

CHAPTER 7-1

WATER RELATIONS: CONDUCTING STRUCTURES

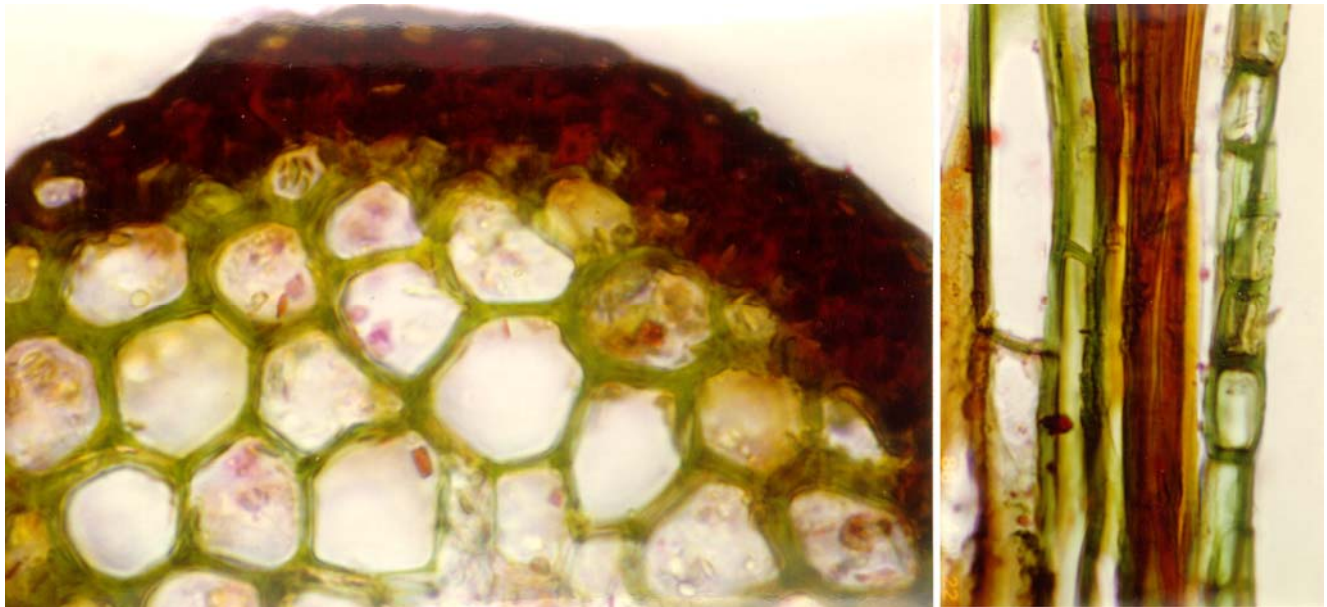


Figure 1. Cross section (**left**) and longitudinal section (**right**) of the moss *Bryoxiphium*, showing in vertical section how cells that appear in cross section to be only parenchyma cells may in fact be elongate cells suitable for conduction. Photo by Isawa Kawai.

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 nonwetland 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* that have conducting systems that almost mimic those of **tracheophytes** (plants having tracheids, *i.e.* the lignified vascular plants).

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

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; Héban 1977) and the variety of perforated and spirally thickened cells typical of xylem. 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 (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.

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.

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 3)? 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 3. *Aloina ambigua* growing in sand. Photo by Michael Lüth.

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 Structure

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 plant (**ectohydric**) (Buch *et al.* 1938). Thallose liverworts, Polytrichaceae, and Mniaceae represent the endohydric group (Buch 1945, 1947; Proctor 2000b). Ectohydric mosses typically maintain a constant internal water content by absorbing water from the external capillary spaces as needed (Proctor 2000b). These two 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.

Although the Anthocerotophyta are 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*. Few liverworts (Marchantiophyta) have specialized conducting tissues in their gametophytes, and none have them in the sporophyte. Nonetheless, conducting strands have been known since 1901 in the thallose liverwort *Pallavicinia lyellii* (Figure 4; Tansley & Chick 1901). As in mosses, *Pallavicinia* strands (Figure 5) closely resemble tracheids, with long cells, tapering ends, and obliquely oriented pits, and they likewise are dead at maturity.



Figure 4. *Pallavicinia lyellii* thallus. Photo by Jan-Peter Frahm.

