

CHAPTER 2-2

LIFE CYCLES: SURVIVING CHANGE



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

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 protection from herbivory, their ability to desiccation, and their life cycle strategies as well as in their physiological behavior, permitting them to occupy a wide variety of niches. 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 the bryophytes. May Father Hedwig save us from those who want to identify them all by numbers!

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

Dominant Generation

One of the ways that plants manage to survive as "immobile" organisms, yet are able to survive the severe changes of seasons, is by having different life cycle stages that are adapted to different conditions. As we progress through the protist and plant kingdoms, we see that most green algae (Chlorophyta), especially in freshwater, spend most of their time in the water and most of them have only one set of chromosomes ($1n$). Although there is much disagreement about evolutionary pathways among photosynthetic organisms, all evolutionary biologists seem

to agree that this **life strategy** was first, with invasion of land and dominant $2n$ organisms both coming later. (The **dominant generation** refers to the most conspicuous and generally the most long-lived generation.) This $1n$ stage is termed the **gametophyte generation** ($1n$ or **haploid** generation that reproduces by gametes in plants) because the generation ends when it produces **gametes** (sexual reproductive structures that have one set of chromosomes and must unite with another of the same species but opposite strain to continue the life cycle) that join to form the $2n$ **zygote** ($2n$ cell resulting from fusion of male and female gametes, *i.e.* from fertilization; Figure 2). Hence, the zygote is the first structure of the $2n$ stage or **sporophyte generation** [**diploid** ($2n$) generation that reproduces by **meiospores** in plants; Figure 2]. The **meiospores** in many bryophytes are able to survive many years in a dry state, thus permitting at least some taxa to live in habitats that only occasionally get moisture.

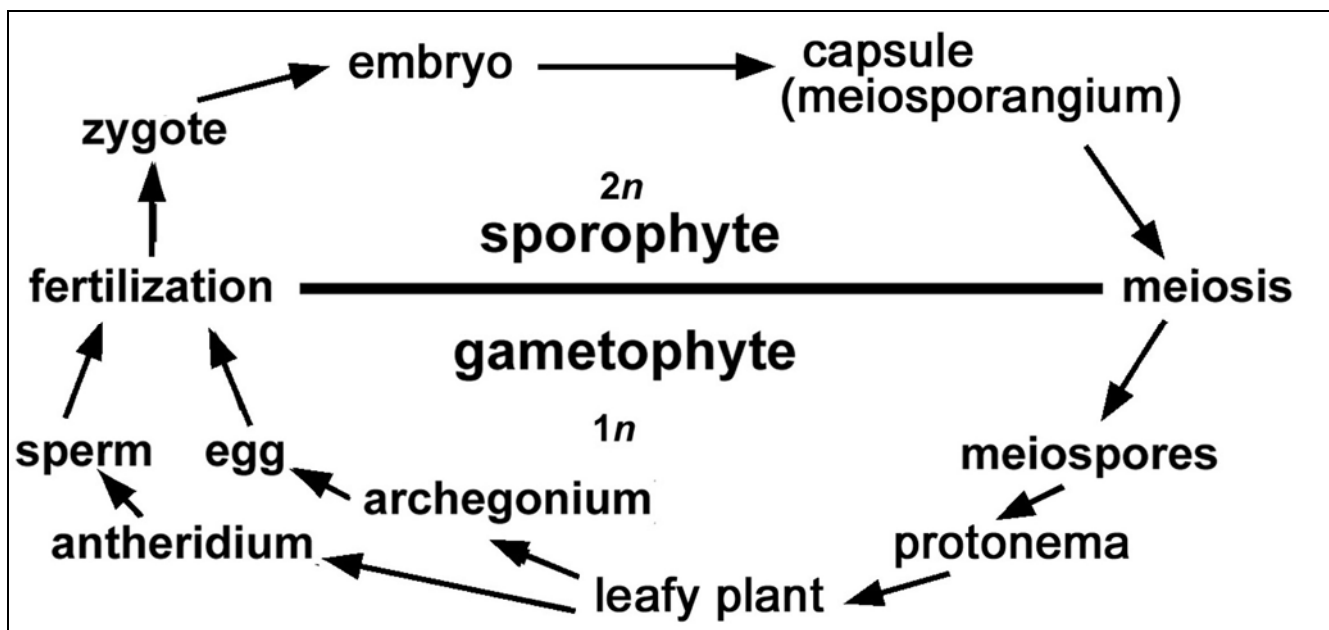


Figure 2. Basic sexual life cycle of a bryophyte. Gemmae or other propagules, not shown here, can occur on the leafy plant or on the protonema (pl. **protonemata**: alga-like, usually filamentous, stage that develops from spores of bryophytes), giving rise to the same generation as its origin. Diagram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

The Life Cycle

The dominant $1n$ condition (the **nuclear condition**, referring to having 1 set of chromosomes, where n represents the number of chromosomes in a complete set) begins as a **spore** (reproductive cell that develops into plant without union with another cell, usually 1-celled), 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 2, Figure 3). 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.

