

# CHAPTER 2-7

## BRYOPHYTA – BRYOPSIDA

---

### TABLE OF CONTENTS

Bryopsida Definition .....	2-7-2
Chromosome Numbers.....	2-7-3
Spore Production and Protonemata .....	2-7-3
Gametophyte Buds .....	2-7-4
Gametophores .....	2-7-4
Location of Sex Organs.....	2-7-6
Sperm Dispersal .....	2-7-7
Release of Sperm from the Antheridium.....	2-7-7
Dispersal to the Archegonium.....	2-7-8
Embryo Development .....	2-7-20
Capsule Development .....	2-7-20
Summary .....	2-7-28
Acknowledgments.....	2-7-28
Literature Cited .....	2-7-28

# 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.

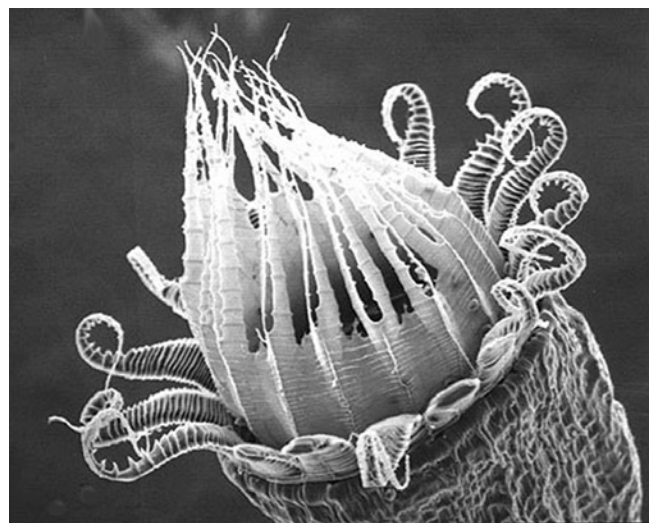


Figure 2. Electron micrograph of the arthrodontous peristome teeth of the moss *Eurhynchium praelongum*. Photo from Biology 321 Course Website, UBC, with permission.



## 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.

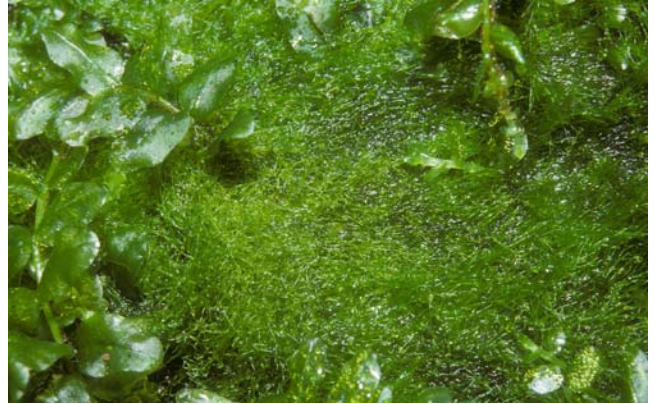


Figure 4. Protonemata among leafy plants of *Plagiomnium*. Photo by Janice Glime.

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.

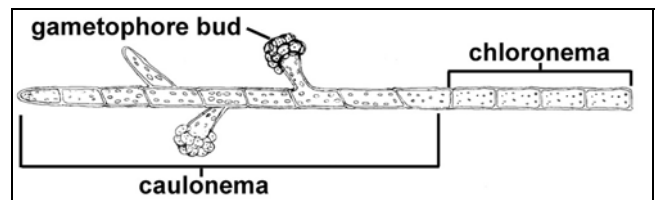


Figure 5. Protonema of moss such as *Funaria hygrometrica* with differentiated caulonema and chloronema. Drawing by Noris Salazar Allen, with permission.

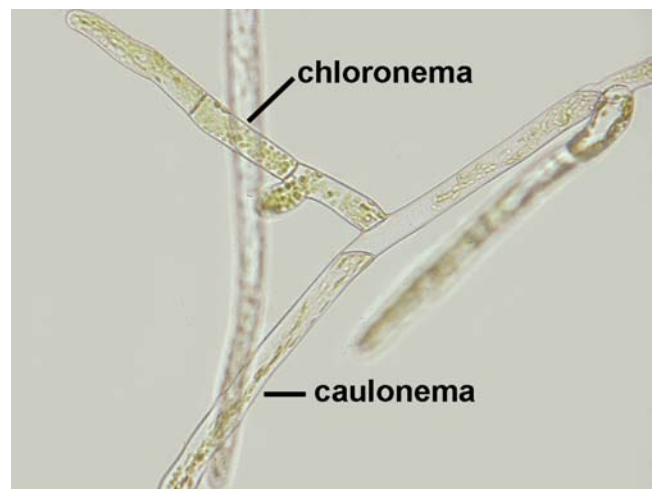


Figure 6. Protonema of *Funaria hygrometrica* showing chloronema (short cells with perpendicular walls and dense chloroplasts) and caulonema (long cells with diagonal cross walls and more dispersed chloroplasts). Photo by Janice Glime.



## 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 7. Moss protonema with young bud. Photo by Chris Lobban, with permission.

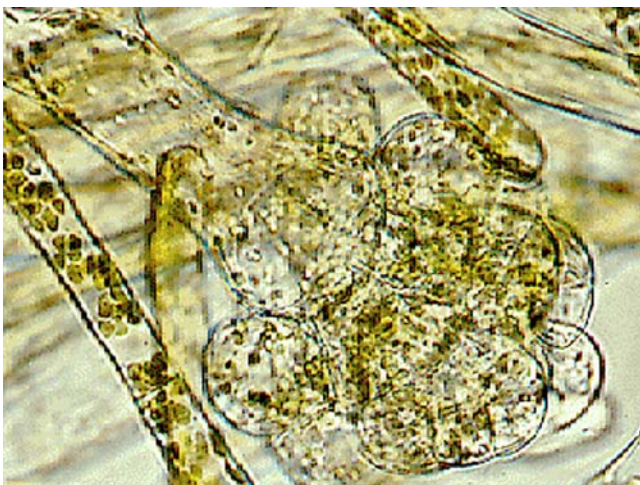


Figure 8. Protonema (caulonema) and young developing bud of the moss *Funaria hygrometrica*. Photo by Martin Bopp, with permission.

As the bud develops, **rhizoids** (Figure 9, Figure 102) 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.

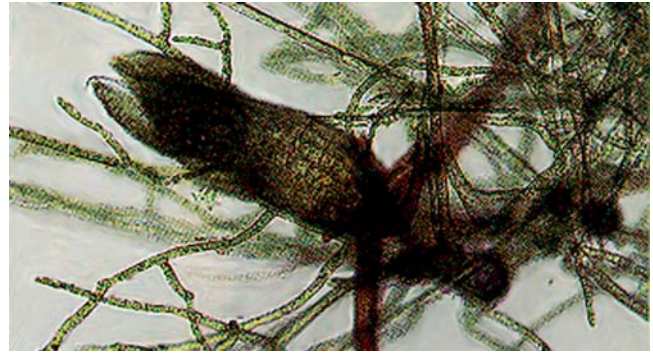


Figure 9. Moss protonema with developed bud. Brown threads are rhizoids. Photo by Janice Glime.

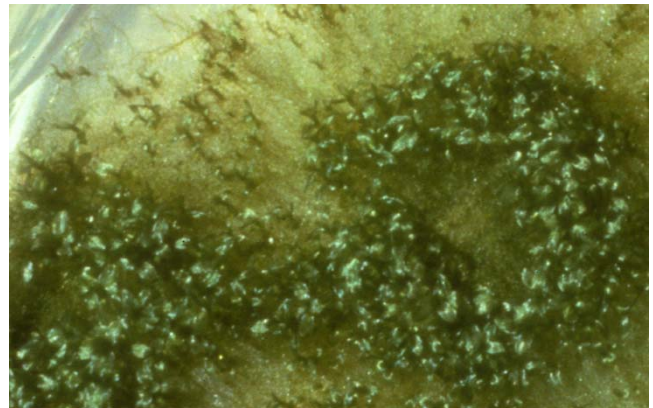


Figure 10. Leafy buds on the protonemata of *Funaria hygrometrica* forming a doughnut shape. Each of these circles of buds is the result of one spore. The hole in the middle is the area where the protonemata is in the chloronema stage and does not produce buds. Photo by Janice Glime.

## Gametophores

The bud develops into the upright (or horizontal) **gametophore**. These plants are leafy **haploid** ( $1n$ ) 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**.

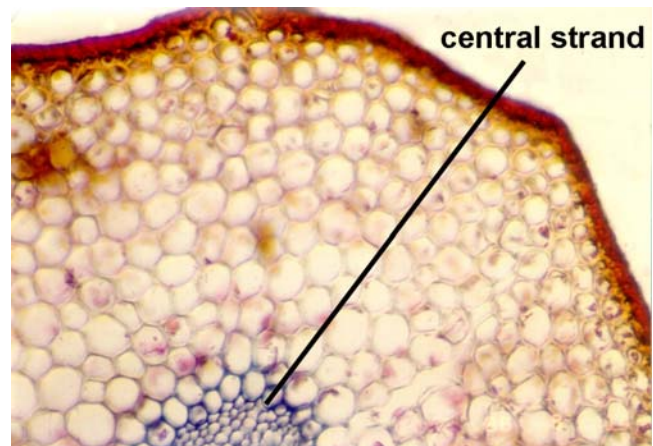


Figure 11. Stem cross section of *Rhizogonium* illustrating central strand of hydroids. Photo by Isawa Kawai, with permission.



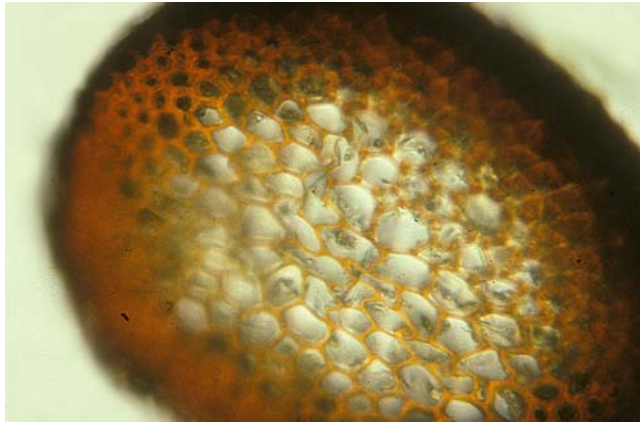


Figure 12. Cross section of stem of the brook moss *Fontinalis dalecarlica* showing absence of central strand and conducting tissues. Photo by Janice Glime.

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. *Brachymerium* 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-wagner.de](http://www.drralf-wagner.de)>, with permission.

