

CHAPTER 2-7

BRYOPSIDA



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

Bryopsida Definition

By far the largest class of Bryophyta (*sensu stricto*) (84% of families) (Goffinet *et al.* 2001) and ~98% of the species, this class 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.

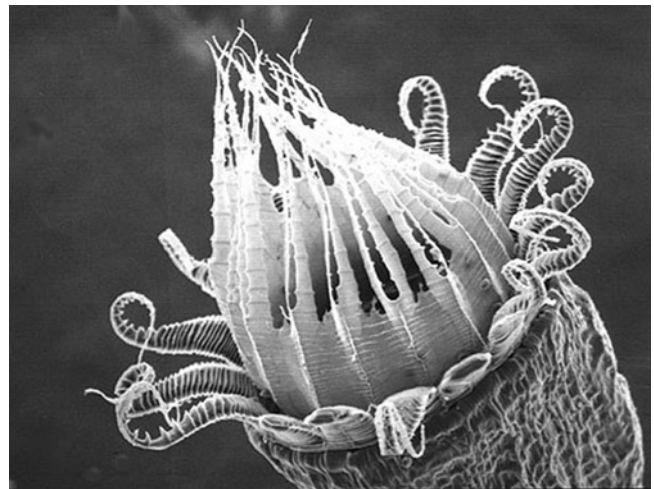


Figure 2. Electron micrograph of the arthrodontous peristome teeth of the moss *Eurhynchium praelongum*. Photo from Biology 321 Course Website, <http://www.botany.ubc.ca/bryophyte/LAB6b.htm>.

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 (Figure 4). This germination process 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.

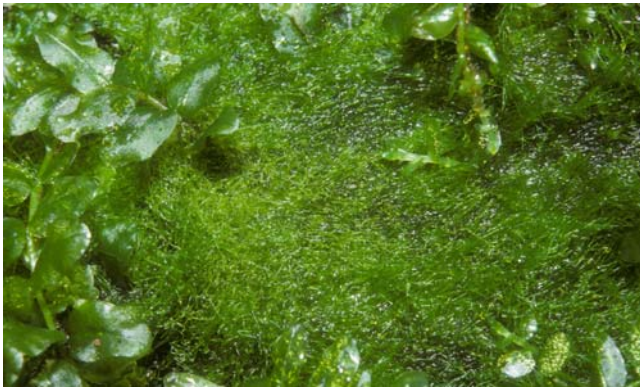


Figure 4. Protonemata among leafy plants of *Plagiommium*. Photo by Janice Glime.

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.

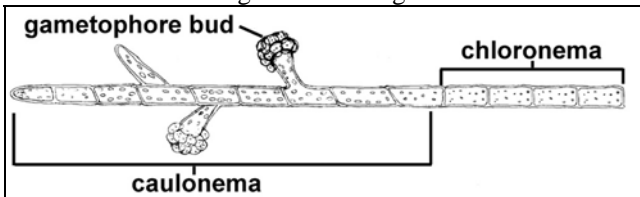


Figure 5. Protonema of moss such as *Funaria hygrometrica* with differentiated caulonema and chloronema. Drawing by Noris Salazar Allen.

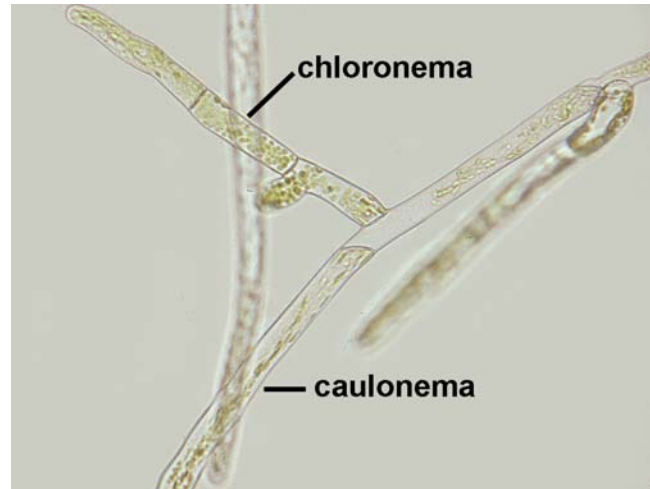


Figure 6. Protonema of *Funaria hygrometrica* showing chloronema (short cells with perpendicular walls and dense chloroplasts) and caulonema (long cells with diagonal cross walls and more dispersed chloroplasts). Photo by Janice Glime.

Gametophore Buds

As the protonema continues to develop and produce buds (Figure 7, Figure 8), 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 9). This provides the possibility for somatic mutations to arise, affording genetic variation among the leafy plants.

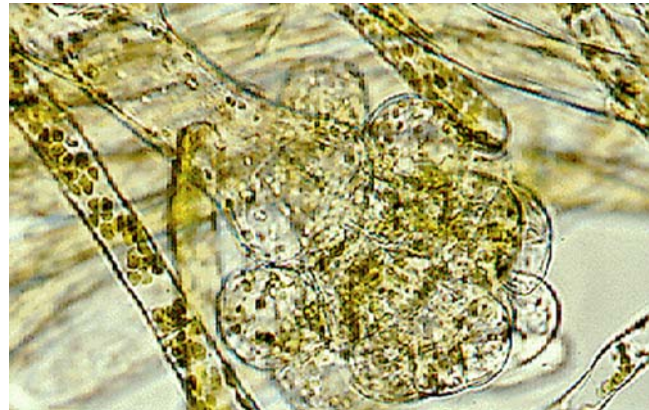


Figure 7. Protonema and young developing bud of the moss *Funaria hygrometrica*. Photo by Martin Bopp.

