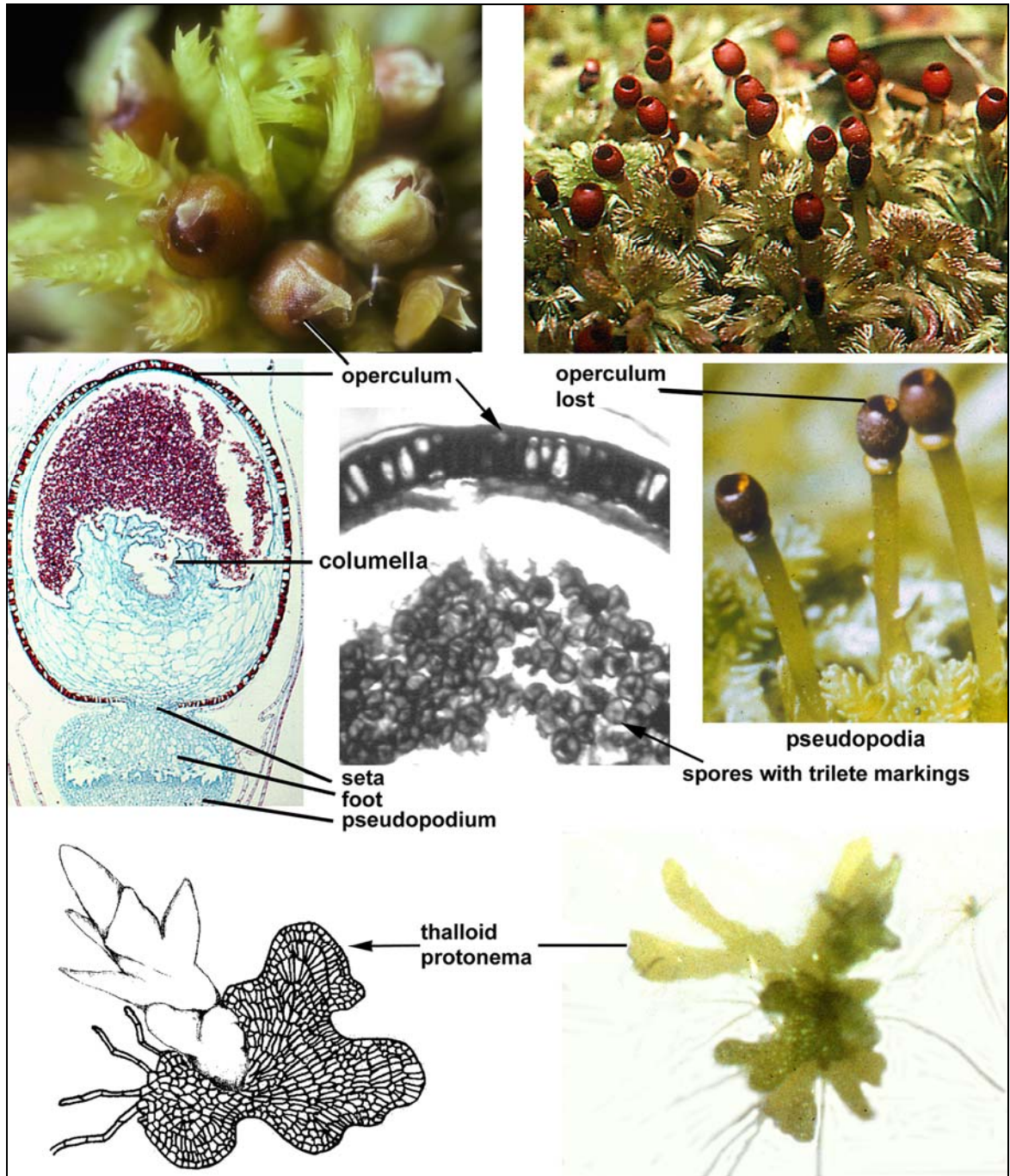

Figure 49. *Sphagnum* life cycle stages. Upper left photo by Zen Iwatsuki; others by Janice Glime. Protonema drawing by Margaret Minahan and Noris Salazar Allen, with permission.

Flatbergiaceae (= Sphagnaceae?)

Shaw (in Shaw *et al.* 2010) separated this family morphologically from **Sphagnaceae** by its efibrillose leaves. It is currently monotypic, with only the species *Flatbergium sericeum*. Currently, however, both Tropicos and The Plant List (Kew) consider this genus to belong in the **Sphagnaceae**. A second species is implicated for the family (Devos *et al.* 2016), based on molecular data. This would transfer *Sphagnum novo-caledoniae* to *Flatbergium novo-caledoniae* (Figure 50).

Figure 50. *Flatbergium novo-caledoniae*. Photo courtesy of Kjell Flatberg.

Ambuchananiaceae

Not many of us get to describe a new order. And certainly no one was expecting one in the **Sphagnopsida**! (Buchanan 2008). But this organism, this moss, was certainly something new! – *Ambuchanania leucobryoides* (Figure 51).

Figure 51. *Ambuchanania leucobryoides* showing similarity to some species of *Sphagnum*. Photo by Lynette Cave, with permission.

Excerpts from correspondence with Rod Seppelt

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

"When I first saw the material I kept trying to put it in Leucobryaceae. Same habit, hence the epithet. Initially I thought I saw a peristome. The leaves did not

---

fit anything in Leucobryaceae. Then the penny dropped – it had no peristome. The position of the archegonia also started to ring bells."...

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

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

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

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

Now, this strange, yet somewhat familiar genus resides not just in a new family, but a new order, the Ambuchananiales. It differs from *Sphagnum* in **lacking fascicles**, being **sparsely branched**, and **lacking the "wood" cylinder** of the stem. Its **leaves** are **partially bistratose** but have those telltale **hyaline** and **photosynthetic cells** (Figure 52-Figure 53). It is anchored by **rhizoids**, a character found in *Sphagnum* only in one epiphytic species. Its **archegonia** are located **terminally** on stems and its **capsules** are **cylindrical**, and likewise perched on an elevated **pseudopodium**.

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

Figure 53. *Ambuchanania leucobryoides* leaf cross section showing hyaline and photosynthetic cells. Photo by Lynette Cave, with permission.

In addition, the genus *Eosphagnum* has been added to the **Ambucananiaceae**, an older species that has been reclassified (Shaw *et al*. 2010). This genus has the single species *E. rigescens* (an older name for *E. inretortum*; Figure 54) (Shaw *et al*. 2016).
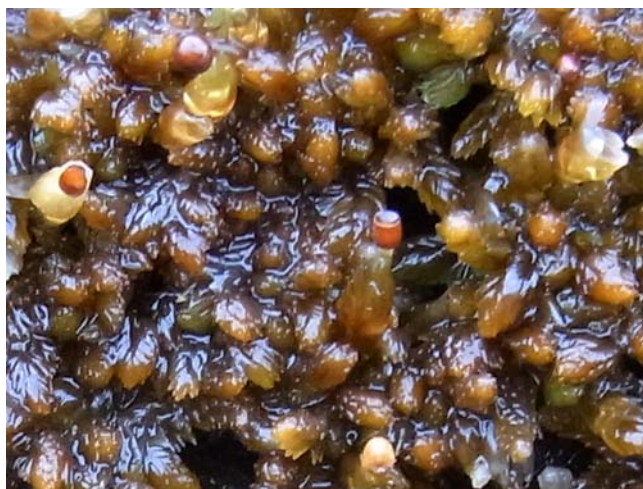

Figure 54. *Eosphagnum rigescens* with capsules. Photo courtesy of Blanka Shaw.

Summary

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

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

Sporophytes remain attached to the gametophyte and produce **spores** by **meiosis**. The stalk supporting the *Sphagnum* sporophyte is a deliquescent extension

of the gametophyte (**pseudopodium**) and it develops after the **capsule** is mature. **Sphagnopsida** lack teeth in the capsule but have an **operculum**, which the capsule sheds explosively.

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

Acknowledgments

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CHAPTER 2-6

BRYOPHYTA - ANDREAEOPSIDA, ANDREAEOBRYOPSIDA, POLYTRICHOPSIDA

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CHAPTER 2-6

BRYOPHYTA - ANDREAEOPSIDA, ANDREAEOBRYOPSIDA, POLYTRICHOPSIDA

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

Andreaeopsida – The Granite Mosses

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

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

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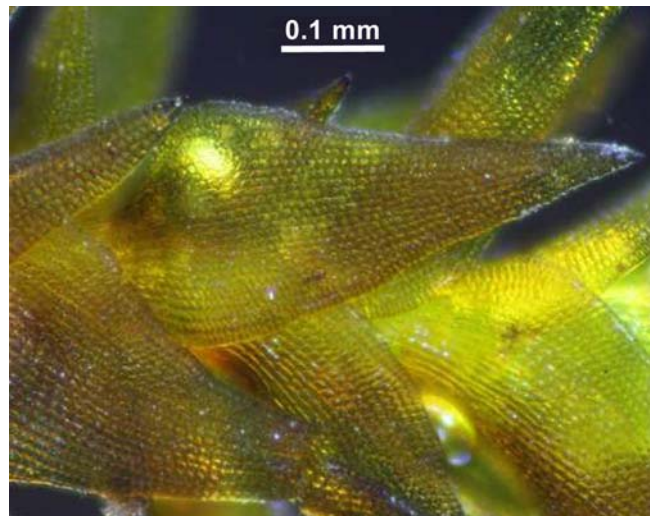

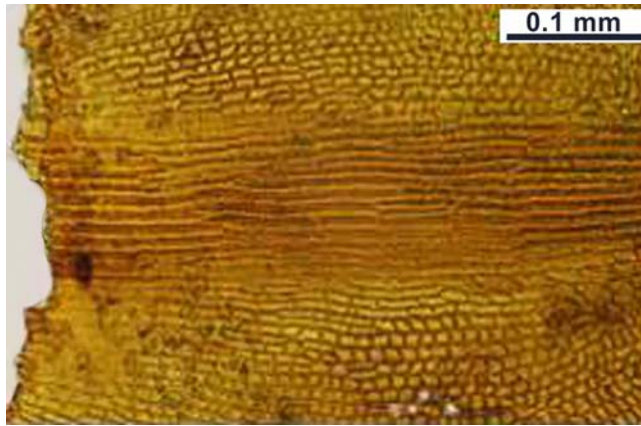Figure 2. *Andreaea mutabilis* leaves with no costa. Photo by Tom Thekathyil, with permission.

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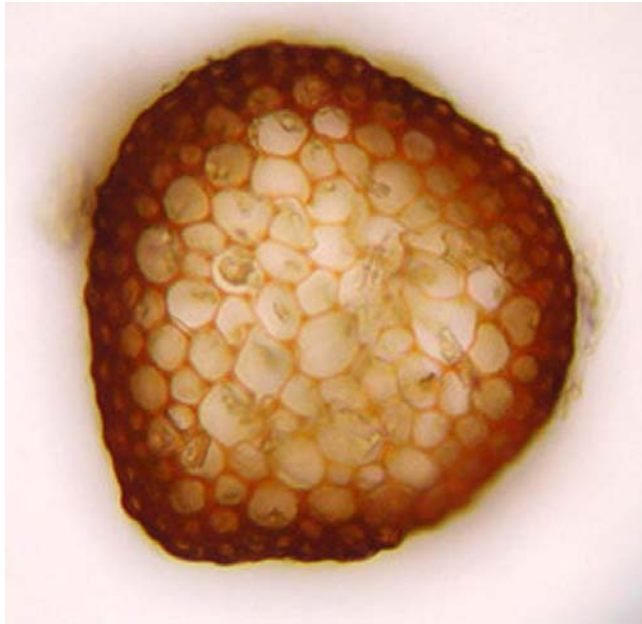

Figure 4. *Andreaea* stem cross sections. Photo from website of Botany Department, University of British Columbia, with permission.

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

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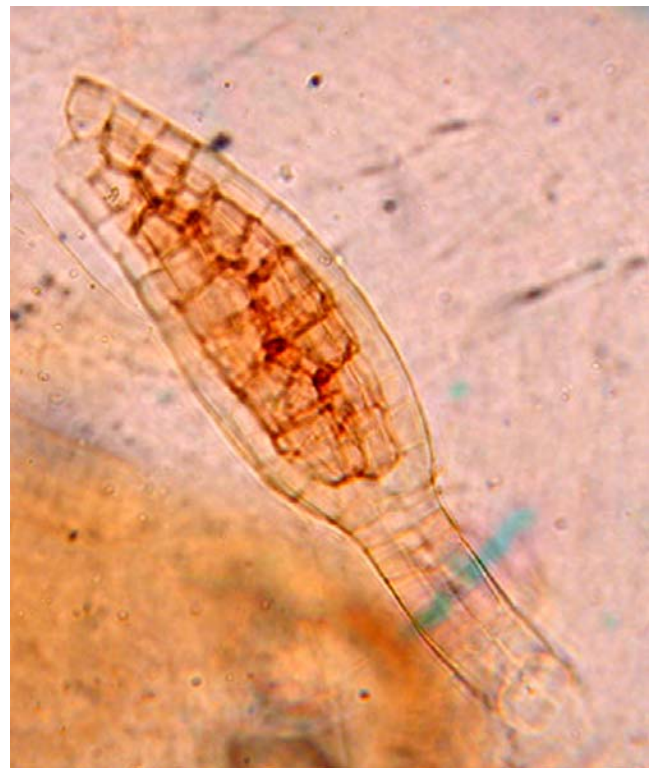

Figure 7. *Andreaea nivalis* antheridium. Photo from website of Botany department, University of British Columbia, with permission.

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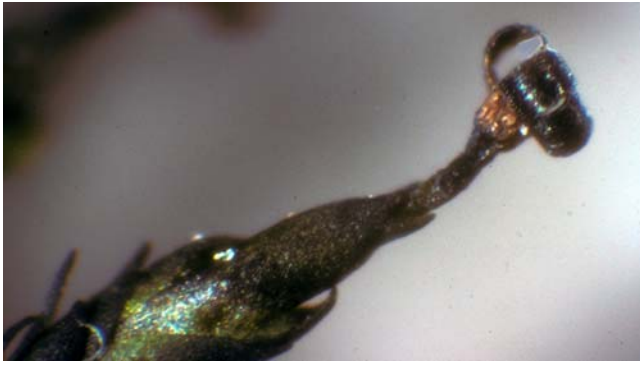
Figure 8. *Andreaea rupestris*, Class **Andreaeopsida**, gametophyte with sporophyte showing four valves of capsule and pseudopodium of gametophyte. Photo by Janice Glime.

Andreaeobryopsida

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

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

Polytrichopsida

With bryophytes, the determination of primitive or advanced often depends on the generation being examined. The gametophyte may have changed considerably while some set of characters of the sporophyte remained constant. And of course, the reverse can be true. The **dioicous** condition (male and female reproductive organs on separate plants) that characterizes **Polytrichopsida** is considered to be primitive (Longton & Schuster 1983), with the

monoicous condition (male and female reproductive organs on the same plant) that is so frequent in **Bryopsida** typically being derived by doubling of the chromosome number.   Likewise, **nematodontous peristome teeth** (having evenly thickened walls and whole dead cells lacking eroded walls, Figure 10) of **Polytrichopsida** would seem to be an earlier development than the arthrodontous condition of Bryopsida.

All members of the class possess an elongate sporophyte **seta**, supporting an **operculate peristomate** capsule, and a **columnar columella**, characters that are more advanced than in Sphagnopsida but typical in Bryopsida. Spores are produced by meiosis in a single event in **sporogenous** tissue that surrounds the columella (Figure 11-Figure 12).
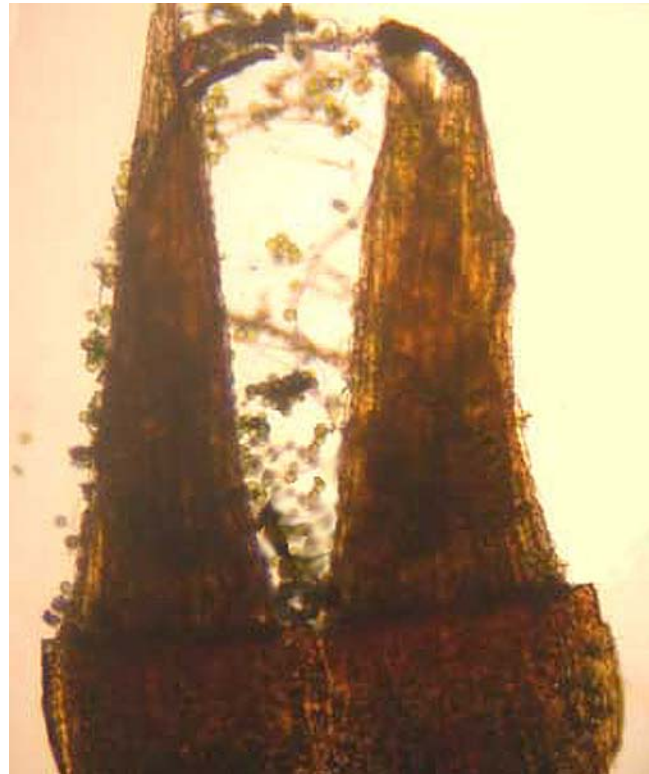

Figure 10. **Nematodontous** peristome teeth of *Tetraphis pellucida* (**Polytrichopsida**). Note the separation at the tips. Photo from Biology 321 Course Website, UBC, with permission.
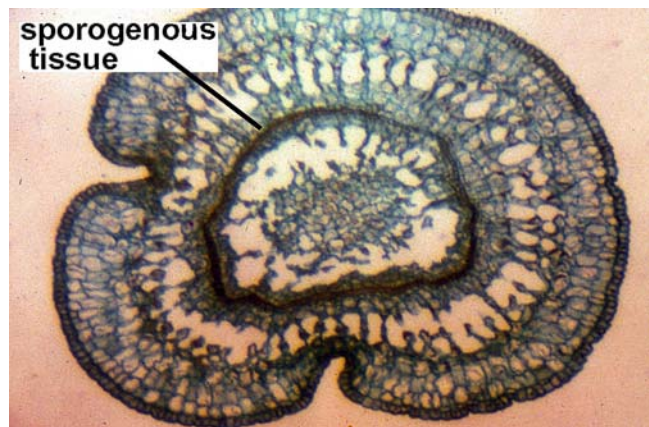

Figure 11. Cross section of immature *Polytrichum* capsule showing sporogenous tissue. Photo by Janice Glime.
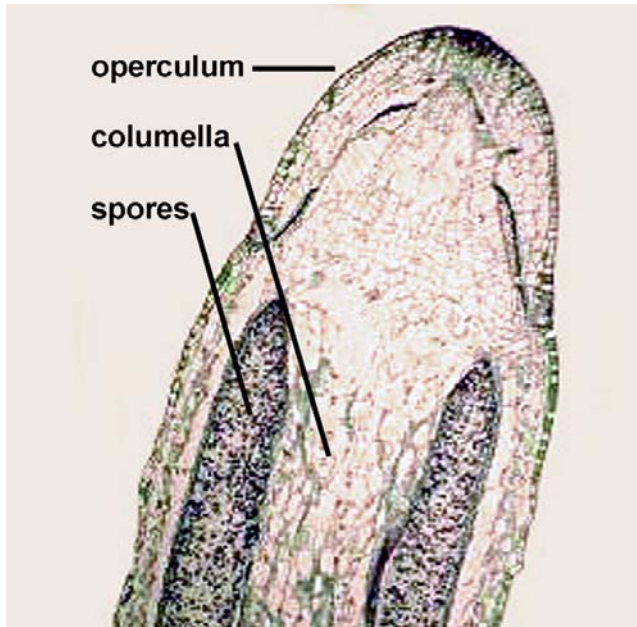
Figure 12. Longitudinal section of *Polytrichum* capsule. Photo by Janice Glime.

