

CHAPTER 2-3

MARCHANTIOPHYTA



Figure 1. *Symphogyna podophylla* (Phylum Marchantiophyta, Class Jungermanniopsida, subclass Metzgeriidae) in New Zealand, showing dorsi-ventral orientation of the thallus and dependent sporophyte. Photo by Janice Glime.

Distinguishing Marchantiophyta

Both the leafy and thallose liverworts are placed in the phylum **Marchantiophyta** (variously known as Hepatophyta, Jungermanniophyta, Hepaticae, and Hepaticopsida), an often inconspicuous group with about 5000 species (Gradstein *et al.* 2001), or as Crum (1991) put it, up to 10,000, "depending on who says it and when," because so many species names described from different parts of the world have proved to be synonyms. As a phylum, Marchantiophyta (Figure 1) are distinguished from the phylum Bryophyta by their **dorsi-ventral orientation**, **unicellular rhizoids**, **inoperculate capsules** (*i.e.* lacking a lid, although there are a few exceptions), **absence of a columella** in the center of the capsule, and **no stomata** in the capsule. They possess a **seta** (stalk on the capsule), as do mosses, but it elongates **after** development of the capsule, whereas in mosses it elongates first. The spores, as in mosses, are all produced simultaneously by meiosis (Figure 7). The capsule, unlike that of most mosses, dehisces typically by **splitting into four valves** (Figure 2), but not in Marchantiopsida, revealing spores mixed with **elaters** (thickened elongate cells with spiral wall thickenings that twist in response to drying; Figure 2, Figure 8).

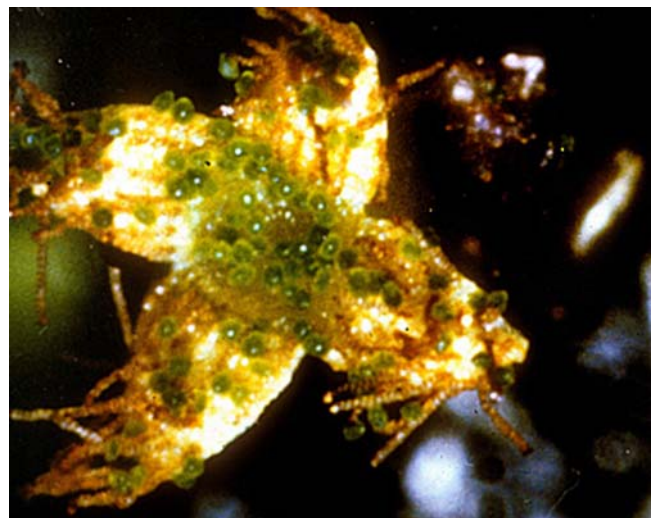


Figure 2. Open valvate capsule of the leafy liverwort *Frullania kagoshimensis* (Class Jungermanniopsida) showing spores and elaters and no columella. Photo by Zen Iwatsuki.

Elaters are notably absent in the thallose liverworts Ricciaceae and Sphaerocarpaceae (*Sphaerocarpos*, *Riella*), although sterile cells exist in the latter. Elaters respond to

changing moisture conditions, most likely rather sudden upon the first splitting of the capsule, and twist and turn among the spores as they dry. When the capsule opens, the elaters are filled with water, but as the capsule dries, so do the elaters. This causes the thin areas of the elaters to be pulled inward, distorting them. As the space between the thickenings is pulled in, the spirals tighten until the entire elater becomes a tight, twisted helix. Physical forces keep trying to untwist them, but adhesion of water inside the elater cell wall resists this extension, creating tension. When the tension of the water column finally breaks, the elater extends to its original shape so violently that it springs free of the capsule, scattering spores as it does so. The pressure in the cellular water just prior to its release can be as high as 200-300 atmospheres in *Lophozia*. In the tiny *Cephaloziella*, spores can travel up to 4-5 cm (Douin 1914 in Schuster 1966) and in *Tritomaria quinquedentata* about 2.5 cm (Meylan in Schuster 1966).

In the leafy liverwort *Frullania dilatata*, elaters are attached to the capsule wall at both ends (Schuster 1966). When the capsule opens, the elaters are stretched, creating tension. Most likely further drying contributes to the tension until the inner ends suddenly release, providing a springboard from which spores are catapulted 1-2 cm above and out of the capsule. However, Schuster feels that most of the contribution of the elaters in this case is to loosen the spore mass.

In *Marchantia*, elaters twist and untwist, based on moisture changes. The capsules do not open along four distinct lines of dehiscence, but rather open irregularly into short lobes that bend back. Elaters twist as they dry and become entangled. When an elater becomes free of the others, it does so with a sudden movement that throws spores from the capsule, although the elater generally remains (Ingold 1939 in Schuster 1966). In other liverworts, such as *Pellia*, the spiral thickenings are not so thick and the movements are too subtle to accomplish much dispersal (Schuster 1966). Rather, release of pressure at the time of dehiscence seems to be responsible for at least some dispersal. However, even the subtle movement of elaters may serve to loosen spores from each other, making dispersal easier when something disturbs the stalk and capsule. (See chapter on dispersal.)

