# CHAPTER 2-7
## BRYOPHYTA – BRYOPSIDA

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CHAPTER 2-7
BRYOPHYTA – BRYOPSIDA

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

**Bryopsida Definition**

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

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 rhizoids.

As the bud develops, rhizoids (Figure 9, Figure 71) form, functioning largely in anchorage, but at least in some mosses, also functioning in moving water and nutrients from substrate to moss. This may be especially important as the atmosphere dries and the rhizoids help to maintain a humid substrate.
Figure 12. Cross section of stem of the brook moss *Fontinalis dalecarlica* showing absence of central strand and conducting tissues. Photo by Janice Glime.

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

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

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

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

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

Figure 17. Hyaline and chlorophyllous cells of *Leucobryum glaucum* leaf. Photo by Ralf Wagner <www.drralf-wagner.de>, with permission.
Some leaves may have borders (Figure 19-Figure 20) which likewise can be one or more layers thick. These leaves often have a multi-layered costa (Figure 19, Figure 21) in the center, or double (Figure 22), or even triple costa. The costa itself (Figure 23) consists of long, narrow cells that offer support and seem to function in moving water more quickly than their wider and often shorter neighboring cells.

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

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

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

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.
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.

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

Sperm Dispersal

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

Release of Sperm from the Antheridium

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

**Dispersal to the Archegonium**

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

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

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

Until somewhat recently we have assumed that in most bryophytes sperm reached the archegonia by splashing or swimming from the antheridia to a landing spot, then swimming the remainder of the way. Closer observation by recent observers indicates that such an inefficient and unsafe method may not be the case for some bryophytes,
and that we should examine others more closely for secrets in their sperm dispersal. Muggoch and Walton (1942) considered the presence of fat in the sperm mass to be a widespread phenomenon, perhaps true of all mosses, and that it was important in permitting insects to carry sperm to female plants. However, there seem to be few observations of such insect dispersal except in Polytrichum (Class Polytrichopsida) and Rosulabryum (=Bryum) capillare (Bryopsida; Figure 28).

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

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

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

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

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

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

Figure 35. Bryum argenteum with sporophytes, signalling successful fertilization. Photo by George Shepherd, through Flickr Creative Commons.
But how do these springtails find the mosses? Flowers provide odors and colors to attract their pollinators. It appears that these mosses also have a way to attract their dispersal agents. When springtails and mites were given choices of plants with mature gametangia vs those that were sterile, fertile plants were chosen over non-fertile ones about five times as often (Beckman 2006) in the cases of both males and females and by both organisms. Cronberg et al. (2006) suggest that fertile plants may attract the invertebrates with sucrose (Pfeffer 1884), starch, fatty acids, and/or mucilage (Harvey-Gibson & Miller-Brown 1927; Paolillo 1979; Renzaglia & Garbary 2001). Ziegler et al. (1988) demonstrated the presence of sucrose in the archegonium exudate of *Bryum capillare* (Figure 28).

A small flurry of research followed this EXCITING finding (Cronberg 2012). Both *Bryum argenteum* (Figure 35) and *Ceratodon purpureus* (Figure 37) sperm are transported by tiny springtails (*Folsomia candida*) (Rosenstiel et al. 2012). Rosenstiel and coworkers (2012) used *Ceratodon purpureus* to examine what attracts sperm dispersers. They found that this species produces volatile compounds – some of those secondary compounds that have evolved tremendous varieties in bryophytes. They were able to demonstrate that some, perhaps many, of these compounds attracted the springtail *Folsomia candida* (Figure 38). The volatile compounds are sex-specific (Figure 40) and definitely increase the rate of fertilization, even when splashing water is provided to facilitate sperm transfer (Figure 39). Although fertilization rates were about the same in treatments of water spray alone and springtails alone, the presence of both more than doubled the rate of using either alone.
Figure 40. Sexual preference of the springtail *Folsomia candida* on *Ceratodon purpureus*. **a.** Petri dishes with 24 assays, 491 springtails. **b.** Samples in an olfactometer with 10 assays, 276 springtails. Vertical lines represent standard error of the mean. *** denotes $p<0.0001$. Modified from Rosenstiel *et al.* 2012.