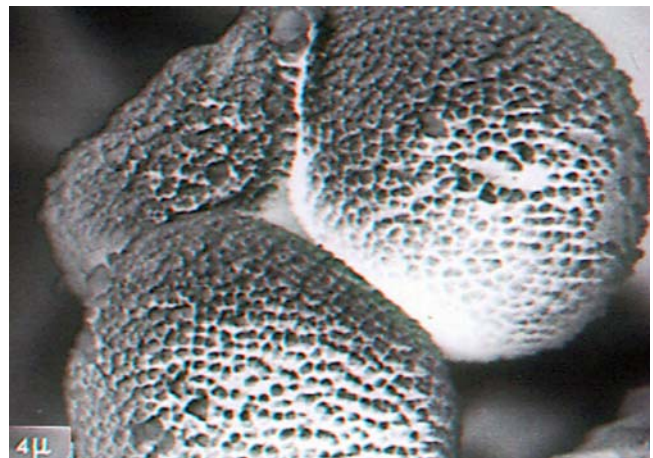


Figure 3. SEM of tetrad of meiospores of *Fontinalis squamosa*, with fourth spore hidden beneath. Photo by Janice Glime

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 4) that develops from the germinating spore. In most mosses, this protonema is truly the "first thread," forming a mat of green filaments, but in most liverworts and Sphagnopsida it becomes more thalloid after a few cell divisions (Figure 4).



Figure 4. **Upper:** Young thalloid protonema of the thallose liverwort *Cyathodium*. Photo by Noris Salazar Allen. **Lower:** Threadlike protonema of the moss *Funaria hygrometrica*. Photo by Janice Glime.



Figure 5. Protonemata, presumably of the moss *Plagiommium*. Photo by Janice Glime.

These protonemata produce buds (Figure 6) and grow into thalloid (thallose liverworts) or leafy plants. These plants are **haploid** (containing one set of chromosomes; $1n$); thus they are the **gametophyte generation** of the life cycle.



Figure 6. Moss protonema with bud. Photo by Janice Glime.

The mature gametophytes are the leafy plants you see, and they produce **antheridia** (sing. **antheridium**; male gamete containers; sperm-containers) and **archegonia** (sing. **archegonium**; multicellular egg-containing structures that later house embryo; Figure 8) on the same or different plants, depending on the species. Antheridia can number up to several hundred in *Philonotis*, but a much smaller number is typical (Watson 1964). Archegonia are generally few, but reach as many as 20-30 in *Bryum*.

The antheridium consists of a layer of cells, the **sterile jacket**, surrounding the **spermatogenous** cells (Figure 7), *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**, produced in large numbers within an antheridium, and the **egg** (non-motile female gamete that is larger than motile sperm), produced singly within an archegonium, must be produced mitotically.

It is then the task of the sperm, with its two **flagella**, to find a film of water within which to swim to the awaiting egg. This is facilitated, most likely in all cases, by the presence of a chemical gradient produced by the archegonium and serving as an attractant. The archegonium is shaped like a flask with a **neck**, 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. It is this disintegration that releases the chemicals that attract the sperm, and the cellular remains provide a fluid medium in which the sperm can swim. Yet it appears that the ability of the sperm to advance any great distance by means of its flagella may be unlikely, if *Riccardia pinguis* is at all representative. Showalter (1926) found that when sperm of that species were placed at one end of a 1 x 0.5 cm pool, the majority still remained at that end of the pool an hour later.

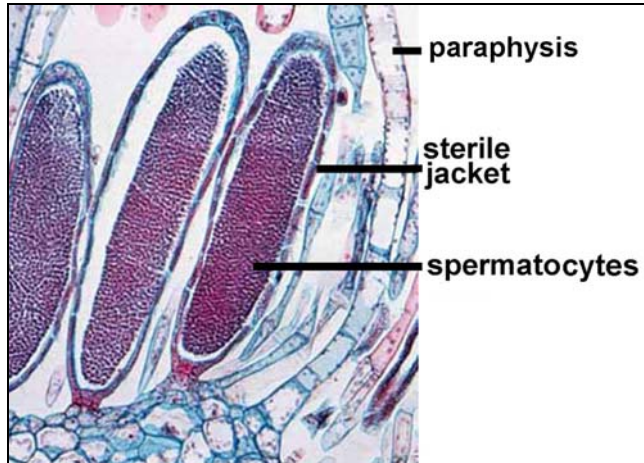


Figure 7. Moss antheridia showing spermatocytes that have been formed by the spermatogenous tissue. Photo by Janice Glime.