The gametophyte is often very specialized, being characterized by stems with a **central strand**, reaching its peak in **Polytrichaceae** (Figure 13), with the presence of **hydroids** (water-conducting cells) and **leptoids** (sugar-conducting cells). The leaves of the class are **all costate** (having a midrib-like structure; Figure 14).
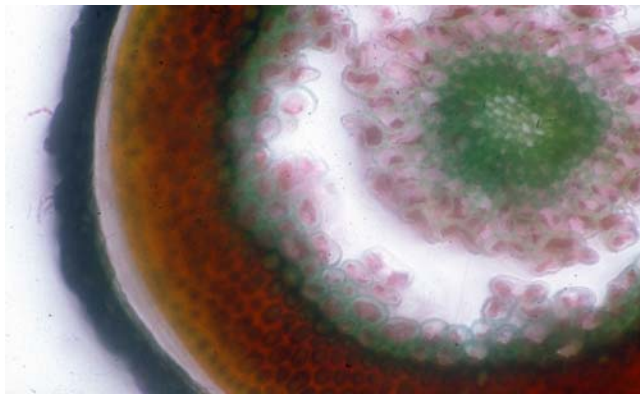

Figure 13. Cross section of a *Polytrichum* stem showing green **hydroids** in center and larger **leptoids** surrounding them. Photo by Izawa Kawai, with permission.

Figure 14. *Tetraphis pellucida* showing leaves with a **costa**. Photo by Des Callaghan, with permission.

Polytrichaceae

In many ways, this family looks like a tracheophyte wanna-be. It attains a greater height than the typical moss and can even stand alone to nearly half a meter in the case of *Dawsonia longifolia* (Figure 15). *Polytrichum commune* (Figure 16) likewise attains similar heights, but only with the support of other individuals, forming a hummock. Even in the cold climate of Macquarie Island, *P. juniperinum* reaches hummock heights of 30 cm (Rod Seppelt, pers. comm. 16 March 2007).

Figure 15. *Dawsonia longifolia* from New South Wales, Australia. Photo by Janice Glime.

The genus *Dawsonia* has many unresolved species, some of which have been moved to a different genus. Even the well known *D. superba* (Figure 15) has been merged into *D. longifolia*. *Dawsonia longifolia* *s.l.* is a native of New Zealand, Australia, and Papua New Guinea and breaks the height record for upright mosses. It grows up to 48 mm in a year and in this study ranged 6-38 cm tall (Green & Clayton-Greene 1981). This compares well with known growth rates of *Polytrichum commune* of 3-5 cm in one growing season (Figure 17) (Sarafis 1971). It occurs in a temperate climate and its growth tracks available moisture and temperature. Its sperm dispersal is aided by an antheridial splash cup, with sperm known to reach females 1.5-2 m from the males in the field, but experimental tests showed they could splash to heights up to 3.3 m in the lab (Clayton-Greene *et al*. 1977)! Ligrone *et al*. (2002) showed that *Dawsonia* responded differently to antibodies used to label the arabinogalactan proteins in the water conducting cells, suggesting that their chemical structure differed from that of other mosses tested. On the other hand, *Dendroligotrichum* (Figure 18) and *Polytrichum* demonstrated a strong reaction in the leptoids (Figure 13; Figure 19) of the stem. These three genera differed in other marker reactions as well, supporting the uniqueness of the **Polytrichopsida**.

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

Figure 16. *Polytrichum commune* with capsules. Photo by George Shepherd, through Creative Commons.

Figure 17. *Polytrichum commune* 2-year growth in Europe. Photo by Michael Lüth, with permission.

Figure 18. *Dendroligotrichum dendroides*. Photo by Jan-Peter Frahm, with permission

Figure 19. *Dendroligotrichum dendroides* stem cross section showing hydroids and leptoids. Photo by Juan Larrain, with permission.

The **Polytrichaceae** lead the way to complexity with their unusual leaf structure, possessing vertical **lamellae** (vertical tiers of cells like the pages of an open book; Figure 20-Figure 22) that provide an interior somewhat resembling that of a maple leaf. In fact, in the genus *Polytrichum*, some members have the outer portion of the blade folded over the lamellae (Figure 23-Figure 24), creating an internal chamber resembling palisade mesophyll surrounded with epidermis. The **cuticle** (in this case, a waxy, water-repellant covering on the outer surface of the leaf; Proctor 1979) of *Polytrichum* is more developed than in most other bryophytes, and *Polytrichum* seems to repel water from its leaves rather than to absorb it (Figure 23), a phenomenon that may prevent the spaces among the lamellae from flooding that would block access of CO_2 to the chloroplasts within. Its rhizoids function not only for anchorage, but also seem to facilitate external water movement.

Figure 20. *Polytrichum ohioense* leaf lamellae in surface view. Photo by John Hribljan, with permission.
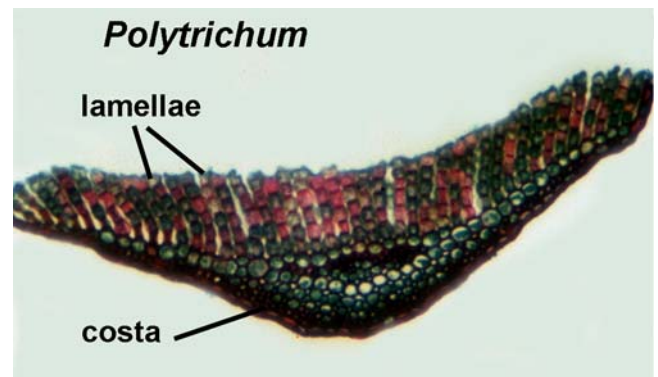

Figure 21. Stained leaf cross section of *Polytrichum* showing vertical lamellae. Photo by Janice Glime.
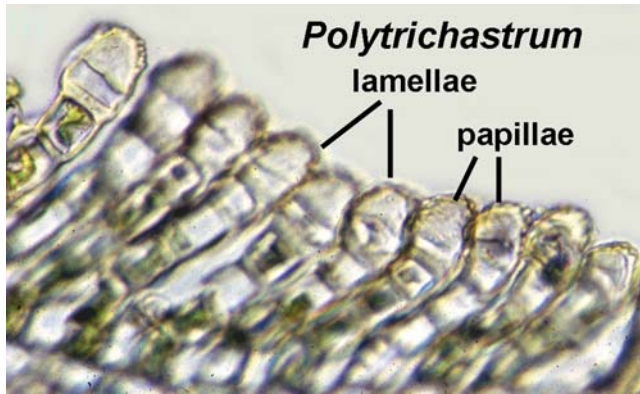
Figure 22. Hand section of *Polytrichastrum alpinum* leaf showing lamellae with papillose terminal cells. Photo by Janice Glime.
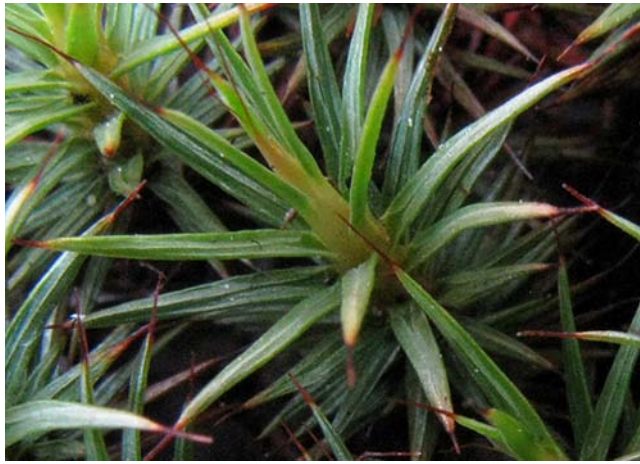

Figure 23. *Polytrichum juniperinum* with waxy leaves and lamina that rolls over the lamellae. Photo by Janice Glime.

Figure 24. *Polytrichum juniperinum* leaf cross section showing lamellae and edges of leaf folded over them. Photo by John Hribljan, with permission.

In some mosses, like *Polytrichum*, the antheridia are in splash **cups** or **platforms** (rosette of leaves from which reproductive units such as sperm, gemmae, or spores can be splashed by raindrops; Figure 25), and when the **sperm** (male reproductive cells; male gametes) are mature, the antheridium (Figure 26) swells and bursts during a rainy period. The bases of the antheridia, in taxa such as *Polytrichum* and *Atrichum* (Figure 33), collect fluid between the sperm tissue and the antheridial jacket (Figure 26) (Bold *et al*. 1987). When the cells at the tip of the sterile jacket open, the antheridial jacket contracts. At this time, the fluid at the bottom acts as a hydraulic ram and forces the sperm out of the antheridium. Once in the open

water of the splash cup, the sperm are splashed from the cup. Hopefully, some of these sperm will splash near the tip of a female plant (Figure 27) and will begin swimming toward the archegonium (Figure 28).
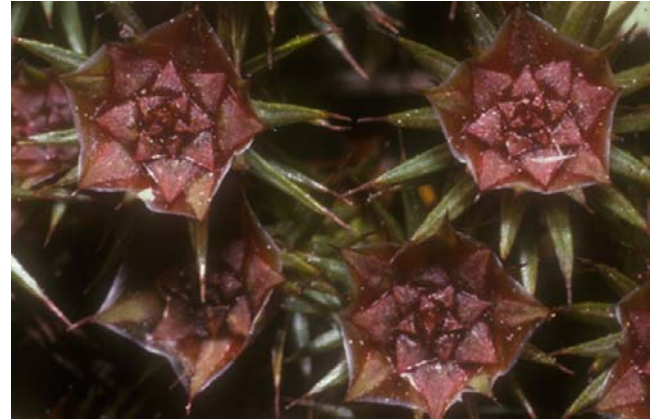

Figure 25. Male plants of *Polytrichum juniperinum* with antheridial splash cups. Photo by Janice Glime.
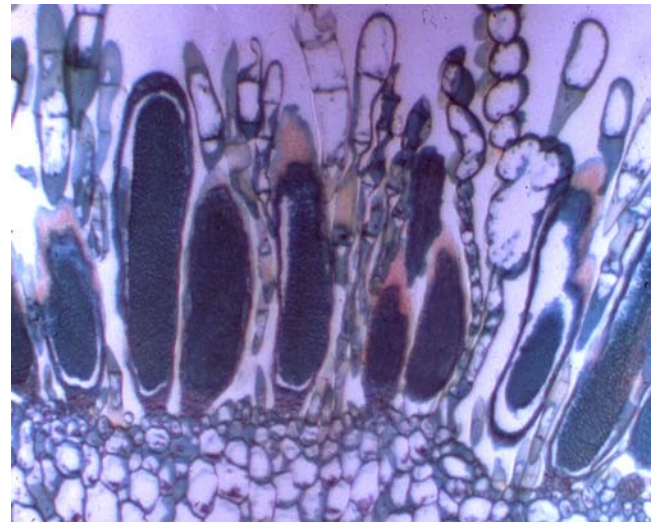

Figure 26. *Polytrichum* antheridial head showing paraphyses and antheridia. Note space where mucilage collects between the dark sperm tissue and the sterile jackets of the antheridia. Photo by Janice Glime.

Figure 27. Female plants of *Polytrichum ohioense* showing the tight leaves at the apex where archegonia are housed. To the right of the female plants, the yellow swollen tips are male plants with unopened antheridial splash cups. Photo by Janice Glime.

Figure 28. Archegonia nestled among terminal leaves of *Polytrichum*. Photo from Michigan State University botany collection, with permission.

But it appears that the sperm of *Polytrichum commune*, and perhaps others, may have some help in this process from another source (Harvey-Gibson & Miller Brown 1927). A variety of invertebrates visit the male splash cups once they are fertile and get the mucilage with sperm stuck on their bodies. While visiting the plants, the insects lap up the mucilage and lick the saline crystals that form on the margins of the perichaetial leaves. The same insects, bodies and limbs smeared with mucilage in which sperms were abundant and motile, likewise appear on female plants. Now, can someone show whether the red color of splash cups (Figure 25) in several members of this family have the ability to attract any dispersal agents?

After fertilization, the zygote divides to form an **embryo** within the **archegonium**. Eventually this sporophyte embryo tissue forms a **foot**, **seta**, and **capsule**. The capsule develops within the **calyptra** (Figure 29-Figure 31), which is the expanded archegonium. The calyptra is essential for normal development in most mosses, and a split on one side can cause asymmetrical development. In the case of *Polytrichum*, the calyptra is very hairy (Figure 31), earning the moss the name of hairy cap moss or goldilocks moss. If it removed early in development, the capsule will not develop properly.

Eventually the **calyptra** (Figure 31) is shed, exposing the capsule. Then the **operculum** (lid) must come off to permit spore dispersal. In this family the capsule has 64 short teeth joined by a membrane (**epiphragm**) that covers

the capsule like skin on a drum (Figure 32). These small spaces permit spores to escape the capsule a few at a time, providing maximum chances for some escaping under the right conditions for dispersal and establishment.

Figure 29. *Polytrichum piliferum*. Young sporophyte with **calyptra** (old archegonium) on top. Photo by Janice Glime.

Figure 30. **Seta** (stalk) of sporophyte with calyptra removed, showing that the capsule has not yet begun to develop. Photo by Janice Glime.

Figure 31. Capsules of *Polytrichum* at maturity, still covered with the calyptra. Photo by Janice Glime.

Figure 32.   Epiphragm of **Polytrichum**.   Photo by Laurie Knight <http://www.flickr.com/photos/laurie-knight>, with permission.

Figure 34.   **Tetraphis pellucida** leaf cross section showing 1-cell-thick lamina and multicellular costa. Photo from botany website, University of British Columbia, with permission.

Figure 33.   **Atrichum undulatum** with antheridial splash cups, another member of the **Polytrichaceae**. Photo by Janice Glime.

Figure 35.   Leafy gametophytes of **Tetraphis pellucida** with gemmae cups on top. Photo by Janice Glime.

Tetraphidaceae

Tetraphis (Figure 35), also in the **Polytrichopsida**, looks more like a typical moss than do other Polytrichopsida, with thin, 1-cell-thick leaves and a costa (Figure 14, Figure 34). **Tetraphis** is unique among mosses in having gemmae (Figure 35-Figure 36) arranged in splash cups at the tips of the stems when sexual reproduction is not in season, arguably a primitive remnant.   These gemmae are asexual bits of plant material that can grow into a new plant. Its most unusual character is that its protonemata are not threads, but rather flaps (Figure 37). Antheridia are borne terminally on the leafy plants (Figure 38), as are the archegonia.   The capsule (Figure 39) has only four long, unjoined, nematodontous teeth (Figure 10, Figure 40).

