CHAPTER 2-2
LIFE CYCLES: SURVIVING CHANGE

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

The General Bryobiotina Life Cycle

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

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

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

Dominant Generation

One of the ways that plants manage to survive as "immobile" organisms, yet are able to survive the severe changes of seasons, is by having different life cycle stages that are adapted to different conditions. As we progress through the protist and plant kingdoms, we see that most green algae (Chlorophyta), especially in freshwater, spend most of their time in the water and most of them have only one set of chromosomes (**1*n***). Although there is much disagreement about evolutionary pathways among photosynthetic organisms, all evolutionary biologists seem to agree that this **life strategy** came first, with both invasion of land and dominant **2*n*** organisms coming later. (The **dominant generation** refers to the most conspicuous and generally the most long-lived generation.) This 1*n* stage is termed the **gametophyte generation** (1*n* or **haploid** generation that reproduces by gametes in plants) because the generation ends when it produces **gametes** (sexual reproductive structures that have one set of chromosomes and must unite with another of the same species but opposite strain to continue the life cycle) that join to form the 2*n* **zygote** (2*n* cell resulting from fusion of male and female gametes, *i.e.* from fertilization; Figure 2). Hence, the zygote is the first structure of the 2*n* stage or **sporophyte generation** [**diploid** (2*n*) generation that reproduces by **meiospores** in plants; Figure 2]. The **meiospores** in many bryophytes are able to survive many years in a dry state, thus permitting at least some taxa to live in habitats that only occasionally get moisture.

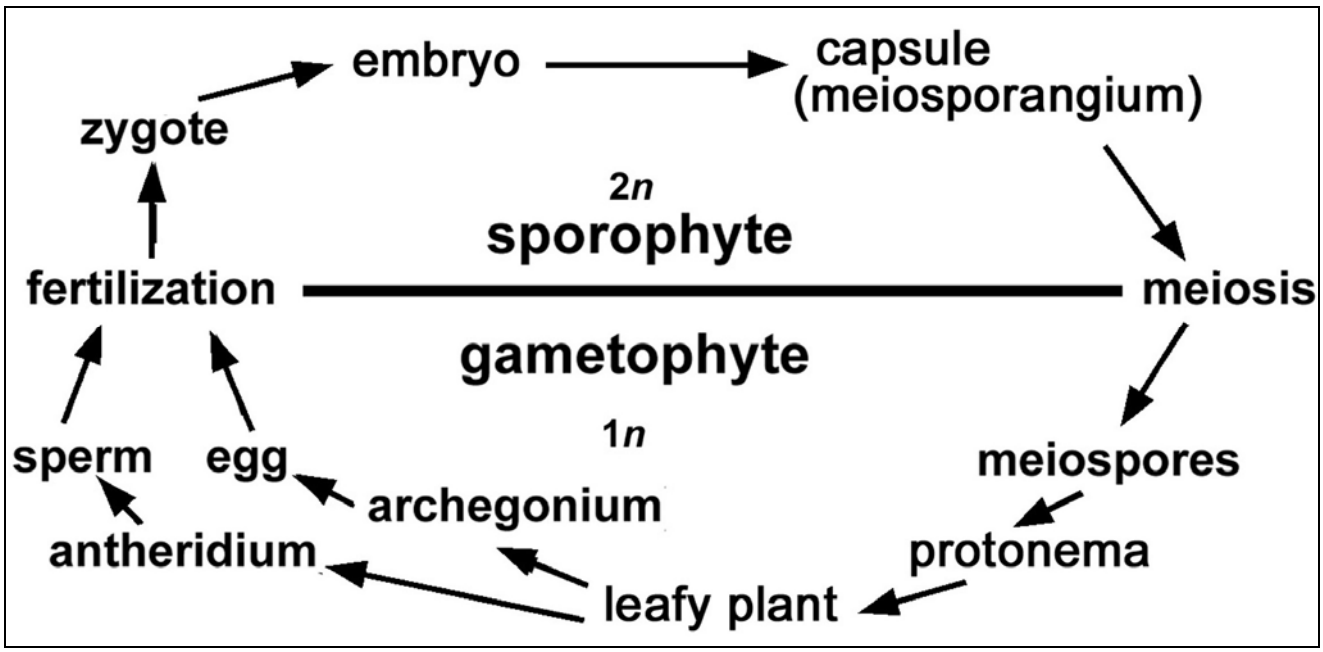

Figure 2. Basic sexual life cycle of a bryophyte. Gemmae or other propagules, not shown here, can occur on the leafy plant or on the protonema (pl. **protonemata:** alga-like, usually filamentous, stage that develops from spores of bryophytes), giving rise to the same generation as its origin. Diagram by Janice Glime.

The Life Cycle

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

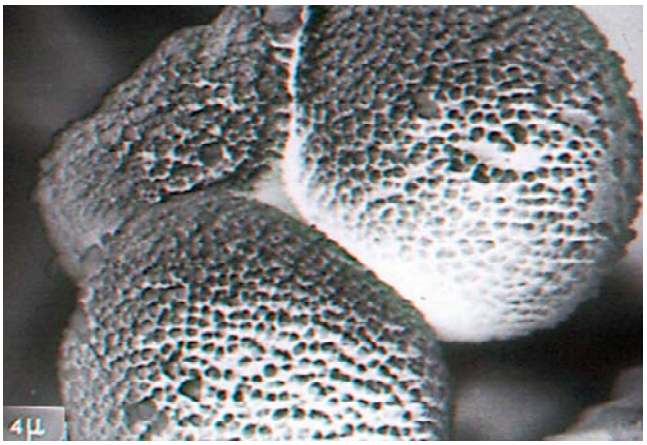

Figure 3. SEM of tetrad of meiospores of aquatic moss ***Fontinalis squamosa***, with fourth spore hidden beneath. Photo by Janice Glime

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

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

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

Figure 6. Thalloid protonema of liverwort ***Sphaerocarpus texanus***. Photo from Plant Actions through Eugenia Ron and Tom Sobota, with permission.

Figure 7. ***Sphagnum*** protonemata on a branch of ***Sphagnum***. Photo by Andras Keszei, with permission.

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

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

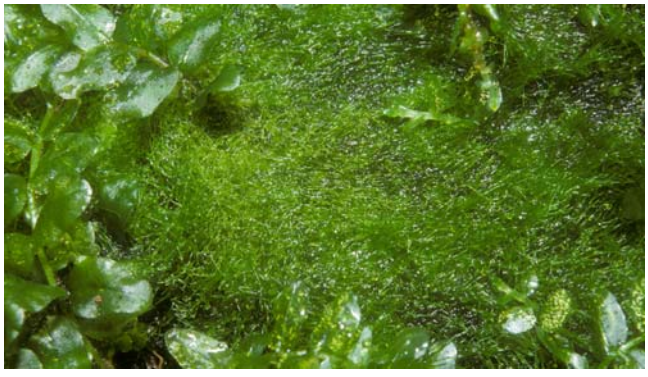

Figure 10. Protonemata of the moss ***Plagiomnium*** sp. Photo by Janice Glime.