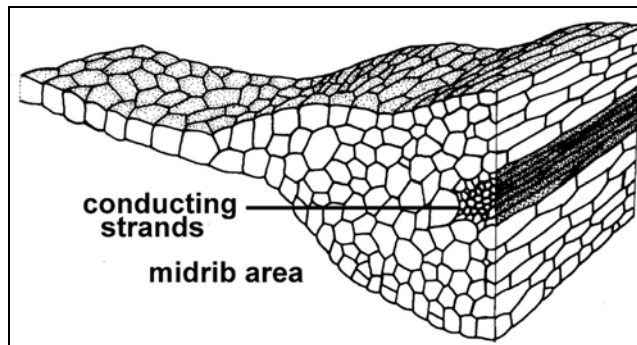


Figure 5. *Pallavicinia lyellii* cross section of thallus. Drawing from Hébant (1977).

Unlike the liverworts, mosses can have conducting cells in both generations (Ligrone *et al.* 2000). In the moss *Takakia* (a primitive moss once thought to be a liverwort; Figure 6) and some liverworts of Calobryales and Pallaviciniaceae (Metzgeriales), 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 11).



Figure 6. Cross section of stem of *Takakia lepidozoides*. Photo with permission from www.botany.ubc.ca/bryophyte/LAB8.htm.

Kawai (1991a) describes the moss stem as having a basic structure much like that of tracheophytes (lignified vascular plants) with an **epidermis** surrounding the **cortex** (Figure 11, top). This basic structure describes most of the pleurocarpous mosses that move internal substances mostly horizontally.

Among the acrocarpous mosses, more complex stems can have a **leptome** (= **leptom**), surrounding the **hydrome sheath**, a **sterome** (= **sterom**), and a **hydrome** (also known as **hadrom** and **hydrom**) (Figure 11). The **leptome** is composed of phloem-like cells called **leptoids**, which are difficult to distinguish from the cortex cells in cross

section. However, in vertical section they resemble phloem sieve cells (Figure 12). **Hydroids** (Figure 12) and **steroids** make up the **central strand** (Zamski & Trachtenberg 1976) and are collectively called the **hydrome** or **hydrom** (Scheirer 1980) and **sterome** (Héban 1977; **sterom** of Zamski & Trachtenberg 1976), respectively. **Hydroids** are water-conducting cells similar to tracheids but lacking any horizontal connections (*i.e.* no pits). **Steroids** are elongate, thick-walled, slender, and fiber-like cells; they can occur in the leaf **costa** (midrib-like strand; Figure 7) and stem.

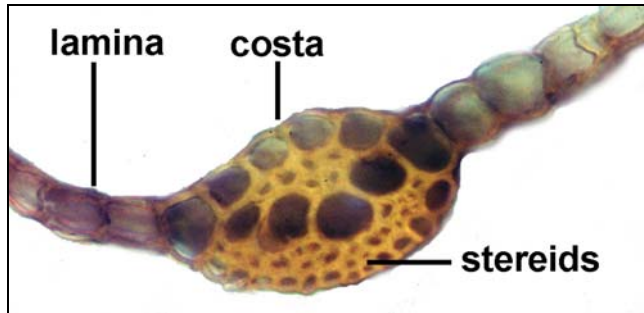


Figure 7. Cross section of moss leaf blade showing arrangement of broad portion (lamina), costa, and supporting steroids. Large cells in costa serve for conduction. Photo by Janice Glime.

The elongated, water-conducting **hydroids** typically occur in groups of 2-3 in bryophyte stems (Héban 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. 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). Hydroids of Bryopsida typically lack perforations. Scheirer (1973) used *Dendroligotrichum* (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* suggests that these end walls are highly permeable (Figure 8), but that substances are unable to move through the lateral walls (Scheirer & Goldklang 1977).

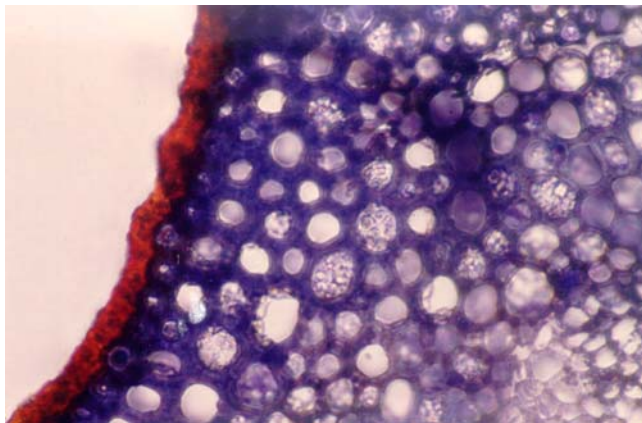


Figure 8. Cross section of *Polytrichum* stem stained with aniline blue to show thin areas in end walls of cells, but these are not in the hydrom. Photo by Isawa Kawai.