Figure 36.   Gemma cup with gemmae of **Tetraphis pellucida**. Photo by Janice Glime.
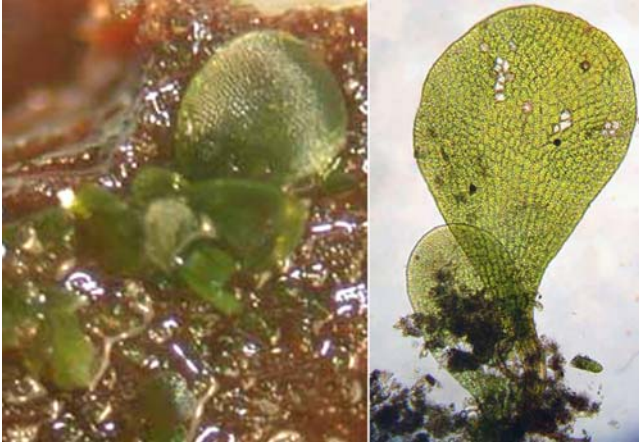
Figure 37. Protonemal flaps of *Tetraphis pellucida*. Photos from University of British Columbia Biology 321 Course Website, with permission.
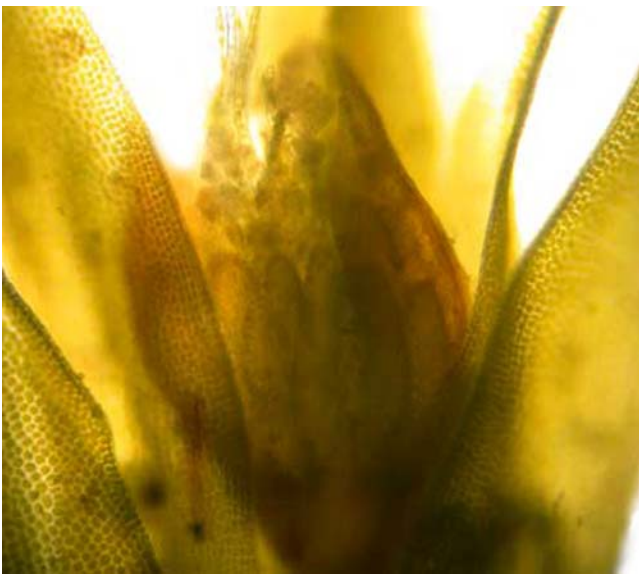

Figure 38. Leaves and antheridia of *Tetraphis pellucida*. Photo from UBC Biology 321 Course Website, with permission.

Figure 39. Capsules of *Tetraphis pellucida* showing calyptra with capsule exposed in the lower third. Photo by Janice Glime.
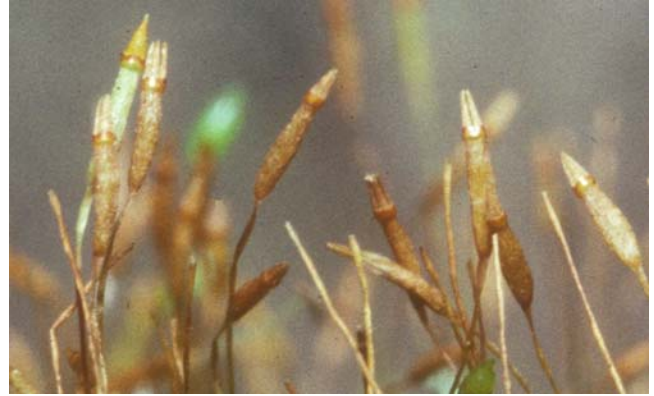

Figure 40. Capsules of *Tetraphis pellucida*, lacking calyptra and **operculum** (lid), exposing the 4 peristome teeth. Photo by Janice Glime.

Buxbaumiaceae – Bug on a Stick

Buxbaumia (Figure 41-Figure 45) is one of the strangest of all mosses. It lacks any leafy stem at all (Figure 41). Its archegonia and antheridia arise directly from the protonema. Hence, its capsules (Figure 43) arise directly from this persistent protonema (Figure 41). They all tend to orient in the same direction (Taylor 1972), most likely in response to the predominant direction of light. Its capsules, although possessing teeth (Figure 44), more typically split across their broad, flattened surface, hence exposing the spores (Figure 45) (Koch *et al*. 2009). Koch and coworkers demonstrated that in *Buxbaumia viridis* (Figure 41) this capsule surface is covered with "massive" wax layers that have embedded and superimposed platelets and granules on them. When these waxy layers peel back, the epidermis peels with them.
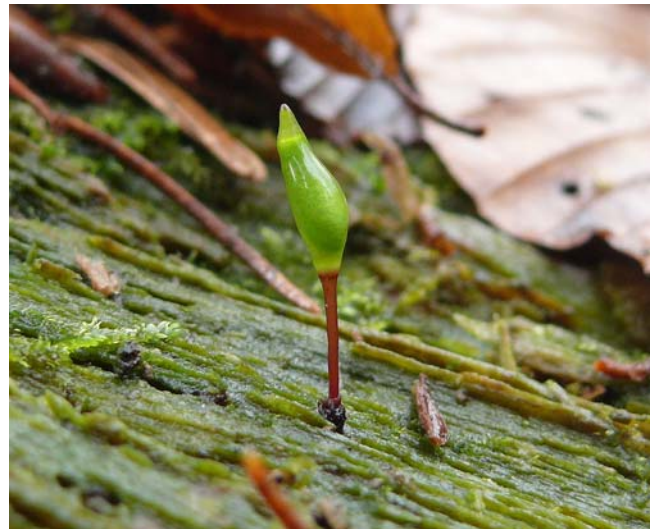

Figure 41. *Buxbaumia viridis* sporophyte and protonema. Photo by Bernd Haynold, through Wikimedia Commons.

The *Buxbaumia* capsule interior is chambered and spongy, somewhat like a spongy mesophyll of Magnoliophyta. It typically occurs with tiny, black leafy liverworts such as *Cephalozia* (Figure 46). Campbell (1918) had considered this moss to be saprophytic, exhibiting almost no chlorophyll, but Mueller (1975) demonstrated dense chlorophyll in the protonema and

considered that to be the primary photosynthetic organ, one that persists throughout the life of the moss. The protonema is not a good competitor, so you can find it after forest fires, on soil banks, on roadsides, and other places that are not very hospitable to plants that could easily overgrow the photosynthetic protonemata. The capsule (Figure 41-Figure 43) is rather unusual, with its broad, flattened side and a rounded side. This strange shape has earned it a number of common names, including humpbacked elves, elf-cap moss, Aladdin's lamp, and bug on a stick.

Figure 42. *Buxbaumia aphylla* on a soil bank with all capsules pointing the same direction. It has been suggested that common habit is advantageous to maximize light absorption by the photosynthetic capsule. Photo by Janice Glime.

Figure 43. Unopened capsule of *Buxbaumia aphylla*, illustrating the flat side with a beaked operculum that has earned it the common names of bug-on-a-stick and Aladdin's lamp moss. Note the absence of a leafy gametophyte. Photo by Michael Lüth, with permission.

Figure 44. *Buxbaumia piperi* capsule showing diminished peristome teeth. Photo from botany website at the University of British Columbia, with permission.

Figure 45. *Buxbaumia aphylla* (Class **Polytrichopsida**) showing flat side of capsule peeled back to expose the spores and spongy interior. Photo by Janice Glime.

Figure 46. *Cephalozia bicuspidata*, member of a genus of tiny liverworts that often occur with *Buxbaumia aphylla*. Photo by Kristian Peters, through Wikimedia Commons.

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

Diphysciaceae

Diphyscium (Figure 47-Figure 54) is distributed mostly in the northern hemisphere (Milne & Klazenga 2012). Its three genera have been reduced to one (Magombo 2002; Goffinet 2012), which has an asymmetrical capsule (Figure 51-Figure 54) of similar shape to that of ***Buxbaumia*** and lacks a leafy female stem except for perichaetial leaves (Figure 54), but the male plant of this genus has large, strap-shaped leaves and leads an independent and separate existence (Figure 47-Figure 50). The capsule opening is quite small and the teeth extrude like a wisp of hairs (Figure 54). The perichaetial leaves are unusual, having a long, excurrent costa and often being fimbriate on the margins (Figure 53-Figure 54). As in ***Buxbaumia***, the capsule shape is responsible for several common names – nut moss, powder gun moss, grain of wheat moss. It shares the phototropic behavior of ***Buxbaumia*** by having its capsules all oriented in one direction with their flat sides facing the direction of the light (Figure 51-Figure 53).

Figure 49. Male plant of ***Diphyscium foliosum*** showing antheridia. Photo modified from botany website and University of British Columbia, with permission.

Figure 50. Cross section of leaf of male plant of ***Diphyscium foliosum*** showing multiple layers and extensive papillae. Photo by Hermann Schachner, through Creative Commons.

Figure 47. Male plant of ***Diphyscium foliosum*** showing strap-shaped leaves. Photo by Hermann Schachner, through Creative Commons.

Figure 48. Leaf of male plant of ***Diphyscium foliosum*** showing weak costa and rows of cells. Photo by Hermann Schachner, through Creative Commons.

Figure 51. ***Diphyscium foliosum*** female plants with young sessile capsules surrounded by perichaetial leaves. These are clumped here among male plants with green, strap-shaped leaves. Photo by Janice Glime.

Figure 52. **Upper:** *Diphyscium foliosum* female plants with young sessile capsules among male plants. Photo by Janice Glime. **Lower:** Mature female *Diphyscium foliosum* plants with capsules showing peristome teeth. Photo by Michael Lüth, with permission.

Figure 53. Capsules and perichaetial leaves of *Diphyscium foliosum*. Photo by Michael Lüth, with permission.

Figure 54. *Diphyscium foliosum* female plant with perichaetial leaves and capsule showing small opening and peristome teeth. Photo by Jan-Peter Frahm, with permission.

Summary

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

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

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

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CHAPTER 2-7
BRYOPHYTA – BRYOPSIDA

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CHAPTER 2-7

BRYOPHYTA – BRYOPSIDA

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

Bryopsida Definition

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

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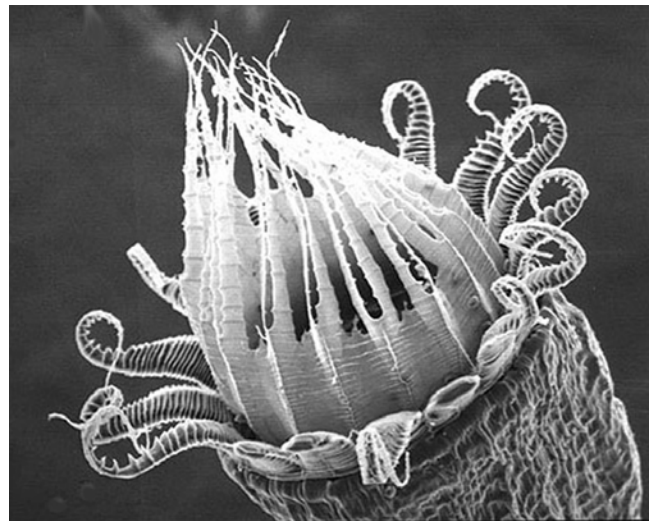

Figure 2. Electron micrograph of the arthrodontous peristome teeth of the moss *Eurhynchium praelongum*. Photo from Biology 321 Course Website, UBC, with permission..

Chromosome Numbers

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

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

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

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

Spore Production and Protonemata

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

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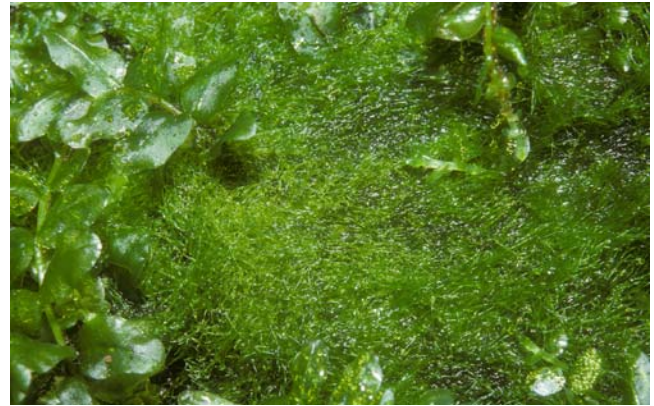

Figure 4. Protonemata among leafy plants of *Plagiomnium*. Photo by Janice Glime.

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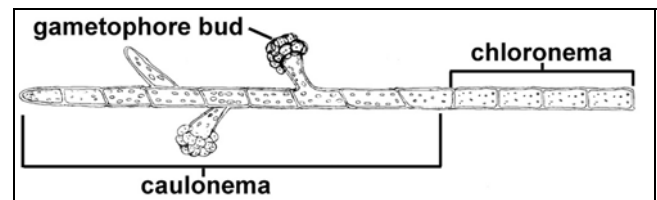

Figure 5. Protonema of moss such as *Funaria hygrometrica* with differentiated caulonema and chloronema. Drawing by Noris Salazar Allen, with permission.
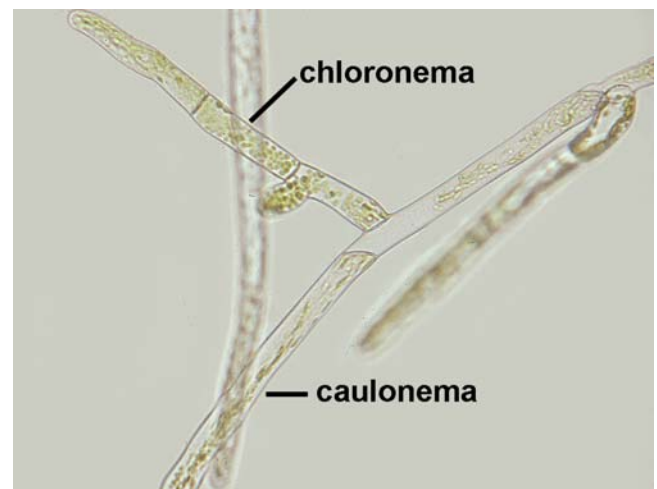

Figure 6. Protonema of *Funaria hygrometrica* showing chloronema (short cells with perpendicular walls and dense chloroplasts) and caulonema (long cells with diagonal cross walls and more dispersed chloroplasts). Photo by Janice Glime.

Gametophore Bud

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

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

Figure 7. Moss protonema with young bud. Photo by Chris Lobban, with permission.
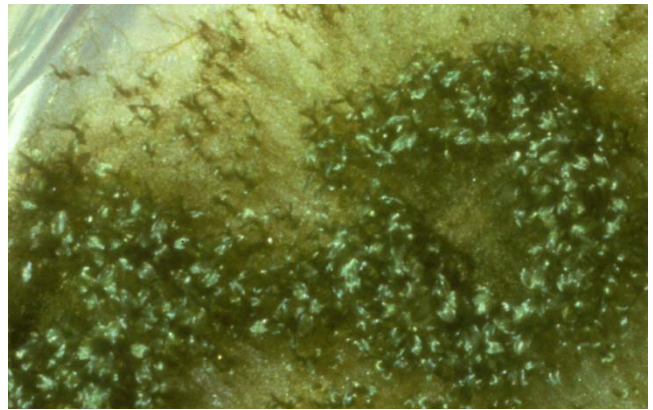
Figure 10.   Leafy buds on the protonemata of *Funaria hygrometrica* forming a doughnut shape. Each of these circles of buds is the result of one spore. The hole in the middle is the area where the protonemata is in the chloronema stage and does not produce buds. Photo by Janice Glime.

Gametophores

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

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

As the bud develops, **rhizoids** (Figure 9, Figure 71) form, functioning largely in anchorage, but at least in some mosses, also functioning in moving water and nutrients from substrate to moss. This may be especially important as the atmosphere dries and the rhizoids help to maintain a humid substrate.
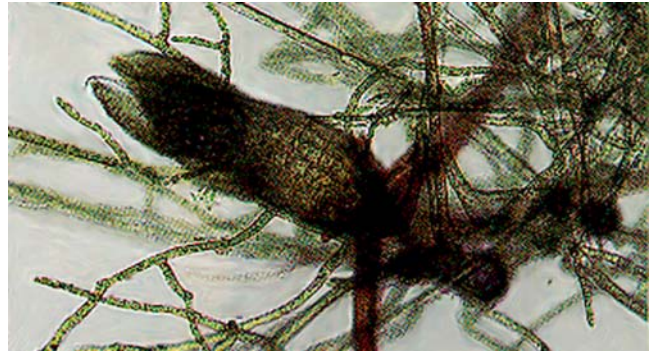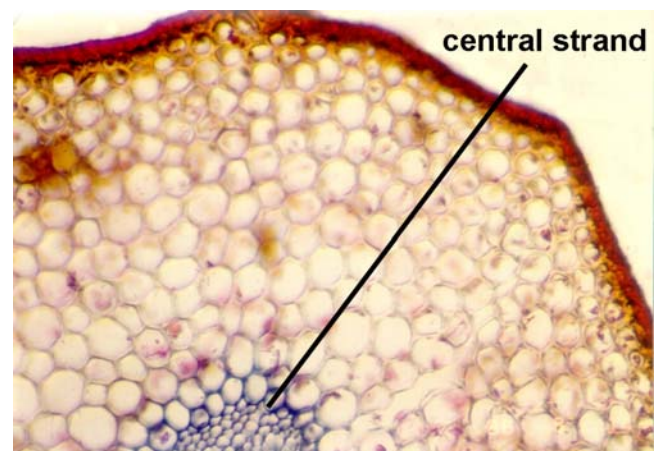

Figure 11.   Stem cross section of *Rhizogonium* illustrating central strand of hydroids.   Photo by Isawa Kawai, with permission.
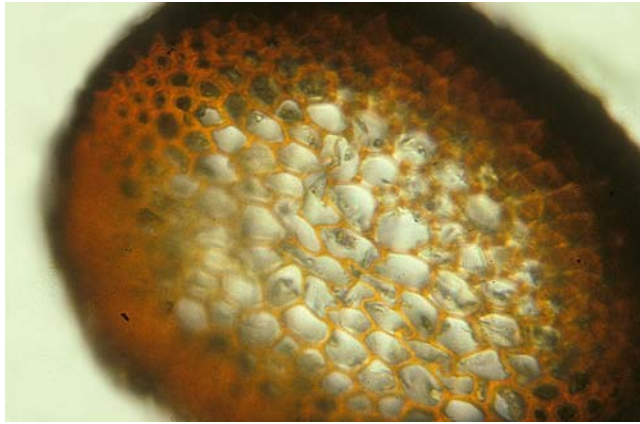
Figure 12. Cross section of stem of the brook moss *Fontinalis dalecarlica* showing absence of central strand and conducting tissues. Photo by Janice Glime.

