

CHAPTER 7-4a

WATER RELATIONS: LEAF STRATEGIES – STRUCTURAL

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Figure 1. *Campylopus introflexus* demonstrating the ability of water to cling and collect on the thin, wiry leaves. Photo by Michael Lüth, with permission.

Much of what we know about water uptake by bryophytes has been through observation. While the observations are probably valid, broad generalizations have emerged and these have been applied to all mosses, especially by non-bryologists, and can lead to inappropriate experiments and conclusions.

Larson (1981) experimented with three species of bryophytes (and 8 lichens) using a "raining" wind tunnel environment to determine the effects of various structures on water uptake and storage. Larson found that the time required to reach saturation did not differ between lichens and mosses, varying from three minutes in the moss *Polytrichum juniperinum* (Figure 2) to over 300 minutes in the lichen *Stereocaulon saxatile*. The rate of absorption increases with the ratio of surface area to weight, making it extremely rapid in finely divided plants. Hence, comparison of leaf structure and plant form become important in considering the role of bryophytes in the water cycling of an ecosystem (Proctor *et al.* 1998; Wu *et al.* 2007).

Schofield (1981) considered leaf shape, arrangement, orientation, surface ornamentation, and detailed anatomy to

be important in influencing water movement. These adaptations are complemented by branch arrangement, stem cortical cells, rhizoid structure, and presence of paraphyllia.



Figure 2. *Polytrichum juniperinum* hydrated (left) and dry (right) showing change in leaf position to wrap around stem. Photo by Michael Lüth, with permission.

Bryophytes hold their water in three ways (Proctor *et al.* 1998): **apoplastic** water in cell-wall capillary spaces and held by matric forces; **symplastic** (internal osmotic) water; external capillary water. For many bryophytes, the external capillary water is a highly important, albeit variable, component. This external water complicates any measurements of relative water content (RWC) because it makes measurement of the bryophyte at full turgor a difficult endeavor. Proctor *et al.* found that full-turgor water ranged from 110% dry weight (dw) in *Syntrichia ruralis* (Figure 3) and *Andreaea alpina* (Figure 4) to 1400% dw or more in *Dumortiera hirsuta* (Figure 5) and *Conocephalum conicum* (Figure 6-Figure 7). Most species had an osmotic potential ($\Psi\pi$) at full turgor of -1.0 to -2.0 MPa, but thallose liverworts had values that were much less negative (-0.35 to -0.64 MPa).



Figure 3. *Syntrichia ruralis* with raindrops, a moss with low water content. Photo by Peggy Edwards, with permission.



Figure 4. *Andreaea alpina*, a moss with low water content. Photo by Andrew Hodgson, with permission.



Figure 5. *Dumortiera hirsuta*, a thallose liverwort that holds a high water content. Photo by Li Zhang, with permission.



Figure 6. *Conocephalum conicum*, a thallose liverwort that holds a high water content. Photo by Robert Klips, with permission.



Figure 7. *Conocephalum conicum* thallus section with pore. From website of the Botany Department, University of British Columbia, with permission.

Pressel *et al.* (2009) pointed out that despite the ancient history of liverworts, we know little about the physiology of their desiccation tolerance. Desiccation causes a number of cytological changes in liverworts, including fragmentation of the vacuole, rounding of the chloroplasts and mitochondria with thylakoids, and cristae becoming rearranged but remaining undamaged, all responses that are similar to those of mosses and **tracheophytes** (non-bryophyte plants; plants with lignified vascular tissue). Furthermore, chlorophyll fluorescence shows half-recovery within minutes to 2 hours, but requires 24-48 hours to reach normal, unstressed values. And like desiccation tolerance in mosses, the de- and repolymerization of the cortical microtubule cytoskeleton

are associated with de- and rehydration. But liverworts have oil bodies, and these play a role unknown in mosses, as will be seen below.

Guerra *et al.* (1992) described the adaptations of xeric mosses in the gypsiferous zones of the southeast Iberian Peninsula, listing 15 modifications for conserving water. I have included these and some of my own observations here.

Overlapping Leaves

Most bryophytes have their leaves inserted at angles on the stem. In some cases, especially leafy liverworts (Figure 8), these are **incubous** in arrangement [leaves overlapping from base to tip like shingles on a roof, with the part of the leaf closer to the stem base being nearer the substrate (ventral) and the more apical side emerging on the upper (dorsal) side of the stem], whereas others are **succubous** [basal edge dorsal, apical edge ventral – the leaf succumbs to the leaf above it].