The Marchantiophyta can be divided into two classes (Figure 11), the **Marchantiopsida** (thallose liverworts; Figure 3, Figure 4) and **Jungermanniopsida**, the latter with two subclasses, the **Metzgeriidae** (mostly thallose liverworts; Figure 12), and the **Jungermanniidae** (mostly leafy liverworts; Figure 14, Figure 15). One could argue that these two classes should actually be separate phyla (Bopp & Capesius 1996), but most modern systematists disagree (Crandall-Stotler & Stotler 2000). Based on 18S rRNA genes for all bryophytes tested, the Marchantiopsida are clearly separated from the Jungermanniopsida, but the latter are in the same clade as the Bryophyta! Furthermore, the orders Metzgeriales and Jungermanniales are indicated on the same branch. We will leave these arguments for the future and describe the two classes of Marchantiopsida and Jungermanniopsida as comprising the Marchantiophyta.

Class Marchantiopsida

The **Marchantiopsida** possess a thallus that is dichotomously forked and generally several cells thick.

The upper (**dorsal**) tissue is loose, resulting from internal air spaces, and generally has pores (Figure 4, Figure 9). The lower (**ventral**) surface usually has two kinds of **rhizoids** (Figure 6), **smooth** ones and those with "pegs" (protrusions inward from the cell wall), and usually has scales. The capsule dehisces irregularly, or less commonly by means of an operculum of thin-walled cells, as in *Cyathodium*.

Members of the Marchantiopsida may have the archegonia raised on an umbrella-like **archegoniophore**, as in Marchantiaceae, or imbedded in the thallus, as in *Ricciocarpos* (Figure 5). Likewise, the antheridia may be imbedded in a splash platform atop an **antheridiophore**, as in *Marchantia*, or imbedded in the thallus, as in *Ricciocarpos*. Such elevation of antheridia within a **splash platform**, the **antheridial head**, in *Marchantia* presumably permits the sperm to be splashed away from the parent to land on the archegonial head that is just beginning to develop and is not yet elevated significantly. In *Marchantia*, this sexual expression is under the control of a small Y chromosome in the male, with no X chromosome, and a single X chromosome in the female (Lorbeer 1934). The life cycle of *Marchantia* is summarized in Figure 10.



Figure 3. *Preissia quadrata* (Marchantiopsida), a thallose liverwort. Photo by Janice Glime.

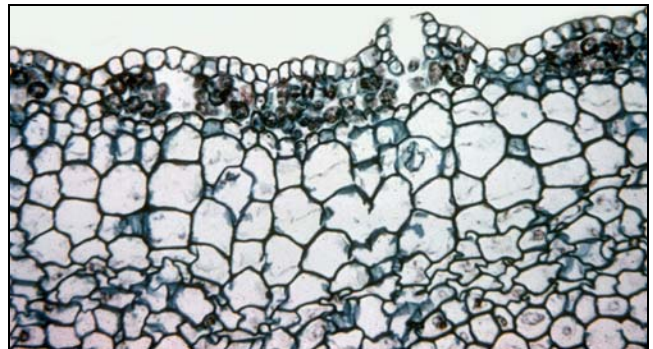


Figure 4. Cross section of thallose liverwort *Marchantia polymorpha* (Marchantiopsida) showing the internal air chambers, pores, and fragments of rhizoids. Note stacks of cells in internal air chambers, resembling spongy mesophyll of a maple leaf. Pores are surrounded with rings of cells 4-5 cells high that can, as a group, curve and close pores in a manner somewhat resembling that of guard cells in leaves. Photo from botany teaching collection, Michigan State University.

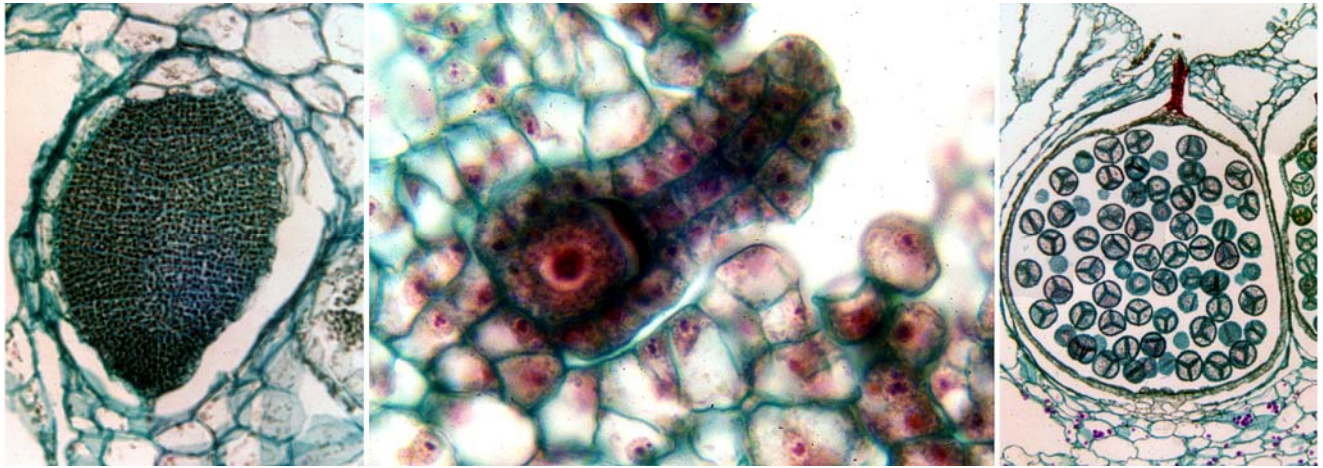


Figure 5. Reproductive structures of *Ricciocarpos natans* (Class Marchantiopsida). **Left:** Antheridium imbedded in thallus. **Middle:** Archegonium imbedded in thallus. **Right:** Spore tetrads in sporophyte imbedded within the thallus and still within the archegonial wall. Photos modified from Triarch.