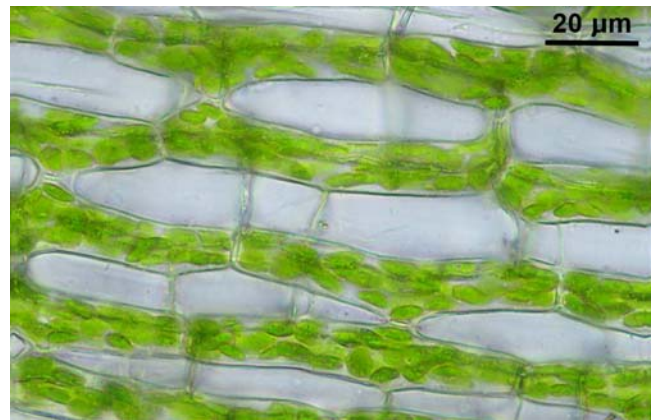


Figure 17. Hyaline and chlorophyllous cells of *Leucobryum glaucum* leaf. Photo by Ralf Wagner <[www.drralf-wagner.de](http://www.drralf-wagner.de)>, with permission.

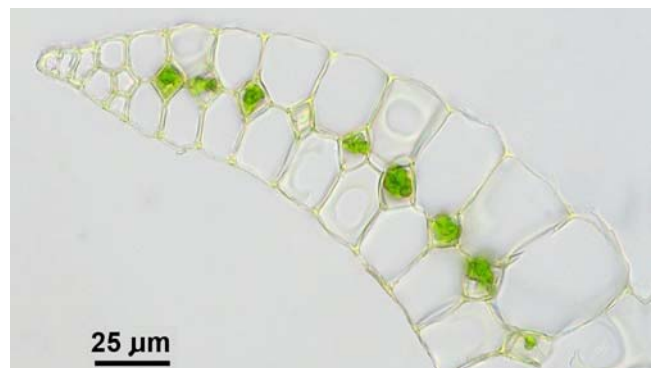


Figure 18. *Leucobryum glaucum* leaf cells. Photo by Ralf Wagner <[www.drralf-wagner.de](http://www.drralf-wagner.de)>, with permission.



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](http://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](http://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.

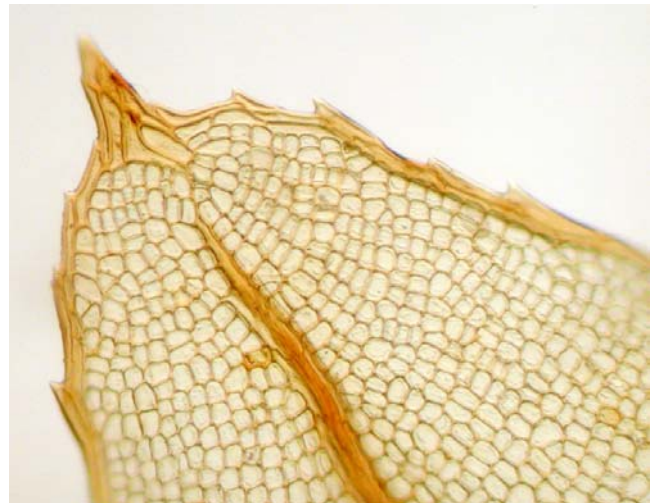


Figure 23. *Mnium marginatum* showing elongate costa cells compared to short lamina cells. Photo by John Hribljan, with permission.

## 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 28). In mosses, antheridia and archegonia may be located at the end of the main stem (Figure 29), at the ends of lateral branches, or along the main stem, either at the ends of very short branches (Figure 30) or nearly sessile (Figure 103). 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 29) (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 31), within about four minutes of placing water into an antheridial cup, dehiscence will occur (Muggech & Walton 1942). The **spermatocytes** (cells in which sperm have differentiated) emerge in a banana-shaped packet (Figure 27, Figure 33) into the water surrounding the antheridium, usually within 4-10 minutes.

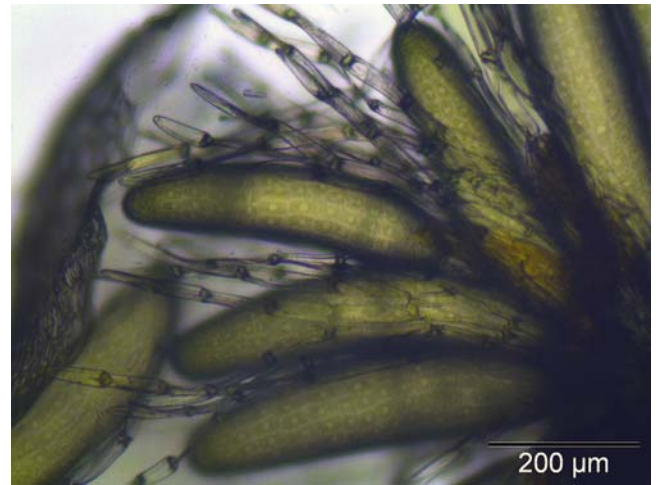


Figure 26. *Hypnum cupressiforme* paraphyses and antheridia. In this species, antheridia occur long the stem. Photo by Kristian Peters, with permission.



Figure 27. *Aloiina ambigua* sperm release, looking like white, gelatinous clouds. Photo courtesy of Llo Stark.





Figure 28. Pleurocarpous moss *Pleurozium schreberi* showing archegonia on short branch along stem. Photo by Janice Glime.

Then, when (or if) that packet 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 packet 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 29. *Ptychostomum capillare* showing antheridial head of male plants. Photo by Michael Lüth, with permission.



Figure 30. *Racomitrium didymum* showing seta, hence archegonium, arising on a short branch. Photo by Michael Lüth, with permission.



Figure 31. *Mnium hornum* male splash cups. Photo by David T. Holyoak, with permission.

Cronberg *et al.* (2008) filmed various stages in the life cycle of *Bryum argenteum*. They found that this species expels its sperm in a mass (Figure 32-Figure 37). The upper cells of the antheridium are expelled and the sperm mass is released. This is a rapid occurrence, followed by a slower activity of sperm escaping from the mass. The sperm have a density close to that of water and thus are easily transported by moving water. When the sperm mass reaches the air surface, the mass disintegrates almost instantly as the mass and surface tension of water react. The surface tension causes a passive dispersal of the sperm for ~2 cm. After 30 minutes, about half the sperm are dead. All are dead after 60 minutes. This might differ in nature where the water chemistry is different.



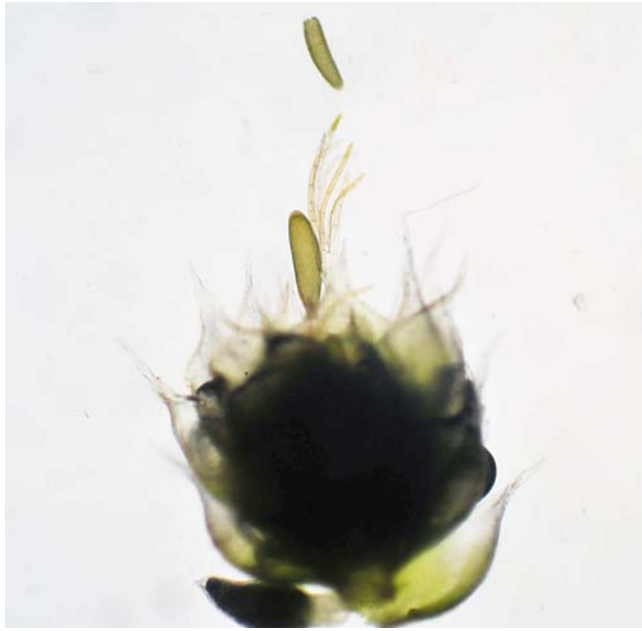


Figure 32. *Bryum argenteum* antheridia with antheridia and sperm masses being released. Photo by George Shepherd through Creative Commons.



Figure 33. *Bryum argenteum* releasing sperm masses from submerged antheridia. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

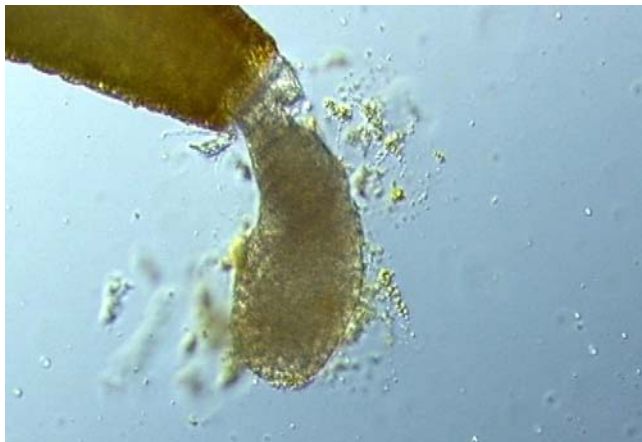


Figure 34. *Bryum argenteum* antheridium with initial explosive sperm mass release. The upper cells of the antheridium are also expelled. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.



Figure 35. *Bryum argenteum* antheridium with final sperm mass release. A few sperm have already left the sperm mass. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.



Figure 36. *Bryum argenteum* perigonium with spent antheridia. Photo by George J. Shepherd through Creative Commons.

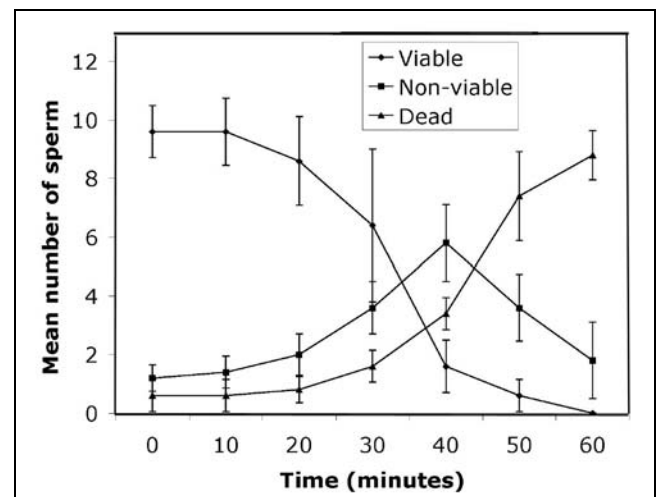


Figure 37. Time lapse of sperm release and viability in *Bryum argenteum*. Modified from Cronberg *et al.* 2008.



Llo Stark has provided us with a time sequence of the release of the sperm packets in *Aloina ambigua* (Figure 38- Figure 40).



Figure 38. *Aloina ambigua* early sperm packet release into the cup formed by the perigonial leaves. Photo courtesy of Llo Stark.



Figure 39. *Aloina ambigua* sperm packet release into the perigonium. Photo courtesy of Llo Stark.