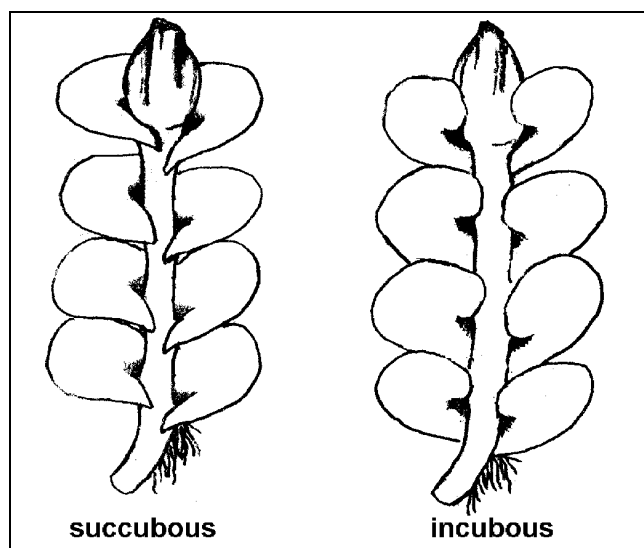


Figure 8. Succubous leaf arrangement of liverworts such as *Jungermannia* (left) and incubous arrangement of those such as *Calypogeja* (right). Note the decurrent leaf bases in the liverwort on the left. Redrawn by Margaret Minahan from Iwatsuki.

Clee (1937) found that in the succubous *Plagiochila asplenioides* var. *major* (Figure 9), water could move up to 3.7 cm in one minute. However, with the incubous arrangement, water moved less than 1 cm per minute. On the other hand, Basile and Basile (1987) questioned the role of the incubous vs. succubous leaf orientation in water conduction. They found that conduction proceeds equally in both orientations and that there is no correlation between the direction of leaf overlap and the angle of the substrate slope where they commonly grow. This seems reasonable since water coming from the top in rainfall would be presented with the opposite direction from water coming from beneath the branch. Hence, we could consider the branches in Figure 8 to be the above and below presentations of the same plant. Certainly if water is available from both above and below, it should make little difference if the plant is succubous or incubous. We need experiments to compare the effect on liverworts that form protruding shelves, those that are growing upright from a substrate, those that are adnate to a vertical surface, and

those that grow horizontally adnate to a substrate. Then we need to compare the direction of the water source – base or tip of plant, dorsal or ventral surface.



Figure 9. *Plagiochila asplenioides* with overlapping, succubous leaves. Photo by Michael Lüth, with permission.

Among mosses, Bowen (1933) considered the erect habit of leaves to hold and conduct more water than spreading leaves. This effect is enhanced if the leaves have **decurrent** bases (extensions of the leaf base down the stem; Figure 8).

Bayfield (1973) found that as water content declined in *Polytrichum commune* (Figure 10), the leaf arrangement changed (see also changes in *Polytrichum juniperinum* Figure 2). As the moisture decreased, the leaves wrapped closer around the stem, seemingly increasing moisture retention, a phenomenon that makes *Hedwigia ciliata* (Figure 11) almost unrecognizable when wet if one is only familiar with the dry state. Bayfield also found that external conduction is possible in the capillary spaces between the stem and the overlapping leaf bases. In the endohydric *Polytrichum* species, the loss of water is controlled by a complex series of changes in the leaf arrangement, whereas in the ectohydric *Racomitrium lanuginosum* (Figure 12-Figure 13), little or no mechanical control is exercised over water loss. It is likely that all *Polytrichum* (Figure 2, Figure 10) species benefit from this movement of the leaves upon drying.



Figure 10. *Polytrichum commune* showing the dry lower leaves that are beginning to wrap around the stem compared to the wide-spreading upper leaves that are well hydrated. Photo by Michael Lüth, with permission.



Figure 11. *Hedwigia ciliata* showing wet leaves (**upper left**) and dry leaves (**diagonally across lower right**) as a result of drying from the edge of the mat inward. The plants were growing on exposed boulders at the base of a cliff. Photo by Janice Glime.



Figure 14. *Campylostelium pitardii* with capsules, a species whose leaves curve or twist when dry. Photo by Proyecto Musgos, through Creative Commons.