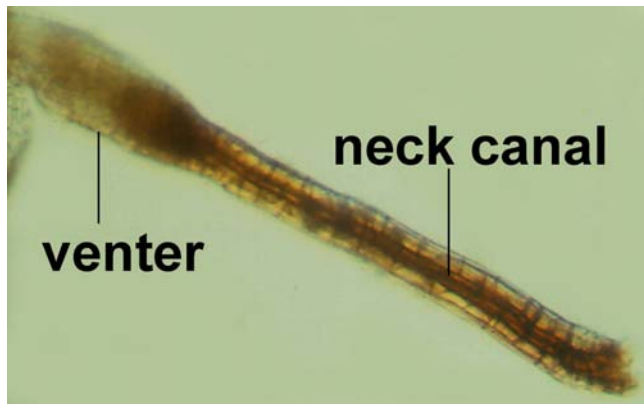


Figure 8. Archegonium of *Fontinalis dalecarlica* showing entry pathway (neck canal) for the sperm. Photo by Janice Glime.

It appears to be typical for sperm to be shed within their spermatocyte cells, squeezed out of the antheridium by the swelling tissues, both **paraphyses** (sterile filaments among the reproductive organs) and the **antheridium** itself, then drifting 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, they seem to disperse readily across the surface of the water, hopefully facilitating their dispersal by splashing raindrops. Yet, this leaves them to fend for themselves once they reach the surface upon which they land, hopefully a female plant or near a female organ. Could it be that they are programmed to avoid wasting energy unless they are within the liquid from a female plant or near a female organ?

We know little about the ability of this archegonial fluid to attract the sperm, but it appears that sucrose may be one of the factors, perhaps the only one, involved (Kaiser *et al.* 1985; Ziegler *et al.* 1988). These researchers found that in *Bryum capillare*, 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.

Once the sperm reaches the **venter** of the archegonium (the bulbous base of the flask), it penetrates the egg and together they form the **zygote**, that first $2n$ cell of the sporophyte. Unlike the algae, the bryophyte retains its zygote in the female **gametangium** (gamete container) and when conditions are right the zygote divides, forming the **embryo** (young plant still contained in archegonium). This embryo continues dividing and then specializing, forming eventually a **foot, stalk, and capsule** (sporangium; spore-container of mosses and liverworts; Figure 9) with a **cuticle** (water-protective layer; Crum 2001), the **mature sporophyte**. Because the base of this sporophyte is still firmly anchored in the gametophyte tissue, the sporophyte is necessarily a parasite on the gametophyte, gaining its nutrition through a joining tissue called the **haustorium**. As a parasite, 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*, *Plagiomnium*, *Rhodobryum*, and *Mittenia plumula*, with as many as nine capsules in *Plagiomnium insigne* (Crum 2001).

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.

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

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

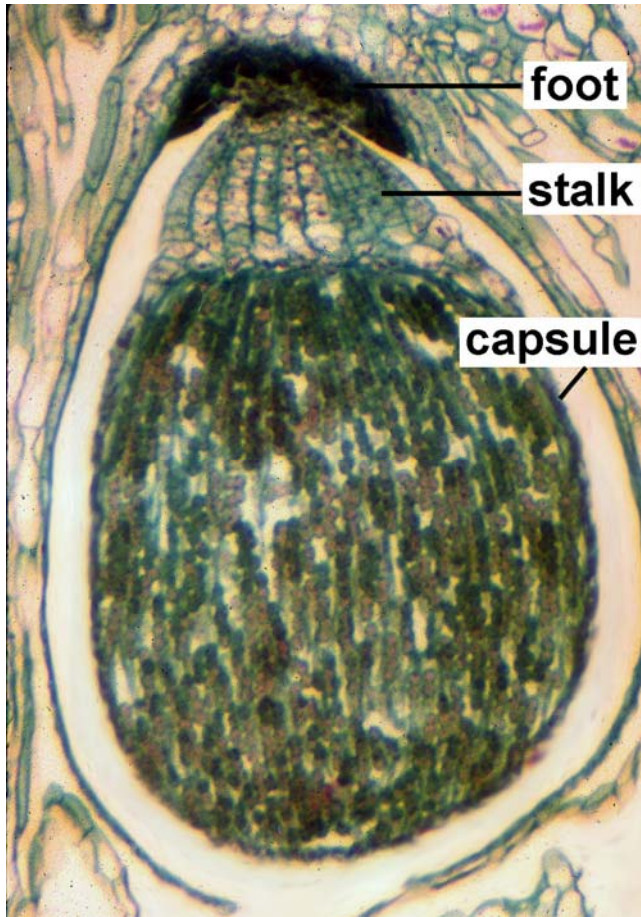


Figure 9. Mature sporophyte of thallose liverwort *Marchantia* showing foot, stalk, and capsule. Photo from botany teaching collection, Michigan State University.