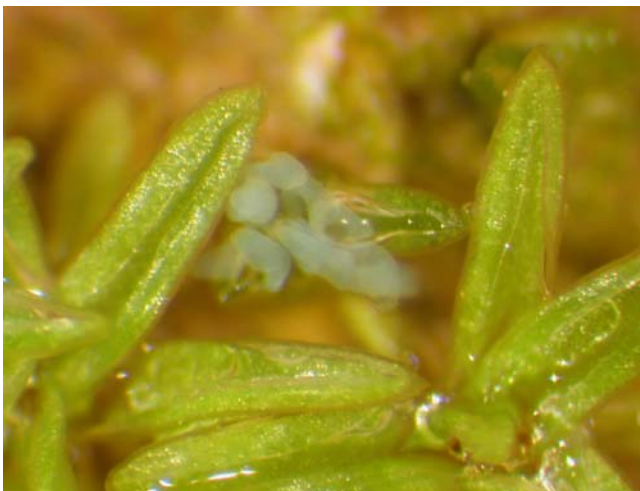


Figure 40. *Aloina ambigua* with distended sperm packets. Photo courtesy of Llo Stark.

## Dispersal to the Archegonium

Some bryophytes seem to have no special means of dispersing their sperm, relying on the water film that surrounds the bryophytes when it rains. Others have developed splash cups or splash platforms that aid in the dispersal of sperm. Andersson (2002) filmed the splashes on splash cups in the moss *Plagiomnium affine* (Figure 41). 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 spermatozooids 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 spermatozooids 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 41. *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 42) 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.





Figure 42. *Plagiomnium ciliare* with splash platforms. Photo by Robert Klips, with permission.

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 researchers 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**; Figure 43) and *Ptychostomum capillare* (syn. = *Bryum capillare*; **Bryopsida**; Figure 29).

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 43). As the invertebrates crawled about the male splash cups, they picked up mucilage and sperm. The researchers 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 mucilage to be a source of food as they "greedily" lapped it up and also licked at saline crystals on the perichaetial leaf margins.

It appears that *Ptychostomum capillare* (Figure 29) 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.



Figure 43. *Polytrichum commune* males with splash cups. Photo by Li Zhang, with permission.

Observations on *Bryum argenteum* (Figure 44-Figure 45) 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*; see Figure 46) or springtails (Collembola: *Isotoma caerulea*, Figure 47) (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 44. *Bryum argenteum* males. Photo by George Shepherd, through Creative Commons.





Figure 45. *Bryum argenteum* with sporophytes, signalling successful fertilization. Photo by George Shepherd, through Flickr Creative Commons.



Figure 46. *Scutovertex sculptus*; *Scutovertex minutulus* is a mite that facilitates sperm dispersal in some bryophytes. Photo by Matthew Shepherd, through Creative Commons.



Figure 47. *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 male and female mosses and by both arthropod 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 *Ptychostomum capillare* (Figure 29). Llo Stark has captured images of this exudation in *Aloina ambigua* (Figure 48-Figure 50).

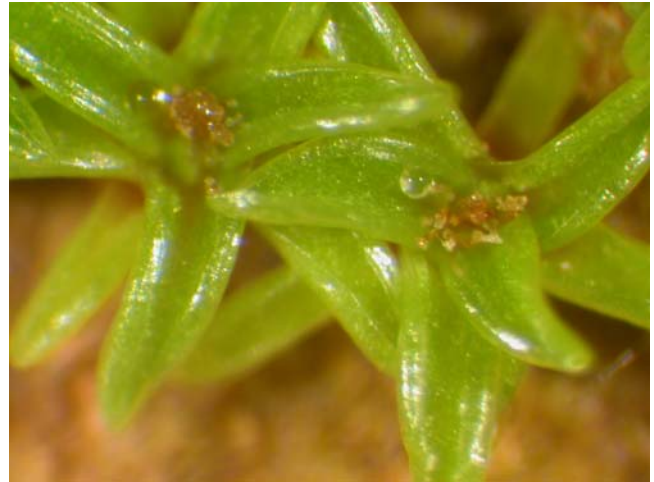


Figure 48. *Aloina ambigua* archegonium exudate. Photo courtesy of Llo Stark.



Figure 49. *Aloina ambigua* archegonia with one showing exudate. Photo courtesy of Llo Stark.

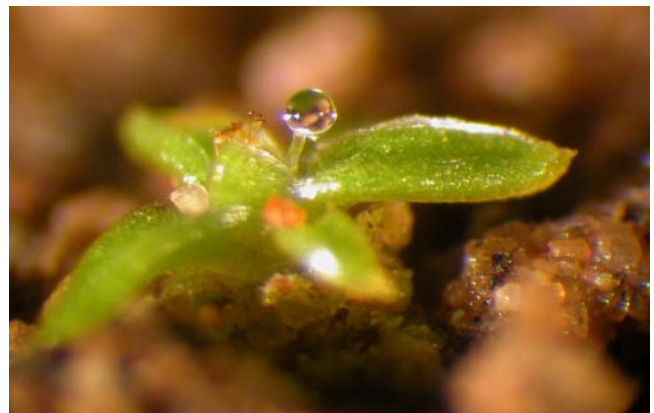


Figure 50. *Aloina ambigua* showing archegonium exudate. Photo courtesy of Llo Stark.



A small flurry of research followed this exciting finding (Cronberg 2012). Both *Bryum argenteum* (Figure 45) and *Ceratodon purpureus* (Figure 51) sperm are transported by tiny springtails (*Folsomia candida*; Figure 52) (Rosenstiel *et al.* 2012). Rosenstiel and coworkers (2012) used *Ceratodon purpureus* to examine what attracts sperm dispersers. They found that this moss 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 52). The volatile compounds are sex-specific (Figure 53) and definitely increase the rate of fertilization, even when splashing water is provided to facilitate sperm transfer (Figure 54). 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 51. *Ceratodon purpureus* showing water drops that could facilitate fertilization. Photo by Jiří Kameníček, with permission.

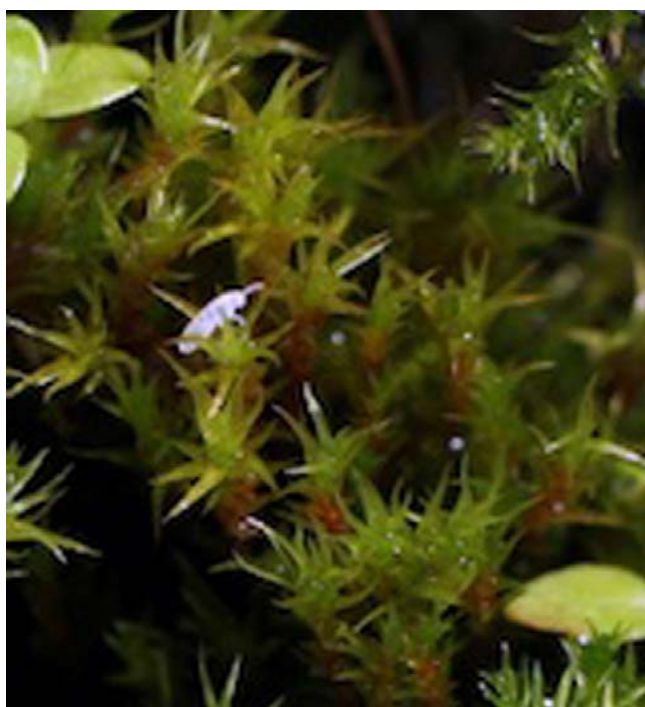


Figure 52. *Folsomia candida* (Collembola) on *Ceratodon purpureus*. Photo by Erin Shortlidge, with permission.

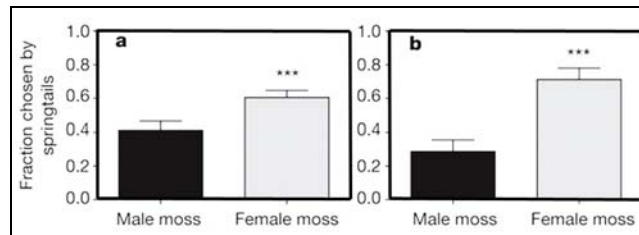


Figure 53. Sexual preference of the springtail *Folsomia candida* on *Ceratodon purpureus*. **a.** Petri dishes with 24 assays, 491 springtails. **b.** Samples in an olfactometer with 10 assays, 276 springtails. Vertical lines represent standard error of the mean. \*\*\* denotes  $p < 0.0001$ . Modified from Rosenstiel *et al.* 2012.

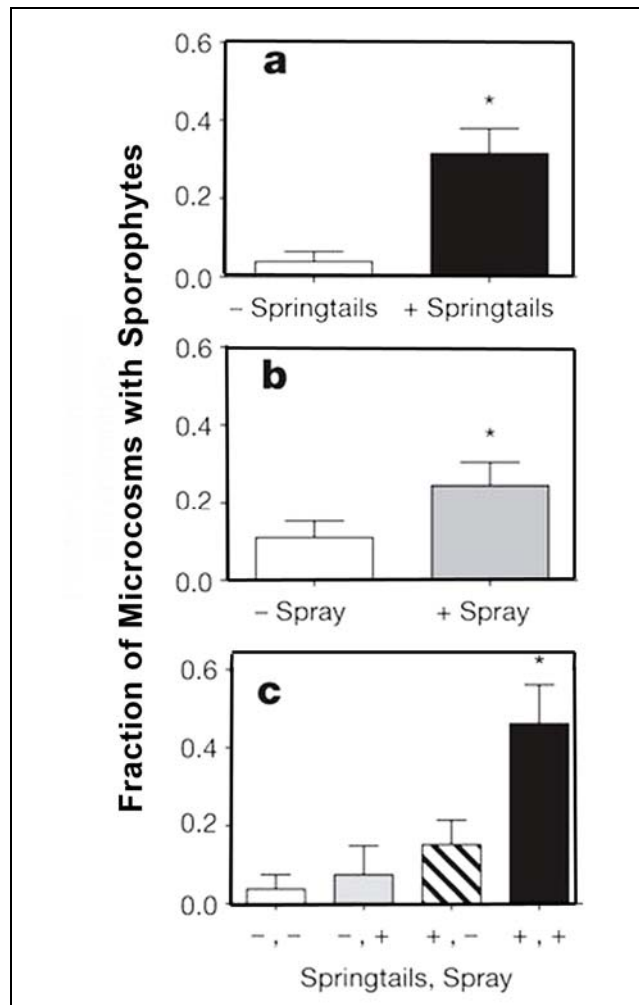


Figure 54. Effect of the springtail *Folsomia candida* vs water spray treatment on fertilization success of *Ceratodon purpureus* and *Bryum argenteum* in 108 microcosms. Vertical lines represent standard error of mean. \* denotes significantly different,  $p < 0.05$ . Modified from Rosenstiel *et al.* 2012.

