# CHAPTER 7-1

# WATER RELATIONS: CONDUCTING STRUCTURES

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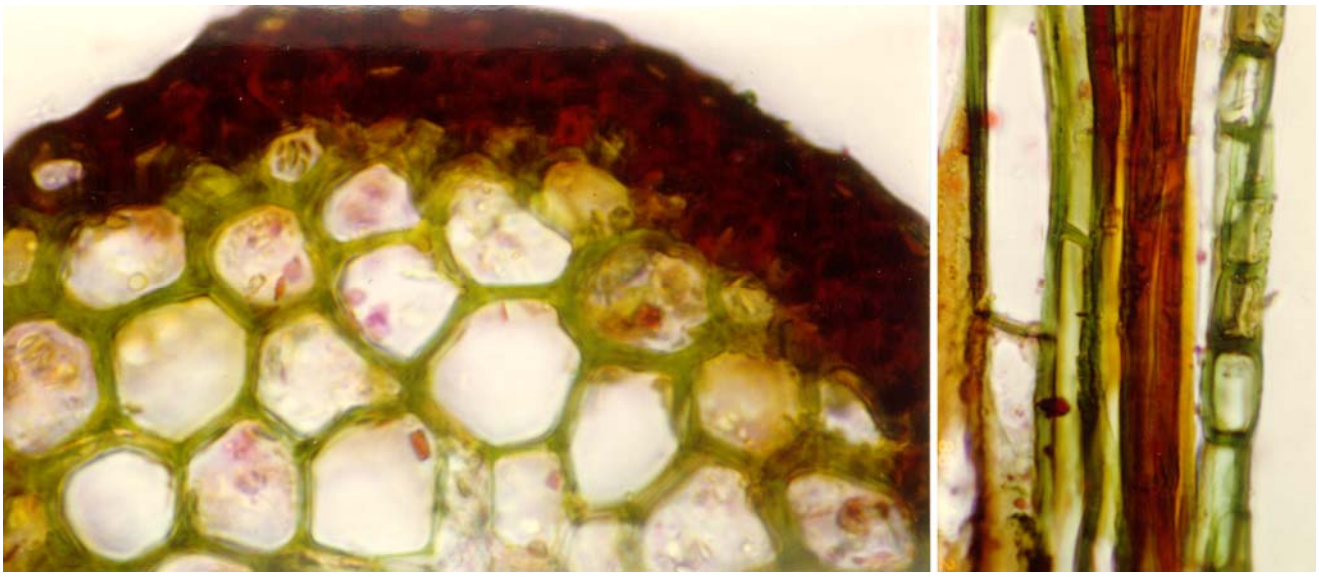

Figure 1. Cross section (**left**) and longitudinal section (**right**) of the moss ***Bryoxiphium***, showing in vertical section how cells that appear in cross section to be only parenchyma cells may in fact be elongate cells suitable for conduction. Photo courtesy of Isawo Kawai.

## Movement to Land

The most obvious need for photosynthetic organisms in their move from water to land was the continued need for water. At this time, most photosynthetic organisms still had a dominant gametophyte, and all indications are that the movement onto land carried with it that gametophytic dominance. As life on land progressed through evolution, plants with sophisticated vascular tissue ultimately developed. At the same time, the gametophyte in these highly vascularized tracheophytes (lignified vascular plants) solved its water problems by ultimately being contained within the protection of sporophytic tissues in the seed plants.

This reduction of the gametophyte might necessarily have forced a reduction in conducting tissues because the surrounding sporophytic tissue on the one hand reduced available space and on the other made vascularization much less necessary in the gametophyte. But in gametophyte-dominant bryophytes, survival on land required a means for getting water, and the nutrients carried with it, from one part of the plant to another. Despite their being the first land plants, as Raven (2002) has put it, plant biologists have taken a "top-down" view of land plants, seemingly expecting the bryophytes to have a simpler version of the same system as tracheophytes.

But bryophytes have been around much longer than tracheophytes, and their gametophytes have remained dominant. Hence, should we not expect them to have evolved means of water movement in the gametophyte generation during all these millennia? First of all, consider the desiccation-tolerant tracheophytes. These are almost all small plants (Raven 2002). Many bryophytes are likewise desiccation tolerant, and they too are small.

## Bryophytes as Sponges

Sponges, both animal and synthetic, gain and retain water through small chambers and capillary spaces. Bryophytes, due to their small size and tiny leaves, are natural arrays of chambers and capillary spaces. As this story unfolds, you will soon see that bryophytes are indeed sponges, aiding their own water needs and in some cases massively affecting the **ecosystem** (interacting community & habitat).

All life needs water, and the most severe stress for organisms venturing onto land was undoubtedly just that. But already, algae had developed means of becoming dormant through zygospores when they faced unfavorable circumstances. However, those first land organisms had to find ways to get water to all their internal parts, and often this water was in very limited amounts. For bryophytes, surviving water loss and prolonged periods of drought was a necessity for survival, so it is not surprising that during their 450 million years of evolutionary history (Proctor 2000a) they have perfected physiological mechanisms that

outdistance those of their tracheophyte counterparts (Oliver *et al*. 2000a). This ability has led plant physiologists to use bryophytes as model systems for the study of desiccation tolerance physiology, even to the extent of attempting to introduce those genes to crop plants (Comis 1992; Oliver *et al*. 2000b). And this use has made it into the agricultural literature with articles such as "Miracle Moss" (Comis 1992).

It appears that despite the typical relegation of bryophytes to the category of "non-vascular," conduction has played a major role in the phylogenetic history of bryophytes. Hedenäs (1999) examined the importance of various character states on the phylogenetic history of **pleurocarpous** mosses (typically the ones that grow horizontally) and determined that, based on redundancy analysis, gametophyte variance relates to characters associated with water conduction. Furthermore, one of the most important environmental variables in this phylogeny was the non-wetland to wetland gradient. On the other hand, Proctor (2000b), in "The bryophyte paradox: Tolerance of desiccation, evasion of drought," points out that a desiccation-tolerant tree is hardly conceivable. Height necessitates highly developed conducting systems that are unnecessary in short plants, and even among the bryophytes, it is the tall ***Dawsonia*** (Figure 2) and ***Polytrichum*** (Figure 3-Figure 4) that have conducting systems that almost mimic those of **tracheophytes** (plants having tracheids, *i.e.* the lignified vascular plants).

Figure 2. ***Dawsonia***, one of the tallest and most highly structured of all mosses. Photo by Janice Glime.

Ecosystem processes cannot be understood without understanding the role of bryophytes and their water relations. A lack of understanding of bryophyte water relations has led ecologists to conduct inappropriate experiments or draw erroneous conclusions about such topics as nutrient cycling and effects of air-borne pollutants on mosses in general in the ecosystem. Mosses such as ***Polytrichum*** (Figure 3-Figure 4), among the most conductive bryophytes in the northern hemisphere, have been used to generalize about the behavior of soil and airborne minerals in mosses during ecosystem processes. But this moss can behave very differently from most of the other genera that carpet forest floors. Puckett (1988) warns that mosses with internal conduction (as in ***Polytrichum***) do not make good monitors. Anderson and Bourdeau (1955) concluded that dew and rain were the main sources of water for bryophytes, excluding the groundwater source so vital for tracheophytes. It is therefore important that ecosystem ecologists, especially those studying water relations and nutrient cycling, have a basic understanding of the variety of ways that bryophytes move water and nutrients.

Figure 3. ***Polytrichum commune*** with capsules 1 Kristian Peters, through Creative Commons.

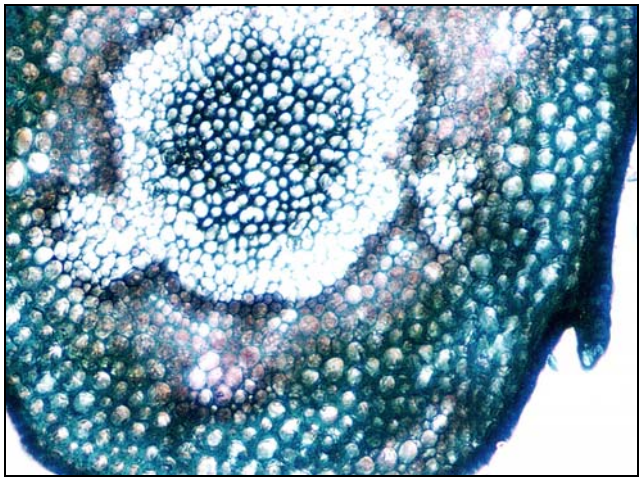

Figure 4. ***Polytrichum*** stem cross section showing central hydrome and surrounding leptome – the essence of its vascular system. Photo courtesy of Isawo Kawai.

Nearly every botany book on the market defines bryophytes as non-vascular plants, distinguishing them in this way from all other embryophytes. In fact, **many bryophytes are vascular**, but **lacking lignin** [associated with cellulose in cell walls of **sclerenchyma** (thick-walled supporting cells), xylem vessels, and tracheids; Hébant 1977] and the variety of perforated and spirally thickened cells typical of xylem. [Note that **lignin-like** compounds bind to cell walls in bryophytes, especially in spores and

elaters (Ligrone *et al*. 2008).] Rather, many bryophytes have unique cells that perform conduction in rather different ways from the "true vascular plants." Kawai has published a series of colored photographs (*e.g.* Figure 1), using specific stains, that illustrate the wide presence and variety of such tissues among many families of mosses (Kawai 1971a, b, c, 1976, 1977a, b, 1978, 1979, 1980a, b, 1981, 1982, 1989, 1991a, b; Kawai & Ikeda 1970; Kawai & Ochi 1987; Kawai *et al*. 1985, 1986; Ron & Kawai 1990). Hence, it is safer to distinguish the bryophytes as non-lignified plants (still waiting to be disproved) or **non-tracheophytes**, and the lignified vascular plants as **tracheophytes**. This puts a slightly new perspective on the way we look at their roles in ecosystems.

When we consider bryophytes, we are tempted to think about wet habitats where mosses grow close to water, basking in the sun of a bog, or cooling off in the spray of a waterfall. Certainly these are habitats where bryophytes are common, but keep thinking. What about those rocks on the cliff or the sand of the dunes (Figure 5)? In fact, can you think of any habitat that has plants but where it is impossible to find mosses? There are not many, and if you visualize some of the rocky habitats in your mind, you realize that these organisms undergo tremendous changes in moisture and temperature, even within a single day, occupying habitats where no vascular plants can survive.

Figure 5. ***Aloina ambigua*** growing in sand. Photo by Michael Lüth, with permission.

If we try to speculate about those first organisms to survive on land, we would probably consider them to be simple organisms with no organized vascular systems. There was no selection pressure for any wasteful vascular tissue while these organisms were living in the water. Water may have been the primary force limiting plants from vast colonization of land. Gray (1985) suggests that it was the ecophysiological tolerance to desiccation, appropriate life cycle strategies, and short vegetative life cycle that permitted widespread colonization during the mid **Ordovician** (~441-504 million years ago) to the mid Early Silurian (~400-440 million years ago) – strategies that describe bryophytes.

Even with so many diverse habitats occupied by plants today, we still consider the move from water to land to have been a major one. Imagine the changes that were necessary. Consider that the greatest overriding challenge was to keep their cells wet. Land plants responded to this challenge in two ways. Some, the ones we traditionally called **vascular plants** (the **tracheophytes**), acquired **lignin**, developed a complex water transport system, and encased themselves in a waxy, waterproof **cuticle**. Others, the **bryophytes**, developed strategies that we are only beginning to understand, including external transport, cell-to-cell transport, and the ability to survive desiccation. In the words of Proctor (2000a), "Bryophytes... evolved desiccation tolerance and represent an alternative strategy of adaptation to life on land, photosynthesizing and growing when water is available, and suspending metabolism when it is not. Limited by mode of life, but also liberated: prominent on hard substrates such as rock and bark, which are impenetrable to roots and untenable to vascular plants. Bryophytes (in species numbers the second biggest group of green land plants) may be seen as mobile phones, notebook computers and diverse other rechargeable battery-powered devices of the plant world – not direct competitors for main-based equivalents, but a lively and sophisticated complement to them."

Bryophytes are adapted to land but restricted in their morphology by a biochemical impasse, *i.e.* the inability to synthesize lignin (Niklas 1976). Because they lack lignin, they lack the tracheids and vessels of other plants, but have produced instead vascular strands with similar elongate shapes. Nevertheless, they are unable to support a large structure or great mass because they lack the strengthening ability of lignin. Because of their importance in both structure and physiology, water relations seem an appropriate place to start in our consideration of the limits imposed on bryophytes, for without that understanding, we cannot understand their other limitations, nor can we fully evaluate their ecological relationships.

## Conducting Structures

Conducting structures are not new expressions in bryophytes. Edwards *et al*. (2003) found at least fourteen types of such structures in mesofossils from a Lochkovian (Lower Devonian) locality in the Welsh Borderland, Shropshire. These are distinguished by variation in the combination of cells in the central strand and the cell wall architecture. The elongate cells may have smooth, uniformly thick or thin walls, walls with smooth projections pointed inward, or bilayered walls. The innermost walls are perforated by pores with the dimensions of plasmodesmata. These perforations are not well organized and some resemble the secondary thickenings most similar to the S-type tracheids of the **Rhyniopsida** (Figure 6-Figure 7), a primitive tracheophyte with lignified vascular tissue. Edwards and coworkers suggest that the imperforate bilayered examples may have been used in water conduction, cells that exhibited globular residues may have facilitated metabolite movement, and smooth-walled elongate cells seemed to be involved in support. Edwards and coworkers were unable to identify these mesofossils to genus, but concluded that there was widespread anatomical diversity among these early bryophytes.

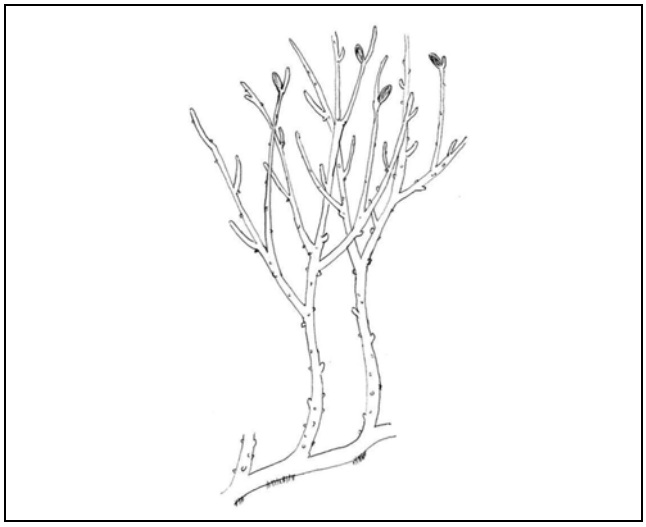

Figure 6. ***Rhynia gwynne-vaughanii*** reconstruction, member of **Rhyniophyta** – an early vascular plant. Photo by Griensteidl, through Creative Commons.

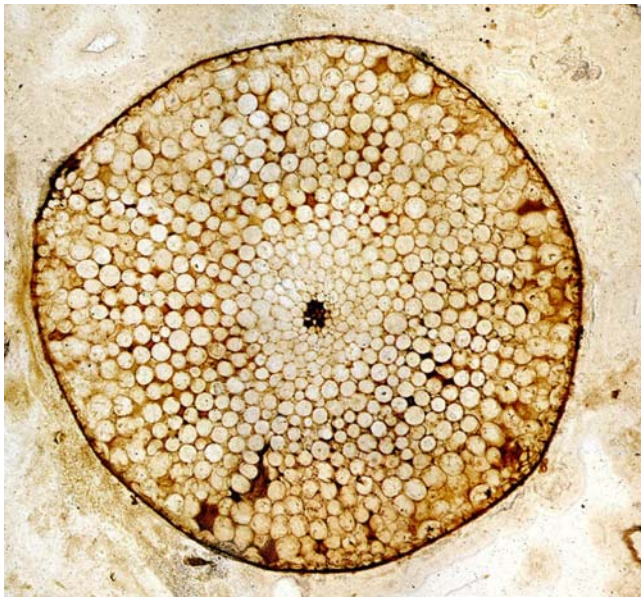

Figure 7. ***Rhynia gwynne-vaughanii*** stem cs fossil. Photo by Plantsurfer, through Creative Commons.

Bryophytes have two paths of water movement, often both in the same plant: internal through a **central cylinder** (**endohydric**) and external along the surface of the leafy or thallose plant (**ectohydric**) (Buch *et al*. 1938). Some thallose liverworts, **Polytrichaceae**, and **Mniaceae** represent the endohydric groups (Buch 1945, 1947; Proctor 2000b), but there are many others with at least some internal conduction. ***Metzgeria furcata*** (Figure 12), a "thallose" liverwort in the **Jungermanniopsida**, and others in the **Marchantiopsida**, have midribs (Figure 13) with enlarged internal cells (Figure 14), but the relative importance of these midrib cells for conduction is largely unknown.

In ***Asterella wilmsii*** (see Figure 8), numerous lipid bodies are present in the thallus cells. Ligrone and Duckett (1994a) suggested that these were associated with the perennation in winter. In the same species, vacuolar microtubule associations resemble the microtubule-based translocation system of many animals, but they differ greatly from the bulk flow known in sieve elements and actin-based cytoplasmic streaming of tracheophytes.

