CHAPTER 2-3
MARCHANTIOPHYTA

TABLE OF CONTENTS

Distinguishing Marchantiophyta ................................................................. 2-3-2
Elaters ........................................................................................................ 2-3-3
Leafy or Thallose? .................................................................................. 2-3-5
Class Marchantiopsida ........................................................................ 2-3-5
Thallus Construction ........................................................................... 2-3-5
Sexual Structures .................................................................................. 2-3-6
Sperm Dispersal .................................................................................... 2-3-8
Class Jungermanniopsida ................................................................. 2-3-12
Metzgeriidae ......................................................................................... 2-3-13
Jungermanniidae .................................................................................. 2-3-14
Summary ............................................................................................... 2-3-22
Acknowledgments ................................................................................. 2-3-23
Literature Cited ..................................................................................... 2-3-23
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.

Because of the long tradition of considering these to be bryophytes, liverworts (and hornworts) are still lumped into that group for a vernacular name instead of creating a new name that is unfamiliar to everyone. As a phylum, Marchantiophyta are distinguished from the phylum Bryophyta by their dorsi-ventral orientation (Figure 1, Figure 12), unicellular rhizoids (Figure 2), inoperculate capsules [i.e. lacking a lid (Figure 3), although there are a few exceptions], absence of a columella in the center of the capsule (Figure 4), 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 (Figure 11-Figure 12), whereas in mosses it elongates first, then develops the capsule. The spores, as in mosses, are all produced simultaneously by meiosis (Figure 5). The capsule, unlike that of most mosses, dehisces typically by splitting into four valves (Figure 6), but not in the class Marchantiopsida, revealing spores mixed with elaters (thickened elongate cells with spiral wall thickenings that twist in response to drying; Figure 6-Figure 7).
Elaters

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 suddenly 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 (Figure 8). In the tiny Cephaloziella (Figure 9), 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* (*Jungermanniopsida*), elaters attach 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 (see Figure 6), providing a springboard from which spores are catapulted 1-2 cm above and out of the capsule. However, Schuster felt that most of the contribution of the elaters in this case is to loosen the spore mass.

In *Marchantia* (Figure 10), elaters twist and untwist, based on moisture changes. The capsules do not open along four distinct lines of dehiscence (compare Figure 10 to Figure 14), but rather open irregularly into short lobes that bend back. Elaters twist as they dry and become entangled (Figure 10). 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* (Figure 11-Figure 13), 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 (Figure 14). (See chapter on dispersal.)
Chapter 2-3: Marchantiophyta

Leafy or Thallose?

The Marchantiophyta can be divided into two classes (Figure 40), the Marchantiopsida (thallose liverworts; Figure 15 & Figure 18) and Jungermanniopsida, the latter with two subclasses, the Metzgeriidae (mostly thallose liverworts; Figure 41), and the Jungermanniidae (mostly leafy liverworts; Figure 47 & Figure 48). 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. I will leave these arguments for the future and describe the two classes of Marchantiopsida and Jungermanniopsida as comprising the Marchantiophyta.
The thallus in Marchantiopsida has some resemblance to the leaf of a tracheophyte. The air chambers have stacks of photosynthetic cells (Figure 18) that resemble the spongy mesophyll of a tracheophyte leaf. The pores permit gas exchange into and out of these photosynthetic cells.

Figure 18. 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, somewhat resembling the spongy mesophyll of a tracheophyte 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, with permission.

Figure 19. *Marchantiopsida* thallus showing multiple layers, rhizoids, and dorsiventral orientation. Photo by Smith through Wikimedia Commons.

Figure 20. *Marchantia polymorpha* thallus pore. Photo by George Shepherd through Creative Commons.

Figure 21. 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>, with permission.

Figure 22. *Marchantia polymorpha* cross section showing ventral surface with scale and rhizoids. Photo from University of British Columbia website, with permission.