Figure 12. *Racomitrium lanuginosum* dry showing twisted leaves and prominence of awns at the leaf tips, but little mechanical control over water loss. Photo by Michael Lüth, with permission.



Figure 13. *Racomitrium lanuginosum* wet showing transparent awns that are much less conspicuous than in dry plants. Photo by Des Callaghan, with permission.

Leaves Curving or Twisting upon Drying

Many species have leaves that curve or twist when they dry, particularly those in xeric habitats. These leaves curve toward the stem and thus reduce the exposed surface area. Among these are *Campylostelium pitardii* (Figure 14), *Phascum cuynetii*, and *Pterygoneurum sampaianum*.

Thickened Leaf

Many leaves partially protect themselves from water loss by having all or part of the leaf more than one cell thick. This is a common character for the borders and costa, where it most likely serves for support and possibly water movement, but in the leaf **lamina**, this reduces the exposed surface area (Figure 17).

Some leaves are **bistratose** in the upper part of the leaf, *i.e.* the part most exposed when the plant is dry. Among these are the xerophytic species *Syntrichia caninervis* (Figure 115) subsp. *spuria*, *Dicranella varia* (Figure 15), and *Didymodon australasiae* (Figure 16) (Guerra *et al.* 1992).



Figure 15. *Dicranella varia*. Note the twisted leaves on the dry mosses in the foreground. Photo by J. C. Schou, with permission.



Figure 16. *Didymodon australasiae* showing leaves curved around the stem in this dry state. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Some species protect the photosynthetic cells with hyaline cells, as in *Leucobryum* (Figure 18) and *Octoblepharum* (Figure 19). *Fissidens grandifrons* (Figure 20) differs from most other members of the genus *Fissidens* by having leaves that are multiple cell layers thick, most likely an adaptation to its habitat in fast-flowing water of streams and waterfalls. *Fissidens* accomplishes a degree of protection and provides capillary water-holding spaces by creating a pocket (Figure 21-Figure 24), giving this region a thickness of two layers of cells; the next leaf toward the apex often fits into this pocket. But this flattened moss nevertheless moves water slowly through its external surface (Table 1).

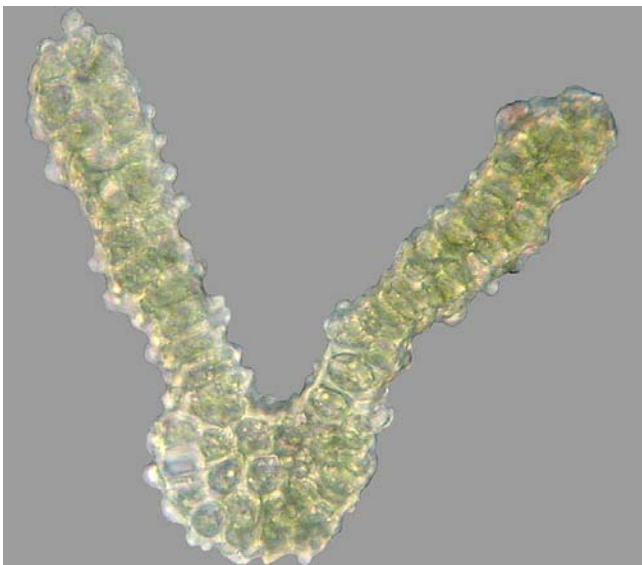


Figure 17. *Grimmia anomala* leaf section showing double layer of cells in parts of the lamina and papillae on the cells. Photo by Michael Lüth, with permission.

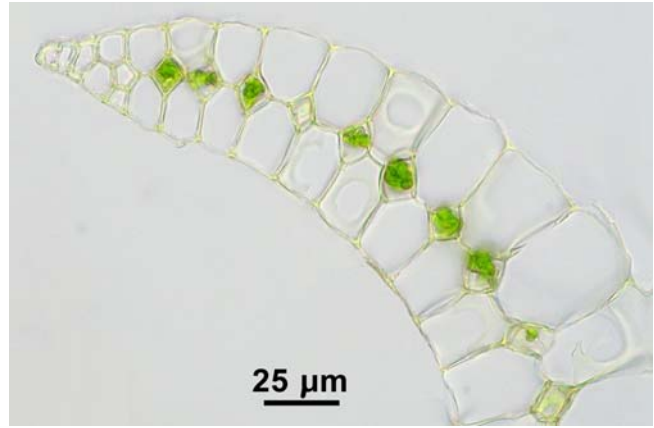


Figure 18. *Leucobryum glaucum* leaf cross section showing multiple layers with outer hyaline cells and central photosynthetic cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

