

CHAPTER 7-3

WATER RELATIONS: PLANT STRATEGIES

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Figure 1. *Tortula muralis* with water drops collected on the leaf awns and setae. Note their collection around the young capsules. Such collection can occur in fog and mist and may serve as the only source of water in some habitats. Photo courtesy of Peggy Edwards.

Water Strategies

Water strategies in bryophytes have been approached in a variety of ways, from splashing gemmae (Brodie 1951) to uptake (Proctor 1981; Rice & Schneider 2004; Rice 2012; Jonas & Dolan 2012; Sand-Jensen & Hammer 2012) to transport (Héban 1977; Mulder *et al.* 2001; Proctor & Tuba 2002; Pressel 2006; Rice 2012) to moving nutrients (Buch 1945, 1947; Proctor 1981) to retention (Kennedy 1993; Mulder *et al.* 2001; Rixen & Mulder 2005).

Mosses often appear to be completely dead, only to be revived by water. Angela Newton (pers. comm., Bryonet) reported that epiphytic mosses in the lowland tropical rainforests, where mosses may appear dead after severe desiccation, recover quickly with actively growing apical and axillary buds on completely dried out plants and even on plants scorched by fire (see Figure 2)! Leaf and stem tissues from xerophytic mosses can regenerate after as many as 19 years of desiccation (Table 1); some spores remain viable after 70 years (Malta 1921). As surmised by Oliver *et al.* (2005), **desiccation tolerance** appears to be a primitive trait that permitted plants to invade land. **Desiccation tolerance (DT)** is the ability of an organism or structure to tolerate and survive after equilibrating to a relative humidity (RH) of $\leq 50\%$ (Alpert & Oliver 2002;

Koster *et al.* 2010). An understanding of this tolerance in modern bryophytes is fundamental to a general understanding of desiccation tolerance.

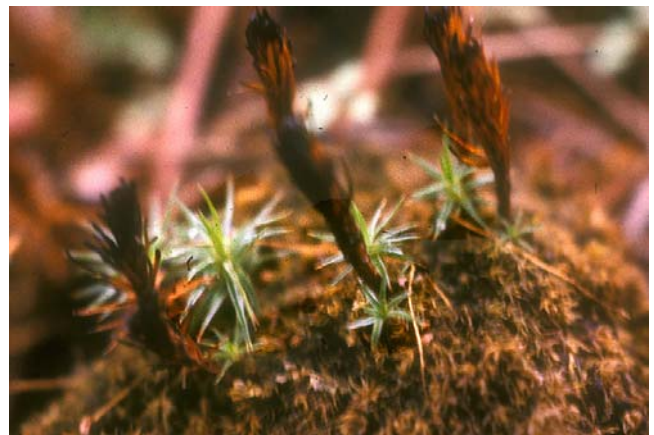


Figure 2. *Polytrichum* showing fresh, green growth one week after a forest fire that scorched adjacent plants in Baraga, Michigan, USA. Photo by Janice Glime.

Table 1. Records of revival after extended periods in a herbarium (Alpert 1982, *Volk 1984, †Glime pers. obs.).

<i>Anoetangium compactum</i>	19 years
<i>Dicranoweisia cirrata</i>	9 years
<i>Riccia canescens</i>	*7 years
<i>Grimmia elatior</i>	5 years
<i>Oxymitra</i>	*4 years
<i>Anomodon longifolius</i>	2 years
<i>Bryum argenteum</i>	2 years
<i>Orthotrichum rupestre</i>	2 years
<i>Grimmia muehlenbeckii</i>	18 months
<i>Andreaea rothii</i>	13 months
<i>Racomitrium lanuginosum</i>	11 months
<i>Syntrichia ruralis</i>	8 months
<i>Fontinalis flaccida</i>	†3 months

Most people who are not very familiar with bryophyte physiology consider them to be plants that require damp or wet habitats. But compared to **tracheophytes** (non-bryophytes; plants with lignified vascular tissue), bryophytes are the ones adapted to drying conditions (Vitt *et al.* 2014). Even in bryophytes that seem to lack physiological desiccation tolerance, morphological or life history adaptations permit them to survive periodic drought.

Although of the known 21,000 species of bryophytes, only 210 have been documented as desiccation tolerant (Wood 2007), but most have never been tested. In fact, Vitt *et al.* (2014) argue that "many members of both moss and liverwort lineages are desiccation tolerant, allowing them to survive in periodically dry habitats, and that in many of the moss lineages this physiological desiccation tolerance is remarkably high." But among seed plants, fewer than 1% of those tested are desiccation tolerant (Proctor & Pence 2002). Among bryophytes, even the aquatic moss *Fontinalis* has at least some desiccation-tolerant species (Glime 1971). For example, *Fontinalis flaccida* survived and grew after three months of drying on a herbarium sheet (pers. obs.). If one considers the types of microhabitats bryophytes occupy, and lack in most species of any kind of water storage organ, we should expect that most have at least some degree of desiccation tolerance. This notion is further supported by the high survival rate of bryophytes despite a high surface-to-volume ratio that facilitates rapid drying (Proctor *et al.* 2007).

Poikilohydry vs Homoiohydric

The strategy of maintaining internal moisture levels that agree closely with the ambient atmospheric levels is a risky physiological strategy and used mostly by lower plants such as bryophytes. Proctor and Tuba (2002) considered there to be two contrasting strategies for land plants to deal with the irregular supply of water they faced on land and that these relate closely to the matter of scale. Tracheophytes use internal transport to carry water from the soil to the distant canopy (**homoiohydric**). **Poikilohydric** bryophytes (and some tracheophytes), on the other hand, depend on desiccation tolerance, becoming dormant when desiccated. Hence, their cells are either **turgid** (swollen) or desiccated. But **desiccation tolerance** (DT) requires a whole series of adaptations to permit the cell to regain its original state. Essential cell components

and their functional relationships must be preserved through the drying-rewetting cycles presented by their environment. In some cases, this tolerance is induced by water stress. This strategy is particularly beneficial on hard substrates such as rocks and on dry soils in seasonally dry climates where lacking roots that would prevent them from obtaining deeper water in soils. Thus, among tracheophytes, this strategy is most common in warm, semiarid climates, whereas in bryophytes the strategy occurs from polar to tropical regions (Proctor & Tuba 2002; Lakatos 2011). The time scale also differs, with tracheophytes requiring one to several days to resume activity whereas bryophytes (and lichens) typically can become dry and rehydrated within an hour or less (Proctor & Tuba 2002).

In bryophytes, external water conduction seems to be present in all species, but is often supplemented by internal conduction. External conduction is typically diffuse (Proctor & Tuba 2002). The plants can survive drying to the point where there is no liquid phase remaining in the cells and water content may be reduced to only 5-10% dry weight (equilibrium water potential of -100 MPa or less). But when these bryophytes are remoistened, mostly normal metabolism returns within minutes to hours. Those capillary spaces between leaves and branches are able to maintain an external water reservoir that is available to the photosynthesizing cells without blocking the free exchange of gasses (Dilks & Proctor 1979; Proctor & Smith 1995; Zotz *et al.* 2000). This relationship seems to be essential to the functioning of the bryophytes. At the same time, cell water content seems to affect photosynthesis in the same way as that in tracheophytes (Dilks & Proctor 1979; Tuba *et al.* 1996; Proctor 2000).

Some mosses, as for example *Barbula convoluta* (Figure 3), can maintain their turgor for some time after rain ceases, an ability that is made possible by contact or proximity to the moist ground surface (Proctor & Tuba 2002). Typically, water is able to reach distant cells either by travelling externally through capillary spaces or internally through free spaces of the cell walls (Figure 4). To permit photosynthesis by making gas exchange possible, many mosses exhibit a water-repellent cuticle on the younger cell surface, preventing them from trapping water droplets there (Kershaw 1972, 1985; Dilks & Proctor 1979; Proctor 1979b; Nash 1996; Tuba *et al.* 1996; Zotz *et al.* 2000) and thus permitting gas exchange.



Figure 3. *Barbula convoluta*, a moss that maintains turgor for a longer time than most mosses following rain. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

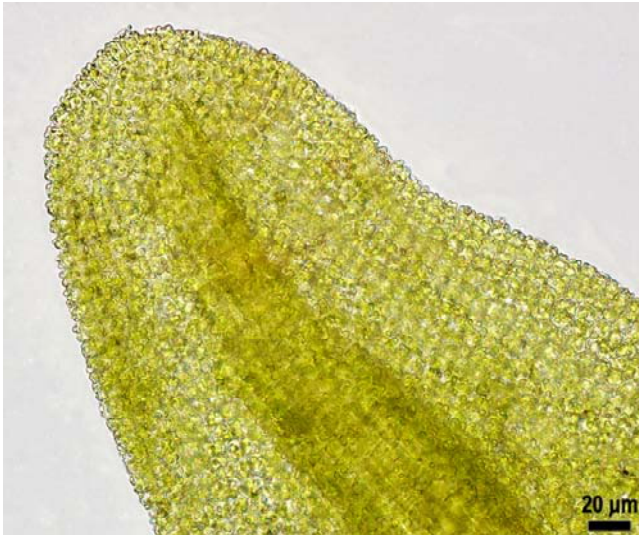


Figure 4. *Barbula convoluta* leaf cells showing small size and papillose surface that hold water longer than large cells. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

In some cases, the physiological desiccation tolerance is induced by water stress (Proctor & Tuba 2002). Both **constitutive** (always present; fully desiccation tolerant) and **inducible** [produced when drying conditions occur; previously known as modified desiccation-tolerant (Oliver *et al.* 1998)] desiccation tolerance exist among plants (Stark *et al.* 2013) and these will be discussed in Chapter 7-6 of this volume.

Cellular structure remains intact in desiccation, but upon rapid uptake of water it can be disrupted. However, in bryophytes the cellular integrity returns rapidly. Photosynthetic activity recovers quickly, perhaps due to protection of the chlorophyll (Tuba 1984; 1985). During desiccation, there seems to be no gene activity, but gene expression occurs rapidly following rehydration. Among these activities is the production of a number of proteins called **rehydrins**. These seem to be involved in stabilizing and reconstituting membranes that have been damaged by dehydration. Oliver *et al.* (2005) suggest that vegetative desiccation tolerance, at least in bryophytes, has changed little from early land invaders and may be using a mechanism that was first used in spores.

Even though many bryophytes tolerate high degrees of desiccation (Dilks & Proctor 1974; Nörr 1974; Dhindsa & Bewley 1976), **water content** and availability are important for potential accumulation of photosynthates (Alpert 1979). Patidar (1988) found that in *Asterella angusta* the moisture content is the most important determinant of **thallus** (flattened, nonvascular plant body) size. In *Plagiochasma appendiculatum* (Figure 5), optimum growth occurs at 60% moisture, whereas branching and growth are able to occur from 10-100% moisture (Vishvakarma & Kaul 1988)! *Reboulia hemisphaerica* (Figure 6), on the other hand, requires 70-80% moisture for optimum growth, with growth and branching occurring from 40 to 90%. In other words, no matter how desiccation tolerant a plant might be, it requires water to grow. Representative water contents of bryophyte plants from a wide range of field habitats in the temperate zone, Great Britain, are given in Table 2.



Figure 5. *Plagiochasma appendiculatum*, a liverwort with both branching and growth throughout the range of 10-100% moisture. Photo by Michael Lüth, with permission.



Figure 6. *Reboulia hemisphaerica*, a liverwort in which growth and branching occur in the range of 40-90% moisture. Photo by Jan-Peter Frahm, with permission.

Mosses grown in fully hydrated conditions afforded by saturated air enjoy optimal growth and development (Davy 1927). They exhibit more rapid development, more stem branching, more numerous rhizoids, smaller leaves, and smaller and fewer cells with larger chloroplasts than mosses existing at less than full saturation. Even at the scale of a single boulder, bryophytes distribute themselves according to their ability to achieve photosynthetic gain. When examining bryophytes that occupied various microsites on exposed granitic boulders, Alpert and Oechel (1987) found that those species that occurred in microsites with lower water availability were able to attain maximum net photosynthetic gain at a lower water content and to recover better from prolonged desiccation than those taxa in less **xeric** (dry) microsites. Alpert (1985, 2000) supports the hypothesis that the reason even **xerophytic** mosses (those adapted to dry habitats) are limited in their ecological distribution is that they often are unable to maintain positive carbon balance during repeated cycles of wetting and drying. Alpert and Oechel (1985) demonstrated this with *Grimmia laevigata* (Figure 7-Figure 8), a desiccation-tolerant plant that was unable to maintain this balance under a natural, highly xeric regime of wetting

and drying in certain microhabitats on exposed granitic boulders in California chaparral. Thus, there is an "inherent trade-off between desiccation tolerance and growth rate."

Table 2. Percent water content (compared to dry mass) of bryophytes at full turgor, not including free external water. Values represent means of two measurements. Table based on Dilks and Proctor (1979); those marked with * from Skre *et al.* (1983) include new growth and 1-year-old growth; those with ⁺ from Proctor (2000).

species	water content, % dry mass
Mosses	
<i>Sphagnum subsecundum</i> *	1225
<i>Pilotrichella ampullacea</i> ⁺	>1200
<i>Hookeria lucens</i>	516
<i>Pleurozium schreberi</i> *	485-625
<i>Hylocomium splendens</i> *	485-545
<i>Brachythecium rutabulum</i>	249
<i>Syntrichia intermedia</i>	233
<i>Homalothecium sericeum</i>	223
<i>Pseudoscleropodium purum</i>	207
<i>Thuidium tamariscinum</i>	203
<i>Dicranum majus</i>	202
<i>Leptodon smithii</i>	187
<i>Rhytidiadelphus loreus</i>	165
<i>Pleurochaete squarrosa</i>	165
<i>Neckera complanata</i>	162
<i>Racomitrium lanuginosum</i>	142
<i>Anomodon viticulosus</i>	141
<i>Polytrichum commune</i> *	95-125
Liverworts	
<i>Pellia epiphylla</i>	1180
<i>Conocephalum conicum</i>	871
<i>Porella platyphylla</i>	230
<i>Plagiochila spinulosa</i>	222
<i>Bazzania trilobata</i>	210



Figure 7. *Grimmia laevigata*, a poikilohydric moss, in its dry state. Photo by Michael Lüth, with permission.



Figure 8. *Grimmia laevigata*, a poikilohydric moss, in its wet state. Photo by Michael Lüth, with permission.

Rod Seppelt (Bryonet 27 June 2022) summarized some of the Antarctic studies on the role of cushions in maintaining water content. Microbial associates within the cushion provide the CO₂ (~2000 ppm) needed for photosynthesis while ambient concentrations are only 350-400 ppm. When temperatures drop to below 0°C at night, the cushion likewise drops until the water in the cushion begins to freeze. Then latent heat is able to elevate the cushion temperature to ~2°C. This provides time before partial denaturing of proteins begins.

Water content in a bryophyte ranges widely throughout the year. For example, Klepper (1963) measured 23.8-258% in *Dicranum scoparium* (Figure 9), Romose (1940) 10-950% in *Homalothecium sericeum* (Figure 10), Morton (1977) 19-214% in *Pseudoscleropodium purum* (Figure 11), and 58-307% in *Dicranum bonjeanii* (Figure 12). Whereas many mosses benefit from high water content, too much water is not good for photosynthesis. Water on the surface blocks CO₂, and most likely high internal water content also interferes with physiological processes (Proctor 2000). Dilks and Proctor (1979) found optima as low as 200% water content and as high as 1500% among the same bryophytes shown in Table 2. Respiration seems to peak around 200% for most of these taxa.



Figure 9. *Dicranum scoparium*, a moss with measured water content ranging 23.8-258%. Photo by Janice Glime.



Figure 10. *Homalothecium sericeum*, a moss with measured water content ranging 19-214%. Photo by David Holyoak, with permission.



Figure 11. *Pseudoscleropodium purum*, a moss with measured water content ranging 19-214%. Photo by Michael Lüth, with permission.



Figure 12. *Dicranum bonjeanii*, a moss with measured water content ranging 58-307%. Photo by Michael Lüth, with permission.

Richardson (1981) divides mosses into three water strategies by habitat: **aquatic**, **mesophytic** (living in continually moist habitats), and **poikilohydric** (organism dries as its habitat dries and resumes normal metabolic activity after rehydration; Figure 8). Unlike most other plants, water content of predominantly poikilohydric bryophyte species is highly related to environmental conditions and weakly regulated by their internal and morphological structures. This strategy permits them to colonize such xeric environments as boulders and tree trunks. In these environments, mosses enjoy release from competition by higher plants, but must still survive the low light intensity created by the trees above.

Some bryophytes do appear to be able to survive in absence of precipitation. In caves in Poland, only 18.1% of the species occurred in very wet places or where there was dripping water, whereas in places that were continuously dry(!), 25% occurred (Jedrzejski & Ziobor 1992). Certainly in those dry places atmospheric humidity must have provided the needed water for these very **hygroscopic** (readily absorbing water from air), **ectohydric** (relying mainly on water transport along external surface of plant by capillarity) bryophytes. Shaun Russell (pers. comm.) found that in montane areas of Africa with virtually no rainfall, fog collected on bryophyte surfaces, providing sufficient water for them to survive. A similar phenomenon occurs in geothermal areas (Figure 13).



Figure 13. *Campylopus holomitrius* with water droplets captured from the "steam" emitted by geothermal vents in New Zealand. Photo by Janice Glime.

The drought-tolerant *Pseudocrossidium crinitum* (= *Barbula aurea*; Figure 14) seems to have compensated for its low water availability by having relatively low levels of light compensation and saturation responses for photosynthesis (Rundel & Lange 1980). Such low levels would permit the moss to carry out photosynthesis early in the morning when dew is available and before high evaporation stress occurs. These aerial sources of water are of little use to tracheophytes that must take water in by their roots, not their leaves.

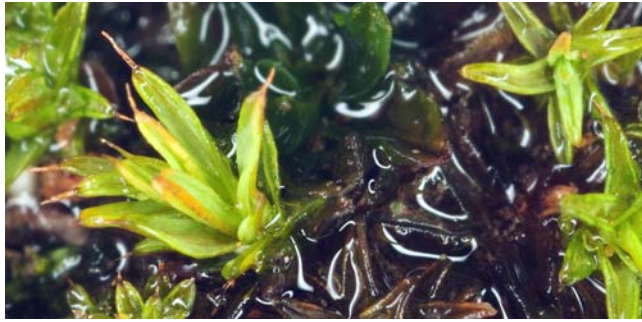


Figure 14. *Pseudocrossidium crinitum*, a xerophyte with low light compensation and saturation levels. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

As one would expect, degree of drought tolerance is generally greatest in plants from dry habitats (Clausen 1952, 1964; Johnson & Kokila 1970; Dilks & Proctor 1974). Seki and Yamaguchi (1985) suggest that on some islands with strong summer winds, Shannon diversity decreases as saturation deficits increase. Richardson (1981) claims that aquatic mosses and those that grow in humid forests are damaged quickly by drought. But even such high humidity plants as *Hookeria lucens* (Figure 15) are able to survive desiccation for days (Horst Tremp, Bryonet).



Figure 15. *Hookeria lucens*, a drought-intolerant moss. Photo by Michael Lüth, with permission.

Glime (1971) found that two aquatic mosses (*Fontinalis* spp.; Figure 16) were able to survive on the stream bank out of water (Figure 17) for up to one year and still grow when rehydrated. However, those dried in the laboratory were apparently dead after only 55 hours, perhaps due to rapid drying. Steere (1976) found that *F. squamosa* (Figure 18) from Alaska could not survive a week of air drying. One reason for apparent differences here is that it is difficult to determine when a moss is dead, and even though all leaves may be dead, the stem may still harbor life. *Fontinalis* is subject to annual emergence when stream level drops (Figure 16), and perhaps slow drying on the stream bank permitted it to become dormant and to preserve sufficient energy to repair its membranes upon rehydration. The rapid drying of a laboratory, with unnaturally low humidity and no acclimation period, may have prevented the necessary physiological changes that could permit it to survive. Oliver and Bewley (1984) have demonstrated that it takes longer for the cellular physiology to return to normal in a rapidly dried bryophyte than in a slowly dried one.



Figure 16. *Fontinalis dalecarlica* and *F. novae-angliae* above water, in Fox Run, New Hampshire, USA. When these mosses were placed away from the stream bed for up to one year, at least some of them survived from all re-submersion dates (Glime & Carr 1974). Photo by Janice Glime.



Figure 17. *Fontinalis antipyretica* in dry stream. Photo by Janice Glime.



Figure 18. *Fontinalis squamosa* on rock above water near Swallow Falls, Wales. Photo by Janice Glime.

A similar pattern of submersion and desiccation is endured by *Hydropogon fontinaloides* in the Amazon basin (Mägdefrau 1973). It hangs from trees during the dry season, but during the wet season it floats in water. The behavior of *Cratoneuron filicinum* (mistakenly published as *Hygrohypnum luridum*; Figure 19), typically a stream margin species, may explain the lab results. This moss was unable to synthesize protein when rehydrated after it was dried quickly over silica gel for one hour (Bewley 1974). However, it was able to tolerate drying down to 33% of its fresh mass when dried slowly, and slow drying for 5 hours to 66% of its fresh mass had no detrimental effects on protein synthesis.



Figure 19. *Cratoneuron filicinum*, a moss that is unable to synthesize protein when rehydrated if it dries too quickly. Photo by Teplov through Arctoa, with permission.

Just what endows bryophytes with the ability to inhabit arid microsites that are totally inhospitable for tracheophytes? As you can see from the foregoing examples, we can divide these adaptations into anatomical/structural, growth/life form, and physiological adaptations.

Life cycle adaptations, a major means for an immobile organism to cope with changing weather and seasons, have been addressed in Chapter 4-6. Schofield (1981) points out that spore germination patterns, protonemal structure, life span, and methods of propagation are all related to the habitat characteristics. Water availability is important to all of these aspects. Multicellular spores are more common in habitats where the spores are subject to desiccation. Protonematal specialization is common in deeply shaded habitats, whereas in mesic habitats the protonemal cells are elongate, *i.e.*, having typical protonematal structure. In the leafy **gametophore** (upright leafy plant), characters such as leaf shape, leaf arrangement and orientation, leaf anatomy, stem cortical cells, hydroids, leptoids, branch arrangement, presence of rhizoids, and presence of paraphyllia all affect water movement. Such small features as surface ornamentation of leaves, stems, and rhizoids affect water absorption and retention and influence habitat specificity.

Role in Ecosystem Water Cycle

In areas where bryophytes dominate the forest floor, their role in the water cycle can be extraordinary. This is especially true where permafrost prevails (Henry Santeford, pers. comm.). Bryophytes hold melt water until they become saturated. At that point in time, all new melt water is suddenly released and can cause flooding. It is important in some areas to be able to predict this flooding regime for the safety of both animals and humans. Hence, we need to understand both holding capacity and evaporation rates of water from the bryophytes.

Penman (1948) helps us to understand evaporation as it might apply to bryophytes. Although he compared evaporation from bare soil, grass, and open water, the principles apply. He suggests that we need to combine two theoretical approaches to evaporation, an aerodynamic basin in which evaporation is due to turbulent transport of vapor by eddy diffusion, and an energy basis in which evaporation is a way of degrading incoming radiation. This approach eliminates the problem of measuring surface temperature and overcomes the problem of estimating effects as if one is measuring evaporation from a lake surface. Using this method, supported by empirical data, indicates that evaporation from grass follows a seasonal cycle relative to that evaporating from open water, a phenomenon Penman attributes to the change in photoperiod.

In other circumstances, bryophytes may prevent the underlying roots from getting water (Beth Scafone, unpubl. data). If there is a quick rain shower, bryophytes act as sponges, trapping the water before it reaches the soil. On the other hand, bryophytes can reduce evaporation of water from the soil following heavy rain, thus permitting the roots to grow for longer periods of time.

Structural Adaptations

When I moved to the Upper Peninsula of Michigan, I was struck by the fact that only red oaks were able to live here. A simple difference in one structure made their survival possible in a cold region with long winters – narrow vessels. Large vessels in other North American species cavitate and the water is unable to reconnect on an appropriate time schedule that permits the oaks to complete their life cycle and gain sufficient energy to continue the establishment of the species.

Watson (1919) warned of the difficulty in dealing with bryophyte identification because of the entirely different appearance they can present in the wet vs dry state. The bryologist must know them in both conditions. I once spent half an hour in an unfamiliar locality trying to identify *Hedwigia ciliata* because I had only seen it dry (Figure 20-Figure 22) and these plants were fully hydrated (Figure 23-Figure 24). The plant may even appear to be dead during drought, only to revive quickly when moistened, resuming its normal functions.



Figure 20. *Hedwigia ciliata* dry at Canyon Falls, Michigan, USA, a state that was very familiar to me. Photo by Janice Glime.



Figure 23. *Hedwigia ciliata* wet, totally changing color and leaf angles from those of the dry form. Photo by Allen Norcross, with permission.



Figure 21. *Hedwigia ciliata* dry, 21 August 2018, Esrey Park, Michigan, USA. Photo by Janice Glime.



Figure 24. *Hedwigia ciliata* wet, contrasting with the grey-green of the dry form. Photo by Bob Klips, with permission.



Figure 22. *Hedwigia ciliata* dry, showing julaceous leaf arrangement and white leaf tips. Photo by Larry Jensen, with permission.

Many studies have demonstrated the importance of anatomy in determining the mechanical properties of plant tissues, including bryophytes (Héban 1977; Rossi *et al.* 1998; Niklas *et al.* 2006; Frenzke *et al.* 2011; Atala & Alfaro 2012; Vincent 2012). Getting water and nutrients into and out of a plant is size dependent. Adaptations vary even within a species due to its plasticity in responding to the environment (Sarafis 1971; Buryová & Shaw 2005). As discussed by Raven and Handley (1987), for plankton organisms, any size above ~50 μm diameter restricts the growth rate because of the greater restriction of uptake by the boundary layer. Thus, for macroscopic aquatic photosynthetic organisms, even favorable velocity of water and plant morphology cannot reduce the boundary layer restrictions on nutrient uptake enough to compensate for the decrease in uptake rate. Movement of nutrients within the plant involves **cyclosis** (cytoplasmic streaming) in algae, phloem and xylem in tracheophytes, and in bryophytes it often involves both cyclosis and transport through leptoids and hydroids.