**Sexual Structures**

Members of the Marchantiopsida may have the archegonia imbedded in the thallus, as in *Ricciocarpos* (Figure 23), or raised on an umbrella-like archegoniophore (Figure 24-Figure 25), as in Marchantiaceae. Likewise, the antheridia may be imbedded in the thallus, as in *Ricciocarpos* (Figure 23), or imbedded in a splash platform atop an antheridiophore (Figure 26-Figure 29), as in *Marchantia*. The archegoniophore and antheridiophore are made by the infolding of the thallus. The "suture" along the vertical surface, and often scales and rhizoids, can be seen along the stalk where they stick out from the stalk (Figure 25). 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 (Figure 27-Figure 31). Once the sperm are in the vicinity of the archegonia, the archegonium attracts them with a protein (Harvey-Gibson & Miller-Brown 1927).
Figure 23. Reproductive structures of *Ricciocarpos natans* (Class Marchantiopsida). **Left:** Antheridium imbedded in thallus. **Middle:** Archegonium imbedded in thallus. **Right:** Spore tetrads (following meiosis) in sporophyte imbedded within the thallus and still within the archegonial wall. Photos modified from Triarch.

Figure 24. *Marchantia polymorpha* archegoniophores. Photo by Janice Glime.

Figure 25. *Marchantia polymorpha* archegoniophore showing scales and rhizoids along the stalk. Photo by Janice Glime.

Figure 26. Antheridiophores of *Marchantia polymorpha* elongating. Photo by Des Callaghan, with permission.

Figure 27. Antheridiophores and developing archegoniophores on thalli of *Marchantia polymorpha*. Note the "button" heads just beginning on some thalli. Photo by Bob Klips, with permission.
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 39.

**Sperm Dispersal**

But just how far can these tiny sperm travel? Showalter (1926) found that the sperm of *Riccardia pinguis* could swim at a rate up to one centimeter in one hour, but more often it was considerably slower. Furthermore, their maximum swimming endurance time was only six hours.

Duckett and Pressel (2009) found that classical knowledge of *Marchantia* fertilization did not always fit reality. Following a fire, *Marchantia polymorpha* (Figure 27) spread rapidly. Both gemmae and sexual reproduction are most likely responsible. Rather than relying entirely on splash from antheridiophores, the sperm are actively discharged from the antheridial heads to as much as 15 cm above it (Shimamura et al 2008). Duckett and Pressel found that every archegoniophore in this large patch had achieved fertilization, some of which were several decimeters from the nearest male. Some archegonial heads bore as many as 30-50 sporophytes with more mature ones near the ends of the arms and younger ones nearer the central stalk. Dye splashed on the antheridial heads landed up to 30 cm away, hardly explaining the distances at which some archegonia were fertilized, more than 90% of the dye solution was readily absorbed by the antheridial heads. The dye quickly moved to the ground level (within
Within an hour the dye had spread throughout the rhizoids of the entire 10 cm diameter colony. Upward movement to archegonial heads was a bit slower but nevertheless reached the heads in 30-60 minutes.

As early as 1950, Benson-Evans observed the remarkable dispersal of spermatozoids from *Conocephalum conicum* (Figure 32). She found that they are "vigorously" dispersed into the air through an ejection mechanism, but also that mites, known as dispersal vectors in other Marchantiales, were probably not involved. She found that the dry antheridia, such as those following a hot day, would eject the spermatozoids in a fine mist that occurred in regular puffs. If these plants were put into direct sunlight, the activity increased enough that the packets of sperm were visible to the unaided eye.