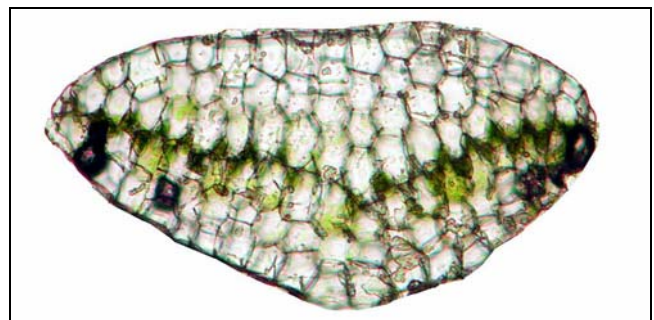


Figure 19. *Octoblepharum albidum* leaf cross section showing multiple layers of hyaline cells. Photo by Michael Lüth, with permission.



Figure 20. *Fissidens grandifrons* leaf cross section showing multiple layers that help this species to survive in torrents of water in waterfalls and snowmelt streams. These layers may also aid its survival when the water recedes, stranding it out of the water. Photo by Li Zhang, with permission.



Figure 21. *Fissidens asplenioides* showing flattened branch with each leaf fitting into the pocket of the one below it. Photo by Michael Lüth, with permission.

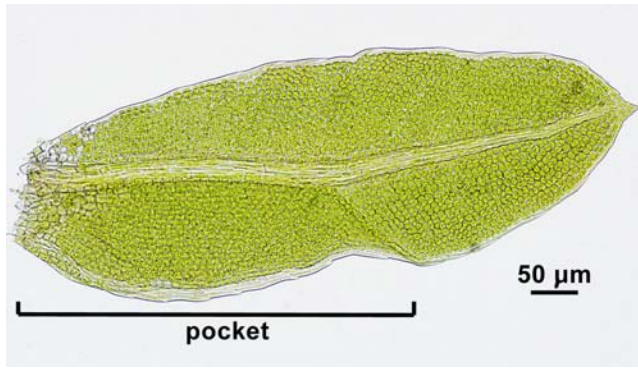


Figure 22. *Fissidens crispus* leaf showing pocket. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 23. *Fissidens taxifolius* leaves showing one leaf fitting into pocket of the next. Photo by Walter Obermayer, with permission.



Figure 24. *Fissidens taxifolius* leaf cross section through pocket. Note that the costa forms the region where the two halves join. Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Concave Leaves

Proctor (1979a) found that many taxa of ectohydric mosses have concave leaves (e.g. Figure 25-Figure 26). When examined in moist weather, the concavities on the upper sides of the leaves will generally be full of water. This helps to solve the problem of gas exchange by exposing one surface to the atmosphere while keeping the other surface bathed in water. And most of the CO₂ needed for photosynthesis comes from respiration in the soil and litter. Gas diffusion in air is about 10⁴ times faster than in water (Proctor 1982). Other mosses, like *Campylopus* (Figure 1) and *Polytrichum* (Figure 2, Figure 10), are able to roll their leaves, like some grasses, when they are dry. In this mode, mosses like *Syntrichia ruralis* (Figure 28) can look much darker and expose less surface area to the atmosphere, whereas the wet cells change the optical properties, making the cell walls more translucent (Glime & Church, unpubl.).



Figure 25. The moss *Scleropodium touretii* illustrating deeply concave leaves. Photo by Michael Lüth.



Figure 26. *Pseudoscleropodium purum* showing concave leaves. Photo by Aimon Niklasson, with permission.



Figure 27. *Syntrichia ruralis* dry. Photo by Janice Glime.



Figure 28. *Syntrichia ruralis* wet. Photo by Janice Glime.

Leaf spreading upon re-moistening is rapid in most bryophytes. Yenhung Li (unpublished data) found that in *Sphagnum* sp., *Ptilium crista-castrensis* (Figure 29), *Pleurozium schreberi* (Figure 30), and *Dicranum polysetum* (Figure 32), the first leaves spread within 1.5 to 2 seconds of receiving water (Table 1). To wet all the leaves in pieces 0.7 cm long required less than 2 minutes for most taxa, but required 24 minutes in *Rhodobryum ontariense* (Figure 31). The highest rate of conduction among the 15 taxa was in *Pleurozium schreberi* (140 mm min⁻¹).