Raven and Handley (1987) consider that the energy cost for transporting nutrients would be higher for those organisms using cyclosis than for those using vascular tissue. They also consider that there is a penalty for height in tracheophytes, causing reduced specific growth rate under both resource-saturated and resource-limited conditions. Coupled with this penalty is reduced resource use efficiency with increased plant height. The reason for these penalties is the need for greater supporting tissue and a greater percentage of the tissue dedicated to vascular tissue. But there is also some compensation. Taller plants can capture more light energy and reach more nutrients and water in the soil. Smaller plants, on the other hand, have a potentially higher specific growth rate under these same resource-limited or resource-saturated conditions. The lack of need for supporting structures, requiring breadth, permits smaller plants such as bryophytes to have all or nearly all of their tissues as photosynthetic tissues. Raven and Handley left us with the challenge to discover the differences in transport needs and solutions resulting from these different morphologies.

In the desert moss *Syntrichia caninervis* (Figure 25), conservation of moisture is paramount, surpassed only by the need for rapid uptake. It can therefore serve as a model for adaptations against desiccation. Its growth form is tufted and its leaves are folded upward and twisted around the stem when dry (Figure 26 (Zheng *et al.* 2010)). The leaf cells are endowed on both the upper and lower surfaces with C-shaped papillae that may have a role in deflecting sunlight to protect the DNA and chlorophyll during dry periods or to reduce the temperature. The leaf costa extends beyond the leaf to form an awn that has forked teeth and is able to capture moisture from the atmosphere. The protonemal cells are small and have thick walls; their cytoplasm is highly concentrated with only a small vacuole.



Figure 25. *Syntrichia caninervis* hydrated, a desert moss that increases its wax content as it ages. Note the awns that can trap atmospheric moisture from fog. Photo from Proyecto Musgo, through Creative Commons.



Figure 26. *Syntrichia caninervis* dry with leaves held close against the stems. Photo by Shari Hagwood, through public domain.

Thallose Liverworts

The structure of most thallose liverworts is so different from that of mosses or leafy liverworts that their water relations warrant separate consideration. They are adapted for predominantly ventral uptake. Thallose liverworts like *Conocephalum conicum* (Figure 27) and *Cyathodium cavernarum* (Figure 28) use ventral appendages (**scales**; Figure 27) to provide capillary spaces that conduct water externally on the underside of the thallus. Marchantialian species use specialized capillary systems on the ventral surface of the thallus to conduct water in either direction. Cell walls of the scales contain **tannins** (McConaha 1939), perhaps acting as an antibiotic.

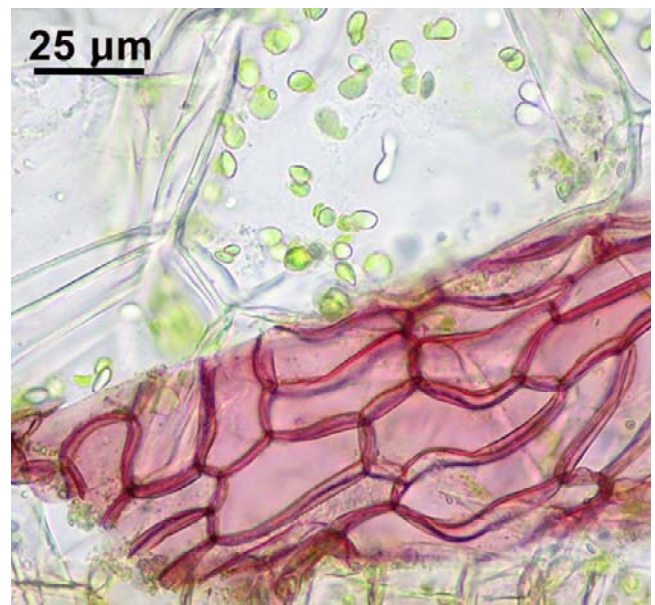


Figure 27. *Conocephalum conicum* ventral scale (purple) that provides capillary spaces for external water movement. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

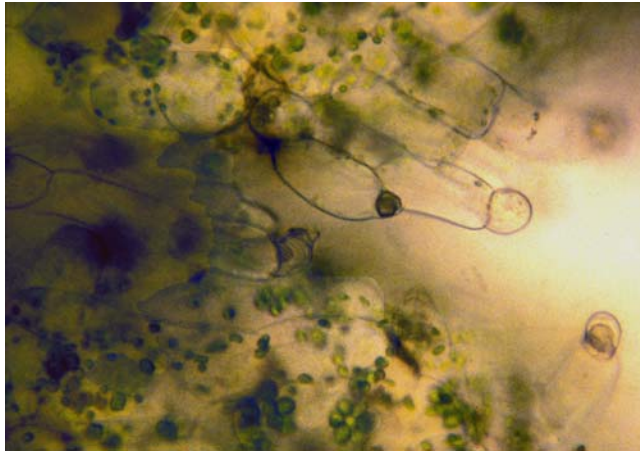


Figure 28. Scales of *Cyathodium cavernarum*. Photo courtesy of Noris Salazar Allen.

Scales

Exposed surfaces of scales and thallus are often reddish-purple due to the flavonoid pigment **phlobaphene**, formed by oxidation of tannic compounds (McConaha 1939), but the role of phlobaphene is not clear. It is possibly a defense against would-be toxins from tannic compounds that contact the ventral surface. (There is evidence that tannins are toxic to bryophytes, not within their cell walls, but when they are able to act on cell constituents.) Since all these ventral surfaces are wettable, these cells are more susceptible to damage by such toxins.

Kürschner (2004) surmised that the anthocyanin pigments in ventral scales (Figure 27) protected the ventral surface from the sun when the thallus was rolled up, as it typically does in many species of *Riccia* (Figure 29-Figure 31). Furthermore, even hyaline scales (Figure 32) of *Riccia* and *Oxymitra* (Figure 33) can reduce desiccation. Some species, especially of *Riccia*, sink into the soil surface as the soil dries, reappearing only after precipitation or heavy dew.



Figure 29. *Riccia beyrichiana* well hydrated and looking succulent. Photo by Michael Lüth, with permission.



Figure 30. *Riccia beyrichiana* drying. Note the loss of succulence in the now thin thallus; the thallus edges are beginning to curl. Photo by David Holyoak, with permission.



Figure 31. *Riccia beyrichiana* dry, showing curling of the thallus. Photo by Andrew Spink, with permission.

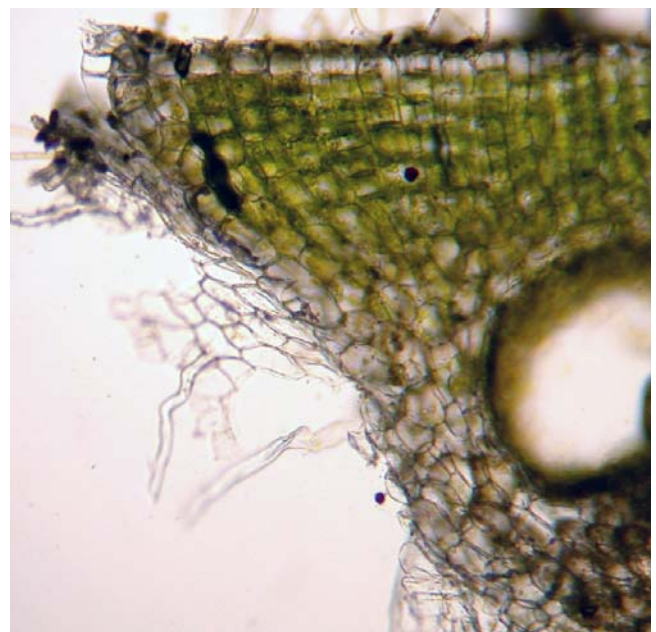


Figure 32. *Riccia sorocarpa* showing scales. Photo from Botany website, UBC, with permission.



Figure 33. *Oxymitra incrassata* showing ventral hyaline scales at the margins. Photo by Michael Lüth, with permission.

This high degree of wettability provides a greater possibility for water entry in thallose forms. For example, in *Marchantia* (Figure 34-Figure 35), water is conducted along the midrib as well as in interstitial spaces between the blade and scales, distributing water throughout the surface of the thallus. Water movement in *Marchantia* is relatively slow, at 0.4 mm per sec, improving slightly in *Lunularia* (Figure 53-Figure 54) and *Reboulia* (Figure 6), to approximately 0.5 mm per sec, despite their less highly developed capillary systems. However, McConaha (1939) found that movement from base to apex in *Conocephalum conicum* s.l. (probably *C. salebrosum*; Figure 36) generally takes only about 20-30 seconds, roughly 1 mm per sec. Despite its slowness, McConaha found this external movement to be much faster than would be possible by internal conduction.



Figure 34. *Marchantia polymorpha* with gemmae cups located on the midrib. Photo by Walter Obermayer, with permission.



Figure 35. *Marchantia polymorpha* ventral surface showing blackish midrib (arrow) and white scales and rhizoids. Photo from Botany website, University of British Columbia, BC, Canada, with permission.



Figure 36. *Conocephalum salebrosum*, where water travels from base to apex in about 20-30 seconds. Photo by Janice Glime.

Rhizoids

Ventral structures seem to be important in this group. In marchantialian liverworts, two types of rhizoids (Figure 37-Figure 38) provide somewhat different functions. The smooth-walled rhizoids (Figure 37-Figure 38) are alive (Duckett & Ligrone 2003) and emerge from beneath the ventral scales (Figure 39), providing contact with the substrate, whereas the **tuberculate** (pegged) rhizoids (Figure 38) are dead (Duckett & Ligrone 2003) and form a capillary system parallel to the thallus beneath each scale (McConaha 1941). The pegged rhizoids begin growth at

right angles to the thallus but change their orientation to follow that of the scales. The pegs, extending into the pegged rhizoid cell, prevent the collapse of the cell when dehydrated, thus maintaining its capillary role (Duckett & Ligrone 2003). When the **archegoniophore** (stalk supporting female reproductive organs) forms, the pegged rhizoids are wrapped within the archegoniophore by the folded thallus (Figure 40) and function in internal water conduction (Duckett & Ligrone 2003). The presence of the pegs also prevents the collapse of this stalk when the thalli dehydrate (Duckett & Ligrone 2003). These rhizoids have an outer layer of pectic material (like that of apples).



Figure 37. *Riccia* sp. with rhizoids on ventral side. Photo by Bernd Haynold, through Creative Commons.

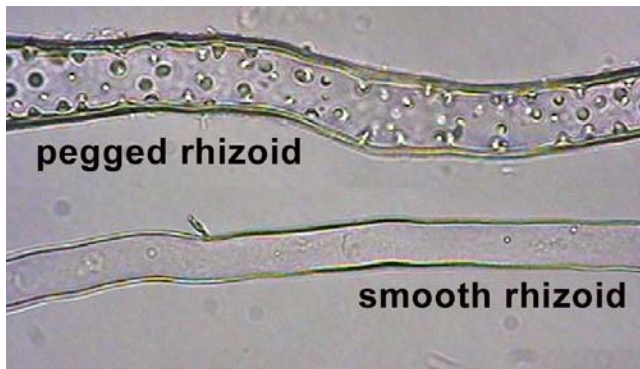


Figure 38. Pegged and smooth rhizoids of *Conocephalum conicum* s.l. Photo by Paul Davison, with permission.

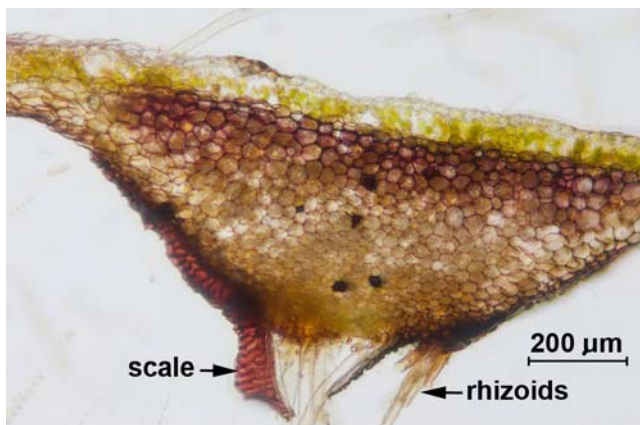


Figure 39. *Preissia quadrata* thallus cross section showing position of scale and rhizoids. Photo by Kristian Peters, with permission.



Figure 40. *Marchantia polymorpha* archegoniophore showing white rhizoids that are incompletely enclosed by the stalk of the archegoniophore. Photo by George Shepherd, through Creative Commons.

Previously treated mostly as a taxonomic anomaly, it appears that these two types of rhizoids have distinctly different functions (Duckett *et al.* 2013). The smooth rhizoids are alive, functioning in nutrition, anchorage, and as entry locations and conduits for fungal symbionts. Their role for fungal entry does indeed require that these rhizoids be alive. The pegged rhizoids, on the other hand, are dead at maturity, a condition first noted by Kamerling (1897), and function as water conduits through these empty tubes. Kny (1890) was the first to suggest that pegs prevent the rhizoid walls from collapse with water loss. Duckett *et al.* (2013), however, were the first to test this hypothesis. The pegs, along with elasticity, seem to provide the ability of the rhizoids to maintain their functional integrity by preventing their collapse when they are dry. This ability is essential to their function in conduction, a role demonstrated by Bowen (1935) and others (McConaha 1939, 1941), who used dyes to show conduction by capillarity and transpiration. The famous German morphologist Goebel (1905) observed that it is the liverworts with high transpiration rates that also have the most highly developed pegged rhizoids. This is in contrast with those of **hygrophilous** (water-loving) taxa such as *Dumortiera* (Figure 41-Figure 42) and *Cyathodium* (Figure 43).



Figure 41. *Dumortiera hirsuta*, a hygrophilous species showing fringe of hairs on thallus and archegonial heads, but lacking the pegged rhizoids and scales of the dry habitat species. Photo by Jan-Peter Frahm, with permission.



Figure 42. *Dumortiera hirsuta* thallus showing smooth rhizoids on the ventral surface. Photo by Chris Lobban, with permission.



Figure 43. *Cyathodium tuberosum*, a simple thallus lacking the complex scales and two types of rhizoids. Photo by Jan-Peter Frahm, with permission.

Among the leafy liverworts, thallose liverworts, and ferns, living rhizoids die and collapse upon dehydration, an irreversible response (Pressel 2007). Duckett *et al.* (2013) concluded that smooth rhizoids of liverworts grow at the apex, a character they share with root hairs, fungal hyphae, and moss protonemata. Furthermore, the smooth rhizoids exhibit considerable endoreduplication of Golgi bodies similar to that in moss caulonemata. They reach lengths that commonly are greater than 20 mm, sometimes reaching 30 mm in *Marchantia polymorpha* (Figure 35), making them the longest cells in liverworts. Duckett and coworkers suggest that this combination of characters may explain their inability to regenerate when damaged (Pressel *et al.* 2008a; Duckett *et al.* 2013).

On the other hand, rhizoids of mosses (and protonemata) can recover from desiccation except at the apical cell (Pressel 2007; Rowntree *et al.* 2007; Pressel *et al.* 2008b). The pegged rhizoids furthermore are devoid of air bubbles when desiccated, a further indication that they are highly resistant to **cavitation** (formation of a space; air blockage, as when water column in xylem becomes

separated by air; collapse of cells), as are the hydroids of mosses (Ligrone *et al.* 2000).

Duckett *et al.* (2013) identified pegged rhizoids in 26 species of thallose liverworts and absence in 5. They compared the diameters of the smooth and pegged rhizoids and measured the time required for dyes to reach the archegonial heads in the taxa compared to time required in several mosses. The rates ranged 30-150 mm h⁻¹ in the thallose liverworts, 28-14 mm h⁻¹ in mosses, and 127-141 mm h⁻¹ in ferns.

Duckett *et al.* (2013) point out that these pegged rhizoids fulfill the three criteria for conduction defined by Raven (1993): dead at maturity, specialized walls, preferential conduction of water. Duckett and coworkers added a fourth criterion, the ability to maintain functional integrity through periods of dehydration, as in moss hydroids (Ligrone *et al.* 2000). This maintenance of functional integrity becomes a problem, because unlike trees and stems, there is no adjacent cell to help in rehydration.

Xerophytic liverworts such as *Riccia* (Figure 44), *Reboulia* (Figure 6), *Targionia* (Figure 45), *Asterella* (Figure 46), and *Lunularia* (Figure 53-Figure 54) have both **tuberculate** (pegged) and smooth rhizoids, scale leaves, and well-defined assimilatory and storage zones, whereas moisture-loving *Dumortiera* (Figure 41), *Cyathodium* (Figure 43), *Pallavicinia* (Figure 47) (Daniels 1998), *Monoclea* (Figure 48), *Neohodgsonia* (Figure 49), and some aquatic *Riccia* species (Figure 50-Figure 51) (Duckett & Ligrone 2003) lack these complex structures. Even in *Marchantia* (Figure 34-Figure 35), with its strong midrib, water moves externally along the midrib and in the spaces between the scales, providing a film of water throughout the thallus (McConaha 1941).



Figure 44. *Riccia sorocarpa* thallus section showing ventral rhizoids, dorsal midribs, and internal photosynthetic layer. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 45. *Targionia hypophylla*, a thallose liverwort with pegged and smooth rhizoids and scales. Photo by Des Callaghan, with permission.



Figure 46. *Asterella saccata* showing scales around the thallus margin. Photo by Jan-Peter Frahm, with permission.



Figure 49. *Neohodgsonia mirabilis* with archegonial heads in New Zealand, a simple thallus lacking the complex scales and two types of rhizoids. Photo by Odontites, through Creative Commons.



Figure 47. *Pallavicinia lyellii*, a simple thallus lacking the complex scales and two types of rhizoids. Photo by Des Callaghan, with permission.



Figure 50. *Riccia fluitans*, an aquatic species with no rhizoids or scales. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 48. *Monoclea* cf. *gottschei* with the salamander *Oedipina gracilis*. This liverwort is a simple thallus lacking the complex scales and two types of rhizoids, but clearly having a waxy surface. Photo by William Leonard, with permission.

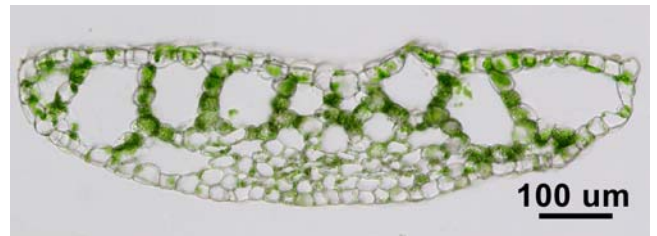


Figure 51. Cross section of thallus of *Riccia fluitans*, an aquatic species with no rhizoids or scales; note the large air spaces for gas exchange and flotation. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

In *Preissia* (Figure 39), it appears that the numerous rhizoids compensate for a less compact arrangement of the capillary system. Volk (1984) found that *Riccia* (Figure 52), a common inhabitant of ephemeral habitats such as flood plains, absorbs water by capillary action among the rhizoids and the lower surface of the thallus. The thallus rolls or folds when it is dry, thus exposing the rhizoids, scales, and/or cilia. These serve both to absorb water and to provide a reflective surface that protects the chlorophyllous (photosynthetic) cells of the thallus. In others, a crystalloid crust serves a similar function of reflectance.

Fungal Partners

Despite their roles in anchorage (smooth rhizoids) and conduction (pegged rhizoids), it seems that smooth rhizoids have a major role in the **endosymbiosis** (internal partnership) of fungi (Pressel *et al.* 2010, 2012; Duckett *et al.* 2013). Our understanding of the value of this partnership is meager. In other plants, fungi serve to increase absorptive surface area and often tap into the roots of a tracheophyte, transferring carbohydrates from plants that reach the canopy to plants that are in the low light beneath them. Such a role remains unknown in the bryophytes, but I am confident that we shall discover that at least some species have this advantage. After all, these partners have been around much longer than the flowering plants, known as **hemiparasites**, that have succeeded in developing this life style. In the leafy liverworts, infections occur exclusively through rhizoids with the Ascomycete *Rhizoscyphus ericae* as partner (Read *et al.* 2000; Pressel *et al.* 2008a, c). This is a widespread fungus that lacks host specificity. Fungal partnerships are discussed in more detail below under "Mosses and Leafy Liverworts."

Main Thallus Structure

Midribs: Seeing the midribs in valleys (Figure 44, Figure 52) makes me think that water is directed from the thallus surface to the midrib in some species. I have to wonder if water is absorbed more easily there. Once the water enters the midrib cells, it can be carried to more distant parts of the thallus more quickly than by travelling through other, shorter thallus cells. It has fewer cell walls to cross.



Figure 52. *Riccia nigrella* showing valleys with midribs that could be used to direct water into the thallus. These valleys facilitate folding when dry. Photo by Des Callaghan, with permission.

The rib of *Lunularia cruciata* (Figure 53-Figure 54) has parenchymatous cells in which plasmodesmata-derived pores are grouped in small, sparse fields, particularly on transverse oblique walls (Giordano *et al.* 1989). This suggests that the rib cells may be able to transport water and other substances through the ends of cells. These longer cells should, then, move water faster than crossing the many walls of the hyaline parenchyma (Figure 55). Giordano and coworkers suggested that the reticulate cells may serve a water-holding role and facilitate lateral distribution by both **symplastic** (within protoplasm) and

apoplastic (outside the protoplasm, in intercellular spaces) conduction of substances arriving by way of the rib. They suggest this mechanism may be present in all members of **Marchantiales** with this thallus construction.



Figure 53. *Lunularia cruciata* indicating rib area (arrows). Photo by Luis Nunes Alberto, through Creative Commons.

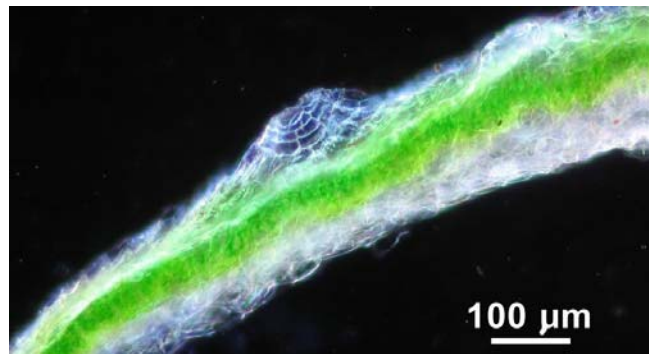


Figure 54. *Lunularia cruciata* thallus showing pore and hyaline parenchyma cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

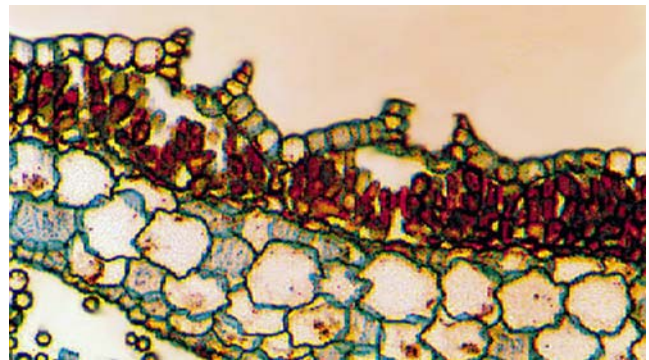


Figure 55. Cross section of *Marchantia* thallus, showing hyaline parenchyma and two pores. Photo from Department of Botany Teaching Collection, Michigan State University, East Lansing, MI, USA.

Rolling Thallus: Midribs may also facilitate rolling of the thallus by creating a crease through the middle of the plant (compare Figure 52 to Figure 56). Rolling conserves water, but at the same time it exposes the ventral surface where scales help to conserve water (Figure 56). Such rolling is common in species of *Riccia* (Figure 56, Figure 84-Figure 85), often supplemented with hairs that cover the thallus.



Figure 56. *Riccia nigrella* with dry thallus folded at the midrib. Compare this to Figure 52. Photo by Michael Lüth, with permission.

Internal Conduction: The liverwort *Lunularia cruciata* (Figure 53-Figure 54) may exemplify a means for water movement between cells in thallose liverworts (Giordano *et al.* 1989). The thallus has **reticulate** (like network) **hyaline** (colorless) **parenchyma** (thin-walled) cells (Figure 54) with between wall thickenings, large **primary pit fields** (thin area in walls of many cells in which one or more pits usually develop) with numerous pores derived from **plasmodesmata** (narrow threads of cytoplasm that pass through cell walls of adjacent cells and allow communication between cells) on unthickened areas of walls.

Spongy Thallus

The spongy thallus of *Riccia cavernosa* (Figure 57) looks like it should have an important adaptive value. The basal layer gives rise to a layer of irregular vertical column of chlorophyllose cells overtopped by colorless epidermal cells (*Riccia cavernosa* 2012). While these might seem to have functions similar to those of *Exormotheca* (Figure 59-Figure 61), instead some of these epidermal and chlorophyllose cells collapse, creating large air spaces at several levels in the tissue of the thallus. The light that reflects from these cavities has a glistening appearance. But does this sequence of events provide any advantage to the plant? At first glance, it looks very much like a sponge, but at a much smaller scale.



Figure 57. *Riccia cavernosa* showing spongy thallus. Photo by Richard Orr, with permission.

The basal pad of isodiametric cells gives rise to a layer of irregular vertical columns of chloroplast-containing cells, topped by colorless oval epidermal cells (*Riccia cavernosa* 2012). But early in development, large air spaces develop at several levels in this tissue due to the collapse of some of the epidermal and chlorenchyma cells. The light reflecting inside these cavities gives the thallus its characteristic glistening appearance.

