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CHAPTER 2-3
MARCHANTIOPHYTA

TABLE OF CONTENTS

CHAPTER 2-3

MARCHANTIOPHYTA

Figure 1. ***Symphogyna podophylla*** (Phylum **Marchantiophyta**, Class **Jungermanniopsida**, subclass **Metzgeriidae**) in New Zealand, showing dorsiventral 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.

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).

Figure 2. ***Fossombronia*** rhizoids. Note that these rhizoids are unicellular, and the ones in this genus are purple by nature. Photo by Paul Davison, with permission.

Figure 3. ***Marchantia polymorpha*** archegonial head showing inoperculate capsule in lower right. Photo by George Shepherd through Creative Commons.

Figure 4. Capsule, lacking cell wall, of ***Marchantia polymorpha***. Photo from Michigan State University Botany Department teaching collection, with permission.

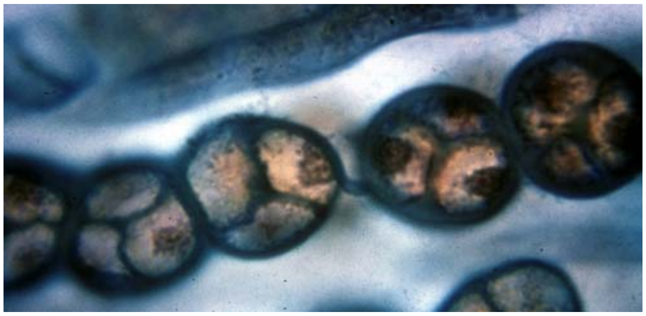

Figure 5. ***Marchantia polymorpha*** spore tetrads and one elater (upper) before spiral thickenings form. Photo from botany teaching collection at Michigan State University, with permission.

Elaters

Elaters are notably absent in the thallose liverworts **Ricciaceae** and **Sphaerocarpales** (***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).

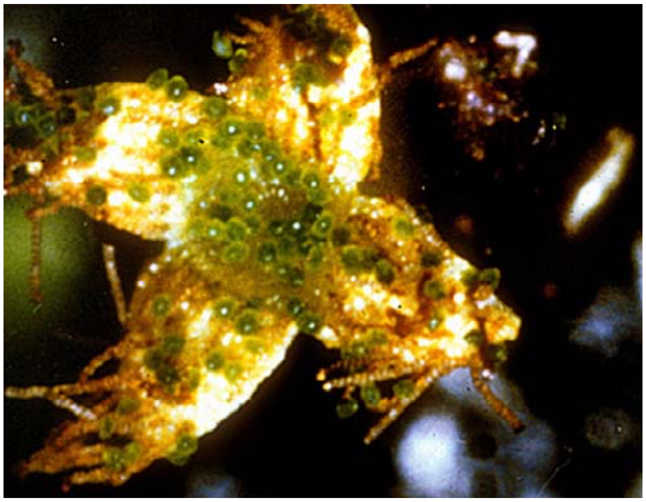

Figure 6. Open valvate capsule of the leafy liverwort ***Frullania kagoshimensis*** (Class **Jungermanniopsida**) showing spores and elaters and no columella. Photo by Zen Iwatsuki, with permission.

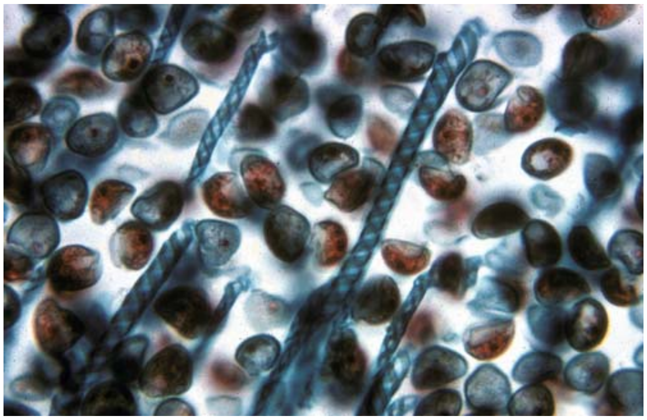

Figure 7. Spores and elaters with spiral thickenings from ***Marchantia polymorpha*** (**Marchantiopsida**). Photo from botany teaching collection at Michigan State University, with permission.

Figure 8. ***Cephaloziella hampeana*** with closed (black) and open (brown) capsules, a genus in which spores can travel 4-5 cm. Photo by David T. Holyoak, with permission.

Figure 9. ***Lophozia incisa*** with capsules, a species whose capsules open after building up pressure of 200-300 atmospheres. Photo by Tab Tannery, through Creative Commons.

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.)

Figure 10. ***Marchantia polymorpha*** archegoniophore showing unopened capsule on right and open capsule on left with elaters emerging. Photo by George Shepherd through Creative Commons.

Figure 11. ***Pellia epiphylla*** (**Jungermanniopsida**) with young capsule emerging from perianth, before seta elongation. Photo through Biopix, through Creative Commons.

Figure 12. ***Pellia epiphylla*** (**Jungermanniopsida**) with capsules on elongated setae, from southern Europe. Photo by Michael Lüth, with permission.

Figure 13. ***Pellia epiphylla*** (**Jungermanniopsida**) with capsule wall peeled back and elaters exposed. Photo by Malcolm Storey from <www.discoverlife.org>, through Creative Commons.

Figure 14. ***Noteroclada confluens*** (**Jungermanniopsida**) elaters and spores. Photo by George Shepherd through Creative Commons.

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 49). 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**.

Figure 15. ***Preissia quadrata*** (**Marchantiopsida**), a thallose liverwort, showing antheridiophores. Photo by Janice Glime.

Class Marchantiopsida

Thallus Construction

The **Marchantiopsida** possess a thallus that is dichotomously forked (Figure 12) and generally has pores (Figure 16-Figure 18). The thallus is several cells thick and the upper (**dorsal**) tissue is loose, resulting from internal air spaces (Figure 18-Figure 20). The lower (**ventral**) surface usually has two kinds of **rhizoids** (Figure 19, Figure 21-Figure 22), **smooth** ones and those with "**pegs**" (protrusions inward from the cell wall), and usually has scales (Figure 22). The capsule dehisces irregularly (Figure 13), or less commonly by means of an operculum of thin-walled cells, as in ***Cyathodium***.

Figure 16. ***Marchantia chenopoda*** pores. Photo by George Shepherd through Creative Commons.

Figure 17. ***Marchantia chenopoda*** pores. Photo by George Shepherd through Creative Commons.

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.

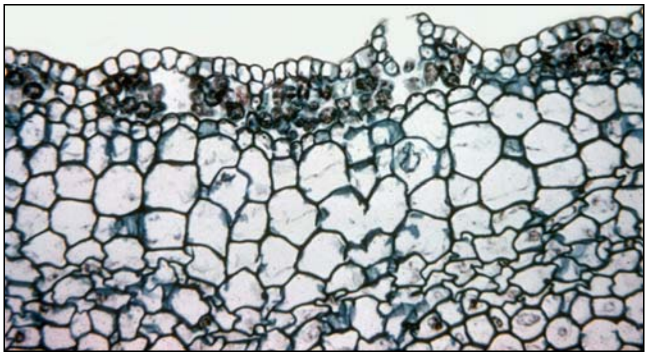

Figure 18. Cross section of thallose liverwort ***Marchantia polymorpha*** (**Marchantiopsida**) showing the internal air chambers, pores, and fragments of rhizoids. Note stacks of cells in internal air chambers, somewhat resembling the spongy mesophyll of a tracheophyte leaf. Pores are surrounded with 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.