As the bud develops, **rhizoids** (Figure 25) 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.

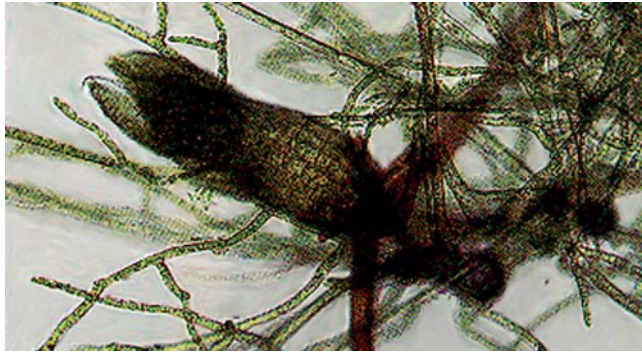


Figure 8. Moss protonema with developed bud. Photo by Janice Glime.

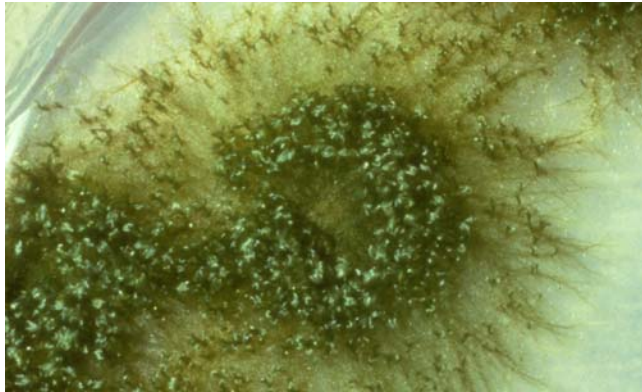


Figure 9. Leafy buds on the protonemata of *Funaria hygrometrica* forming a doughnut shape. Each of these circles of buds is the result of one spore. The hole in the middle is the area where the protonemata is in the chloronema stage and does not produce buds. Photo by Janice Glime.

Gametophores

The bud develops into the upright (or horizontal) **gametophore**. These plants are leafy **haploid** ($1n$) plants; thus, they are the **dominant gametophyte generation** of the life cycle. The stem may have a **central strand** (Figure 10), or lack it (Figure 11); this strand may or may not have **hydroids**.

Their leaves, more accurately known as **phyllids** (but rarely called that), are usually in **more than three rows**, but there are exceptions with two or three rows. 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 12), or alternating **hyaline** (colorless) and photosynthetic layers as in *Leucobryum*, or just multiple layers of tissue, sometimes in patches. Some may have borders which likewise can be one or more layers thick. These leaves often have a multi-layered **costa** (Figure 13) in the center, or double, or even triple costa. The **costa** itself (Figure 25) 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.

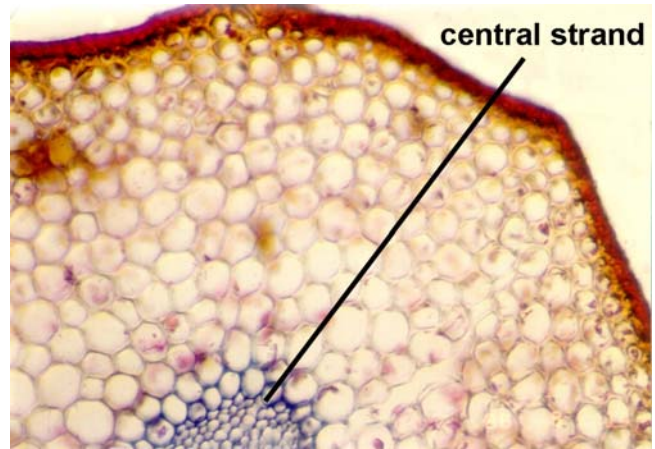


Figure 10. Stem cross section of *Rhizogonium* illustrating central strand of hydroids. Photo by Isawa Kawai.

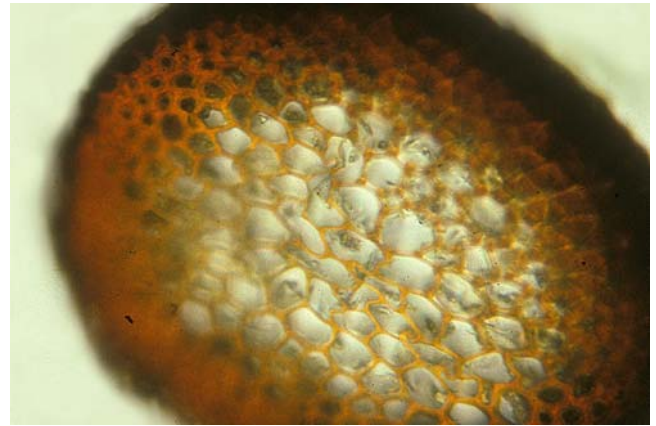


Figure 11. Cross section of stem of the brook moss *Fontinalis dalecarlica* showing absence of central strand and conducting tissues. Photo by Janice Glime.



Figure 12. Pockets in leaf of *Fissidens arnoldii*. Photo by Michael Lüth.