Figure 29. *Ptilium crista-castrensis*, a moss that rewets quickly. Photo by Michael Lüth, with permission.



Figure 30. *Pleurozium schreberi*, a feather moss that rewets quickly. Photo by Janice Glime.



Figure 31. *Rhodobryum ontariense*, a moss that rewets very slowly. The dense cluster of leaves are all at the top of the stem. Photo by Janice Glime.



Figure 32. *Dicranum polysetum*, a boreal forest moss that rewets quickly. Photo by O. V. Ivanov, with permission.

Table 1. Mean time required for leaf spreading and conduction rate after rewetting along 0.7 cm branches in 15 species of bryophytes (n = 30 & 10 respectively). Based on Yenhung Li, unpublished data.

Species	sec for spreading	conduction mm/min
<i>Ptilium crista-castrensis</i>	2	0.93
<i>Dicranum polysetum</i>	2	70.00
<i>Pleurozium schreberi</i>	5	140.00
<i>Hedwigia ciliata</i>	5	11.48
<i>Climacium dendroides</i>	8	21.00
<i>Fontinalis duriaei</i>	9	2.60
<i>Dicranella heteromalla</i>	10	11.48
<i>Lophozia barbata</i>	10	24.1
<i>Anomodon attenuatus</i>	14	0.06
<i>Fontinalis antipyretica</i> var. <i>gigantea</i>	26	27.5
<i>Porella platyphylla</i>	34	0.75
<i>Sphagnum</i> sp.	90	6.0
<i>Bryum pseudotriquetrum</i>	149	0.82
<i>Fissidens adianthoides</i>	284	0.08
<i>Rhodobryum ontariense</i>	1421	0.06

Li found some indication that small leaves can spread more quickly than large ones, at least in *Fontinalis*. *Fontinalis duriaei* (Figure 33) has smaller and thinner leaves than does *F. antipyretica* var. *gigantea* (Figure 34-Figure 35), and *F. duriaei* can spread its leaves in 1/3 the time required for *F. antipyretica* var. *gigantea*. However, the difference may be due to the stiffness of the keel (leaf fold; Figure 35) in *F. antipyretica* var. *gigantea*, whereas *F. duriaei* has flat leaves.



Figure 33. *Fontinalis duriaei*, a species with flat, relatively narrow leaves that spread more quickly than larger leaves with a keel in *Fontinalis antipyretica* var. *gigantea*. Photo by Janice Glime.

Among the slowest species to re-wet in Li's study were *Fissidens adianthoides* (Figure 36) and *Rhodobryum ontariense* (Figure 31), both for rate of conduction and leaf wetting. *Fissidens adianthoides* has leaves that are large and partly two-layered. There is little overlap between the leaves in this genus except at the two-layered pocket (Figure 37), and Church and Nelson (unpubl data) noted that when the leaves of *F. adianthoides* are dry there is little or no overlap even at the pocket. Therefore, lack of capillary space may account for its slow response. The slowness of *Rhodobryum ontariense*, which has all its leaves crowded at the top of the stem like a palm tree (Figure 31), may likewise be explained by lack of capillary spaces (Figure 38). Below the crowded rosette of leaves at the apex are very reduced scale-like leaves along the stem, providing little capillary space and rendering it the slowest among the 15 species observed by Li. It required 123 minutes for the water to travel 0.7 cm up the stem! Although Li's data indicate a slight trend for rapid conduction to be coupled with rapid leaf spreading, there are enough exceptions to indicate that the relationship is not so simple.



Figure 34. *Fontinalis antipyretica* showing keeled leaves that spread slowly but that conduct water externally relatively rapidly. Photo by Jan-Peter Frahm, with permission.



Figure 35. *Fontinalis antipyretica* leaf showing keel (lower side of image). Photo by Malcolm Storey, through Creative Commons.



Figure 36. *Fissidens adianthoides*, a moss providing little capillary space, hence slow external conduction. Photo by Niels Klazenga, with permission.