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

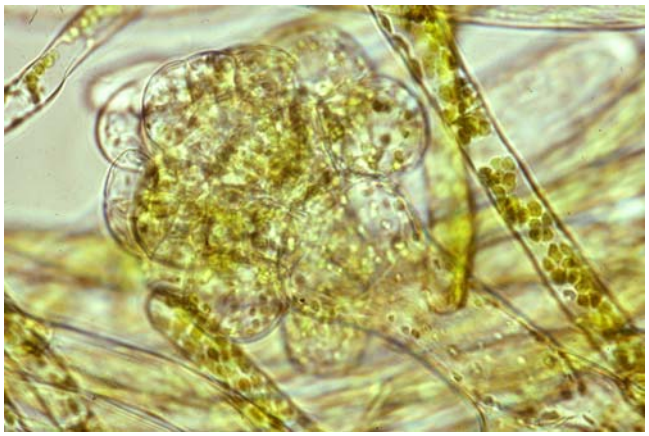

Figure 11. Moss ***Funaria hygrometrica*** protonemal bud. Photo by Janice Glime.

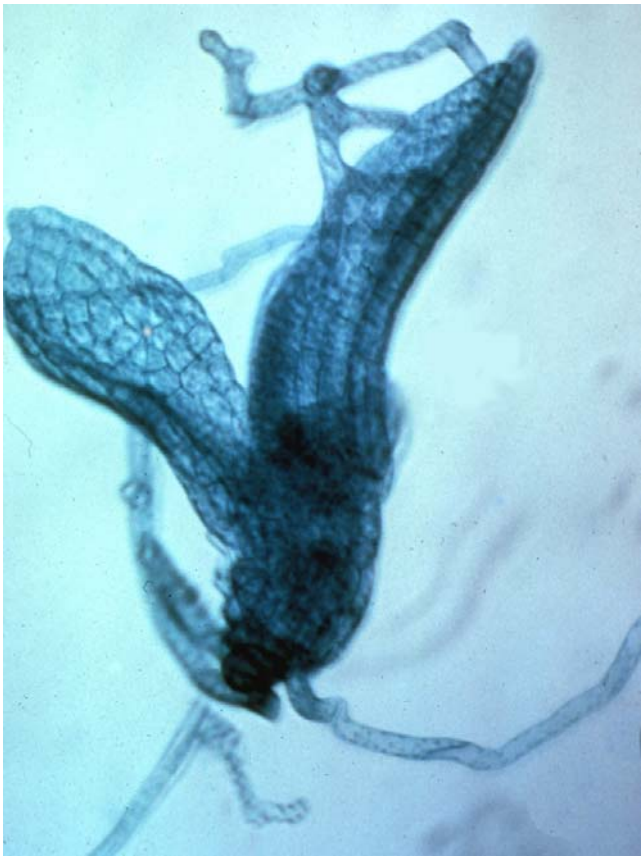

Figure 12. Moss protonema with bud. Photo by Janice Glime.

The mature gametophytes are the leafy plants you see (Figure 13-Figure 19). They produce **antheridia** (sing. **antheridium**; male gamete containers; sperm-containers; Figure 20-Figure 27) and **archegonia** (sing. **archegonium**; multicellular egg-containing structures that later house embryo; Figure 31-Figure 37) on the same or different plants, depending on the species. Antheridia can number up to several hundred in ***Philonotis***, but a much smaller number is typical (Watson 1964). Archegonia are generally few, but can reach as many as 20-30 in ***Bryum***.

Figure 13. Leafy liverwort ***Porella navicularis*** male branches. Photo from botany website at the University of British Columbia, with permission.

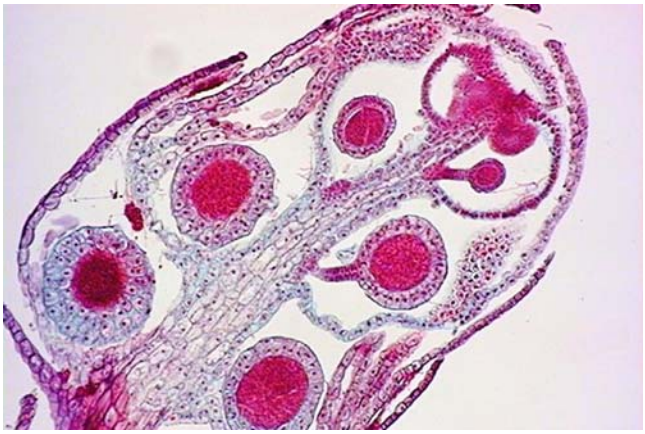

Figure 14. Leafy liverwort ***Porella*** antheridia in antheridial branch. Photo by Paul Davison, with permission.

Figure 15. ***Porella navicularis*** female with arrow indicating perianth. Photo from botany website at the University of British Columbia, with permission.

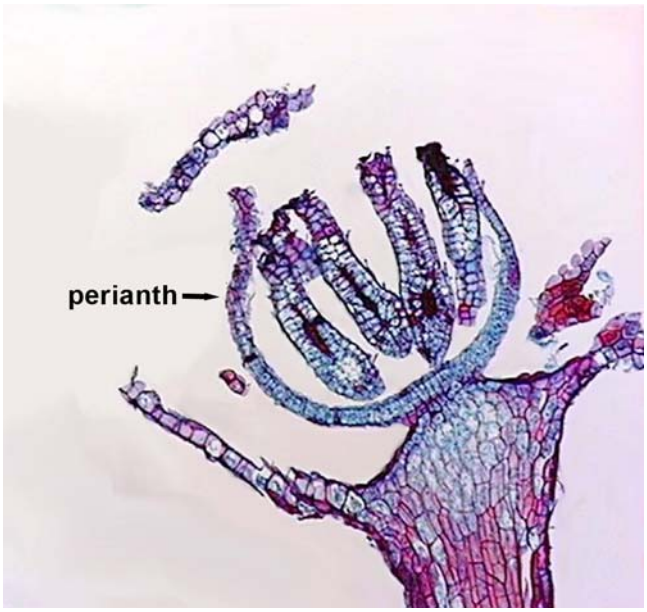

Figure 16. ***Porella*** archegonia in perianth. Photo by Paul Davison, with permission.

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

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

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

The **antheridium** consists of a layer of cells, the **sterile jacket**, surrounding the **spermatogenous** cells (Figure 21), *i.e.*, those that divide to form the **spermatocytes** (sperm-containing cells). If you remember that this is the gametophyte generation and, therefore, already in the haploid state, you will realize that the **sperm** (Figure 27-Figure 30), produced in large numbers within an **antheridium** and released as a mass (Figure 28), and the **egg** (non-motile female gamete that is larger than motile sperm), produced singly within an **archegonium**, must be produced by **mitosis** (ordinary cell division).

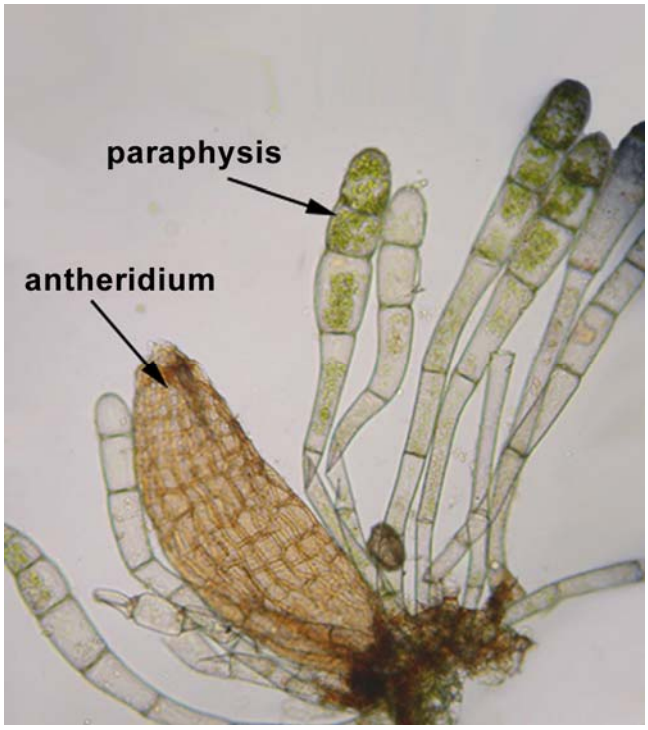

Figure 20. ***Plagiomnium insigne*** antheridium and paraphyses. Photo from Botany 321 website at the University of British Columbia, with permission.