Figure 13. Cross section of Bryopsida leaf showing one cell thick lamina (blade) portion and thickened costa. Photo by Janice Glime.

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 14) are generally those upright mosses with terminal sporangia. They usually are unbranched or sparsely branched. **Pleurocarpous** mosses (Figure 15), 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 14. *Barbula unguiculata*, an **acrocarpous** moss. Setae originate at the apex of the previous year's growth. Photo by Michael Lüth.



Figure 15. *Pleuroziopsis ruthenica*, a **pleurocarpous** moss. Photo by Janice Glime.

The upright or sprawling stems of the gametophyte produce **antheridia** (sperm-containers) and **archegonia** (egg-containers). In mosses, antheridia and archegonia

may be located at the end of the main stem, at the ends of lateral branches, or along the main stem, either at the ends of very short branches or nearly sessile (Figure 26). Often the chloroplasts of the antheridial jacket cells are converted into chromoplasts as the antheridia mature, causing the characteristic red-orange color (Bold *et al.* 1987; see Figure 16).

Sperm Dispersal

The dispersal of the sperm from the antheridium is an interesting phenomenon. In *Mnium hornum*, 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. 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. This 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. Muggoch and Walton considered this 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 *Bryum* (or *Rosulabryum*) *capillare* (Bryopsida; Figure 16).



Figure 16. *Bryum capillare* showing antheridial head of male plants. Photo by Michael Lüth.

It appears that *Bryum capillare* 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* 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 17) (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 17. *Isotoma caerulea*, a springtail that is instrumental in fertilizing *Bryum argenteum*. Photo by Katrina Hedlund.

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).

Anderson (2002) managed to catch the dispersal of *Plagiomnium affine* 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 18, Figure 26, Figure 27) 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.

Splash cups and platforms seem to be rare in monoicous taxa (exceptions include species of *Brachymerium* and *Rosulabryum* 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. However, other things can create splash. Jonathan Shaw (pers. comm.) has considered that *F. hygrometrica* 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 she 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.

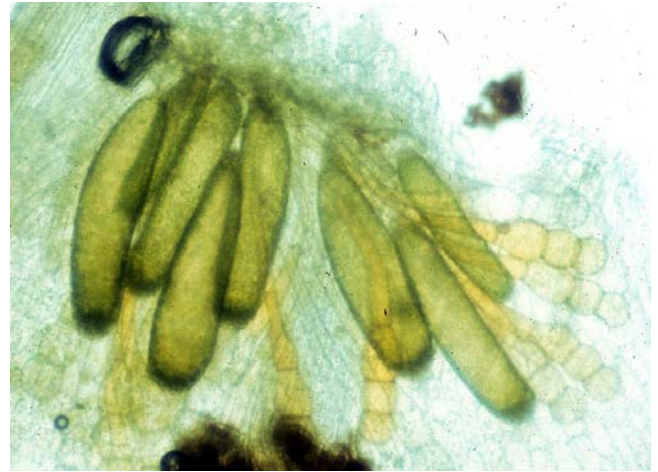


Figure 18. Mature **antheridia** and **paraphyses** of the moss *Rhizomnium*. Photo by Janice Glime.

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), which has well-developed splash cups 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) and **perichaetia** (modified leaves enclosing

female reproductive structures) sometimes attracts invertebrates.

One might expect that many antheridia burst as they and their surrounding **paraphyses** 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?

If animal dispersal is so rare, then how, in this vast world, does an unintelligent sperm find an archegonium (Figure 19) 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 26) leading down to the **egg**, 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** of the archegonium to the egg. The exact nature of this liquid is unknown, but it seems that sugars 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 19. Archegonia of the moss *Fontinalis duriaei*. Photo by Janice Glime

Embryo Development

When a sperm reaches and fertilizes an egg, the resulting **diploid** (having two sets of chromosomes; $2n$) **zygote** begins dividing by **mitosis** to form an **embryo** that starts to stretch the archegonium (Figure 20). 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 26). So the calyptra is a $1n$ covering over the $2n$ 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 21). **Meiosis** occurs in the mature capsule, producing haploid ($1n$) 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 – Splachnaceae – by insects) and grow into new gametophytes.

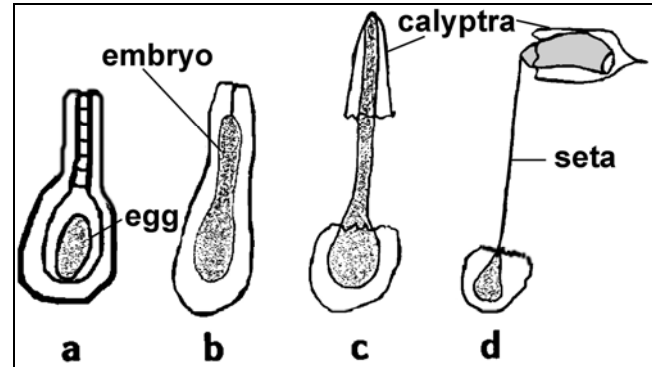


Figure 20. Development of the calyptra of a moss. **a.** egg in archegonium, with neck canal cells not yet disintegrated. **b.** archegonium after fertilization and early development of embryo, showing elongation of the archegonium as embryo grows. **c.** elongated seta with calyptra perched on top of it before capsule has developed. **d.** mature capsule with calyptra and fully elongated seta. **c & d** indicate the remains of the venter of the archegonium at the base of the sporophyte. Drawings by Janice Glime.