Shimamura *et al.* (2008) have successfully filmed the remarkable dispersal of sperm from the antheridia (Figure 32) of *Conocephalum conicum* (Figure 32). In *Conocephalum*, there is no splash platform, and instead the sperm are ejected from the antheridium in a cloud that rises into the air several centimeters (Shimamura 2008), a phenomenon originally described by Cavers (1903), and again by Muggoch & Walton (1942) and Benson-Evans (1950). In Hiroshima, Japan, these sperm are typically dispersed in April to May. Shimamura (pers. comm. 2008) relayed to me that they were able to detect many airborne sperm on a sunny day after a rain shower. After a week of dry, sunny conditions, sperm were dispersed following a rainy day, resulting in most of the mature antheridiophores being empty. In the lab, antheridia can be persuaded to release their sperm by misting them. The intense lighting for photography also seemed to help. Initially, the sperm in these droplets are non-motile. Touching the droplets causes them to swim (Masaki Shimamura, Bryonet 3 January 2008), suggesting that these might be packets that must be broken for the sperm to begin swimming (Muggoch & Walton 1942) (see Figure 79).

At this stage, the archegoniophore has not extended and the archegonia are near the main thallus (Figure 33), making transfer of sperm easier. As in our traditional understanding of *Marchantia*, the archegoniophore elongates following fertilization (Figure 34) and the capsules form on the underside of the archegonial head (Figure 35-Figure 37), extending from the archegonial wall. Des Callaghan has provided us with a film of liverwort sperm swimming <http://youtu.be/Jdh8flxvZgk>, demonstrating how they are able to reach the archegonia. Splashing can bring them close to the archegonia, but they must swim to reach the archegonial neck and enter it.

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**Figure 32.** *Conocephalum conicum* males showing antheridial heads. The polygon shapes delineate the internal chambers and the tiny dot visible in the middle of some is the pore. Photo by John Hribljan, with permission.

**Figure 33.** *Conocephalum conicum* showing young archegoniophores, probably before they are mature enough for fertilization. Photo by Dick Haaksma, with permission.

**Figure 34.** *Conocephalum conicum* archegoniophores with elongated stalks. Photo by Janice Glime.

**Figure 35.** *Conocephalum conicum* (Marchantiopsida) archegoniophores with capsules. Photo by Hermann Schachner through Wikimedia Commons.
Like *Marchantia* (Figure 18, Figure 20), *Conocephalum* has a spongy photosynthetic layer in the thallus (Figure 38). The life cycle for *Marchantia* applies equally well to *Conocephalum*, except for the lack of an antheridiophore, and is illustrated in Figure 39. Sexual structures of *Cyathodium spruceanum* (*Marchantiopsida*) are illustrated in Figure 46. Examples of species of *Marchantiopsida* and *Jungermanniopsida* are in Figure 40.

Figure 36. Mature archegonial head of *Conocephalum salebrosum*, showing capsules. Photo by Barry Stewart, with permission.

Figure 37. *Conocephalum conicum* capsules on ventral side of archegonial head. Photo by Hermann Schachner through Wikimedia Commons.

Figure 38. Cross section of thallus of *Conocephalum conicum* showing photosynthetic cells. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.
Figure 39. 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.
Class Jungermanniopsida

Jungermanniopsida lack dichotomous forking, internal air spaces, dorsal pores, ventral scales, and pegged rhizoids. They may be ribbon-like, thallose, or leafy. Many have oil bodies (isoprenoid essential oils). The role of oil bodies is unclear, but they may help to prevent desiccation damage or to protect against UV light. Yet, those seem like strange functions if the oil bodies disappear upon drying. On the other hand, species that typically live in dry habitats seem less subject to oil body disappearance. Goebel and Balfour (1905) suggested that they are the source of the unique odors found in many of the liverworts, particularly the thallose taxa. The Jungermanniopsida are divided into two subclasses: Metzgeriidae and Jungermanniidae.
Metzgeriidae

Plants in the subclass **Metzgeriidae** (Figure 41-Figure 45) are thalloid or ribbon-like, except that some members of *Fossombronia* (Figure 44) appear leafy, while having only one initial cell instead of 2-3 as in other members (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 as in **Jungermanniidae**. Cells often have oil bodies (Figure 49), although these disappear upon drying.