Ballooning of Epidermis

In some species of *Riccia* (Figure 29-Figure 32) the epidermal cells are balloon-like (Figure 58) and may contribute to protection from desiccation (Kürschner 2004). However, I wonder if those cells don't provide a greater role in focussing the light into the thallus to the chlorophyllous cells when the thallus is hydrated. Kürschner suggested that the chimney-like, hyaline air chambers of *Exormotheca* (Figure 59-Figure 61) may also have a function in protecting the underlying tissue during dehydration.



Figure 58. *Riccia atromarginata* showing balloon epidermal cells. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 59. *Exormotheca pustulosa* showing ballooning of epidermal cells. Photo by Jonathan Sleath, with permission.



Figure 60. *Exormotheca welwitschii* showing ballooning of epidermal cells. Photo by Michael Lüth, with permission.



Figure 61. *Exormotheca* thallus section showing columns of photosynthetic tissue and ballooning surface. Photo by Wilhelm Barthlott, with permission.

Cuticle

For many years we considered the cuticle to be absent in bryophytes, with scattered references referring to them, but with no definitive data on their surface chemistry. However, not only are waxy cuticles present, but waxes are present on the leaves and thalli, albeit in less noticeable quantity than in tracheophytes. In fact, Brockington *et al.* (2013) considered the cuticle in the thallose liverwort *Marchantia polymorpha* (Figure 34) to be "an overlooked innovation in land plants."

Knowing that *Marchantia polymorpha* (Figure 34-Figure 35) has a cuticle, one should not be surprised that the shiny thallose liverwort *Monoclea gottschei* (Figure 48) and the hornwort *Notothylas orbicularis* (Figure 62) have an **osmiophilic layer** (refers to lipid-containing bodies; a cuticle) with structural resemblance to that of early developmental stage tracheophyte cuticles (Cook & Graham 1998).



Figure 62. *Notothylas orbicularis*, a species with a demonstrated osmiophilic layer, *i.e.* cuticle. Photo by Michael Lüth, with permission.

What emerged as more interesting in this study is that not all of these bryophyte versions are created equal. In the liverwort *Monoclea gottschei* (Figure 48) the layer is nodular, in the hornwort *Notothylas orbicularis* (Figure 62) it can be either nodular or sheetlike, and in *Sphagnum fimbriatum* (Figure 63) it is sheetlike with regular ridges that run parallel to the edges of the "thalli" (Cook & Graham 1998). It appears that cuticle is ancient, and Cook and Graham suggest that it may have arisen before the charophycean algae and bryophytes diverged from their common ancestor.



Figure 63. *Sphagnum fimbriatum*, a species with a cuticle. Photo by Michael Lüth, with permission.

The thallose liverwort *Plagiochasma rupestre* (Figure 64) has a non-wettable thallus endowed with hydrophobic wax globules, preventing it from absorbing water through its surface (Kürschner 2004). Instead, it uses the pegged rhizoids for water uptake, a phenomenon that may be common to all members of **Marchantiales**. This dorsal surface wax may have an important role in preventing water logging in the underlying air chambers.



Figure 64. *Plagiochasma rupestre* thallus showing smooth rhizoids on edges and waxy surface. Photo by Hugues Tinguy, with permission.

The presence of a cuticle on the upper surface of a thallose liverwort raises the question of water absorption in these species. But based on the foregoing discussions of scales and rhizoids, we know that it occurs predominantly through the ventral surface, facilitated by the scales and rhizoids. Presumably there is no cuticle on that surface, but that does not yet seem to have been demonstrated.

In the **Polytrichaceae**, waxes may serve a different function. Rather than keeping water in, the leaves of these species must keep water out to permit maximum photosynthesis (Figure 65) (Clayton-Greene *et al.* 1985). Their lamellae provide extra photosynthetic tissue, but water can become trapped there due to the capillary spaces. This protection from water is further enhanced by the rolled margins (Figure 66) of species like *Polytrichum juniperinum* (Figure 67).

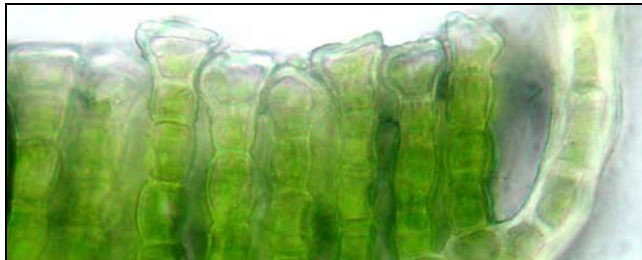


Figure 65. *Polytrichastrum pallidisetum* showing leaf lamellae where photosynthesis occurs. Note thickened end cells that help keep water from entering capillary spaces between lamellae. Photo by Michael Lüth.

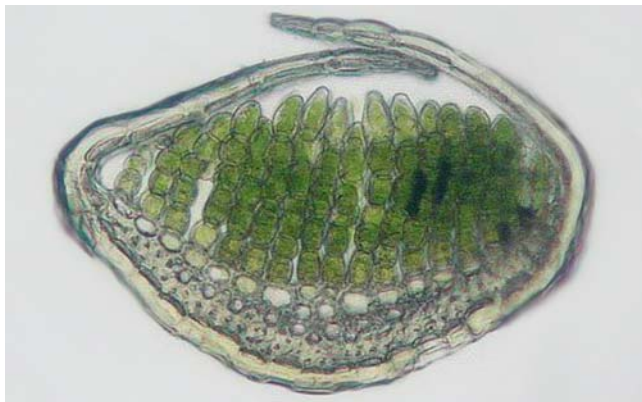


Figure 66. *Polytrichum hyperboreum* showing inrolled leaf margins that cover the lamellae and protect them from water logging in the capillary spaces. Photo by Michael Lüth, with permission.



Figure 67. *Polytrichum juniperinum* showing lamellae and leaf edge that is rolled over them to help keep water out of the capillary spaces. Photo by John Hribljan, with permission.

Pores

The wonderful ventral efficiency of rhizoids and scales is often challenged by a dorsal (upper) surface that does little to conserve water. In fact, this dorsal surface water loss may facilitate the movement of water and nutrients through the plant, as it does in leafy tracheophytes. The pores on the dorsal surface function much as do the stomata of tracheophyte leaves in losing water (Figure 55, Figure 73). Maier-Maercker (1982) found that *Conocephalum conicum* (Figure 36) loses water through transpiration from these dorsal thallus pores (Figure 68), accumulating radioactively labelled ions in the cells surrounding the air pores.

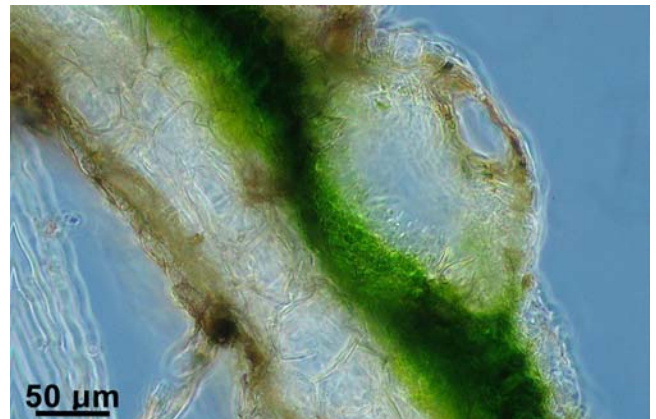


Figure 68. *Conocephalum conicum* pore section. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

The single-layered leaves of leafy liverworts and most mosses preclude the presence of stomata there as they would provide only a hole through the leaf, hardly a useful character. Even multicellular layers of moss leaves have no use for stomata because there is no chamber where the gases may gather. But thallose liverworts meet those two requisites – multiple cell layers (Figure 69) and chambers internally (Figure 70). Furthermore, as mentioned above for *Marchantia polymorpha* (Figure 34), the thallus has a cuticle that can at least to some degree repel water. Hence we might presume that it likewise is somewhat resistant to gas exchange, creating a problem for photosynthesis.

Raven (2002) provided evidence that stomata evolved from pores of an epidermis over plant organs at least three cell layers thick, with intercellular gas chambers, and with a cuticle. In this anatomical arrangement, the presence of pores most likely confers an adaptive advantage for photosynthesis.



Figure 69. *Conocephalum conicum* photosynthetic cells under epidermis, showing thallus that is more than three cell layers thick. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

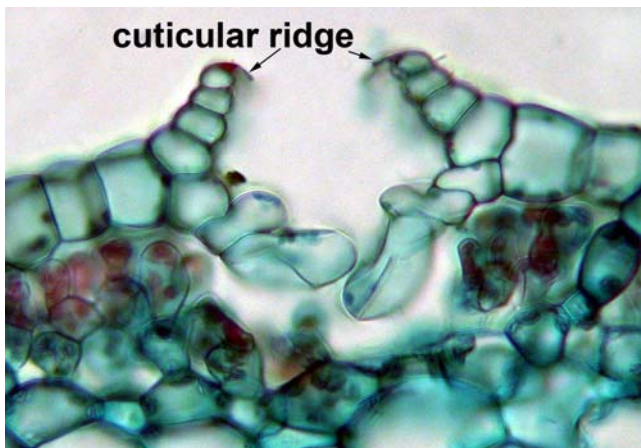


Figure 70. *Marchantia polymorpha* thallus pore in longitudinal section, showing cuticular ridge. Cells stained with purple are photosynthetic cells. Note the chamber beneath the pore. Photo by George Shepherd, through Creative Commons.

In some cases, thalloid liverworts seem to lose great quantities of water, 2-3 times that of leaves of the weeping birch tree *Betula pendula* (McConaha 1941). Under extreme conditions, they transpire equivalent to their total content of water in an hour. One reason for this rapid transpiration rate is the areolation of the thallus that creates a large surface area where water can be lost. The pores in these thalli (Figure 71), permitting contact between outside air and internal moisture, have only limited ability to close, thus being a major source of water loss. McConaha (1941) claims that the ventral specializations compensate for the losses from dorsal areolation and pores. Proctor (1980) found that these areolate thalli have internal resistances similar to those of mesophytic leaves of flowering plants (Proctor 1980). As in the flowering plants, the water loss is correlated with pore size and density.



Figure 71. *Marchantia chenopoda* pores showing rim of cuticle projecting into the pore opening. The polygons outline the internal chambers that create the areolation. Photo by George Shepherd, through Creative Commons.

But the photosynthetic cells project into these chambers beneath the pores (Figure 70), and flooded cells cannot exchange gases freely. It should be no surprise then that the openings themselves prevent the entrance of water into the chamber. Their small size (Figure 71) contributes to this. In the absence of a wetting agent, the cohesive forces of water make the aggregation of water molecules too large to enter the holes. This smallness of the hole is further enhanced by the presence of a **cuticular ridge** (Figure 71-Figure 74) that not only narrows the entrance, but that also repels the water, *i.e.* is **hydrophobic**.

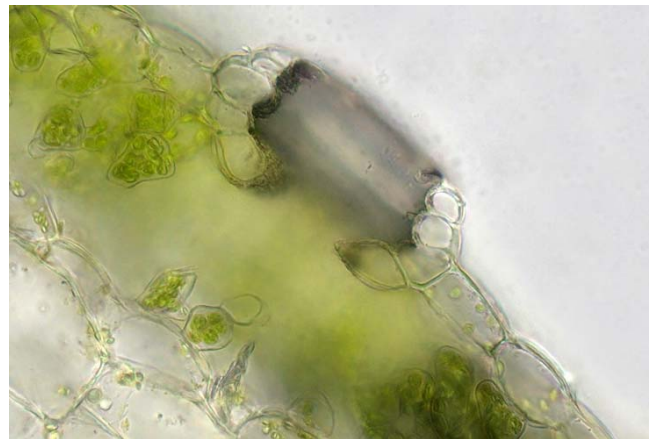


Figure 72. *Marchantia polymorpha* pore in longitudinal section. Photo by Walter Obermayer, with permission.

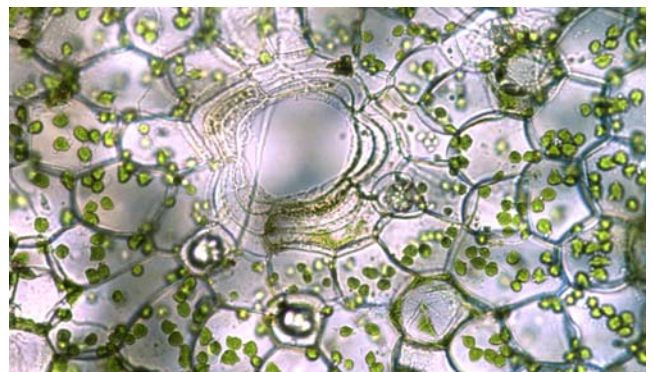


Figure 73. Pore opening in thallus of *Cyathodium cavernarum*, showing cuticular ridge. Photo courtesy of Noris Salazar Allen.

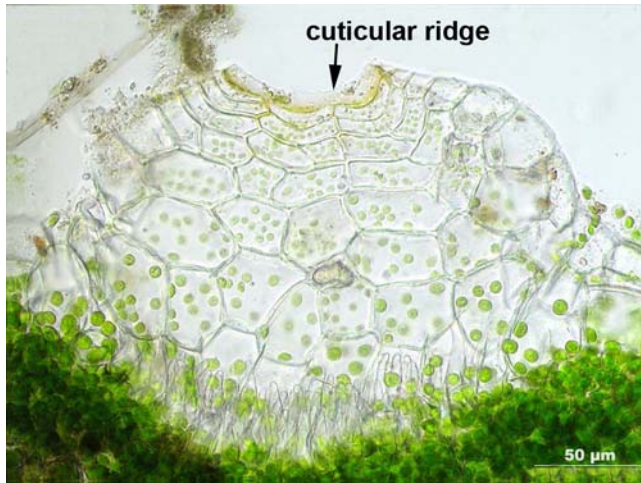


Figure 74. *Conocephalum conicum* pore longitudinal section showing the cuticular ridge. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

Schönherr and Ziegler (1975) found that of the fourteen thallose liverwort species they studied, twelve of them have such **hydrophobic** (repelling water) ridges, and that **cutin** is present in these ridges. Furthermore, the researchers considered the pores in these species to be "perfect" in keeping water out of the thallus. *Plagiochasma rupestre* (Figure 75) and *P. peruvianum*, on the other hand, lack such ridges and liquids are able to enter the thallus through the pores. While the waxes and small size of the holes keep water out, the water in vapor form within the thallus is able to escape through the pores, along with oxygen, while CO₂ enters. Therefore, the openings must maximize carbon gain per unit water loss (Raven 2002).



Figure 75. *Plagiochasma rupestre*, a thallose liverwort with no cuticular ridge on its pores, but with a waxy cuticle on the thallus. Photo by Michael Lüth, with permission.

While these pores are an advantage for a hydrated, photosynthesizing thallus, they are a liability for a drying thallus due to the loss of water vapor. But at least some of

the liverworts seem to be able to partially control the opening. This is accomplished by curving of the stack of cells surrounding the opening, creating partial closure. In *Preissia* (Figure 76-Figure 77, Figure 39), the barrel-shaped pores (Figure 77) change shape to accomplish control of water loss (Lepp 2008). When turgid with water, the cells at the bottom of the barrel keep the pore open, but when the conditions are dry, the cells lose their turgor and collapse, narrowing the opening at the bottom of this barrel. Those in *Marchantia* (Figure 70-Figure 72) behave similarly (Raven *et al.* 2005). A further aid, presumably, is the ability to fold the upper side of the thallus inward, as discussed above, creating a less exposed surface and slowing the rate of water loss.



Figure 76. *Preissia quadrata* thallus showing pores (light-colored dots). Photo by Jan-Peter Frahm, with permission.



Figure 77. *Preissia quadrata* thallus showing pores with cuticular ridges. Photo by Kristian Peters, with permission.

Archegoniophores and Antheridiophores

In thallose liverworts, the horizontal orientation cannot serve as a model for water movement in the vertical **archegoniophore**. As determined by Duckett *et al.* (2013), the archegoniophore has more efficient water movement than the stems of mosses. They attribute this to the efficiency of movement through the rhizoids and capillary spaces among them, as well as the hydrophobic nature of the thallus surface surrounding these rhizoids (Figure 78).

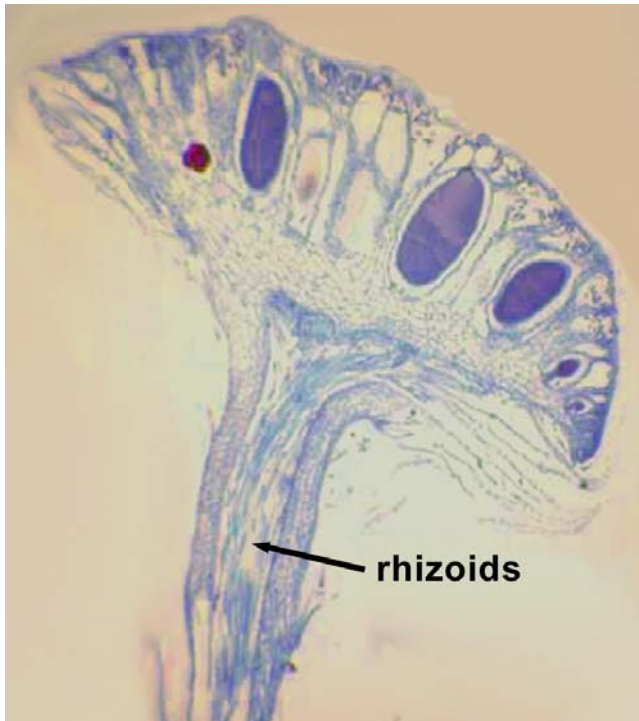


Figure 78. *Marchantia polymorpha* antheridial head showing location of rhizoids within the antheridiophore. Photo from Botany website of the University of British Columbia, BC, Canada, with permission.

The importance of this rhizoid-thallus combination for the archegoniophore is suggested by comparing its response to drought with that in mosses. For example, *Marchantia* (Figure 79) archegoniophores and heads can remain fully hydrated for several hours in full sunlight at 20-30°C while the shoots of neighboring *Polytrichum commune* (Figure 80) with their bases in standing water become wilted and must have added rainwater to recover (Duckett *et al.* 2013), suggesting an efficient system of transport in the archegoniophore.



Figure 79. *Marchantia polymorpha* archegoniophore and archegonial head. Note rhizoids along stalk (archegoniophore) where they emerge from the folded thallus that makes the stalk. Photo by George Shepherd, through Creative Commons.



Figure 80. *Polytrichum commune*, a moss that wilts in full sun despite its wet substrate and colonial habit. Photo by Michael Lüth, with permission.

Duckett *et al.* (2013) suggest that the length of the archegoniophore is limited to a maximum of 7-10 cm (in *Conocephalum*; Figure 81) because of the problems of air bubbles in the mucilaginous matrix surrounding the pegged rhizoids in the grooves of the archegoniophore, a condition analogous to an embolism in the vessels of tracheophytes (see Canny 2001 a, b).



Figure 81. *Conocephalum conicum* with tall archegoniophore. Photo by Adolf Ceska, with permission.

Antheridiophores provide yet a different mechanism (Duckett & Pressel 2009). Present only in the genus *Marchantia*, they present an antheridial head (Figure 82) on a stalk that is much shorter than that of the mature archegoniophore, rarely exceeding 30 mm. Rather than being hydrophobic, the heads are highly hydrophilic and absorb raindrops much like a sponge. Whereas upward flow occurs in the stalk during dry periods, downward flow carries the motile sperm toward the archegonia on immature (shorter) archegoniophores (Figure 83) during rainfall.



Figure 82. *Marchantia polymorpha* with antheridial heads where water is absorbed like a sponge. Photo by Rudolf Macek, with permission.



Figure 83. *Marchantia polymorpha* young archegoniophores that receive sperm from temporarily taller antheridiophores. Photo by Rudolf Macek, with permission.

Dormancy

Volk (1984) found that when *Riccia* (Figure 84-Figure 85) has less than 150 mm of rainfall per year, it requires other means to survive, and it seems that dehydration/dormancy is the solution (Figure 84-Figure 85). Some thallose *Riccia* species are able to survive up to 7 years in this dehydrated state, enduring temperatures up to 80°C. The annual species compensate for this water loss by producing huge numbers of spores, taking advantage of their ornamentation for distribution by animals.



Figure 84. *Riccia sorocarpa* in a fresh, active state. <www.aphotofauna.com>, with permission.



Figure 85. *Riccia sorocarpa* in a dry, dormant state. Photo by Michael Lüth, with permission.

Mosses and Leafy Liverworts

We typically think first about structural adaptations for water retention, so we will start there. Sarafis (1971) considered that *Polytrichum commune* (Figure 80) had four ways of controlling water loss:

1. Community level – gregariousness
2. Plant level – leaf density & size, plant height
3. Organ level – leaf movement and inrolling
4. Molecular level – wax on leaf surface

These all relate to structure, but internal structure and cellular level physiology are additionally important.

Vitt *et al.* (2014) consider the avoidance strategies of mosses to differ somewhat from those of liverworts and hornworts. Leaf arrangement has greater variation in mosses. Xerophytic leaves and stems often possess large **trigones** (thickenings in corners of cell walls; Figure 86) and nodular intermediate thickenings on interior walls, forming branched **vittae** (like costa, but 1 cell thick) in the lamina of leaves such as those of *Herbertus aduncus* (Figure 87-Figure 88) that enhance water uptake and storage, often with protruding **papillae** on their dorsally exposed, superficial walls. Xerophytic stem cells are thick-walled. These wall adaptations consist mostly of hemicelluloses, pectins, and cellulose, substances that would facilitate apoplastic water uptake, movement, and retention (Proctor 1979a). Water spreads over the leaves that have papillae, filling the spaces next to the leaf surface, but leaving the tips of the papillae dry to facilitate gas exchange. In taxa from moist but intermittently dry habitats, the outer cell walls are typically exposed but water-repellent. In *Nowellia* (Figure 89), *Marsupella* (Figure 90), and *Solenostoma* (Figure 91) with concave, overlapping leaves, surface tension may account for this repellent property (Proctor, 2009), but in other cases, thin coats of epicuticular waxes are hydrophobic (Duckett & Soni 1972; Heinrichs *et al.* 2000). And what is the function of the pore-like connections between cells (Figure 92) in more mesic mosses like *Dicranum scoparium*?

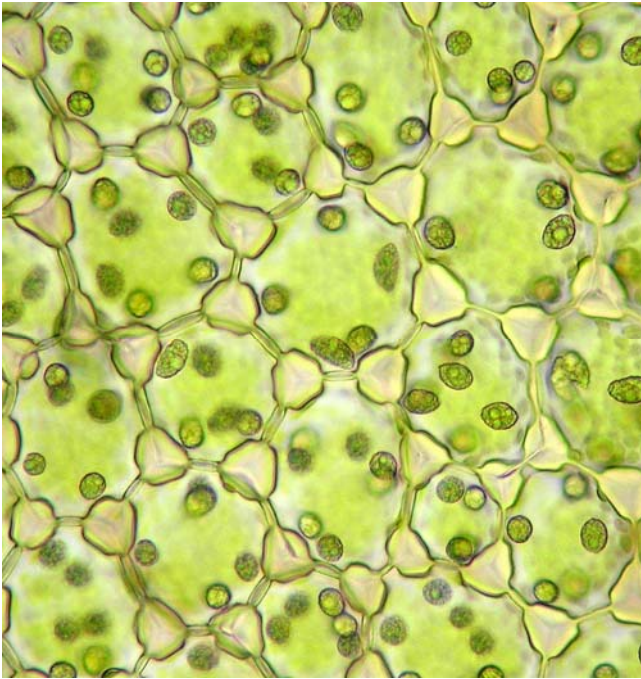


Figure 86. *Heteroscyphus conjugatus* leaf cells showing trigones. Photo by David Tng, with permission.



Figure 87. *Herbertus aduncus* in a temperate rain forest. Photo by Ian Cruickshank, through Creative Commons.

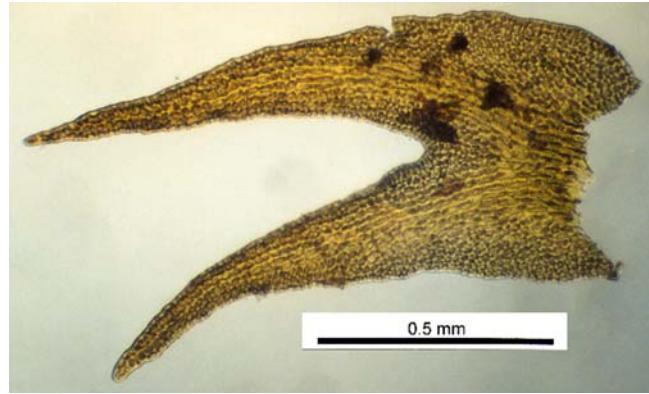


Figure 88. *Herbertus aduncus* leaf showing vitta in each leaf lobe. Photo by David H. Wagner, with permission.



Figure 89. *Nowellia curvifolia* showing deeply concave, overlapping leaves where water becomes trapped. Photo by Štěpán Koval, with permission.



Figure 90. *Marsupella emarginata* showing concave leaves that can trap a drop of water. Photo by Hermann Schachner, through Creative Commons.



Figure 91. *Solenostoma hyalinum* showing overlapping, concave leaves that can trap water. Photo by David T. Holyoak, with permission.



Figure 93. *Racomitrium lanuginosum*, an ectohydric moss with little control over water loss. Photo by Hermann Schachner, through Creative Commons.