The **calyptra** 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 has been shed, the **operculum** (lid) of the capsule is exposed. This 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. But a few are **cleistocarpous** (indehiscent; lacking a regular means of opening), thus lacking an operculum.



Figure 21. *Aloina rigida* with stalk and capsule and with foot imbedded in gametophyte tissue. Photo by Michael Lüth.

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 22, Figure 23). 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. The sporophyte capsule usually has a **columella** (Figure 22) that is columnar like those in Polytrichopsida, providing structure.

Unlike the valvate capsules of liverworts and some moss classes, the sporophytes of the Bryopsida are photosynthetic. 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).

These stages of the life cycle are summarized in Figure 24.

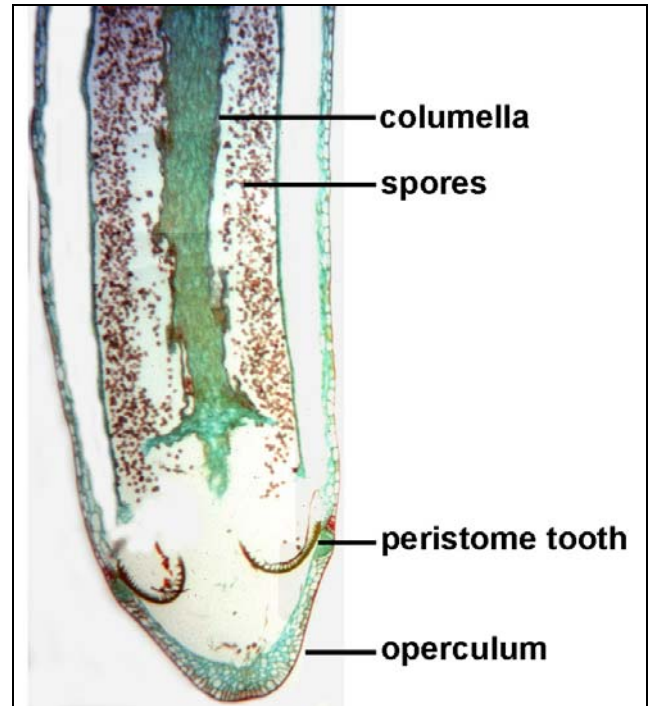


Figure 22. Section of *Mnium* capsule. This capsule actually hangs down, so teeth are on the bottom of the picture. Photo by Janice Glime.

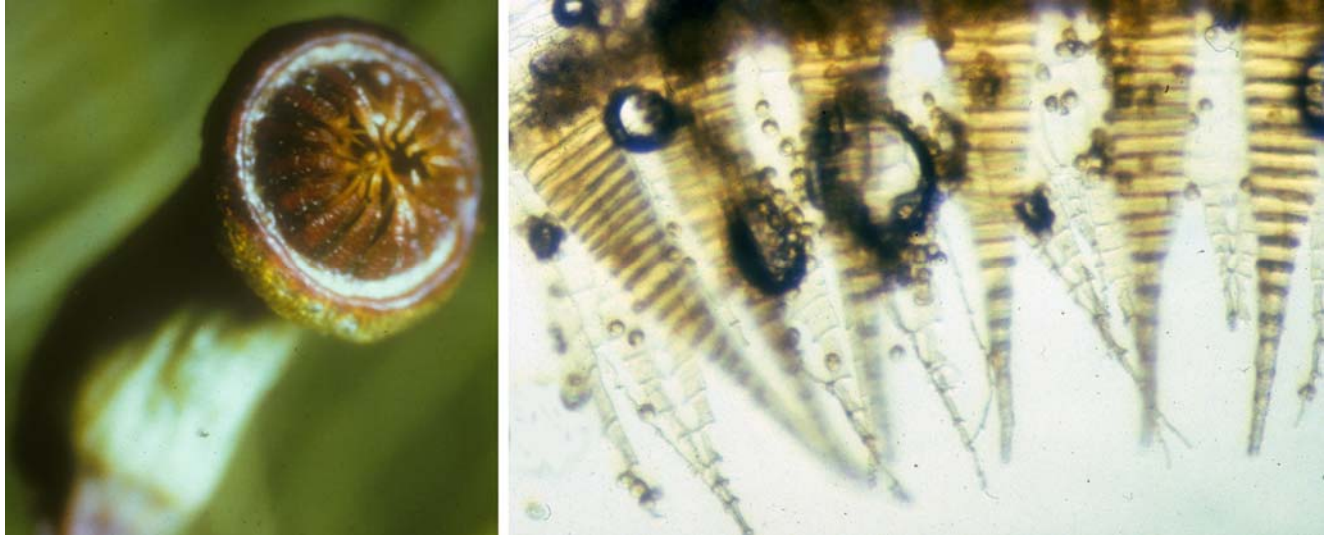


Figure 23. Arthrodontous peristome teeth. **Left:** peristome of *Bartramia pomiformis*. Photo by Zen Iwatsuki. **Right:** spores and peristome teeth of *Trichostomum* showing cell thickenings. Photo by Janice Glime.