Figure 8. ***Asterella*** sp.; ***Asterella wilmsii*** produces numerous lipid bodies in the thallus cells. Photo by Brian du Preez, through Creative Commons.

Ligrone and Duckett (1994b) also found that food conducting cells in both gametophytes and sporophytes of bryoid mosses have a polarized organization and an axial system of endoplasmic microtubules. The polarity corresponds with a source to sink gradient with distal cellular ends (toward the sink) containing denser cytoplasm than that at the proximal ends. The cytoplasmic polarity and endoplasmic microtubules are unique in the plant kingdom, but are reminiscent of arrangements seen in animal neurons and in fungi.

The arrangement of the microtubules seems to aid in rapid rehydration, at least in ***Polytrichastrum formosum*** (Figure 9) (Pressel *et al*. 2006). It is this arrangement that permits rapid re-establishment of the cytoplasmic architecture of the leptoids (Figure 58). This reassembly of the endoplasmic microtubule systems establishes the time frame for recovery.

Figure 9. ***Polytrichastrum formosum***, a species that experiences rapid rehydration due to its arrangement of microtubules. Photo by Daniel Cahen, through Creative Commons.

But even in conduction structures, mosses once again exhibit diversity. In both ***Polytrichum juniperinum*** (Figure 10) and ***Mnium hornum*** (Figure 11) decapitation greatly reduces cellular polarity (Ligrone & Duckett 1996a). But only in ***Mnium*** was there a disappearance of endoplasmic microtubules, loss of longitudinal alignment of organelles, and accumulation of abundant starch when subjected to decapitation. And in ***Polytrichum*** starch accumulated in the cortical parenchyma cells.

Figure 10. ***Polytrichum juniperinum***, a species that loses much of its polarity when decapitated. Photo by Bob Klips, with permission.

Figure 11. ***Mnium hornum***, a species that experiences rapid rehydration due to its arrangement of microtubules. Photo by Hermann Schachner, through Creative Commons.

***Sphagnum*** seems to have found yet another way to accomplish formation of conducting cells. The cytology is very similar to that in bryoid mosses, but the development of the central strand (Figure 37-Figure 40, Figure 42-Figure 45) of the stem in ***Sphagnum*** is not homologous with that known in other mosses (Ligrone & Duckett 1998b).

Furthermore, mosses differ from liverworts in location of their conduction elements (Ligrone *et al*. 2000). In mosses, these occur in both the gametophyte and sporophyte. In liverworts, however, they occur only in the gametophyte. In the liverworts, the **Calobryales** and **Pallaviciniaceae** have water-conducting cells with walls that are perforated by pores derived from plasmodesmata. In the mosses, this type of water-conducting cell is known only from ***Takakia*** (Figure 25-Figure 27), a moss initially considered to be a liverwort until its sporophyte was discovered.

In the liverwort ***Symphogyna africana***, conducting cells have a different path or origin (Ligrone & Duckett 1996b). The cortical microtubules, wall microfibrils, and secondarily modified plasmodesmata are consistently aligned to form helices of about 45º, reminiscent of flowering plant vessels. Ultimately, the cytoplasm dissolution causes lysis of all cellular membranes, with membrane-bounded fibrillar material becoming deposited onto the walls. When the plugs of amorphous electron-transport material dissolves, open pits form. This formation of conducting elements resembles, in some aspects, the formation of vessels in flowering plants.

Conduction to other parts of the bryophytes has a similar polarized transport, facilitating long-distance movement of nutrients (Ligrone *et al*. 2000). This occurs in rhizoids and caulonemata and in the thallus parenchyma cells of at least some liverworts.

Diversity presents again when we compare cell wall components, equalling the diversity found in "higher" plants (Ligrone *et al*. 2002). Not only were there differences among the orders, diversity occurred within the order **Polytrichales**. Furthermore, the water-conducting cells of ***Takakia*** (Figure 25-Figure 27) are not homologous with those of other mosses, nor are they homologous with the ***Haplomitrium*** (Figure 28) or metzgerialean liverworts.

Broadly speaking, imperforate bilayered examples may have been involved in water conduction, cells with globular residues with or without pitting involved in metabolite movement, and smooth-walled examples with or without projections involved in support.

In liverworts, conducting tissues are restricted to the gametophyte, whereas in mosses, they are sometimes also in the sporophyte (Ligrone *et al*. 2000). Among the liverworts, the **Calobryales** and **Pallaviciniaceae** in the **Metzgeriales** have water-conducting cells with walls perforated by pores derived from plasmodesmata. The **hydroids** (water-conducting cells) of bryoid mosses are imperforate. In the **Polytrichaceae**, there is an axial system of microtubules in the **leptoids** (food-conducting cells) and in the parenchyma cells of the stems and setae of other mosses such as ***Sphagnum***, representing the variety of expression of conducting cells in the bryophytes..

Figure 12. ***Metzgeria furcata*** thallus with midrib. Photo by Des Callaghan, with permission.


Figure 13. ***Metzgeria furcata*** thallus showing distinct midrib with elongated cells and one layer of parenchyma cells in the thallus. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

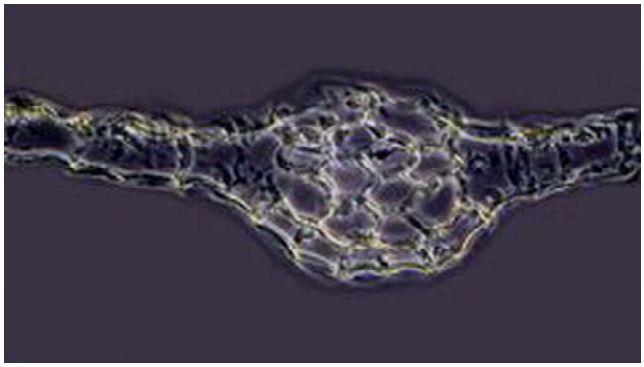

Figure 14. ***Metzgeria furcata*** thallus cross section at midrib. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Ectohydric mosses typically maintain a constant internal water content by absorbing water from the external capillary spaces as needed (Proctor 2000b). The ectohydric and endohydric modes each require their own structural adaptations. Lacking lignin, xylem is not possible. Furthermore, in the lignified vascular plants, it is the sporophyte generation that carries out organized internal conduction, and the gametophyte, with rare exception, does not. By contrast, in bryophytes it is the leafy gametophyte that must obtain and conduct water and nutrients about the plant, although conduction also occurs in the moss sporophyte (Ligrone *et al*. 2000; see Chapter 5-9).

Although the hornworts (**Anthocerotophyta**) have been considered by some to be reduced from more advanced plants, water-conducting tissue is unknown in this phylum (Ligrone *et al.* 2000), although Hébant (1977) reported the presence of cells resembling phloem sieve cells (leptoids?) in ***Dendroceros*** (Figure 15). Likewise, few liverworts (**Marchantiophyta**) have specialized conducting tissues in their gametophytes (Figure 16-Figure 22), and none have them in the sporophyte. Nonetheless, conducting strands have been known since 1901 in the thallose liverwort ***Pallavicinia lyellii*** (Figure 23; Tansley & Chick 1901). As in mosses, ***Pallavicinia*** conducting strands (Figure 24) closely resemble tracheids, with long cells, tapering ends, and obliquely oriented pits, and they, like xylem cells, are dead at maturity (Richardson 1981).

Figure 15. ***Dendroceros borbonensis***, a hornwort (**Anthocerotophyta**). Photo by Jan-Peter Frahm, with permission.

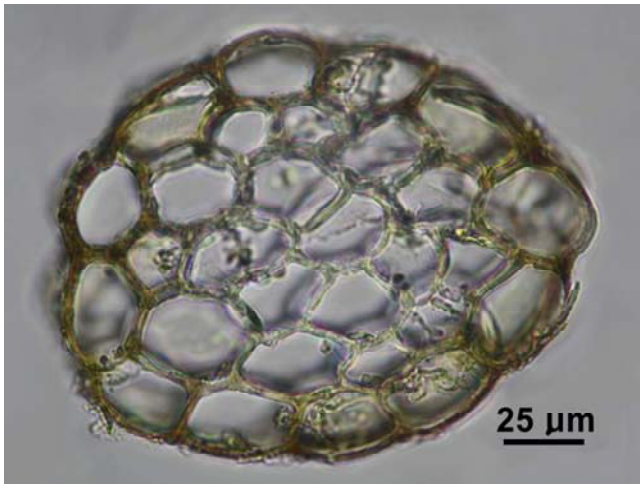


Figure 16. ***Kurzia*** sp. (leafy liverwort, **Jungermanniopsida**) stem cross section. Photo by Tom Thekathyil, with permission.

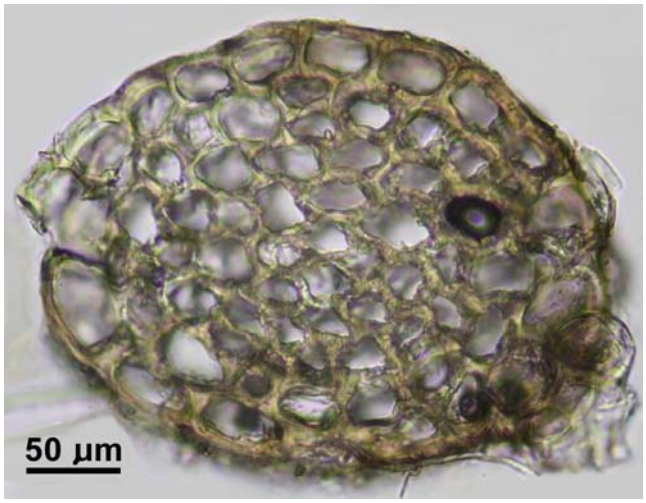


Figure 17. ***Lepidozia*** sp. (leafy liverwort, **Jungermanniopsida**) stem cross section. Photo by Tom Thekathyil, with permission.

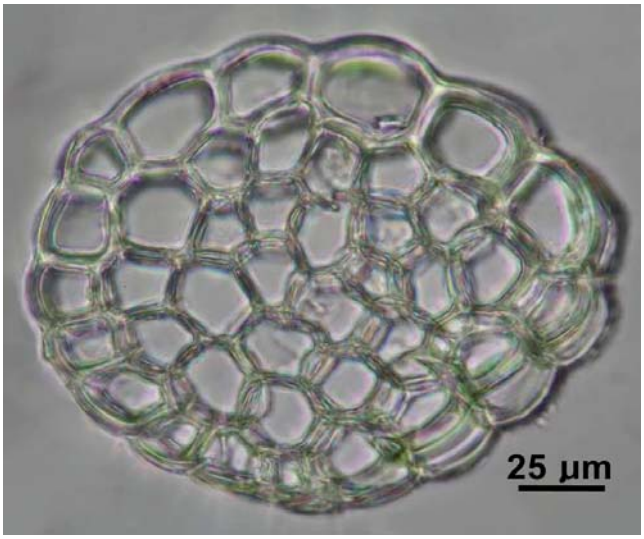


Figure 18. ***Telaranea pallescens***, a leafy liverwort in the **Lepidoziaceae** (**Jungermanniopsida**), stem cross section. Photo by Tom Thekathyil, with permission.

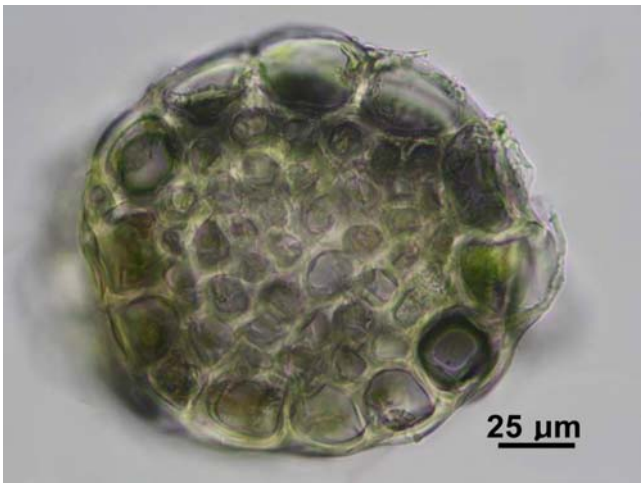


Figure 19. ***Telaranea tridactylis***, a leafy liverwort in the **Lepidoziaceae** (**Jungermanniopsida**), stem cross section. Photo by Tom Thekathyil, with permission.

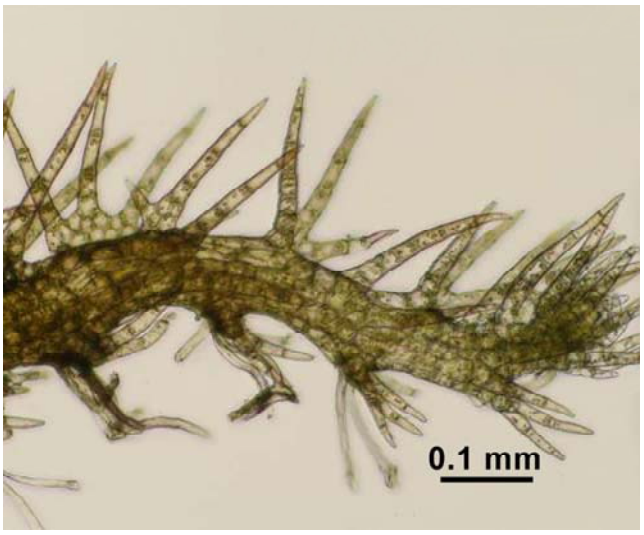


Figure 20. ***Temnoma palmata***, a leafy liverwort (**Pseudolepicoleaceae**, **Jungermanniopsida**). Photo by Tom Thekathyil, with permission.

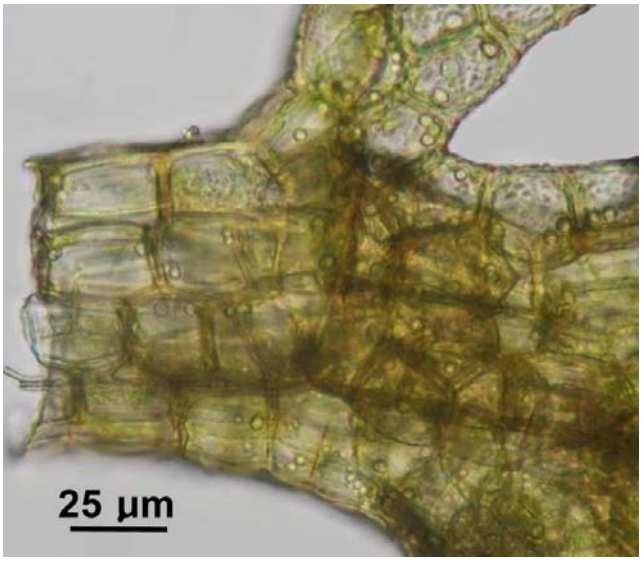


Figure 21. ***Temnoma palmata*** stem showing parenchyma cells and leaf base. Photo by Tom Thekathyil, with permission.

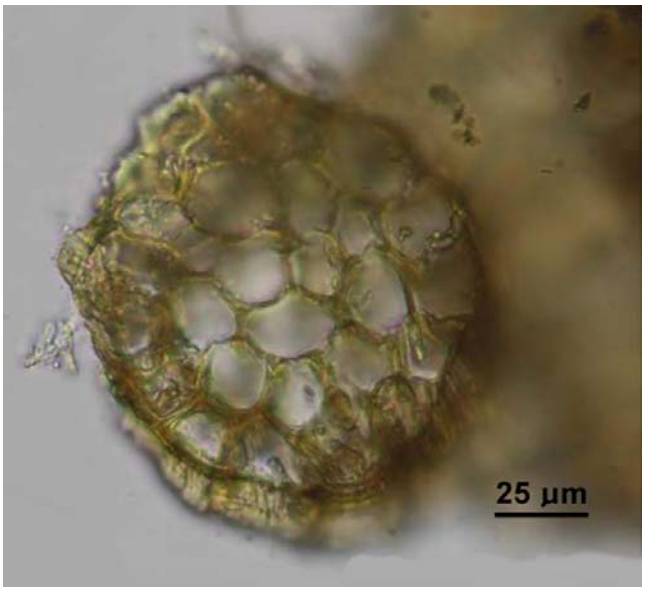


Figure 22. ***Temnoma palmata*** stem cross section. Photo by Tom Thekathyil, with permission.

Figure 23. ***Pallavicinia lyellii*** thallus. Photo by Jan-Peter Frahm, with permission.

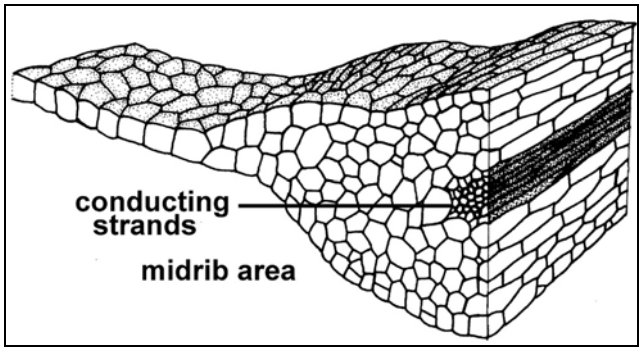


Figure 24. ***Pallavicinia lyellii*** cross section of thallus. Drawing from Hébant (1977).