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

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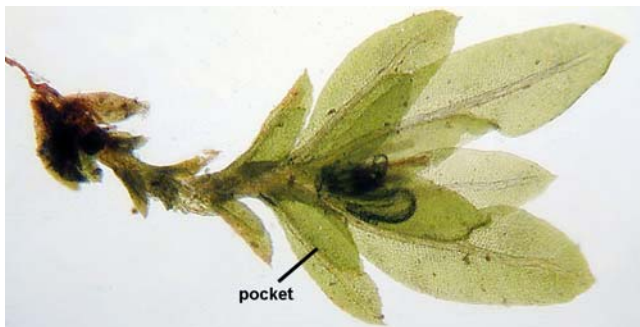

Figure 14. Pockets in leaf of *Fissidens arnoldii*. Note the leaves in two rows. Photo by Michael Lüth, with permission.

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

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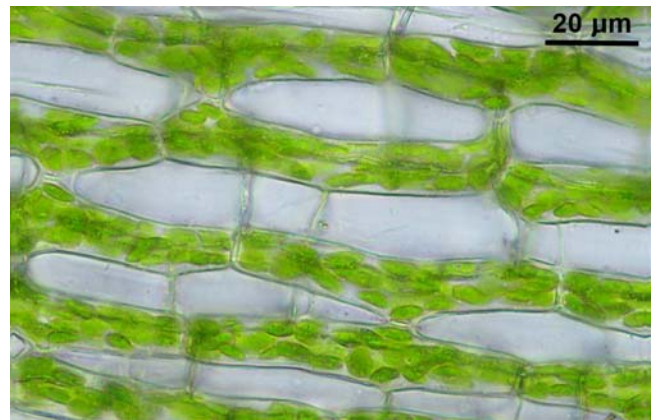

Figure 17. Hyaline and chlorophyllous cells of *Leucobryum glaucum* leaf. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.

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

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

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

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

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

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

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

Location of Sex Organs

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

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

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

The upright or sprawling stems of the gametophyte produce **antheridia** (sperm-containers; Figure 26) and **archegonia** (egg-containers; Figure 27). In mosses, antheridia and archegonia may be located at the end of the main stem (Figure 28), at the ends of lateral branches, or along the main stem, either at the ends of very short branches (Figure 29) or nearly sessile (Figure 72). One can determine the position of archegonia most easily by finding the base of the seta. Often the chloroplasts of the antheridial jacket cells are converted into chromoplasts as the antheridia mature, causing the characteristic red-orange color (Figure 28) (Bold *et al.* 1987).

Sperm Dispersal

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

Release of Sperm from the Antheridium

The release of the sperm from the antheridium is an interesting phenomenon. In ***Mnium hornum*** (Figure 30),

within about four minutes of placing water into an antheridial cup, dehiscence will occur (Muggoch & Walton 1942). The **spermatocytes** (cells in which sperm have differentiated) emerge in a banana-shaped package into the water surrounding the antheridium, usually within 4-10 minutes.
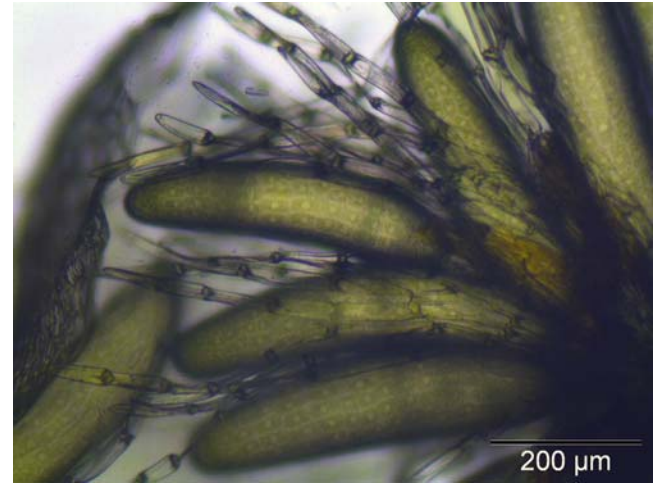

Figure 26. ***Hypnum cupressiforme*** perichaetial leaves, paraphyses, and antheridia. In this species, antheridia occur long the stem. Photo by Kristian Peters, with permission.

Figure 27. Pleurocarpous moss ***Pleurozium schreberi*** showing archegonia on short branch along stem. Photo by Janice Glime.

Then, when (or if) that package connects with the water-air interface, the sperm spread apart rapidly to form a surface layer of regularly spaced sperm (Muggoch & Walton 1942). This movement of sperm emerging from an antheridium is shown in a film by Serge Hoste <http://users.pandora.be/serge.hoste1/>. This spreading

suggests that some substance with a low surface tension might be present in the sperm package because the mass spreads much like an oil spill. The behavior suggests that there is a small amount of fat present in the sperm mass.

Figure 28. *Rosulabryum capillare* showing antheridial head of male plants. Photo by Michael Lüth, with permission.

Figure 29. *Racomitrium didymum* showing seta, hence archegonium, arising on a short branch. Photo by Michael Lüth, with permission.

Figure 30. *Mnium hornum* male splash cups. Photo by David T. Holyoak, with permission.

Dispersal to the Archegonium

Some bryophytes seemed to have no special means of dispersing on their sperm, relying on the water film that surrounded the bryophytes when it rained. Others have developed splash cups or splash platforms that aid in the dispersal of sperms. Andersson (2002) filmed the splashes on these splash cups in the moss *Plagiomnium affine* (Figure 31). Andersson observed that water fills the splash cup capillary spaces among the antheridia and paraphyses up to the bottom of the cup. He determined that for a striking raindrop to have the space needed to develop, the diameter of the drop should be 1 mm or less, a size common in most rain showers. The impact of the drop causes the ripe antheridia to rupture, causing the spermatozoids to reach the bottom of the splash cup through the capillary spaces created by the heads of the paraphyses. The drop of rain incorporates water from the bottom of the splash cup, thus including the spermatozoids that are entering the cup. These droplets can travel 100 mm or more as they rebound from the cup, thus effecting fertilization of nearly all female gametangia within about 80 mm. Since the fertilization period in southwestern Sweden lasts about three weeks, this is usually sufficient time for one or more appropriate rainfalls to occur and facilitate dispersal.

Figure 31. *Plagiomnium affine* splash cups. Photo by Peter Gigiegl. Permission pending.

Duckett and Pressel (2009) demonstrated that falling raindrops on the antheridiophores of the liverwort *Marchantia polymorpha* were not very effective, so the even softer splash platforms of mosses may be even less effective, or certainly not any better. Measurements from fertilized females to nearest male have provided us with some estimates, as for example that of *Plagiomnium ciliare* (Figure 32) for 5.3 cm (Reynolds 1980). But Reynolds did find that artificial rainfall could splash over 10 cm and concluded that measurements to nearest male most likely underestimated the distances sperm could travel from a splash cup or platform.

Until somewhat recently we have assumed that in most bryophytes sperm reached the archegonia by splashing or swimming from the antheridia to a landing spot, then swimming the remainder of the way. Closer observation by recent observers indicates that such an inefficient and unsafe method may not be the case for some bryophytes,

and that we should examine others more closely for secrets in their sperm dispersal. Muggoch and Walton (1942) considered the presence of fat in the sperm mass to be a widespread phenomenon, perhaps true of all mosses, and that it was important in permitting insects to carry sperm to female plants. However, there seem to be few observations of such insect dispersal except in **Polytrichum** (Class **Polytrichopsida**) and **Rosulabryum** (=**Bryum**) **capillare** (**Bryopsida**; Figure 28).

Figure 32. **Plagiomnium ciliare** with splash platforms. Photo by Robert Klips, with permission.

The idea that invertebrates may disperse sperm is not entirely new. Harvey-Gibson and Miller-Brown (1927) observed various invertebrates visiting the fertile shoots of **Polytrichum commune** (Figure 33). As they crawled about the male splash cups, they picked up mucilage and sperm. They then observed that the same insects would appear on female plants with abundant sperm smeared on their bodies and legs in the mucilage. The invertebrates seemed to consider the mucilage to be a source of food as they "greedily" lapped it up and also licked at saline crystals on the perichaetial leaf margins.

Figure 33. **Polytrichum commune** males with splash cups. Photo by Li Zhang, with permission.

It appears that **Rosulabryum** (=**Bryum**) **capillare** (Figure 28) may indeed be fertilized, at least some of the time, by animals. When covered by a fine net to discourage winged insects and other creatures, females were not fertilized, but when the net was removed, fertilization occurred 2 m(!) from the nearest males (Gayat 1897). However, it is difficult to rule out the possibility of raindrops in this case, or even squirrels, for that matter. Raindrops are likely to trap the mucilage with its sperm load in the tiny capillary spaces of the net. The success of fertilization would depend on the success of these drops getting bounced from one plant to another, and that bounce would surely be inhibited by such a filter to diminish the impact and retain the mucilage.

Observations on **Bryum argenteum** (Figure 34-Figure 35) are more conclusive. Cronberg *et al.* (2006), in an experiment in which male and female plants were separated by 0, 2, and 4 cm, demonstrated that help from such agents as invertebrates are essential. These treatment distances were combined either with no animals, or with mites (Acarina: **Scutovertex minutus**) or springtails (Collembola: **Isotoma caerulea**, Figure 36) (Cronberg *et al.* 2006; Milius 2006). After three months, those females in contact with male plants (0 cm) produced sporophytes. Those without this contact (2 or 4 cm) and without either animal group produced no sporophytes. But those housed with springtails or with mites produced numerous sporophytes, with springtails being the more effective conveyor. Springtails are more mobile than mites, and in this experiment, more sporophytes were produced at greater distances when springtails were available as dispersal agents.

Figure 34. **Bryum argenteum** males. Photo by George Shepherd, through Creative Commons.

Figure 35. **Bryum argenteum** with sporophytes, signalling successful fertilization. Photo by George Shepherd, through Flickr Creative Commons.

Figure 36. *Isotoma caerulea*, a springtail that is instrumental in fertilizing *Bryum argenteum*. Photo by Katrina Hedlund, with permission.

But how do these springtails find the mosses? Flowers provide odors and colors to attract their pollinators. It appears that these mosses also have a way to attract their dispersal agents. When springtails and mites were given choices of plants with mature gametangia vs those that were sterile, fertile plants were chosen over non-fertile ones about five times as often (Beckman 2006) in the cases of both males and females and by both organisms. Cronberg *et al*. (2006) suggest that fertile plants may attract the invertebrates with sucrose (Pfeffer 1884), starch, fatty acids, and/or mucilage (Harvey-Gibson & Miller-Brown 1927; Paolillo 1979; Renzaglia & Garbary 2001). Ziegler *et al*. (1988) demonstrated the presence of sucrose in the archegonium exudate of *Bryum capillare* (Figure 28).

A small flurry of research followed this EXCITING finding (Cronberg 2012). Both *Bryum argenteum* (Figure 35) and *Ceratodon purpureus* (Figure 37) sperm are transported by tiny springtails (*Foisomia candida*) (Rosenstiel *et al*. 2012). Rosenstiel and coworkers (2012) used *Ceratodon purpureus* to examine what attracts sperm dispersers. They found that this species produces volatile compounds – some of those secondary compounds that have evolved tremendous varieties in bryophytes. They were able to demonstrate that some, perhaps many, of these compounds attracted the springtail *Folsomia candida* (Figure 38). The volatile compounds are sex-specific (Figure 40) and definitely increase the rate of fertilization, even when splashing water is provided to facilitate sperm transfer (Figure 39). Although fertilization rates were about the same in treatments of water spray alone and springtails alone, the presence of both more than doubled the rate of using either alone.

Figure 37. *Ceratodon purpureus* showing water drops that could facilitate fertilization. Photo by Jiří Kameníček, with permission.
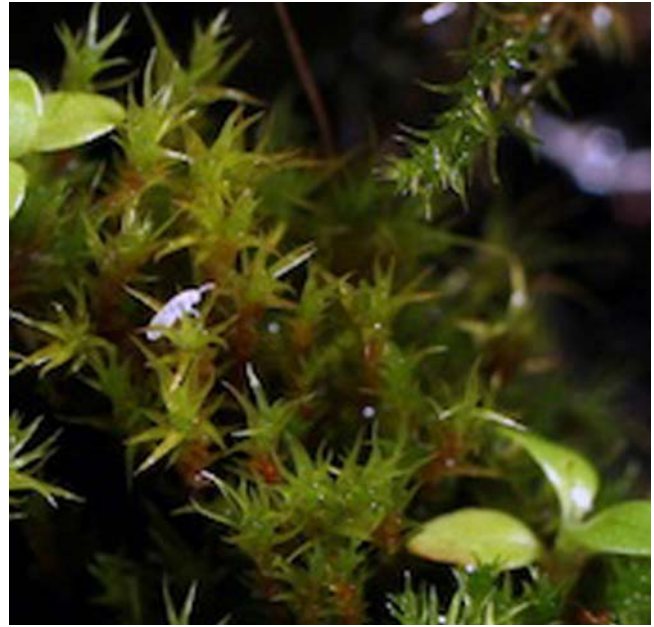

Figure 38. *Folsomia candida* (Collembola) on *Ceratodon purpureus*. Photo by Erin Shortlidge, with permission.
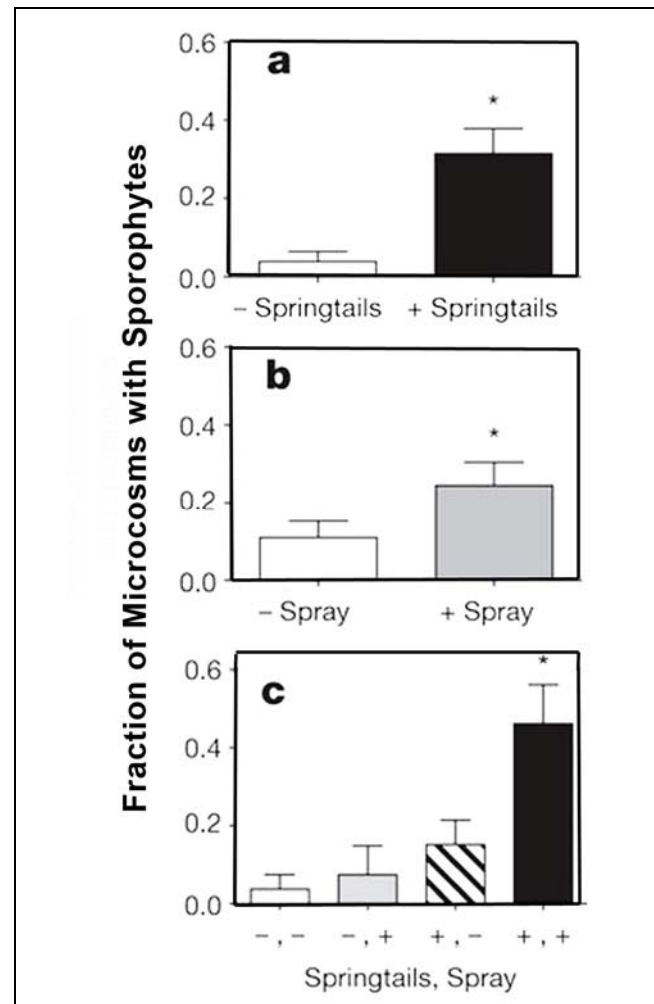

Figure 39. Effect of the springtail *Folsomia candida* vs water spray treatment on fertilization success of *Ceratodon purpureus* and *Bryum argenteum* in 108 microcosms. Vertical lines represent standard error of mean. * denotes significantly different, $p < 0.05$. Modified from Rosenstiel *et al*. 2012.
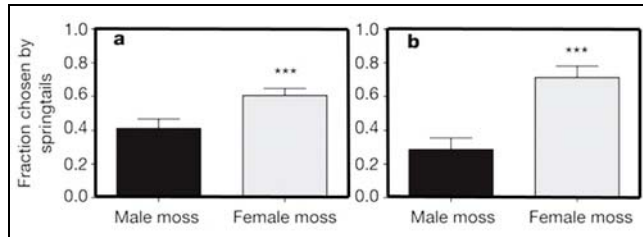
Figure 40. Sexual preference of the springtail *Folsomia candida* on *Ceratodon purpureus*. **a.** Petri dishes with 24 assays, 491 springtails. **b.** Samples in an olfactometer with 10 assays, 276 springtails. Vertical lines represent standard error of the mean. *** denotes $p<0.0001$. Modified from Rosenstiel *et al*. 2012.

Splash cups and splash platforms help to launch the sperm in many acrocarpous taxa, with spreading upper leaves serving to facilitate the launch. Richardson (1981) estimated that raindrops could splash these sperm only about 5 cm in small mosses, but up to 2 m in large ones. In mosses without antheridial splash cups or platforms, dispersal distances are typically short. Pleurocarpous mosses are not arranged in such a way as to offer much of a boost to raindrops containing sperm. In *Hylocomium splendens* (Figure 41), sperm have a long distance record of only 11.6 cm (Rydgren *et al*. 2005).

Figure 41. *Hylocomium splendens* in autumn. Photo by Petr Brož, through Wikimedia Commons.