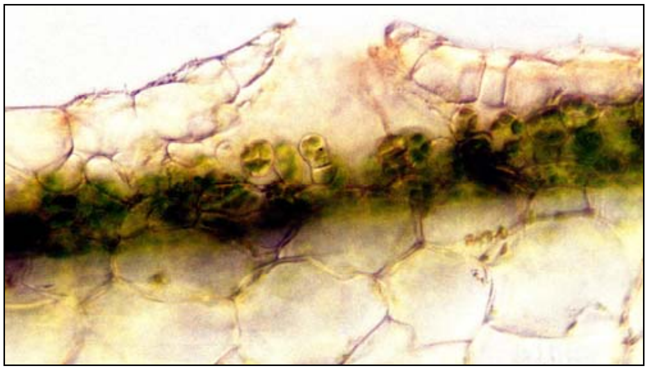

Figure 20. ***Marchantia polymorpha*** thallus pore. Photo by George Shepherd through Creative Commons.

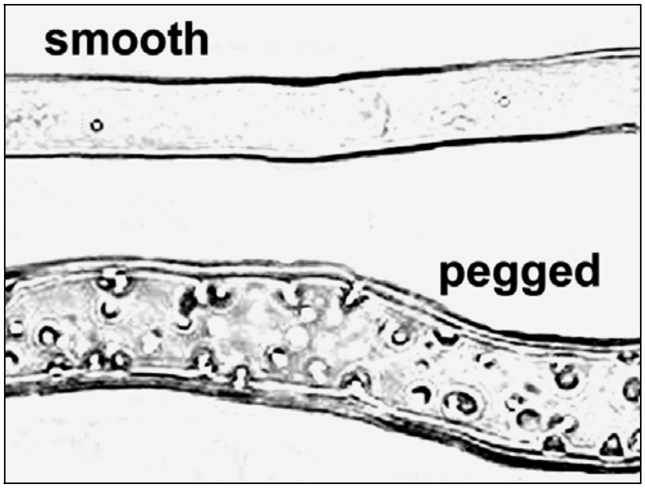

Figure 21. Smooth and pegged rhizoids of ***Conocephalum conicum*** in the Class **Marchantiopsida**. Photo with permission, modified from web site of Paul Davison, <www2.una.edu/pdavis/bryophytes.htm>, with permission.

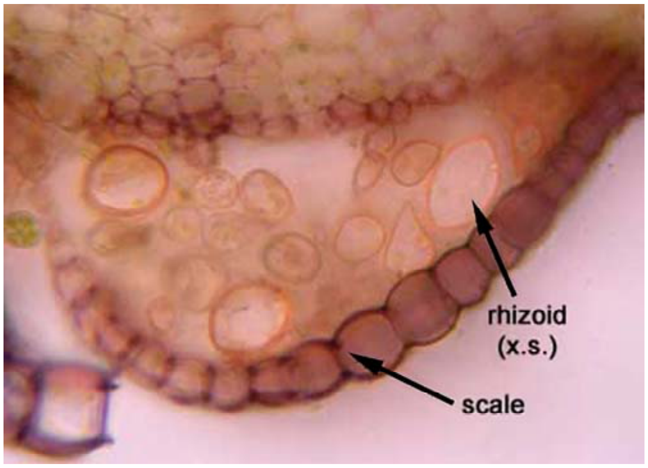

Figure 22. ***Marchantia polymorpha*** cross section showing ventral surface with scale and rhizoids. Photo from University of British Columbia website, with permission.

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 28-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.

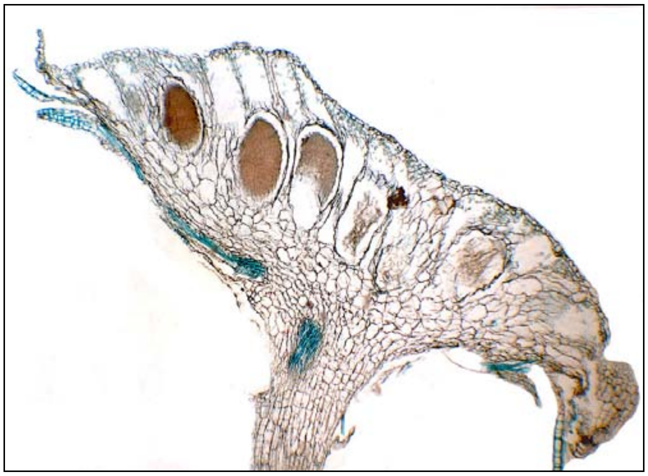

Figure 28. ***Marchantia polymorpha*** antheridial head. Photo by George Shepherd through Creative Commons.

Figure 29. ***Marchantia polymorpha*** antheridium opening to the upper surface of the antheridial head. Photo from Michigan State University teaching collection, 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.

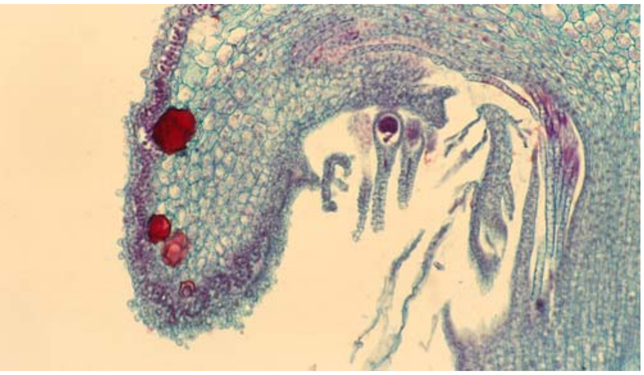

Figure 30. **Archegonial head** of ***Marchantia polymorpha*** with archegonia hanging down from the under side. Photo by from Plant Actions through Eugenia Ron Alvarez, with permission.

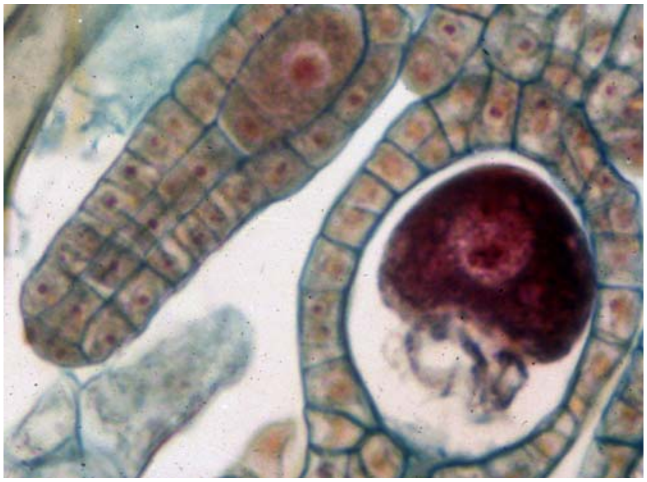

Figure 31. ***Marchantia polymorpha*** archegonia. **Left** archegonium has unfertilized egg; **right** archegonium has zygote. Photo by Janice Glime.

Sperm Dispersal

But just how far can these tiny sperm travel? Showalter (1926) found that the sperm of ***Riccardia pinquis*** 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 minutes). 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 <http://www.youtube.com/watch?v=ALGDLzWcvnU> 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 80).

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.

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.

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.

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.