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 55), sperm have a long distance record of only 11.6 cm (Rydgren *et al.* 2005).



Figure 55. *Hylocomium splendens* in autumn. Photo by Petr Brož, through Wikimedia Commons.

Insect dispersal of sperm is not unique to *Ceratodon purpureus* (Figure 52). Ignatov (1921) reported that the luminous moss, *Schistostega pennata* (Figure 56), has several kinds of visitors who facilitate sperm dispersal. This species is **cladoautoicous** (male and female reproductive structures on separate stems, connected only by the protonema; Figure 57-Figure 59). Thus, the sperm must be dispersed to a different stem. In addition to movement in a drop of water when the antheridium bursts (Figure 60), in the Moscow Province of Russia this dispersal is facilitated by a variety of small arthropods, including mites in the families **Damaeidae** (e.g. *Damaeus lengersdorfi*, Figure 61, Figure 62) **Oribatulidae** (e.g. *Oribatula tibialis*, Figure 63-Figure 64), **Astegistidae** (e.g. *Furcoribula furcillata*, Figure 65), and **Ceratozetidae** (e.g. *Melanozetes mollicomus*, Figure 66), and springtails *Orchesella bifasciata* (Figure 67) and *Entomobrya nivalis* (Figure 68) in the family **Entomobryidae**. The arthropods use the antheridial contents as food. This activity is facilitated by the barely hidden antheridia of *Schistostega pennata*, unlike those of most mosses that are well protected by perigonia.



Figure 56. *Schistostega pennata* showing individual stems. Photo by Martine Lapointe.

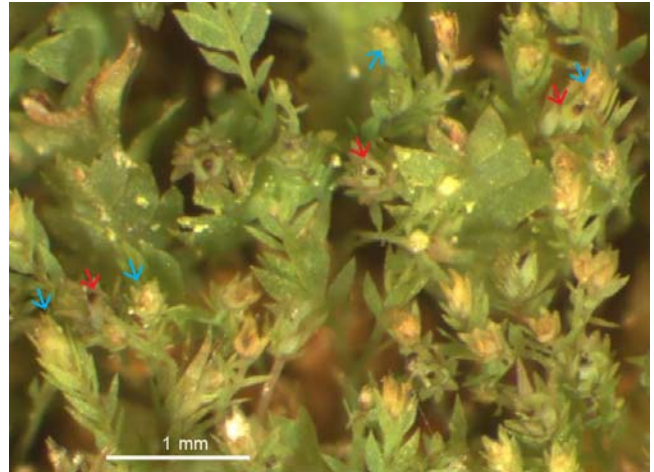


Figure 57. *Schistostega pennata* male (blue) and female (red) plants. Photo by Misha Ignatov, with permission.

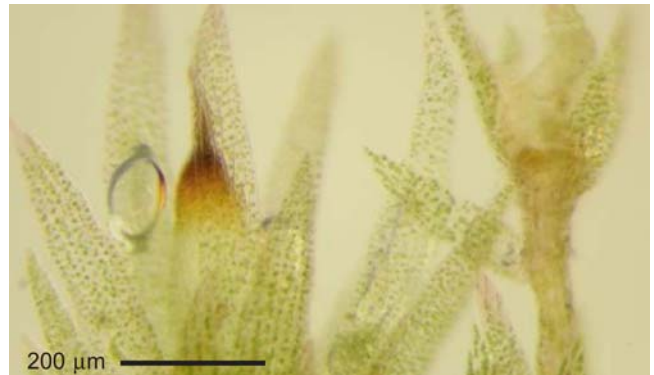


Figure 58. *Schistostega pennata* female (left) and male (right) plants. Photo by Misha Ignatov, with permission.

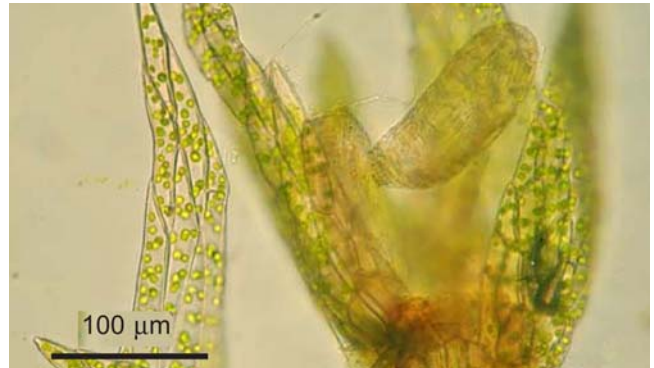


Figure 59. *Schistostega pennata* male plants showing antheridia. Photo by Misha Ignatov, with permission.

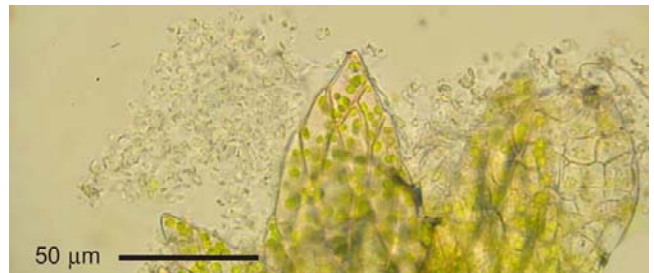


Figure 60. *Schistostega pennata* antheridia dispersing sperm. Photo by Misha Ignatov, with permission.





Figure 61. *Schistostega pennata* with young mite of *Damaeus lengersdorfi* approaching antheridia and eating contents. Photo by Misha Ignatov, with permission.



Figure 64. *Oribatula tibialis* from *Schistostega pennata*. Photo by Misha Ignatov, with permission.

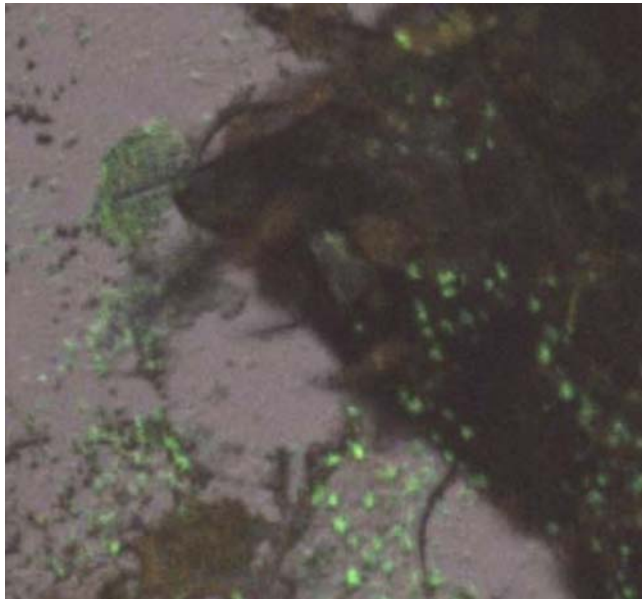


Figure 62. *Damaeus lengersdorfi* with sperm (with green DAPI stain) after visiting *Schistostega pennata*. Photo by Misha Ignatov, with permission.



Figure 63. The mite *Oribatula tibialis* feeding on *Schistostega pennata* antheridia. Photo by Misha Ignatov, with permission.

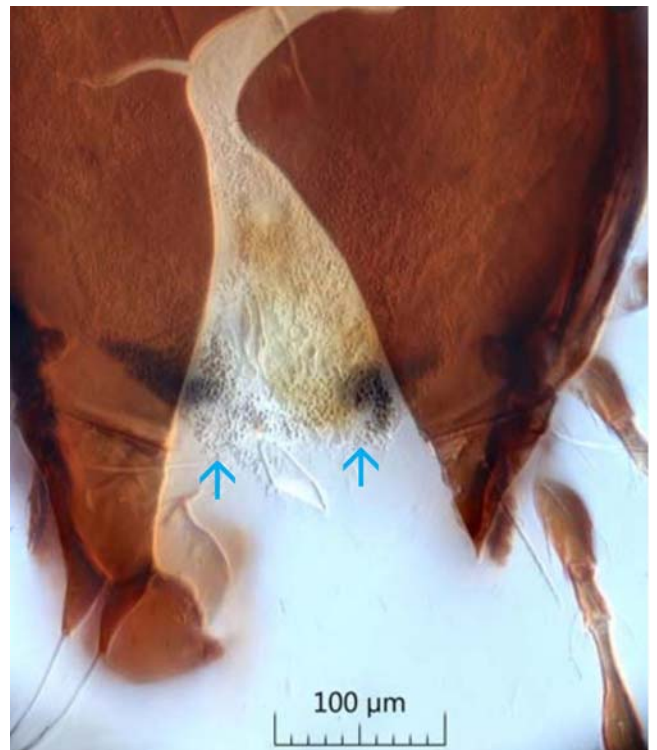


Figure 65. *Furcoribula furcillata* esophagus with sperm (dark) and ovate spores from *Schistostega pennata*. Photo by Misha Ignatov, with permission.



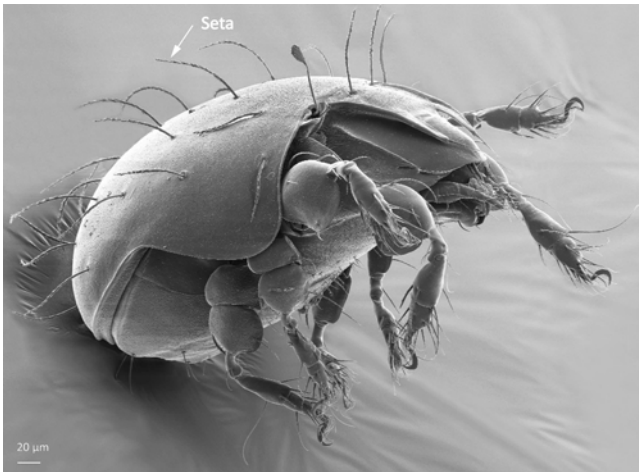


Figure 66. *Melanozetes mollicomus*, a mite known to feed on antheridia of *Schistostega pennata*. Photo by Anna Seniczak, through Creative Commons.



Figure 67. *Orchesella bifasciata*, a springtail that feeds on antheridia of *Schistostega pennata*. Photo by Arne Fjellberg, through Creative Commons.



Figure 68. *Entomobrya nivalis*, a springtail that feeds on antheridia of *Schistostega pennata*. Photo by Ben Armstrong, through Creative Commons.

Anderson (2000) managed to catch the dispersal of *Plagiommium affine* (Figure 41) 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 69, Figure 101, Figure 103) 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 69. 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 *Brachymerium* (Figure 70) and *Rosulabryum* (Figure 71) 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 70. *Brachymerium* sp. showing splash platform. Photo by Michael Lüth, with permission.