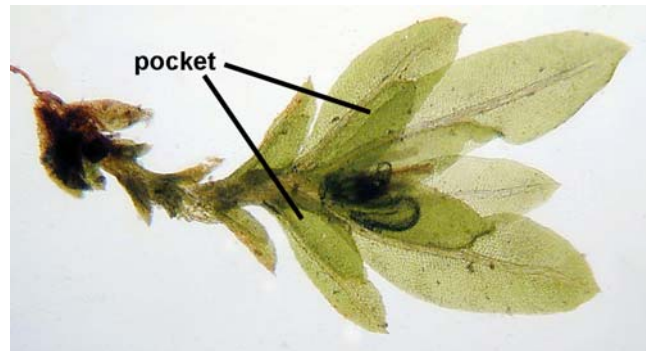


Figure 37. *Fissidens arnoldii* showing the overlap created by leaf pockets where the leaf blade has two, but separated, layers. Photo by Michael Lüth, with permission.



Figure 38. *Rhodobryum ontariense* dry, with its leaves twisted upward. Note the bare stem that seemingly provides no capillary spaces for external conduction. Photo by Michael Lüth, with permission.

Cucullate Leaves

Cucullate is hooded or boat-shaped, referring to the apex of leaves in this case. The cavity created by this leaf form is able to hold water, in part due to surface tension. An example of this is the moss *Phascum cuynetii*; some *Sphagnum* (Figure 39) species also have cucullate leaves.



Figure 39. *Sphagnum* sp. from the Neotropics showing cucullate leaves. Photo by Michael Lüth, with permission.

Plications

Plications, or Japanese fanfolds, in the leaf may reduce evaporation by reducing the exposed area and creating nearly dead space between the folds. On the other hand, it might simply be a means of neatly folding the leaf as it dries and loses the turgidity that kept it concave. These plications are present in *Brachythecium* (Figure 40), *Coscinodon* (Figure 41-Figure 43), and *Hamatocaulis vernicosus* (= *Drepanocladus vernicosus*; Figure 44), among others. Some taxa exhibit these only as they are drying or dry, so the system is responsive to water loss. When it is rehydrated, the plications permit the leaf to expand.



Figure 40. *Brachythecium* leaves showing plications. Photo by Bob Klips, with permission.

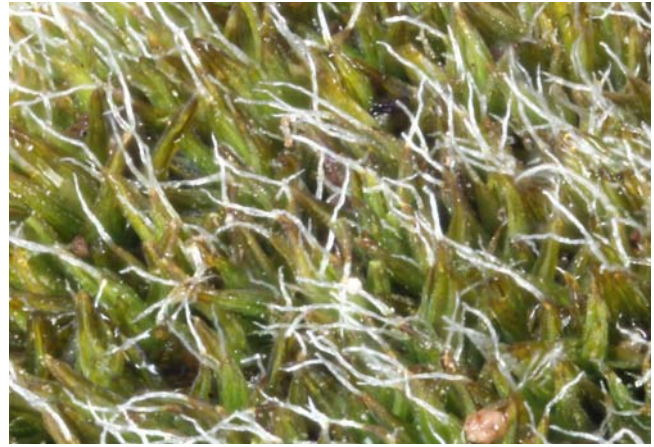


Figure 41. *Coscinodon cribrosus*. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

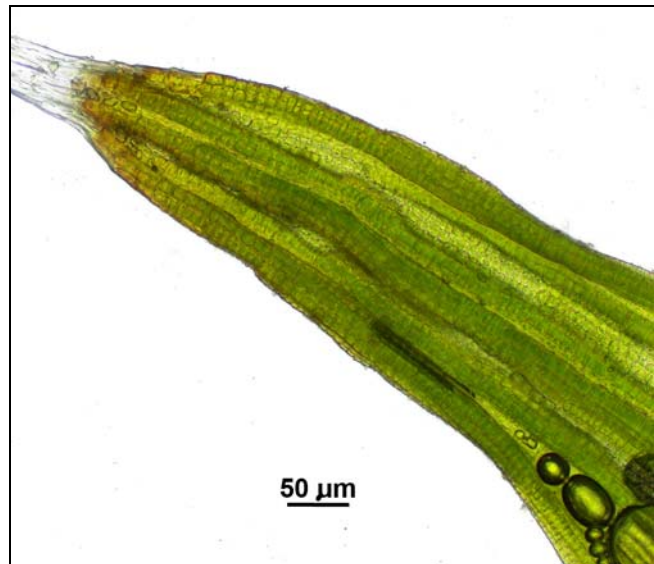


Figure 42. *Coscinodon cribrosus* leaf with plications. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 43. *Coscinodon cribrosus* leaf cross section showing plications. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 44. *Hamatocaulis vernicosus* showing plications at arrow. Photo by Des Callaghan, with permission.