Unlike the liverworts, as already noted mosses can have conducting cells in both generations (Ligrone *et al.* 2000). In some liverworts of **Calobryales** and in **Pallaviciniaceae** of the **Metzgeriales** (Figure 23-Figure 24) and the moss ***Takakia*** (a primitive moss once thought to be a liverwort; Figure 26), there exist water-conducting cells with perforated walls derived from **plasmodesmatal pores** (Ligrone *et al*. 2000), but these do not seem to be organized into a distinctive **central strand** (group of elongate cells forming central axis of stems and thalli of some bryophytes, usually thin-walled and often colored; Figure 58). Furthermore, the water conducting cells of ***Takakia*** (Figure 25-Figure 27) do not seem to be homologous with either the hydroids of other mosses or with those of the **Metzgeriales** or the leafy liverwort ***Haplomitrium*** (Figure 28), lending support to its basal lineage (Ligrone *et al*. 2000).

Figure 26. ***Takakia lepidozioides*** showing rhizomes and stems. Photo from the Herbarium of Hiroshima University, with permission.

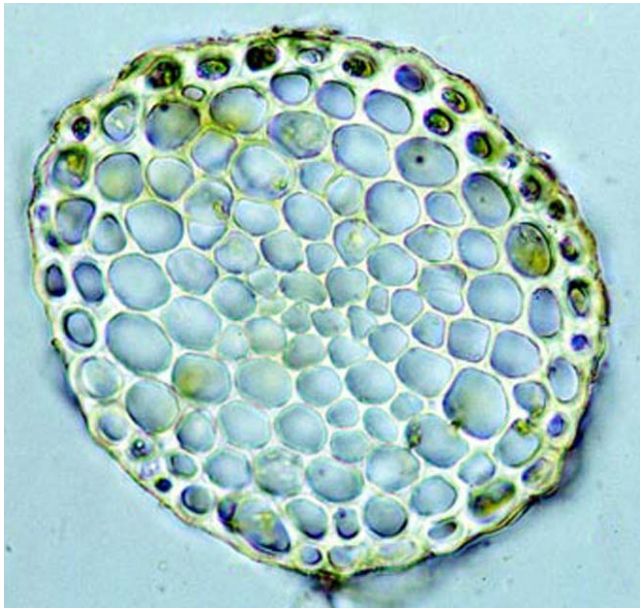

Figure 25. ***Takakia lepidozioides*** stem cross section. Photo from the Herbarium of Hiroshima University, with permission.

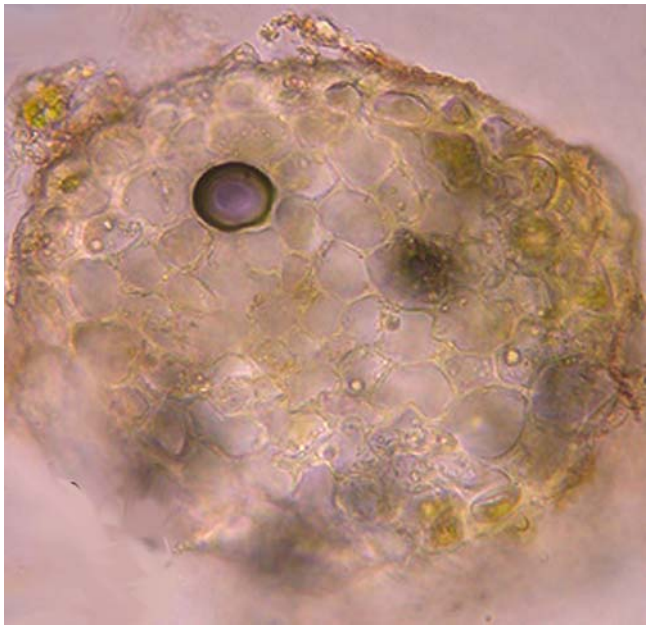

Figure 27. Cross section of stem of ***Takakia lepidozioides*** showing no evidence of a central strand. Photo with permission from Botany website, UBC.

Figure 28. ***Haplomitrium gibbsiae*** showing stems that lack a central strand. Photo by Jan-Peter Frahm, with permission.

***Dendroligotrichum dendroides*** (Figure 29, Figure 49, Figure 73) can reach 60 cm height and transports water **endohydrically** (internally) (Atala & Alfaro 2012). Its water-conducting **hydrome** follows Murray's law, *i.e.* the sum of the radii of the conduits to the third power (Σr3) is maintained across branching of these conduits. This means that the conduction system is optimized for maximal water transport per unit of 'vascular' tissue biomass. As the vascular tissue ascends toward the apex, there is **acropetal** (base to apex) tapering and an increase in conduit number at ascending levels. Since this architecture is similar to that of tracheophytes, Atala and Alfaro reasoned that it had undergone the same selection pressures in its evolution.

Figure 29. ***Dendroligotrichum dendroides***, a moss with non-lignified vascular tissue. Photo by Felipe Osorio-Zúñiga, with permission.

## Leptomes and Hydromes

Kawai (1991a) describes the moss stem as having a basic structure much like that of tracheophytes with an **epidermis** surrounding the **cortex** (Figure 30-Figure 31). This basic structure describes most of the **pleurocarpous** mosses that move internal substances mostly horizontally.

Among the **acrocarpous** mosses (those mostly upright mosses with the sporophyte at the stem apex), more complex stems can have a conducting cylinder in the center of the stem. This cylinder connects the base of the stem to the apex, but in most cases it is not connected to the leaves by any sort of leaf trace. The center of this conducting cylinder is comprised of **hydroids** and **stereids**, making up the **central strand** (Figure 32) (Zamski & Trachtenberg 1976). As you can guess from the name, **hydroids** are water-conducting cells. They are somewhat similar to tracheids but lack any horizontal connections (*i.e.* no pits) and are not lignified. And as you will see later, their chemistry and development are different from that of tracheids. Hydroids collectively make up the **hydrome** (also known as **hadram** or **hydrom)** (Scheirer 1980).

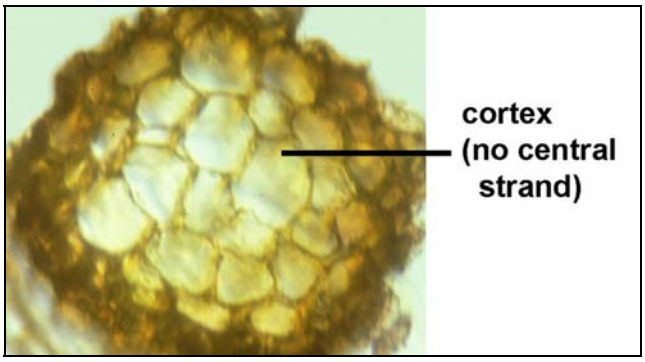


Figure 30. ***Trichodon cylindricus*** stem cs showing lack of central strand. Photo by Janice Glime.

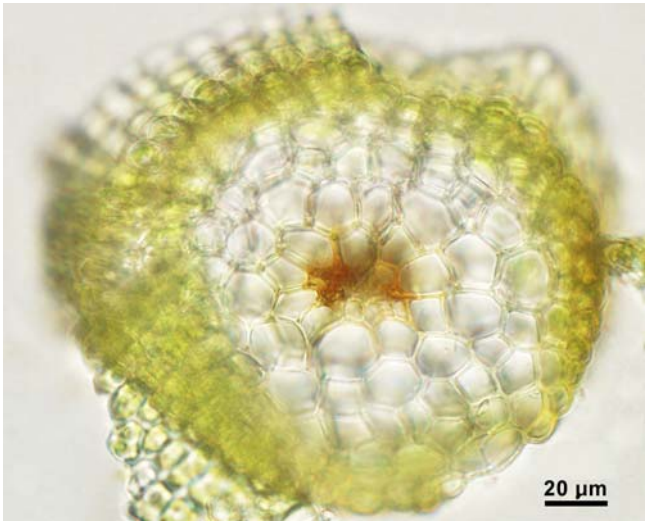


Figure 31. ***Molendoa sendtneriana*** (acrocarpous; **Pottiaceae**) stem cross section showing a central tissue that is differentiated. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

**Stereids** are elongate, thick-walled, slender, and fiber-like cells that add support to the stem, typically arranged in a cylinder around the hydrome. The stereids are collectively known as the **sterome** (Hébant 1977) (also known as sterom; Zamski & Trachtenberg 1976). They can also occur in the leaf **costa** (midrib-like strand; Figure 61), as will be discussed below, where they also serve as support.

Hébant (1977) describes the living parenchyma cells around the central strand in the **Polytrichaceae** to be a **hydrom sheath**, a term originated by Tansley and Chick (1901). This seems like an unnecessary term with only limited usage. However, Hébant reports that both starch grains and oil droplets are frequent in these cells. In ***Polytrichum commune*** (Figure 3), these cells have accelerated enzyme activity at the same time the protoplasts of the hydroids degenerate. Furthermore, some members of the **Polytrichaceae** have stereids among the

central strand cells. These have acid phosphatase activity in ***Dawsonia longifolia*** (Figure 2), suggesting they may have a role in the maturation of the hydroids.

Whereas the hydrome is relatively common, the **leptome** (also known as leptom; Figure 32) is less well known. The simple structure of its cells (**leptoids**) makes them difficult to distinguish from cortex parenchyma cells in cross section, but in vertical section they can be seen as longer cells surrounding the central strand and somewhat resembling phloem sieve cells (Figure 1, Figure 56). Their function, like that of phloem cells, is for photosynthate conduction, but they may also transport hormones or other substances. These cells in the **Polytrichales** (Figure 35) have oblique sieve plates, organized marginal endoplasmic reticulum, and partial nuclear degeneration (Scheirer 1975; Crandall-Stotler 1980).

In mosses like the **Mniaceae** (Figure 32-Figure 34) and **Polytrichaceae** (Figure 35), distinguishing the hydroids is fairly easy. However, not all distinctive cells in the center of the stem are hydroids. In other mosses, small to large cells comprise a distinctive central tissue (Figure 31), but we have no experiments to demonstrate their functions in conduction. It was not until 2002 (Ligrone *et al*. 2002) that immunocytological testing revealed the nature of the central tissue cell walls of 8 mosses and 4 liverworts. Little follow-up work has occurred, hence much of our understanding is still conjecture.

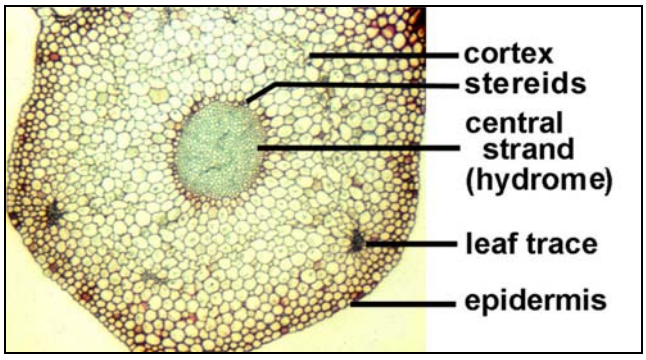


Figure 32. ***Plagiomnium*** (**Mniaceae)** stem cross section illustrating well-developed central strand. Photo by Janice Glime.

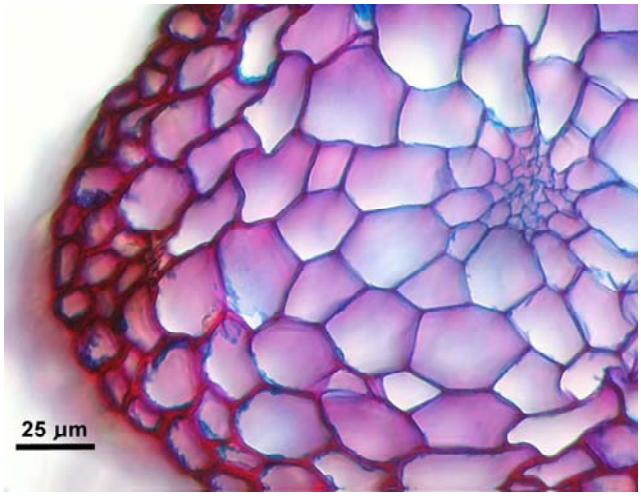


Figure 33. ***Plagiomnium ellipticum*** stem cross section showing central strand with **hydroids**. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

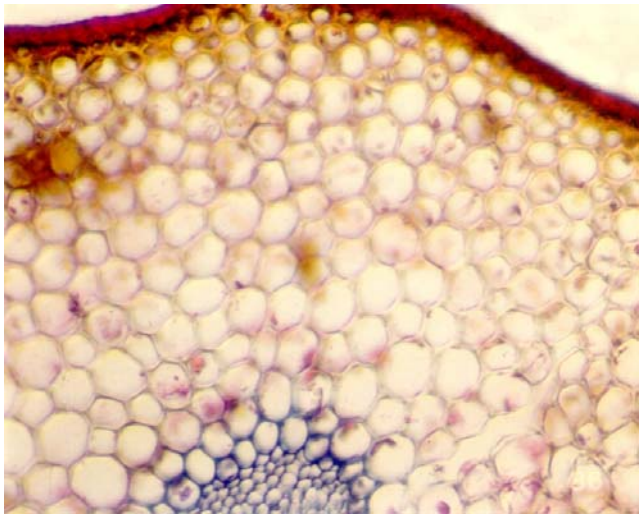

Figure 34. ***Rhizogonium*** (**Mniaceae**) stem cross section showing **hydroids** (stained blue in center). Photo courtesy of Isawo Kawai.

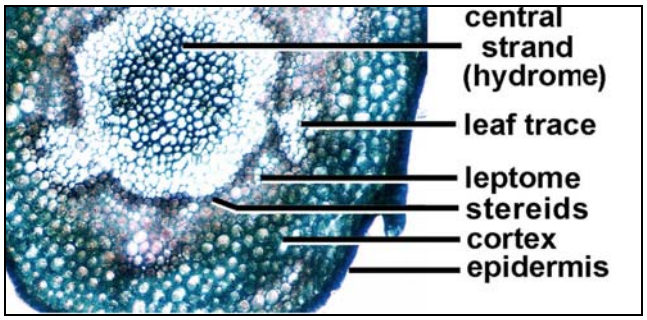


Figure 35. ***Polytrichum*** stem cross section illustrating well-developed central strand. Photo courtesy of Isawo Kawai.

Consider, for example, the genus ***Sphagnum*** (Figure 36). Central cells can vary considerably among species (Figure 37-Figure 42) and can be much smaller than the outer layer that comprises the epidermis (Figure 43). Yet these small cells of the central core are not conducting cells (Hébant 1977). Instead, ***Sphagnum*** typically uses its descending branches as wicks because they form capillary spaces around the stem (Figure 36).

Figure 36. ***Sphagnum obtusum*** showing descending branches that help to create capillary spaces and the wicking activity for upward movement of water. Photo by Michael Luth, with permission.

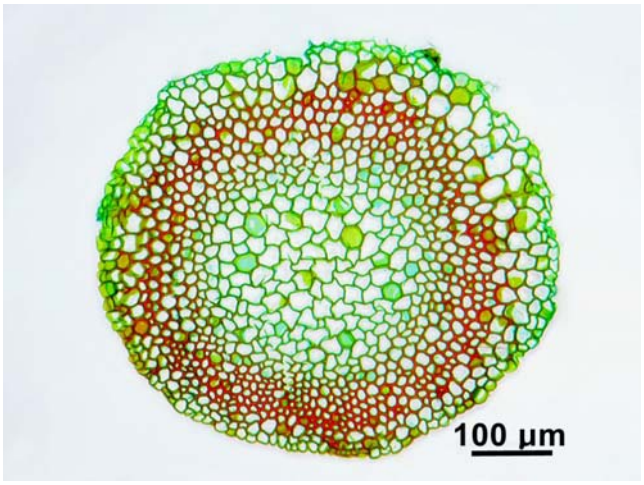


Figure 37. ***Sphagnum obtusum*** stem cross section with larger parenchyma cells in the center, surrounded by smaller thick-walled cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

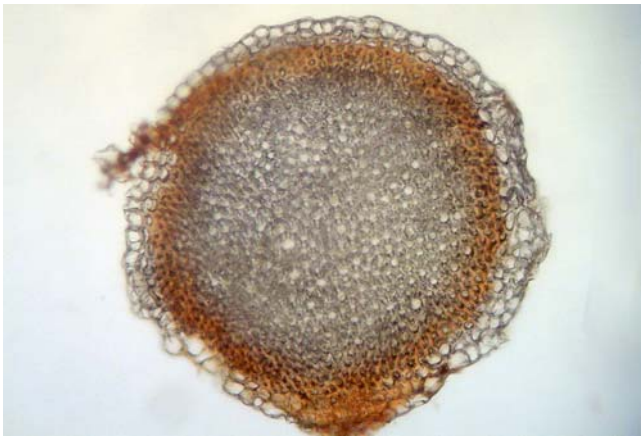

Figure 38. Stem cross section of ***Sphagnum contortum*** with three distinct cell types but no hydroids. Photo by Michael Lüth, with permission.