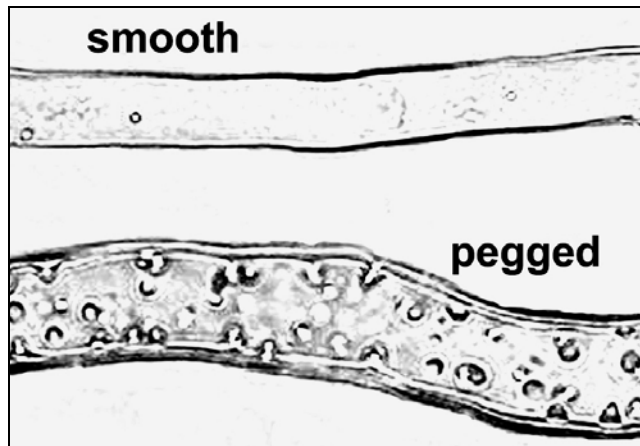


Figure 6. Smooth and pegged rhizoids of *Conocephalum conicum* in the Class Marchantiopsida. Photo with permission, modified from web site of Paul Davison, www2.una.edu/pdavis/bryophytes.htm.



Figure 7. *Marchantia polymorpha* (a thallose liverwort in Marchantiopsida) spore tetrads and elaters before spiral thickenings form. Photo from botany teaching collection at Michigan State University.

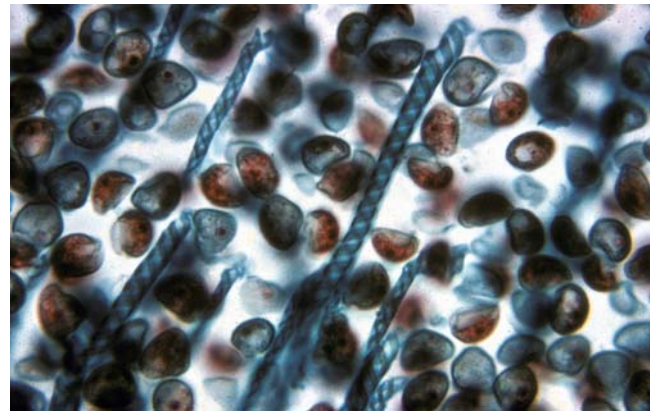


Figure 8. Spores and elaters with spiral thickenings from *Marchantia polymorpha*, a thallose liverwort (Marchantiopsida). Photo from botany teaching collection at Michigan State University.



Figure 9. *Conocephalum conicum*, a thallose liverwort in the Marchantiopsida. The polygon shapes delineate the internal chambers and the tiny dot visible in the middle of some is the pore. Photo by Janice Glime.