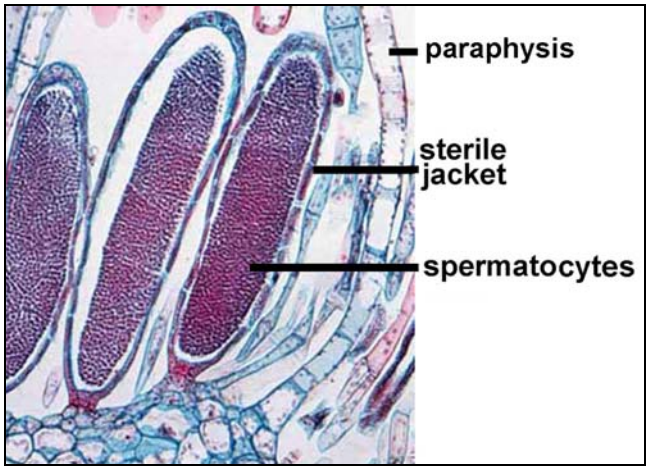

Figure 21. Moss **antheridia** showing **spermatocytes** that have been formed by the **spermatogenous tissue**. Photo by Janice Glime.

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

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

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

Figure 25. ***Fissidens bryoides* antheridia** on a special branch. Photo by Dick Haaksma, with permission.

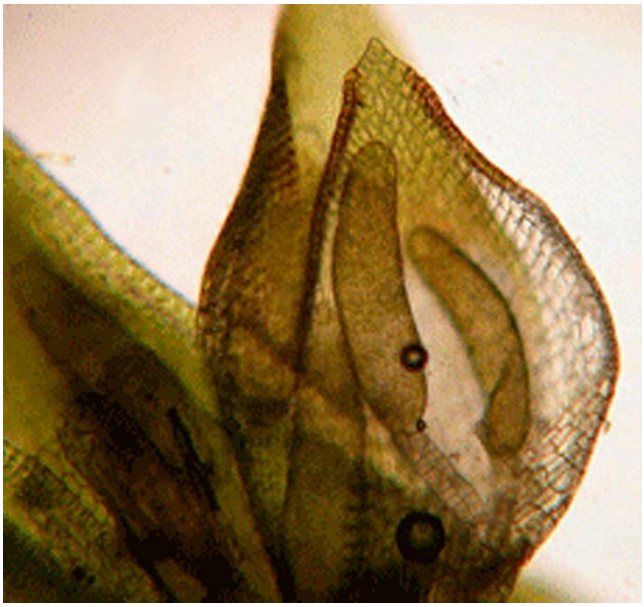

Figure 26. ***Orthotrichum pusillum* antheridia** nestled among leaves. Photo by Bob Klips, with permission.

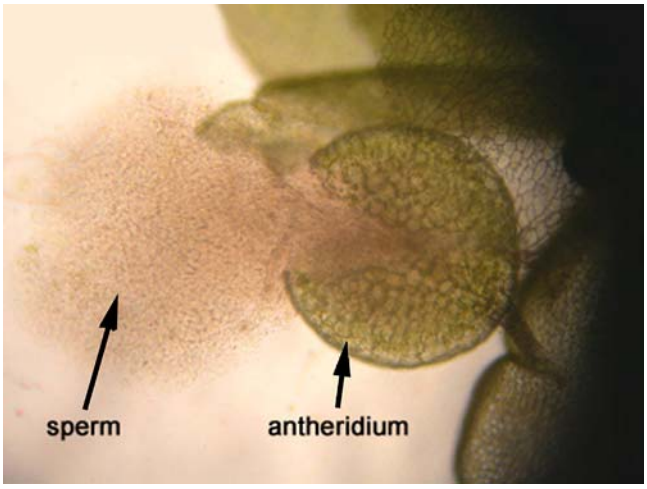

Figure 27. ***Porella navicularis*** **antheridium** releasing **sperm** as a mass. Photo by Jonathan Choi from Botany 321 website at the University of British Columbia, with permission.

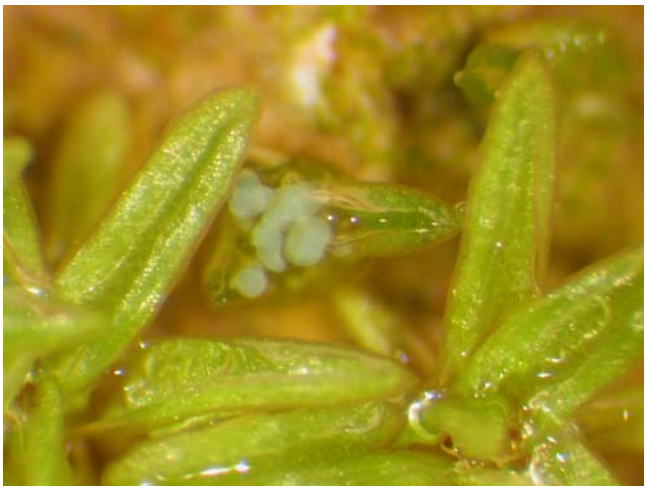

Figure 28. ***Aloina ambigua*** sperm release in packages. Photo courtesy of Llo Stark.

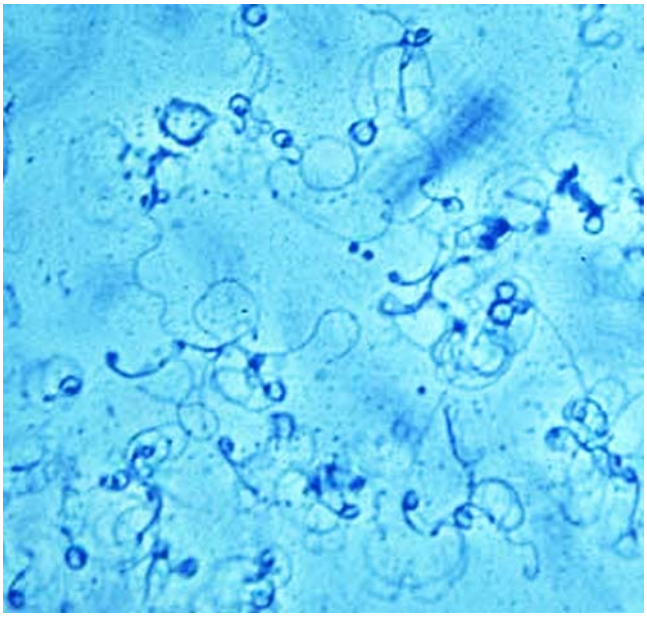

Figure 29. ***Marchantia polymorpha*** **sperm**. Photo from Botany 321 website at the University of British Columbia.