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

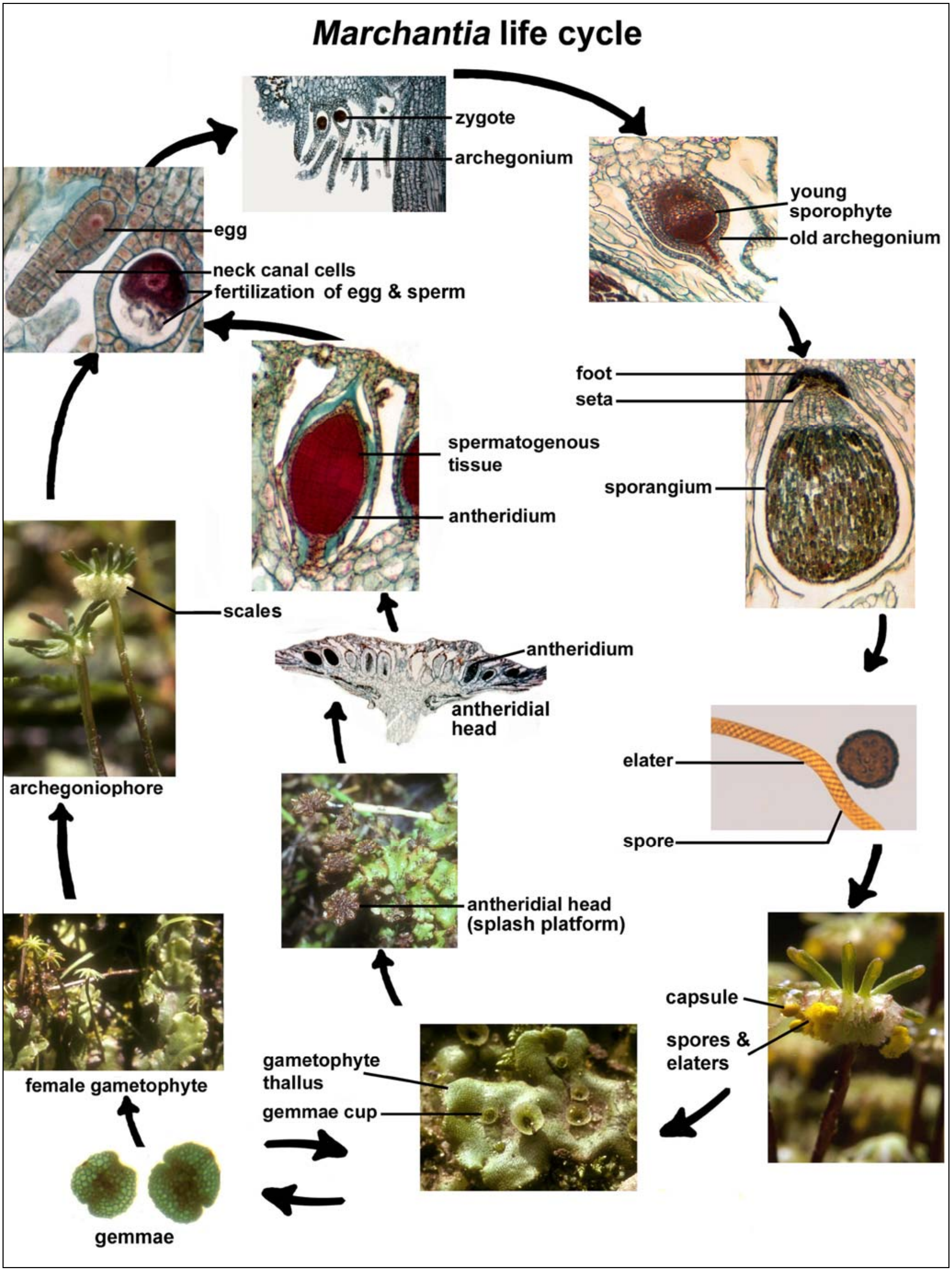

Figure 39. Life cycle of ***Marchantia polymorpha***, showing dominance of the gametophyte generation. Photos by Janice Glime, photomicrographs from botany teaching collection of Michigan State University, and spore and elater modified from photo by Noris Salazar Allen.

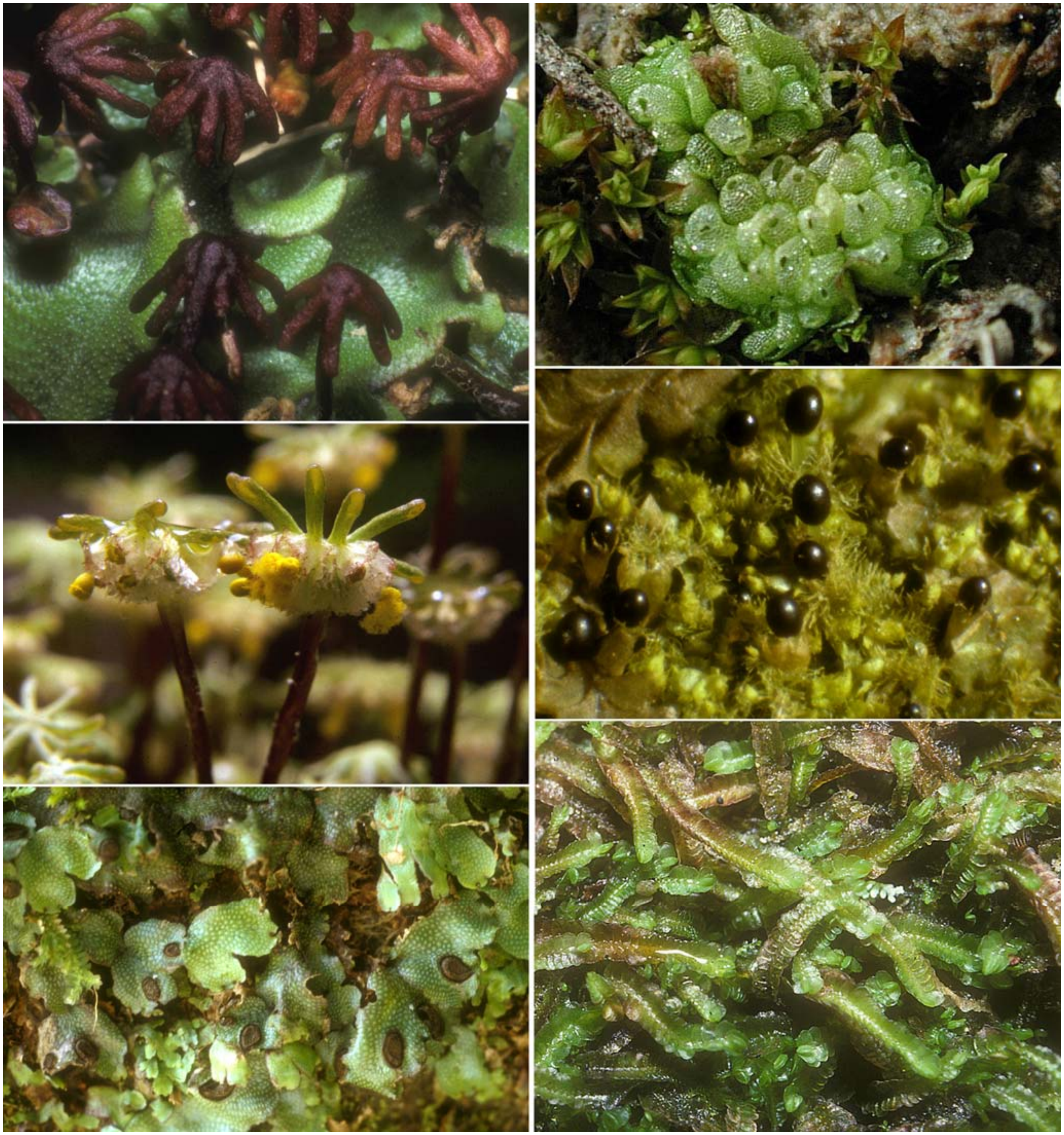

Figure 40. Examples of **Marchantiophyta**. **Left: Marchantiopsida** – **left upper:** ***Marchantia polymorpha*** with archegoniophores; **left middle:** mature sporophytes hanging from archegoniophores of ***Marchantia polymorpha***; **left lower:** ***Conocephalum conicum*** showing antheridial patches on the thallus. **Right upper:** ***Sphaerocarpus texanus*** thallus (**Marchantiopsida**) with involucres surrounding 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 of ***Sphaerocarpus texanus*** by Michael Lüth, with permission.