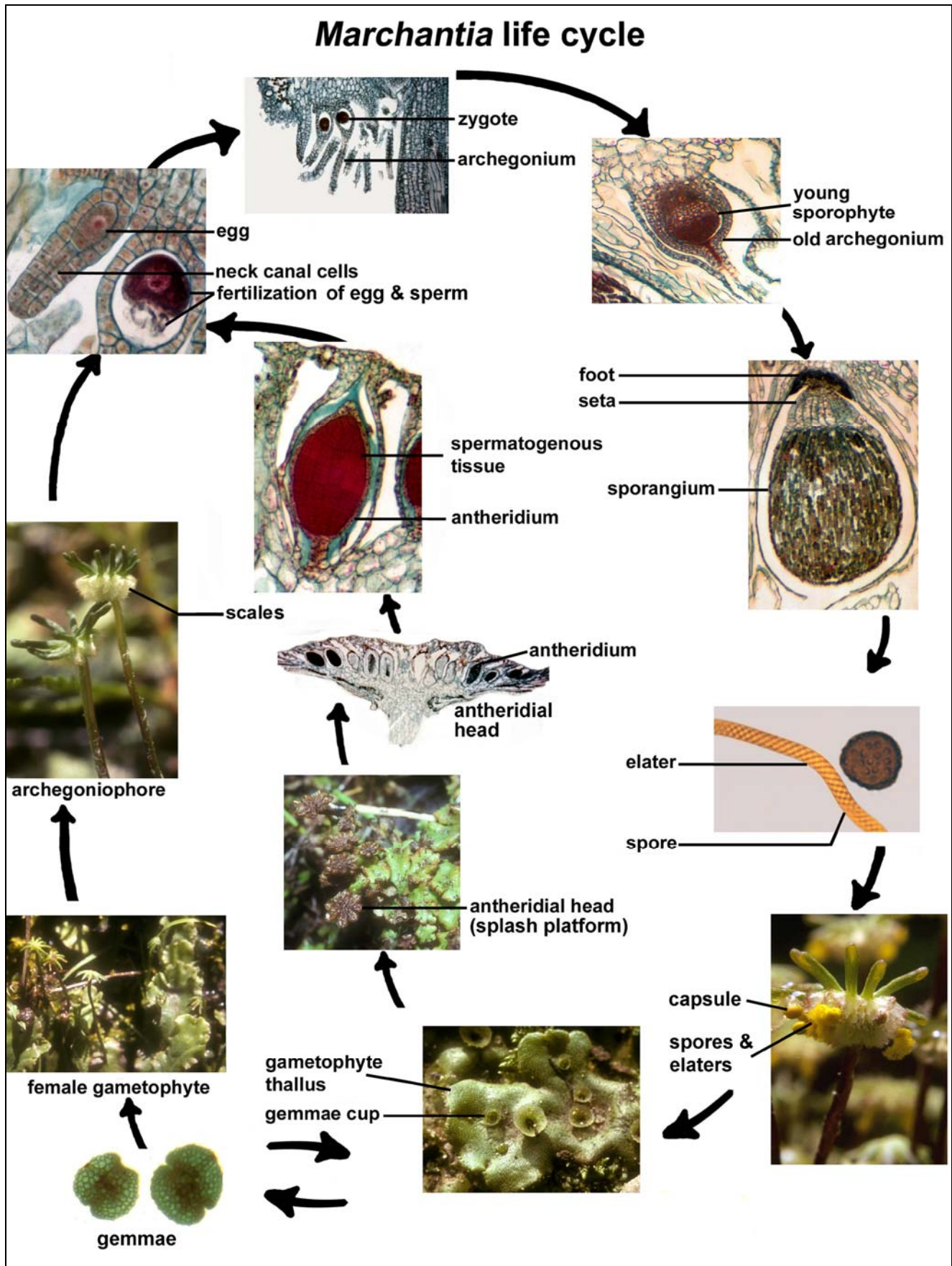


Figure 10. Life cycle of *Marchantia polymorpha*, showing dominance of the gametophyte generation. Photos by Janice Glime, photomicrographs from botany teaching collection of Michigan State University, and spore and elater modified from photo by Noris Salazar Allen.