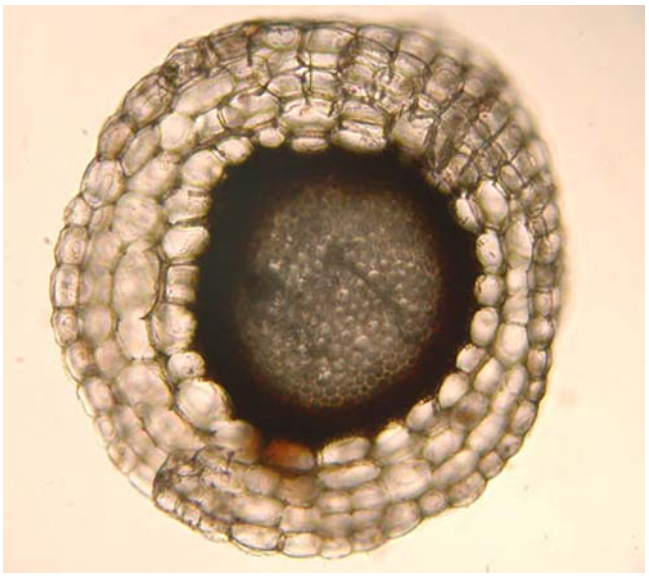

Figure 39. ***Sphagnum*** stem cross section with small-celled central core, dark band of cells, and 3-4 layers of outer hyaline cells. Photo from Botany website, University of British Columbia, Canada, with permission.

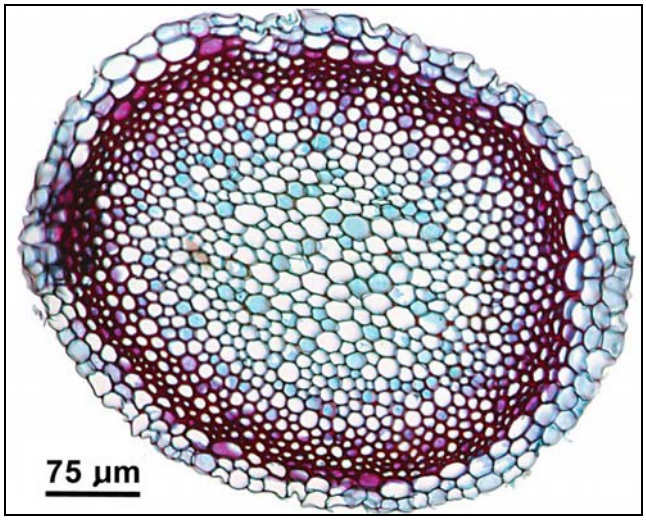


Figure 40. ***Sphagnum squarrosum*** stem cross section with central parenchyma cells, a strengthening layer, and two distinct layers of hyalocysts. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

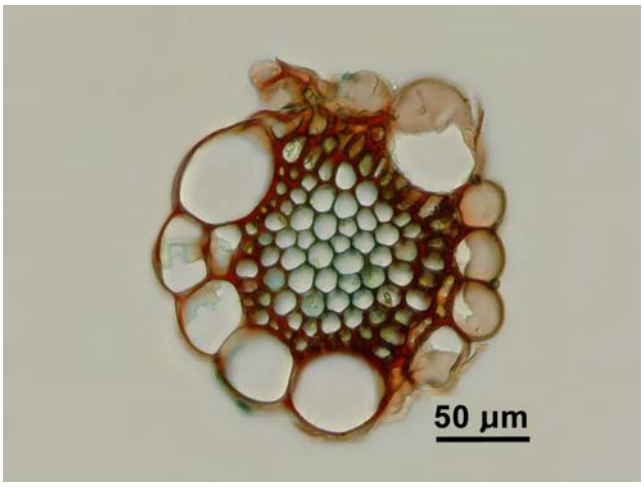


Figure 41. ***Sphagnum squarrosum*** branch cross section showing very different outer hyaline cells and overall appearance from that of the stem in Figure 40. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

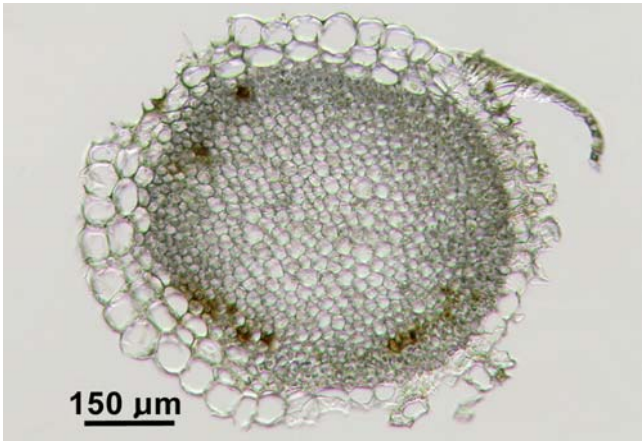


Figure 42. ***Sphagnum fimbriatum*** stem cross section showing only two kinds of cells: central core and outer hyaline cells (**hyalodermis**). Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

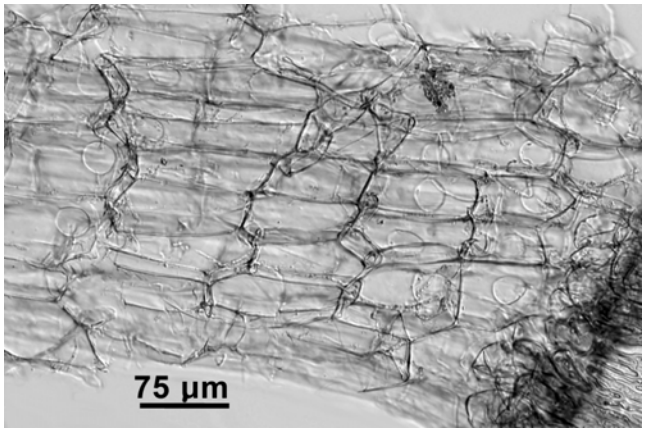


Figure 43. Longitudinal view of ***Sphagnum fimbriatum*** stem hyalodermis showing pores. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Schimper (1857) determined that the hyaline outer cells of stems and the hyaline cells of leaves in ***Sphagnum*** were dead at maturity (Figure 44). Furthermore, they have true perforations strengthened by spiral fibers (Figure 45). Branches are smaller than the stem and typically have a single outer hyaline layer and smaller, often thick-walled cells in the central core (Figure 46-Figure 47).

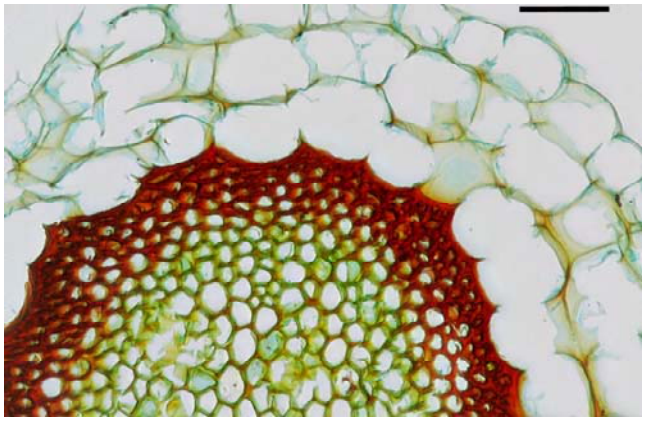

Figure 44. ***Sphagnum papillosum*** stem cross section with central core and dead outer layers of hyalocysts. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

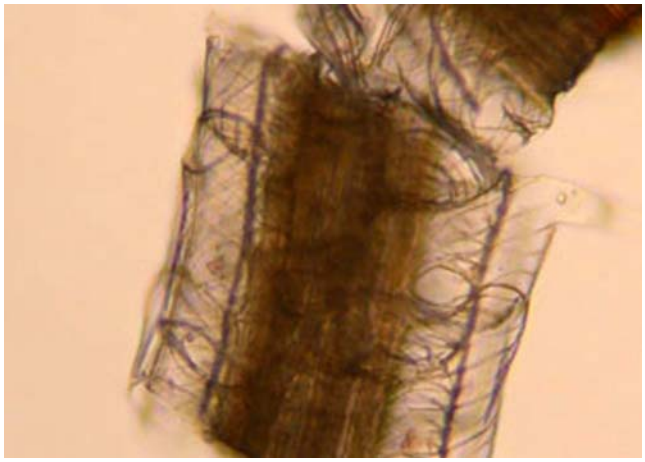

Figure 45. Longitudinal view of ***Sphagnum papillosum*** stem showing **central core** and outer hyaline cells (**hyalocysts**) with **fibrils** and **pores**. Photo from Botany website, University of British Columbia, Canada, with permission.

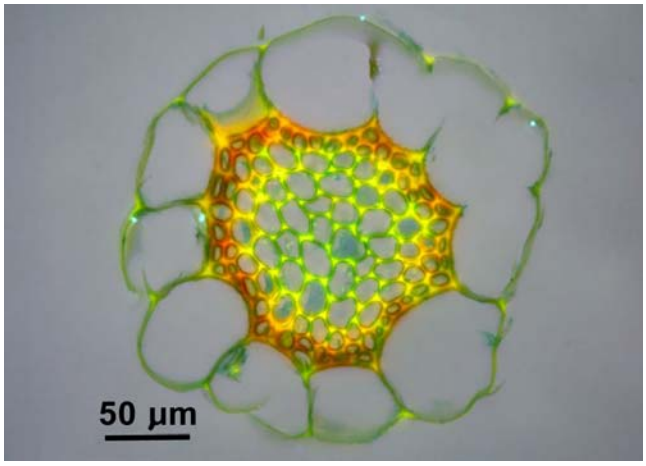


Figure 46. ***Sphagnum papillosum*** branch cross section demonstrating its differences from the stem in Figure 44. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

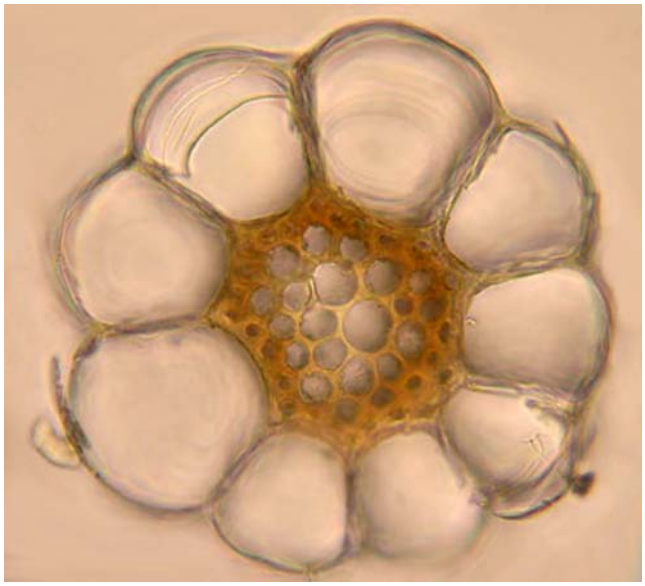

Figure 47. ***Sphagnum papillosum*** branch cross section. Photo from Botany website, University of British Columbia, Canada, with permission.

Schnepf (1973) later found that microtubules are fundamental in the development of the spiral thickenings of ***Sphagnum*** by lifting the plasmalemma off the wall to form an extraplasmatic space in which wall material is accumulated. The wall area where the pore will form becomes progressively thinner until only the cuticle remains. The cuticle eventually ruptures, making a pore. The protoplasts likewise eventually disappear.

The **Marchantiophyta** lack water-conducting cells except for two families of leafy and two of thallose liverworts (Ligrone *et al*. 2000, 2002). These conducting cells are formed by protoplasmic degeneration due to acid phosphatases, as in the mosses, but their wall development is different from that of the mosses (Crandall-Stotler 1980). They lack wall hydrolysis but possess numerous plasmodesmata-derived pores on all walls and never develop polyphenolic compounds (Hébant 1978). No food-conducting cells are known among the **Marchantiophyta** (Figure 48).

Figure 48. ***Porella navicularis*** (**Marchantiophyta**, **Jungermanniopsida** – a leafy liverwort) stem cross section showing absence of central strand. Photo from Botany website, University of British Columbia, Canada, with permission.

## Hydroids

The elongated, water-conducting **hydroids** typically occur in groups of 2-3 in bryophyte stems (Hébant 1970); they are similar to tracheids, but lack lignin and secondary wall thickenings (Taylor 1988). Consequently, hydroids are usually thin-walled (Zamski & Trachtenberg 1976) and lack the helices and other thickenings typical of tracheids. Vanderpoorten and Goffinet (2009) sum up three major differences between hydroids of bryophytes and the tracheids and vessels of tracheophytes: hydroids lack secondary wall patterns; bryophyte lignin-like polymers are not cell-specific as they are in tracheophytes and are more likely to offer protection against microbes; hydroids collapse during water stress, making them highly resistant to cavitation (drop in vascular pressure due to vapor pockets resulting from desiccation) (Ligrone *et al.* 2000). This combination creates a fundamental difference in response to drying, with bryophytes being desiccation tolerant and tracheophytes preventing desiccation by pumping water from the soil, closing stomata, and reducing water loss with a waxy cuticle (Vanderpoorten & Goffinet 2009).

Table 1. Comparison of percentage of structural components of tree leaves and of plants of the moss ***Polytrichastrum*** (=*Polytrichum*) ***ohioense***. From Lawrey 1977.

| Litter type | soluble carb | hemi-cellulose | cellulose | "lignin" | ash |
|---|---|---|---|---|---|
| *Pinus resinosa* leaves | 35.41 | 13.44 | 19.37 | 23.56 | 3.68 |
| angiosperm tree leaves | 43.89 | 11.59 | 20.43 | 11.04 | 6.97 |
| ***Polytrichastrum ohioense*** | 16.51 | 14.07 | 24.37 | 12.90* | 4.24 |

*Not a true lignin in mosses.

Hydroids senesce at maturity and become dead, empty cells, like those of xylem, with slanted end walls that abut on the end wall of the next cell, as in tracheids (Richardson 1981). This change from living cells to empty dead cells is a result of acid phosphatase activity that degenerates the protoplasm (Crandall-Stotler 1980). Hydroids of **Bryophyta** typically lack perforations but sometimes have secondary polyphenolic thickenings on the lateral walls of cells (Scheirer 1975). Scheirer (1973) used ***Dendroligotrichum*** (Figure 49) (**Polytrichopsida**) to demonstrate that hydrolysis leaves behind only cellulose remains of the primary walls of end walls of hydroids. Subsequent examination by electron-dense crystals of Prussian blue on the end walls in ***Polytrichum commune*** (Figure 50) suggests that these end walls are highly permeable (see Figure 51), but that substances are unable to move through the lateral walls (Scheirer & Goldklang 1977).

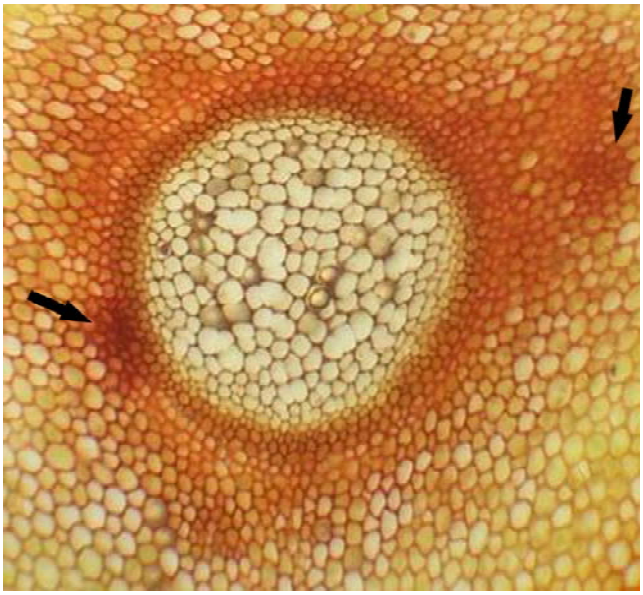

Figure 49. ***Dendroligotrichum dendroides*** stem cross section showing hydroids in center (**brown walls and mostly empty**), surrounded by stereids (**brown walls and interior brown**) and leptoids (**rusty-colored walls and contents**). Note vascular branches (**arrows**) that go into the cortex. The central strand has a few sclereids (thick walls) and these are living cells. Photo by Juan Larrain, with permission.

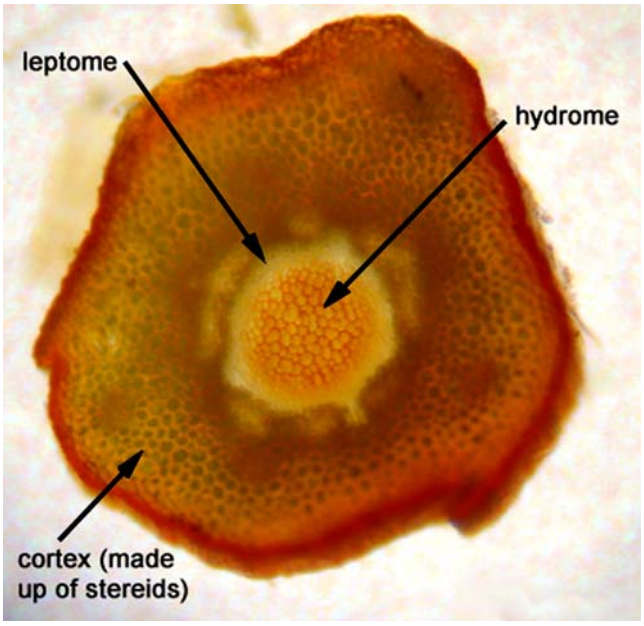


Figure 50. ***Polytrichum commune*** stem cross section. Photo by Julie Chou from Botany website, University of British Columbia, Canada, with permission.