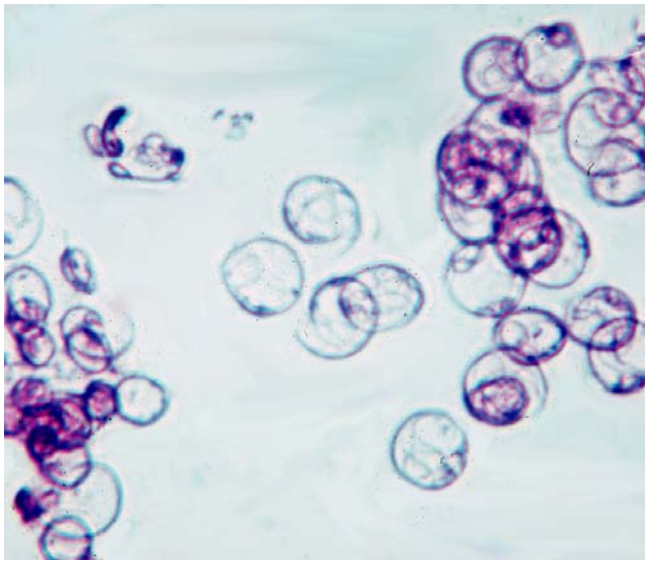

Figure 30. Stained bryophyte **sperm**. Photo by Janice Glime.

It is then the task of the **sperm** (Figure 29-Figure 30), with its two **flagella**, to find a film of water within which to swim to the awaiting egg in the **archegonium** (Figure 31-Figure 37). This is facilitated, most likely in all cases, by the presence of a chemical gradient produced by the archegonium and serving as an attractant (Figure 34). The archegonium is shaped like a flask with a **neck** (Figure 31), albeit a short one in some taxa. This neck has an outer layer of cells and a middle layer, the **neck canal cells** that disintegrate prior to fertilization, leaving this area as the **neck canal** (Figure 31). It is this disintegration that releases the chemicals that attract the sperm, and the cellular remains provide a fluid medium in which the sperm can swim. This fluid exudes from the archegonium (Figure 34) and can serve as a chemical gradient. Yet it appears that the ability of the sperm to advance any great distance by means of its flagella may be unlikely, if ***Riccardia pinguis*** is at all representative. Showalter (1926) found that when sperm of that species were placed at one end of a 1 x 0.5 cm pool, the majority still remained at that end of the pool an hour later, retaining motility up to 6 hours. Cronberg *et al*. (2008) showed the timescale of sperm deterioration (Figure 38).

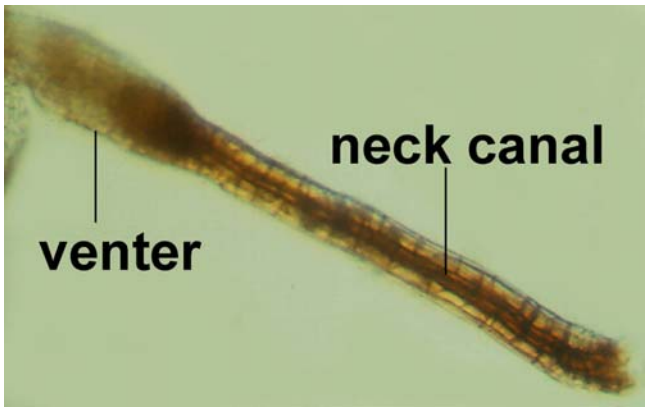

Figure 31. **Archegonium** of ***Fontinalis dalecarlica*** showing entry pathway (**neck canal**) for the sperm. Photo by Janice Glime.

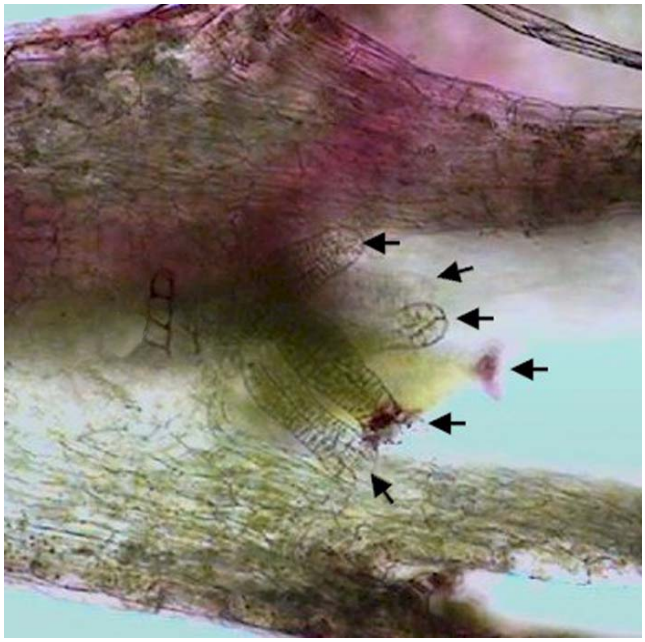

Figure 32. Terminal **archegonia** (arrows) of leafy liverwort ***Jungermannia evansii***. Photo by Paul Davison, with permission.

Figure 33. Immature archegonia of leafy liverwort ***Lophocolea cuspidata***. Photo from Botany 321 website at the University of British Columbia, with permission.

Figure 34. ***Aloina ambigua*** showing archegonial exudate. Photo courtesy of Llo Stark.

Figure 35. ***Pleurozium schreberi*** archegonia with two developing embryos, on short side branch. The large one is likely to be the only one to mature. Photo by Janice Glime.

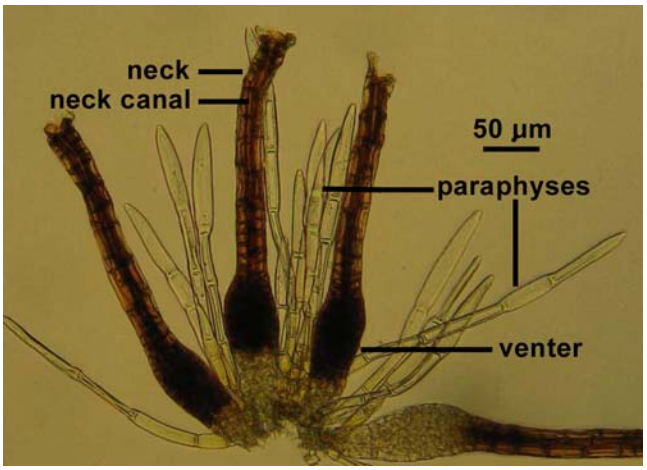

Figure 36. Moss ***Zygodon intermedius*** archegonia with paraphyses. Photo by Tom Thekathyil, with permission.

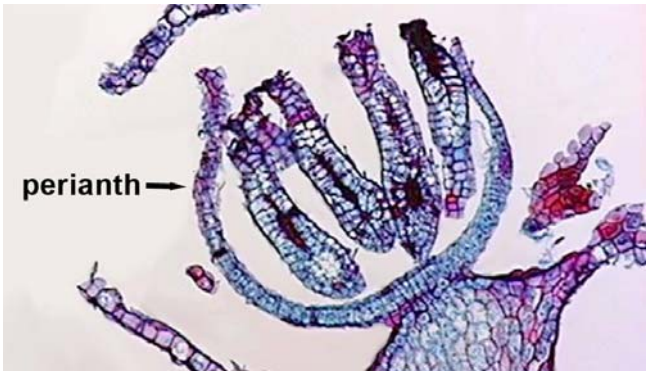

Figure 37. ***Porella*** archegonia in perianth. Photo by Paul Davison, with permission.