Figure 10. *Bartramia pomiformis* showing leafy gametophytes and sporophyte capsules. Photo by Janice Glime.

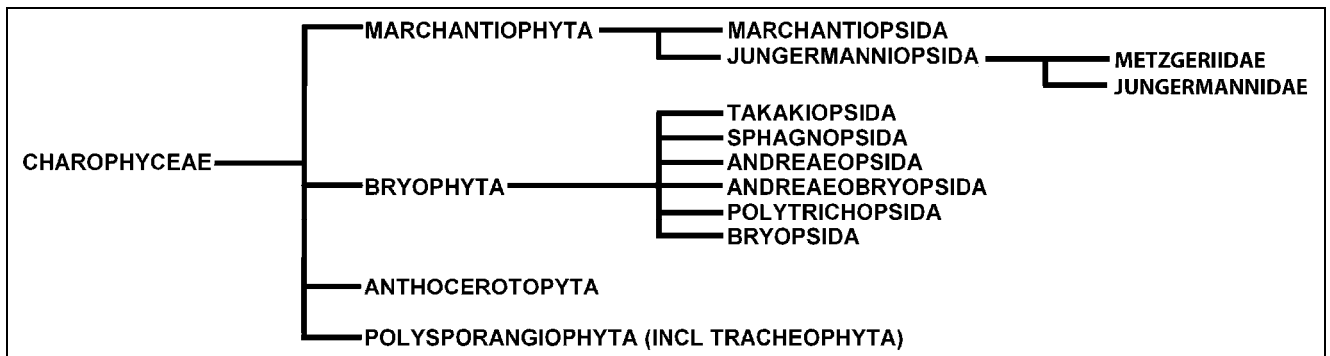


Figure 11. Schematic representation of the Bryobiotina phyla and classes related to other members of the Plant Kingdom (Polysporangiophyta), based on Shaw & Goffinet (2000).

Summary

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

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

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

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.

Literature Cited

Crum, H. 2001. Structural Diversity of Bryophytes. University of Michigan Herbarium, Ann Arbor, 379 pp.

- Farley, J. 1982. Gametes and spores. Ideas about sexual reproduction 1750-1914. Johns Hopkins University Press, Baltimore, 299 pp.
- Garcia-Ramos, G., Stieha, C., McLetchie, N., and Crowley, P. 2002. Maintenance of sexes under metapopulation dynamics: Modeling a liverwort case. Abstracts of the 87th Annual Meeting of the Ecological Society of America and the 14th Annual International Conference of the Society for Ecological Restoration, August 4-9, 2002, Tucson, AZ.
- Kaiser, K., Outlaw, W. H. Jr., and Ziegler, H. 1985. Sucrose content of receptive archegonia of the moss *Bryum capillare* Hedw. *Naturwissenschaften* 72: 378-379.
- Krazakowa, M. 1996. Review of genetic investigations on bryophytes in Poland. *Cryptog. Bryol. Lichénol.* 17: 237-240.
- 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.
- Niklas, K. J. 1976. Plant evolution and the reciprocity model. *Ann. Bot.* 40: 1255-1264.
- Shaw, A. J. and Goffinet, B. 2000. *Bryophyte Biology*. Cambridge University Press. 476 pp.
- Showalter, A. M. 1926. Studies in the cytology of the Anacrogynae. 1. Antherozoids. *Ann. Bot.* 40: 691-707.
- Watson, E. V. 1964. Sexual reproduction. In: *The Structure and Life of Bryophytes*. Hutchinson University Library. London, pp. 106-119.
- Wiencke, C. and Schulz, D. 1978. The development of transfer cells in the haustorium of the *Funaria hygrometrica* sporophyte. *Bryophytorum Bibliotheca* 13: 147-148.
- Ziegler, H., Kaiser, K., and Lipp, J. 1988. Sucrose in the archegonium exudate of the moss *Bryum capillare* Hedw. *Naturwissenschaften* 75: 203.