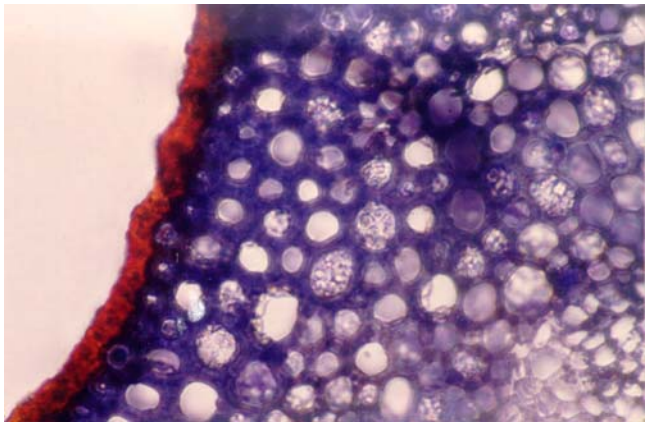

Figure 51. Cross section of ***Polytrichum*** stem stained with aniline blue to show thin areas in end walls of cortical cells. Photo courtesy of Isawo Kawai.

To understand any relationship between hydroids of bryophytes and tracheids or vessels of tracheophytes, we must understand their structure. We can consider that part of their structural development is similar to that of tracheophytes because they, like xylem cells, are dead at maturity (Richardson 1981). But is their chemical nature similar? It appears that the bryophytes have derived their water conducting cells in a variety of ways.

Hébant (1973a) found that strong activity of acid phosphomonoesterases occurs in the differentiating water-conducting cells of various mosses and at least one liverwort. But a lesser activity is also present in leptome cells and certain parenchyma cells of some **Polytrichales**.

Some chemical labelling tests gave similar results in as divergent taxa as ***Takakia*** (Figure 25-Figure 27) and ***Polytrichum*** (Figure 50-Figure 51), but different results in ***Mnium*** (Figure 74) (Ligrone *et al*. 2002). And Ligrone and coworkers found labelling of both water-conducting cells and parenchyma cells in ***Haplomitrium*** (Figure 107), but only of water-conducting cells in ***Polytrichum***. Ligrone *et al*. found that the arabinogalactan protein (AGP) antibody labelled the water-conducting cells in all Bryophyta tested (8 species) except the large polytrichaceous moss ***Dawsonia*** (Figure 52). No labelling occurred in the liverworts (4 species). Hence, it appears that the chemicals present are similar, but that they occur at different places within the plants.

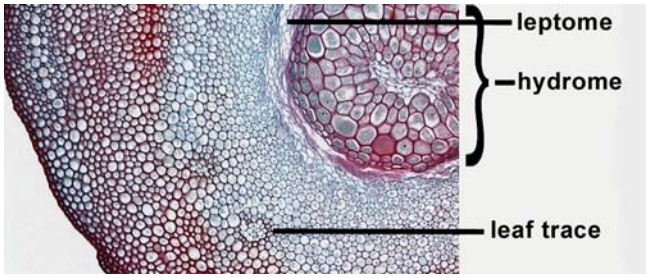


Figure 52. ***Dawsonia*** stem cross section to show hydrome, leptome, and leaf traces. Photo from Wikimedia Creative Commons.

Differences in labelling between the water-conducting cells and the cortical cells appeared to be mostly quantitative in these few species (Ligrone *et al*. 2002). On the other hand, electron microscopy revealed clearly distinct differences in the location of the antibodies within the cell walls of these two cell types, suggesting that their presence in a particular location was tissue specific in its regulation. Even within the **Polytrichaceae** (Figure 49-Figure 52) there is considerable diversity in the immunocytochemistry. In short, the bryophytes have a widely diverse chemistry in their conducting cells, but as such, they differ strongly from those of tracheophytes. Ligrone *et al*. (2002) consider the presence of several carbohydrate antigens in the cell walls of hydroids to indicate that hydrolysis of non-cellulosic polysaccharides is not part of the maturation process, a strong contrast to that in tracheophytes (see Hébant 1977).

Accompanying these chemical differences are differences in structure. True **perforation plates** (end walls of vessels) have not been found in **Polytrichaceae** (Figure 49-Figure 52) (Frey & Richter 1982) or most other mosses (Hébant 1973b). Consequently, Frey and Richter (1982) set out to discover them in mosses. In the dendroid moss ***Canalohypopterygium tamariscinum*** (Figure 53), they found structures resembling perforation plates of *Ephedra* (Gnetophyta), although they were not numerous and were restricted in location to branching areas. Perhaps this type of vascular structure permits them to be dendroid, lacking the close structure of leaves along the stem needed for capillary action. Smith (1964) had already demonstrated perforations in the conducting elements of the liverwort ***Symphyogyna circinata*** (Figure 54). Furthermore, pits are known, particularly in end walls, from ***Haplomitrium*** (Figure 107) [considered to be basal to leafy liverworts (Crandall-Stotler & Stotler 2000)] and ***Takakia*** (Figure 25-Figure 27) (now classified as a primitive moss in the **Takakiopsida**), as confirmed by electron microscope.

Figure 53. ***Canalohypopterygium tamariscinum***. Photo by Pieter Pelser, with online permission for educational use.

Although hydroids do not seem to contain true lignin, as do tracheophyte xylem cells, they do contain a polyphenolic cell wall component that functions similarly to lignin (Pressel *et al*. 2010). This compound protects the wall from hydrolytic attack and aids in internal transport of water. In ***Rhacocarpus purpurascens*** (Figure 55), Edelman *et al*. (1998) found walls composed of "mainly

lignin, **hemicellulose** (H-bonded to cellulose in plant cell walls), and cellulose in a ratio of ca. 9:8:5." Although the resonance spectrum indicated various characteristics typical of lignin, some specific peaks associated with known lignin compounds were missing. Thus the question remains, is this true lignin?

Figure 54. ***Symphyogyna circinata***. Photo by Filipe Osorio, with permission.

Figure 55. ***Rhacocarpus purpurascens***, a moss that produces a cell wall substance similar to lignin. Photo by Michael Lüth, with permission.

## Leptoids

**Leptoids** (Figure 56) are very similar to phloem sieve cells, and in fact, Behnke (1975) calls them just that. Taylor (1988) considers that in some cases they are nearly identical to protophloem cells of certain tracheophytes. They, along with parenchyma cells, comprise the **leptome** (=leptom) (Hébant 1970, 1974; Behnke 1975; Figure 32). We know that they are typical in the **Polytrichaceae**, but have also been found in ***Sphagnum***, **Hookeriaceae**, **Neckeraceae**, and **Orthotrichaceae** (Ligrone & Duckett 1994b, 1998a; Duckett & Ligrone 2003). Except in the setae of a few species (Hébant 1974), leptoids have not been found in the arthrodontous mosses (considered more advanced) and are unknown in liverworts. It is likely that they are much more common than we realize because in cross section without stain they appear no different from the unspecialized parenchyma cells.

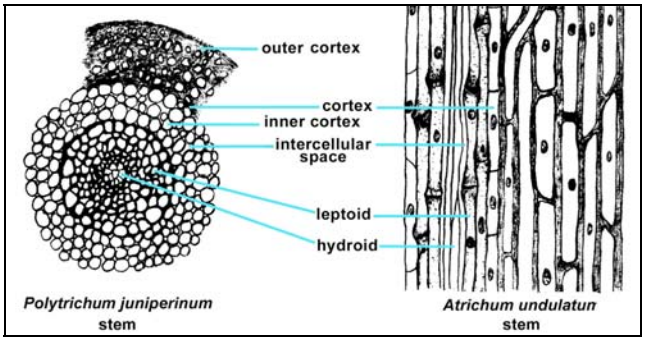


Figure 56. Cross section of ***Polytrichum juniperinum*** and longitudinal section of ***Atrichum undulatum*** stem to illustrate parts of central strand (leptoids and hydroids) and stem structures. Drawings by Margaret Minahan, modified from Hébant (1977).

In the moss family **Polytrichaceae** (Figure 56, Figure 58), leptoids have an axial system of microtubules with polarized cytoplasmic organization (Ligrone *et al*. 2000). In other mosses, including ***Sphagnum*** (Figure 36-Figure 47), such organization may also occur in stem and seta parenchyma cells. Even rhizoids and caulonemata of mosses and liverworts and thallus parenchyma cells of liverworts may have a similar organization for transporting nutrients **symplastically** (through cells, inside the membrane) for longer distances. But, as will be seen later in this chapter, these food and water conducting cells are fundamentally different from the phloem sieve cells and tracheids of tracheophytes. Nevertheless, Ligrone *et al*. (2002) found that the cell wall and tissue complexity of bryophytes are "on a par with higher plants."

The **leptoids** are distinct in vertical section by their elongate shape and slightly oblique end walls (Figure 59) (Behnke 1975). At maturity, the nucleus degenerates, as in phloem sieve cells (Richardson 1981), but protoplasm remains. In ***Polytrichum*** (Figure 56), the leptoids are not connected end-to-end by sieve plates or pores as in tracheophytes, but by numerous **plasmodesmata**. However, Cortella and coworkers (1994) considered the thin areas of central strand parenchyma cells to be primary pit fields in ***Hookeria lucens*** (Figure 57) stems and suggest that these cells have a conducting function.

Figure 57. ***Hookeria lucens***. Photo by Jiří Kameníček, with permission.

Even the development of leptoids seems similar to that of phloem sieve cells. During leptoid maturation in **Polytrichaceae**, **ribosomes** (centers of protein synthesis) disintegrate and nuclei become smaller and inactive, although they do not dissolve completely as in tracheophytes; mitochondria persist. The parenchyma cells contain starch-storing chloroplasts. As in their tracheophyte counterparts, leptoids move carbohydrates and other substances away from the apex.

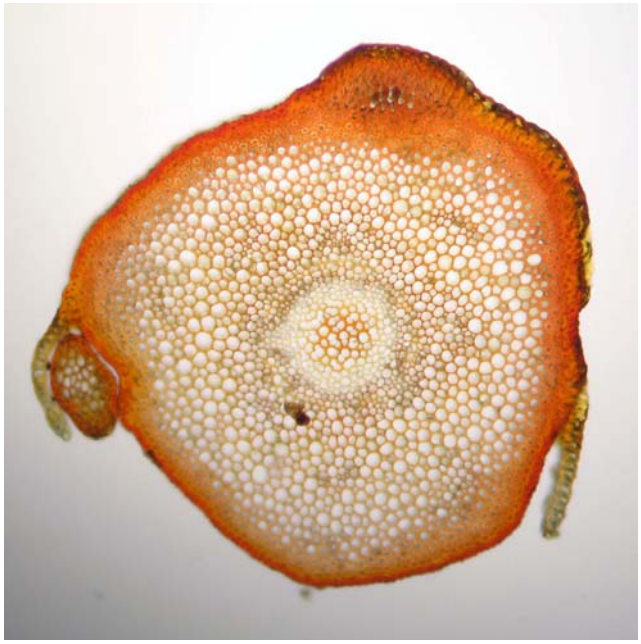

Figure 58. ***Polytrichastrum formosum*** stem cross section showing central **hydroids** (**with orange walls in center**) and considerable differentiation in the cells of the **central strand**. **Leptoids** are present outside the central strand and are not discernible in cross sectional view. Photo from Botany website, University of British Columbia, Canada, with permission.

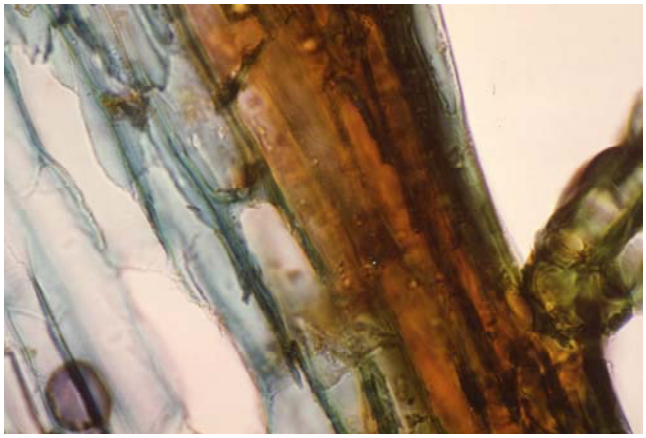

Figure 59. ***Hypnum*** sp., a pleurocarpous moss, stem longitudinal section. Note the long cell with what appear to be broken side walls, a disintegrating diagonal cross wall, and a partially missing protoplast. This appears to be a **leptoid**, but we need conduction tests to verify it. Photo courtesy of Isawo Kawai.

## Rhizome

The **rhizome** (underground, horizontal stem connecting upright plants), on the other hand, has **hypodermal** and **radial strands** but lacks connecting traces and a sterome. The **hypodermis** (Figure 60), also present in some stems, consists of one to several layers of distinct cells just beneath the epidermis and may be thick-walled or colored.

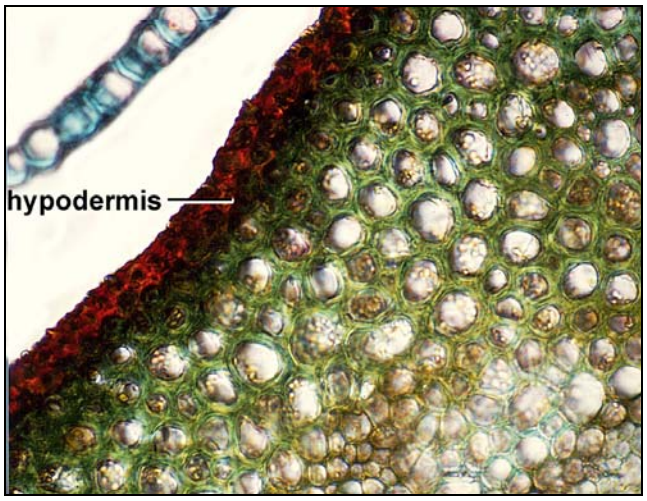


Figure 60. ***Polytrichum*** stem cross section showing **hypodermis**. Photo courtesy of Isawo Kawai.

Long-distance transport brings its own set of problems. These plants can undergo transpiration, causing them to lose water (Raven 2003). In some liverworts and many mosses, but not hornworts, there are dead cells in the tissues. These may function in long-distance **apoplastic** (outside cell membranes) water transport. Symplastic transport, on the other hand, seems to have a high resistance to flow, emphasizing the importance of apoplastic movement.

## Leaves

In most tracheophytes, the leaf is a critical structure in creating the movement of water from the roots to the tops of tall plants. This movement, known as the **transpiration stream**, requires the loss of water from the leaf, creating a vapor pressure deficit that brings water upward like someone sucking on a straw. But bryophytes typically do things quite differently, as we shall see in a later sub-chapter. They typically take in water from above, not below, hence requiring a new look at the role of leaves in water movement. It appears that the greatest need is not to move water to the leaves, but rather to move substances made in the leaves to other parts of the plants.

## Costa

Within the leaf, water may move cell to cell among the **lamina** cells (Figure 61), but many leaves have a **costa** (Figure 61-Figure 62) that is often accompanied by supporting **stereid** cells (Figure 63). Unlike the midrib of ferns and seed plants, the costa does not branch and rebranch to deliver water or other substances to or from cells of the leaf lamina (Figure 62), although in some taxa, for example ***Hygrohypnum*** (Figure 64), it may have one or more branches. Nevertheless, the costa has elongate cells

that we might expect to facilitate a more rapid movement of water within the leaf (Figure 62), but does it?

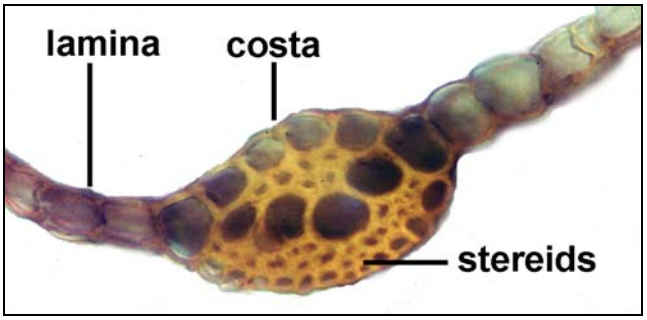


Figure 61. Cross section of moss leaf blade showing arrangement of broad portion (lamina), costa, and supporting stereids. Large cells in costa serve for conduction. Photo by Janice Glime.