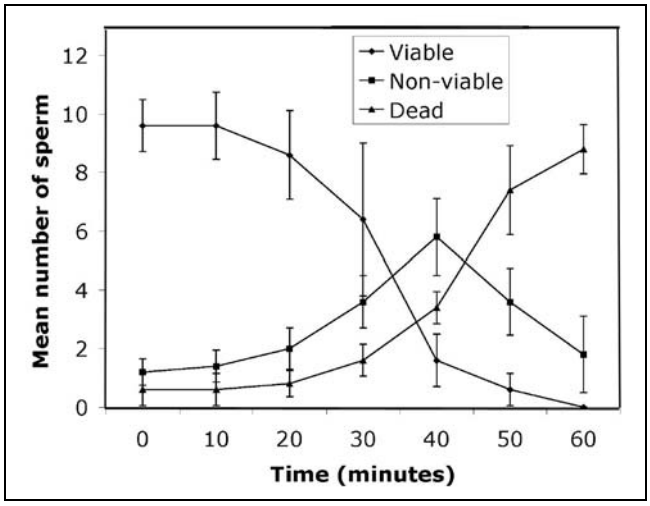

Figure 38. Time lapse of sperm release in ***Bryum argenteum***. Modified from Cronberg, Hans Berggren, & Rayna Natcheva 2008.

But that does not mean that all species have such short sperm longevity. In their experiments with the **paroicous** (having archegonia and antheridia on same branch) ***Pohlia nutans*** (Figure 39-Figure 40), a widespread moss that tolerates the high temperatures of geothermal areas and the extremes of the Antarctic, Rosenstiel and Eppley (2009) found that 20% of the sperm were still viable after 100 hours in DI or rainwater. They furthermore found that longevity was not affected by 22-60ºC, but at 75ºC it was significantly shortened. Dilution reduced viability. This longevity is much longer than anticipated, but it may not be representative of bryophytes with more narrow ecological distributions.

Figure 39. ***Pohlia nutans*** **perigonia** (modified leaves around antheridia in bryophytes). This species is usually **paroicous**. Photo by Michael Lüth, with permission.

Figure 40. ***Pohlia nutans*** with capsules, a widespread moss from geothermal areas to the Arctic. Photo by Michael Lüth, with permission.

It appears to be typical for sperm to be shed within their spermatocyte cells as a mass, being squeezed out of the antheridium by the swelling tissues (Figure 41-Figure 43). Both **paraphyses** (sterile filaments among the reproductive organs; Figure 20-Figure 24) and the **antheridium** (Figure 20-Figure 27) itself, swell. Then the spermatocytes drift to the top of the splash apparatus. It seems usual that the sperm do gain distance from the antheridium when they reach the surface of the surrounding water, especially in a splash cup, and break away from their enclosing spermatocyte cell membrane (Muggoch & Walton 1942). At that point, the sperm seem to disperse readily across the surface of the water, hopefully facilitating their dispersal in splashing raindrops. Yet, this leaves them to fend for themselves once they reach the surface upon which they land, hopefully that of a female plant or near a female organ. Could it be that they are programmed to avoid wasting energy unless they are within the liquid from a female plant or near a female organ?

Figure 41. ***Bryum argenteum*** releasing sperm masses from antheridia. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

Figure 42. ***Bryum argenteum*** antheridium with initial explosive sperm mass release. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

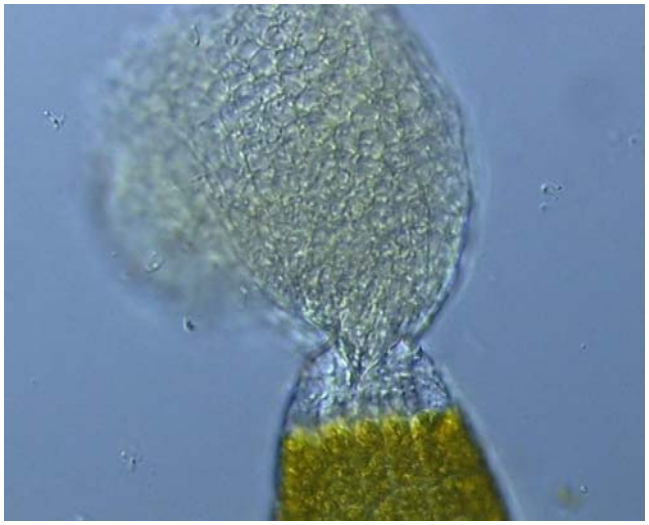

Figure 43. ***Bryum argenteum*** antheridium with final sperm mass release. Photo by Nils Cronberg, Hans Berggren, & Rayna Natcheva, with permission.

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

We know little about the ability of the archegonial fluid to attract the sperm, but it appears that **sucrose** may be one of the factors, perhaps the only one, involved (Kaiser *et al.* 1985; Ziegler *et al*. 1988). These researchers found that in the moss ***Bryum capillare*** (Figure 44), once the neck canal cells of the archegonium had disintegrated, the leaves and the archegonia contained less than 20% of the sucrose found in the intact neck region. There was virtually no fructose in the intact archegonium, but the glucose concentration rose after the receptive period ended.

Figure 44. ***Bryum capillare*** with capsules. Photo by David Holyoak, with permission.

Once the sperm reaches the **venter** of the archegonium (the bulbous base of the flask; Figure 45), it penetrates the egg and together they form the **zygote** (Figure 46), the first 2*n* cell of the sporophyte. Unlike an alga, the bryophyte retains its zygote in the female **gametangium** (archegonium) and when conditions are right the zygote divides, forming the **embryo** (young plant still contained in archegonium). This embryo continues dividing (Figure 47) and then specializing, forming eventually a **foot**, **stalk**, and **capsule** (sporangium; spore-container of mosses and liverworts; Figure 47) with a **cuticle** (water-protective layer; Crum 2001), which together constitute the **mature sporophyte** (Figure 48-Figure 58).

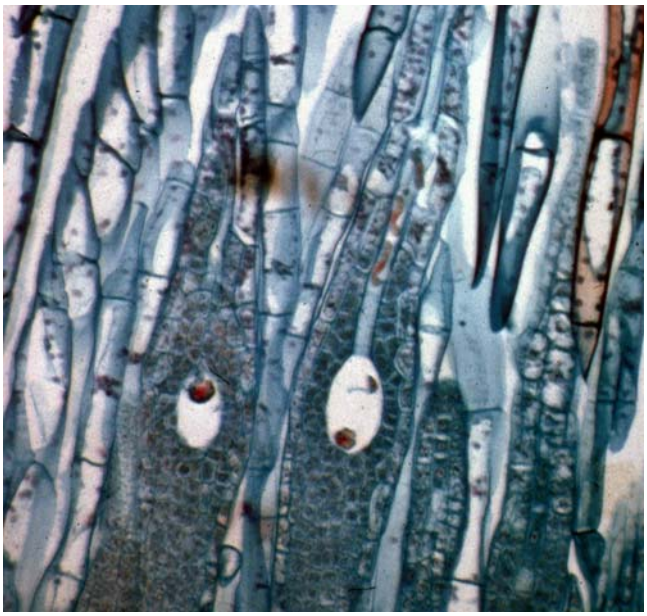

Figure 45. Moss ***Polytrichum*** archegonia. The archegonium on the right has an egg in the bottom of the venter and a biflagellate sperm near the neck. Two more sperm are in the neck canal of the archegonium on the right. Photo from botany teaching collection, Michigan State University, with permission.