Figure 41. Thallose liverwort *Metzgeria conjugata* in the Class **Jungermanniopsida**, subclass **Metzgeriidae**. Photo by Michael Lüth, with permission.

Figure 42. *Metzgeria furcata* thallus cross section. Photo by Ralf Wagner <www.dr-rafl-wagner.de>, with permission.

Figure 43. Neotropical *Metzgeria*. Photo by Michael Lüth, with permission.

Figure 44. *Fossombronia 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, with permission.

Figure 45. *Pellia*, a thalloid liverwort in the class **Jungermanniopsida**, subclass **Metzgeriidae**. Note the watery, colorless setae with the globose, inoperculate capsules. a: undehisced capsules and setae. b: capsule splitting into four valves. c: dehisced capsules showing four valves. d: dehisced capsule (left) looking fuzzy due to elaters and undehisced capsule (right). Photos a, c, & d by Janice Glime. Photo b by Michael Lüth, with permission.
Figure 46. *Cyathodium spruceanum* (Marchantiopsida). **Left:** male plants; R = male receptacles. **Right:** female plants; ES = sporophytes; arrows = involucres. Photos courtesy of Noris Salazar Allen.

**Jungermanniidae**

Members of the subclass *Jungermanniidae* are leafy and usually branching. These are the leafy liverworts. They often have reduced underleaves (Figure 47) 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 48). The leaves typically have oil bodies (Figure 49), membrane-bound, terpene-containing organelles unique to liverworts, in all their cells, although these usually disappear upon drying.

Figure 47. *Calypogeia integristipula* (Class *Jungermanniopsida*) showing the dorsiventral orientation of the plant and the underleaves. Photo by Michael Lüth, with permission.

Figure 48. *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 49. 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, with permission.

In the leafy liverworts, the leaf may be folded to create a pocket or pouch (lobule; Figure 50), usually on the lower side, but the smaller lobe may occur on the upper side in such genera as *Scapania* (Figure 51). Rhizoids, unlike those in the *Metzgeriidae*, usually occur in clumps at bases of underleaves (Figure 52).

In all the bryophyte phyla, the spore is a meiospore (produced by meiosis and therefore 1n; Figure 53-Figure 55). These structures can be variously decorated and their size and decorations can contribute to their dispersal ability. Germination (Figure 55) in liverworts is apparently inhibited inside the capsule, thus occurring only after capsule dehiscence (splitting apart) and spore dispersal (Figure 56-Figure 58).

Figure 50. *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, with permission.

Figure 51. *Scapania gracilis* showing leaves folded up to the dorsal side. Photo by Jan-Peter Frahm, with permission.

Figure 52. *Chiloscyphus polyanthus* with a clump of rhizoids at the base of the underleaf. Photo by Paul Davison, with permission.

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Figure 53. *Porella navicularis* capsule with meiospores and elaters. Photo from University of British Columbia website, with permission.
Figure 54. Noterocladia confluens (Metzgeriidae) meiospores and elaters. Photo by George Shepherd, through Creative Commons.

Figure 55. Fossombronia angulosa protonema emerging from spore. Photo by Plant Actions through Eugenia Ron Alvarez, with permission.

Figure 56. Lophocolea capsule. Photo by George Shepherd, through Creative Commons.

Figure 57. Lophocolea capsule dehiscing. Photo by George Shepherd, through Creative Commons.

Figure 58. Lophocolea capsule fully open into four valves. Photo by George Shepherd, through Creative Commons.

The spore, once finding a suitable condition of moisture and lighting, germinates (Figure 55-Figure 60). Here, the liverwort sporeling differs from that of most mosses. In liverworts the protonema is variable, even within orders, with the protonema ranging from filamentous to thalloid, but mostly forming only a few cells (Figure 63-Figure 60).

In the leafy liverworts Frullania moniliata and Drepanolejeunea, as in all Porellales, the protonema is formed within the spore (endosporic); in Cephalozia otaruensis it is an ectosporic filamentous protonema; in most of the liverworts it is ectosporic (developing outside the spore) and thalloid (Figure 60-Figure 64) (Nehira 1966).