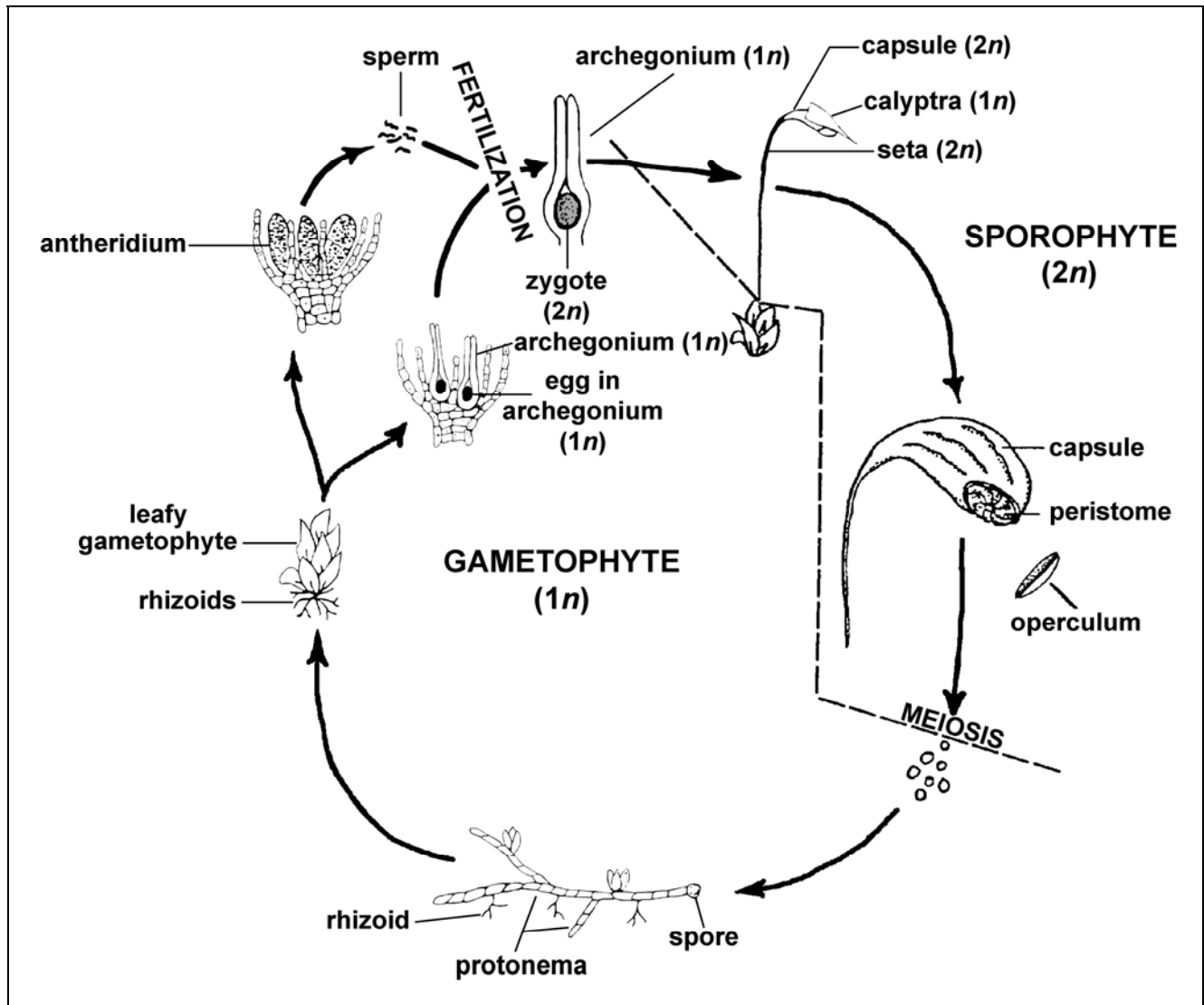


Figure 24. Life cycle of the moss *Funaria hygrometrica*. Drawn by Shelly Meston.