Figure 71. *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 72) 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 72. *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. For example, *Desmatodon randii* and *D. urainicus* are both self-compatible when grown from a single spore (Lazarenko & Lesniak 1972; Lazarenko 1974). *Desmatodon randii*

retained vigorous fertility for 15 generations of self crossing in the lab (Lazarenko 1974). On the other hand, it also gave rise to a spontaneous **apogamous** (development of sporophyte without gamete union) haploid line that continued the line vegetatively.

The suggestion of selfing is even supported by the scarcity of splash platforms in monoicous taxa. And in desert habitats, the monoicous condition prevails, presumably due to the scarcity of water for sperm dispersal (Stark 1983). Nevertheless, means exist to ensure at least some cross fertilization in monoicous taxa (Longton & Miles 1982; Ramsay & Berrie 1982). Such means include having antheridia placement below the archegonia on the same stem (Longton & Miles 1982) or on different stems or branches, and differences in timing of maturity of male and female gametangia. Despite the greater opportunity for selfing, Lefebvre (1969) found evidence in the **Plagiotheciaceae** that not only do monoicous species have a wider distribution, they also have greater phenotypic variability than that found in dioicous species in the family.

Longton and Miles (1982) suggest that the greater distance between male and female gametangia in **autoicous** (male & female gametangia in separate clusters) species provides a greater opportunity for out-crossing. But a close neighbor is likely to be part of the same clone or grown from a spore from the same parent. Nevertheless, this permits mutations to be remixed and passed to a new generation and thus provide at least some genetic mixing.

Lazarenko and Lesniak (1972) found that *Physcomitrella patens* from wild strains was self compatible, but certain mutant strains were self incompatible. On the other hand, they found that monosporic cultures of *Desmatodon cernuus* were sterile when grown in 24-hour light (these are long-day plants preferring 16 hours daylight), demonstrating the importance of environmental conditions, especially in new locations.

Ashton and Cove (1977) have also demonstrated possible mechanisms of compatibility by using mutants. They have shown that many **auxotrophs** (requiring an additional nutrient) of *Physcomitrella patens* are self-sterile. They obtained a diploid strain by aposporus regeneration from a hybrid sporophyte and the progeny accomplished self-fertilisation. Outcrossing would most likely supply the right genes to complement the missing one(s), but half the forthcoming spores would still be expected to carry the mutation. There would be a quick selection against the mutants in the next generation of gametophytes if the missing or mutant gene was needed by the gametophyte. The big advantage for monoicous taxa is that their nearest neighbors can always provide gametes of the opposite sex. (See fuller discussion in Chapter 3-4 of this volume.)

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, until recently it appears that the only documented case of such animal transport of sperm was in *Polytrichum commune* (Polytrichopsida; Figure 73), which has well-developed splash cups (Figure 73) 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 74) and **perichaetia** (modified leaves enclosing female reproductive structures; Figure 75) sometimes attract invertebrates.



Figure 73. *Polytrichum commune* antheridial splash cups. Photo by Michael Lüth, with permission.



Figure 74. *Fissidens bryoides* antheridia along stem where they are surrounded by **perigonia**. Photo by Dick Haaksma, with permission.



Figure 75. *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 76). 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 77), 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 76. Female *Dawsonia longifolia* (= *D. superba*). Photo by Jan-Peter Frahm, with permission.



Figure 77. *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 78) 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 78. 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 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 79; Figure 103) leading down to the **egg** in the **venter** (Figure 79), 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 (Figure 48-Figure 50), creating a chemical gradient. The sperm follows the concentration gradient toward the archegonium and finally swims down the **neck canal** (Figure 79) 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!

Gayat (1897 in Clayton-Greene *et al.* 1977) experimented with *Ptychostomum capillare* (Figure 29) 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 73-Figure 75) the paraphyses (Figure 79) 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.

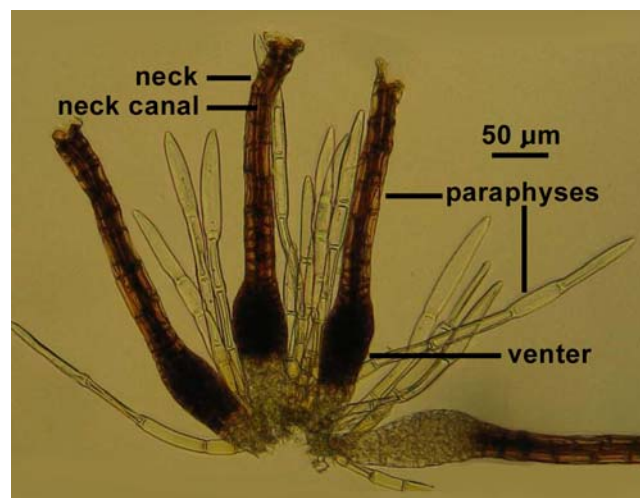


Figure 79. Archegonia of *Zygodon intermedius*. Photo by Tom Thekathyl, with permission.

## Archegonial Reception

Cronberg *et al.* (2008) described the opening of the archegonium in *Bryum argenteum* (Figure 44) as sudden. The top of the archegonium ruptures and the upper cells fold outward, creating a small funnel leading to the neck canal (e.g. Figure 80-Figure 81). At the same time, the archegonium releases a fluid.



Figure 80. Archegonia of the moss *Fontinalis dalecarlica*, showing the funnel-like tip. Photo by Janice Glime.



Figure 81. *Rhodobryum roseum* perichaetium showing archegonium with funnel tip (arrow). Photo by George J. Shepherd, through Creative Commons.

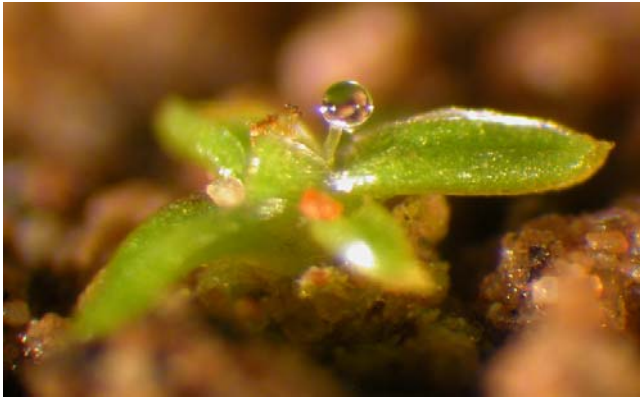


Figure 82. *Aloina ambigua* showing archegonial exudate. Photo courtesy of Llo Stark.

Sexual strategies are covered in Chapter 3-1 of this volume.

## 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 83). 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 103). 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 84). **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 – *e.g.* Splachnaceae – by insects) and grow into new gametophytes.

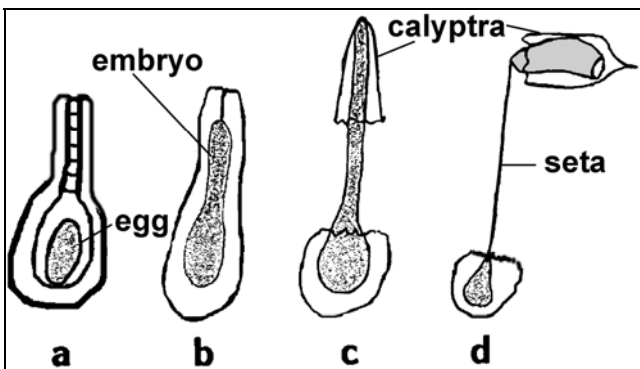


Figure 83. Development of calyptra of a moss. **a.** egg in archegonium, with neck canal cells not yet disintegrated. **b.** archegonium after fertilization and early development of embryo, showing elongation of archegonium as embryo grows. **c.** elongated seta with calyptra perched on top of it before 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 84. *Aloina rigida* with stalk and capsule and with foot imbedded in gametophyte tissue. Photo by Michael Lüth, with permission.

The **calyptra** (Figure 85) 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 85) has been shed, the **operculum** (lid) of the capsule is exposed (Figure 86). 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.

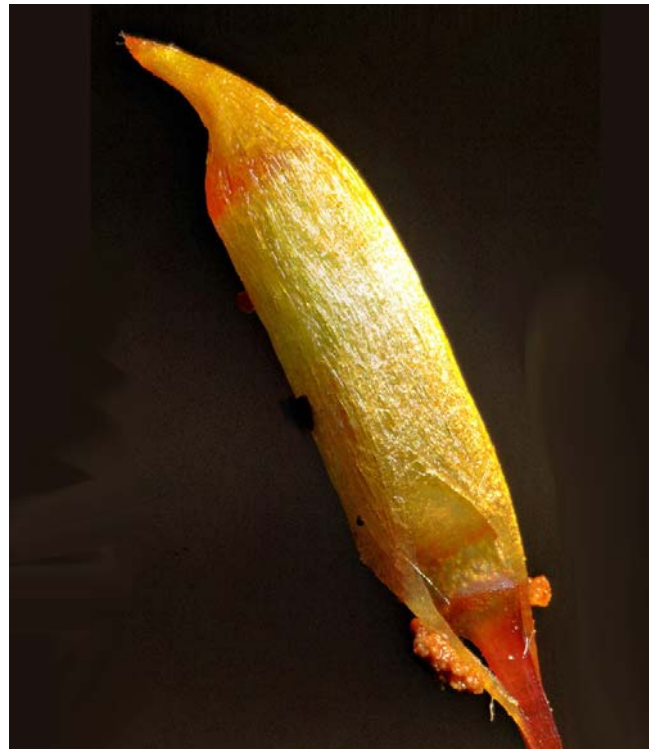


Figure 85. *Polytrichum* sp. with calyptra covering the capsule. Photo by George Shepherd, through Creative Commons.





Figure 86. *Polytrichum* sp. capsule with calyptra removed, showing operculum. Photo by George Shepherd, through Creative Commons.

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; Figure 87), thus lacking an operculum (Figure 89). Capsules in these taxa open by irregular breakage of the capsule. Llo Stark (pers. comm. 22 March 2023) describes this in *Physcomitrella patens* as highly fragile capsule walls that break up very quickly after the capsules are mature.



Figure 87. *Pleurophascum grandiglobum* with cleistocarpous capsules. Photo by Yordle Ziggs, through Creative Commons.