Anderson (2000) managed to catch the dispersal of *Plagiomnium affine* (Figure 31) on video to see the effectiveness of the splash platform of that moss. Although many drops will miss the tiny platform completely, a few manage full hits. Impact causes a "crown" of water to form, like dropping a rock into a lake. The capillary spaces between the antheridia and adjoining **paraphyses** (sing. **paraphysis:** sterile filaments located among reproductive organs; Figure 42, Figure 70, Figure 72) fill with water.

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

Figure 42. Mature **antheridia** and **paraphyses** of the moss *Rhizomnium* sp. Photo by Janice Glime.

Splash cups and platforms seem to be rare in monoicous taxa [exceptions include species of *Brachymenium* (Figure 43) and *Rosulabryum* (Figure 44) per John Spence], suggesting fertilization is accomplished with close neighbors. For most Bryopsida, however, there is no antheridial splash cup or platform, so seemingly sperm must swim all the way.

Figure 43. *Brachymenium* sp. showing splash platform. Photo by Michael Lüth, with permission.

Figure 44. *Rosulabryum laevifilum* with splash platform. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

However, other things can create splash. Jonathan Shaw (pers. comm.) has considered that *Funaria. hygrometrica* (Figure 45) has wide-spreading bracts surrounding the antheridia and the flexible nature of these bracts permits them to bend back and create an effective cup from which sperm in that species might be splashed. Angela Newton (pers. comm.) has suggested that platform surfaces among the more dendroid and shelf-forming taxa could be viewed as water-trapping mechanisms that would promote surface flow and dripping to the next level down as a mode of transporting sperm between individual plants or parts of plants. One complication in this arrangement is that the complex texture would act to trap water drops rather than encouraging them to splash out and away. However, in some of the plants with large smooth leaves, these leaves might act as springboards, but Newton considered that in such a case the water drops would be unlikely to carry sperm, although they might carry the smaller kinds of vegetative propagules. Nevertheless, sperm that had gotten as far as a leaf might benefit from this splash as well.

Figure 45. *Funaria hygrometrica* males showing splash apparatus. Photo by James K. Lindsey, with permission.

Now it would seem that monoicous taxa might not need a partner since they have one built in. This suggestion is even supported by the scarcity of splash platforms in these taxa. But the fact is that many monoicous taxa are self-incompatible (Longton & Miles 1982; Ramsay & Berrie 1982; Mishler 1988; Kimmerer 1991). The big advantage for them is that their nearest neighbors can always provide gametes of the opposite sex.

Whereas flowering plants frequently rely on animals, especially insects, to transport their male gametophytes, and ultimately the sperm, to the female reproductive organ, this seems rarely to be the case in bryophytes. Surprisingly, it appears that the only documented case of such animal transport of sperm is in *Polytrichum commune* (Polytrichopsida; Figure 46), which has well-developed splash cups (Figure 46) for the purpose of sperm dispersal. Nevertheless, it was in this species that Harvey-Gibson and Miller-Brown (1927) found motile sperm on the bodies of small arthropods (flies, leafhoppers, mites, spiders, and springtails) on both male and female reproductive inflorescences. Schofield (1985) suggests that mucilage produced in both the **perigonia** (modified leaves enclosing male reproductive structures; Figure 47) and **perichaetia** (modified leaves enclosing female reproductive structures; Figure 48) sometimes attract invertebrates.

Figure 46. *Polytrichum commune* antheridial splash cups. Photo by Michael Lüth, with permission.

Figure 47. *Fissidens bryoides* antheridia along stem where they are surrounded by **perigonia**. Photo by Dick Haaksma, with permission.

Figure 48. *Polytrichum commune* female showing tight perichaetial leaves at the tips of plants. Photo by Michael Lüth, with permission.

Clayton-Greene *et al*. (1977) used laboratory tests to determine the distance sperm could travel from the large moss *Dawsonia longifolia* (=*D. superba*) (Figure 49). Field investigations indicated that this species uses a splash cup mechanism. Field data of sporophyte production

indicated that capsules seldom develop on females located more than 1.5-2 m from any male. They found similar results in the lab when they dropped water from a height of up to 3.3 m. In experimental heights ranging from 150 to 330 cm, travel distances ranged from 105 to 230 cm, indicating that height of water drop positively affects dispersal distance. But in the smaller *Polytrichum ohioense* (Figure 50), sperm in experiments only landed up to 61 cm from the source when water was dropped from ~1 m (Clayton-Greene *et al.* 1977). Clayton-Greene *et al.* suggested that smaller drops could act like an aerosol spray and float in air, achieving greater distances.

Figure 49. Female *Dawsonia longifolia* (=*D. superba*). Photo by Jan-Peter Frahm, with permission.

Figure 50. *Polytrichum ohioense* males with new growth from old splash cups. Photo by Janice Glime.

One might expect that many antheridia burst as they and their surrounding **paraphyses** (Figure 51) swell from a desiccated state to a hydrated state during early minutes of a precipitation event. Could it be that the same external capillary forces that carry water rapidly to other parts of the plant could move sperm, thus reducing the energy requirements for getting these tiny cells to their destinations? Or are these forces to be reckoned with, forcing the sperm to swim against a current?

Figure 51. Antheridia and paraphyses of *Rhizomnium* sp. Photo by Janice Glime.

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

If animal dispersal is so rare, then how, in this vast world, does an unintelligent sperm find an archegonium (Figure 52) and an egg? Fortunately for the moss, the archegonium at this time has dissolved the **neck canal cells** (entry canal through neck to egg in base of archegonium; Figure 53; Figure 72) leading down to the **egg** in the venter (Figure 53), and the resulting liquid provides a chemical attractant for the sperm.

Meanwhile, the egg exudes mucilage into the cavity of the venter (Lal *et al.* 1982). When the canal opens, the liquid exudes from the opening of the neck, creating a chemical gradient. The sperm follows the concentration gradient toward the archegonium and finally swims down the **neck canal** (Figure 53) of the archegonium to the egg. The exact nature of this liquid is unknown, but it seems that sugars (Harvey-Gibson & Miller-Brown 1927) and sometimes boron are necessary. It seems also likely that something specific, perhaps a protein, might guide the sperm to the correct species. Otherwise, it would seem that in spring, when so many species are producing sexual structures, some of these sperm would find their way into the wrong archegonium – or perhaps they do!
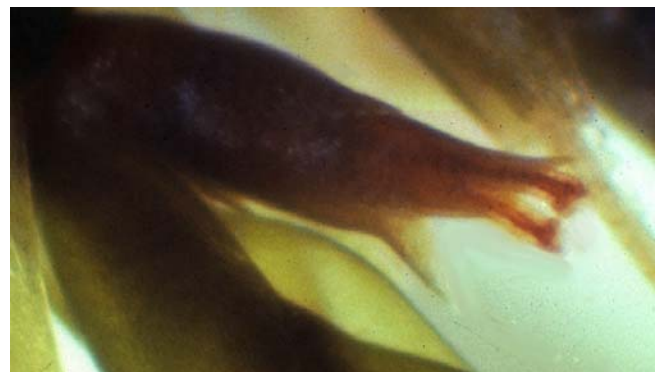

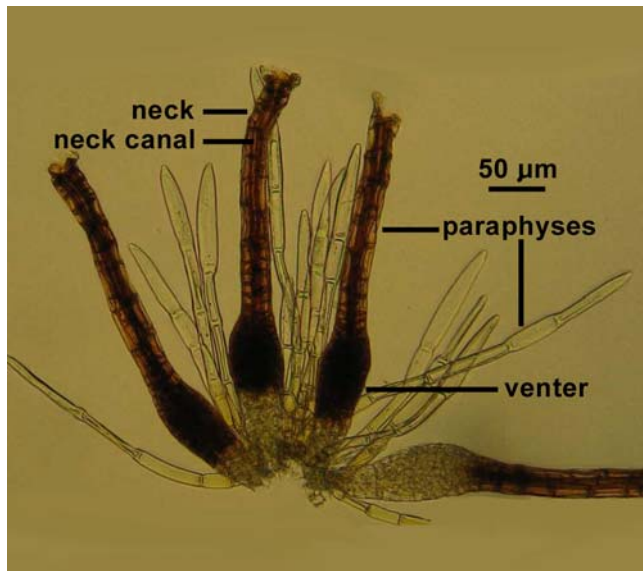Figure 52. Archegonia of the moss *Fontinalis dalecarlica*. Photo by Janice Glime.

Figure 53. Archegonia of *Zygodon intermedius*. Photo by Tom Thekathyil, with permission.

Gayat (1897 in Clayton-Greene *et al*. 1977) experimented with **Bryum** (**Rosulabryum**) *capillare* (Figure 28) and found that when the plants were covered with a fine net, female plants located 2 m from males had no fertilization, but when the net was removed, giving insects access to the females, these same plants did have fertilization.   Harvey-Gibson and Miller-Brown (1927) found that in *Polytrichum commune* (Figure 46-Figure 48) the paraphyses (Figure 53) of both males and females exuded mucilage, but contained no sugar.   These gametangial areas were "constantly" visited by oribatid mites, two species of Collembola (springtails), a small midge (Diptera), a leaf hopper (Cicadidae), an aphid, and a spider.   They found that the insects "greedily" lap the mucilage and their body parts become smeared with the mucilage excretion.   This adhering mucilage contains actively motile sperm.   These sperm-carrying invertebrates were also located on female plants.

Embryo Development

When a sperm reaches and fertilizes an egg, the resulting **diploid** (having two sets of chromosomes; 2*n*) **zygote** begins dividing by **mitosis** to form an **embryo** that starts to stretch the archegonium (Figure 54).   But the archegonium cannot stretch indefinitely, and as the embryo gets larger, the archegonium finally tears.   Here, mosses and liverworts differ.   In most mosses, part of the archegonium remains perched on top of the developing **embryo** (young sporophyte).   This separated piece of archegonium is the **cap** you often see on top of the capsule and is now called a **calyptra** (Figure 72).   So the calyptra is a 1*n* covering over the 2*n* capsule.

The emerging embryo grows into the sporophyte of the moss.   The mature sporophyte has a **capsule** and **stalk** (**seta**), with a **foot** embedded into the gametophyte tissue (Figure 55).   **Meiosis** occurs in the mature capsule, producing haploid (1*n*) spores, as in all plants.   Note that this is a major difference from meiosis in animals, which results in gametes.   These spores are dispersed from the capsule by wind (or in a few cases – *e.g.* Splachnaceae – by insects) and grow into new gametophytes.
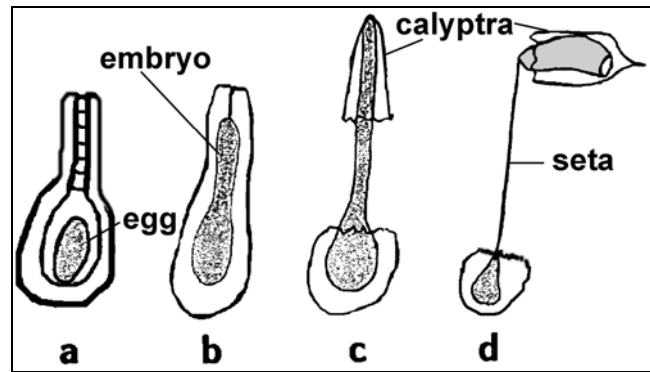

Figure 54.   Development of calyptra of a moss.   **a.** egg in archegonium, with neck canal cells not yet disintegrated.   **b.** archegonium after fertilization and early development of embryo, showing elongation of archegonium as embryo grows.   **c.** elongated seta with calyptra perched on top of it before capsule has developed.   **d.** mature capsule with calyptra and fully elongated seta.   **c & d** indicate remains of venter of archegonium at base of sporophyte.   Drawings by Janice Glime.

Figure 55.   *Aloina rigida* with stalk and capsule and with foot imbedded in gametophyte tissue.   Photo by Michael Lüth, with permission.

The **calyptra** (Figure 56) that covers the capsule of mosses most likely plays multiple roles.   We know that in many species, normal development ceases if the calyptra is removed (Paolillo 1968; French & Paolillo 1976a, b).   One could assume that it provides protection from UV light and other environmental influences, as well as changing the internal environment, and that these influences are important in shaping the further development of the capsule, as will be discussed in another chapter.

Capsule Development

In mosses, once the calyptra (Figure 56) has been shed, the **operculum** (lid) of the capsule is exposed (Figure 57).   As a result of this exposure, the environment is considerably changed for remaining development.   Gas exchange could be easier, moisture relations can change, and the constraining effect of the size and shape of the capsule might change.

The exposed operculum must come off before the spores can be dispersed.   The **dehiscence** of the operculum is usually facilitated by drying of the capsule that causes it to shrink and compress the contents.   This creates a distortion that forces the operculum to pop off, at least in some species.   But a few are **cleistocarpous** (indehiscent; lacking a regular means of opening), thus lacking an operculum (Figure 58).   Capsules in these taxa open by decay.

Figure 56. *Polytrichum* sp. with calyptra covering the capsule. Photo by George Shepherd, through Creative Commons.

Figure 57. *Polytrichum* sp. capsule with calyptra removed, showing operculum.   Photo by George Shepherd, through Creative Commons.

Figure 58. *Pleurophascum grandiglobum* showing capsules with no operculum. Photo by Niels Klazenga, with permission.

Just under the lid of most moss capsules you will find the **peristome teeth** (in mosses, fringe of teeth around opening of capsule, involved in spore dispersal; Figure 59-Figure 67). These are usually **hygroscopic** (responding to humidity changes) and may flex back and forth in response to moisture changes to aid in gradual dispersal. In most cases, these function best as the capsule is drying, but in some taxa moisture actually facilitates dispersal. Perhaps their best role is in preventing the spores from all exiting the capsule at the same time, as happens in the liverworts and *Sphagnum* and most likely also in the mosses with valvate capsules.   They often form spaces between the teeth, creating a salt shaker appearance (Figure 67). The sporophyte capsule usually has a **columella** (Figure 62, Figure 65) that is columnar like those in Polytrichopsida, providing structure. Most mosses also have an **annulus** (Figure 60) just below the peristome. This annulus aids in dehiscence of the operculum.

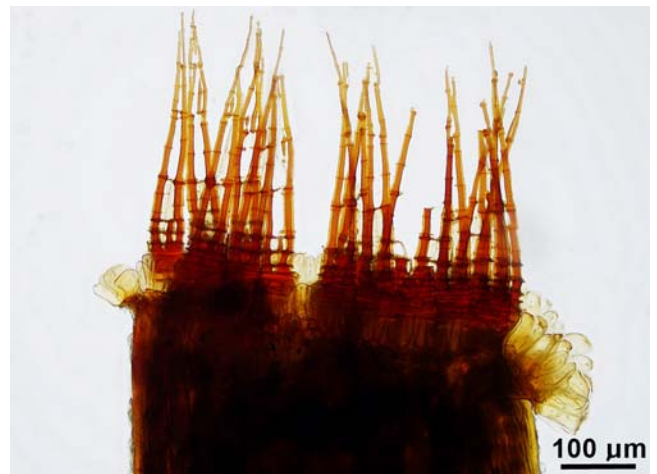Figure 59. Moss peristome. Photo by Laurie Knight, with permission.

Figure 60. *Ceratodon purpureus* peristome with annulus peeling back at its base on each side. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 61.   *Schistidium rivularis* sporophyte zoom view showing operculum dehiscence. Photo by Betsy St. Pierre, with permission.

Figure 62.   *Schistidium rivularis* sporophyte showing operculum dehiscence with columella still attached.   This continued attachment is unusual. Photo by Betsy St. Pierre, with permission.