True **perforation plates** (end walls of vessels) have not been found in Polytrichaceae (Frey & Richter 1982) or most other mosses (Héban 1973). Consequently, Frey and Richter (1982) set out to discover them in mosses. In the dendroid moss *Canalohypopterygium tamariscinum*, they found structures resembling perforation plates of *Ephedra*, although they were not numerous and were restricted in location to branching areas. Perhaps this type of vascular structure permits them to be dendroid (Figure 9), lacking the close structure needed for capillary action along the stem. Smith (1964) had already demonstrated perforations in the conducting elements of the liverwort *Symphogyna circinata*. Furthermore, pits are known, particularly in end walls, from *Haplomitrium* [considered to be basal to leafy liverworts (Crandall-Stotler & Stotler 2000)] and *Takakia* (now classified as a primitive moss in the Takakiopsida), as confirmed by electron microscope.



Figure 9. *Hypopterygium novae-seelandiae* showing dendroid growth habit. Photo by Janice Glime.

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. This compound protects the wall from hydrolytic attack and aids in internal transport of water. In *Rhacocarpus purpurascens*, 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?

True **leaf traces** (conducting cells connecting the leaf costa to the hydrom; Figure 11) exist in some Polytrichaceae, whereas in the Mniaceae they are **false leaf traces** that do not connect with the leaf costa (Figure 11). The **rhizome** (underground, horizontal stem connecting upright plants), on the other hand, has **hypodermal** and **radial strands** but lacks leaf traces and a sterome. The **hypodermis** consists of one to several layers of distinct cells just beneath the epidermis and may be thick-walled or colored (Figure 10).

Leptoids (Figure 12) 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** (Héban 1970, 1974; Behnke 1975; Figure 11). We know

that they are typical in the Polytrichaceae, but have also been found in *Sphagnum*, Hookeriaceae, Neckeraceae, and Orthotrichaceae (Ligrone & Duckett 1994, 1998; Duckett & Ligrone 2003). 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. The leptoids are distinct in vertical section by their elongate shape and slightly oblique end walls (Behnke 1975). At maturity, the nucleus degenerates, as in phloem sieve cells (Richardson 1981). In *Polytrichum*, 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* stems and suggest that these cells have a conducting function.

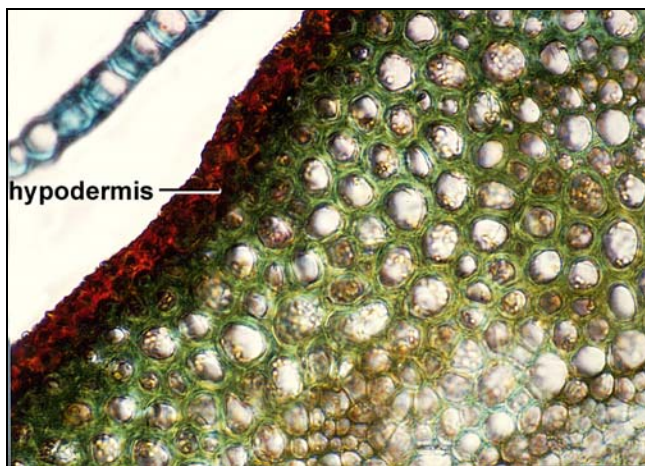


Figure 10. *Polytrichum* stem cross section showing hypodermis. Photo by Isawa Kawai.

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, they move carbohydrates and other substances away from the apex.