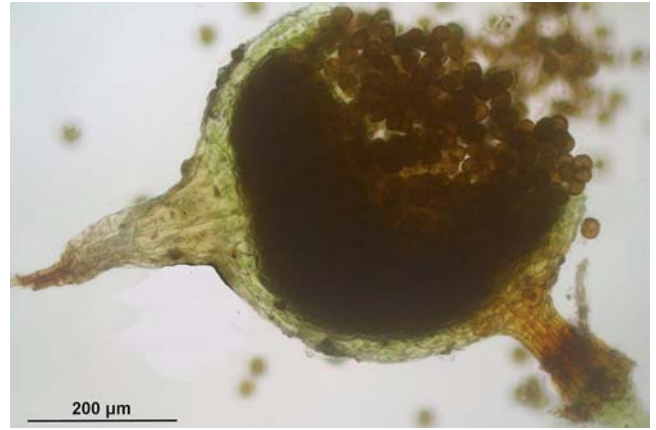


Figure 88. *Physcomitrella patens* cleistocarpous capsule opening. Photo by Hermann Schachner, through Creative Commons.

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 90-Figure 98). 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 96). The sporophyte capsule usually has a **columella** (Figure 93, Figure 97) that is columnar like those in Polytrichopsida, providing structure. Most mosses also have an **annulus** (Figure 91) just below the peristome. This annulus aids in dehiscence of the operculum.



Figure 89. *Pleurophascum grandiglobum* showing capsules with no operculum. Photo by Niels Klazenga, with permission.





Figure 90. Moss peristome. Photo by Laurie Knight, with permission.

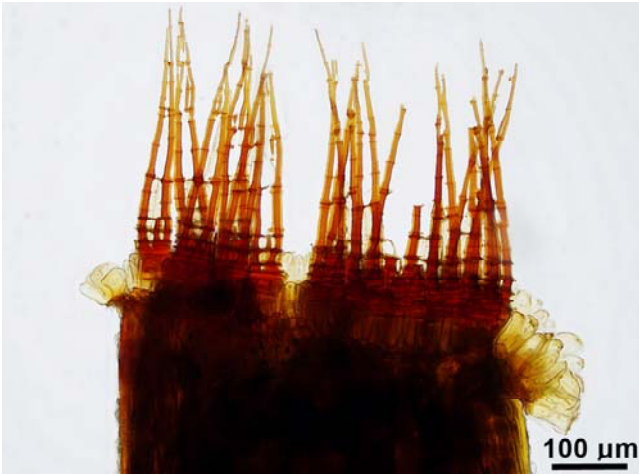


Figure 91. *Ceratodon purpureus* peristome with annulus peeling back at its base on each side. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 92. *Schistidium rivularis* sporophyte view showing operculum dehiscence. Photo by Betsy St. Pierre, with permission.



Figure 93. *Schistidium rivularis* sporophyte showing operculum dehiscence with columella still attached. This continued attachment is unusual. Photo by Betsy St. Pierre, with permission.



Figure 94. *Schistidium crassipilum* open capsules with teeth spreading. Photo by Jan-Peter Frahm, with permission.

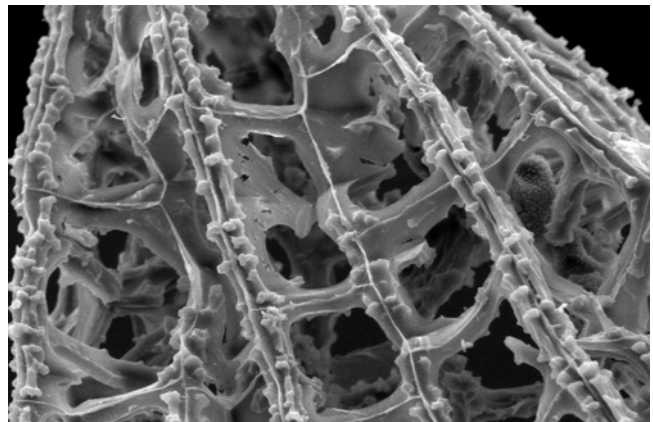


Figure 95. SEM of *Fontinalis* peristome illustrating the elaborate lattice structure. Note a few spores nestled within it. Photo by Misha Ignatov, with permission.



Figure 96. Perfect peristome showing inner (endostome) and outer (exostome) peristome with spores. Photo by George Shepherd, with permission.



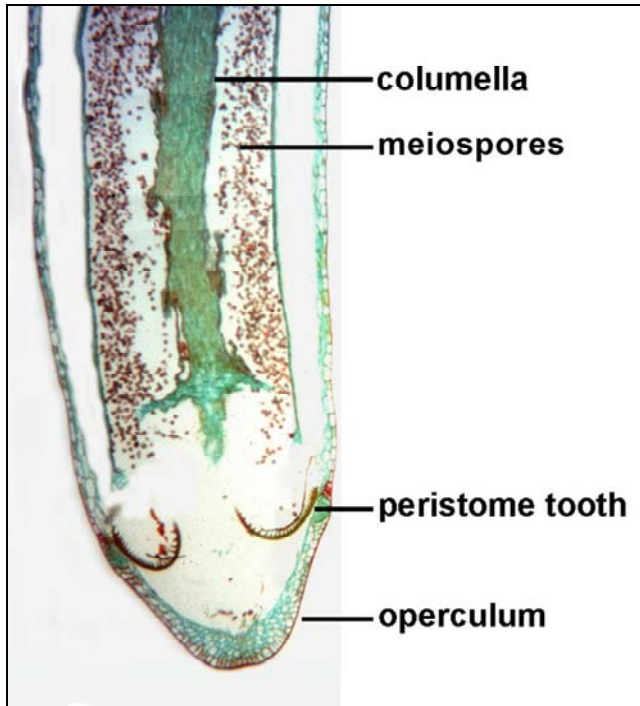


Figure 97. Section of *Mnium* capsule. This capsule actually hangs down, so teeth are on the bottom of the picture. Photo by Janice Glime.

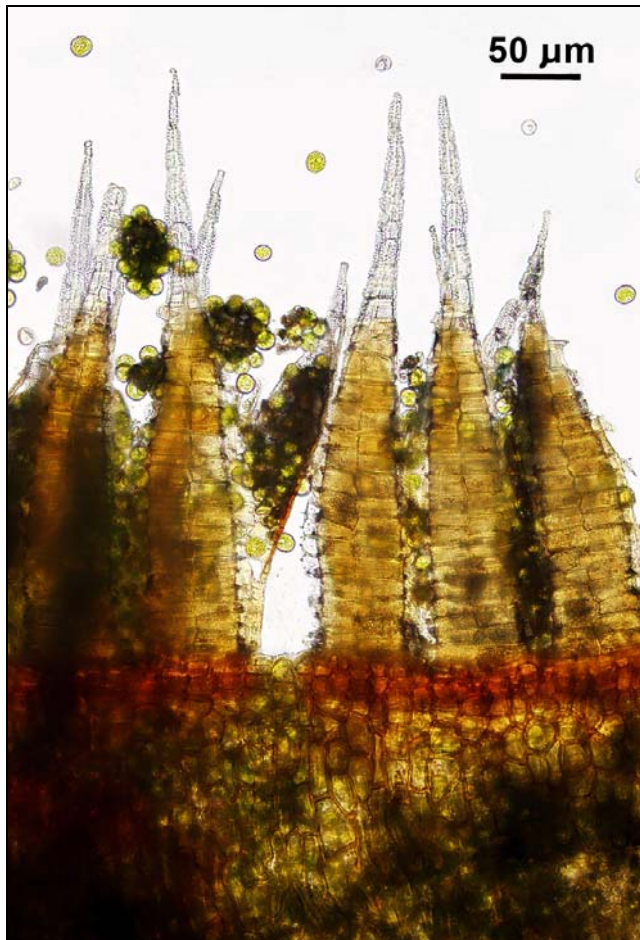


Figure 98. *Rosulabryum laevifilum* peristome and spores. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

A very recent study by Zanatta *et al.* (2018) has revealed that some mosses are **xerochastic** (and others are **hygrochastic** (**hydrochastic**; **hydrochastique**). That is, some peristome teeth flex and open as the surrounding moisture decreases (**xerochastic**) and others respond and open in response to increasing moisture (**hygrochastic**). In their study of 16 species, they found that all nine species with **perfect peristomes** [having both **endostome** (inner peristome) and **exostome** (outer peristome); Figure 96] exhibited xerochastic behavior, opening at around 90% RH upon drying, but initiating closing (exostome teeth bending inward toward endostome) around 50-65% RH as humidity increased. On the other hand, five species with specialized peristomes displayed hygrochastic behavior, opening as RH increased and closing as it decreased. Opening started at about 70% RH; closing started when humidity decreased below about 94%. But *Pseudoamblystegium subtile* possesses a specialized peristome while exhibiting xerochastic behavior. Behavior of the peristome in *Orthothecium rufescens* could not be classified as it was unclear whether teeth were clearly closing or opening. In three species, the humidity initiating position changes was dependent on age. These interesting observations need to be expanded to many more species from a wide range of habitats to determine if there is any relationship to habitat.

Unlike the valvate capsules of liverworts and some moss classes, the sporophytes of the Bryopsida are photosynthetic (Figure 99). 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 99. *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 100 and Figure 101. Structures involved in the life cycle and in general morphology are illustrated in Figure 102- Figure 105.