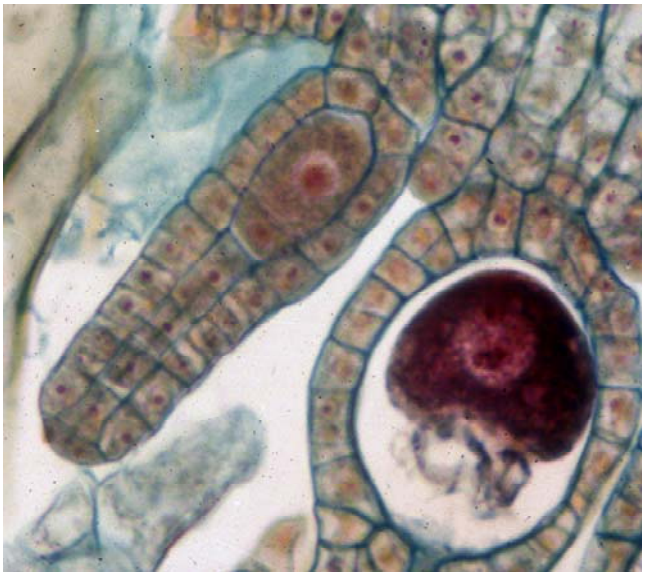

Figure 46. Thallose liverwort ***Marchantia polymorpha*** fertilization. Archegonium on left is young and neck canal cells have not broken down yet. The egg cell is in the swollen venter. On the right is an egg that is fusing with the sperm during fertilization. Photo from botany teaching collection at Michigan State University, with permission.

Because the base of this sporophyte is still firmly anchored in the gametophyte tissue, the sporophyte is at least partially a parasite on the gametophyte, gaining at least some of its nutrition through a joining tissue called the **haustorium**. Being contained in the gametophyte, the zygote necessarily competes for energy, as well as space, with other zygotes or embryos, and thus it is not surprising that multiple capsules are rare. Notable exceptions occur in the mosses ***Dicranum*** (Figure 1), ***Plagiomnium*** (Figure 59), ***Rhodobryum*** (Figure 60), and ***Mittenia plumula***, with as many as nine capsules in ***Plagiomnium insigne*** (Figure 59) (Crum 2001).

Consideration of the sporophyte as a parasite on the gametophyte is controversial. Some botanists find this to be an obvious interpretation, but others are adamantly opposed to such a label. Part of this reasoning against the relationship as parasitic is because most sporophytes, at least in mosses, are photosynthetic until the spores near maturity. They also argue that the fitness of the gametophyte is tied to the fitness of the sporophyte with, in at least some monoicous species, the same genome. Llo Stark (pers. comm. 25 February 2023) has also found that the strategy for desiccation tolerance can change shortly after fertilization, changing from constitutive protection to inducible protection. He suggests that this could cause the release of sugars that are moved to the sporophyte. The same dilemma of terminology applies to the human embryo, but the case against calling it a parasite in bryophytes seems stronger due to the photosynthetic ability of many sporophytes, at least in Anthocerotophyta and most Bryophyta.

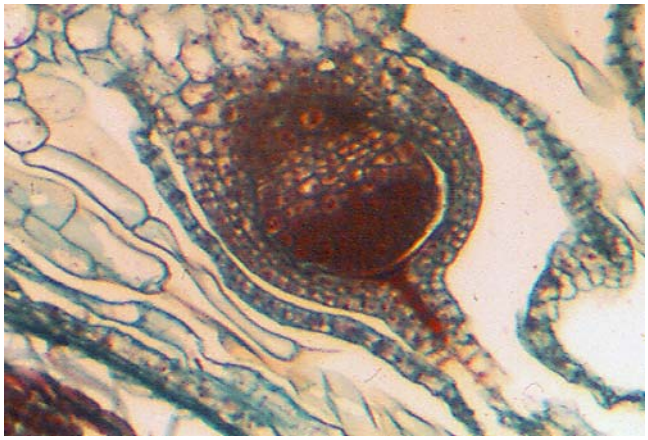

Figure 47. Thallose liverwort ***Marchantia polymorpha*** embryo in archegonium, showing development of the **foot**, **seta**, and **sporogonium**. Note the red-stained **neck canal** of the archegonium. Photo by Janice Glime.

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

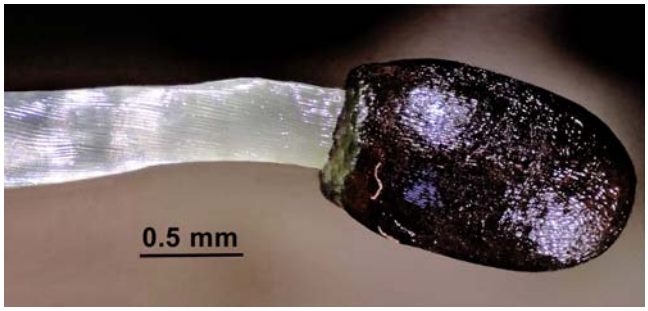

Figure 48. Liverwort ***Blasia pusilla*** capsule and stalk. Photo by Walter Obermayer, with permission.

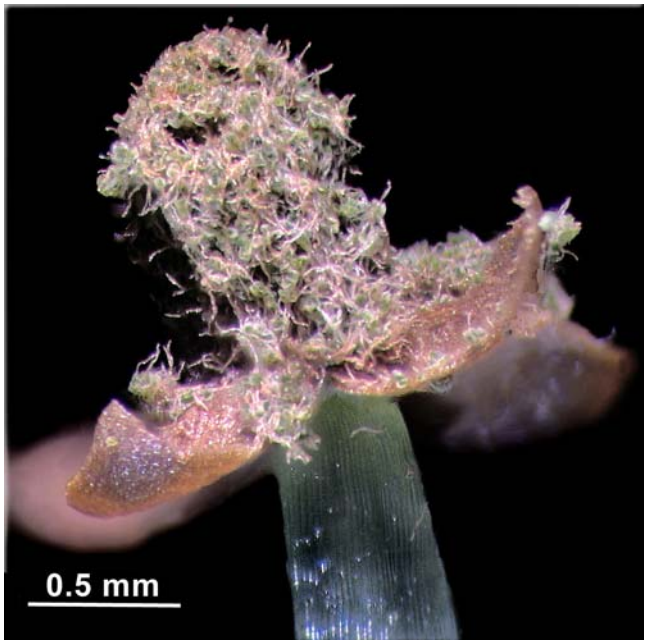

Figure 49. Liverwort ***Blasia pusilla*** open capsule showing spores and elaters. Photo by Walter Obermayer, with permission.

Figure 50. Liverwort ***Lophocolea cuspidata*** capsule with elongated seta. Photo from Botany 321 website at the University of British Columbia, with permission.

Figure 51. Moss ***Orthotrichum stramineum*** capsule with calyptra. Photo by Des Callaghan, with permission.

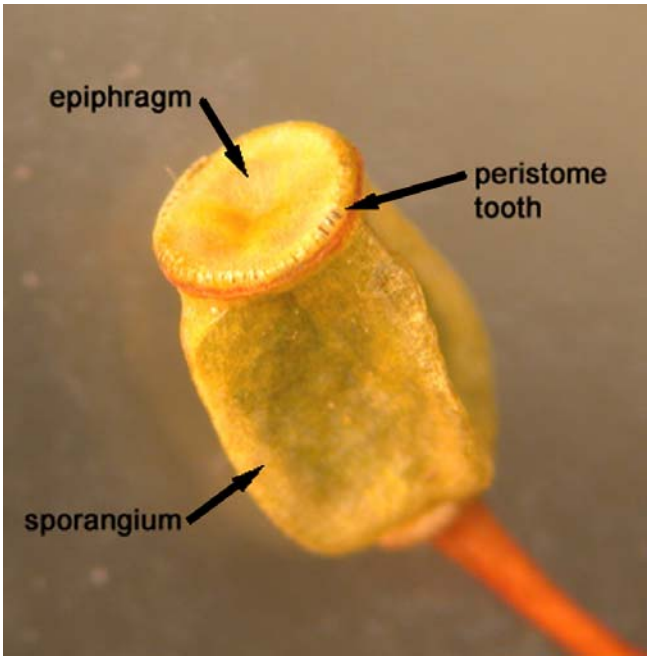

Figure 52. ***Polytrichum commune*** capsule. Photo from Botany 321 website at the University of British Columbia, with permission.