Liverworts differ markedly from mosses not only in most species having a thalloid rather than filamentous protonema (exceptions in some Cephaloziaaceae), 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). [See Glime (1970) for a new plant produced by a fragment in Scapania undulata (Figure 65)]. Nevertheless, in all bryophytes the sporeling is quite different in structure and appearance from the mature gametophyte that will develop from it.
Chapter 2-3: Marchantiophyta

But what links the thallose liverworts to the leafy ones? Steenbock et al. (2011) reported an interesting find from Vancouver Island, British Columbia, Canada. In the Eocene flora, they found a liverwort unlike any currently known, either as fossils or extant. This liverwort had three-ranked leaves arranged in a spiral, with the underleaves larger than the lateral leaves. The rhizoids were in fascicles associated with all three ranks of leaves. These and other characters caused them to name a new family, the Appianaceae, based on the name of the type locality at the
Appian Way. This arrangement of leaves is reminiscent of the leaf arrangement in *Haplomitrium* (Figure 66-Figure 67). The genus *Treubia* (Figure 68) is yet another unusual liverwort (Anonymous 2010) and appears to be one of the basal groups among liverworts. This liverwort might be described as a thallus with leaves. It is intermediate between thallose and leafy liverworts and is most closely related to *Haplomitrium*.

Within the Jungermanniopsida, the *gametophore*, or mature gametophyte, can be either of two forms, depending on the family. The thalloid form has a blade-like appearance and usually produces its antheridia and archegonia within the thallus. The leafy liverworts produce their antheridia (Figure 69-Figure 72) and archegonia (Figure 73-Figure 78) along branches.
Figure 72. *Porella* sp. branch showing location of antheridia. Photo by Paul Davison, with permission.

Figure 73. *Lophocolea cuspidata* in its log habitat. Photo from Botany 321 at University of British Columbia website, with permission.

Figure 74. *Jungermannia evansii* archegonia at leaf base. Photo by Paul Davison, with permission.

Figure 75. *Lophocolea cuspidata* archegonia. Photo from Botany 321 at University of British Columbia, website, with permission.

Figure 76. *Porella* archegonia in perianth. Photo by Paul Davison, with permission.

Figure 77. *Porella navicularis* archegonium. Photo by Jannah Nelson through Botany 321, University of British Columbia website, with permission.
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 79). This is at a much faster rate of 20 mm per minute (Muggoch & Walton 1942).

By contrast to these earlier observations of Muggoch and Walton (1942), 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 80). 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 where the capsule enlarges. This is of little advantage, it would seem, until the sporophytes are mature and the spores ready for dispersal. When the spores are mature, the capsules (sporangia) split (with very few exceptions having a lid), revealing the spores and elaters (in Marchantiophyta, 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 (Figure 81), 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 82-Figure 84) that soon withers away. The capsule itself opens by four valves and usually contains elaters.

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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 contrast to the Marchantiopsida taxa that may have thalloid stalks supporting the archegonia and ultimately the capsules (e.g. Marchantia), and the sporophyte stalk remains small and is typically not visible among elevated scales and thallus, in the Jungermanniopsida the sporophyte stalk is conspicuous. In leafy taxa (Jungermanniidae) 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 (Figure 84), 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 85-Figure 90) or on the thallus of thallose taxa (Figure 91). These permit the plants to reproduce asexually in places where sexual reproduction is unsuccessful. As will be discussed in a later chapter, this is especially important when the sexes are on separate plants. These gemmae are often useful for taxonomic purposes because they have a variety of shapes and colors.
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.
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Chapter 2-3: Marchantiophyta 2-3-23


Chapter 2-3: Marchantiophyta 2-3-23


Chapter 2-3: Marchantiophyta 2-3-23


Chapter 2-3: Marchantiophyta 2-3-23