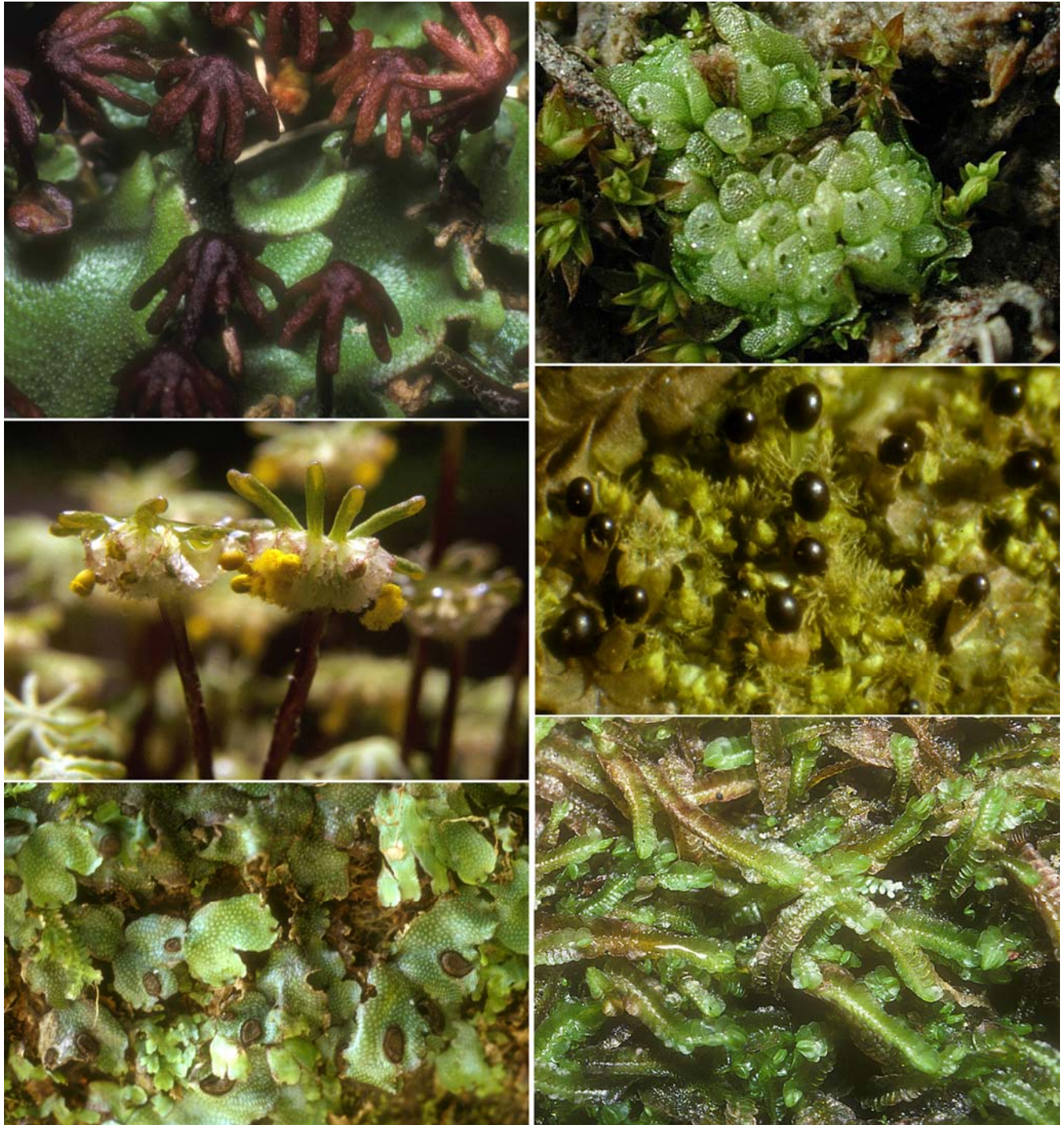


Figure 11. Examples of Marchantiophyta. **Left:** Marchantiopsida – **left upper:** *Marchantia polymorpha* with archegoniophores; **left middle:** mature sporophytes hanging from archegoniophores of *Marchantia polymorpha*; **left lower:** *Conocephalum conicum* showing antheridial patches on the thallus. **Right upper:** *Sphaerocarpus texanus* thallus (Marchantiopsida) with perigonia holding archegonia; **right middle:** *Blepharostoma trichophylla* (Jungermanniopsida), a leafy liverwort with finely divided leaves and protruding sporophyte capsules; **right lower:** *Odontoschisma prostratum* (Jungermanniopsida), a leafy liverwort. Photos by Janice Glime; upper right photo by Michael Lüth.

Class Jungermanniopsida

Two classes comprise the Jungermanniopsida. The subclass **Metzgeriidae** (Figure 12, Figure 13, Figure 19) are thalloid [except that *Fossombronina* appears leafy while having only one initial cell instead of 2-3 as in others (Figure 18, Renzaglia 1982)], but despite their thalloid nature, other features seem to place the Metzgeriidae within the Jungermanniopsida. They lack true dichotomous forking (although pseudodichotomies occur), and their tissues are solid, lacking internal air spaces. They also lack dorsal pores and **ventral scales**, and the **rhizoids** are all smooth and never in clumps. Cells often have **oil bodies** (Figure 17), although these disappear upon drying.

Members of the subclass **Jungermanniidae** are leafy and usually branching. They often have reduced underleaves (Figure 14) that at least in some cases can develop into a third row of normal leaves if the plant is supplied with an ethylene inhibitor (Basile & Basile 1983). The leaves are never more than one cell thick, never have a costa or rib, and unlike the mosses, are often toothed or lobed (Figure 15).

In the leafy liverworts, the leaf is only one-cell-thick but may be folded to create a pocket or pouch (**lobule**; Figure 16), usually on the lower side, but the smaller lobe may occur on the upper side in such genera as *Scapania*. The leaf cells generally contain **oil bodies**, membrane-bound, terpene-containing organelles unique to liverworts, but don't look for them in dry plants – they typically disappear. Rhizoids, unlike those in the Metzgeriidae, usually occur in clumps at bases of underleaves.

In all the phyla, the spore is a meiospore. These structures can be variously decorated and their size and decorations can contribute to their dispersal ability. Germination in liverworts is apparently inhibited inside the capsule, thus occurring only after **dehiscence** (splitting apart) and dispersal.

The spore, once finding a suitable condition of moisture and lighting, germinates. Here, the liverwort

sporeling differs from that of most mosses. In liverworts it is variable, even within orders, with the protonema ranging from **filamentous** to **thalloid**, but mostly forming only a few cells (Figure 20, Figure 21). In the leafy liverworts *Frullania moniliata* and *Drepanolejeunea*, as in all Porellales, the protonema is formed within the spore; in *Cephalozia otaruensis* it is a filamentous protonema; in many others it is thalloid (Nehira 1966). Liverworts differ markedly from mosses not only in most species having a thalloid rather than filamentous protonema (exceptions in some Cephaloziaceae), but in producing only one upright plant per protonema. Furthermore, unlike many mosses, they never produce protonemal **gemmae** or other protonemal **propagules** (Schofield 1985) and rarely reproduce by fragments (Crum 2001). Nevertheless, in all bryophytes the sporeling is quite different in structure and appearance from the mature gametophyte that will develop from it.



Figure 12. Thallose liverwort *Metzgeria conjugata* in the Class Jungermanniopsida, subclass Metzgeriidae. Photo by Michael Lüth.



Figure 13. *Cyathodium spruceanum*. **Left:** male plants; R = male receptacles. **Right:** female plants; ES = sporophytes; arrows = involucres. Photos by Noris Salazar Allen.



Figure 14. *Calypogeia integristipula* (Class Jungermanniopsida) showing the dorsiventral orientation of the plant and the underleaves. Photo by Michael Lüth.