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 50), 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-ralf-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.

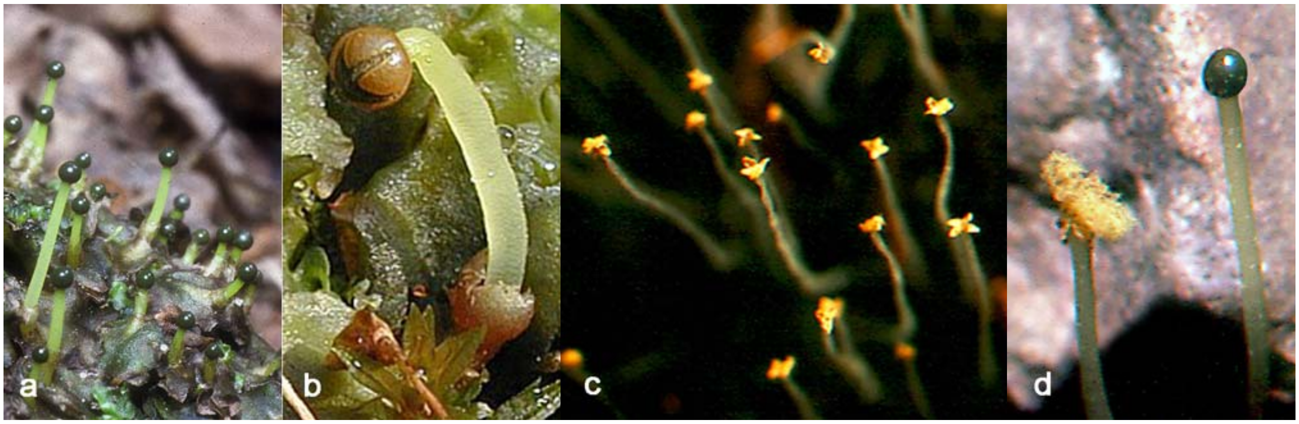

Figure 45. ***Pellia***, a thalloid liverwort in the class **Jungermanniopsida**, subclass **Metzgeriidae**. Note the watery, colorless setae with the globose, inoperculate capsules. **a:** undehisced capsules and setae. **b:** capsule splitting into four valves. **c:** dehisced capsules showing four 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-Figure 49). The leaves typically have oil bodies (Figure 50), 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 stolons on the ventral side. Photo by Janice Glime.

Figure 49. ***Bazzania trilobata***; note the two-ranked leaves and top-bottom (**dorsi-ventral**) orientation. Photo by Janice Glime.

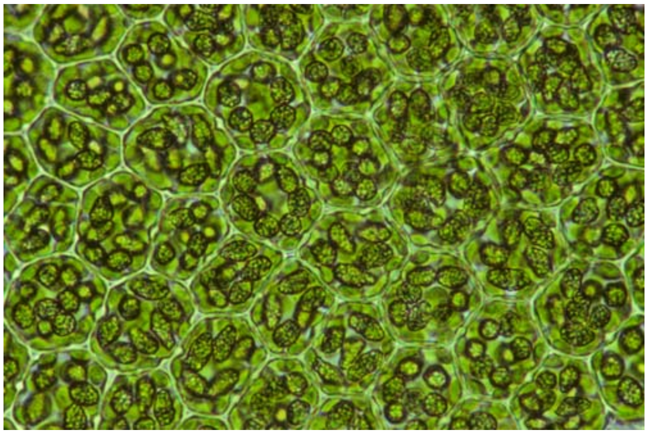

Figure 50. Leaf cells of the leafy liverwort ***Frullania davarica*** (**Jungermanniopsida**). Note the oil bodies resembling bunches of grapes and the numerous small chloroplasts clumped around the periphery of cells. Cell walls also have **trigones** (swellings in the walls). Photo by Zen Iwatsuki, with permission.

In the leafy liverworts, the leaf may be folded to create a pocket or pouch (**lobule**; Figure 51), usually on the lower side, but the smaller lobe may occur on the upper side in such genera as ***Scapania*** (Figure 52). Rhizoids, unlike those in the **Metzgeriidae**, usually occur in clumps at bases of underleaves (Figure 53).

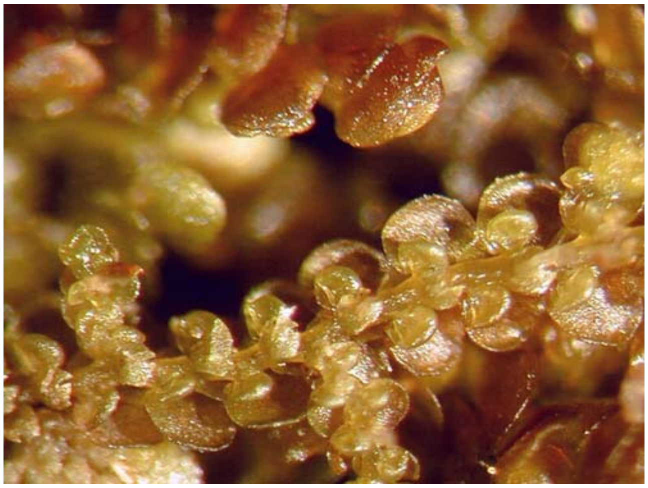

Figure 51. ***Frullania dilatata*** (Class **Jungermanniopsida**), a leafy liverwort showing the ventral (under) side of the stem with hood-shaped lobules under each leaf and underleaves on the stem. Photo by Michael Lüth, with permission.

Figure 52. ***Scapania gracilis*** showing leaves folded up to the dorsal side. Photo by Jan-Peter Frahm, with permission.

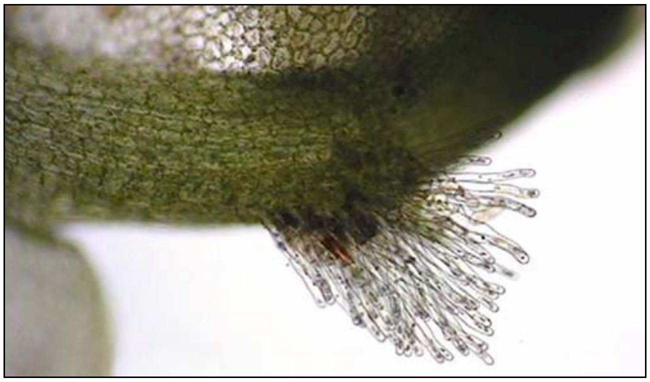

Figure 53. ***Chiloscyphus polyanthus*** with a clump of rhizoids at the base of the underleaf. Photo by Paul Davison, with permission.