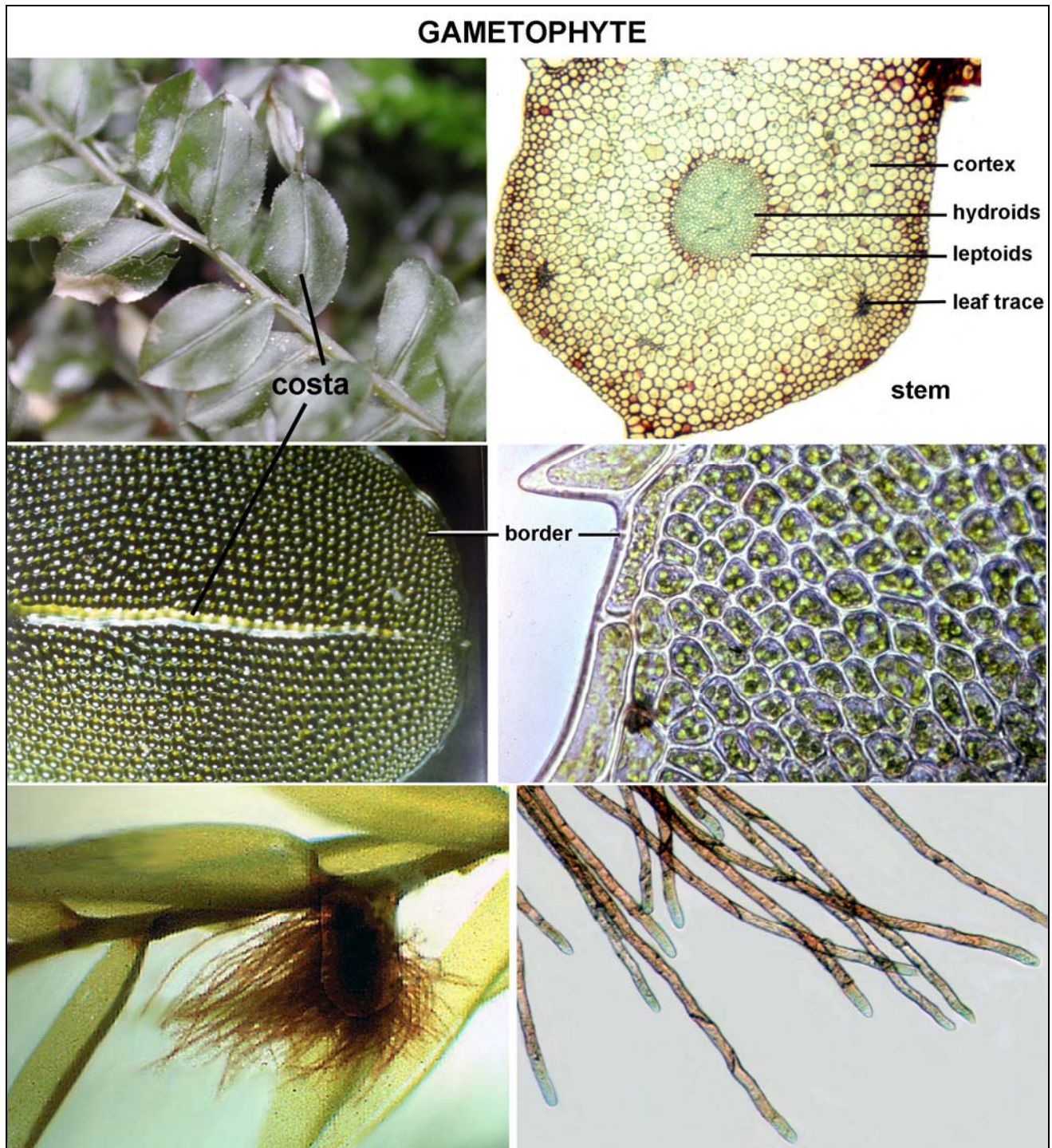


Figure 25. Vegetative characters (gametophyte) of Class Bryopsida. **Upper Left:** *Plagiomnium medium* stem and leaves. Photo by Michael Lüth. **Upper right:** *Plagiomnium* stem cross section showing central strand of hydroids. Note smaller darkened areas in stem cortex that are leaf traces. Photo 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. **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.