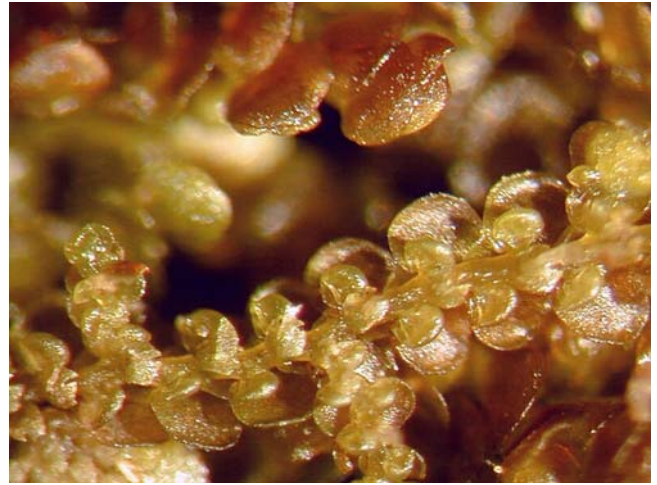


Figure 16. *Frullania dilatata* (Class Jungermanniopsida), a leafy liverwort showing the ventral (under) side of the stem with hood-shaped lobules under each leaf and underleaves on the stem. Photo by Michael Lüth.



Figure 15. *Bazzania trilobata*, a leafy liverwort in the Class Jungermanniopsida. Note the two-ranked leaves and top-bottom (dorsi-ventral) orientation. Photos by Janice Glime.

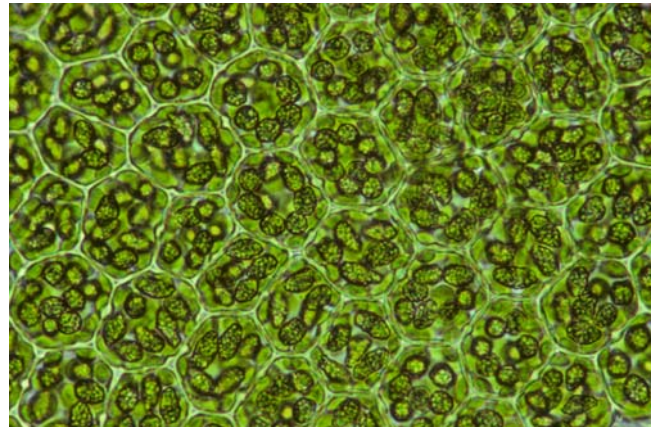


Figure 17. Leaf cells of the leafy liverwort *Frullania davarica* (Jungermanniopsida). Note the oil bodies resembling bunches of grapes and the numerous small chloroplasts clumped around the periphery of cells. Cell walls also have **trigones** (swellings in the walls). Photo by Zen Iwatsuki.



Figure 18. *Fossombronina husnotii*, a "leafy" liverwort in the Jungermanniopsida, subclass Metzgeriidae. Some members of this genus appear thallose (but ruffled), and their single apical initial and developmental pattern suggest a transition between the two growth types within the Jungermanniopsida. Photo by Michael Lüth.

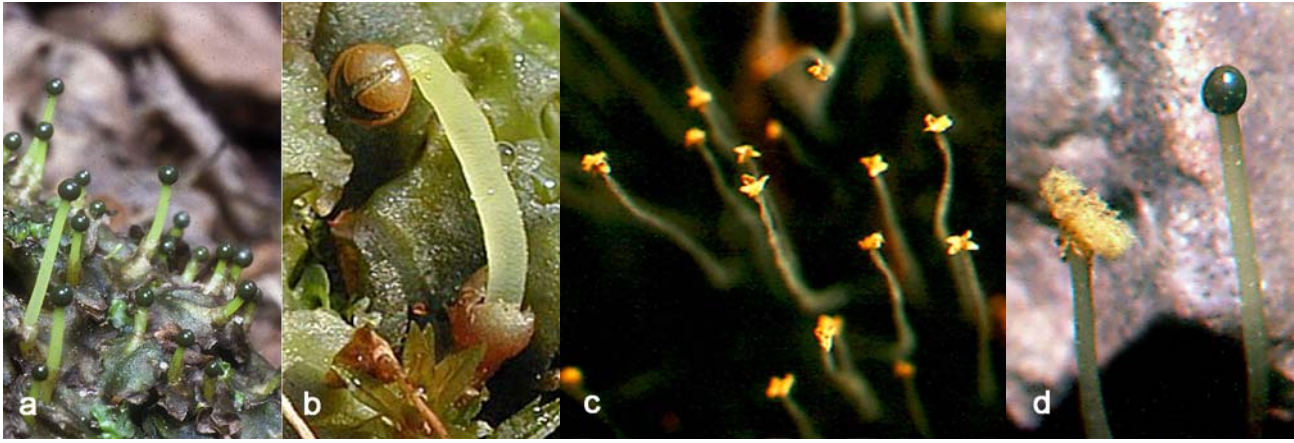


Figure 19. *Pellia*, a thaloid liverwort in the class Jungermanniopsida, subclass Metzgeriidae. Note the watery, colorless setae with the globose, inoperculate capsules. **a**: undehiscent capsules and setae. **b**: capsule splitting into four valves. **c**: dehiscing capsules showing four valves. **d**: dehiscing capsule (left) looking fuzzy due to elaters and undehiscent capsule (right). Photos a, c, & d by Janice Glime. Photo b by Michael Lüth.



Figure 20. Germinated spore and protonema stage of thaloid liverwort *Cyathodium foetidissimum*. Photo by Noris Salazar Allen.