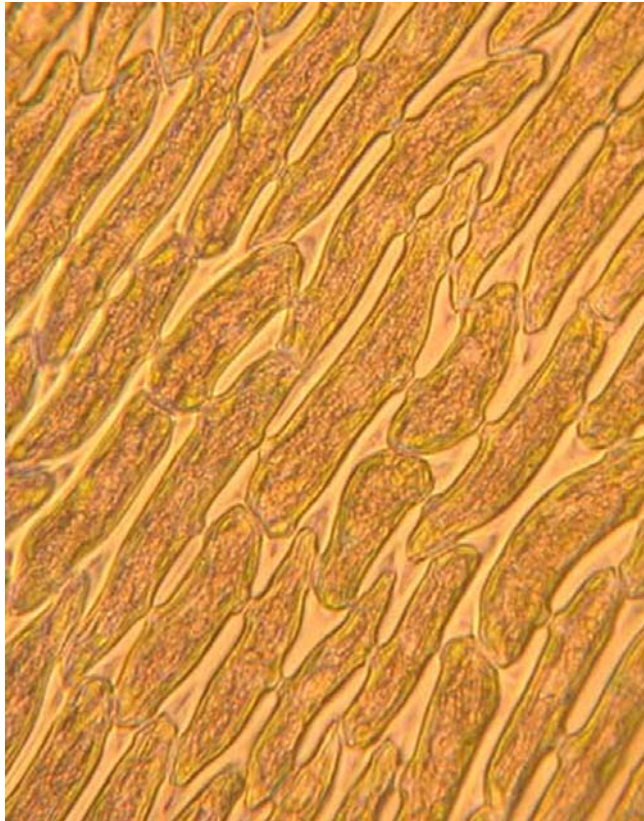


Figure 92. *Dicranum scoparium* cells showing pore-like connections between cells. Photo from Botany website, UBC, with permission.

Bayfield (1973) considered that water loss in endohydric *Polytrichum commune* (Figure 80) to be controlled by its leaf arrangement changes. This was accompanied by changes in water potential deficit of the shoots, with conduction being primarily internal under high evaporative flux and external under moderate flux. The ectohydric *Racomitrium lanuginosum* (Figure 93), by contrast, has little control over its water loss.

After examining 439 taxa of pleurocarpous mosses, Hedenäs (2001) reported that most differences in taxonomic character states between environments relate to two functions: 1) water conduction and retention; 2) dispersal. Those morphological characters that seem important for water relations relate to **stem central strand** (Figure 94-Figure 95), **leaf costa type** (Figure 96-Figure 97), **paraphyllia** (Figure 98), **pseudoparaphyllia** (Figure 99), **alar cells** (Figure 96), and **leaf orientation** (Figure 20-Figure 24, Figure 100-Figure 102). The latter two also relate to the **ability to change leaf orientation during drying** (Figure 103-Figure 105). But if acrocarpous mosses (upright mosses with terminal sporophytes) had been included, surely many more characters might be added, as it is mostly acrocarpous mosses that occupy the most xeric of habitats.

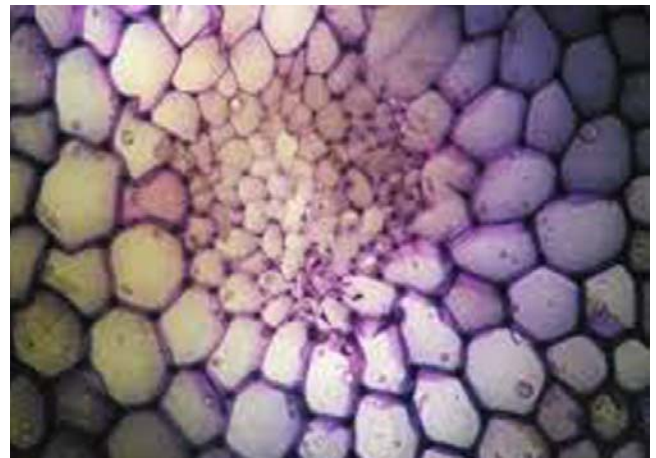


Figure 94. *Haplomitrium* sp. stem cross section with central strand that disappears in wet habitats. Photo by Rachel Murray and Barbara Crandall-Stotler, with permission.

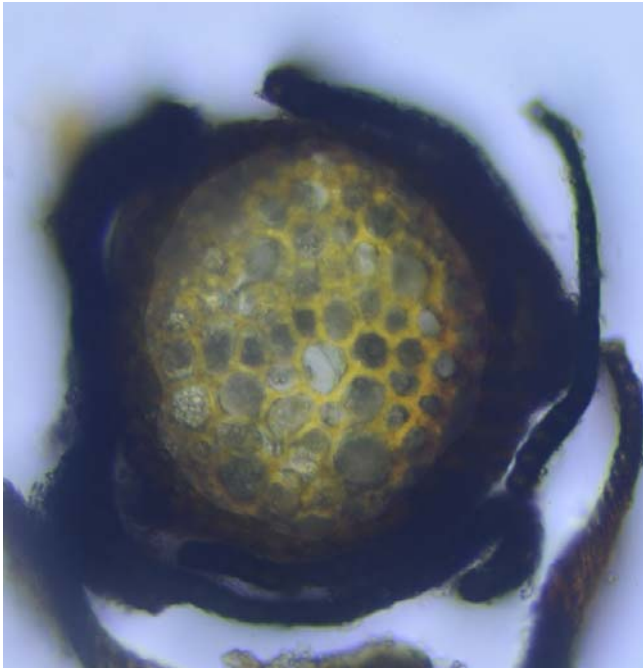


Figure 95. *Andreaea rothii* stem cs showing absence of central strand of conducting cells. Photo by Randal, through Creative Commons.

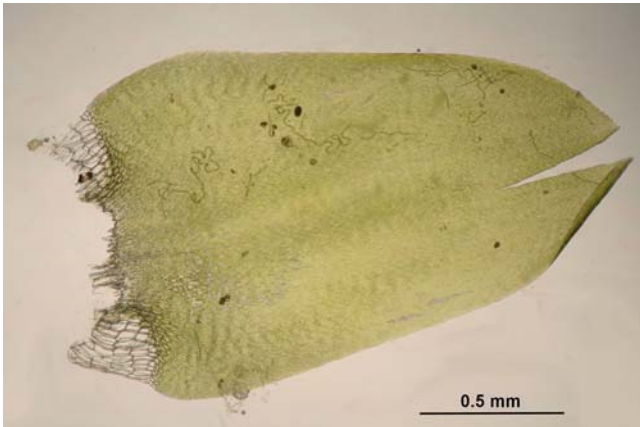


Figure 96. *Calliergonella cuspidata* leaf showing alar cells and absence of costa. Swelling of alar cells upon hydration can physically push the leaf away from the stem. Photo by Hermann Schachner through Creative Commons.



Figure 97. *Bryhnia-graminicolor* leaf showing costa and prorate cells. Photo by Bob Klips, with permission.

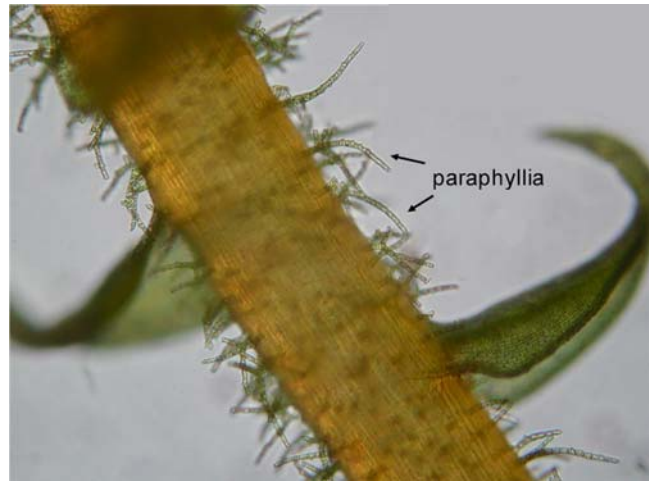


Figure 98. *Thuidium paraphyllia* on stem. Photo by Paul Davison, with permission.

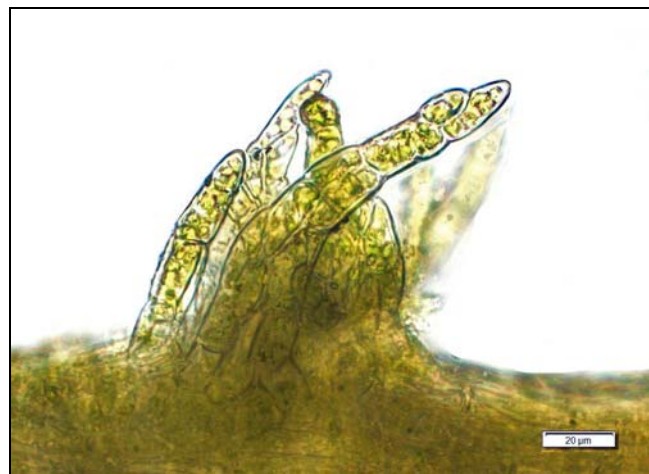


Figure 99. *Homomallium mexicanum* pseudoparaphyllia surrounding a branch bud. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 100. *Calypogeia muelleriana* showing overlapping leaves in two rows, making the branches flattened. Photo from Botany Website, UBC, with permission.



Figure 101. *Thelia asprella* showing leaves adhering tightly to stems and branches (**julaceous**). Photo by Bob Klips, with permission.



Figure 102. *Polytrichum formosum* male showing spreading leaves in wet condition. Photo by Andrew Spink, with permission.



Figure 103. *Polytrichum formosum* dry, showing leaves tightly wrapped around the stem. Photo by Sharon Pilkington, with permission.

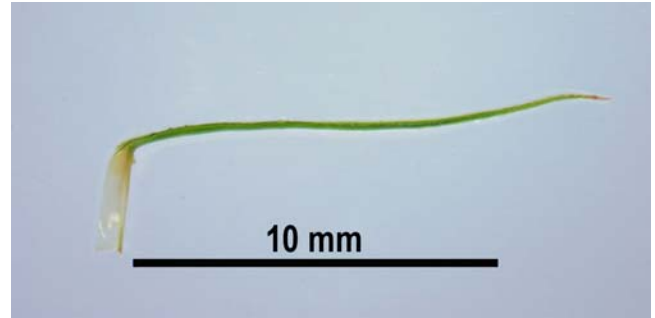


Figure 104. *Polytrichastrum formosum* leaf showing the hyaline basal cells that facilitate the spreading of the leaf when hydrated. Photo courtesy of Norbert Ethan.



Figure 105. *Polytrichastrum formosum* leaves with lowest leaf holding water at its base.. Photo courtesy of Norbert Ethan.

One feature of structural adaptations is that many are **plastic**, *i.e.* they can change depending on their growing conditions (Buryová & Shaw 2005). For example, **conducting strands** are absent in the liverworts *Moerckia flotoviana* (Figure 106) and *Haplomitrium hookeri* (Figure 94, Figure 107) under high humidity or liquid culture (Héban 1977). **Hair points** (colorless, hair-like extensions at leaf tip) of *Schistidium apocarpum* (Figure 108) likewise are absent in humid conditions (Figure 109).



Figure 106. *Moerckia blyttii*, a thallose liverwort that doesn't develop conducting cells in wet habitats. Photo by Michael Lüth, with permission.



Figure 107. *Haplomitrium hookeri*, a liverwort that doesn't develop its central strand in wet habitats. Photo by Des Callaghan, with permission.

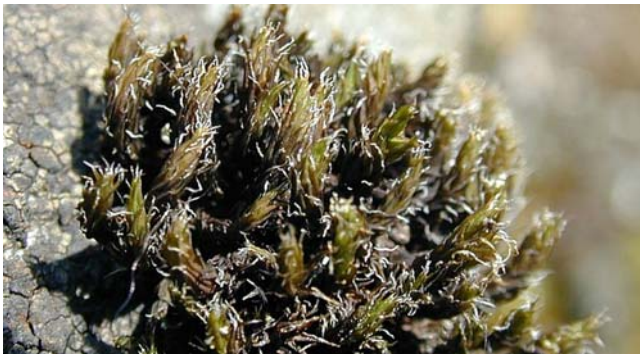


Figure 108. *Schistidium apocarpum* with hyaline hair points, on an exposed rock. Photo by Michel Lüth, with permission.



Figure 109. *Schistidium apocarpum* without hyaline hair points, growing in a more shaded or moist environment. Photo by Jan-Peter Frahm, with permission.

Rhizoids are less well developed or absent in wet conditions (Smith 1988), even in the same species. In *Andreaea blyttii* (Figure 110), increased moisture results in longer, wider leaves that are more curved with longer cells in the basal margin, wider **costae** (midrib of leaf), and longer stems, but with a decrease in number of leaves per stem (Heegaard 1997). Even in typically aquatic taxa such as *Drepanocladus* (*sensu lato*), leaves become longer, and falcation (leaf curvature) is lost in submersed leaves (Figure 111) compared to those grown out of water (Figure 112), and the reduced light in submersed conditions results in greater **internode** distances (distances between leaf insertions) (Lodge 1959). A similar response is seen in *Fontinalis* (Figure 113). It is interesting that increases in

salt concentration increase cell length in this genus. Plasticity itself is an important adaptation.



Figure 110. *Andreaea blyttii*, a moss that changes its leaf morphology in response to moisture changes. Photo by Michael Lüth, with permission.



Figure 111. *Drepanocladus aduncus* with straight leaves resulting from growing under water. Photo by Michael Lüth, with permission.



Figure 112. *Drepanocladus aduncus* with falcate leaves resulting from growing above water. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

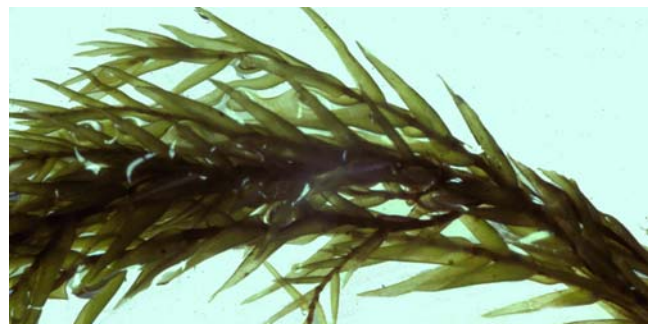


Figure 113. *Fontinalis novae-angliae* with normal submersed leaves. Photo by Janice Glime.



Figure 114. *Fontinalis novae-angliae* with leaves grown out of water, but wet, exhibiting an atypical falcate habit. Photo by Janice Glime.

Proctor (2010) reminds us that adaptations are subject to phylogenetic constraints and that entire clades may represent adaptations to desiccation. All plants must obtain water and CO₂, but there are multiple ways that this can be achieved.

Growth Form

Growth form is important both for obtaining and retaining water. For example, *Grimmia pulvinata* (Figure 115) forms cushions. In this moss, and most likely others with this growth form, size matters. As the clump grows larger, the surface to volume ratio decreases as the larger cushion is accompanied by greater height in the center. This reduces exposed area for gas exchange, but it also reduces the portion exposed to the atmosphere for water loss. In *Grimmia pulvinata* the larger cushions have lower area-based evapotranspiration rates due to a higher boundary-layer resistance, but the relative water storage capacity per dry weight does not change (Zotz *et al.* 2000). Consequently, the hydrated period is considerably longer in larger cushions. And as predicted, the CO₂ exchange rate decreases with increasing size of the cushion, with both net photosynthesis and dark respiration decreasing.



Figure 115. *Grimmia pulvinata* showing cushion form that conserves water. Photo by Michael Lüth, with permission.

Living in **clumps** affects the ability to gain and to retain moisture. The cushion growth form decreases the

surface to volume ratio, thus reducing surface water loss. Clump shape is important in this relationship, particularly in ameliorating wind effects (Proctor 1981; Zotz *et al.* 2000; Rice *et al.* 2001; Rice & Schneider 2004; Rice 2012). But for this system to work, the surface must be as smooth as possible. Greater roughness, resulting from protruding shoots, increases the turbulent air flow, thus increasing evaporation (Proctor 1981; Rice & Schneider 2004). A consequent advantage to the cushion growth form and its retention of water is the slowing of the drying rate (Sand-Jensen & Hammer 2012).

Fortunately, this is a self-regulating condition. As a shoot emerges from the surface, the greater exposure and greater evaporation cause its growth to attenuate. Even herbivores might contribute to this evening, choosing the protruding branch because it is easier to munch on. Hence, the surrounding mosses are able to catch up in length, returning the clump to its smooth structure. Thus, moisture limitations create a more matted clump with a smoother surface, limiting turbulent flow and wind penetration into the clump (Longton 1979; Guerra *et al.* 1992; Nakatsubo 1994).

Nakatsubo (1994) examined the importance of the growth form of sub-alpine mosses in controlling their evaporative water loss. The xerophytic species were comprised of large cushions and compact mats. Mesophytic species from the coniferous forest floor were represented by smooth mats, wefts, and tall turfs. The evaporation rate per dry weight was much less in the xerophytic species than in the mesophytic species. However, when compared on a basal area, the evaporation rates were similar. One advantage of the xerophytic species was their ability to increase weight per basal area without increasing roughness.

The density of the clumps seems to be a plastic character that can be modified by the environment (Gimingham & Birse 1957; LaFarge-England 1996; Bates 1998; Rossi *et al.* 2001). For example, the endohydric *Polytrichum juniperinum* var. *alpestre* (Figure 116), when in humid habitats, forms a looser clump structure with greater roughness than when in drier habitats (Birse 1957).



Figure 116. *Polytrichum juniperinum* var. *alpestre* showing contacting leaves of adjoining shoots in moist habitat. Photo by Des Callaghan, with permission.

Elumeeva *et al.* (2011) set out to determine the important characters that maintained moisture in sub-Arctic bryophytes. They found that individual shoot properties seemed to have little effect on colony water retention capacity. That is, leaf cell wall properties, water retention capacity, and desiccation rate of shoots made little difference in the water relations of the colony. Rather, the colony desiccation rate was determined by the density of the water-saturated colony. The desiccation rate of the individual shoot had a marginally significant negative effect on the colony rate.

In *Polytrichastrum formosum* (Figure 102), the plants are relatively tall and arranged in loose clumps. Nevertheless, the leaves of adjoining shoots touch, permitting water drops to be trapped by the resulting web. Drop size is an important consideration in conducting experiments using artificial rain. Raindrops usually range 0.5 mm (light rain) to 5 mm (heavy rain) (Best 1950; Brandt 1989; Yakubu *et al.* 2016). Using this size range, Zajaczkowska *et al.* (2016) determined that clumps of *P. formosum* were able to retain almost 60% of the applied water. When water was applied to the tips, water ran down the shoots and continued to run down until about 2 minutes after the water application ceased. When a drop lands on a leaf, it is more likely to be trapped by the leaf axil or by a leaf. Thus these clumps are benefitted by the catchment web formed by the overlapping leaves.

With these clump advantages, we might ask why so many mosses use other growth forms that are less compact. But moisture is not the only need for the mosses. A compact nature reduces light penetration, reduces CO₂ diffusion into the clump, and increases shoot-to-shoot competition for nutrients (Bates 1989; Rice 2012).

Mulder *et al.* (2001) explored the role of species richness on biomass, then compared it when these communities were exposed to experimental drought. They found that under drought conditions biomass increased with greater species richness. They determined that the interaction was facilitative rather than niche complementarity or the result of sampling effects. Survivorship increased for almost all species as richness increased, with the least drought-resistant species receiving the most benefit in biomass. Rixen and Mulder (2005) found similar results in the Arctic tundra.

Stems and Branches

Most stem and branch arrangements relate to growth form or life form (see Chapter 4-5 of this volume). However, in some cases there is internal or structural modification, exemplifying the plasticity of some bryophytes. For example, *Philonotis fontana* (Figure 117- Figure 118) exhibits variation among populations in leaf dimensions, whereas their cell dimensions show little response to differences in water regime or light level (Buryová & Shaw 2005).



Figure 117. *Philonotis fontana*, a species whose leaf dimensions vary with habitat. Photo by Des Callaghan, with permission.

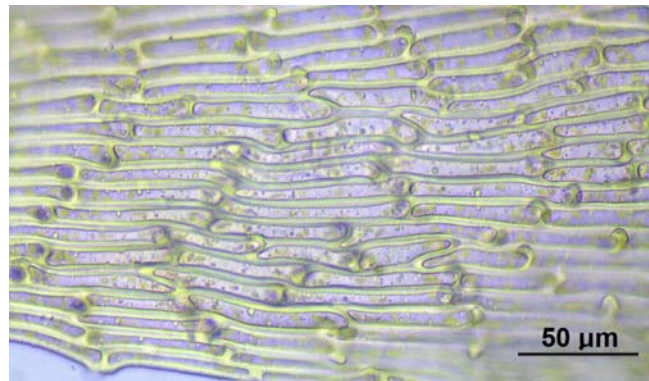


Figure 118. *Philonotis fontana* leaf lamina showing cells. These cells vary little in dimensions in different water or light regimes. Photo by Kristian Peters, through Creative Commons.

Overlapping leaves from neighboring shoots help in the support of the mosses in a clump. In stems, the alternating layers of stiff and soft structures, such as those of the **Polytrichaceae**, the strength benefits from the **periodic component materials** (Vincent 2012) that occur in many biological structures and provide stronger mechanical features (Dunlop *et al.* 2011; Fratzl *et al.* 2016). This layering provides the stem with both supportive strength and flexibility that prevents breakage. In *Polytrichastrum* (Figure 102) and other members of the **Polytrichaceae**, the thicker cell walls surrounding the stem provide a higher bending strength (Niklas 1992), much like a paper straw compared with a paper lollipop stick (the former bends; the latter breaks). We also know that a lollipop stick made with twisted paper threads is stronger than a solid, non-twisted one, and that many trees likewise gain strength this way. This possibility needs to be explored in bryophytes.

Schröder (1886) considered the ability of moss stems to resprout from a dormant stem to be one method for withstanding prolonged drought. I had a similar experience with the aquatic moss *Fontinalis dalecarlica* (Figure 119). In this case, the moss was boiled for 14 hours a day for two

weeks in the lab, then returned to the stream. One year later, new growth was present on this moss that was still attached to the numbered rock used in the boiling treatment. Such ability of stem tips to recover from environmental stresses have been largely overlooked.

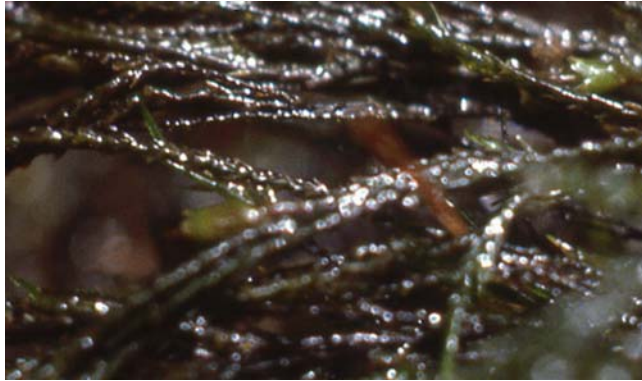


Figure 119. *Fontinalis dalecarlica* with from Fox Run, New Hampshire, USA, where a plant similar to this produced a green leaf one year after being boiled for 14 hours a day for two weeks. Photo by Janice Glime.

Sphagnum: Li and coworkers (1992) examined the responses of two closely related *Sphagnum* hummock species, *S. magellanicum* (Figure 120) and *S. papillosum* (Figure 121), to distance from water surface and related these responses to structural and physiological adaptations of the two species. They found that both species increase growth in length as water becomes more available, *i.e.* as the distance from water level decreases. Likewise, dry mass is maximal under wet conditions, with new branches being a major mass contributor, especially in *S. papillosum*. Furthermore, while experimenting with effects of distance from water on *S. magellanicum* and *S. papillosum*, Li and coworkers found that dry conditions result in wider stems (Figure 122), with thicker hyaline layers (Figure 123-Figure 124), than stems with apical capitula near the water surface (Figure 132), presumably increasing both absorption and water-holding ability.



Figure 120. *Sphagnum magellanicum*, a hummock species with efficient water movement. Photo by Michael Lüth, with permission.



Figure 121. *Sphagnum papillosum*, a species with inefficient water movement. Photo by David Holyoak, with permission.

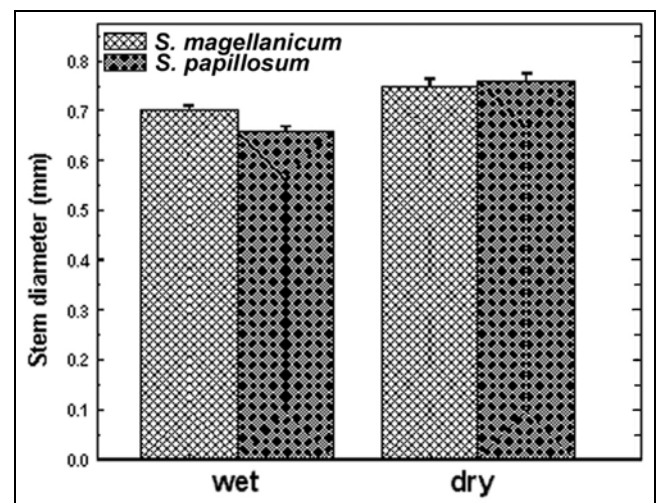


Figure 122. Effect of water level (water availability) on stem diameter in *Sphagnum magellanicum*, a more desiccation-resistant species, and *S. papillosum*, a more desiccation-tolerant species. Wet denotes 0 cm initial distance of capitulum from water; dry denotes 10 cm initial distance. Bars represent standard errors; stem diameter in dry treatment is significantly greater (Figure 123) in both species. From Li *et al.* 1992.

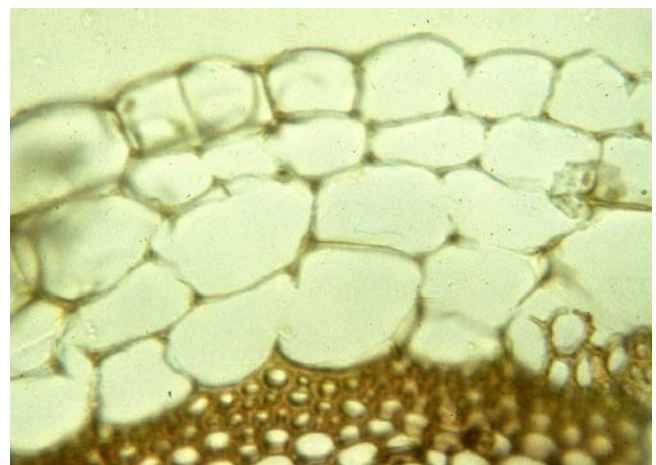


Figure 123. *Sphagnum magellanicum* stem at highest level (5) above water surface. Photo courtesy of Yenhung Li.