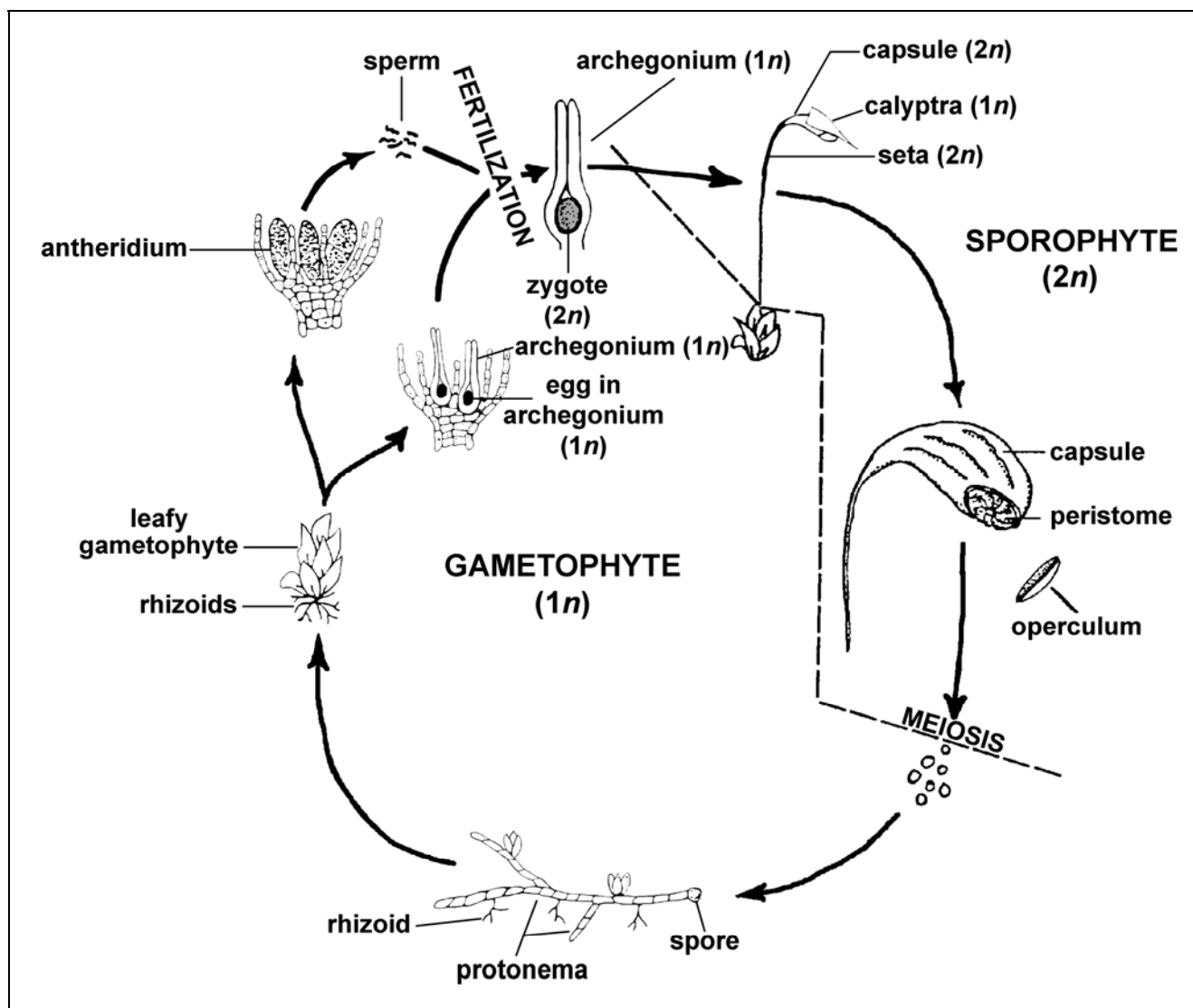


Figure 100. Life cycle of the moss *Funaria hygrometrica*. Drawn by Shelly Meston, with permission.

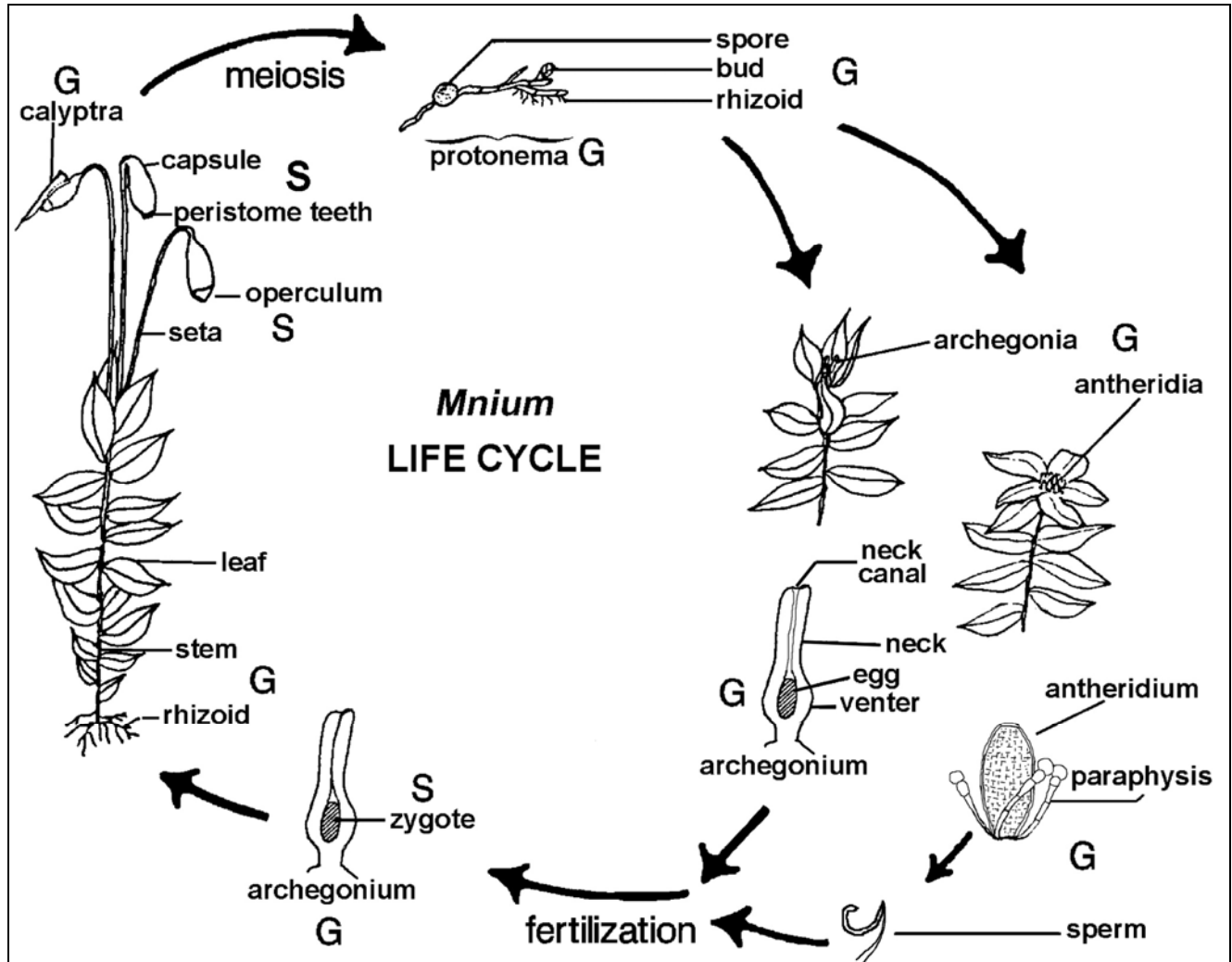


Figure 101. Life cycle of a moss such as *Mnium* (Bryopsida). **G** represents Gametophyte; **S** represents Sporophyte. Drawings by Allison Slavick, Noris Salazar Allen, and Janice Glime, with permission.



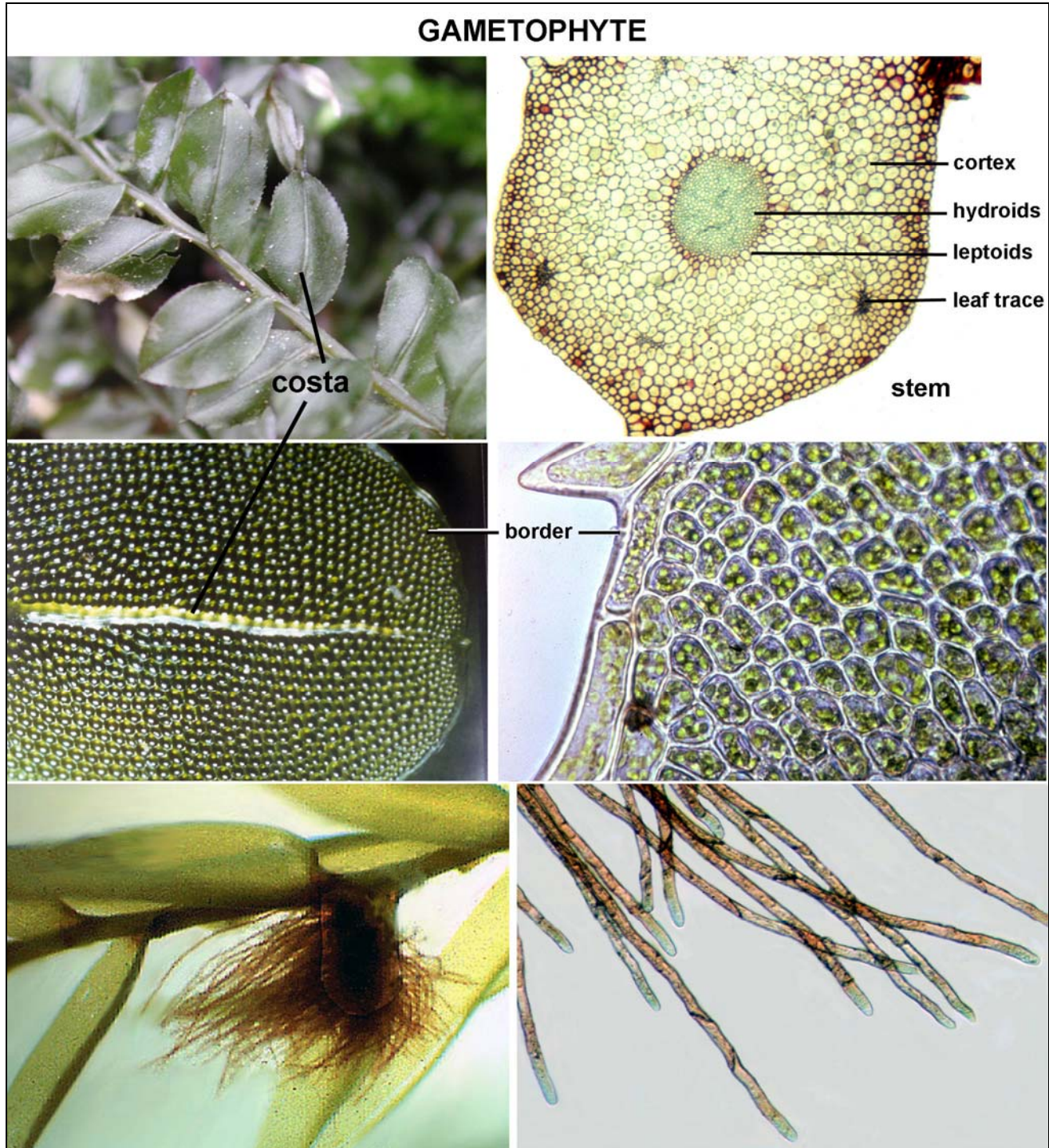


Figure 102. Vegetative characters (gametophyte) of Class Bryopsida. **Upper Left:** *Plagiomnium medium* stem and leaves. Photo by Michael Lüth, with permission. **Upper right:** *Plagiomnium* stem cross section showing central strand of hydroids. Note smaller darkened areas in stem cortex that are leaf 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.