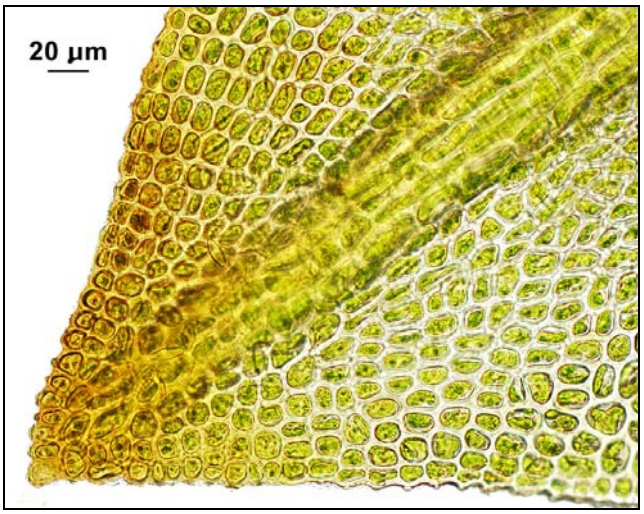


Figure 62. ***Crumia latifolia*** leaf showing elongate costa cells and nearly isodiametric lamina cells. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

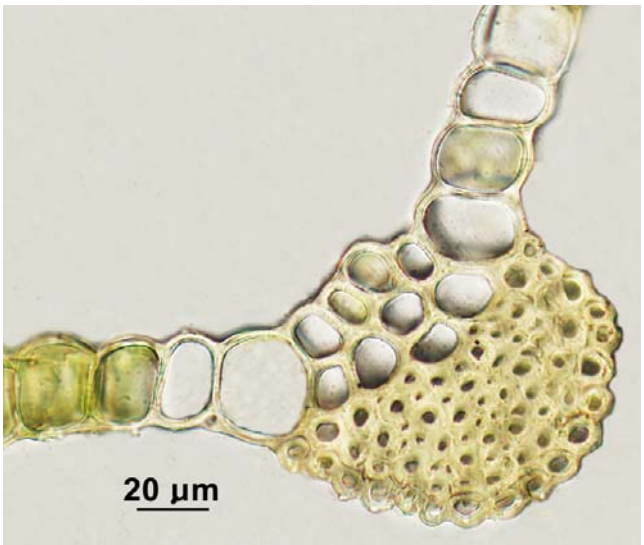


Figure 63. ***Crumia latifolia*** leaf cross section showing enlarged costa with many stereids supporting the conducting cells. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

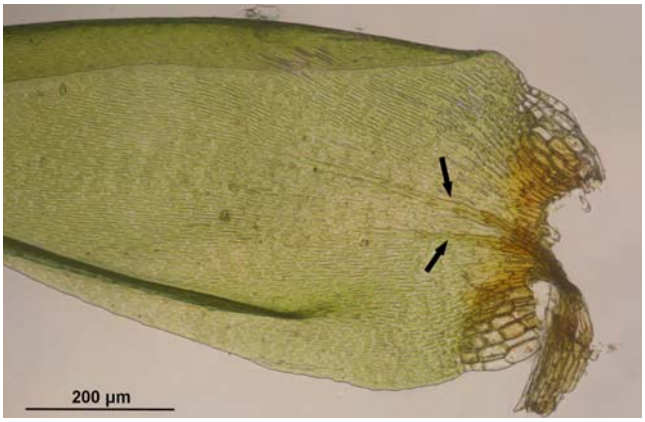


Figure 64. ***Hygrohypnum eugyrium*** leaf showing two branches of the costa (**arrows**). Photo by Hermann Schachner, through creative Commons.

On closer examination of the costa, we find that those elongate cells are living cells with oblique end walls, thin cell walls, and living protoplasm (Hébant 1977)! These are not hydroids, but are **leptoids**. Hence, it appears that in addition to its supporting role, the costa can have the role of conducting substances from the leaf toward the stem. (We will see shortly how this system connects to the leaf traces in the stem.) It appears that the costa should not have a role in conduction of water.

### *Sphagnum*

***Sphagnum*** (Figure 65) has the most unusual water system in its leaves of any bryophyte. Its leaves have two types of cells, and rarely a border in addition. These two types are the water-holding, colorless, dead **hyaline** cells and the green **chlorophyllose** (**photosynthetic**) cells (Figure 66-Figure 67). The hyaline cells serve as water reservoirs for the photosynthetic cells. Their walls have true perforations and are strengthened by spiral thickenings, suggesting the structure of tracheophyte vessels (Figure 66-Figure 67) (Hébant 1977). The pores (perforations) begin with a thinning of an area of the cell wall and presence of a thin membrane. Eventually these rupture to create the pore, using the process already described above for the hyaline cells of ***Sphagnum*** stems.

Figure 65. ***Sphagnum*** leaves showing the patterning caused by the network of chlorophyllose cells and hyaline cells. Photo by Michael Lüth, with permission.

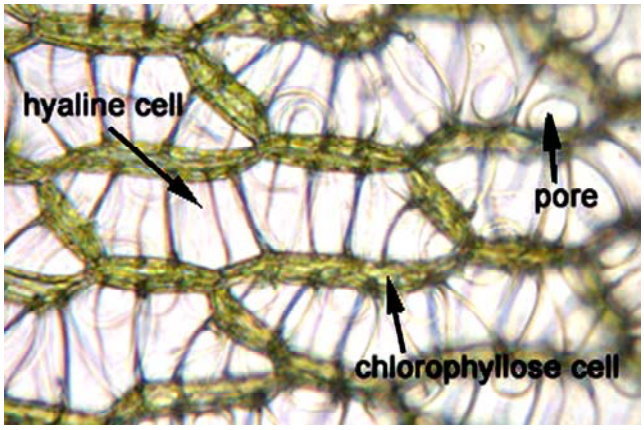


Figure 66. ***Sphagnum*** cells showing hyaline cells with spiral thickenings and pores, intermixed with chlorophyllose cells. Photo from Botany website, University of British Columbia, Canada, with permission.

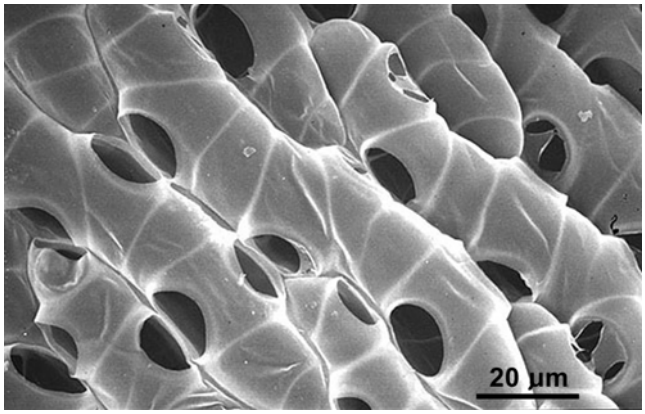


Figure 67. ***Sphagnum*** hyaline cells with spiral fibrils and pores. The photosynthetic cells are hidden by the hyaline cells in this leaf. Photo from Botany website, University of British Columbia, Canada, with permission.

## Leafy Liverworts

Leafy liverwort leaves never have a costa (Figure 68), leaving us to assume that transport of water and other substances in the leaves, if needed, is cell-to-cell transport through ordinary leaf parenchyma cells. But in this group (**Jungermanniopsida**), leaves are never more than one cell thick, giving all cells direct exposure to water from the atmosphere or other surroundings.

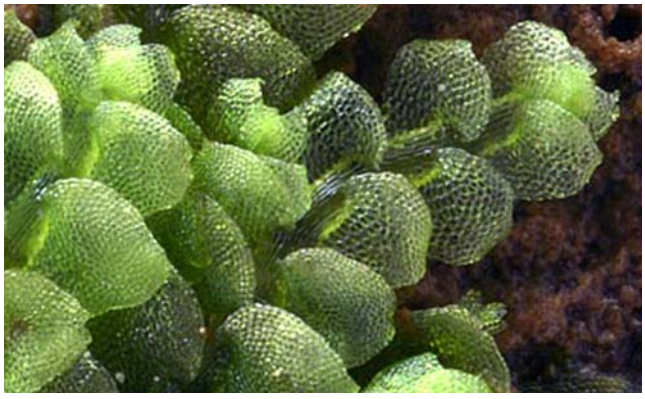

Figure 68. ***Calypogeia fissa*** (**Jungermanniopsida**) showing absence of costa in leaves and one-cell-layer leaf thickness. Photo by Des Callaghan, with permission.

We might also ask the role of **underleaves** (Figure 69) in this group. These may be non-existent (*e.g.* ***Jamesoniella***, Figure 70) to quite large (*e.g.* ***Porella***, Figure 71). Underleaves may be an evolutionary left over with no function, but their persistence suggests they may offer some advantages in water retention. They create capillary spaces on the under side of the stem and thus may aid in water retention. This space may also aid water uptake by holding water, but in many cases this would require that the stem (Figure 72) absorb the water. It would be interesting to experiment with different types of underleaves to see how they affect water uptake, especially by the stem, and how long they are able to hold a water reservoir.


Figure 69. ***Calypogeia integristipula*** demonstration of underleaves. Photo by Michael Lüth, with permission.

Figure 70. ***Jamesoniella undulifolia*** showing absence of underleaves (**arrow**). Photo by David T. Holyoak, with permission.

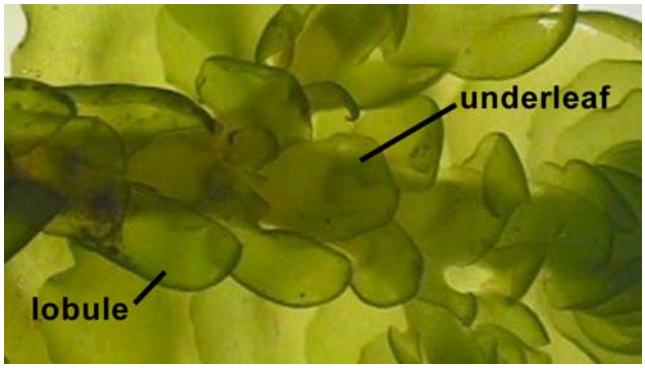


Figure 71. ***Porella platyphylla*** showing its large underleaf and lobule. Photo by Paul Davison, with permission.

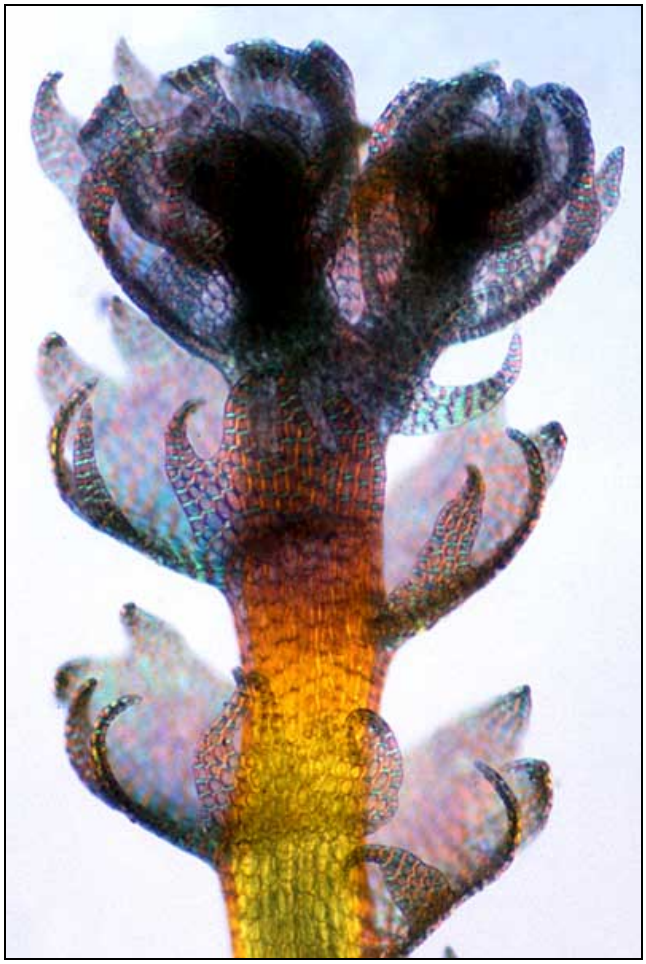

Figure 72. Leafy liverwort showing parenchymatous cells of stem. Photo by Bill Malcolm, with permission.

Another water reservoir in a number of leafy liverworts is the **lobule** (Figure 71). This structure, present in ***Frullania***, ***Porella***, **Lejeuneaceae**, and others can create a small reservoir of water suitable for small aquatic invertebrates such as rotifers and Protozoa to carry out their entire life cycle. These are discussed further in Chapter 7-4.

## Leaf Traces

Conduction from stems into leaves is typically through the parenchyma cells of the stem cortex, as will be described in a later sub-chapter. True **leaf traces** (conducting cells connecting the leaf costa to the hydrome; Figure 73) exist in some **Polytrichales**, but in other cases they do not quite reach that far. In the **Mniaceae** and **Splachnaceae** there are **false leaf traces** (Figure 74) that extend into the cortex from the leaf but do not connect with the central strand of the stem (Figure 75) (Hébant 1977). In ***Funaria hygrometrica***, some specimens have true leaf traces that reach the central strand, and others do not.

Hébant (1969) found that in ***Polytrichum*** (Figure 4), the true leaf traces extend from the leaf costa toward the central strand, but they become reduced near the central strand. Nevertheless, Hébant (1969) found that 7-8 hydroids of each leaf trace could connect to the central strand in grassland ***Polytrichum commune*** (Figure 50). This connection, however, seems to be related to water availability. In bog populations, only three hydroids form the connection. For specimens grown under water, no leaf traces connected to the central strand.

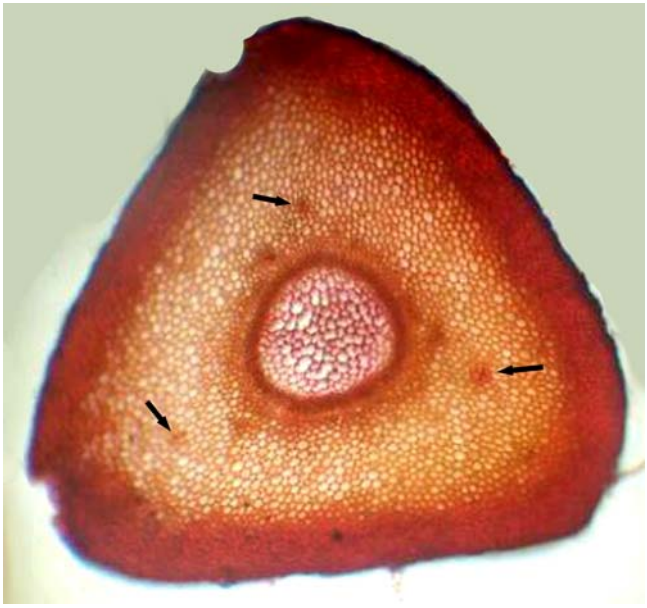

Figure 73. ***Dendroligotrichum dendroides*** stem cross section showing leaf traces in the cortex (**arrows**). Photo by Juan Larrain, with permission.

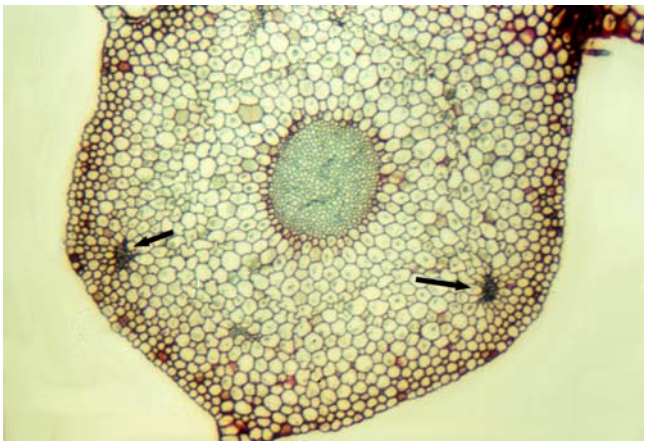

Figure 74. ***Mnium*** stem cross section showing distinct central strand and false leaf traces (**arrow**) that do not connect directly to the leaves. Photo by Janice Glime.

Figure 75. ***Rhizomnium glabrescens*** leaf cross section showing hydroids in center and stereids near the outer margins. In this family (**Mniaceae**), the central strand produces false leaf traces that do not connect to the costa of the leaf. Photo from Botany website, UBC, with permission.

But wait! Many kinds of leaves have a **costa**, the rib that extends part way or all the way down the center of the leaf. But the costa cells are fairly wide cells, albeit elongated, and contain a living protoplast (Hébant 1977). The end walls are oblique and have numerous plasmodesmata. They are in fact **leptoids**, not hydroids, and do not seem to have an important water conducting function in many mosses, if any. Rather, they conduct **photosynthate** and other substances from the leaf to the stem. These materials are thus deposited in the stem tissue. Could these actually connect with leptoids in the stem, permitting transport to stem tips or to rhizomes? In fact, in ***Polytrichum commune*** they do connect to the leptoids of the stem axis. Why then are there hydroids in the leaf traces? What do they connect? Is there any correlation between having a costa with leptoids and a stem with a central strand? Do all leaf leptoids connect with stem leptoids? So little we know...

## Rhizoids

Rhizoids have generally been assumed to function in attachment and little else. However, depending on the species and habitat, they may have important roles in water movement as well.

All liverworts except ***Haplomitrium*** (Figure 28) produce smooth, unicellular rhizoids. Duckett *et al*. (2013) reviewed the **pegged** and **smooth rhizoids** (Figure 76-Figure 78) of the complex thallose liverworts and noted that their roles differ. The mature smooth rhizoids of all liverworts remain alive. This permits them to function in nutrition, anchorage, and as conduits for mycobiont entry (Figure 77). They also collapse when dehydrated, a condition that is irreversible. Pegged rhizoids, on the other hand, are dead at maturity, permitting them to function in a "highly effective internalized external water-conducting system." This works especially well in the archegoniophores (Figure 79-Figure 80) of such liverworts as ***Marchantia***. They are cavitation-resistant with elastic walls that permit them to retain functional integrity during desiccation.