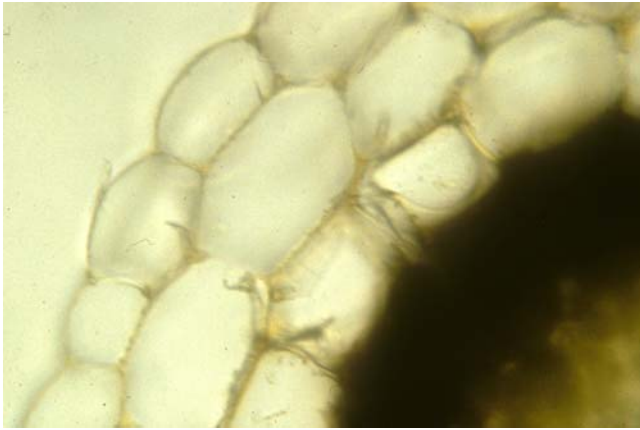


Figure 124. *Sphagnum magellanicum* stem at level 3 above water surface. Photo courtesy of Yenhung Li.

Sphagnum has pores in its stem (Figure 125), in most species, and has very rapid movement of water externally up the stem by capillary action, adapting it for its annual cycle of being stranded well above water level in many species. Some species of *Sphagnum* have special **retort cells** (Figure 126) on the stems for absorbing water.

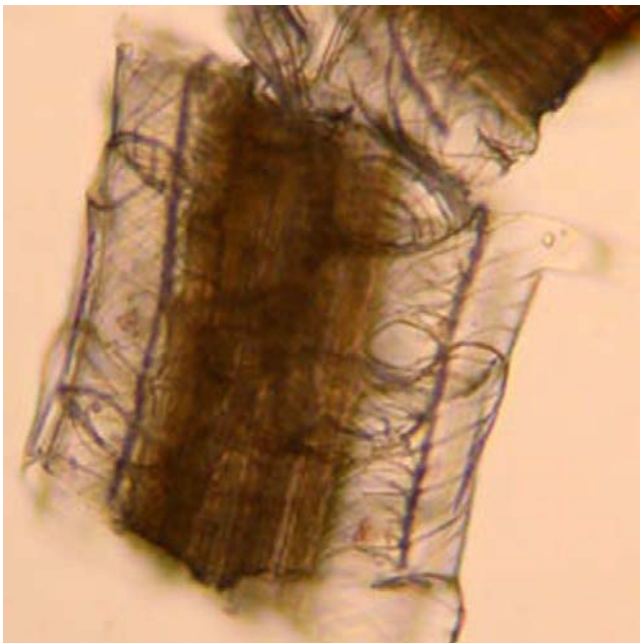


Figure 125. *Sphagnum papillosum* stem showing pores. The spiral thickenings of stem cells are unique in this moss. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Daniels (1989) found that while there is little differentiation between **spreading** and **pendant** branches (Figure 127-Figure 128) among *Sphagnum* plants growing in pools, hummock plants have more closely spaced **fascicles** (groups of branches), comparatively short spreading branches, and thin, closely appressed pendant branches (Figure 128). Pendant branches help to preserve stem water and maintain the wick effect as water level drops. Daniels determined that leaves of pendant branches on submerged plants photosynthesize actively, while those of hummock plants do not. He found that the two species growing in wet hollows (*Sphagnum cuspidatum*; Figure

129) or as wet carpets (*Sphagnum recurvum*; Figure 130) had the highest percentage of unbranched stems. The low hummock species *Sphagnum papillosum*, on the other hand, had up to six **capitula** (terminal clump of branches; Figure 131) per stem; the two species growing in the high-humidity, shaded wet woodland exhibited intermediate degrees of branching.

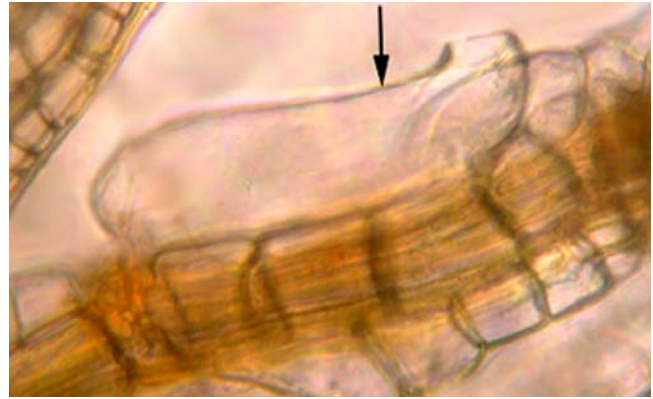


Figure 126. Retort cell (arrow) of *Sphagnum*, showing pore. Photo from Botany website, University of British Columbia, BC, Canada, with permission.



Figure 127. *Sphagnum teres* indicating two major branch types, compact capitulum, and joining of branches into fascicles. Photo by Michael Lüth, with permission.



Figure 128. Spreading branches and pendant branches on two hummock *Sphagnum* species. **Left:** *S. magellanicum*. **Right:** *S. papillosum*. Photos courtesy of Yenhung Li.



Figure 129. *Sphagnum cuspidatum*, a species from hollows with a high percentage of unbranched stems as seen in the single capitula. Photo by J. C. Schou, with permission.



Figure 130. *Sphagnum recurvum*, a species of wet carpet with a high percentage of unbranched stems, as seen in the single capitula. Photo by J. C. Schou, with permission.



Figure 131. *Sphagnum papillosum* with branched capitula. Photo by J. C. Schou, with permission.

Sphagnum magellanicum (Figure 120) has greater ability to move and hold water than does *S. papillosum* (Figure 121) (Li *et al.* 1992). Therefore, when they grow together in the same hummock, *S. magellanicum* will not only stay wet longer, but if it is dominant it will keep *S.*

papillosum wet (Figure 132). However, it will fail to do so if *S. papillosum* is dominant (Figure 132). This is further supported by lab experiments in which *S. magellanicum* moved water farther externally in 20 hours than did *S. papillosum* (Figure 133; Figure 134).



Figure 132. Predominately *Sphagnum papillosum* (olive colored) lower on the hummock (left side of picture) causes both species to be dry, whereas predominately *S. magellanicum* (red) higher on the hummock (upper right side of picture) keeps both species wet. Photo by Janice Glime.

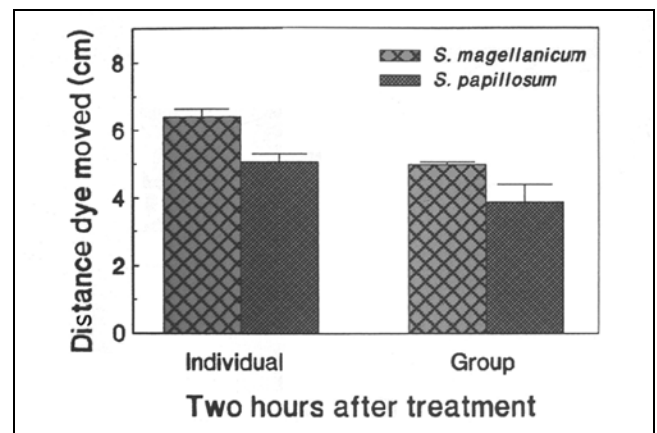


Figure 133. Comparison of distance travelled by dye after 20 hours in two *Sphagnum* species from lower (*S. papillosum*) and higher (*S. magellanicum*) positions in the hummock. Group refers to those kept together at field density with half of each species. From Li *et al.* 1992.

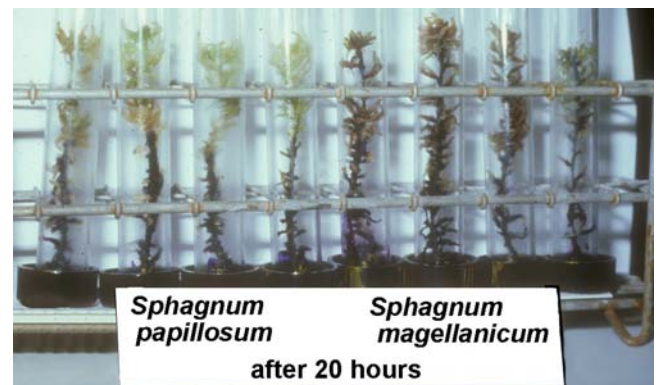


Figure 134. Comparison of upward transport in a low (left) and high (right) hummock species of *Sphagnum*. Movement of water is indicated by purple dye. Photo courtesy of Yenhung Li.

Central Strand

In addition to the structural adaptations of stems and branches already described, the vascular system itself may be modified. The **central strand** (Figure 135) is typically composed of hydroids that are elongated and impose fewer cell end walls through which water must travel. Héban (1973) found that variation occurred in the vascular elements, particularly in length and diameter, degree of inclination of end walls, and structure of the walls themselves. For example, whereas walls of hydroids are usually thin, they can be very thick, as in the swollen walls of hydroids in the setae of *Dicranum scoparium* (Figure 136) or the lateral walls of hydroids in the gametophyte central strand of the **Polytrichales** (Figure 137). But insufficient data exist to relate these variations to adaptive function.

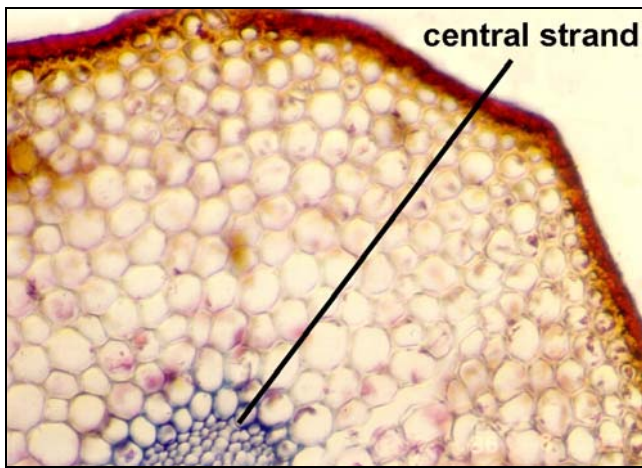


Figure 135. Stem cross section of *Rhizogonium* showing narrow cells of central strand. Photo courtesy of Isawo Kawai.

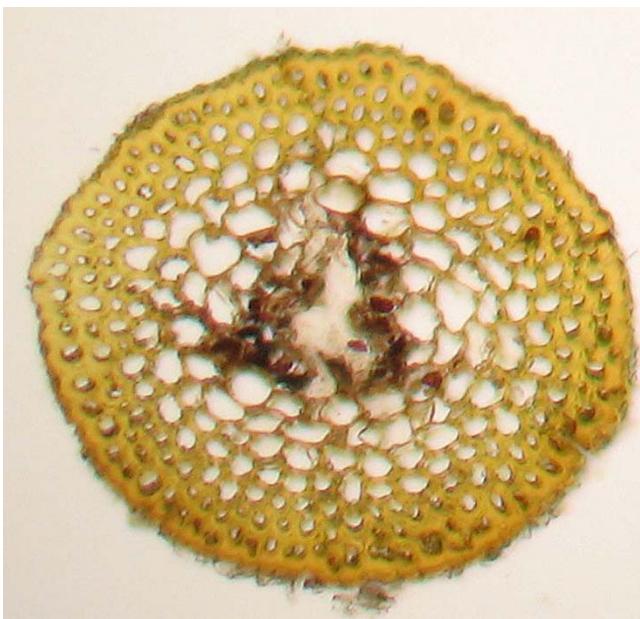


Figure 136. *Dicranum scoparium* seta cross section showing hydroids. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

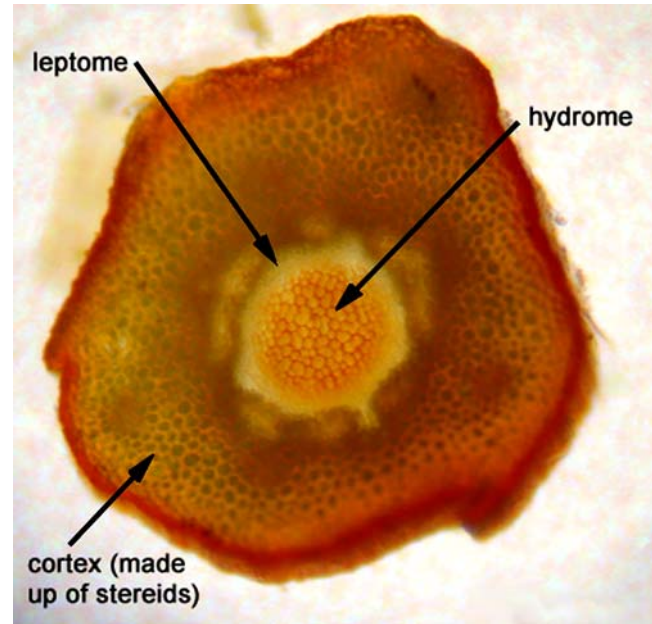


Figure 137. *Polytrichum commune* stem cross section showing central strand. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Using several references for comparison, Héban (1977) showed that the number of hydroids within the *Polytrichum commune* (Figure 80) central strand (Figure 137) can vary with habitat, following an apparent moisture gradient. In a pseudo-alpine grassland he reports 900 hydroids in the central strand, peat bog 400, cultivated in artificial peat 280, and cultivated under water 70. There is no clear indication as to how these numbers affect the rate of conduction, but one would presume that more hydroids conduct more water.

Although in general, leafy liverworts lack conducting tissues in both leaves and stems (Crandall-Stotler 2014), *Haplomitrium* seems to be an exception. At least it possesses a differentiated central strand (Figure 94). But there seem to be no experiments to demonstrate how well this actually serves as conducting tissue.

Rhizoids and Tomentum

Rhizoids and **tomentum** (layer of matted woolly down on surface of plant; Figure 138) are adapted for water uptake. Pressel and Duckett (2011) found that rhizoids of all representatives they tested in **Polytrichales**, **Dicranales**, and **Bryales** (Figure 139) were **hydrophilic** (tendency to be wetted by water). For example, there is a sharp contrast between the leaves with a waxy cuticle in **Bartramiaceae** (Figure 140) and the highly hydrophilic tomentum-forming rhizoids (Figure 140) with papillae.



Figure 138. *Rhizomnium magnifolium* showing dense brown rhizoidal tomentum on lower half of stem. Photo by Michael Lüth, with permission.



Figure 139. *Bryum pseudotriquetrum* (Bryales) showing dense rhizoidal tomentum along stem. Photo by Misha Ignatov, with permission.



Figure 140. *Breutelia chrysocoma* (Bartramiaceae) showing rhizoidal tomentum. Photo by Michael Lüth, with permission.

Mosses with dense rhizoids or **tomentum** (Figure 138–Figure 140) seem to be well equipped to retain and conduct water by capillary action. Smith (1988) found that *Bryum pseudotriquetrum* (= *Bryum algens*; Figure 139), with a dense rhizoidal tomentum (Figure 139), held significantly more water than colonies with sparse rhizoids. But the tomentose form lost water more rapidly per unit dry mass than did the ones with sparse rhizoids. Could this be attributed mostly to loss of water from the tomentum? In *Schistidium antarctici* (Figure 141), the xeric form has less densely packed shoots and thicker cell walls that maintain

lower water content than the high-water-holding-capacity hydric turf form. Mosses in Smith's study took several times longer to drop to minimal water contents than did lichens in the same conditions.



Figure 141. *Schistidium antarctici*, a moss that becomes morphologically modified by moisture conditions. Photo courtesy of Rod Seppelt.

In acrocarpous mosses, rhizoids are produced all the way around the base of the stem, serving on the lower parts for anchorage, and in mosses like the **Polytrichaceae**, for limited conduction (Odu 1978). Rhizoids further up the stem provide capillary spaces that can both store water and facilitate movement. In pleurocarpous mosses, rhizoids appear only on the side of the stem (Figure 142) toward the substrate (Odu 1978), except in the case of those in flowing water (Glime 1987). In *Fontinalis* (Figure 143), where rhizoids have a critical function in anchorage and this aquatic moss may encounter its substrate in any direction from the stem, the individual rhizoids grow in a spiral (Figure 144) until they encounter the substrate, then form multiple branches (Figure 145) in a small space and cement themselves to the substrate, presumably offering no function of water movement (Glime 1987).



Figure 142. *Hygroamblystegium fluviatile* rhizoids on one side of stem. Photo by Janice Glime.

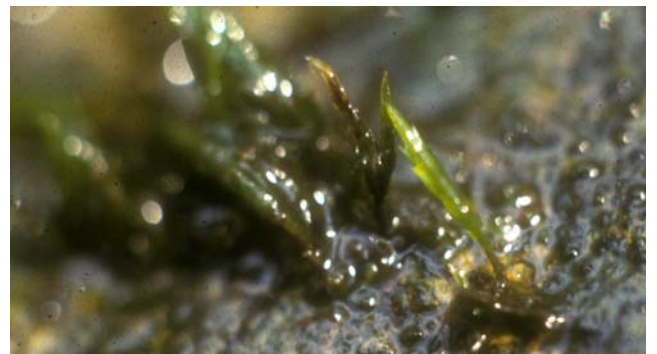


Figure 143. *Fontinalis novae-angliae* cemented to the rock by its rhizoids. Photo by Janice Glime.



Figure 144. *Fontinalis squamosa* rhizoids growing in a spiral where they are suspended above the substrate. Photo by Janice Glime.

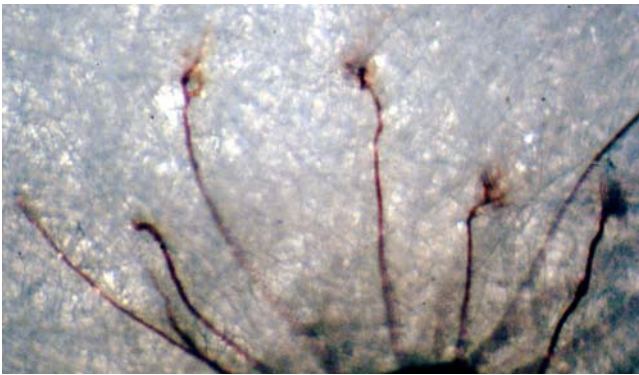


Figure 145. *Fontinalis squamosa* rhizoid tips branching when they encounter a paper towel substrate. Photo by Janice Glime.

Higuchi and Imura (1987) cultured three moss species to determine the effects of submersion on the rhizoid characters. The thickness, surface decorations, and positions where the rhizoids arise appear to be stable in altered moisture conditions, but in *Macromitrium gymnostomum* the mucilage that is present in terrestrial cultures is lost in water culture. Rhizoids generally are not produced on submersed mosses in standing water (Odu 1978). Could it be that ethylene, which inhibits their development, cannot escape easily? This conserves energy, because it would seem that they are needed neither for anchorage nor absorption and conduction. In flowing water they need anchorage and the flow would prevent ethylene from accumulating, if that is the mechanism.

Surprisingly, Trachtenberg and Zamski (1979) found a cuticle on the rhizoids of *Polytrichum juniperinum* (Figure 146), sharply contrasting with roots and root hairs of tracheophytes, which serve as absorbing organs and have no waxy cuticle. This suggests that they may play little role in water uptake, but rather prevent water loss to the substratum. This raises questions about how widespread this cuticle is on rhizoids of other taxa and how it affects the capillary action they might otherwise afford. Perhaps they play only a role in conservation of water and not in its uptake. Or are these cuticles designed to provide capillary spaces that hold water around the rhizoids and facilitate uptake?



Figure 146. *Polytrichum juniperinum* males, a moss that has a cuticle on its rhizoids. Photo by Jan-Peter Frahm, with permission.

It is noteworthy that the leafy liverwort *Haplomitrium* (Figure 94, Figure 107, Figure 153) lacks rhizoids (Duckett *et al.* 2013). On the other hand, *Treubia* (Figure 147-Figure 148) appears to possess rhizoids that facilitate nutrient uptake (Field *et al.* 2014). These unusual liverworts have leaves in three equal ranks and use underground stems (**rhizomes**) for anchorage and for fungal associations. All other liverworts produce **unicellular** (having only one cell) rhizoids (Figure 149). But only the thallose liverworts produce two types. Mosses, on the other hand, have multicellular rhizoids that can branch (Figure 150).



Figure 147. *Treubia lacunosa* dorsal view. Photo by Jan-Peter Frahm, with permission.



Figure 148. *Treubia lacunosa* with sporophyte, a species with underground stems. Photo courtesy of Jeff Duckett & Silvia Pressel.



Figure 149. *Cephalozia* sp. rhizoids showing that they are one-celled. Photo by Jan Fott, with permission.



Figure 150. *Bryum stirtonii* rhizoid showing multiple cells, papillae, and branching. Photo by Michael Lüth, with permission.

Mucilage

Stem apices are protected by mucilage secreted by specialized hairs (Berthier *et al.* 1974). This mucilage seems to play a strong role in protecting the actively dividing tissue, permitting fragments to survive long periods of desiccation until they are able to grow again, and most likely playing a role in water retention, especially for the critical apical cells.

In liverworts and the moss *Takakia* (Figure 151) there are **slime papillae** (Figure 152) that may serve a water absorption/retention function as well. The leafy liverwort *Haplomitrium* (Figure 153) produces extensive mucilage on its rhizomes (Figure 153-Figure 154). It is interesting that these slime papillae appear in the green alga *Coleochaete* (Figure 155), the genus that seems most closely related to embryophytes, causing one to wonder if slime papillae may have been a prerequisite for land adaptation in early plants.



Figure 151. *Takakia lepidozioides*, a moss with slime papillae. From the Herbarium of Hiroshima University, Hiroshima, Japan, with permission.



Figure 152. Stem of *Takakia lepidozoides* showing slime papillae that might serve in water absorption and retention. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

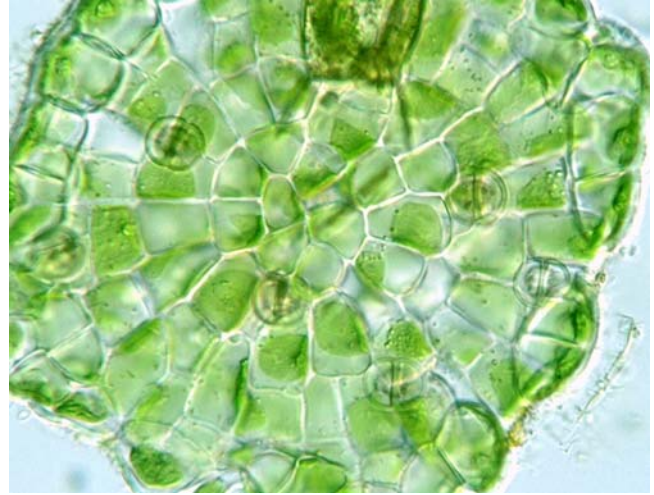


Figure 155. *Coleochaete* thallus, an extant green alga that has the most characters in common with bryophytes. Photo by Yuuji Tsukii, with permission.



Figure 153. *Haplomitrium gibbsiae* leafy plant with mucous on its rhizomes. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 154. *Haplomitrium gibbsiae* rhizome with mucous. Photo courtesy of Jeff Duckett and Silvia Pressel.

The thallose liverwort *Conocephalum conicum* (Figure 27, Figure 36, Figure 68) has mucilage ducts in its thallus. Clee (1943) suggests that these may aid in water retention.

Cuticles and Waxes

Bryophyte leaves have frequently been described as lacking a cuticle. However, this ancient concept has proven to be false. Even leafy liverworts can have a cuticle. The details of the leaf cuticle will be discussed in the next subchapter, but we need to consider how such a cuticle might affect the whole plant water movement. Loss of water from leaves can create a transpiration stream that draws water upward, but in most bryophytes the greater movement of water is external. Hence, it is not surprising that little is known of the effects of a transpiration stream on water movement in bryophytes. It would be interesting to know if stems have a cuticle, but I am aware of no studies that isolated the stems to look for it. For now, we will concentrate on other aspects of water movement.

Capillary Spaces

Although several adaptations to holding water seem to exist [porose leaf cells, ridges, folds, sheathing leaf bases (Figure 156), rhizoids, tomentum], Proctor (1979a) contends that most of the water is held in the larger capillary spaces between the moss shoots. Small amounts of dew that accumulate at the moss tip (Figure 157), *i.e.* the growing region, may be critical to survival (Lange 1969; Kappen *et al.* 1979). Hair points that wrap around the succeeding leaves above (Figure 158) help to deflect light and reduce evaporative loss by creating a diversion for air currents. Proctor (1980) experimented by removing hair points and found that when present they reduced water loss by 35% in *Grimmia pulvinata* (Figure 115) and *Syntrichia montana* (= *S. intermedia*; Figure 159). Thus far, it has been difficult to demonstrate that papillae afford any such advantage (Frey & Kürschner 1991). Nevertheless, in leaves they can act as a rapid capillary water movement system (Proctor 1979a; Longton 1988; Pressel & Duckett 2011).



Figure 156. *Bartramia ithyphylla* illustrating the sheathing leaf base that provides capillary spaces that can hold water. Photo by Michael Lüth, with permission.



Figure 159. *Syntrichia montana* showing long hair points that can reduce evapotranspiration by up to 35%. Photo by Michael Lüth, with permission.



Figure 157. *Campylopus introflexus* showing water droplets at tips of plants. Hair points, like fine wires and spider webs, provide locations where the cohesive, adhesive water droplets can cling. Photo by Jan-Peter Frahm, with permission.



Figure 158. *Polytrichum piliferum* illustrating leaf hairs that overlap the next leaf and help shield it from light, at the same time creating capillary spaces. Photo by Michael Lüth, with permission.