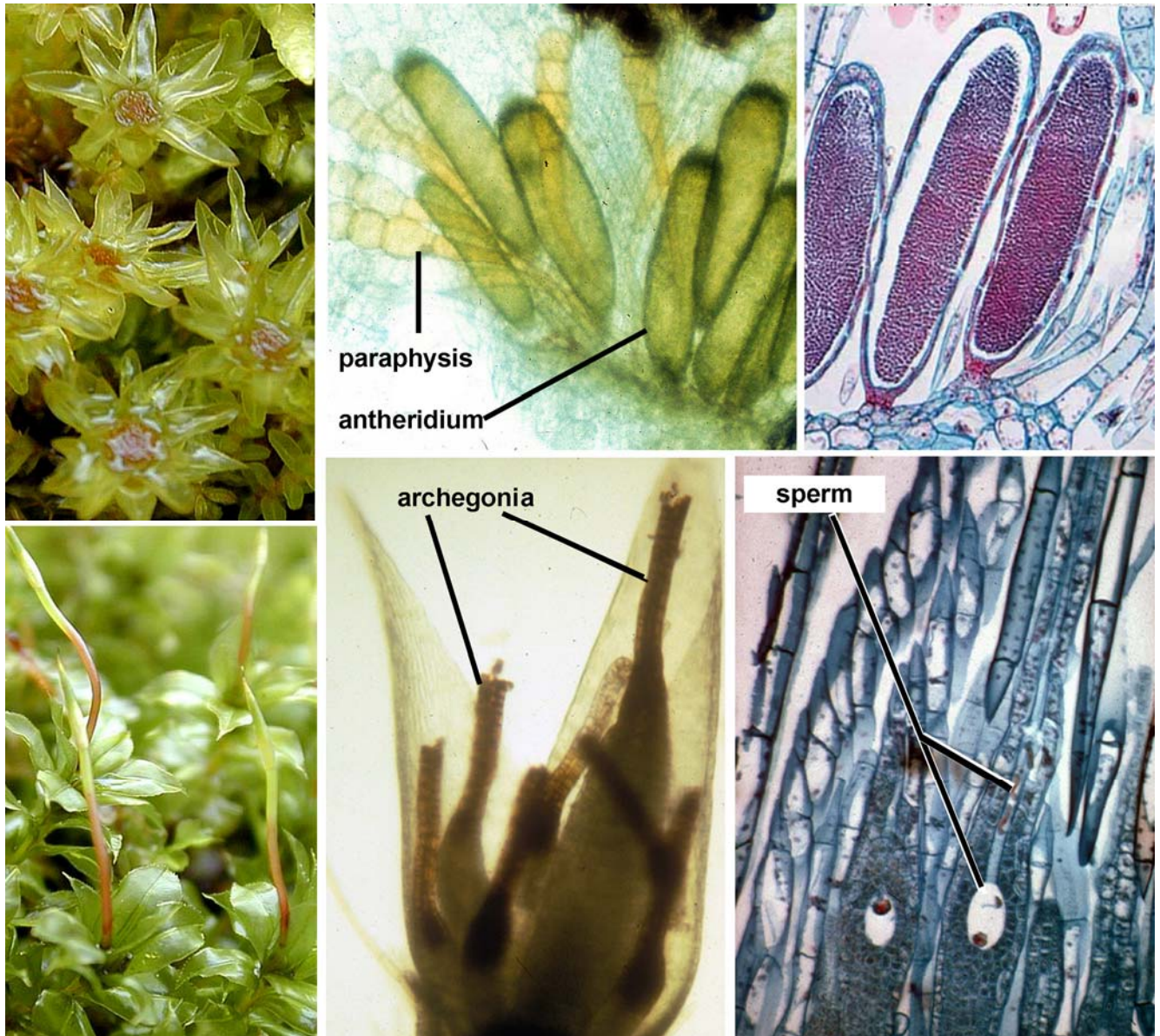


Figure 103. Sexual reproduction of mosses. **Upper row** shows male reproductive parts. Splash platforms (**left**) of *Mnium hornum* in which antheridia may be located, or they can be among ordinary leaves (**center**); among the antheridia are paraphyses (**center** and **right**) that help in retaining water and in forcing sperm out of the antheridia at maturity. **Lower row** shows female reproductive parts. Perichaetial leaves and young sporophytes of *Plagiommium 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.

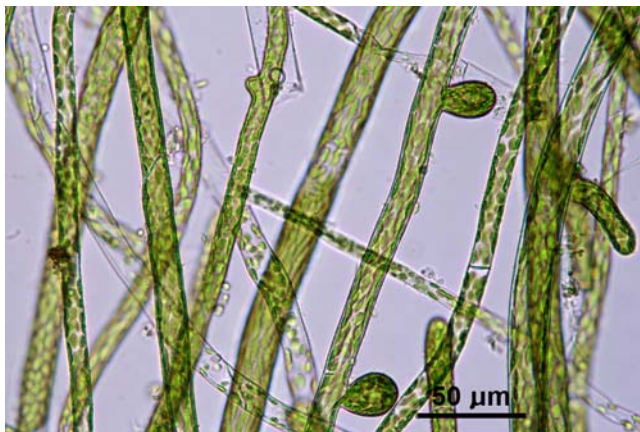


Figure 104. Moss protonemata. Photo by Jan Fott, with permission.



Figure 105. 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**. Sperm escape as a mass when the antheridium bursts. In some species, arthropods facilitate transfer of sperm from the antheridium to the archegonium. 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. A **perfect peristome** has two rows of teeth and seems to respond to drying by opening the teeth. The **specialized peristomes** tested generally respond to drying by closing the teeth.

**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. Betsy St. Pierre has been taking pictures for me and contributed several for this chapter. Llo Stark kindly offered his images of archegonial exudate and sperm packet release; he also has provided a review and valuable comments on this chapter.

## Literature Cited

- Anderson, L. E. 2000. Great discoveries in bryology and lichenology. Charles E. Allen and sex chromosomes. *Bryologist* 103: 442-448.
- Andersson, K. 2002. Dispersal of spermatozooids from splash-cups of the moss *Plagiomnium affine*. *Lindbergia* 27: 90-96.
- Ashton, N. W. and Cove, D. J. 1977. The isolation and preliminary characterization of auxotrophic and analogue resistant mutants of the moss *Physcomitrella patens*. *Molec. Gen. Genet.* 154 : 87- 95.
- 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.
- Clayton-Greene, K. A., Green, T. G. A., and Staples, B. 1977. Studies of *Dawsonia superba*. 1. Antherozoid dispersal. *Bryologist* 80: 439-444.
- 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.
- Crawford, M., Jesson, L. K., and Camock-Jones, P. J. 2009. Correlated evolution of sexual system and life-history traits in mosses. *Evolution* 63: 1129-1142.
- Cronberg, N. 2012. Animal-mediated fertilization in bryophytes - parallel or precursor to insect pollination in angiosperms? *Lindbergia* 35: 76-85.
- Cronberg, N., Natcheva, R., and Hedlund, K. 2006. Microarthropods mediate sperm transfer in mosses. *Science* 313: 1225.
- Cronberg, N., Natcheva, R., and Berggren, H. 2008. Observations regarding the life cycle of silvermoss *Bryum argenteum*. In: Mohamed, H., Baki, B. B., Nasrulhaq-Boyce, A., and Lee, P. K. Y. (eds.). *Bryology in the New Millennium*. University of Malaya, Kuala Lumpur, pp. 347-352.
- Crum, H. 2001. *Structural Diversity of Bryophytes*. University of Michigan Herbarium, Ann Arbor, 379 pp.
- Duckett, J. G. and Pressel, S. 2009. Extraordinary features of the reproductive biology of *Marchantia* at Thursley Common. *Field Bryology* 97: 1-10.
- 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'archegore 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.
- Ignatov, M. S., Ignatova, E. A., Makarova, O. L., and Potapov, M. B. 2021. *Schistostega* "pollinators" and their attraction [Kak *Schistostega* привлекает "опылителей"]. *Arctoa* 30: 451-462.

- Kimmerer, R. W. 1991. Reproductive ecology of *Tetraphis pellucida*. I. Population density and reproductive mode. *Bryologist* 94: 255-260.
- 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.
- Lazarenko, A. S. 1974. Some considerations on the nature and behavior of the relict moss, *Desmatodon randii*. *Bryologist* 77: 474-477.
- Lazarenko, A. S. and Lesniak, E. N. 1972. Comparative study of two moss sibling species: *Desmatodon cernuus* (Hub.) BSG and *Desmatodon ucrainicus* Laz. (contribution to the problem of infrastructure of the moss species). *Zh. Obshch. Biol.* 2013: 657-667.
- Lefebvre, J. 1969. Fertilité et souplesse adaptative chez les Plagiotheciaceae de Belgique. *Rev. Bryol. Lichenol.* 36: 162-166.
- Longton, R. E. and Miles, C. J. 1982. Studies on the reproductive biology of mosses. *J. Hattori Bot. Lab.* 52: 219-240.
- 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.
- Newton, M. E. 1980. Chromosome studies in some Antarctic and sub-Antarctic bryophytes. *Brit. Antarct. Surv. Bull.* 50: 77-86.
- Newton, M. E. 1989. A Practical Guide to Bryophyte Chromosomes. No. 2. British Bryological Society.
- 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.
- Przywara, L. and Kuta, E. 1995. Karyology of bryophytes. *Polish Bot. Stud.* 9: 1-83.
- Ramsay, H. P. 1982. The value of karyotype analysis in the study of mosses. *J. Hattori Bot. Lab.* 53: 51-71.
- Ramsay, H. P. and Berrie, G. K. 1982. Sex determination in bryophytes. *J. Hattori Bot. Lab.* 52: 255-274.
- 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.
- Reynolds, D. N. 1980. Gamete dispersal in *Mnium ciliare*. *Bryologist* 83: 73-76.
- Richardson, D. H. S. 1981. *The Biology of Mosses*. John Wiley & Sons Inc., N. Y., 220 pp.
- Rosenstiel, T. N., Shortlidge, E. E., Melnychenko, A. N., Pankow, J. F., and Eppley, S. M. 2012. Sex-specific volatile compounds influence microarthropod-mediated fertilization of moss. *Nature* 489: 431-433.
- Rydgren, K., Cronberg, N., and Økland, R. H. 2005. Factors influencing reproductive success in the clonal moss, *Hylocomium splendens*. *Oecologia* 147: 445-454.
- Schofield, W. B. 1985. *Introduction to Bryology*. Macmillan Publishing Co., New York, 431 pp.
- Verma, S. K. and Kumar, S. S. 1983. Cytological observations on some West Himalayan mosses - VIII. *Bryologist* 86: 121-129.
- 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.
- Zanatta, F., Vanderpoorten, A., Hedenäs, L., Johansson, V., Patiño, J., Lönnell, N., and Hylander, K. 2018. Under which humidity conditions are moss spores released? A comparison between species with perfect and specialized peristomes. *Ecol. Evol.* 8: 11484-11491.
- Ziegler, H., Kaiser, K., and Lipp, J. 1988. Sucrose in the archegonium exudate of the moss *Bryum capillare* Hedw. *Naturwissenschaften* 75: 203.