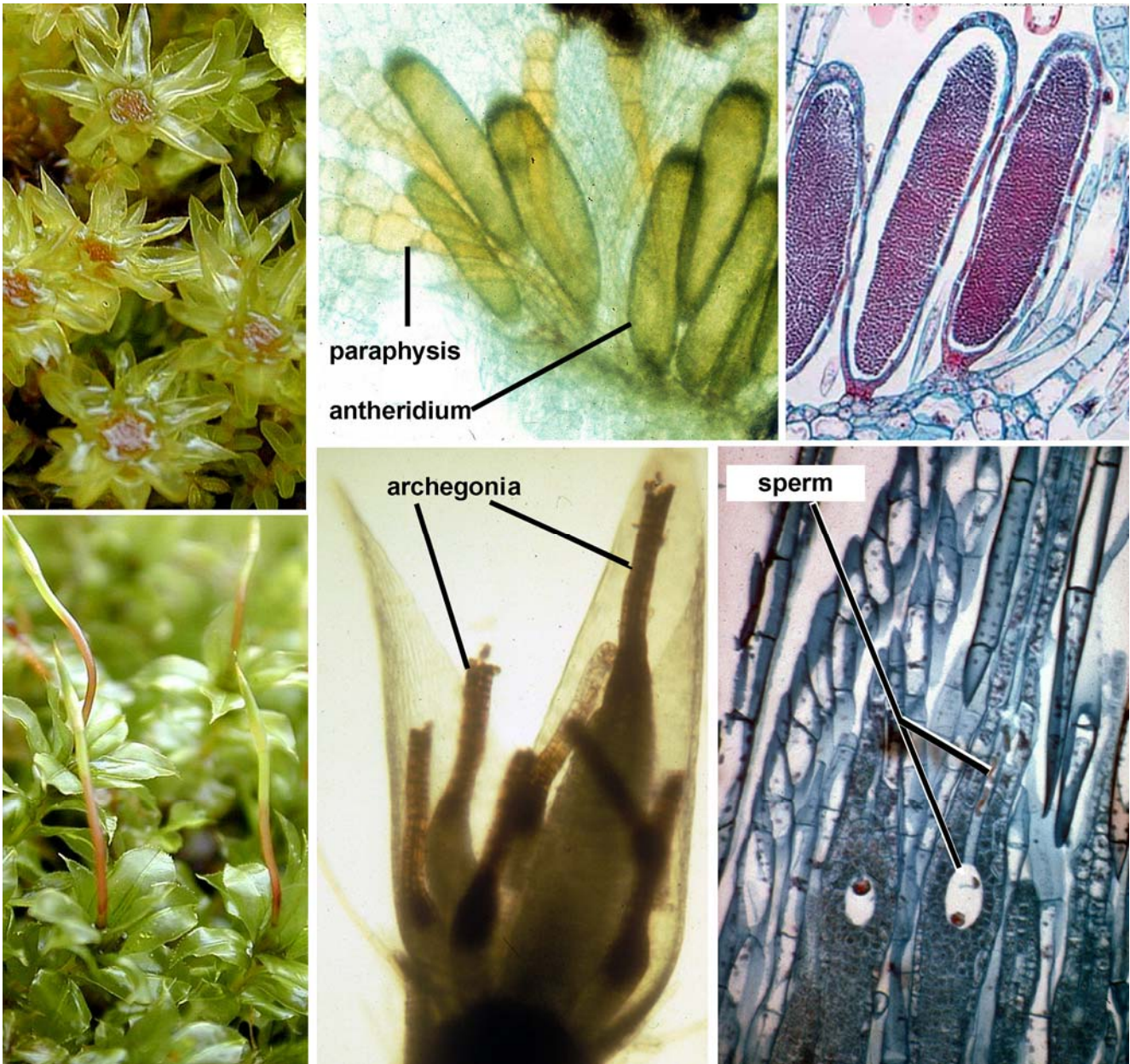


Figure 26. Sexual reproduction of mosses. **Upper row** shows male reproductive parts. Splash platforms (**left**) of *Mnium hornum* in which antheridia may be located, or they can be among ordinary leaves (**center**); among the antheridia are paraphyses (**center** and **right**) that help in retaining 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; photomicrographs by Janice Glime.

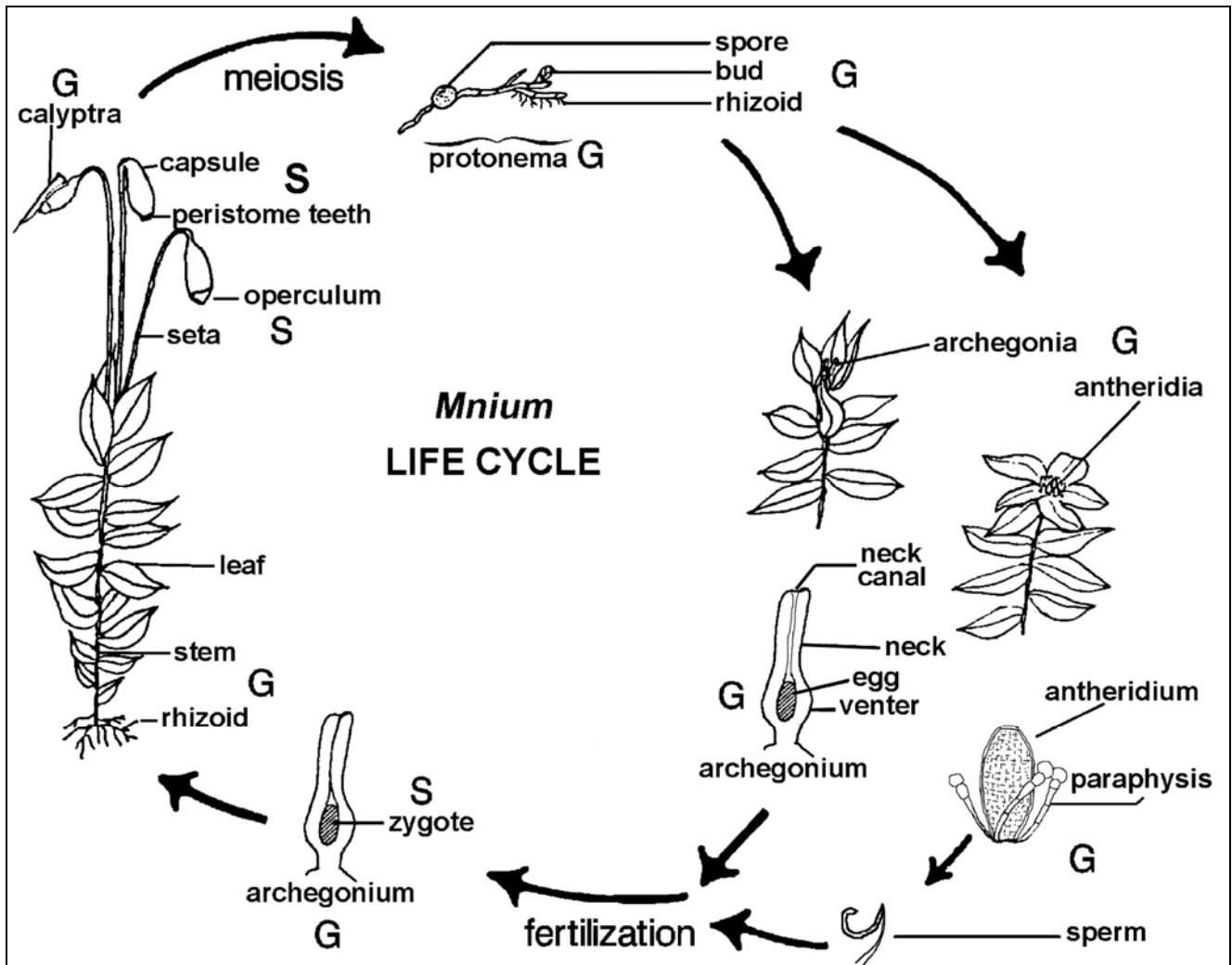


Figure 27. Life cycle of a moss such as *Mnium* (Bryopsida). **G** represents Gametophyte; **S** represents Sporophyte. Drawings by Allison Slavick, Noris Salazar Allen, and Janice Glime.