In all the bryophyte phyla, the spore is a **meiospore** (produced by meiosis and therefore 1*n*; Figure 54-Figure 56). These structures can be variously decorated and their size and decorations can contribute to their dispersal ability. Germination (Figure 56) in liverworts is apparently inhibited inside the capsule, thus occurring only after capsule **dehiscence** (splitting apart) and spore dispersal (Figure 57-Figure 59).

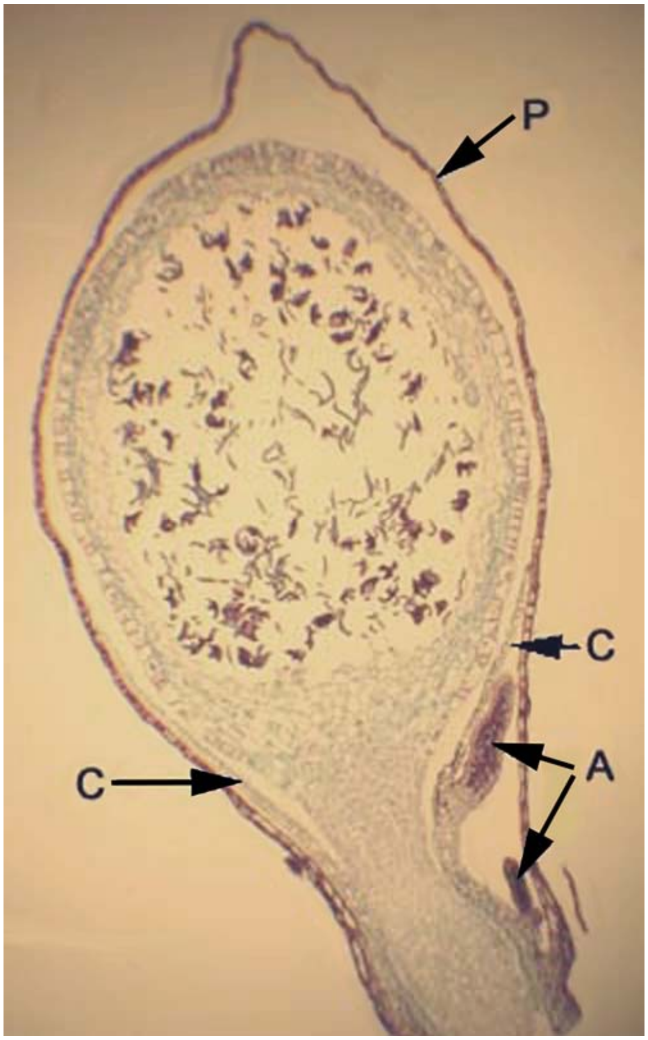

Figure 54. ***Porella navicularis*** capsule with meiospores and elaters. Photo from University of British Columbia website, with permission.

Figure 55. ***Noteroclada confluens*** (Metzgeriidae) meiospores and elaters. Photo by George Shepherd, through Creative Commons.

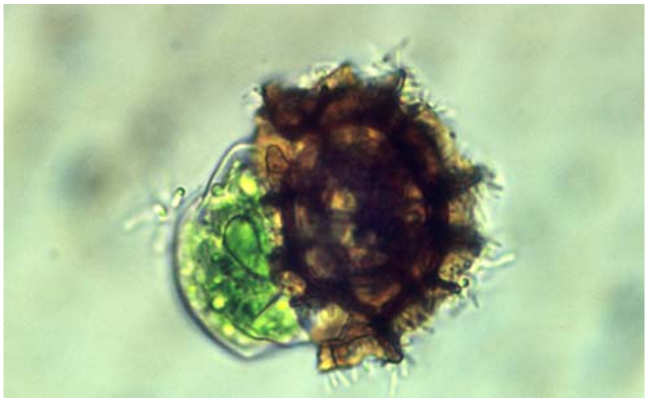

Figure 56. ***Fossombronia angulosa*** protonema emerging from spore. Photo by Plant Actions through Eugenia Ron Alvarez, with permission.

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

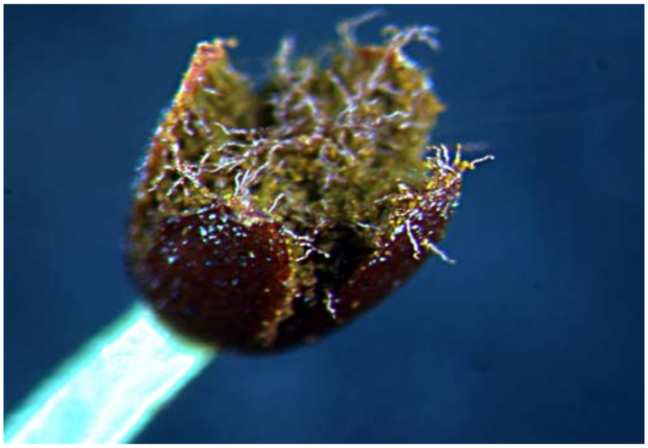

Figure 58. ***Lophocolea*** capsule dehiscing. Photo by George Shepherd, through Creative Commons.

Figure 59. ***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 56-Figure 61). 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 64-Figure 61).

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 61-Figure 65) (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). [See Glime (1970) for a new plant produced by a fragment in ***Scapania undulata*** (Figure 66)]. Nevertheless, in all bryophytes the sporeling is quite different in structure and appearance from the mature gametophyte that will develop from it.

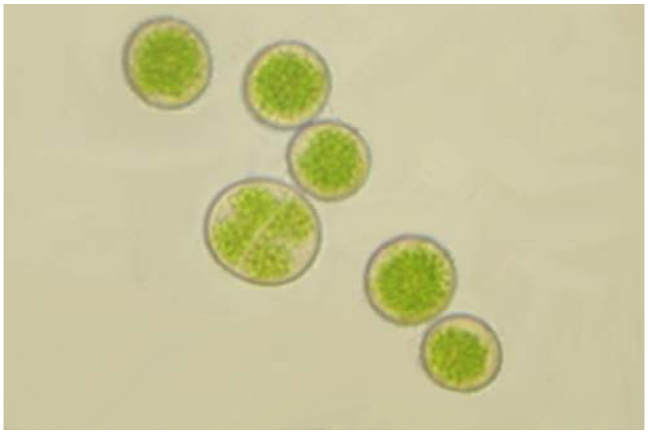

Figure 60. ***Radula recubans*** spores and protonema. Photo by Adaíses Simone Maciel da Silva, with permission.

Figure 61. ***Radula recubans*** protonema. Photo by Adaíses Simone Maciel da Silva, with permission.

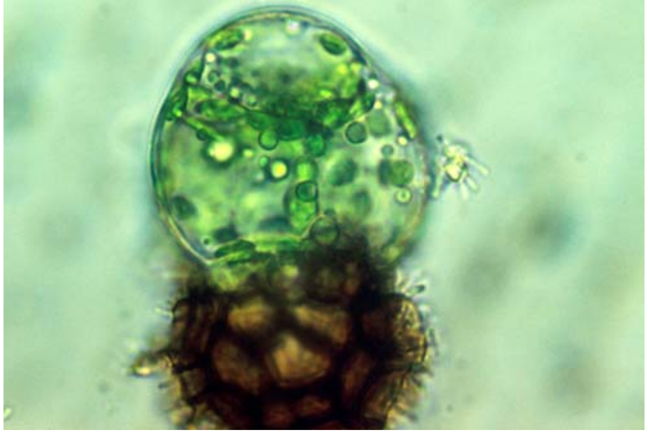

Figure 62. ***Fossombronia angulosa*** protonema. Photo by Plant Actions through Eugenia Ron, with permission.