Figure 160. *Trichocolea tomentella* dry, a leafy liverwort with finely divided leaves and paraphyllia. Photo by Hermann Schachner, through Creative Commons.

The leafy liverwort *Trichocolea* (Figure 160-Figure 162) is highly adapted to take advantage of capillary action. Its leaves are highly dissected and **paraphyllia** (leaflike appendages between the leaves; see Figure 163) are abundant, permitting this species to act like a sponge. Zehr (1979) observed that it experienced only short-term vapor deficits in its moist habitat and thus was able to grow anytime temperatures were above freezing. Paraphyllia such as those in *Hylocomium splendens* (Figure 164-Figure 165) and *Thuidium tamariscinum* (Figure 166) create capillary spaces much like a tomentum. Other mosses such as **Mniaceae** utilize **paraphyses** (Figure 167) among the archegonia and antheridia to conserve water, using the same capillary principle.



Figure 161. *Trichocolea tomentella* wet, a leafy liverwort with finely divided leaves and paraphyllia. Note the numerous capillary spaces afforded by the filamentous divided leaves. Photo by Jan-Peter Frahm, with permission.

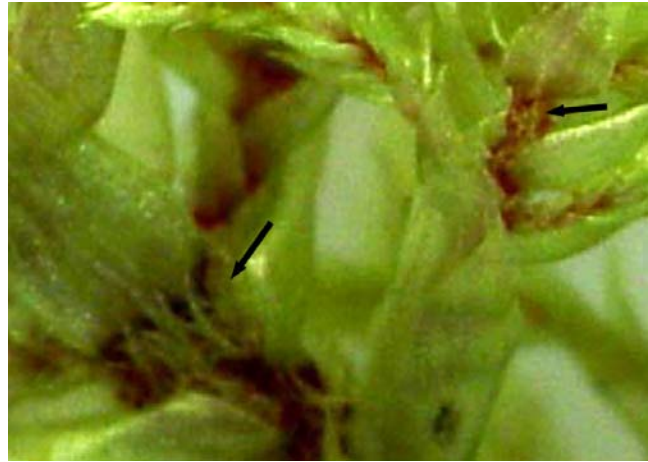


Figure 164. *Hylocomium splendens* showing paraphyllia on stem. Photo by Rosalina Gabriel, with permission.

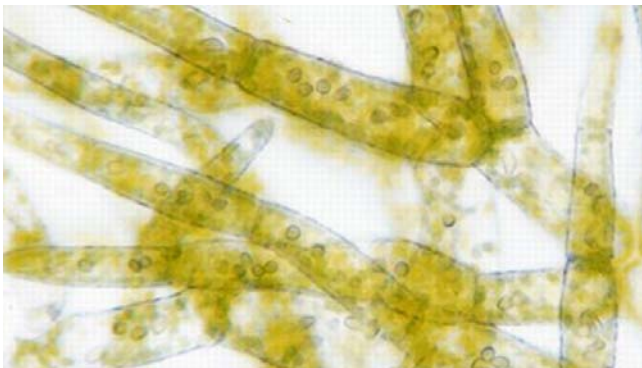


Figure 162. *Trichocolea tomentella* cells of divided leaves. Photo by Malcolm Storey from Discover Life <www.discoverlife.org>, through Creative Commons.



Figure 165. *Hylocomium splendens* paraphyllia. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

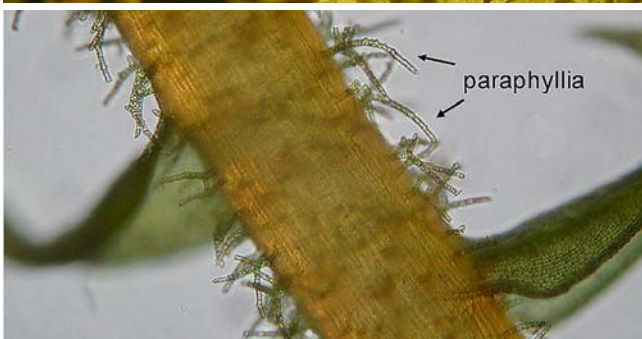


Figure 163. *Thuidium recognitum* showing branched paraphyllia on the stem and branches. Photos by Michael L  th (upper) and Paul Davison (lower), with permission.



Figure 166. *Thuidium tamariscinum*, showing paraphyllia on stem (arrows). Photo by Brian Eversham, with permission.

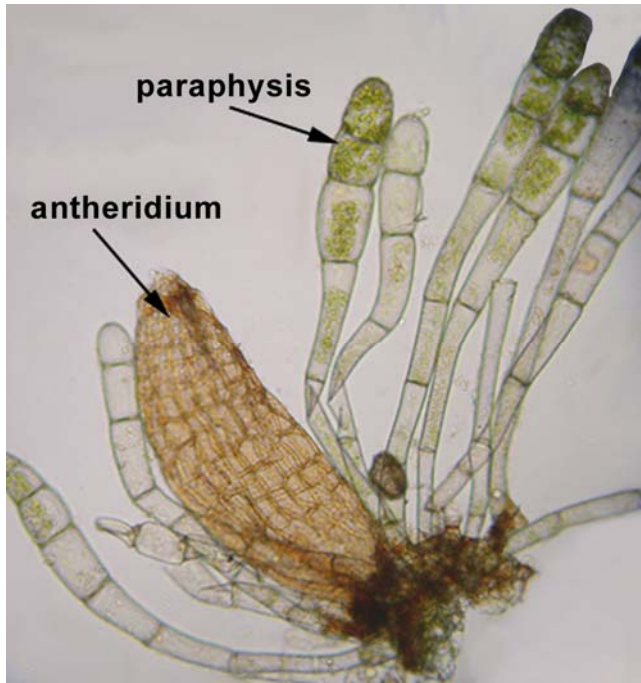


Figure 167. *Plagiomnium insigne* antheridia and paraphyses that create capillary spaces. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Cellular Structure

Sun-exposed rock surfaces and similar habitats require the greatest degree of desiccation tolerance. One such desiccation-tolerant species is *Andreaea rothii* (Figure 168-Figure 170), a small, blackish cushion moss that grows on hard, acidic mountain rocks. It is able to recover and photosynthesize after 12 months of desiccation at 32% relative humidity at 20°C (Proctor & Tuba 2002). Similar tolerance is exhibited by the small cushions of *Grimmia pulvinata* (Figure 171-Figure 172) on dry wall tops, *Racomitrium lanuginosum* (Figure 93; Figure 173-Figure 175) of mountain and subarctic fellfields (Figure 173), and *Syntrichia ruralis* (Figure 176-Figure 177) of dry sand dunes and steppe grasslands. A common characteristic among these and other tolerant mosses is their small or narrow cells with dense contents and small vacuoles. Their leaf surfaces are readily wetted and the leaves quickly expand within minutes of rewetting.



Figure 168. *Andreaea rothii* in cushions on rocks, a habitat that frequently presents desiccating conditions. Photo by Claire Halpin, with permission.



Figure 169. *Andreaea rothii* showing tightness of the stems in the cushion. Photo by Štěpán Koval, with permission.

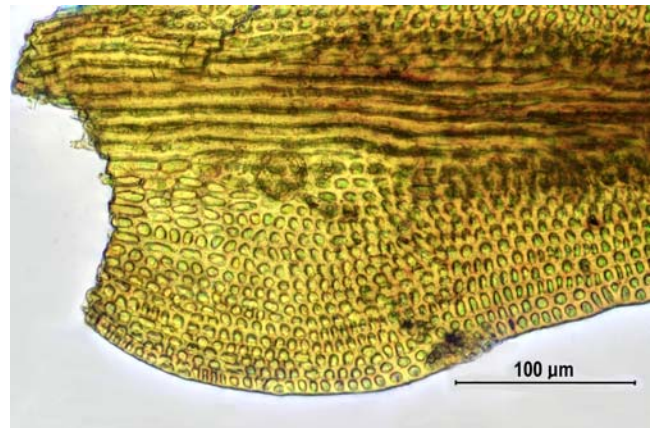


Figure 170. *Andreaea rothii* leaf cells showing small size and isodiametric shape. Photo by Claire Halpin, with permission.



Figure 171. *Grimmia pulvinata* with capsules, forming a cushion on the top of a wall. Photo by Michael Becker, through Creative Commons.

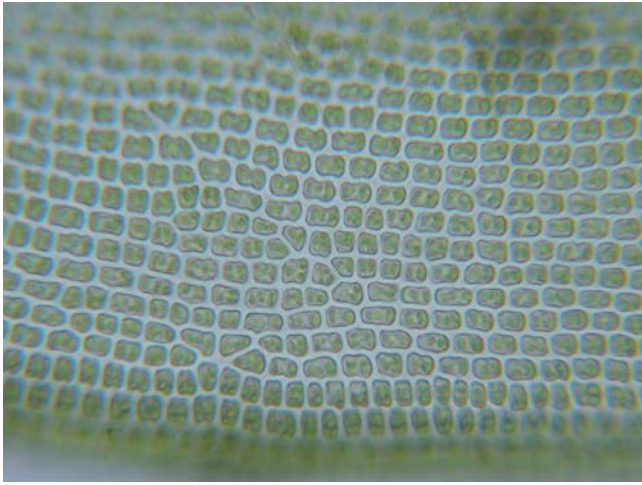


Figure 172. *Grimmia pulvinata* showing small, isodiametric leaf cells. Photo by Claire Halpin, with permission.

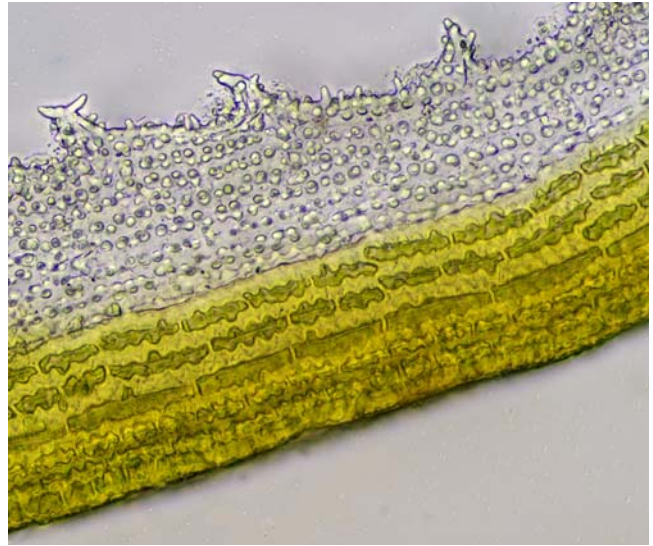


Figure 175. *Racomitrium lanuginosum* leaf cells showing wavy margins, thick walls, and cell elongation. Photo by Claire Halpin, with permission.



Figure 173. *Racomitrium lanuginosum* on rocky field. Photo by Brucedc, through Creative Commons.



Figure 176. *Syntrichia ruralis* in their usually dry habitat of a rock crevice. Photo by Darkone, through Creative Commons.



Figure 174. *Racomitrium lanuginosum* cushion on rock. Photo by Hugues Tinguy, with permission.



Figure 177. *Syntrichia ruralis* isodiametric leaf cells with papillae (creating darker spots on the cells). Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

Liverworts in general are less desiccation tolerant than mosses, but some are able to survive frequently dry habitats (Clausen 1952). The leafy liverwort *Porella platyphylla* (Figure 178-Figure 182) grows in dry but shaded habitats on dry calcareous rock or base-rich bark. It recovers completely after 60 days of desiccation at 50% relative humidity (Hinshiri & Proctor 1971). Other leafy liverworts such as *Frullania dilatata* (Figure 183-Figure 185) and *Gymnomitrium* spp. (Figure 186-Figure 187) grow on sun-exposed rocks. But the leafy liverwort *Porella platyphylla* has moderate cell size and large vacuoles, contrasting with what seems to be typical in DT mosses (Marshall *et al.* 1998).



Figure 178. *Porella platyphylla* in crevice. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.



Figure 179. *Porella platyphylla* on vertical rock, an infrequently wet habitat. Photo by Joanne Denyer, with permission.



Figure 180. *Porella platyphylla* showing rolled leaf edges of a drying plant. Photo by Hermann Schachner, through Creative Commons.



Figure 181. *Porella platyphylla* ventral view showing lobules that hold water droplets and keep the photosynthetic tissue hydrated. Photo by Hermann Schachner, through Creative Commons.

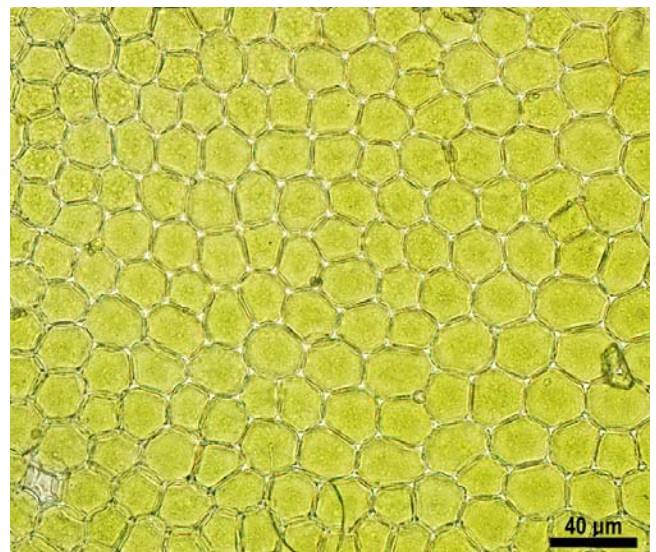


Figure 182. *Porella platyphylla* leaf cells showing larger but still isodiametric size. Note trigones at the corners, places where capillary water can be held. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.



Figure 183. *Frullania dilatata* on tree trunk, a frequently dry habitat. Photo by Bernd Haynold, through Creative Commons.



Figure 184. *Frullania dilatata* showing the closely overlapping leaves that trap capillary water in this xerophyte. Photo by Bernd Haynold, through Creative Commons.

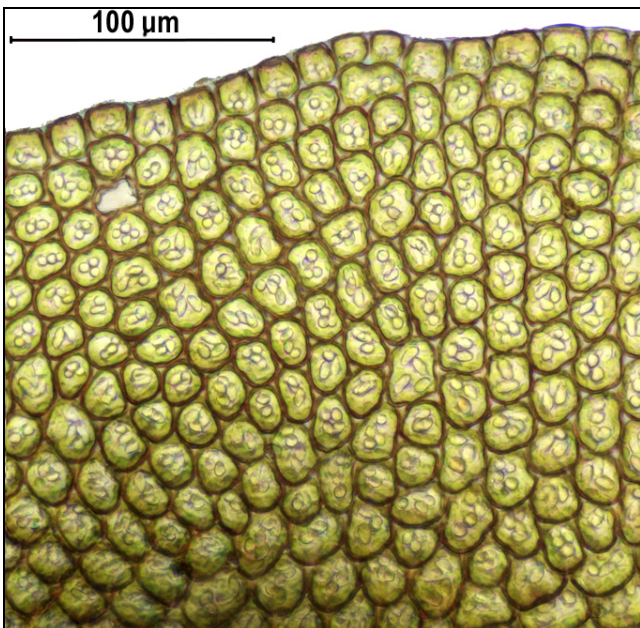


Figure 185. *Frullania dilatata*, a xerophytic liverwort, showing isodiametric leaf cells with oil bodies and **trigones**. Photo by Claire Halpin, with permission.



Figure 186. *Gymnomitrium* sp. on tree trunk, a xeric habitat. Photo by Claire Halpin, with permission.

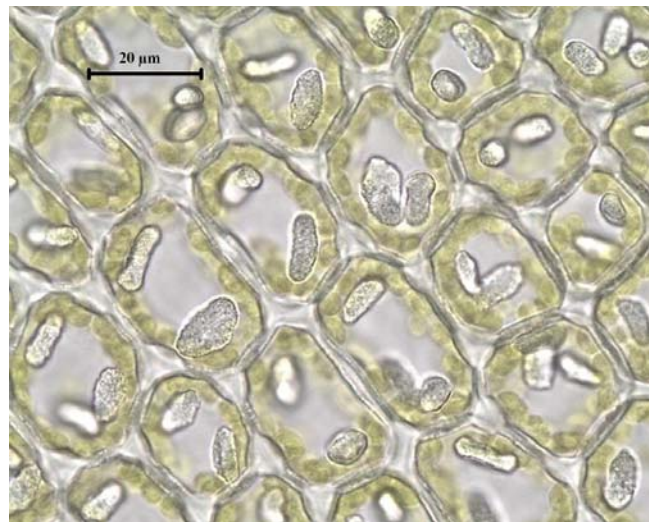


Figure 187. *Gymnomitrium concinnatum* leaf cells with oil bodies. The cell walls have adequate spaces and **trigones** for water storage. Photo by Hugues Tinguy, with permission.

Although 50% relative humidity seems to be the level commonly used for determining desiccation tolerance, some structures, and possibly some species, can tolerate even lower levels.

Fungal Partners

Fungal partners associated with roots have been termed **mycorrhizae**, and the same term is applied to fungi that serve as fungal partners to bryophytes. The existence

of these relationships has been mostly overlooked until recently, although we have recognized for quite some time that many bryophytes had fungi associated with them. Hence, our knowledge of their importance to the bryophyte is meager. It is likely that they serve a similar role to that in tree roots in scavenging a wide area for water, minerals, and perhaps organic nutrients. But I would also consider it likely that at least some of them play a role similar to that in the **hemiparasites** such as Indian pipe (*Monotropa uniflora*). That is, for those bryophytes living in dense shade, they could find a third partner that has more access to light – a leafy tracheophyte – that provides photosynthate that can be transferred from the tracheophyte, by way of the fungus, to the bryophyte. I am afraid I can see no substance that is likely to be produced by the bryophyte that is useful to the tracheophyte, making the bryophyte also a hemiparasite. Nevertheless, such a 3-way linkage remains to be demonstrated.

In an attempt to unravel the evolution of the fungal symbioses of bryophytes, Pressel *et al.* (2010) examined the ancient basal bryophytes *Treubia* (Figure 147-Figure 148) and *Haplomitrium* (Figure 153-Figure 154). In these liverworts they found intracellular fungal lumps, inter cellular hyphae, and thick-walled spores. Unlike the well known glomerophytes found as symbionts in thallose liverworts and lower tracheophytes, these were more ancient fungi (Figure 188-Figure 189).

In leafy liverwort families sister to the **Schistochilaceae**, the Ascomycete fungus *Rhizoscyphus ericae* occurs in the rhizoids (Pressel *et al.* 2010). This fungus has a wide range of hosts, including flowering plants in the Ericales (includes blueberries and heath plants) and an Antarctic species of the leafy liverwort *Cephaloziella* (Figure 190). Figure 191 shows a member of the **Ascomycota** inhabiting the leafy liverwort *Mylia anomala*. In the **Basidiomycota**, the genus *Sebacina* (Figure 192) is associated with leafy liverworts, but this fungus is host specific. Neither of these liverwort fungi seems to digest its host, whereas the **Basidiomycota** in the thallose liverworts of **Aneuraceae** have regular colonization and digestion cycles. The hornworts also demonstrate mycorrhizal relationships with fungi, but thus far there is no evidence that such a mycorrhizal relationship exists in mosses. It might be worth looking for it in **Polytrichaceae** and **Sphagnaceae**.

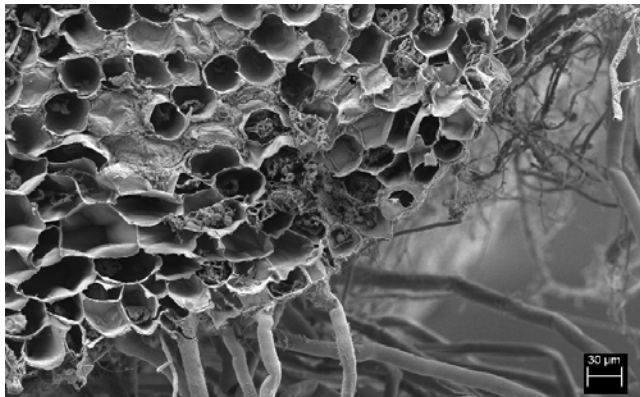


Figure 188. SEM of *Treubia* cross section showing the number of cells with resident fungi. Photo courtesy of Jeff Duckett and Silvia Pressel.

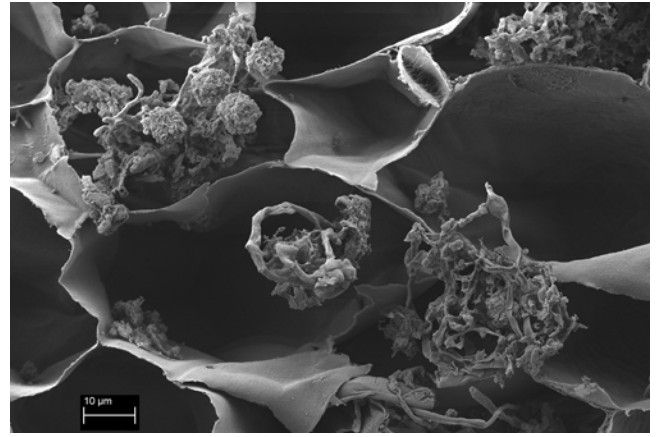


Figure 189. SEM of *Treubia* cross section with fungi in cells. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 190. *Cephaloziella elachista*; an Antarctic species in this genus serves as one of the hosts of the fungus *Rhizoscyphus ericae*. Photo from Earth.com, with permission.

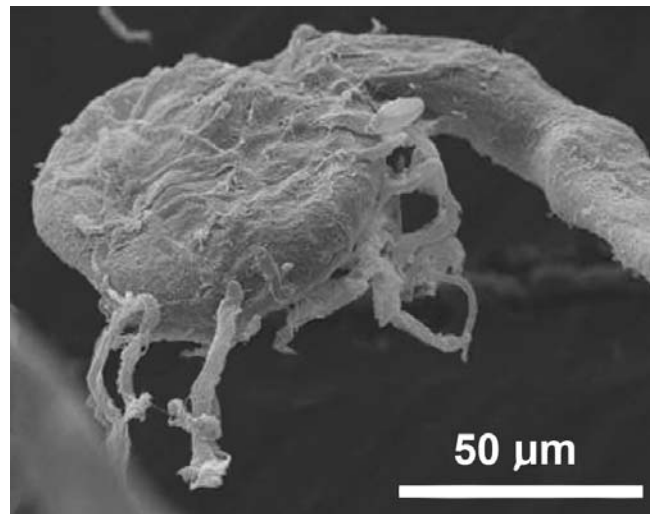


Figure 191. Swollen rhizoid tip with **Ascomycota** in leafy liverwort *Mylia anomala*. Photo courtesy of Silvia Pressel and Jeff Duckett.



Figure 192. *Sebacina incrustans*, member of a genus of basidiomycete fungi that is associated with leafy liverworts. Photo by James K. Lindsey, with permission.

We are at a very early stage in our understanding of mycorrhizae in bryophytes. In tracheophytes these associations permit the host plant to gain water and nutrients from a much wider area by accepting these from a fungus that has grown over a wide area, as much as 15 hectares, weighing 10,000 kg (Smith *et al.* 1992). Their role in bryophytes is less clear, but the ancient origin of this association suggests that by now it could be quite sophisticated and beneficial.

Protonema

The protonema stage of mosses is a delicate threadlike stage in which every cell is surrounded by air with the potential for creating desiccation. But is it really so delicate?

In experiments, Pressel and Duckett (2010) demonstrated that protonemata can survive slow drying but not fast drying. This suggests that during slow drying there is time to manufacture something that protects the cells from the effects of desiccation. Indeed, pre-treatment with abscisic acid permits the protonemata to survive fast drying as well. During slow dehydration the cells undergo profound changes, including vacuolar fragmentation, reorganization of endomembrane domains, changes in cell wall thickness, changes in plastid morphology, changes in mitochondria morphology, and a controlled dismantling of the cytoskeleton. During fast drying, these events do not occur or are incomplete. The abscisic acid permits the rapidly drying cells to partially mimic their behavior during slow drying, permitting them to survive.

Leafy Liverwort Gemmae

Liverworts have leaf gemmae that are usually small structures along the leaf margins. Germination on the leaf is not desirable, so it is no surprise that they have a means of preventing it. This prevention may relate to their hydrophobic surface (Duckett & Ligrone 1995). In *Odontoschisma denudatum* (Figure 193), the wall

chemistry changes during maturation, with an increase in electron-opacity.



Figure 193. *Odontoschisma denudatum* with gemmae on apical leaves (yellowish). Photo by Jan-Peter Frahm, with permission.

Sporophyte

When we examine mature sporophytes with their capsules and spores, we don't give a second thought to the dangers of drying out. But we are misled by this resistant mature sporophyte. Rather, based on studies of field-collected gametophytes of *Microbryum starckeanum* (Figure 194) and *Tortula inermis* (Figure 195) (both species of dry habitats) with immature sporophytes, McLetchie and coworkers found that the sporophyte generation is more sensitive to desiccation and thermal stress than is the leafy gametophyte (McLetchie & Stark 2006; Stark *et al.* 2007). This may of course differ in species with a different phenology in different environmental conditions, but it bears questioning our perception of the importance of desiccation during sporophyte development. This need for desiccation tolerance of the sporophyte may be especially important for species like those of *Polytrichum* (Figure 80) that require as much as 20 months for sporophyte development and span an entire year of weather conditions (Arnell 1905; Longton 1972).



Figure 194. *Microbryum starckeanum*, a species in which the sporophyte is more sensitive to desiccation than is the gametophyte. Photo from BBS website, with permission.



Figure 195. *Tortula inermis* dry leaves and immature capsules, a species in which the young capsules are more sensitive to desiccation than are the gametophytes. Photo by Michael Lüth, with permission.