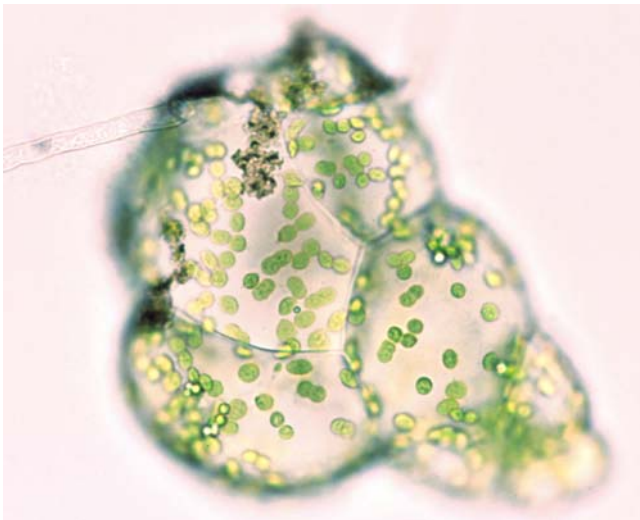


Figure 21. Thaloid protonema of the thallose liverwort *Cyathodium foetidissimum*. Photo by Noris Salazar Allen.

Within the Jungermanniopsida, the **gametophore**, or mature gametophyte, can be either of two forms, depending on the family. The thaloid form has a blade-like appearance and usually produces its antheridia and

archegonia within the thallus. The leafy liverworts produce their antheridia and archegonia along branches (Figure 22).

Mucilage filaments usually occur among the gametangia (Schofield 1985), presumably helping them to retain water and to help squeeze the antheridia when it is time for sperm to emerge.

Once reaching a female plant, the biflagellate sperm presumably swim, in all cases, to the archegonium. In some genera, for example the thallose *Aneura* (Marchantiopsida), it may take several hours for the sperm to travel a mere 10 mm (Showalter 1925 in Walton 1943). In fact, in many taxa, it is the **spermatocytes** (cells that become converted into sperm), prior to sperm release, that travel across the thallus by means of surface tension over the free water surface (Figure 22). This is at a much faster rate of 20 mm per minute (Muggoch & Walton 1942).

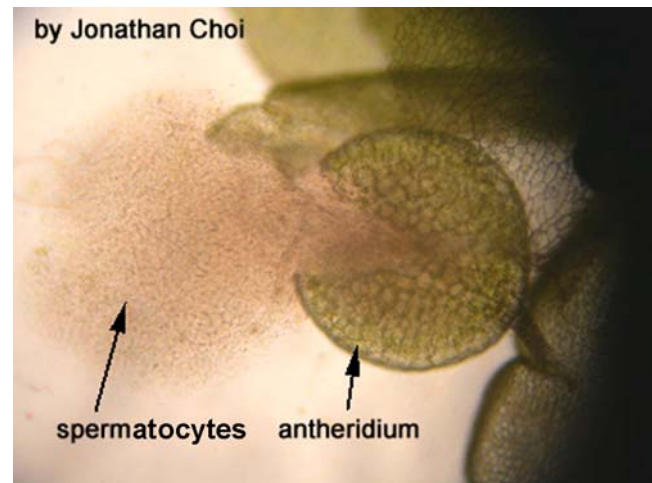


Figure 22. *Porella navicularis* releasing sperm. Photo with permission from Botany 321 website, www.botany.ubc.ca/bryophyte/LAB8.htm.

By contrast to these earlier observations of Muggoch and Walton, in *Pellia*, the emerging **spermatocytes**, in this case housing the sperm within a membrane) emerge from the dehiscing antheridium in grey masses. These masses spread rapidly across the wet surface, breaking apart as they reach the surface, with sperm emerging in about 15 seconds. It takes only 15 seconds for these spermatocytes

to reach the archegonial **involucre** (protective sheath of tissue of thallus origin surrounding single antheridium, archegonium, or sporophyte; Figure 23). Another 15 minutes is required for the free sperm to emerge from the spermatocyte. Thus, the sperm disperse and are ready to enter the archegonia in little more than 15 minutes from the time of antheridial dehiscence. Such rapid movement could not be achieved by the slow-swimming sperm, which would require hours to achieve the same distance, often failing to reach their destination before the necessary water was gone.

Following fertilization, the stalk supporting the archegonial head elongates and elevates the archegonial head several cm above the thallus. This is of little advantage, it would seem, until the sporophytes are mature and the spores ready for dispersal. At this time, the capsules (sporangia) split (with very few exceptions having a lid), revealing the spores and **elaters** (in liverworts, elongate one-celled structures with two spiral thickenings and associated with spores).

In Jungermanniidae, the antheridia are not imbedded, but occur at the bases of leaves, whereas the archegonia are at the ends of stems or branches, surrounded by a **perianth**, and that is again surrounded by an **involucre** of two **bracts** and often a **bracteole**, all of which are often joined. The capsule develops inside the **perichaetium** (modified leaves that surround the archegonia), but ultimately sits atop an elongate, **hyaline** (colorless), delicate **seta** (stalk; Figure 19) that soon withers away. The capsule itself opens by four valves and usually contains **elaters**.