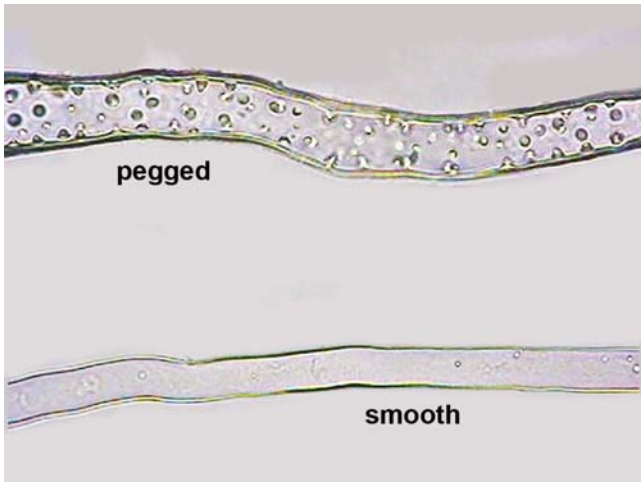


Figure 76. ***Conocephalum conicum*** pegged and smooth rhizoids. Photo by Paul G. Davison, with permission.

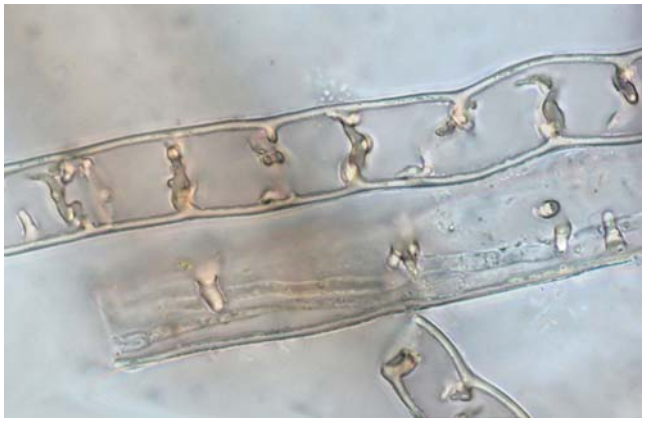

Figure 77. ***Marchantia polymorpha*** pegged rhizoid with fungus. Photo by Walter Obermayer, with permission.

Figure 78. ***Marchantia polymorpha*** ventral surface showing rhizoids. Photo from Botany Website, UBC, with permission.

Figure 79. ***Marchantia polymorpha*** with rhizoids whowing on the stalk where they are not included within the inrolled thallus. Photo by George Shepherd through Creative Commons.

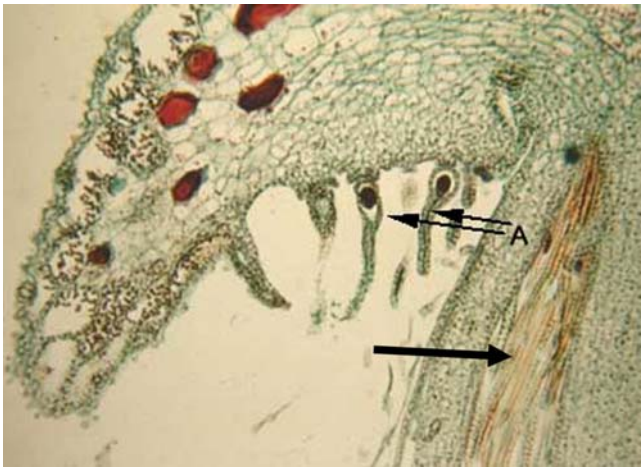


Figure 80. ***Marchantia polymorpha*** archegoniophore, with A indicating archegonia. The large arrow indicates the rhizoids rolled inside the stalk. Photo from Botany Website, UBC, with permission.

But to what degree do rhizoids in bryophytes facilitate the uptake of water and nutrients? Jones and Dolan, as recently as 2012, concluded that there was little direct evidence on nutrient uptake by bryophyte rhizoids. Nevertheless, they suggested that their functions include water transport in some mosses and liverworts. As far as I know, we lack experimental studies to tell us the magnitude of uptake.

Rhizoids can also serve as perennating organs (Frey & Kürschner 2011), often producing propagules.

## Sporophyte Conduction

In tracheophytes, it is the sporophyte that has the vascular tissue, and in the setae of mosses, one might find conducting tissues (a central strand) even when it is absent in the gametophyte. This should not be too surprising since the gametophyte is much better adapted to absorbing water from the atmosphere than the cuticle-endowed sporophyte. It is most likely necessary for a number of substances to be transported from the gametophyte into the sporophyte as it develops. And as we might expect, these conducting strands in setae are best developed in the **Polytrichaceae** (Hébant 1977), a family in which the peristome exhibits the more primitive character of nematodontous teeth.

Is perhaps no coincidence that a species with a vascularized stem also has a vascular seta. This seems to be the case in ***Plagiomnium undulatum*** (Figure 81).

On the other hand, leptoids can occur in the setae of some arthrodontous mosses even when they are absent in the gametophytes. Nevertheless, leptoids of setae, unlike those of tracheophytes, show less differentiation than in their gametophytic counterparts. In the setae of the **Polytrichaceae**, leptoids are not intermixed with specialized parenchyma cells and apparently lack enlarged plasmodesmata in their end walls, as seen in gametophytes of some taxa (Hébant 1974). To add interest to the picture, the leptoids are present in forms that are transitional between the parenchyma cells and the fully differentiated leptoid cells (Hébant 1974).

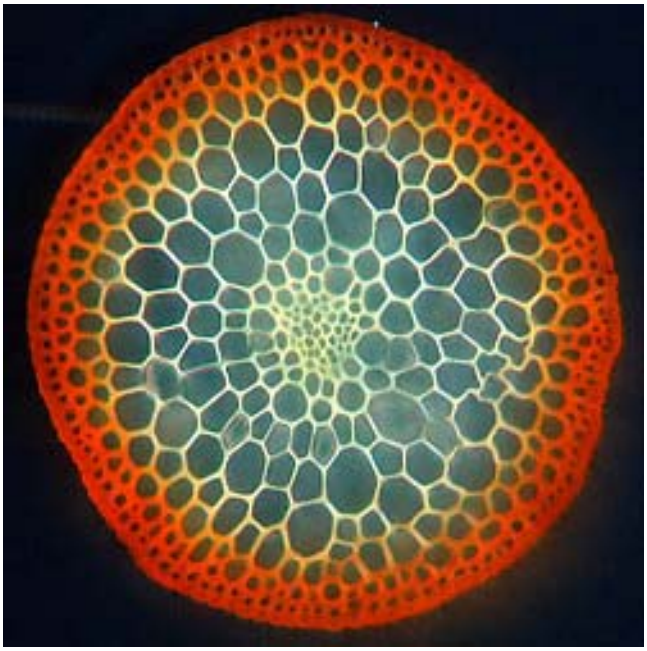

Figure 81. ***Plagiomnium undulatum*** seta cs showing central conducting strand. Photo by Norbert J. Stapper, with permission.

Meager evidence exists for the presence of **leptoids** in setae of other genera. Among these are ***Funaria***, ***Meesia***, and ***Splachnum*** (Hébant 1977). In ***Tortula muralis*** (Figure 82), Favali and Gianni (1973) have claimed that the leptoids are intermixed with the parenchyma cells in the seta and a similar claim was put forth by Bassi and Favali (1973) for ***Mnium orthorrhynchum***, but Hébant (1977) was unable to find any convincing evidence that this was true in either case.

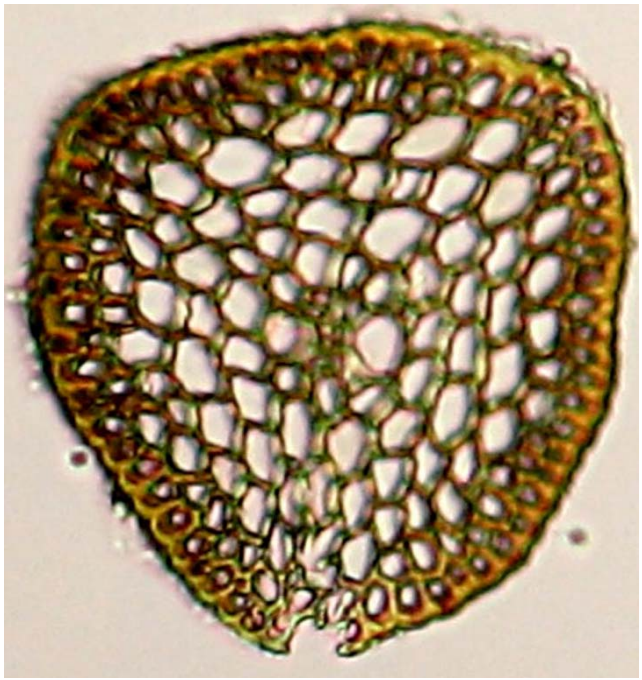

Figure 82. ***Tortula muralis*** seta cross section showing modified cells in center of seta. Photo from Botany website, University of British Columbia, Canada, with permission.


Figure 83. ***Tortula muralis*** or ***plinthobia*** stem cs. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Stem sections indicate that at least a central strand is present in the acrocarpous mosses ***Dicranum scoparium*** (an **arthrodontous** moss; Figure 84-Figure 85) and ***Tetraphis pellucida*** (a **nematodontous** moss; Figure 86-Figure 87). The presence of leptoids cannot be determined from these views, nor can the function of the central strand. Cross sections of these setae can be compared with stems of the same species in Figure 82-Figure 87.

Figure 85. ***Dicranum scoparium*** stem cross section showing differentiated central tissue with hydroids, but representing a genus where leptoids are often absent. There appear to be hydroids that are breaking up, possibly surrounded by a narrow band of leptoids. Photo from Botany website, University of British Columbia, Canada, with permission.

Figure 84. ***Dicranum scoparium*** seta cross section showing broken center with modified cells similar to those of stem (Figure 85). Leptoids do not seem to be visible. Photo from Botany website, UBC, with permission.

Figure 86. ***Tetraphis pellucida*** seta cross section. In this case, most of the cortex is occupied with thick-walled supporting cells. Hydroids occur in the middle. Photo from Botany website, University of British Columbia, Canada, with permission.

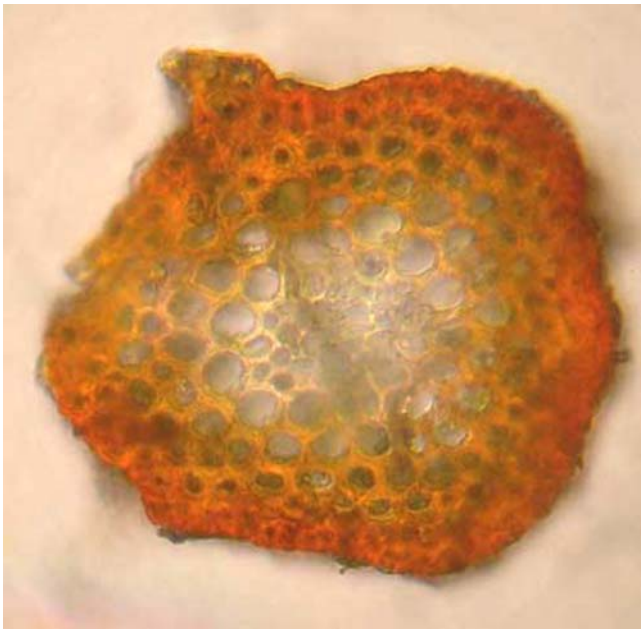

Figure 87. ***Tetraphis pellucida*** stem cross section. As in the seta (Figure 86), most of the cortex is occupied with thick-walled supporting cells. Hydroids occur in the middle but occupy a larger area than in the seta. Photo from Botany website, University of British Columbia, Canada, with permission.

Hébant (1977) pointed out that no electron microscope study existed on the histology of the conducting tissue of the capsule. He could offer little on its organization, stating that the conducting strand terminates shortly after it enters the capsule. In ***Funaria hygrometrica*** and ***Polytrichum commune*** the hydroids terminate within the capsule as a small ampulla, but such an ampulla is absent in ***Dawsonia***, ***Dendroligotrichum***, and ***Fissidens***.

## Adaptation and Evolution

The hydroids and leptoids present interesting evolutionary implications, since it appears that they are primitive characters that are lost in more advanced bryophyte taxa (Hébant 1970; Behnke 1975). Unlike most tracheophytes, the mosses retain conducting cells in both generations, but the haploid generation is the first to lose leptoids evolutionarily, as in ***Funaria*** (Behnke 1975), a moss that still has a central strand in the stem (Malcolm & Malcolm 2006) and leptoids in its setae (Hébant 1977).

### Being Acrocarpous

Some acrocarpous mosses may lack a central strand. For example, ***Leptodontium flexifolium*** (Figure 88-Figure 89) grows on acid substrata but lacks the central strand (Figure 89), but it has a leaf costa (Figure 88). Even the ubiquitous ***Ceratodon purpureus*** (Figure 90), a moss that occurs on substrata from roadsides and exposed rocks to pools in the Antarctic, lacks a central strand (Figure 91), and likewise has a costa (Figure 92-Figure 93). Other taxa that frequently become dry, like ***Grimmia*** species (Figure 94) also often lack specialized cells in the center of the stem (Hébant 1977).

Figure 88. ***Leptodontium flexifolium***, an acrocarpous moss. Photo by Des Callaghan, with permission.

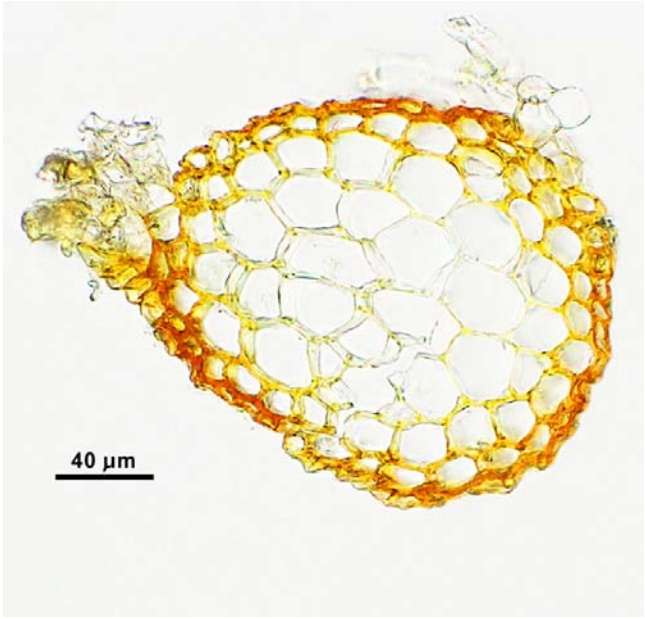


Figure 89. ***Leptodontium flexifolium*** stem cross section showing absence of hydroids. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

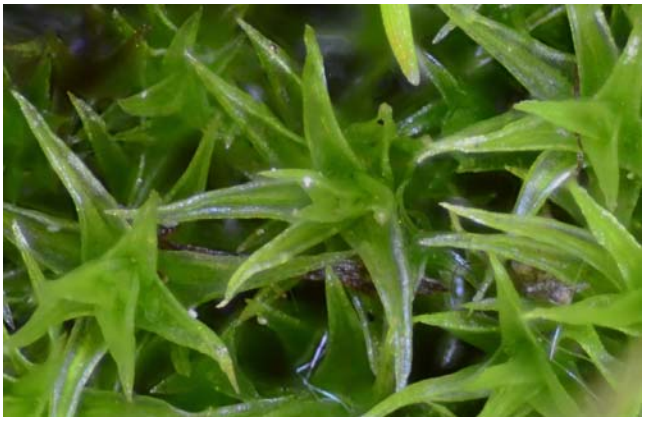

Figure 90. ***Ceratodon purpureus*** leaves. Photo by Don Loarie, through creative Commons.

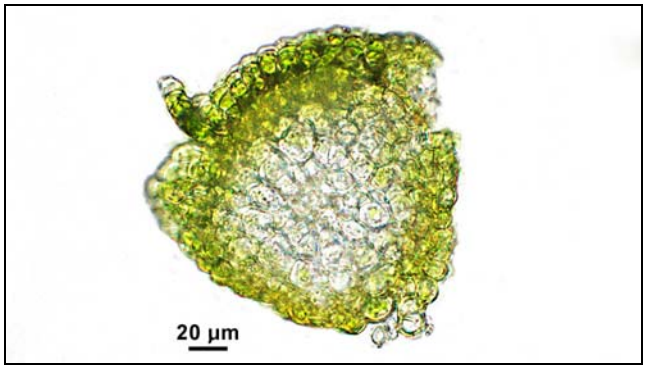


Figure 91. ***Ceratodon purpureus*** stem, a moss with a wide range of habitats from dry fields to Antarctic pools, yet it lacks hydroids. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 92. ***Ceratodon purpureus*** showing distinct costa. Photo by Malcolm Storey, through Creative Commons.