Figure 63. ***Fossombronia caespitiformis*** protonema. Photo by Plant Actions through Eugenia Ron, with permission.

Figure 64. ***Sphaerocarpus texanus*** protonema. Photo by Plant Actions through Eugenia Ron, with permission.

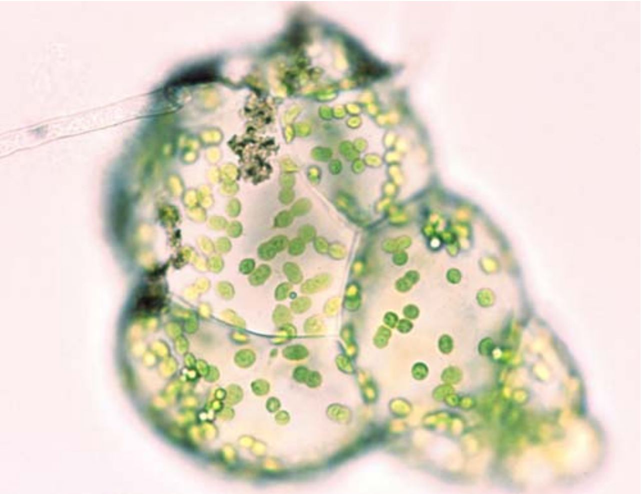

Figure 65. Thalloid protonema of the thallose liverwort ***Cyathodium foetidissimum***. Photo courtesy of Noris Salazar Allen.

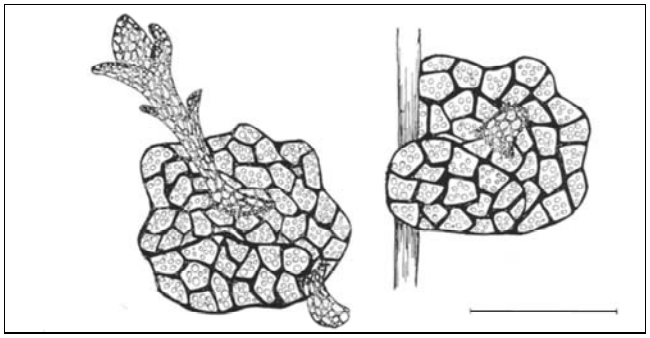

Figure 66. ***Scapania undulata*** showing young plant and two beginnings of plants from leaf fragments. Drawings by Flora Mace from Glime 1970.

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 67-Figure 68). The genus ***Treubia*** (Figure 69) 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***.

Figure 67. ***Haplomitrium gibbsiae*** plants demonstrating the three-ranked leaves in this family. Photo by Jan-Peter Frahm, with permission.

Figure 68. ***Haplomitrium hookeri*** showing young capsules. Photo by David Holyoak, with permission.

Figure 69. ***Treubia lacunosa***. Photo by Jan-Peter FFrahm, with permission.

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 70-Figure 73) and archegonia (Figure 74-Figure 79) along branches.

Figure 70. ***Porella navicularis*** antheridial branch. Photo from Botany 321 University of British Columbia website, with permission.

Figure 71. ***Lophocolea cuspidata*** male branch showing location of antheridia among leaves. Photo from Botany 321 at University of British Columbia website, with permission.

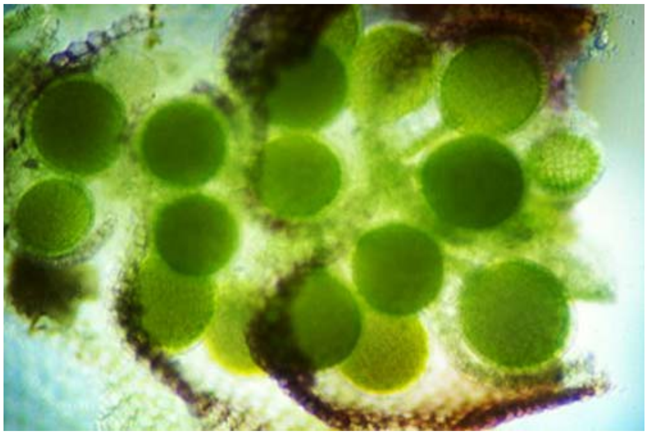

Figure 72. ***Lophozia capitata*** antheridia. Photo by Paul Davison, with permission.

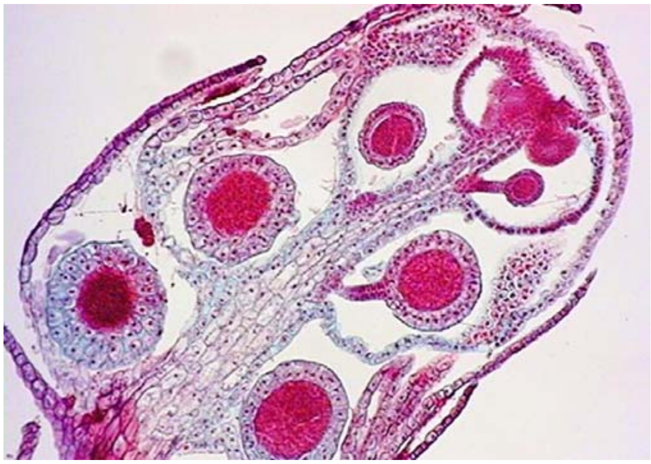

Figure 73. ***Porella*** sp. branch showing location of antheridia. Photo by Paul Davison, with permission.

Figure 74. ***Lophocolea cuspidata*** in its log habitat. Photo from Botany 321 at University of British Columbia website, with permission.

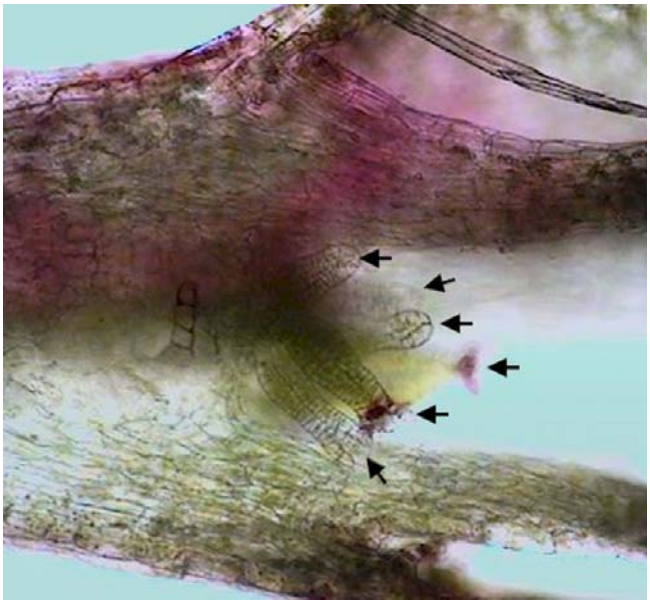

Figure 75. ***Jungermannia evansii*** archegonia at leaf base. Photo by Paul Davison, with permission.

Figure 76. ***Lophocolea cuspidata*** archegonia. Photo from Botany 321 at University of British Columbia, website, with permission.