Figure 63.   *Schistidium crassipilum* open capsules with teeth spreading. Photo by Jan-Peter Frahm, with permission.
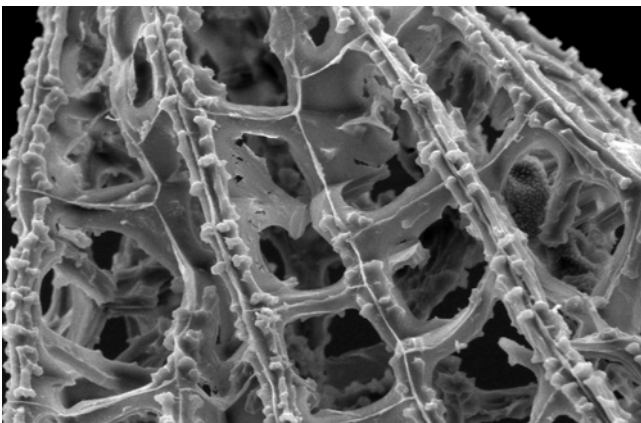

Figure 64.   SEM of *Fontinalis* peristome illustrating the elaborate lattice structure. Note a few spores nestled within it. Photo by Misha Ignatov, with permission.
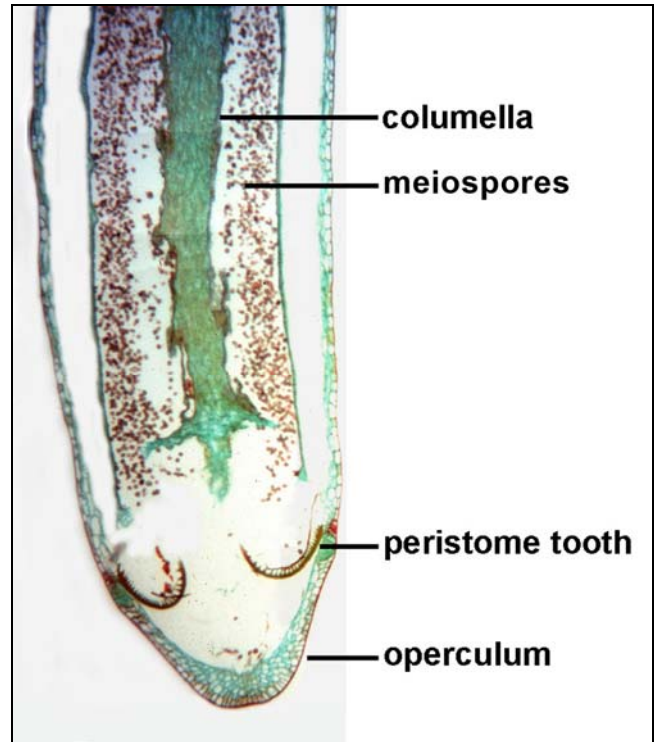
Figure 65. Section of *Mnium* capsule. This capsule actually hangs down, so teeth are on the bottom of the picture. Photo by Janice Glime.
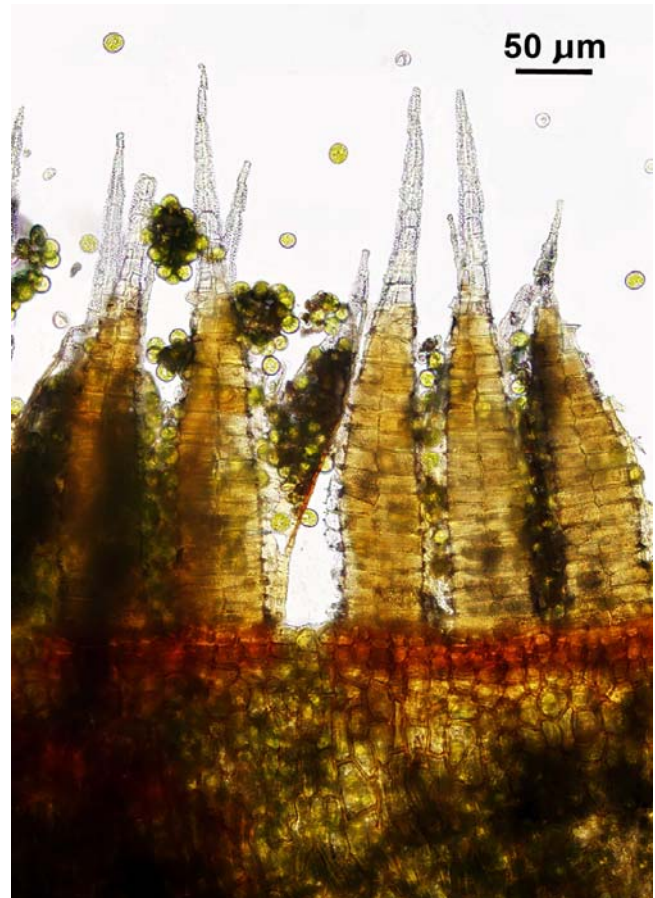
Figure 66.   *Rosulabryum laevifilum* peristome and spores. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 67. Peristome showing inner and outer peristome with spores. Photo by George Shepherd, with permission.

Unlike the valvate capsules of liverworts and some moss classes, the sporophytes of the Bryopsida are photosynthetic (Figure 68). The same pigments often occur in both generations: chlorophylls *a* and *b*, carotene, lutein, violaxanthin, and zeaxanthin (Freeland 1957). Even the ratio of chlorophyll *a* to *b* is approximately the same – about 2.5:1 (Rastorfer 1962). Nevertheless, the gametophyte contains a higher chlorophyll concentration than does the sporophyte and the ratio of photosynthesis to respiration is likewise higher in the gametophyte. Despite its photosynthetic abilities, the sporophyte still depends on the gametophyte for some of its carbohydrates (Krupa 1969).

Figure 68. ***Bryum gemmiferum*** capsules showing photosynthetic green immature capsules and darker ones with maturing spores. Photo by David Holyoak, with permission.

The stages of the life cycle are summarized in Figure 69 and Figure 70. Structures involved in the life cycle and in general morphology are illustrated in Figure 71-Figure 74.
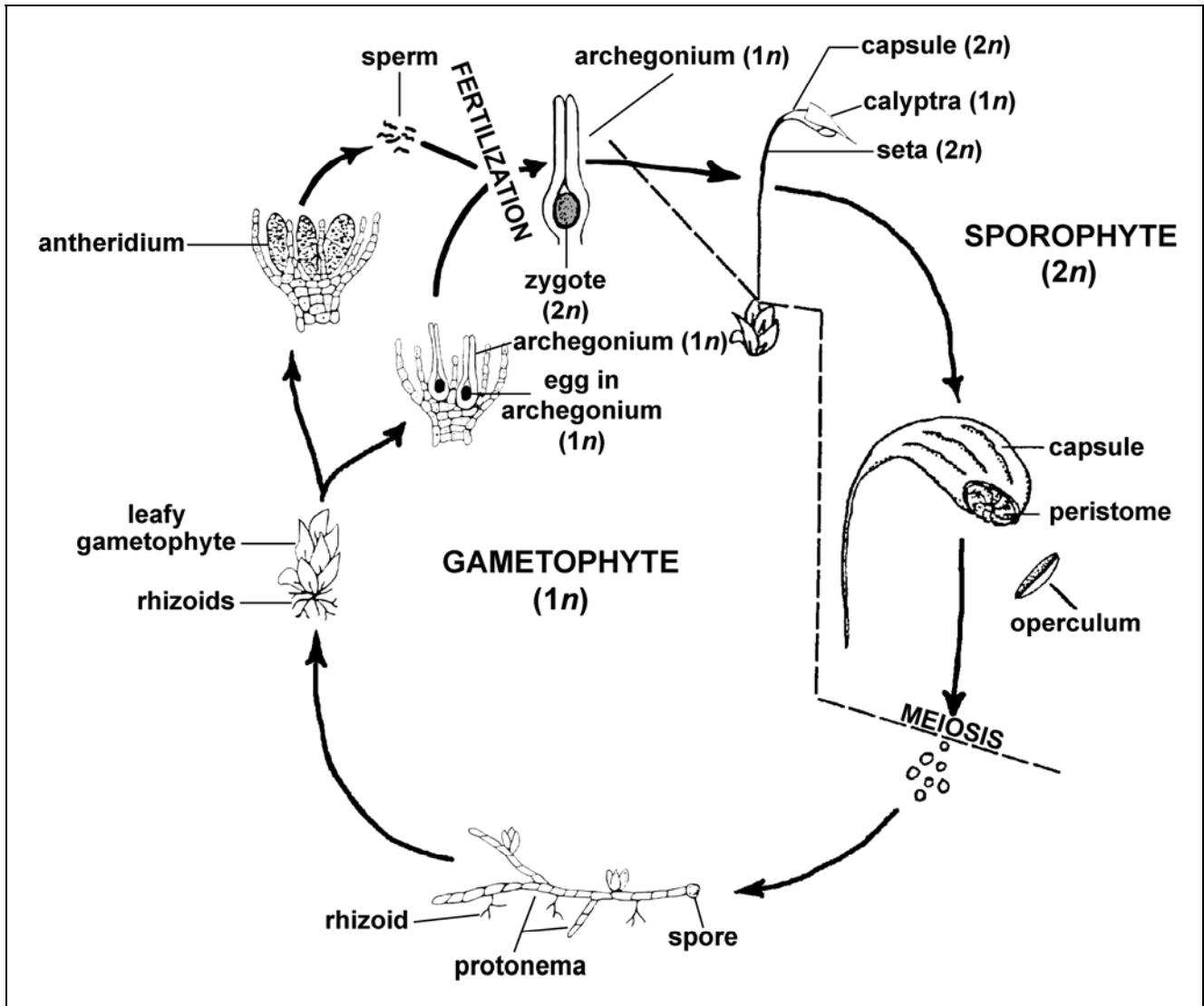
Figure 69. Life cycle of the moss *Funaria hygrometrica*. Drawn by Shelly Meston, with permission.
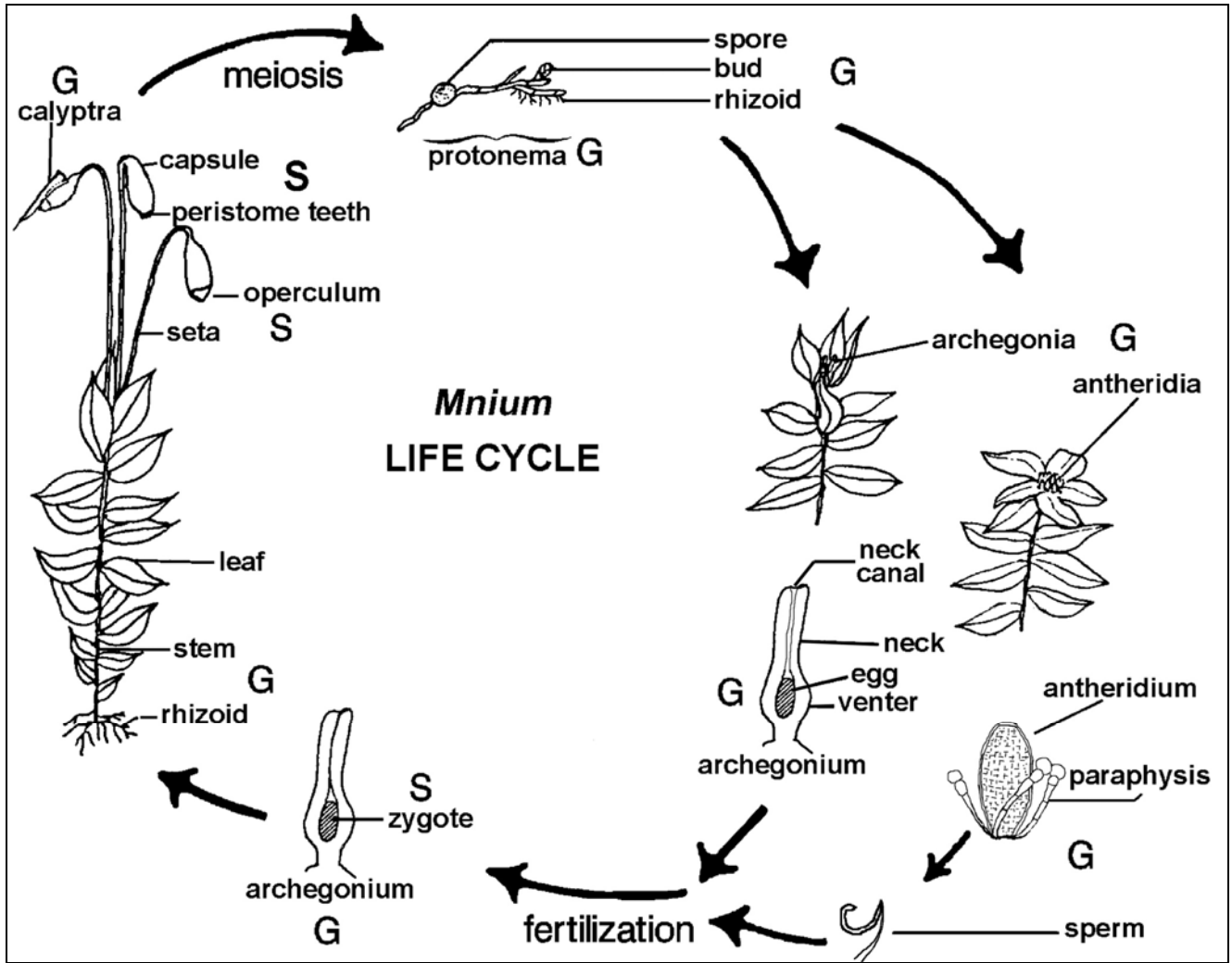
Figure 70. Life cycle of a moss such as *Mnium* (Bryopsida). **G** represents Gametophyte; **S** represents Sporophyte. Drawings by Allison Slavick, Noris Salazar Allen, and Janice Glime, with permission.
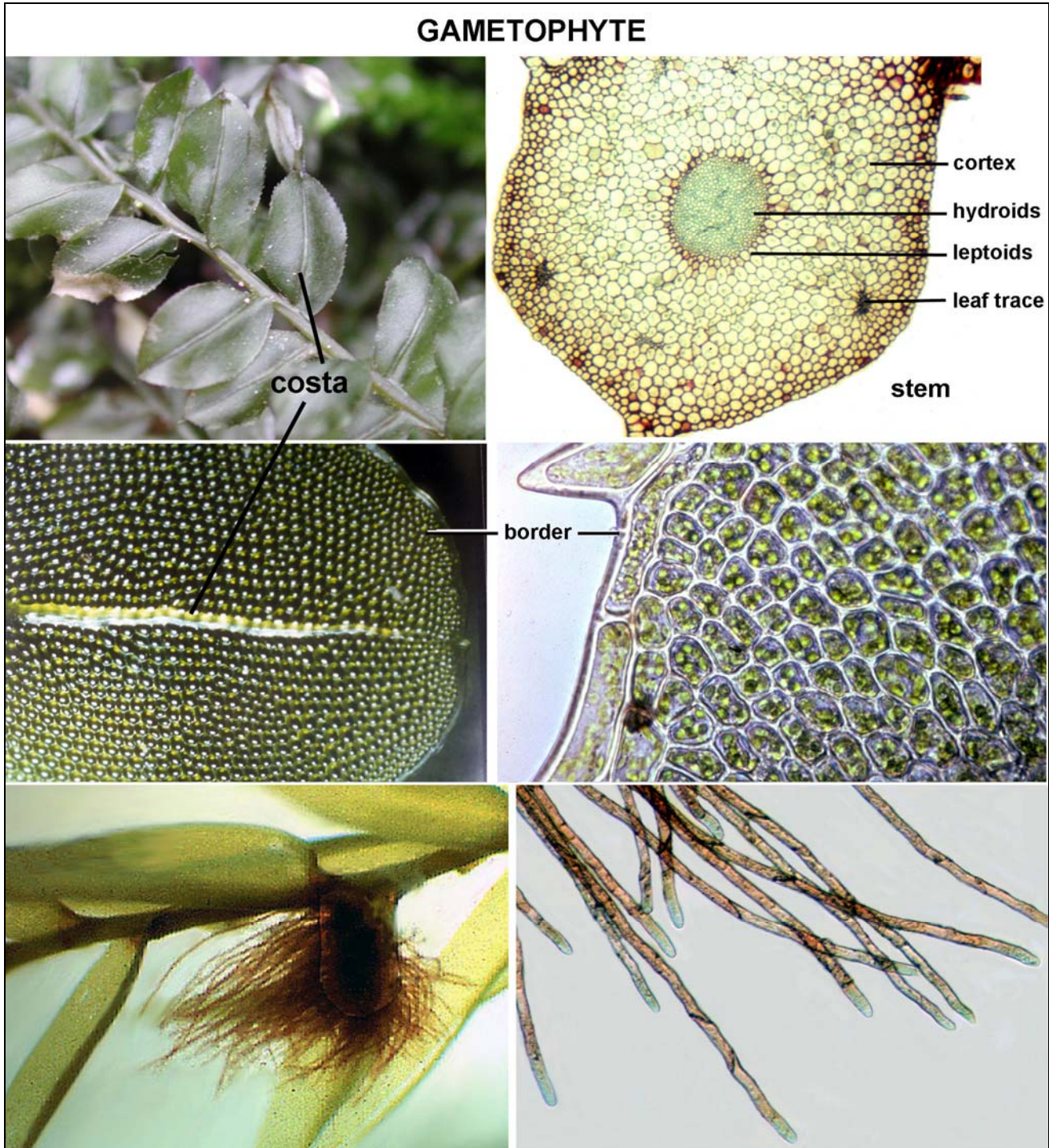
Figure 71. Vegetative characters (gametophyte) of Class Bryopsida. **Upper Left:** *Plagiomnium medium* stem and leaves. Photo by Michael Lüth, with permission. **Upper right:** *Plagiomnium* stem cross section showing central strand of hydroids. Note smaller darkened areas in stem cortex that are leaf traces. Photo by Janice Glime. **Middle Left:** Leaf of *Rhizomnium* illustrating a border, small, roundish cells, and a distinct costa. Tip of leaf lacking a costa, illustrating elongate cells and undifferentiated apical leaf cells. Photo by Zen Iwatsuki, with permission. **Middle Right:** Portion of *Plagiomnium* leaf showing border. Photo by Janice Glime. **Lower Left:** *Fontinalis* stem, leaves, and tuft of rhizoids. Photo by Janice Glime. **Lower Right:** Microscopic view of rhizoids showing single cell thickness and diagonal cross walls. Photo by Janice Glime.
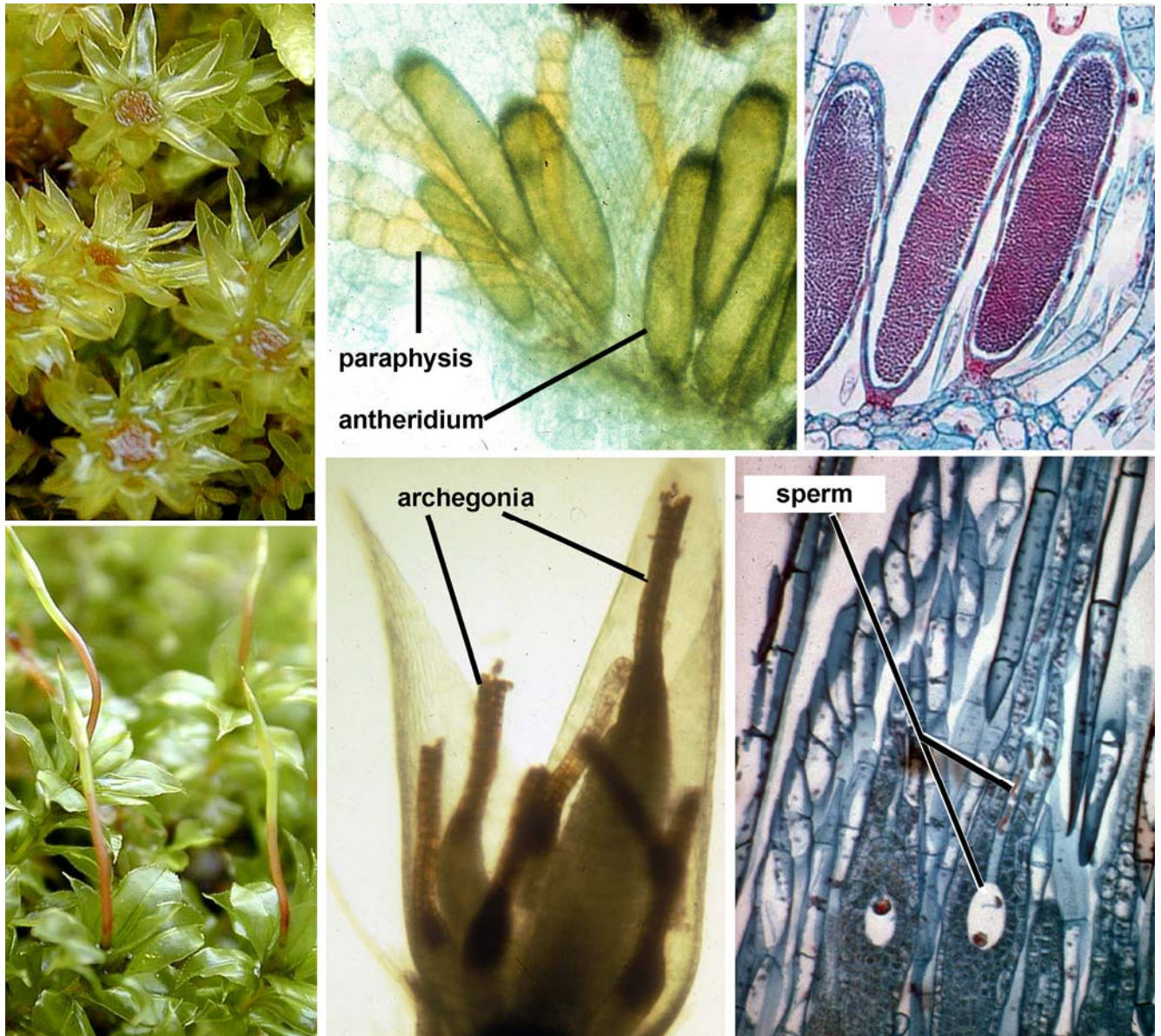
Figure 72. Sexual reproduction of mosses. **Upper row** shows male reproductive parts. Splash platforms (**left**) of *Mnium hornum* in which antheridia may be located, or they can be among ordinary leaves (**center**); among the antheridia are paraphyses (**center** and **right**) that help in retaining water and in forcing sperm out of the antheridia at maturity. **Lower row** shows female reproductive parts. Perichaetial leaves and young sporophytes of *Plagiomnium cuspidatum* (**left**), archegonia from leaf bases of *Pleurozium schreberi* (**center**), and a section of archegonia (**right**) with sperm in the neck canal. Plant photos by Michael Lüth, with permission; photomicrographs by Janice Glime.
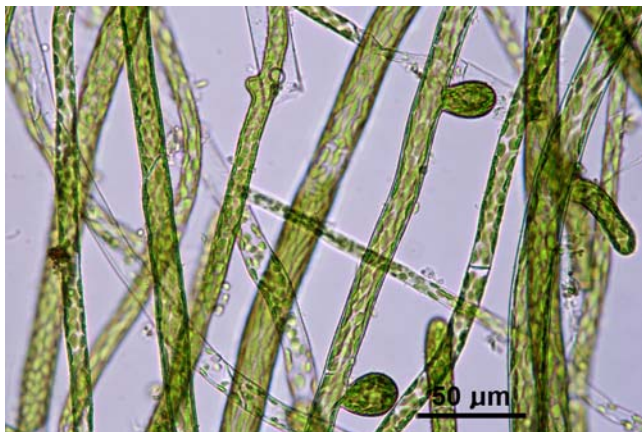