It appears that the embryonic sporophytes are the stage most susceptible to desiccation stress (Stark 2002, 2005). Nevertheless, some desert mosses have embryonic sporophytes that can tolerate desiccation for long periods, most likely benefitting from **desiccation hardening** (development of resistance to desiccation) (Stark *et al.* 2014). Several examples exist from non-desert mosses, although the tie to desiccation is unclear. In the boreal forest moss *Hylocomium splendens* (Figure 164-Figure 165) (Callaghan *et al.* 1978) and desert moss *Syntrichia caninervis* (Figure 25) (Stark *et al.* 2000), the number of aborted sporophytes outnumbers that of mature sporophytes. Similarly, in the boreal forest moss *Pleurozium schreberi* (Figure 196) 38% of the sporophytes aborted (Longton & Greene 1969).



Figure 196. *Pleurozium schreberi*, a boreal forest moss with a high percent of abortions. Photo by Michael Lüth, with permission.

Calyptra Protection

If we imagine the hairy calyptrae of such mosses as *Polytrichum* (Figure 197), we must ask ourselves how the calyptra avoids absorbing water and holding it against the capsule, creating water logging, or contrarily, draws water from the capsule due to capillary spaces created by the hairs. In other words, why doesn't it behave like a bath towel? To answer this question, we will look at calyptra development, timing, structure, and its ultimate role.



Figure 197. Hairy calyptra on capsule of *Polytrichum juniperinum*. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

The **calyptra** develops from the archegonium, which expands as the embryo develops. In some cases, the calyptra falls early in capsule expansion, but in others, such as *Polytrichum* (Figure 197), it may remain until the spores are ready for dispersal. One might then question the role of the calyptra in protecting the embryo through to development of spores. Budke *et al.* (2012) demonstrated that the maternal calyptra provides protection of early post-embryonic sporophytes against desiccation, but that later development of the capsule may incur cuticle development that protects as the capsule emerges from the calyptra. This demonstrates that the calyptra cannot be considered a vestigial structure, but rather that it is essential in preventing desiccation. Haig (2013) agrees that the presence of the calyptra delays the onset of transpiration. Hence, it is prudent to examine the calyptra characters that may provide this desiccation protection.

Cuticle: In *Funaria hygrometrica* there is a 4-layered cuticle on the calyptra for its duration (Figure 198) (Budke *et al.* 2012). Budke *et al.* (2011, 2012, 2013) demonstrated that the cuticle on this calyptra conferred significant protection to the developing sporophyte.



Figure 198. *Funaria hygrometrica* showing calyptra that has a 4-layered cuticle. Photo by Fred Essig, with permission.

Hairs: There appear to be two kinds of hairs on calyptrae, "true" hairs (Figure 197) and undeveloped archegonia. In *Fontinalis*, the calyptral hairs develop from aborted archegonia whose eggs (Figure 199) were presumably not fertilized (Glime unpubl.). This results in a small number of "hairs" near the base of the calyptra.



Figure 199. *Fontinalis squamosa* calyptra with young archegonium SEM. Photo by Janice Glime.

The hairs on the calyptrae in taxa such as *Polytrichum* (Figure 197) and *Orthotrichum* (Figure 200) could

function to prevent desiccation during early development or to deter herbivory both early and late in development, but earlier in development they could also serve important functions for the archegonium, helping to conserve moisture to protect the egg or other uses we haven't considered. I haven't followed the development in taxa other than *Fontinalis* (Figure 199), but the hairs seem too large and numerous in most taxa to be just a lingering of the archegonia or associated paraphyses. If they continue to elongate as the calyptra develops, then there may be some advantage that would favor that prolonged use of energy for their development.



Figure 200. *Orthotrichum stramineum* with calyptra showing long hairs. Photo by Des Callaghan, with permission.

Cuticle

It is likely that many bryophyte sporophytes have a **cuticle**. For example, the large, waxy-looking capsule of *Buxbaumia viridis* (Figure 201), and most likely the other members of the genus, has a layered cuticle (Koch *et al.* 2009). And in *B. viridis* this cuticle is waxy with massive wax layers having small embedded and superimposed platelets and granules on top of this complex. Although until recently the only documented sporophyte cuticles had been those of the **Polytrichales**, this complex of cuticle components is common in various groups of tracheophytes.

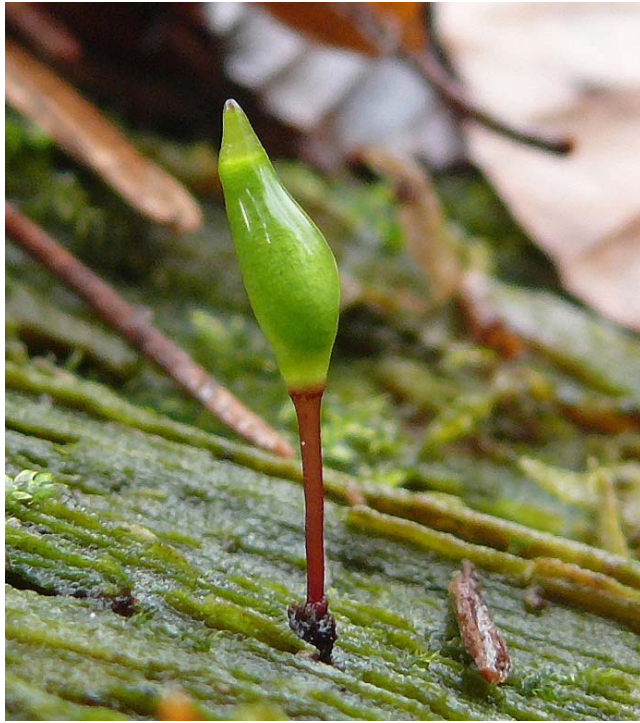


Figure 201. *Buxbaumia viridis* capsule showing shiny, waxy cuticle. Photo by Bernd Haynold, through Wikimedia Commons.

Pressel and Duckett (2011), suspecting that capsule waxes were more common than those of these two groups, examined a wider array of taxa, particularly those with shiny surfaces. They demonstrated that *Bartramia* (Figure 202), *Plagiopus* (Figure 203-Figure 204), and *Mnium* (Figure 205-Figure 207) invested as much in surface waxes of the capsule as did *Polytrichum* (Figure 197). They interpreted these waxes as having a role in preventing accumulated water from depressing gas exchange in the capsules, that is, prevention of water logging.



Figure 202. *Bartramia pomiformis* capsule showing waxy surface. Photo by Walter Obermayer, with permission.



Figure 203. *Plagiopus oederiana* with capsules showing waxy surface. Photo by Michael Lüth, with permission.



Figure 204. *Plagiopus oederiana* waxy capsule with calyptra at near maturity. In this case, the calyptra does little to protect the nearly mature capsule, most likely making the cuticle more important. Photo by Janice Glime.



Figure 205. *Mnium* sp. with water on young capsules, illustrating the potential for water logging. Photo by Alan S. Heilman, through Creative Commons.

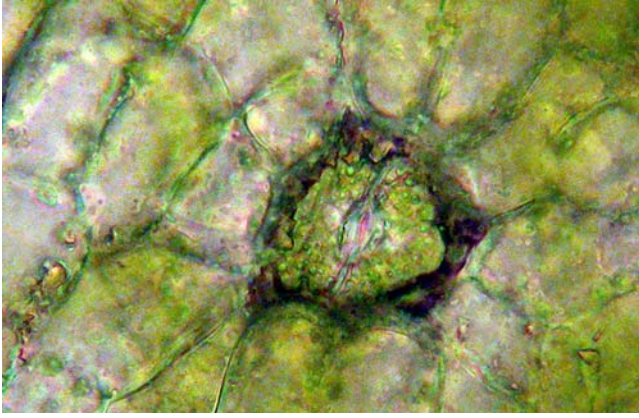


Figure 206. *Orthotrichum pusillum* immersed stoma on calyptra. Photo by Bob Klips, with permission.



Figure 207. *Mnium hornum* with capsule showing waxy surface. Photo by J. C. Schou, with permission.

In the moss genus *Orthotrichum* (Figure 200) many species have immersed stomata (Figure 206). These openings are surrounded by protruding cells that maintain an air space between the capsules and the calyptra (which remains attached and covers most of the capsule until the spores are ripe; Figure 200) (Pressel & Duckett 2011). The waxes repel the water on the capsule and prevent it from being drawn under the calyptra by capillary action. That is, a primary role for these surface waxes may be to prevent water logging in this and other species.

But this cuticle story apparently does not begin with the capsule. The young sporophyte is covered by a calyptra. And as noted earlier, in *Funaria hygrometrica* (Figure 198, Figure 208-Figure 211) this calyptra is covered by a waxy cuticle four layers thick at all stages, hence providing protection long before the developing sporophyte develops its own cuticle that ultimately arises on the sporangium (Budke *et al.* 2012). When the calyptra cuticle is removed during periods of low moisture, the sporophyte suffers significant damage, including decreased survival, increased tissue damage, incomplete sporophyte development, more peristome malformations, and decreased reproductive output (Budke *et al.* 2013). This is in contrast to the conclusion of Pressel and Duckett (2011) that the cuticles function primarily to prevent water logging. I have for my entire career as an ecologist failed to understand why ecologists get into so many arguments over two or more different explanations for the same thing, in this case the presence of stomata. There seems to me to be no evolutionary argument against multiple functions for the same thing, at the same or at different times. Just consider the many functions of our brains, or the many uses for fingernails.

Budke *et al.* (2012) examined the development of the cuticle on both the calyptra and the capsule, using *Funaria hygrometrica* (Figure 198, Figure 208-Figure 211) as a model organism. These researchers found that the sporophyte cuticle does not mature until the formation of the capsule.



Figure 208. *Funaria hygrometrica* with expanding archegonia (now calyptrae) with young sporophytes still mostly protected within the perichaetial leaves. Photo by Andrew Spink, with permission.



Figure 209. *Funaria hygrometrica* young sporophytes and calyptrae emerging from the protection of the perichaetial leaves. Photo by Michael Lüth, with permission.



Figure 210. *Funaria hygrometrica* mature capsules that have lost the calyptrae. Photo by Robert Klips, with permission.



Figure 211. *Funaria hygrometrica* mature capsule showing waxy surface. Photo by Sarah Gregg, with permission.

As among leaves, the capsule waxes vary in structure. In *Tetradontium brownianum* (Figure 212), there are fine rods around the stomata, whereas in *Pylaisia polyantha* (Figure 213) there are both rods and fine whorls (Pressel & Duckett 2011).



Figure 212. *Tetradontium brownianum*, a species with fine rods in the cuticle around the stomata of the capsules. Photo by Michael Lüth, with permission.



Figure 213. *Pylaisia polyantha* capsule, a species with both rods and fine whorls in the cuticle around the stomata. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Peristome: Peristome teeth likewise have cuticles, with differences related to habitat conditions at the time of spore discharge (Pressel & Duckett 2011). In *Polytrichales*, the spores are dispersed when raindrops pounce on the diaphragm (**epiphragm**; Figure 214) that connects the teeth (Watson 1971). For this mechanism to work, the teeth must not only remain dry, but must repel water so that it does not block the small openings between the teeth where spores must exit (Pressel & Duckett 2011).



Figure 214. Top view of *Polytrichum* epiphragm showing the 64 adherent teeth. Water splashing on the membranous epiphragm (like a child on a trampoline) disperses the spores. Photo by George Shepherd, through Creative Commons.

On the other hand, most mosses disperse their spores when it is dry. Water is taken up and lost rapidly from between the ornamentation on these peristomes (Pressel & Duckett 2011). These include all **Bryopsida** they tested: *Amblystegium* (Figure 215), *Bryum* (Figure 139), *Coscinodon* (Figure 216), *Dicranella* (Figure 217), *Didymodon* (Figure 218), *Fissidens* (Figure 219), *Funaria* (Figure 220), *Grimmia* (Figure 115), *Hypnum* (Figure 221), *Mnium* (Figure 205-Figure 207), *Rhynchostegium* (Figure 222), *Schistidium* (Figure 109), *Syntrichia* (Figure 25), *Tortula* (Figure 1, Figure 195). These water gains and losses permit rapid closure in wet conditions and accelerate opening under dry conditions.



Figure 215. *Amblystegium serpens* capsules. Photo by Michael Lüth, with permission.

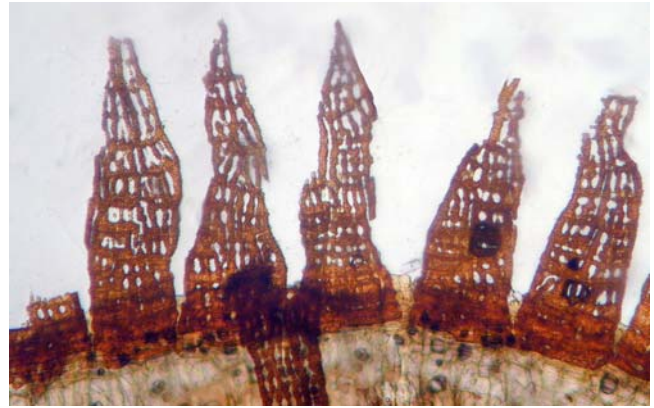


Figure 216. *Coscinodon cribrus* peristome. Photo by Michael Lüth, with permission.



Figure 217. *Dicranella varia* capsule showing peristome. Photo by Kristian Peters, through Wikimedia Commons.



Figure 218. *Didymodon rigidulus* with capsules. Photo by Hermann Schachner, through Creative Commons.

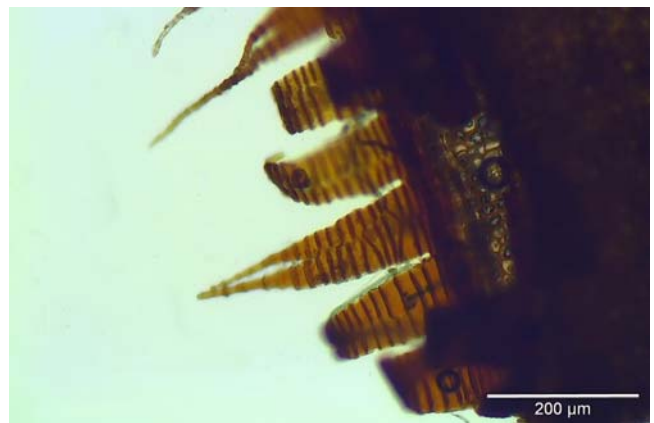


Figure 219. *Fissidens adianthoides* peristome. Photo by Kristian Peters, with permission.

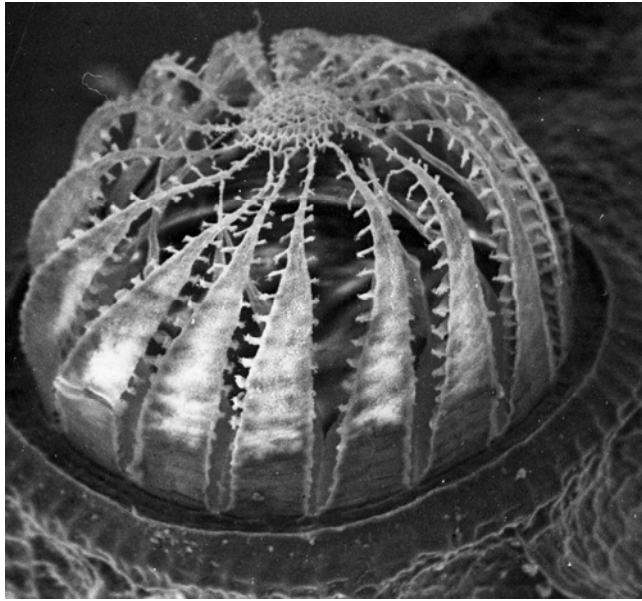


Figure 220. Peristome teeth of *Funaria hygrometrica*, a species in which teeth move in response to drying conditions and spores escape from the spaces between the teeth. Photo by George Shepherd, through Creative Commons.

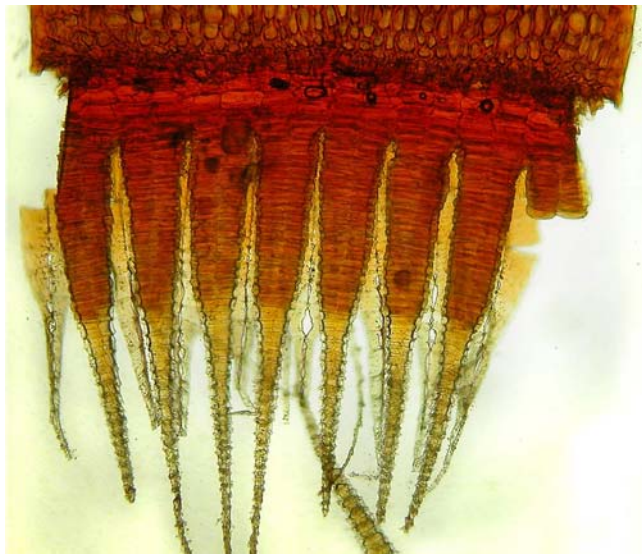


Figure 221. *Hypnum cupressiforme* peristome. Photo by Walter Obermayer, with permission.



Figure 222. *Rhynchoszegium confertum* with capsules. Photo by Michael Lüth, with permission.

But what happens in capsules with no teeth or only rudimentary peristomes? As an example, in *Weissia* (Figure 223) water is prevented from entering the capsule by a highly water-repellent capsule rim (Figure 223). If water entered the capsule, it could cause premature germination or interfere with ultimate dispersal.



Figure 223. *Weissia fallax* capsule showing rudimentary peristome. Note the waxy appearance of the reddish annulus around the teeth. Photo by Michael Lüth, with permission.

Guard Cells and Stomata

Capsules of many (most?) mosses have guard cells and stomata. The guard cells usually resemble those of tracheophytes, having a doughnut shape, and surrounding the **stoma** (opening; Figure 206, Figure 224). These are mostly located at the base of the capsule. In addition to the cuticle, we might expect the **guard cells** to play a role in water relations of the capsule. After all, the stomata and guard cells have existed through 400 million years of land plant evolution (Chater *et al.* 2011).

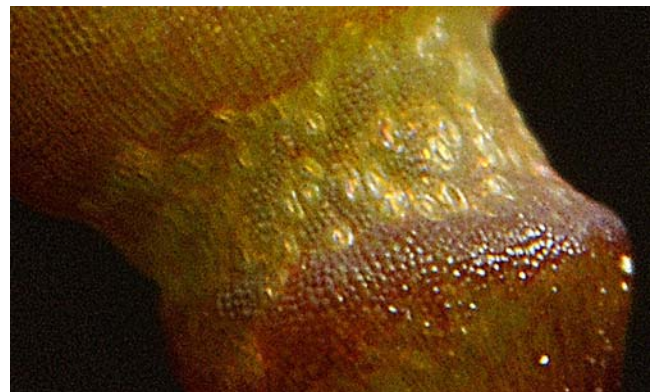


Figure 224. *Polytrichum* stomata on capsule base. Photo by George J. Shepherd, through Creative Commons.

Like the cuticle, the role of the pores and stomata has been overlooked in bryophytes. Although we have known about the stomata in moss capsules for a long time, and used them as taxonomic characters in genera such as *Orthotrichum*, we have largely ignored their function, failing even to ask what it might be.

When thinking about adaptations to drought, we usually think of the survival of the gametophyte. What danger could there be to a dry capsule full of spores, right? But before that capsule is full of spores, it is a photosynthetic body in need of water. Perhaps the young seta with no capsule has little problem, but once the capsule starts to differentiate, water needs most likely increase dramatically. And once meiosis begins, water needs are critical. An interruption during meiosis could lead to a variety of anomalies, many of which could cause spore death.

Paton and Pearce (1957) reviewed the early literature on stomata in bryophytes, pointing out that in *Sphagnum* they do not mature. In fact, the capsule pores of *Sphagnum* are considered **pseudostomata** (Figure 225-Figure 227). Their function seems to be limited, facilitating capsule dehydration, shape change, and dehiscence (Duckett *et al.* 2009; Merced 2015). This is not surprising, because in *Sphagnum*, the seta is only a few cells high (Figure 228). Instead, the capsule is elevated on a **pseudopodium** (Figure 228-Figure 229) that is developed from the gametophyte. This pseudopodium does not extend until the capsule is mature. Hence, the role of the pseudostomata to create a transpiration stream for nutrient transport would seem futile. Rather, Duckett and coworkers (2009) provide evidence that the pseudostomata remain open when the capsule is mature, causing the capsule to dry and shrink, forcing the spores out.

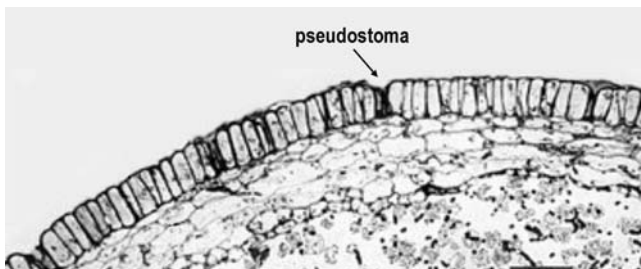


Figure 225. *Sphagnum* pseudostomata in capsule. Modified from photo by Amelia Merced, with permission.

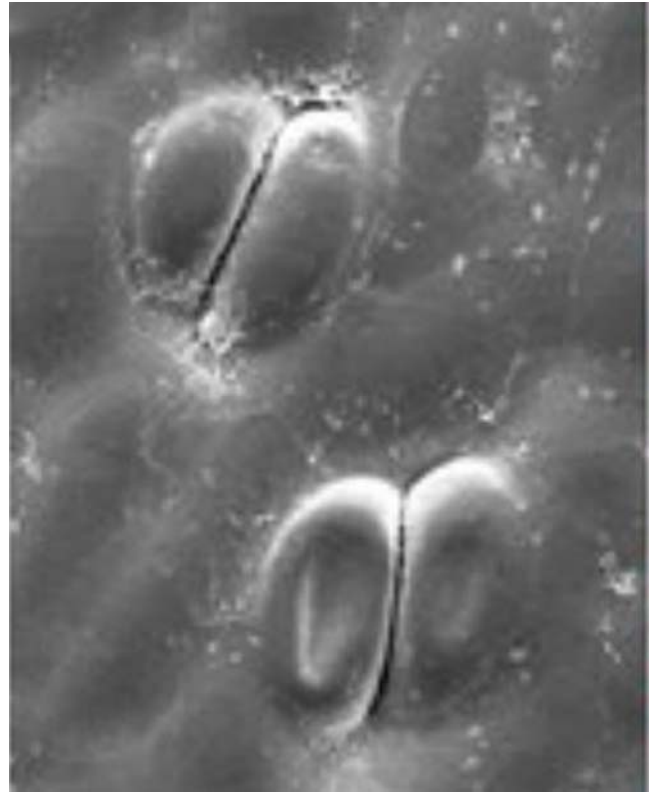


Figure 226. *Sphagnum* pseudostomata (SEM) in capsule. Photo by Amelia Merced, with permission.

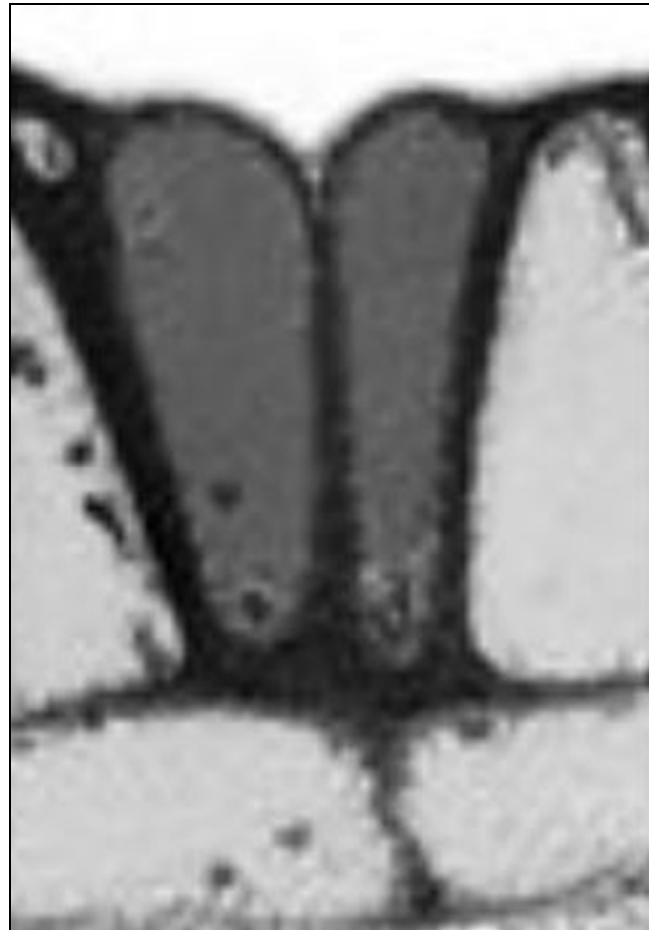


Figure 227. *Sphagnum* pseudostomata in capsule section. Photo by Amelia Merced, with permission.

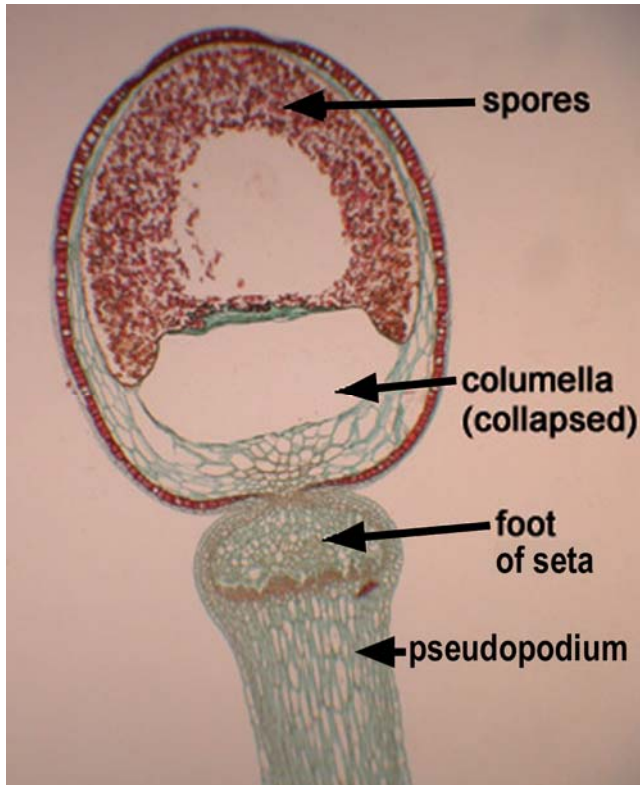


Figure 228. *Sphagnum* sporangium on pseudopodium. Photo from Botany website, UBC, with permission.