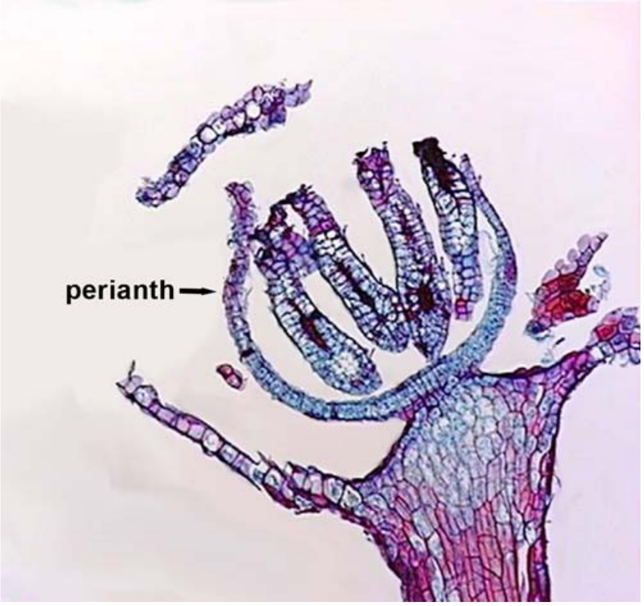

Figure 77. ***Porella*** archegonia in perianth. Photo by Paul Davison, with permission.

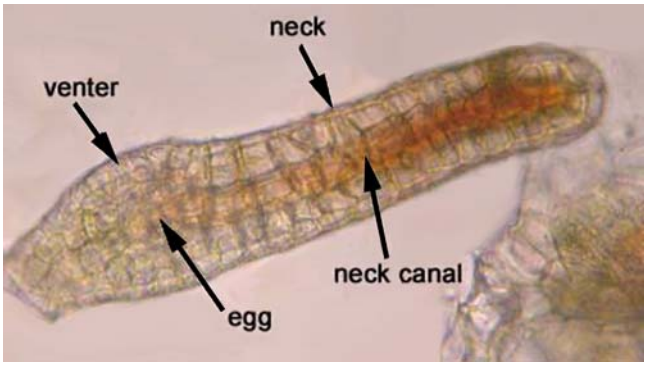

Figure 78. ***Porella navicularis*** archegonium. Photo by Jannah Nelson through Botany 321, University of British Columbia website, with permission.

Figure 79. ***Pellia epiphylla*** archegonium. Photo by Plant Actions through Eugenia Ron Alvarez, 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 80). This is at a much faster rate of 20 mm per minute (Muggoch & Walton 1942).

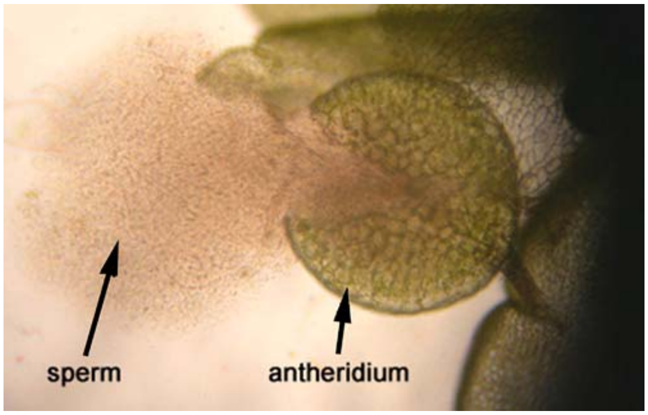

Figure 80. ***Porella navicularis*** (**Jungermanniopsida**) antheridium expelling sperm. Photo by Jonathan Choi, through Botany 321 University of British Columbia website, with permission.

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 81). 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.

Figure 81. ***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, with permission.

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 82), 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 83-Figure 85) that soon withers away. The capsule itself opens by four valves and usually contains **elaters**.

Figure 82. ***Frullania*** sp. perianth. Photo by George Shepherd, through Creative Commons.

Figure 83. ***Porella navicularis*** with young sporophyte emerging, through Botany 321 University of British Columbia website, with permission.

Figure 84. ***Lophocolea cuspidata*** perianth and developing sporophyte. Photo through Botany 321 University of British Columbia website, with permission.

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 85), using turgor pressure within the delicate cells to maintain this position. This **seta** supports and extends the capsule of most mosses and liverworts.

Figure 85. ***Lophocolea heterophylla*** with mature sporophytes. Photo by David Holyoak, with permission.

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 86-Figure 91) or on the thallus of thallose taxa (Figure 92). 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.

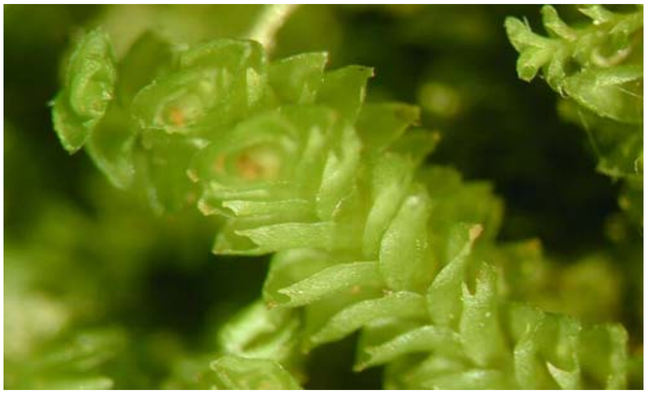

Figure 86. ***Tritomaria exsecta*** (**Jungermanniidae**) showing gemmae on leaf tips (**light brown**; see also Figure 87). Photo by Michael Lüth, with permission.

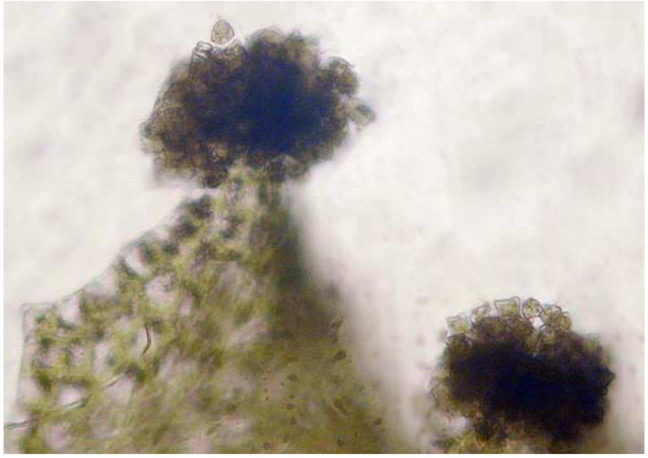

Figure 87. Microscopic view of ***Tritomaria exsectiformis*** leaf tips with gemmae. Photo by Michael Lüth, with permission.

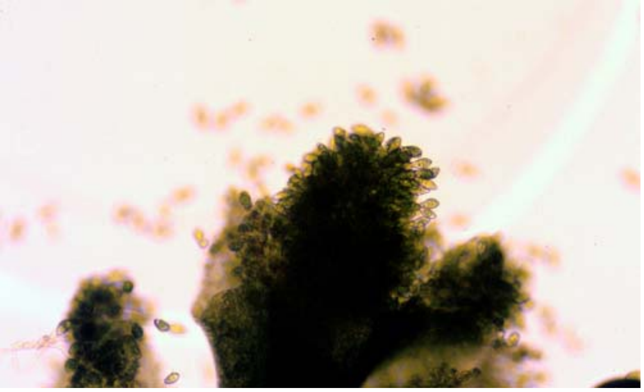

Figure 88. ***Scapania aspera*** gemmae on leaf tips. Photo from PlantActions through Eugenia Ron Alvarez, with permission.