Figure 73. Moss protonemata. Photo by Jan Fott, with permission.

Figure 74. Moss protonema. Photo by Jan Fott, with permission.

Summary

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

The life cycle of Bryopsida involves a **protonema** that is usually threadlike and develops from the germinating spore, developing numerous **buds** and **gametophores**. Gametophores produce **archegonia** and/or **antheridia** and the **embryo** develops within the archegonium.

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

Vegetative reproduction is common among bryophytes. Bryophyta can reproduce by **fragments** as well as specialized asexual structures and thus add a new dimension to life cycle strategies.

Acknowledgments

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CHAPTER 2-8

ANTHOCEROTOPHYTA

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Figure 1. *Notothylas orbicularis* thallus with involucres. Photo by Michael Lüth, with permission.

Anthocerotophyta

These plants, once placed among the bryophytes in the Anthocerotae, now generally placed in the phylum **Anthocerotophyta** (hornworts, Figure 1), seem more distantly related, and genetic evidence may even present them as more like ferns as we understand them better (Hori *et al.* 1985; Sherman *et al.* 1991; Nickrent *et al.* 2000; Knoop 2004; Groth-Malonek 2005). Yet other chemical evidence places them close to the liverworts (Hanson *et al.* 1999); they lack isoprene emission, as do liverworts, whereas mosses and ferns possess it. However, such characters may prove to be retained or lost adaptively and contribute little to phylum level relationships.

The hornworts are divided into two classes (Stotler & Crandall-Stotler 2005), a concept supported by molecular data (Frey & Stech 2005). **Anthocerotopsida** is the largest and best known of these, with two orders and three families. The second class is **Leiosporocerotopsida**, a class with one order, one family, and one genus. The genus *Leiosporoceros* differs from members of the class **Anthocerotopsida** by having the Cyanobacterium *Nostoc* in longitudinal canals. In the other hornworts, the *Nostoc* colonies are scattered in discrete globose colonies (Villarreal A. & Renzaglia 2006).

As in other Bryobiotina, the gametophyte in the Anthocerotophyta is the dominant generation, but then, there are a few ferns in which the gametophyte might also be considered dominant. Hornworts differ from Marchantiophyta in having typically only **one chloroplast per cell** in the thallus, **lacking oil bodies**, and possessing a **pyrenoid** (a proteinaceous body serving as a nucleus for starch storage and common in green algae) (Figure 2).

Figure 2. Hornwort cells showing single chloroplast, doughnut-shaped pyrenoid in center, and absence of oil bodies. Photo by Chris Lobban, with permission.

Some **Anthocerotophyta** have interesting adaptations to help them get the most from their environmental resources. The **pyrenoid**, present in many taxa, has a concentration of Rubisco, and this permits it to concentrate CO_2 (Hanson *et al*. 2002). Furthermore, the thallus typically has colonies of *Nostoc* (Figure 3-Figure 5), a member of the Cyanobacteria, embedded within the tissues and providing a conversion of atmospheric nitrogen into a form the hornwort can use. This fixed nitrogen is transferred from the gametophyte thallus to the sporophyte. Furthermore, if the gametophyte happens to be grown in the dark, and the sporophyte is illuminated, it can transfer the photosynthate to the gametophyte (Bold *et al*. 1987). And that sporophyte can have twice the photosynthetic carbon fixation of the gametophyte (Thomas *et al*. 1978)!

Figure 3. Probably *Megaceros* with *Nostoc* colonies. Photo by Chris Lobban, with permission.
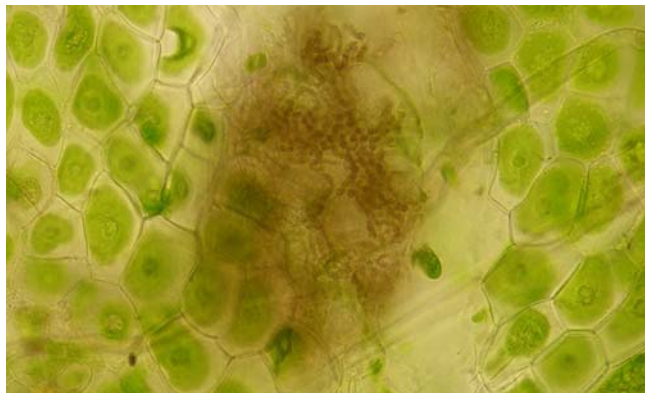

Figure 4. *Nostoc* (brown cells) in hornwort. Photo by Chris Lobban, with permission.
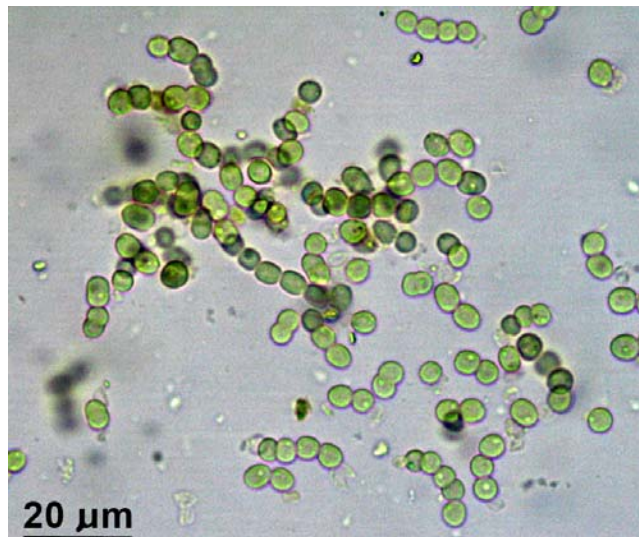

Figure 5. *Nostoc* from *Anthoceros agrestis*. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

At least some members have associated fungi. Ligrone (1988) reported fungi in association with *Phaeoceros laevis*. The fungus colonized the parenchyma cells except at the growing tips of the thallus and epidermal cells. The infected cells increased their cytoplasmic contents, but the chloroplast lost starch and the pyrenoids disappeared. The chloroplast became branched and these branches intermingled with the arbuscular fungal hyphae.

The sporophyte is like that of *Sphagnum* in **lacking a sporophyte stalk** (seta) on the capsule (Figure 6) and like the Bryophyta in having a **columella** (Figure 7-Figure 8) that is not in liverworts. The capsule also has **stomata** surrounded by two kidney-shaped **guard cells** (Figure 9), characters shared with Bryophyta. Instead of elaters, they have **pseudoelaters** (arising from division of a pseudoelater mother cell and outnumbering spores; Figure 10) of one, two, or four cells, usually with **no spiral thickenings** [except *Megaceros* and *Dendroceros* (Renzaglia 1978)] (Figure 11). The pseudoelaters probably provide nutrition, at least initially, but at maturity they twist, contributing to dehiscence and dispersal (Renzaglia 1978).

Figure 6. *Phaeoceros* showing gametophyte thalli at base and horn-like sporophytes. Photo by Janice Glime.
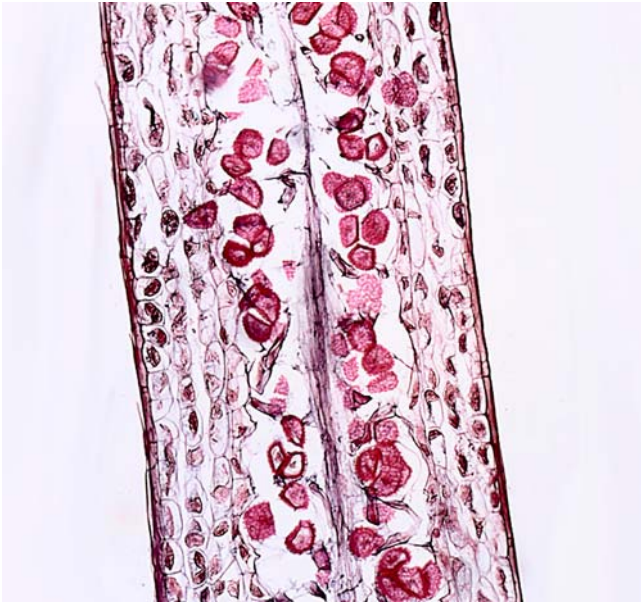
Figure 7. **Anthoceros** sporophyte longitudinal section showing spores and spore tetrads. Note central columella. Photo by George Shepherd, through Creative Commons.
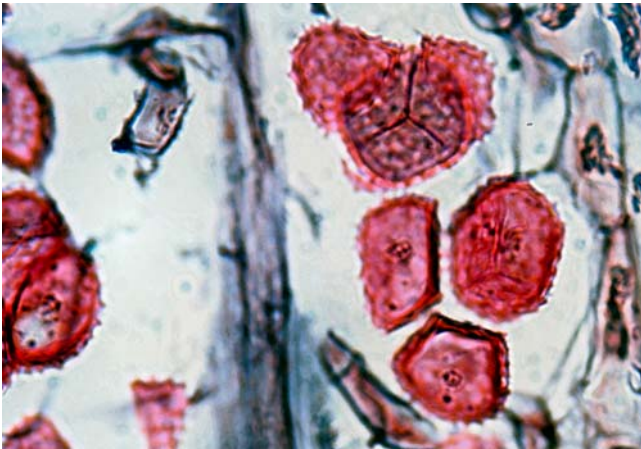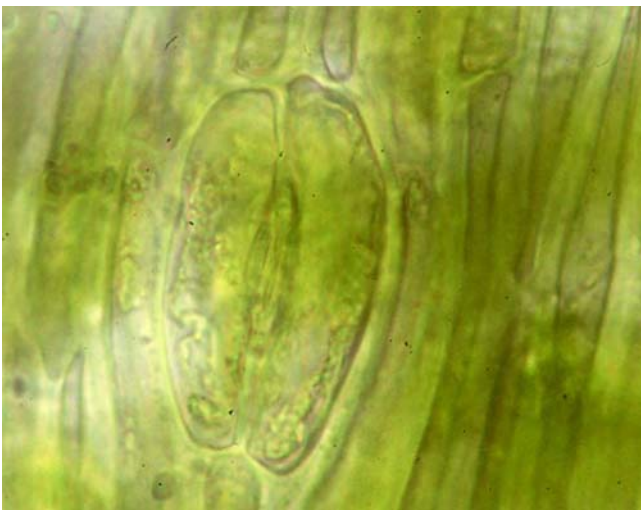

Figure 8. **Anthoceros** sporophyte longitudinal section showing spores and spore tetrads. Note central columella. Photo by George Shepherd, through Creative Commons.

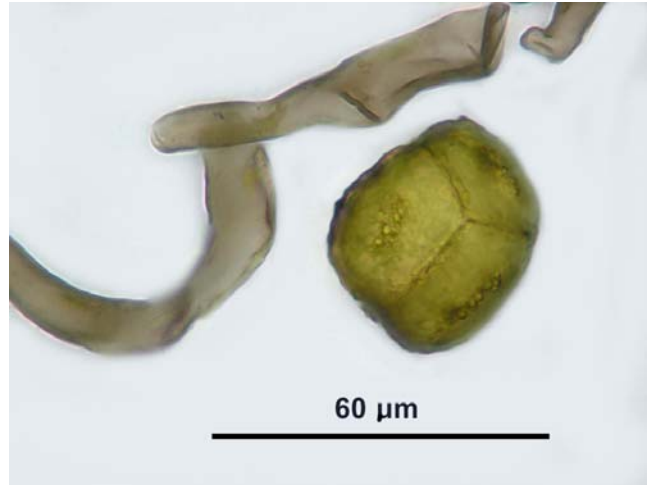Figure 9. Stoma and guard cells on sporophyte of **Anthoceros angustata**. Photo by Hironori Deguchi from <www.digital-museum.hiroshima-u.ac.jp>, with permission.

Figure 10. **Phaeoceros** spore and pseudoelater. Photo by David H. Wagner, with permission; scale modified by Janice Glime.
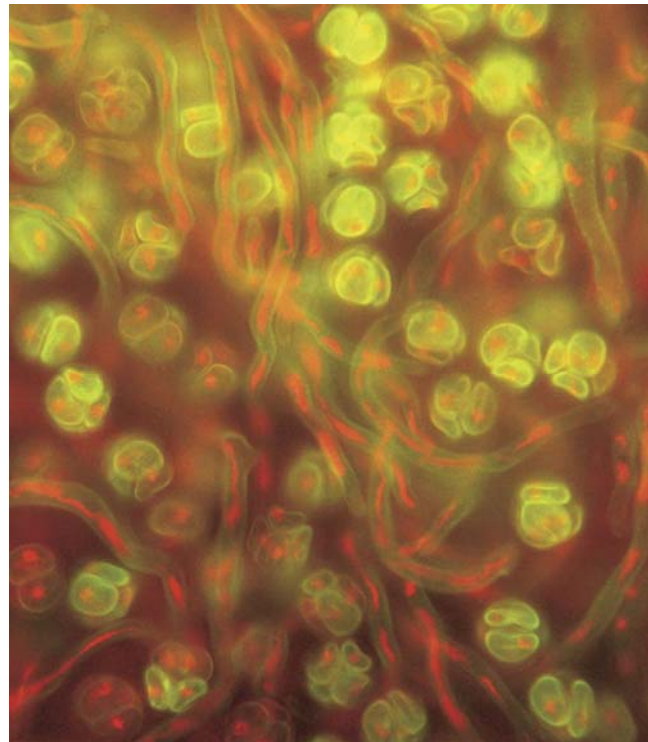

Figure 11. **Leiosporoceros dussii** spores and pseudoelaters using fluorescence microscopy. Note the absence of spiral thickenings in the elaters. Photo by Andrew Blackwell, and Juan Carlos Villarreal A., Southern Illinois University, with permission.