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

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

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

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

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

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

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

Figure 44. *Rosulabryum laevifilum* with splash platform. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.
However, other things can create splash. Jonathan Shaw (pers. comm.) has considered that *Funaria hygrometrica* (Figure 45) has wide-spreading bracts surrounding the antheridia and the flexible nature of these bracts permits them to bend back and create an effective cup from which sperm in that species might be splashed. Angela Newton (pers. comm.) has suggested that platform surfaces among the more dendroid and shelf-forming taxa could be viewed as water-trapping mechanisms that would promote surface flow and dripping to the next level down as a mode of transporting sperm between individual plants or parts of plants. One complication in this arrangement is that the complex texture would act to trap water drops rather than encouraging them to splash out and away. However, in some of the plants with large smooth leaves, these leaves might act as springboards, but Newton considered that in such a case the water drops would be unlikely to carry sperm, although they might carry the smaller kinds of vegetative propagules. Nevertheless, sperm that had gotten as far as a leaf might benefit from this splash as well.

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

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

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

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

Clayton-Greene et al. (1977) used laboratory tests to determine the distance sperm could travel from the large moss *Dawsonia longifolia* (= *D. superba*) (Figure 49). Field investigations indicated that this species uses a splash cup mechanism. Field data of sporophyte production
indicated that capsules seldom develop on females located more than 1.5-2 m from any male. They found similar results in the lab when they dropped water from a height of up to 3.3 m. In experimental heights ranging from 150 to 330 cm, travel distances ranged from 105 to 230 cm, indicating that height of water drop positively affects dispersal distance. But in the smaller *Polytrichum ohioense* (Figure 50), sperm in experiments only landed up to 61 cm from the source when water was dropped from ~1 m (Clayton-Greene *et al.* 1977). Clayton-Greene *et al.* suggested that smaller drops could act like an aerosol spray and float in air, achieving greater distances.

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

![Figure 50](image.png) Figure 50. *Polytrichum ohioense* males with new growth from old splash cups. Photo by Janice Glime.

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

![Figure 51](image.png) Figure 51. Antheridia and paraphyses of *Rhizomnium* sp. Photo by Janice Glime.

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

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

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

![Figure 52](image.png) Figure 52. Archegonia of the moss *Fontinalis dalecarlica*. Photo by Janice Glime.
Gayat (1897 in Clayton-Greene et al. 1977) experimented with *Bryum (Rosulabryum) capillare* (Figure 28) and found that when the plants were covered with a fine net, female plants located 2 m from males had no fertilization, but when the net was removed, giving insects access to the females, these same plants did have fertilization. Harvey-Gibson and Miller-Brown (1927) found that in *Polytrichum commune* (Figure 46-Figure 48) the paraphyses (Figure 53) of both males and females exuded mucilage, but contained no sugar. These gametangial areas were "constantly" visited by oribatid mites, two species of Collembola (springtails), a small midge (Diptera), a leaf hopper (Cicadidae), an aphid, and a spider. They found that the insects "greedily" lap the mucilage and their body parts become smeared with the mucilage excretion. This adhering mucilage contains actively motile sperm. These sperm-carrying invertebrates were also located on female plants.

**Embryo Development**

When a sperm reaches and fertilizes an egg, the resulting diploid (having two sets of chromosomes; 2n) zygote begins dividing by mitosis to form an embryo that starts to stretch the archegonium (Figure 54). But the archegonium cannot stretch indefinitely, and as the embryo gets larger, the archegonium finally tears. Here, mosses and liverworts differ. In most mosses, part of the archegonium remains perched on top of the developing embryo (young sporophyte). This separated piece of archegonium is the cap you often see on top of the capsule and is now called a calyptra (Figure 72). So the calyptra is a 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 55). 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.