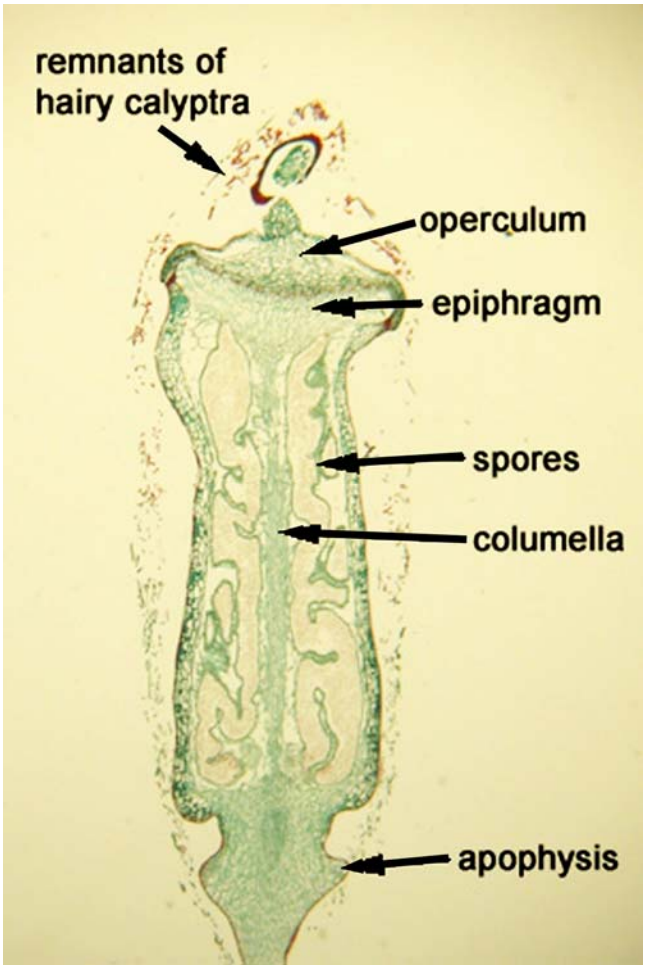

Figure 53. ***Polytrichum commune*** capsule longitudinal section. Photo from Botany 321 website at the University of British Columbia, with permission.

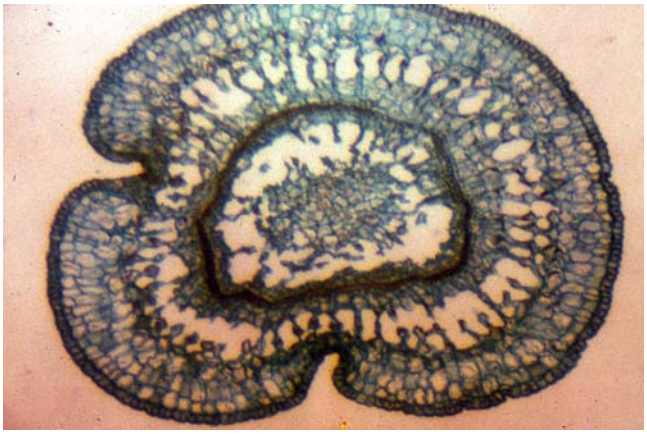

Figure 54. ***Polytrichum*** capsule cross section. The blue center is the columella. The dark circle around it is the developing sporogenous tissue. Photo by Janice Glime.

Figure 55. ***Bartramia pomiformis*** showing leafy gametophytes and sporophyte capsules. Photo by Janice Glime.

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

The details of the foregoing structures differ among the phyla of **Bryobiotina** and in many cases form the basis for separating the phyla. These are best understood by examining each phylum and class in greater detail.

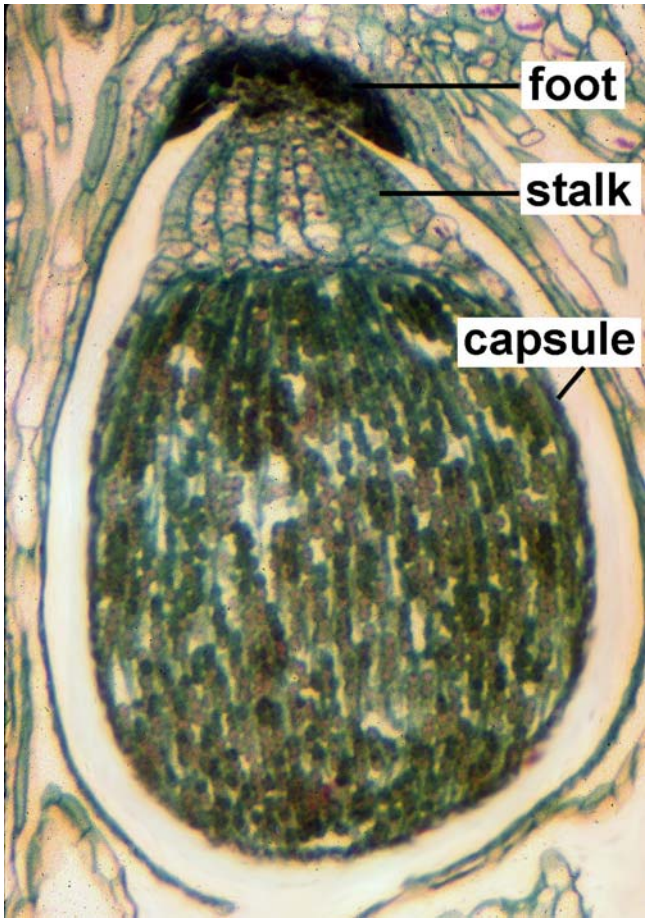

Figure 56. Mature sporophyte of thallose liverwort ***Marchantia polymorpha*** showing **foot**, **stalk**, and **capsule**. Photo modified from botany teaching collection, Michigan State University, with permission.

Figure 57. ***Gigaspermum repens*** capsule showing spores. Photo by David Tng, with permission.

Figure 58. Longitudinal section through mature ***Fontinalis squamosa*** capsule, showing green spores. Photo by Janice Glime.

Figure 59. ***Plagiomnium insigne*** **sporophytes**, illustrating multiple sporophytes on one shoot. Photo from Botany 321 website at the University of British Columbia, with permission.

Figure 60. ***Rhodobryum roseum*** with multiple capsules from one shoot. Photo by Michael Lüth, with permission.

Life Cycle Controls

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

For example, in ***Mnium hornum*** (Figure 61) there is an endogenous rhythm that coincides approximately with the seasonal cycle (Newton 1972). Short days delay gametangial production, but when 7.25-hour days are maintained, neither 10 nor 20°C is capable of completely suppressing the gametangia. Newton interpreted this to mean that the short days of winter maintain coordination with the seasons. In ***Plagiomnium undulatum*** (Figure 62), archegonial induction responds to long days (7.25-12 hours at 10°C). Males are also long-day plants, but in addition they require a diurnal temperature fluctuation.