By contrast to the mosses, liverworts lack a split-off **calyptra** (covering of capsule formed from upper part of torn archegonial wall) and the capsule matures while it is still immersed among the protecting leaves. As the capsule (sporangium) expands, the archegonial wall is ruptured and remains at the base of the sporangial stalk. In the Marchantiopsida taxa having thalloid stalks supporting the archegonia and ultimately the capsules (e.g. *Marchantia*), the sporophyte stalk remains small and is typically not visible among elevated scales and thallus, whereas in the Jungermanniopsida it is conspicuous. In leafy taxa and other thalloid taxa this sporangial stalk elongates only after the capsule matures. The stalk elongates (in leafy liverworts) by rapid (3-4 days) elongation of the watery stalk (**seta**) cells (Bold *et al.* 1987) and extends the capsule away from the plant, using turgor pressure within the delicate cells to maintain this position. This **seta** supports and extends the capsule of most mosses and liverworts.

The spores are all of equal maturity and all ready for dispersal at the same time (Schofield 1985). Once the spores are shed, the deliquescent stalk soon collapses and the capsule disintegrates.

Liverworts frequently produce gemmae that occur on leaves of leafy liverworts (Figure 24, Figure 25) or on the thallus of thallose taxa (Figure 26). These permit the plants to reproduce asexually in places where sexual reproduction is unsuccessful. As will be discussed later, this is especially important when the sexes are on separate plants.

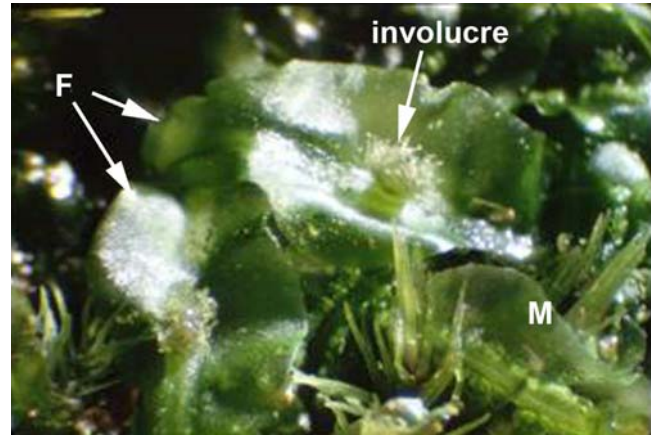


Figure 23. *Pallavicinia lyellii* (Metzgeriidae) showing filamentous fringe of the involucre where archegonia are located on the thallus. **F** denotes female gametophyte; **M** denotes male gametophyte. Photo by Noris Salazar Allen.



Figure 24. *Tritomaria exsecta* (Jungermanniidae) showing gemmae on leaf tips. Photo by Michael Lüth.

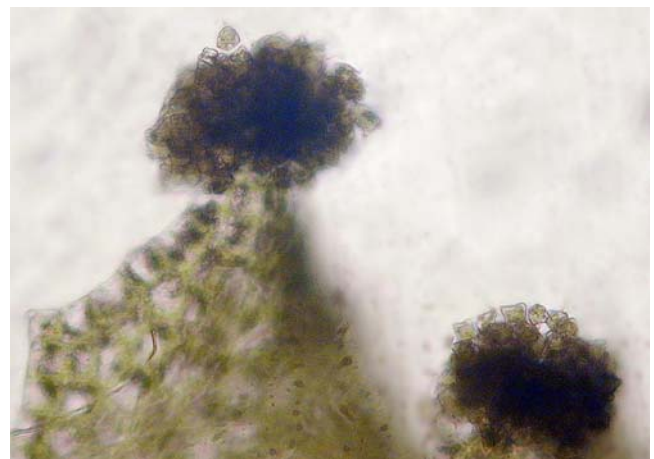


Figure 25. Microscopic view of *Tritomaria exsectiformis* leaf tips with gemmae. Photo by Michael Lüth.



Figure 26. Arrow indicates gemmae on the thallus of *Blasia pusilla*. Photo by Michael Lüth.

Summary

Marchantiophyta are distinguished from the phylum Bryophyta by their **dorsi-ventral orientation, unicellular rhizoids, inoperculate capsules, absence of a columella, and no stomata** in the capsule. Marchantiophyta are generally considered to have two classes: **Marchantiopsida** (thallose liverworts) and **Jungermanniopsida**, including **Metzgeriidae** (thallose liverworts) and **Jungermanniidae** (leafy liverworts).

Marchantiophyta have a dominant gametophyte generation with a dependent, short-lived sporophyte. The life cycle involves a **protonema** that develops from the germinating spore, becoming thalloid or globose in most liverworts. The protonema produces a **bud** that develops into a **leafy or thallose plant**.

Gametophytes produce **archegonia** and/or **antheridia** and the **embryo** develops within the archegonium.

Sporophytes remain attached to the gametophyte and produce **spores** by **meiosis**. Marchantiophyta produce spores from the sporophyte only once, *i.e.* simultaneously. These spores are dispersed, in most genera, by **elaters** that are produced among the spores and that have spiral thickenings, causing them to twist as moisture changes.

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. Rob Gradstein suggested clarifications and Christine Cargill provided important information and references. Heino Lepp of the Australian National Herbarium shared his preliminary website information on elaters with me, helping me to find original sources on their mechanisms of dispersal.

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