Figure 229. *Sphagnum* with pseudopodium and capsule. Photo from Botany Website, UBC, with permission.

Stomata also are absent in the liverworts (but can have thallus pores), present in at least some hornworts (Figure 238-Figure 241), and absent in the moss order **Andreaeales** (Figure 230-Figure 231) (Paton & Pearce 1957). As in the tracheophytes, the number of guard cells associated with a stoma is usually two (Figure 224-**Error! Reference source not found.**). Known exceptions (single circular guard cells) occur in **Funariaceae** (Figure 198, Figure 208-Figure 211, Figure 232) and *Buxbaumia aphylla* (Figure 233). Larger numbers of guard cells (3-4) occur but do not seem to be consistent in any single taxon and are thus considered an anomaly.



Figure 230. *Andreaea rothii* with capsules that have no stomata. Photo by Jan-Peter Frahm, with permission.

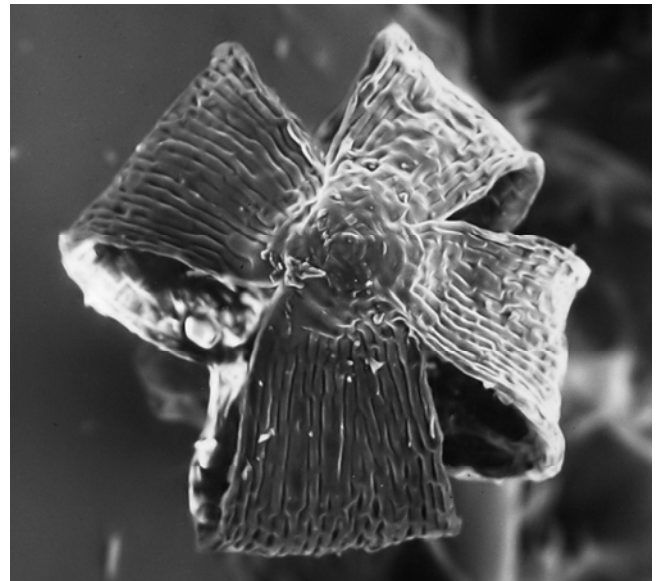


Figure 231. *Andreaea* capsule SEM, a capsule that lacks stomata. Photo by George Shepherd, through Creative Commons.

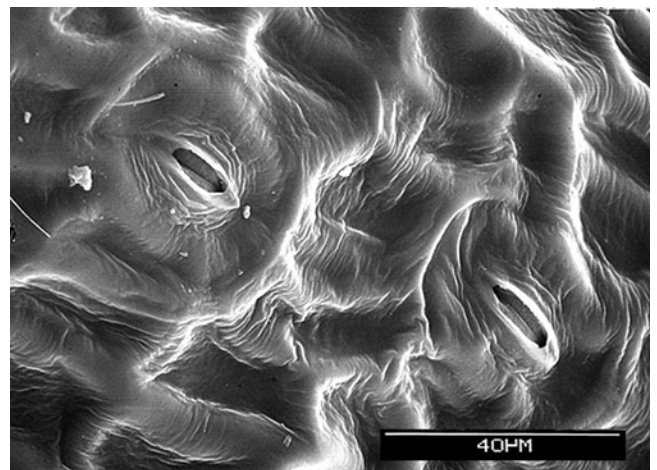


Figure 232. *Funaria hygrometrica* stomata showing circular guard cells. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 233. *Buxbaumia aphylla* capsules, a species with single circular guard cells. Photo by Štěpán Koval, with permission.

The walls of the guard cells are strongly cuticularized (Paton & Pearce 1957). The number of stomata in capsules that have been examined varies from 4 to over 200. Species with a long seta generally have more stomata than species with a short seta or immersed capsules. This supports the hypothesis that they are needed to provide an adequate transpiration stream to transport nutrients from the leafy gametophyte to the sporophyte capsule (Haig 2013), but both are adaptations that would support wind dispersal.

Guard cells are usually located at the base of the capsule. In reality, they tend to be located below the area covered by the calyptra, where gas exchange and water loss are possible. This is consistent with a role to permit water loss, but could they also serve in gas exchange? It appeared that the capsule guard cells did not respond to changes in humidity (Copeland 1902). Rather, they are only able to close when the sporophyte is dehydrated or reopen when it is remoistened. This is consistent with their potential role in bringing nutrients upward.

In the moss *Physcomitrella patens* (Figure 234-Figure 236), the stomata of the sporophytes do indeed respond to environmental signals with the hormone abscisic acid (ABA) serving as a signalling component. In fact, the genes controlling ABA in *P. patens* can be moved to mutant *Arabidopsis thaliana* (flowering plant) that has lost its ABA-regulatory gene and cause stomata in that plant to behave normally. When *P. patens* mutants lack the ABA regulatory gene, the response to ABA is greatly reduced.

But wait! While ABA may affect guard cell closure in *Physcomitrella patens* (Figure 234-Figure 236), it appears that the guard cells in mosses have a somewhat different mechanism to function. First of all, there seems to be no potassium-regulating mechanism (Duckett *et al.* 2010a). Instead, their primary role seems to be to permit water to escape when the capsule is mature (Boudier 1988; Beerling & Franks 2009; Duckett *et al.* 2009, 2010b). This loss of water causes the capsule to become distorted enough to force the rather stiff circular cap (**operculum**) to pop off, exposing the spores (Figure 237).



Figure 234. *Physcomitrella patens* with sporophyte. Photo by Ralf Reski Lab through Wikipedia Commons.

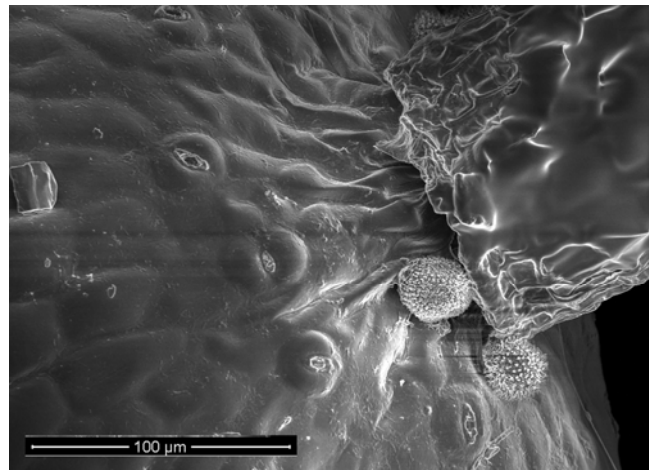


Figure 235. *Physcomitrella patens* capsule stomata SEM. Photo courtesy of Jeff Duckett and Silvia Pressel.

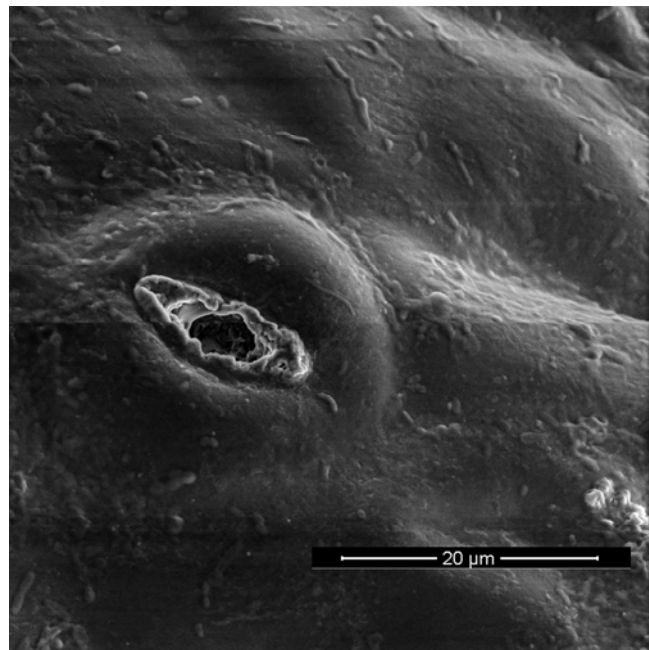


Figure 236. SEM of *Physcomitrella patens* stoma. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 237. *Physcomitrella patens* with open capsules. Photo by Hermann Schachner, through Creative Commons.

It appears that the stomata endow the capsule with multiple advantages. Loss of water during development could be important to create a transpiration stream that moves nutrients upward from the gametophyte to the capsule of the sporophyte, especially in mosses (Haig 2013). If this interpretation is correct, the water loss is essential to maintain continuous movement of water and associated nutrients upward. In fact, Haig interprets the elevation of the capsule on an elongated seta to be an adaptation that increases the movement of water by placing the capsule into the zone of turbulent air above the quiet boundary layer. The placement of the stomata at the base of the capsule gives them exposure while the calyptra reduces water loss from the part of the capsule where spores are developing.

Ziegler (1987) pointed out that in some mosses the sporophyte guard cells have thick walls and do not open and close. This type of guard cell occurs in species that have reduced photosynthetic tissue in the capsule and have been considered evolutionarily reduced. Bryophyte guard cells also differ from those of tracheophytes in that they are larger than the surrounding cells, whereas in tracheophytes they are smaller.

Paton and Pearce (1957) found that the stomata become functionless at a relatively early stage in capsule development, suggesting that this loss in function protects the developing spores against desiccation. They were able to demonstrate this early loss of function in the hornwort *Anthoceros* (Figure 238-Figure 239) and in mosses in the *Bryales*. Based on their studies on the hornwort *Phaeoceros* (Figure 240), Duckett and Ligrone (2003) say no to the function of capsule guard cells in gas exchange, at least in hornworts; they could find no response to moisture changes or to ABA in the hornwort *Phaeoceros* stomata (Figure 241). But if providing a nutrient stream through water transport is to be ruled out, we need experiments that block the stomata to compare with development in capsules that have not had them blocked.



Figure 238. *Anthoceros agrestis* with capsules. Photo by Michael Lüth, with permission.

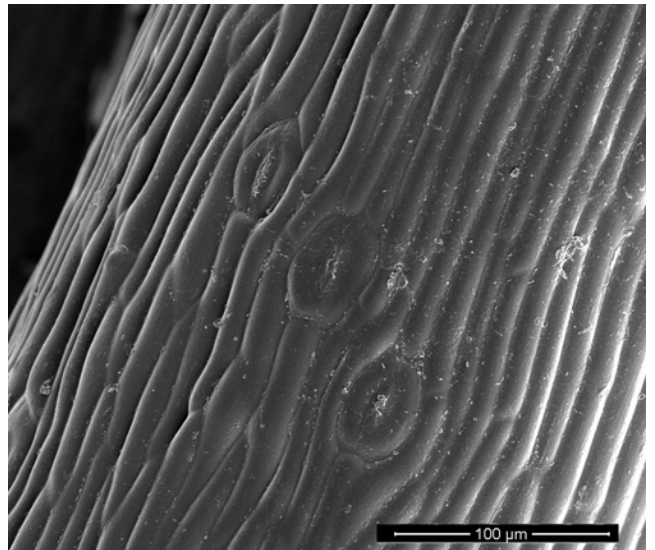


Figure 239. *Anthoceros punctatus* SEM image of sporophyte showing stomata. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 240. *Phaeoceros laevis* with sporophytes dehiscent. Photo by Bob Klips, with permission.

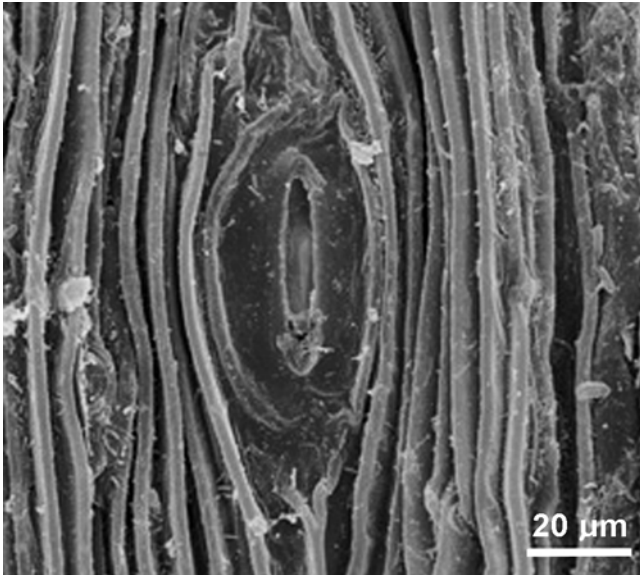


Figure 241. *Phaeoceros laevis*, open stoma flanked by desiccated and shrunken epidermal cells well above dehiscence point. Photo courtesy of Jeff Duckett, Ken P'ng, Karen Renzaglia, and Silvia Pressel.

On the other hand, in greenhouse-grown *Funaria hygrometrica* (Figure 242) the stomata (Figure 232) open on the fourth day of capsule expansion (Garner & Paolillo 1973). By the fifth day, continuing through the tenth day, they close in darkness and reopen in light. They also can be closed by the application of abscisic acid (ABA) (Garner & Paolillo 1973; Chater *et al.* 2011). Thus far we have no evidence to demonstrate the usefulness of this opening and closing. It could enhance gas exchange; it could control water loss during the critical stages of meiosis; and it could serve as a transpiration stream to bring nutrients from the gametophyte. And the function could change or disappear at maturity.



Figure 242. *Funaria hygrometrica* capsules. Photo by Li Zhang, with permission.

Indeed it appears that the function changes as the *Funaria hygrometrica* (Figure 232, Figure 242) capsule ripens. As maturity approaches, the stomatal responsiveness declines and about half the stomata remain open day and night (Garner & Paolillo 1973)! Furthermore, more stomata become exposed when the calyptra is shed (Duckett *et al.* 2009, 2010a). The stomata no longer provide a mechanism to conserve water.

Further complicating our interpretation of stomatal function during capsule development is the apparent lack of relationship between the presence of stomata and habitat. In the liverworts, stomata are totally absent. But liverworts produce mature capsules before elongation of the stalk occurs, negating the necessity for long distance translocation of nutrients and being consistent with the observations of Paton and Pearce (1957) that fewer stomata occurred on moss capsules with short or absent setae than on those with emergent, longer setae. The widespread absence of stomata in at least some species among so many moss taxa [*e.g.* *Atrichum* (Figure 243), *Pogonatum* (Figure 244), *Acaulon* (Figure 245), *Campylopus* (Figure 246), *Leucobryum* (Figure 247), *Cinclidotus* (Figure 248), *Discelium* (Figure 249), *Nanomitrium*, *Fontinalis* (Figure 250), *Tetraphis* (Figure 251), *Catoscopium* (Figure 252), *Cyclodictyon* (Figure 253), *Leucodon* (Figure 254) (Paton & Pearce 1957)] suggests they are not essential for gas exchange. Furthermore, since most of these genera have long setae, one could argue against their function in creating a transpiration stream for nutrient transport. One might also argue that the well developed vascular tissue in both gametophytes and sporophyte setae of the **Polytrichaceae** makes the presence of stomata to create a transpiration stream unnecessary for nutrient transport, yet some members of the family have stomata and guard cells. And the stomata in tracheophytes are certainly necessary to maintain function of the xylem tissue in these larger plants. But there is no rule that says they can't serve different functions at different times or in different species.



Figure 243. *Atrichum crispulum* capsules – in a genus in which at least some species lack stomata. Photo by Bob Klips, with permission.



Figure 244. *Pogonatum urnigerum* capsules, member of a genus in which some species lack stomata. Photo by Kristian Peters, with permission.



Figure 247. *Leucobryum glaucum* with mature capsules, member of a genus in which capsules often lack stomata. Photo by Janice Glime.



Figure 245. *Acaulon muticum* with capsules, a genus in which species lack stomata. Photo by Michael Lüth, with permission.



Figure 248. *Cinclidotus fontinaloides*, a species that lacks stomata. Photo by Michael Lüth, with permission.



Figure 246. *Campylopus nivalis* capsules, a species that lacks stomata. Photo by Michael Lüth, with permission.



Figure 249. *Discelium nudum* capsule, a genus in which at least some members lack stomata. Photo by Des Callaghan, with permission.



Figure 250. *Fontinalis squamosa* var *curnowii* with capsules, in a genus that lacks capsule stomata. Photo by David Holyoak, with permission.



Figure 251. *Tetraphis pellucida* capsule, in a genus that lacks stomata. Photo by Walter Obermayer, with permission.



Figure 252. *Catoscopium nigrum* with capsules, in a genus that lacks capsule stomata. Photo by Hermann Schachner, through Creative Commons.



Figure 253. *Cyclodictyon bicolor* with capsules, in a genus that lacks capsule stomata. Photo by Amelia Merced, with permission.



Figure 254. *Leucodon sciuroides* with capsules, in a genus that lacks capsule stomata. Photo by Hermann Schachner, through Creative Commons.

Merced and Renzaglia (2013) demonstrated the remarkable similarity between stomata in the highly developed *Oedipodium* (Figure 255) and the very reduced *Ephemerum* (Figure 256) capsules. The capsule structure differs, with *Oedipodium* having extensive spongy tissue along the capsule apophysis where stomata are concentrated and *Ephemerum* lacks such tissue but has minimal substomatal cavities. Although *Oedipodium* (Figure 255) has numerous long-pored stomata and *Ephemerum* has few round-pored stomata, the stomatal ultrastructure and wall thickenings of these two taxa are quite similar. Both have sporophytes with a cuticle that is thicker on the guard cells and extends on the walls surrounding the stomata. When the capsules are older, epicuticular waxes and pectin clog the pores, closing them much like the stomata of fir trees in winter. Merced and Renzaglia argue that the cuticle, water-conducting cells, and spongy tissues of *Oedipodium* all support the role of stomata in facilitating gas exchange and water transport as the sporophyte develops. They also contend that the existence of stomata exclusively on capsules may indicate a function in drying and dispersal of spores.



Figure 255. *Oedipodium griffithianum* with young capsules, a species with a well developed spongy apophysis and many stomata. Photo by Des Callaghan, with permission.



Figure 256. *Ephemerum recurvifolium* with capsules, a moss that lacks a spongy apophysis and has few stomata. Photo by Tomas Hallingback, with permission.

Hence, we have four potential functions for the stomata of capsules. These include a role in creating a transpiration stream to aid in nutrient transport, prevention of water logging that inhibits gas exchange, regulation of gas exchange, and drying that contracts the capsule and aids in spore expulsion.

Spores

Spore physiological adaptations are seldom discussed. Fan *et al.* (2023) have just published a study that compares spore germination of six peatland bryophytes under various water regimes. They found that frequent dry-wet cycling reduced spore germination more than less frequent cycling. And habitat mattered. Hummock species such as *Sphagnum capillifolium* (Figure 257) and *S. fuscum* (Figure 258) had a greater spore germination percentage after continuous dry treatment, whereas the hollow species [*S. angustifolium* (Figure 259), *S. squarrosum* (Figure 260), *S. subsecundum* (Figure 261)], had the opposite response, with highest germination following the wet treatment. Both hummock and hollow species exhibited the greatest spore viability after the dry treatment, and viability gradually decreased with the increased frequency of dry-wet cycling. Hummock species had greater %germination than did hollow species (Figure 262).



Figure 257. *Sphagnum capillifolium*, a hummock species. Photo by Bernd Haynold, through Creative Commons.



Figure 258. *Sphagnum fuscum*, a hummock species. Photo by Jutta Kapfer, with permission.



Figure 259. *Sphagnum angustifolium*, a species of hollows. Photo by Mark Rahill, with permission.



Figure 260. *Sphagnum squarrosum*, a species of hollows. Photo by Keto Gyekis, with online permission.



Figure 261. *Sphagnum subsecundum*, a species of hollows. Photo by Mark Rahill, with permission.

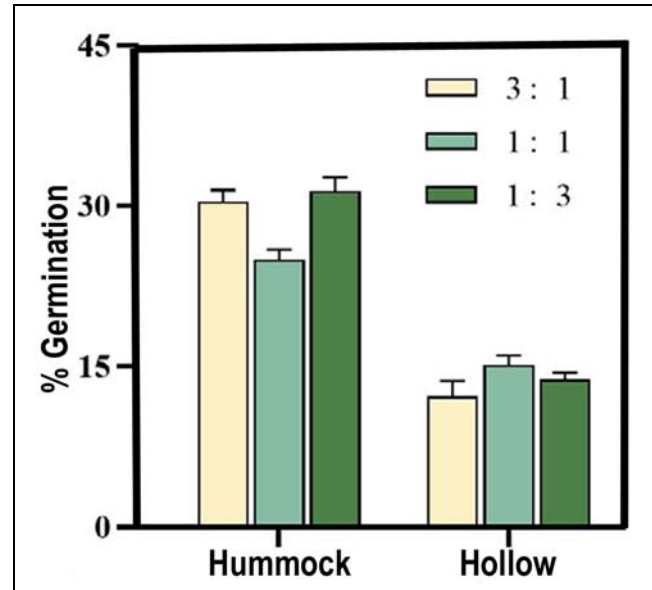


Figure 262. Mean spore viability + standard error following different wet-dry cycle regimes of six peatland *Sphagnum* species. 3:1, 1:1, and 1:3 respectively represent the ratio of days of dry and wet treatment in dry-wet cycling. $n=5$. Image modified from Fan *et al.* 2023.

Hummock vs hollow species seem to have evolved different responses to wetting. Hummocks that have sufficient oxygen and intermittent flooding are more suitable for high spore germination percentage of *Sphagnum* spores than the continuously waterlogged hollows (Sunberg & Rydin 2000). But Feng *et al.* (2017) found that in *S. fallax*, (Figure 263) more wet-dry cycling promoted higher spore germination rates. Furthermore, Feng and coworkers suggested that the strong microbial activity of the intermittently flooded environments could facilitate spore germination by breaking down the spore wall.



Figure 263. *Sphagnum fallax*, a species in which spore germination rates benefit by frequent wet-dry cycles. Photo by Hermann Schachner, through Creative Commons.

It appears that the **Gaia hypothesis** may be operating at many levels in the ecosystem, and that the bryophytes are no exception. Their behavior with such companion

species as bacteria permits the combination to act as a super organism.

Summary

Poikilohydric bryophytes depend on desiccation tolerance (**DT**), becoming dormant when desiccated. Bryophytes gain water in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. When fully hydrated, their water content is typically high, up to more than 1200% of their dry mass. When dry, they can survive months to many years. Structural adaptations of stems and whole plants such as **growth form, branch and leaf arrangements, rhizoidal tomentum, mucilage, central strand, hydroids, paraphyllia, ventral scales, cuticles, and stomata** aid in moving water, facilitating entry, or reducing loss.

In xerophytic bryophytes, leaves and stems often possess large **trigones** and **nodular intermediate thickenings** on interior walls. Some liverworts have branched **vittae** such as those of *Herbertus aduncus* that enhance water uptake and storage. **Papillae** create capillary spaces to hold water on leaf surfaces. Leaf cells are usually small and basal **alar cells** help the leaf change positions to be near the stem upon drying. Xerophytic stem cells are thick-walled. These wall adaptations consist mostly of hemicelluloses, pectins, and cellulose, substances that would facilitate apoplastic water uptake, movement, and retention.

Thallose liverworts benefit from ventral transport by **rhizoids** and **scales**. The dorsal surface is covered by a **cuticle** but gas exchange may occur through pores overlying photosynthetic chambers. The pores are ringed by cells with cuticular ridges that prevent water drops from entering but that allow water vapor to escape, as well as admitting CO₂ and expelling O₂. Midribs may help to gather and direct water both externally and internally. Some have **ballooning cells** on the epidermis. For many taxa, dormancy is a "last resort" to avoid the effects of desiccation.

Fungal partners occur in both thallose and leafy liverworts, but their role is not known. Smooth rhizoids facilitate fungal entry; pegged rhizoids transport water and the pegs prevent collapse upon drying.

In mosses and leafy liverworts, **growth form** can help in both movement and conservation of water. Clumps reduce transpiration and provide additional capillary spaces. **Mixed species** can help each other, especially if one is good at moving water and one is good at retaining it. Mosses may have a **central strand** where water moves, but this is apparently absent in all liverworts except the **Haplomitriopsida**. **Leaf cuticles** occur in both mosses and liverworts and may repel water to avoid water logging or reduce loss by transpiration. **Rhizoids** and **tomentum** help in the movement of water upward. **Mucilage** in some liverworts, especially **Haplomitriopsida**, can be of great value in holding water about the plants.

The **protonema** can usually withstand slow drying. Like the guard cells in some stomata, it is responsive to **ABA**. **ABA** may be linked to **inducible desiccation**

tolerance in the gametophores. **Constitutive desiccation tolerance** is the most common form of desiccation tolerance in bryophytes, but as the plants age they may switch to inducible desiccation tolerance. **Hardening** can occur following slow drying and may last more than a few days.

The sporophyte and calyptra both have **cuticles**, and at least in *Funaria hygrometrica*, the cuticle in the calyptra matures first, helping the calyptra to protect the young embryo. Calyptra hairs, thallus hairs, paraphyllia, and paraphyses all function to help in movement of water and reduce rate of drying. Capillary spaces provided by these can further facilitate absorbing and holding water, bathing the tissues in water and reducing water loss.

The sporophytes of most(?) mosses and hornworts have **guard cells** and **stomata** that cease to open and close at sporophyte maturity. Their function(s) are ambiguous, but they may contribute to creating a transpiration stream to move nutrients upward, regulating capsule hydration during development, and drying the capsule prior to dehiscence and dispersal.

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