Revolute and Involute Margins

Just as elongate cells of the border permit leaves to become contorted as they dry, the involute (Figure 45-Figure 48) and revolute (Figure 49-Figure 50) margins add structural support to the margin that causes contortions when the leaf dries (Figure 50). This contorted condition is known as **crispate**.



Figure 45. *Weissia controversa* that has recently been wet, showing **involute** leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 46. *Weissia controversa* dry, showing **crispate** leaf arrangements. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

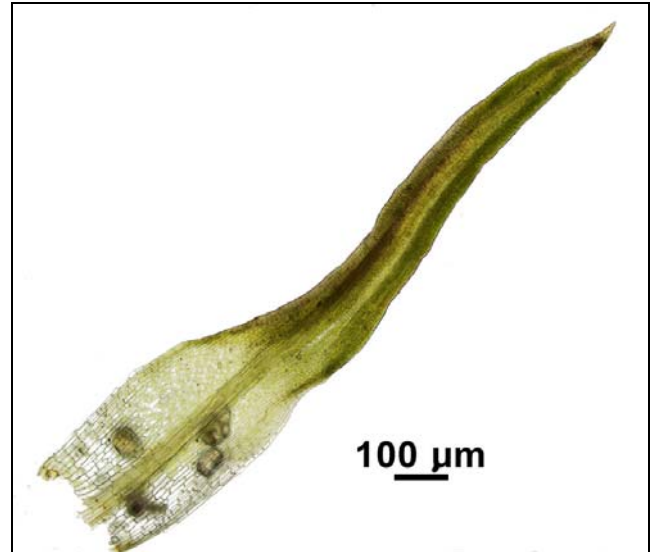


Figure 47. *Weissia controversa* leaf showing **involute** margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

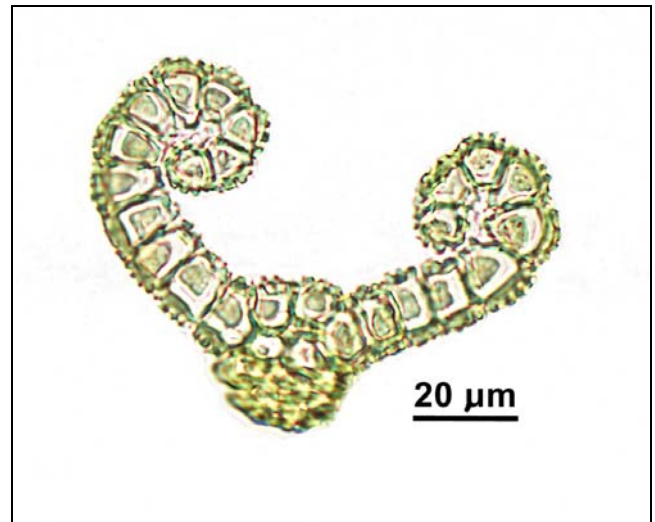


Figure 48. *Weissia controversa* leaf cross section showing **involute** leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 49. *Ceratodon purpureus* leaf cross section showing **revolute** leaf margin. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 50. *Bryoerythrophyllum recurvirostrum* leaf showing strong costa and **revolute** leaf margin that cause its **crispate** appearance when dry. Photo by Michael Lüth, with permission.

Both **Pottiaceae** and **Grimmiaceae** exhibit crisp, contorted leaves where the lamina is able to shrink and the leaf can roll with marginal rolling increasing as the plants dry (Kürschner 2004). The leaves wind spirally around the stem as they dry, reducing water loss and protecting the chlorophyll and DNA from excessive sunlight. The untwisting of the leaves provides another service – removal of trapped sand particles and other particles held by the leaves. When the lamina folds inward, it reduces desiccation. Kürschner suggests that the shiny costa may increase reflection of sunlight, further reducing desiccation. In these two families that occupy dry, open habitats, parallel evolution has adapted them to their similarly dry niches.

Borders

Borders are usually elongate cells that may be light in color or heavily pigmented. But in some species, the leaf margin may be heavily pigmented with chlorophyll in multiple cell layers. Such is the case in species of *Pseudocrossidium* (Figure 51-Figure 54) (Kürschner 2004). These species have marginal cells that form a well developed chlorophyllous region (Figure 52). They are protected by the **revolute** (rolled under; Figure 52-Figure 53) leaf margin that helps to maintain their hydration (Herzog 1926; Kürschner 2004).