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

I appreciate the comments and suggestions of Karla Werner, who offered a beginner's perspective. Noris Salazar Allen offered constructive criticisms on the taxonomic descriptions and helped with the proof reading and life cycle diagrams.

Literature Cited

- Anderson, L. E. 2000. Great discoveries in bryology and lichenology. Charles E. Allen and sex chromosomes. *Bryologist* 103: 442-448.
- Beckman, M. 2006. The birds, the bees, and the mites. *ScienceNOW Daily News* 901: 1 Accessed on 3 September at <http://sciencenow.sciencemag.org/cgi/content/fujll/2006/901/1>.
- Bold, H. C., Alexopoulos, C. J., and Delevoryas, T. 1987. *Morphology of Plants and Fungi*. Harper & Row, Publishers, Inc., New York, NY. 912 pp.
- Buck, W. R. and Goffinet, B. 2000. Morphology and classification of mosses. In: Shaw, J. A. and Goffinet, B. (eds.). *Bryophyte Biology*. Cambridge University Press, pp. 71-123.
- Buck, W. R., Goffinet, B., and Shaw, A. J. 2000a. Novel relationships in pleurocarpous mosses as revealed by cpDNA sequences. *Bryologist* 103: 774-789.
- Buck, W. R., Goffinet, R. B., and Shaw, A. J. 2000b. Testing morphological concepts of orders of pleurocarpous mosses (Bryophyta) using phylogenetic reconstructions based on trnL-trnF and rps4 sequences. *Molec. Phylogen. Evol.* 16: 180-198.
- Cox, C. J., Goffinet, B., Newton, A. E., Shaw, A. J., and Hedderson, T. A. J. 2000. Phylogenetic relationships among the diplolepidous-alternate mosses (Bryidae) inferred from nuclear and chloroplast DNA sequences. *Bryologist* 103: 224-241.
- Cronberg, N., Natcheva, R., and Hedlund, K. 2006. Microarthropods mediate sperm transfer in mosses. *Science* 313: 1225.
- Crum, H. 2001. *Structural Diversity of Bryophytes*. University of Michigan Herbarium, Ann Arbor, 379 pp.
- Freeland, R. O. 1957. Plastid pigments of gametophytes and sporophytes of Musci. *Plant Physiol.* 32: 64-66.
- French, J. C. and Paolillo, D. J. Jr. 1976a. Effect of the calyptra on intercalary meristematic activity in the sporophyte of *Funaria* (Musci). *Amer. J. Bot.* 63: 492-498.
- French, J. C. and Paolillo, D. J. Jr. 1976b. Effect of light and other factors on capsule expansion in *Funaria hygrometrica*. *Bryologist* 79: 457-465.
- Gayat, L. A. 1897. Recherches sur le developpement de l'archegone chez les Muscinees. *Ann. Sci. Nat. Ser. 8*, 3:161-285. In: Clayton-Greene, K. A., Green, T. G. A., and Staples, B. 1977. Studies of *Dawsonia superba*. 1. Antherozoid dispersal. *Bryologist* 80: 439-444.
- Goffinet, B., Cox, C. J., Shaw, A. J., and Hedderson, T. A. J. 2001. The Bryophyta (mosses): Systematic and evolutionary inferences from an rps4 gene (cpDNA) phylogeny. *Ann. Bot.* 87: 191-208.
- Harvey-Gibson, R. J. and Miller-Brown, D. 1927. Fertilization of Bryophyta. *Ann. Bot.* 41: 190-191.
- Krupa, J. 1969. Photosynthetic activity and productivity of the sporophyte of *Funaria hygrometrica* during ontogenesis. *Acta Soc. Bot. Poloniae* 38: 207-215.
- Lal, M., Kaur, G., and Chauhan, E. 1982. Ultrastructural studies on archegonial development in the moss *Physcomitrium cyathicarpum*. *New Phytol.* 92: 441-452.
- Milius, S. 2006. Moss express. Insects and mites tote mosses' sperm. *Science News* 170: 148.
- Muggoch, H. and Walton, J. 1942. On the dehiscence of the antheridium and the part played by surface tension in the dispersal of spermatocytes in Bryophyta. *Proc. Roy. Soc. London Sec. B Biol. Sci.* 130: 448-461.
- Paolillo, D. 1968. The effect of the calyptra on capsule symmetry in *Polytrichum juniperinum* Hedw. *Bryologist* 71: 327-334.
- Paolillo, D. J. Jr. 1979. On the lipids of the sperm masses of three mosses. *Bryologist* 82: 93-96.
- Pfeffer, W. 1884. *Untersuchungen aus dem botanischen Institut in Tübingen* 1: 363.
- Rastorfer, J. R. 1962. Photosynthesis and respiration in moss sporophytes and gametophytes. *Phyton* 19: 169-177.
- Renzaglia, K. S. and Garbary, D. J. 2001. Motile gametes of land plants: Diversity, development, and evolution. *CRC Crit. Rev. Plant Sci.* 20(2): 107-213.
- Schofield, W. B. 1985. *Introduction to Bryology*. Macmillan Publishing Co., New York, 431 pp.
- Vitt, D. H. 1984. Classification of the Bryopsida. In: Schuster, R. M. (ed.). *New Manual of Bryology*, Vol. 2. The Hattori Botanical Laboratory, Nichinan, Japan, pp. 696-759.