**Capsule Development**

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

The exposed operculum must come off before the spores can be dispersed. The dehiscence of the operculum is usually facilitated by drying of the capsule that causes it to shrink and compress the contents. This creates a distortion that forces the operculum to pop off, at least in some species. But a few are cleistocarpous (indehiscent; lacking a regular means of opening), thus lacking an operculum (Figure 58). Capsules in these taxa open by decay.
Just under the lid of most moss capsules you will find the **peristome teeth** (in mosses, fringe of teeth around opening of capsule, involved in spore dispersal; Figure 59- Figure 67). These are usually **hygroscopic** (responding to humidity changes) and may flex back and forth in response to moisture changes to aid in gradual dispersal. In most cases, these function best as the capsule is drying, but in some taxa moisture actually facilitates dispersal. Perhaps their best role is in preventing the spores from all exiting the capsule at the same time, as happens in the liverworts and *Sphagnum* and most likely also in the mosses with valvate capsules. They often form spaces between the teeth, creating a salt shaker appearance (Figure 67). The sporophyte capsule usually has a **columella** (Figure 62, Figure 65) that is columnar like those in Polytrichopsida, providing structure. Most mosses also have an **annulus** (Figure 60) just below the peristome. This annulus aids in dehiscence of the operculum.

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

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

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

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

Figure 60. *Ceratodon purpureus* peristome with annulus peeling back at its base on each side. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.
Figure 61. *Schistidium rivularis* sporophyte zoom view showing operculum dehiscence. Photo by Betsy St. Pierre, with permission.

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

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

Figure 64. SEM of *Fontinalis* peristome illustrating the elaborate lattice structure. Note a few spores nestled within it. Photo by Misha Ignatov, with permission.

Figure 65. Section of *Mnium* capsule. This capsule actually hangs down, so teeth are on the bottom of the picture. Photo by Janice Glime.

Figure 66. *Rosulabryum laevifilum* peristome and spores. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.
A very recent study by Zanatta *et al.* (2018) has revealed that some mosses are *xerochastic* and others are *hygrochastic*. 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 67] 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 68). The same pigments often occur in both generations: chlorophylls *a* and *b*, carotene, lutein, violaxanthin, and zeaxanthin (Freeland 1957). Even the ratio of chlorophyll *a* to *b* is approximately the same – about 2.5:1 (Rastorfer 1962). Nevertheless, the gametophyte contains a higher chlorophyll concentration than does the sporophyte and the ratio of photosynthesis to respiration is likewise higher in the gametophyte. Despite its photosynthetic abilities, the sporophyte still depends on the gametophyte for some of its carbohydrates (Krupa 1969).
Figure 69. Life cycle of the moss *Funaria hygrometrica*. Drawn by Shelly Meston, with permission.
Figure 70. Life cycle of a moss such as *Mnium* (Bryopsida). **G** represents Gametophyte; **S** represents Sporophyte. Drawings by Allison Slavick, Noris Salazar Allen, and Janice Glime, with permission.
Figure 71. Vegetative characters (gametophyte) of Class Bryopsida. **Upper Left:** *Plagiomnium medium* stem and leaves. Photo by Michael Lüth, with permission. **Upper right:** *Plagiomnium* stem cross section showing central strand of hydroids. Note smaller darkened areas in stem cortex that are leaf traces. Photo by Janice Glime. **Middle Left:** Leaf of *Rhizomnium* illustrating a border, small, roundish cells, and a distinct costa. Tip of leaf lacking a costa, illustrating elongate cells and undifferentiated apical leaf cells. Photo by Zen Iwatsuki, with permission. **Middle Right:** Portion of *Plagiomnium* leaf showing border. Photo by Janice Glime. **Lower Left:** *Fontinalis* stem, leaves, and tuft of rhizoids. Photo by Janice Glime. **Lower Right:** Microscopic view of rhizoids showing single cell thickness and diagonal cross walls. Photo by Janice Glime.
Figure 72. Sexual reproduction of mosses. Upper row shows male reproductive parts. Splash platforms (left) of *Mnium hornum* in which antheridia may be located, or they can be among ordinary leaves (center); among the antheridia are paraphyses (center and right) that help in retaining water and in forcing sperm out of the antheridia at maturity. Lower row shows female reproductive parts. Perichaetial leaves and young sporophytes of *Plagiomnium cuspidatum* (left), archegonia from leaf bases of *Pleurozium schreberi* (center), and a section of archegonia (right) with sperm in the neck canal. Plant photos by Michael Lüth, with permission; photomicrographs by Janice Glime.

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

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

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

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