Figure 89. ***Anastrophyllum hellerianum*** with terminal leaf gemmae. Photo by Des Callaghan, with permission.

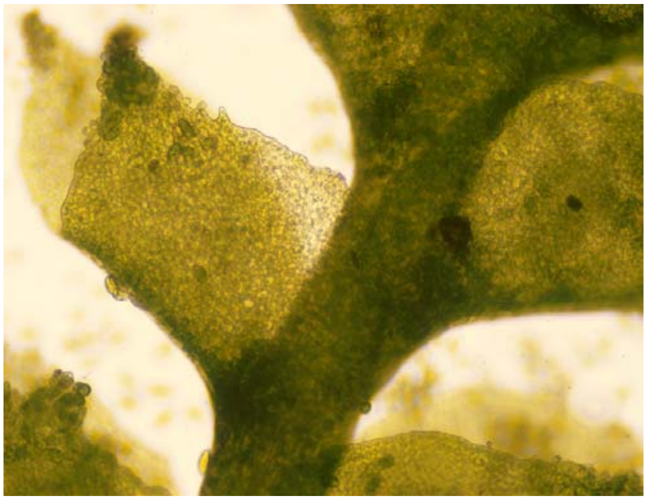

Figure 90. ***Scapania aspera*** with gemmae on leaves. See Figure 91. Photo from PlantActions through Eugenia Ron Alvarez, with permission.

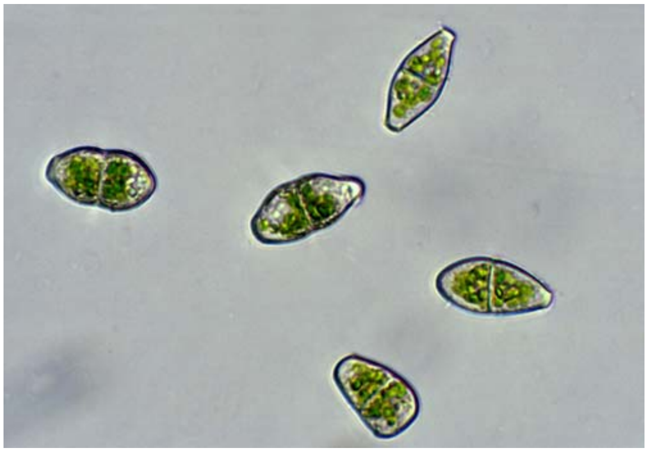

Figure 91. Gemmae of ***Scapania aspera***. Photo from PlantActions through Eugenia Ron Alvarez, with permission.

Figure 92. Arrow indicates gemmae on the thallus of ***Blasia pusilla*** (Metzgeriidae). Photo by Michael Lüth, with permission.

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.

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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. Eugenia Ron Alvarez and Tomas Sobota secured permission for me to use images from the PlantActions website and to obtain the original images. Norbert Stapper helped me get an email address needed to obtain permission to use an image. George Shepherd has made many wonderful images available through Creative Commons. As in most of these chapters, images from Michael Lüth and Des Callaghan have been invaluable. Noris Salazar Allen has provided me with several morphological images. Wilf Schofield helped me to obtain permission to use images from the Botany Website at the University of British Columbia. 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. Thank you to Llo Stark for alerting me to errors and formatting problems in this chapter.

Literature Cited

Anonymous. 2010. *Treubia* – Making leaves their own way. Botanical Heritage, Botanical Oddities, Bryophytes, Molecular Evolution, Plant Morphology 9 January 2010. <http://tasmanianplants.com/2010/01/treubia-making-leaves-their-own-way/>.

Basile, D. V. and Basile, M. R. 1983. Desuppression of leaf primordia of *Plagiochila arctica* (Hepaticae) by ethylene antagonist. Science 220: 1051-1053.

Benson-Evans, K. 1950. Dispersal of antherozoids in *Fegatella*. Nature (London) 165: 324-325.

Bold, H. C., Alexopoulos, C. J., and Delevoryas, T. 1987. Morphology of Plants and Fungi. Harper & Row, Publishers, Inc., New York, NY, 912 pp.

Bopp, M. and Capesius, I. 1996. New aspects of bryophyte taxonomy provided by a molecular approach. Bot. Acta 109: 368-372.

Cavers, F. 1903. On asexual reproduction and regeneration in Hepaticae. New Phytol. 2: 121-165.

Crandall-Stotler, B. and Stotler, R. E. 2000. Morphology and classification of the Marchantiophyta. In: Shaw, A. J. and Goffinet, B. (eds.). Bryophyte Biology. Cambridge University Press, Cambridge, pp. 21-70.

Crum, H. 1991. Liverworts and Hornworts of Southern Michigan. University of Michigan Herbarium, Ann Arbor, Michigan, 233 pp.

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

Duckett, J. G. and Pressel, S. 2009. Extraordinary features of the reproductive biology of *Marchantia* at Thursley Common. Field Bryol. 97: 2-11.

Glime, J. M. 1970. An observation on the vegetative reproduction of *Scapania undulata*. Bryologist 73: 624-625.

Goebel, K. and Balfour, I. B. 1905. Organography of Plants, Especially of the Archegoniata and Spermaphyta. Part 2. Clarendon Press, Gloucestershire, UK.

Gradstein, S. R., Churchill, S. P., Salazar Allen, N. 2001. Guide to the Bryophytes of Tropical America. Memoirs of the New York Botanical Garden Vol. 86: 577 pp.

Harvey-Gibson, R. J. and Miller-Brown, D. 1927. Fertilization of Bryophyta. *Polytrichum commune* (Preliminary note). Ann. Bot. Lond. 41: 190-191.

Lorbeer, G. 1934. Die Zytologie der Lebermoose mit besonderer Berücksichtigung allgemeiner Chromosomenfragen. I. Jahrb. Wiss. Bot. 80: 567-818.

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.

Nehira, K. 1966. Sporelings in the Jungermanniales. J. Sci. Hiroshima Univ. B. Div. 2, 11(1): 1-49.

Renzaglia, K. S. 1982. A comparative developmental investigation of the gametophyte generation in the Metzgeriales (Hepatophyta). Bryophytorum Bibliotheca 24: 358 pp.

Schofield, W. B. 1985. Introduction to Bryology. Macmillan Publishing Co., New York, 431 pp.

Schuster, R. M. 1966. The Hepaticae and Anthocerotae of North America, East of the Hundredth Meridian. I. Columbia University Press, New York, 802 pp.

Shimamura, Masaki. 2008. Airborne sperm of liverworts. Accessed 28 November 2012. <http://www.youtube.com/watch?v=ALGDLzWcvnU>

Shimamura, M., Yamaguchi, T., and Deguchi, H. 2008. Airborne sperm of *Conocephalum conicum* (Conocephalaceae). J. Plant Res. 121: 69-71.

Showalter, A. M. 1925. Fertilization in hepatics. Bot. Soc. Amer., Meeting Kansas City, Dec. 29-31.

Showalter, A. M. 1926. Studies in the cytology of the Anacrogynae. 1. Antherozoids. Ann. Bot. 40: 691-707.

Steenbock, C. M., Stockey, R. A., Beard, G., and Tomescu, A. M. F. 2011. A new family of leafy liverworts from the middle Eocene of Vancouver Island, British Columbia, Canada. Amer. J. Bot. 98: 998-1006.

Walton, J. 1943. How the sperm reaches the archegonium in *Pellia epiphylla*. Nature 3845: 51.