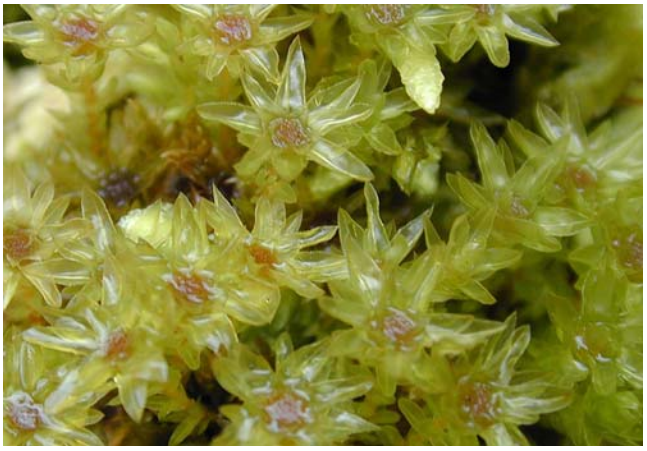

Figure 61. ***Mnium hornum*** showing antheridia that cease production in response to short days. Photo by Michael Lüth, with permission.

Figure 62. ***Plagiomnium undulatum*** with **antheridia** that respond to long days and diurnal temperature fluctuations. Photo by Jan-Peter Frahm, with permission.

Generation Time

The concept of generation time is well known even to the layperson. We know that in humans it means the time from birth to becoming a parent, and for the population we average the data from everybody. I like the Wikipedia definition: The average difference in age between parents and offspring when the population is at the stable age distribution. For plants, it seems the best definition is one complete life cycle. Llo Stark (Bryonet 20 February 2014) agrees with this implied spore-to-spore definition, but he suggests expanding it to include shoot fragment or fragment of a protonema as the starting point instead of a spore. For example, he and John Brinda have found that it takes only 5-6 months for a shoot fragment of ***Aloina ambigua*** (Figure 63) to produce viable spores. In this rapid cycle, only 40 days are required for the sporophyte to develop. On the other hand, Stenøien (Bryonet 21 February 2014) suggests that the average length of time required to replace an individual is a workable definition of generation time. But Lars Hedenäs (Bryonet 21 February 2014) cautions us that we rarely know what this means in any specific case.

Figure 63. ***Aloina ambigua***, a moss with a short generation time of only 5-6 months. Photo by Hermann Schachner, through Creative Commons.

But do we have information for many, or even any, bryophytes on the amount of time required to progress from spore or fragment germination to spore production? This is easy for annual bryophytes, but for perennials, few have been grown from spore to mature capsule and field observations would be based mostly on colonists because spores are an important part of their life strategy. And some bryophytes further complicate this by rarely or never producing capsules, forcing us to guess based on gametangial maturation time. However, once fertilization occurs, sporophyte maturation can proceed rapidly as in the annuals, or take 15 months as in some ***Polytrichum*** (Figure 64) species.

Figure 64. ***Polytrichum commune*** sporophytes, in 4 cases covered by the gametophyte calyptra. Photo by Michael Lüth, with permission.

Even "annuals" might cause problems. For example, ***Buxbaumia*** (Figure 65-Figure 66) is usually considered an annual because the sporophyte lasts only one year and there is no leafy gametophore. But Hancock and Brassard (1974) found that despite the annual disappearance of the sporophyte, the protonema remained for several years.

Figure 65. ***Buxbaumia aphylla*** with mature capsules. Photo by Jan-Peter Frahm, with permission.

Figure 66. ***Buxbaumia aphylla*** with capsule wall peeled back and interior exposed. The greenish ground cover is caused by protonemata that will survive the winter and form new plants. Photo by Janice Glime.

Let us take an example first given by Hans Stenøien and carried further by Lars Hedenäs (Bryonet 21 February 2014). If a moose walks across a bog and kills a ***Sphagnum*** (Figure 67) shoot, the empty space created will most likely be filled by an expanding neighboring shoot. The probability is high that the neighbor originated by branching from the now dead shoot. This means the same individual survives despite the death of one of its shoots. Do we know anything about the frequency of this happening?

Figure 67. ***Sphagnum capillifolium***, a moss that spreads by branches. Photo by David Holyoak, with permission.

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

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

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

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

Rod Seppelt (Bryonet 2 January 2022) has suggested what might be the shortest "generation time" for a bryophyte. When in Alaska, he found a population of ***Riccia cf. cavernosa*** (Figure 68) on a floodplain about a week after the water receded. These were very small plants, suggesting their origin from spores rather than dormant thalli. It was late autumn, and a new submersion was imminent due to upstream rains. He collected more plants about two weeks later and found mature spores in the thalli. He estimated that these plants went from spore to producing mature sporangia in just 2-3 weeks!

Figure 68. ***Riccia cavernosa***, a species that can apparently complete its life cycle in less than 3 weeks on a floodplain. Photo by Richard Orr, with permission.

Importance

So why is it important to understand generation time of a bryophyte? The question about the length of a generation was raised by Jon Shaw who wanted to know the generation time in ***Sphagnum*** (Figure 67). As Hans Stenøien and Richard Zander summarized on Bryonet (21 February 2014), understanding generation times (and population sizes) enables us to use population genetic models to infer the action of evolutionary processes. Likewise, phylogenetic models enable us to infer evolutionary relationships. From these, we can infer migration rates and divergence time between lineages.

Longevity and Totipotency

Bryophyte longevity can be difficult to define because unlike most other plants, they die at the bottom and continue growing at the tip. Furthermore, they may seem dead, yet still be capable of life. For example, I have boiled ***Fontinalis*** (Figure 69) for two weeks, replaced it in its native stream, and found a few new leaves on one stem tip a year later, whereas all the original leaves were brown or gone.

Figure 69. ***Fontinalis dalecarlica***, a species that can survive two weeks of boiling because of its totipotency. Photo by J. C. Schou, through Creative Commons.

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

We know that ***Sphagnum*** (Figure 67) continues growing for hundreds of years, but only the recent few years of growth seem to be alive. But is that really true?

Recent studies in polar regions suggest that parts of some bryophytes can retain life for 1500 years under ice (LaFarge *et al*. 2013; Roads *et al*. 2014). Working in the Arctic, LaFarge *et al*. (2013) were able to grow new gametophytes from two species of buried bryophytes: ***Aulacomnium turgidum*** (Figure 70) ~400 years old and ***Bartramia ithyphylla*** (Figure 71) ~460 years old.

Figure 70. ***Aulacomnium turgidum***, a species found buried in Arctic ice cores. Photo by Michael Lüth, with permission.

Figure 71. ***Bartramia ithyphylla***, a moss found in ice cores from the Arctic. Photo by Michael Lüth, with permission.

Then Roads *et al*. (2014) found new growth of ***Chorisodontium aciphyllum*** (Figure 72-Figure 73) in Antarctic cores at 138 cm, a layer they interpreted to be ~1500 years old! They found that after 55 days the ***Chorisodontium aciphyllum*** grew *in situ* at the base of their ice core at 110 cm. Protonemata developed on the rhizoids at the base in 22 days. (See also Miller 2014; Zimmer 2014).

Figure 72. ***Chorisodontium aciphyllum*** showing the extensiveness of a mat. Photo through Creative Commons.

Figure 73. ***Chorisodontium aciphyllum*** showing upper live green parts and lower dead or dormant parts. Photo through Creative Commons.

Summary

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

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

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

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 reviewed an early draft. Peter Convey and Catherine La Farge entered an email discussion with me on their own finds and concerns about available data on the ice core finds. Thank you to Llo Stark for improving the wording in several parts of the chapter.

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