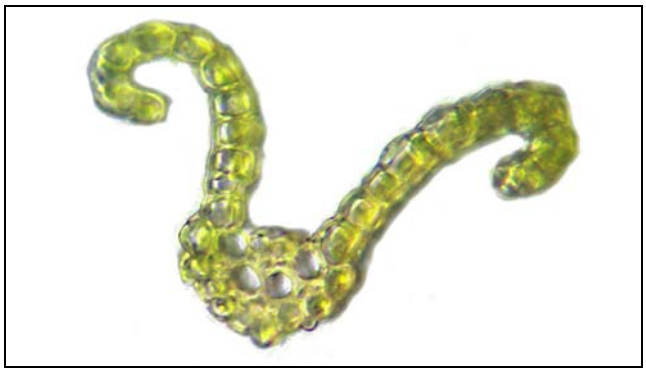

Figure 93. ***Ceratodon purpureus*** leaf cross section showing costa and involute margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

## Being Pleurocarpous

**Pleurocarpous** taxa that grow close to the ground may have less need for hydroids when all their leaves are more or less equally placed to gain water, as can be seen in ***Calliergonella lindbergii*** (=*Hypnum lindbergii*; Figure 95). Pleurocarpous mosses (Figure 95-Figure 98) have fewer problems in getting wet and sharing water among cells because they grow horizontally, compared to the need for upright mosses to distribute water, especially tall ones that grow alone, like ***Dawsonia*** spp. (Figure 2). On the other hand, these mosses may have evolved the loss of hydroids before our extant species existed and have not regained their hydroids, as might be the case for ***Hylocomium splendens*** (Figure 97-Figure 98), a moss that grows in fairly open wefts, but lacks a central strand. Nevertheless, it would seem that the pleurocarpous mosses still need to transport photosynthate and hormones, among other things. Hence, we should expect leptoids in many, if not all, pleurocarpous mosses. Unfortunately, it is hard to find information on leptoids in these taxa. The same need, and lack of information, could be said for leafy liverworts.

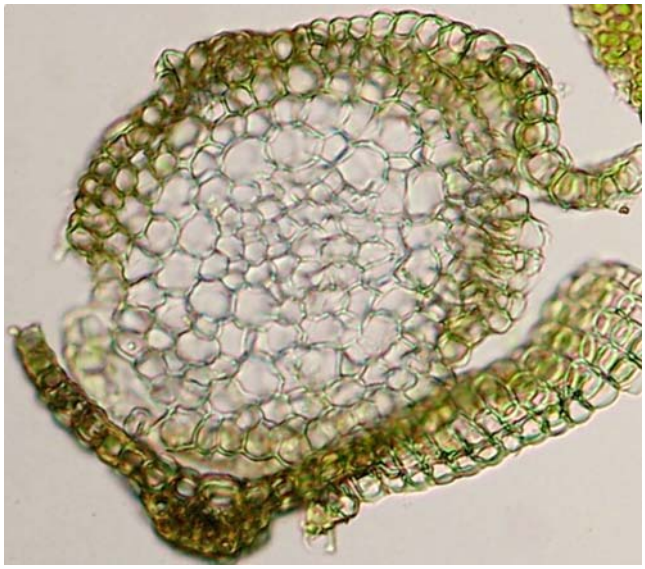

Figure 94. ***Grimmia pulvinata*** stem cross section showing little differentiation in the central cells of the cortex. Are these hydroids? This genus can have hydroids or lack them. The tissues flaking away from the stem are leaf cross sections. Photo from Botany website, UBC, with permission.

Figure 95. ***Calliergonella lindbergii*** forming a thick mat. Photo by Michael Lüth, with permission.

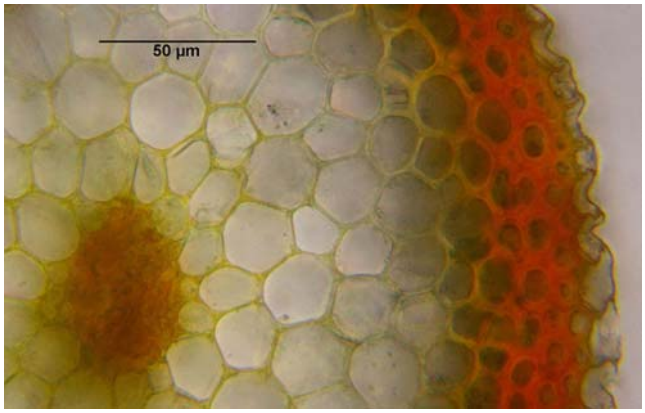


Figure 96. ***Calliergonella lindbergii***, a pleurocarpous moss, stem cross section showing a small area of differentiated central tissue. Photo by Hermann Schachner, through Creative Commons.

Figure 97. ***Hylocomium splendens***, showing its open growth habit that will permit easy escape of water. This moss grows in an almost dendroid pattern, but together with many stems that form wefts. Photo by Dale Vitt, with permission.

Figure 98. ***Hylocomium splendens***, a pleurocarpous moss, stem cross section showing absence of any hydroids or central strand. Photo from Botany website, University of British Columbia, Canada, with permission.

In ***Climacium*** (Figure 99), the stem has very reduced strands of conducting tissue (Hébant 1977). This moss stands upright like a small tree. The stem is nearly naked, making external upward transport limited. Hence this moss must rely on water that lands on the leaves. Instead of specialized water conducting cells, ***Climacium*** species have good supporting tissues in their stems, permitting the stem to support the leafy tree-like portion.

Figure 99. ***Climacium dendroides*** showing the nearly naked supporting stem. Photo by Keith Bowman, with permission.

## Aquatic

It should be no surprise that aquatic taxa like ***Fontinalis*** (Figure 100-Figure 102) lack hydroids. Likewise, in ***Touwia*** (Figure 103), a pleurocarpous moss in the **Neckeraceae**, there is no cross-sectional evidence of a central strand (Figure 104). Rather, like ***Fontinalis***, this streambed moss has many thick-walled cortex cells that help to protect the stem from breakage in stream flow. Its leaves likewise have a thick **costa** (Figure 105) that can resist the ravages of flow. But even in such epiphytic taxa as ***Neckera crispa*** conducting cells are lacking, suggesting an evolutionary loss early in this branch. Taxa like ***Touwia*** with a strong costa but no conducting cells in the stem suggest that the costa cells that are elongate in a leaf where other cells are shorter may serve a function more important than conduction – that of supporting tissue, and may sometimes serve both functions. It is likely that they also have regenerative ability.

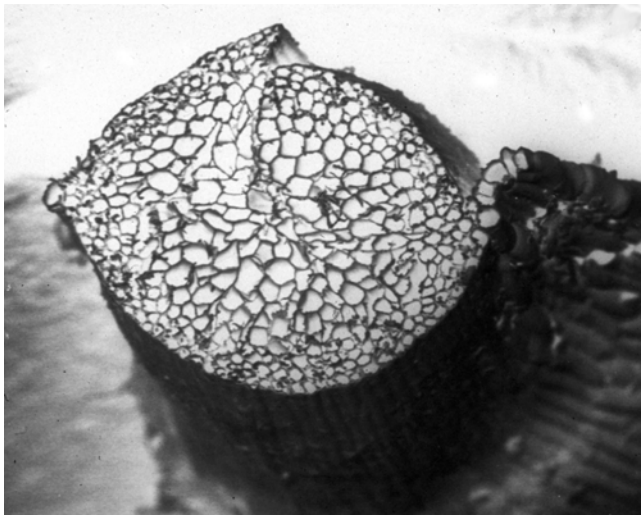

Figure 100. ***Fontinalis squamosa*** SEM image of stem cross section, showing the absence of specialized cells in the center of the stem. Photo by Janice Glime.

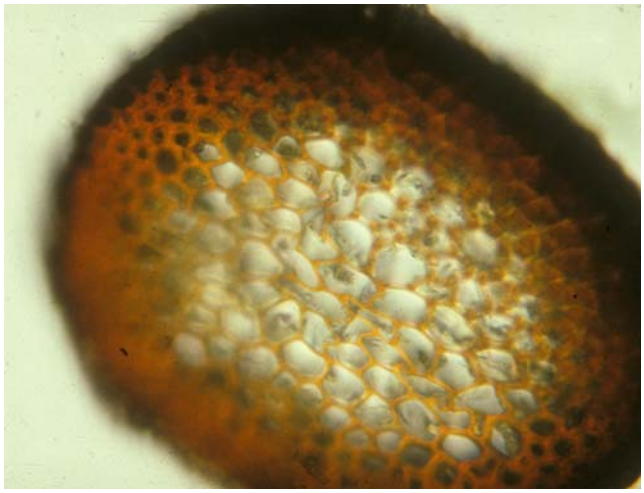

Figure 101. ***Fontinalis dalecarlica*** stem cross section showing absence of hydroids. Note the thick-walled outer cortical cells that give this stem the strength needed to survive in the rapidly flowing water of mountain streams. Photo by Janice Glime.

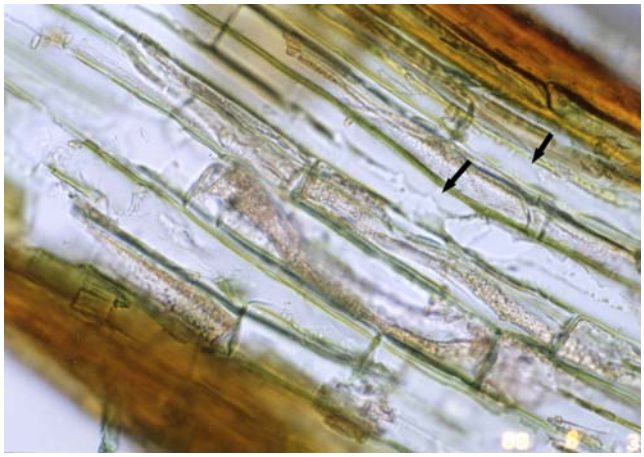

Figure 102. Longitudinal section of stem of ***Fontinalis gracilis*** showing elongated, thin-walled cells of the cortex. The cells at the arrows appear to be particularly long. Could they be leptoids? Photo by Isawo Kawai, with permission.

Figure 103. ***Touwia laticostata*** (?) branches showing leaves with thick costae. Note the remaining costae on the lower branch after it suffered abrasion. Photo courtesy of Andi Cairns.

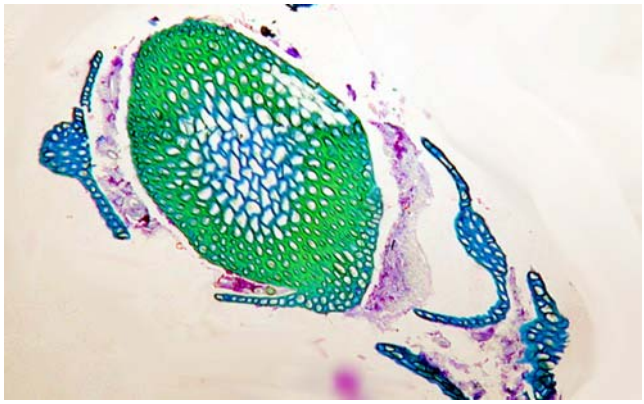

Figure 104. The moss ***Touwia laticostata*** (?) stem (lacking discernible hydroids) and leaves with thick costa. Photo courtesy of Andi Cairns.

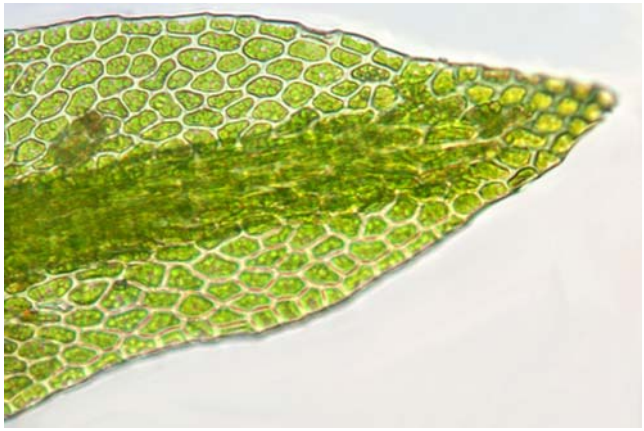

Figure 105. ***Touwia laticostata*** (?) leaf showing thick costa. Photo courtesy of Andi Cairns.

## Using a Partner

**Epiphyllous** bryophytes have an unusual habitat on their host leaves. Water usually does not stay and is even repelled by the host leaf surface. ***Radula flaccida*** (Figure 106) has at least partially solved the problem by producing rhizoids that penetrate the host leaf cuticle and epidermal cells, extending into the tissues of the host (Berrie & Eze

1975). Berrie and Eze found that both water and dissolved phosphorus salts can be obtained from the host leaf. Hence, it appears that the liverwort is at least partially a parasite (Hébant 1977).

Figure 106. ***Radula flaccida*** habit with gemmae, growing on a leaf. Photo by Michaela Sonnleitner, with permission.

Throughout the kingdoms we see examples where two organisms share responsibilities in their mutual survival. Among these partners, the fungi seem to have perfected the strategy, making it possible for plants to greatly increase their available surface area without expending the effort to build the needed tissues. Such is the case for some bryophytes, a partnership for which we have limited understanding. Among those with such a relationship is the genus ***Haplomitrium*** (Figure 107) (Carafa *et al*. 2003). ***Haplomitrium*** secretes mucilage (Figure 108) from its underground rhizomes, forming an environment that harbors fungal hyphae. In ***H. gibbsiae*** (Figure 107), the fungus is restricted to the epidermal cells where it forms lumps, but in ***H. ovalifolium*** it also infects the adjacent cortical cells, forming lumps. Through such partnerships, these species can gain access to both deeper and wider sources of nutrients in the sol substrate.

In tracheophytes, this partnership strategy has been used by a number of **hemiparasites** that partner with a fungus that partners with a tree or shrub. This arrangement permits them to gain carbohydrate energy from the photosynthesizing canopy while living in the darker environment under its protective cover. Our knowledge of bryophyte partnerships is still too primitive to ascertain how important this relationship is in permitting many bryophytes to subsist in such low light conditions.

Figure 107. ***Haplomitrium gibbsiae*** leafy plant showing slimy rhizomes. Photo courtesy of Jeff Duckett and Silvia Pressel.

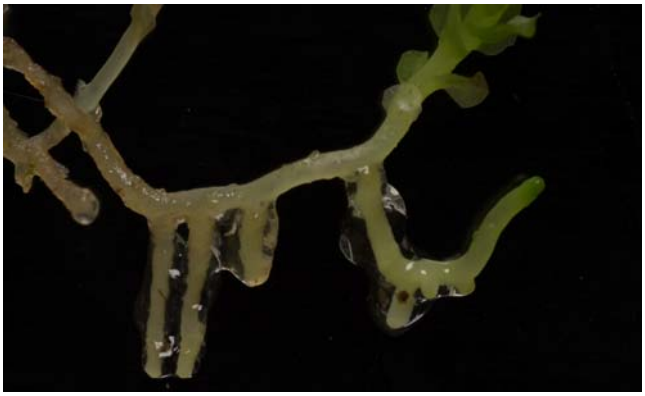

Figure 108. ***Haplomitrium gibbsiae*** rhizomes covered with thick mucous. Photo courtesy of Jeff Duckett and Silvia Pressel.

## Summary

Movement onto land required means of obtaining and retaining water. Bryophytes, reputedly the first colonizers, often are not the nonvascular plants we once thought them to be. They often possess **hydroids**, surrounded by **stereids**, that conduct water and together comprise the **hydrome**. Hydroids lack lignin and spiral thickenings, distinguishing them from tracheids and vessels of tracheophytes. **Leptoids** that conduct sugars, arranged as in tracheophytes, with the water-conducting cells surrounded by the sugar-conducting cells, are less well known because they are distinguishable in longitudinal section. In a few mosses, these stem conducting tissues connect by leaf traces to the leaves. Bryophytes usually have a thin **cuticle**, but it seems to lack wax in most cases. **Rhizoids**, although anchoring the plants as do roots, typically do not serve in obtaining water, but exceptions exist. **Acrocarpous** species more commonly have a central conducting strand, whereas **pleurocarpous** mosses remain close to the substrate and a central strand may not be useful.

Bryophytes function like sponges in the ecosystem by holding water and maintaining moisture in the soil below. But they also absorb water like a sponge, using capillary spaces. At times when water is limiting, the bryophytes are able to survive through their exceptional desiccation tolerance.

Mosses may have a **costa** (rib similar to a midrib) in the leaf, but it does not branch to reach all the cells (as in most tracheophytes) and may not always serve a conduction role. This is connected to the stem vascular strands only in the **Polytrichaceae**. Thallose liverworts may have a midrib to transport water and other substances, but leafy liverworts have no evidence of water-conducting cells in the stem and no **costa** in the leaf.

Even sporophytes have elongated cells in the seta. In younger sporophytes these may be important in conduction of nutrients to the developing capsule.

Aquatic species presumably do not need conduction since they are bathed in water. But they still need to move solutes and especially sugars from leaves to other locations. Some bryophytes have mycorrhizal associates that help take in water and

minerals. Others are connected by rhizomes that permit them to "scavenge" by obtaining photosynthate from connected stems that are in more favorable positions.

## Acknowledgments

This chapter has benefitted from the help of Beth Scafone and Medora Burke-Scoll, who read the manuscript for clarity. Linda Luster checked the literature citations, proofread, and made glossary suggestions from a layperson's perspective. Jean Faubert suggested problems in the original chapter and reviewed the revised chapter for me. Isawo Kawai sent me a large parcel of images of stained stem sections. Jeff Duckett and Silvia Pressel invited me to peruse their digital image library for images I could use.

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