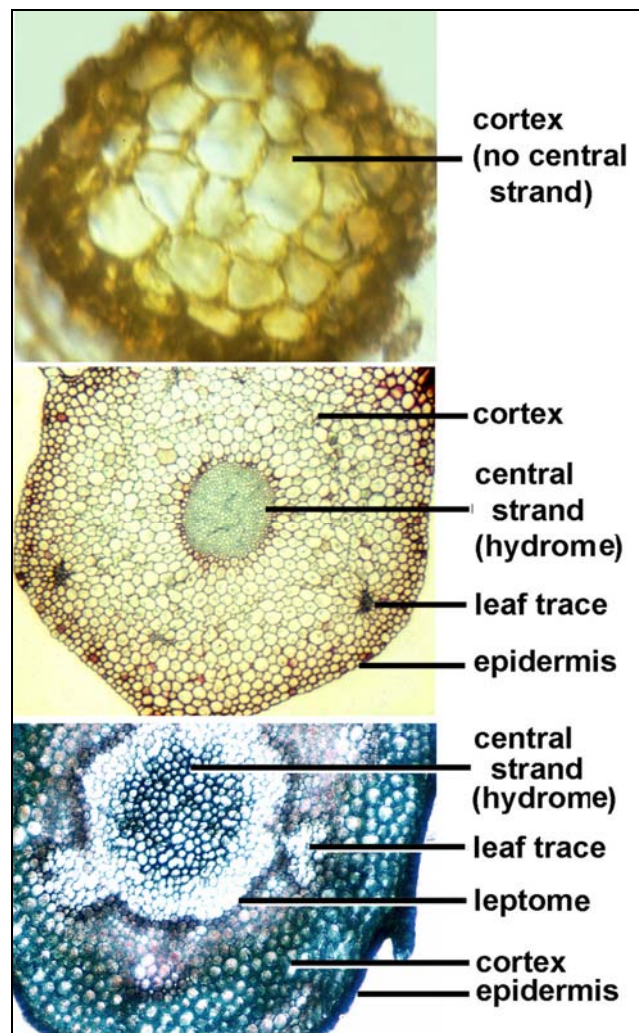


Figure 11. Stem cross sections illustrating lack of central cylinder and well-developed cylinders. **Top:** *Trichodon cylindricus*. Photo by Janice Glime. **Center:** *Plagiomnium*. Photo by Janice Glime. **Bottom:** *Polytrichum*. Photo courtesy of Isawa Kawai.

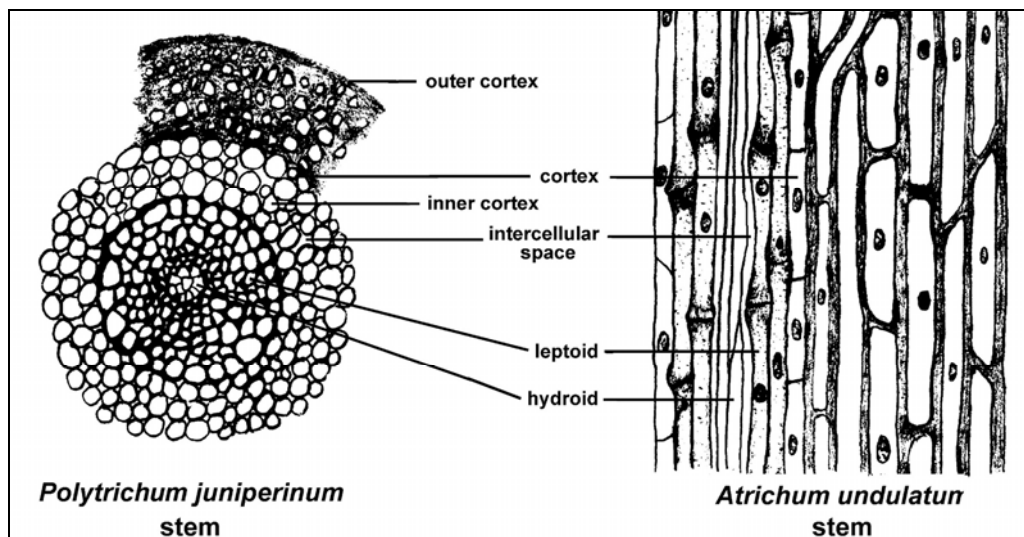


Figure 12. Cross section of *Polytrichum juniperinum* and longitudinal section of *Atrichum undulatum* stem to illustrate parts of central strand (leptoids and hydroids) and stem structures. Drawings by Margaret Minahan, modified from Héban (1977).

The hydroids and leptoids present interesting evolutionary implications, since it appears that they are primitive characters that are lost in more advanced bryophyte taxa (Héban 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). Furthermore, leptoids of setae, unlike those of tracheophytes, show less differentiation than in their gametophytic counterparts. In the seta they are not intermixed with specialized parenchyma cells and apparently lack enlarged plasmodesmata in their end walls, as seen in gametophytes of some taxa (Héban 1974). Except in the setae of a few species (Héban 1974), leptoids have not been found in the arthroodontous mosses (considered more advanced) and are unknown in liverworts. 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 (Héban 1974).

Summary

Bryophytes often are not the nonvascular plants we once thought them to be. They often possess **hydroids** that conduct water and **leptoids** that conduct sugars, arranged as in tracheophytes, with the water-conducting cells surrounded by the sugar-conducting cells. They 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.

Acknowledgments

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