Meiosis is **continuous**, occurring at the base of the capsule, causing the tip of the sporophyte to have more mature spores than the base (Figure 12-Figure 14), a feature unique to the Anthocerotophyta. Dispersal results as the **capsule splits** into valves from the top down (Figure 25), and consistent with its development, this peeling back of the capsule occurs slowly over time, retaining the lower spores while dispersing the upper ones. The valves twist in response to moisture changes, perhaps aiding in dispersal. The **spores mature progressively** from top to bottom of the capsule (Figure 13) as the capsule splits and **continues**

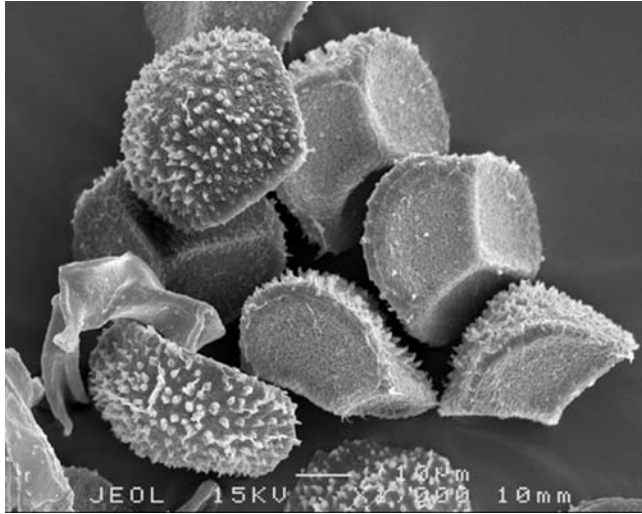**to grow at its base**, unlike any other Bryobiotina (Figure 26).

Figure 12. SEM of ***Phaeoceros carolinianus*** meiospores. Photo by Christine Cargill at Trin Wiki.

Figure 13. Hornwort sporophyte foot in gametophyte tissue. Note that basal portion of the sporophyte contains sporogenous tissue; those above have undergone meiosis. Oval area at the base of the sporophyte is the foot, imbedded in the gametophyte. Photo by Michael W. Clayton. Permission pending
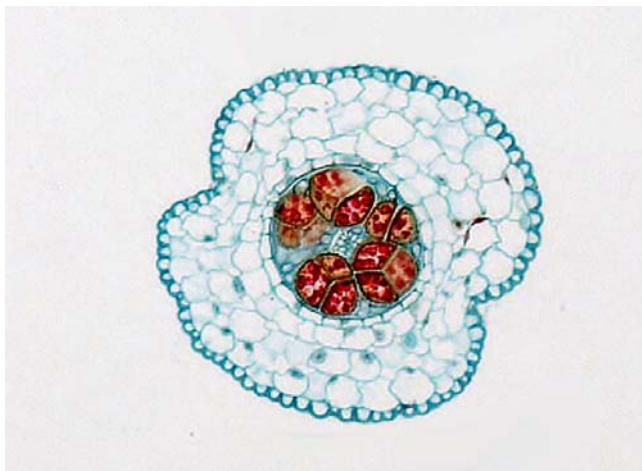

Figure 14. ***Anthoceros*** sporophyte cross section, showing meiospores and columella. Photo from Botany 321 website at University of British Columbia, with permission.

Dendroceros is a tropical genus that is unusual among the Anthocerotophyta by growing on tree bark and leaves. Furthermore, it produces multicellular green spores (Figure 15) (Schuette & Renzaglia 2010). Schuette and Renzaglia suggest that the precocious development of the spore, resulting in **endospory**, permits it the time and resources necessary to survive the desiccating habitat where it lives.
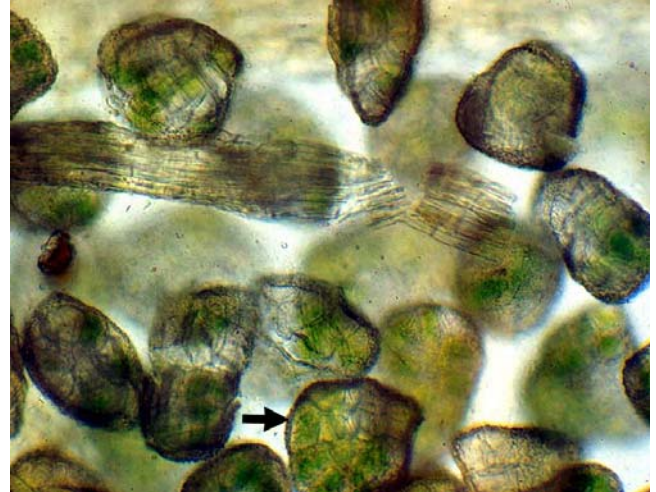

Figure 15. ***Dendroceros tubercularis*** endospores. Photo by Karen Renzaglia, with permission.

Spores in **Anthocerotophyta** germinate to form a short **protonema** that does not remain threadlike, but gets areas that are more three-dimensional, resembling a tuber (Figure 16).

Figure 16. ***Anthoceros dichotomus*** protonema. Photo from Plant Actions through Eugenia Ron Alvarez, with permission.

The mature gametophyte thallus resembles that of a club moss (Lycopodiophyta) in that the **antheridia** may occur in groups within a chamber (Figure 17-Figure 23). The archegonia are likewise embedded within the thallus, again like those of the club mosses. The structure of the archegonium is illustrated in Figure 24.

Figure 17.　Hornwort **antheridia**, illustrating the clustering. Photo by Tom Thekathyil, with permission.
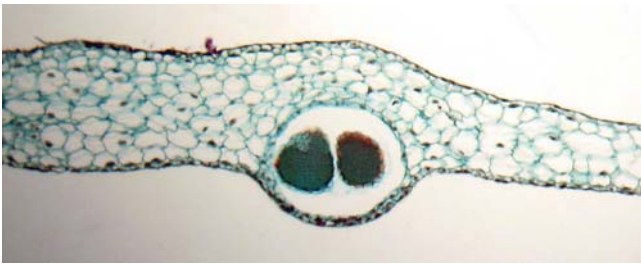

Figure 18.　**Antheridia** in thallus of hornwort.　Photo from Botany 321 website at University of British Columbia, with permission.
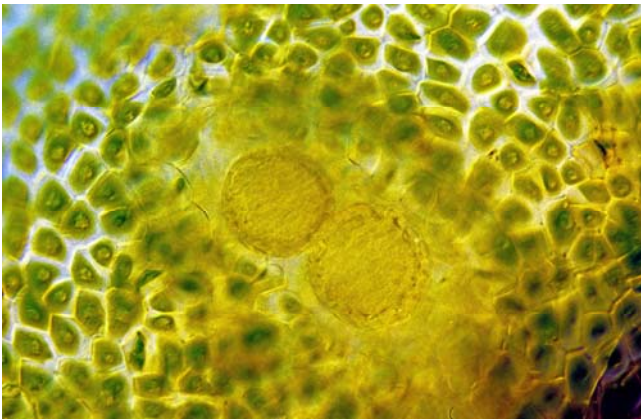

Figure 19.　*Phaeoceros* gametophyte with **antheridia**.　Photo by George Shepherd, through Creative Commons.
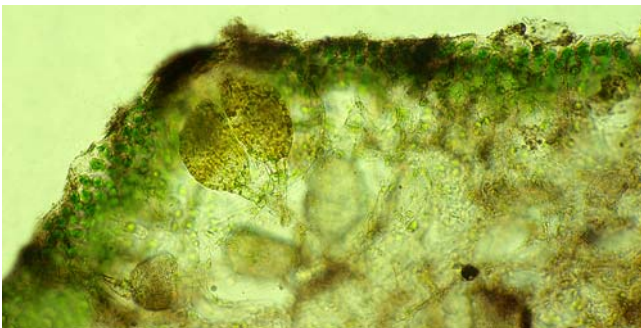

Figure 20.　*Anthoceros punctatus* **antheridia**.　Photo from Plant Actions website through Eugenia Ron Alvarez, with permission.
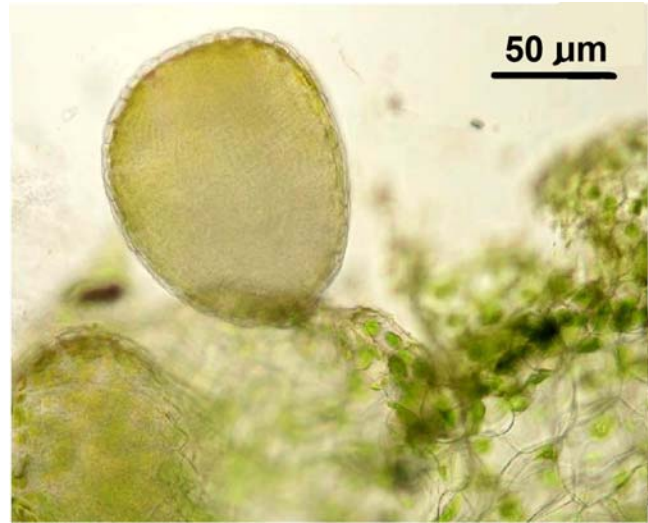

Figure 21.　**Antheridium** of a hornwort.　Photo by Hatice Ozenoglu Kiremit, with permission.
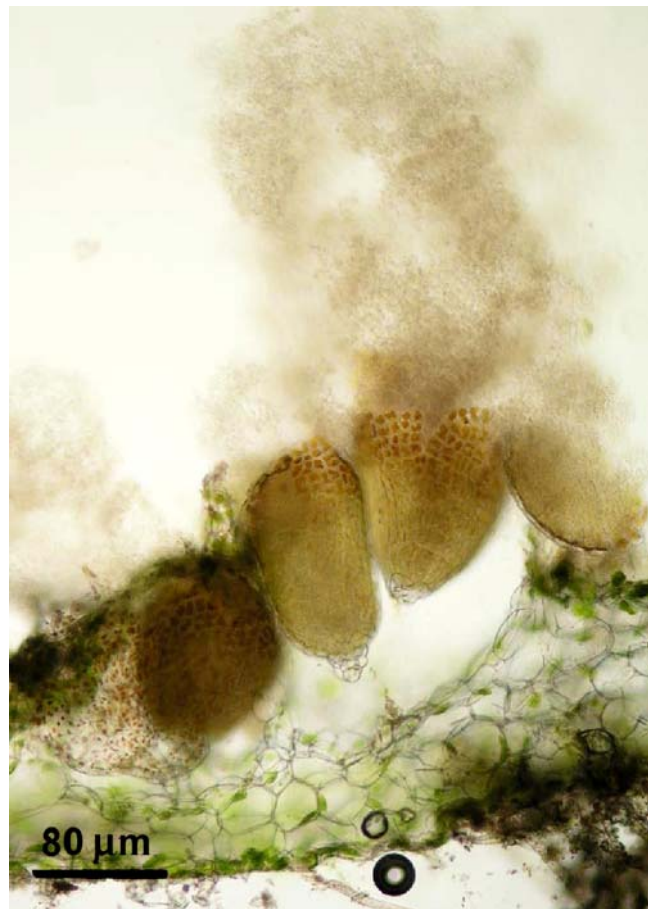

Figure 22.　**Antheridia** of a hornwort dispersing its sperm. Photo by Hatice Ozenoglu Kiremit, with permission.

Figure 23. Antheridium of hornwort (probably ***Phaeoceros carolinianus***) expelling sperm. Tom Thekathyil (pers. comm. 17 September 2009) reported that sperm were still alive several hours later. Photo by Tom Thekathyil, with permission.
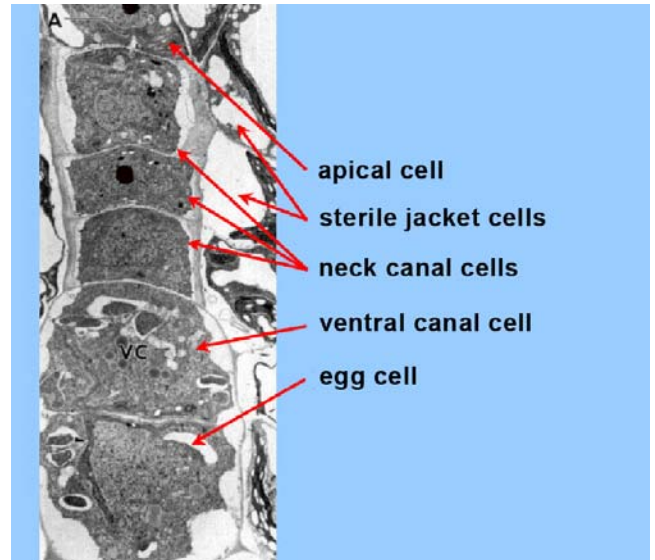

Figure 24. Hornwort archegonium. Photo from Science Land Plant website at Southern Illinois University, with permission.

Figure 25. ***Phaeoceros oreganus*** sporophytes showing the splitting tips of mature capsules. Photo by Li Zhang modified in Photoshop.

Figure 26. Anthocerotophyta – hornworts. **Upper left:** *Anthoceros bulbicosus* thallus and undehisced sporophyte. **Upper right:** cleared section of gametophyte thallus, collar, and hornlike sporophyte. **Lower left:** Cross section of *Anthoceros* thallus. Although the sporophyte is complex, the gametophyte is quite simple, perhaps indicating reduction. Note the lack of specialized tissues and absence of air chambers. **Lower right:** Older sporophyte of *Phaeoceros carolinianus* showing yellow color near tips of sporophyte due to mature spores. Upper left and lower right photos by Michael Lüth; upper right and lower left photos by Janice Glime.

Table 1. Comparison of the phyla of Bryobiotina. Amplified from Crandall-Stotler (1996) and Gradstein *et al.* (2001).

Character	Marchantiophyta	Bryophyta	Anthocerotophyta
Protonema	Mostly globose or thalloid, forming one bud; no gemmae	Filamentous, forming many buds; may produce gemmae	Globose, forming one bud; no gemmae
Gametophyte form	Leafy shoot or thallus; thallus simple or with air chambers; dorsi-ventral	Leafy shoot	Simple thallus; dorsi-ventral
Branches	Developing from leaf initial cells or inner stem cells, rarely stem epidermis	Developing from stem epidermis	
Leaf origin	2 initial cells (1 in Calobryales & Metzgeriales)	1 initial cell	
Leaf arrangement	Leaves in two or three rows, ventral row usually of different size	Leaves usually in spirals	Not applicable
Leaf form	Leaves unistratose, divided into 2+ lobes, no costa	Leaves unistratose in most, undivided, costa present in some	Thallose
Leaf/thallus cells	Usually isodiametric, have trigones; numerous chloroplasts	Often elongate, rarely possess trigones; numerous chloroplasts	No trigones; 1-4 large chloroplasts
Special organelles	Complex oil bodies often present	Simple, small oil bodies or none	Single plastids with pyrenoids
Gemmae	Common on leaves	Common on leaves, stems, rhizoids, or protonemata	Absent
Water conducting cells	Present only in a few simple thalloid forms	Present in both gametophytes and sporophytes of many	Absent
Rhizoids	Hyaline, one-celled	Brown, multicellular	Hyaline, one-celled
Gametangial position	Apical clusters (leafy forms) or on upper surface of thallus	Apical clusters	Sunken in thallus, scattered
Paraphyses	Usually lacking; often have mucilage filaments	Usually associated with antheridia & archegonia	Lacking
Growth of sporophyte	Apical	Apical	Grows continuously from basal meristem
Stomata	Absent in both generations, but pores present on some gametophyte thalli	Present on sporophyte capsule	Present in both sporophyte and gametophyte
Seta	Hyaline, elongating just prior to spore release, rigid when turgid, deliquescent	Photosynthetic, emergent from gametophyte early in development in Bryopsida & Polytrichopsida, rigid due to cell structure, persistent; not elongating in Sphagnopsida – pseudopodium present	Absent
Calyptra	Ruptures & remains at base of seta, lacks influence on capsule shape	Ruptures & persists at apex of seta & capsule, influences capsule shape	Lacking
Capsule	Undifferentiated, spherical or elongate; jacket uni- or multistratose; often with transverse or nodular thickenings	Complex with operculum, theca and neck; jacket multistratose; lack transverse or nodular thickenings	Undifferentiated, horn-shaped; jacket multistratose
Sterile cells in capsule	Spirally thickened elaters	Columella	Columella and pseudoelaters
Capsule dehiscence	Into 4 valves; spores shed simultaneously	At operculum & peristome teeth in Bryopsida & Polytrichopsida, spores shed over extended period; valvate in Takakiopsida, Andreaeopsida, & Andreaeobryopsida; lacking peristome in Sphagnopsida	Into 2 valves; spores mature & shed over extended period
Chemistry	Monoterpenes, sesquiterpenes, & diterpenes; lunularic acid	Triterpenes; ABA	Terpenoids(?)

Summary

The traditional bryophytes are classified into three phyla (Marchantiophyta, Bryophyta, Anthocerotophyta) that can be placed in the subkingdom Bryobiotina. **Anthocerotophyta** (hornworts) differ in having a sporophyte that is shaped like horn and continues to grow at the base as spores mature and are dispersed at the apex.

Anthocerotophyta have a **dominant gametophyte** generation. Gametophytes produce **archegonia** and/or **antheridia** and the **embryo** develops within the archegonium.

Sporophytes remain attached to the gametophyte and produce **spores** by **meiosis** over a prolonged period of time, with the youngest spores at the base. **Pseudoelaters** are produced along with the spores, but are formed by mitosis and remain 2*n*. **Capsules** split longitudinally and peel backward from the tip.

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