So if the costa conducting cells all have protoplasm (**leptoids**), this leaves us with the question of water transport within the leaf. **Leaf borders** with elongate cells such as those in *Atrichum* (Figure 55) and the **Mniaceae** (Figure 56) provide benefits similar to those of the costa and seem to speed the movement of water from the base of the leaf to more distal parts, or in some cases from the tip toward the middle, but unfortunately, I have been unable to find any published study to verify this memory. Other roles are discussed in Chapter 7-4.



Figure 51. *Pseudocrossidium crinitum* hydrated. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

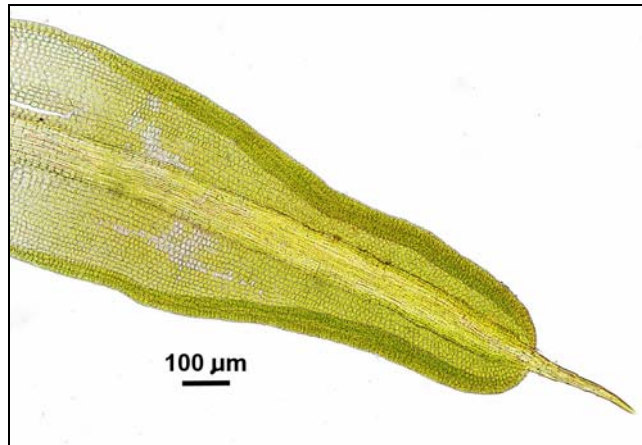


Figure 52. *Pseudocrossidium crinitum* underside of leaf showing thickened, revolute, chlorophyllous margin. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

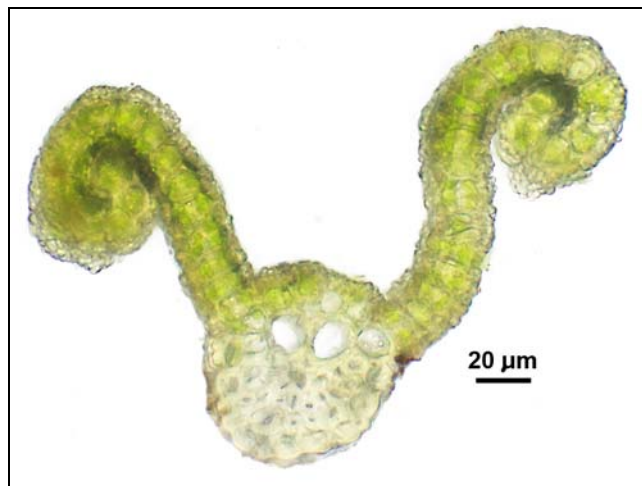


Figure 53. *Pseudocrossidium crinitum* leaf cross section showing revolute margin. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 54. *Pseudocrossidium revolutum* showing curled leaves and revolute margins in dry condition. Photo from Proyecto Musgo, through Creative Commons.



Figure 55. *Atrichum selwynii* leaf showing border with elongated cells and double border teeth. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

toward each other, the leaf to become somewhat concave, and the leaf to become contorted.



Figure 57. *Atrichum altecristatum* drying (lower plants) and moist (upper plants). Photo courtesy of Eric Schneider.



Figure 56. *Plagiomnium affine* leaf border showing elongate cells compared to wider but shorter leaf lamina cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

It appears that long border cells (Figure 56) are able to move water and facilitate uptake. But they may provide an additional role in the wet to dry state transition of the leaf in at least some taxa (Lowell 1998). When the leaf of *Atrichum undulatum* (Figure 57) is wet, the elongate cells of the border are turgid and extend the leaf lamina out into a nearly straight surface. But as the leaf dries, the opposing forces of the drying leaf cells and the border result in the contorted leaf shape that is exhibited by the dry *Atrichum undulatum* leaf (Figure 57). The margins roll toward each other and the tip rolls toward the base, creating a "boat" shape. The border acts much like a wire sewn into the edges of a cloth ribbon, but somewhat more flexible.

In *Atrichum* (Figure 57) the leaf is **prestressed**; that is, it has a natural dry state that is highly convoluted, but when wet the turgor forces it to become straight (Lowell 1998). Thus, when the leaf dries, the leaf itself contorts into a form that is able to trap and hold water next to the leaf and stem surface. As Lowell describes it, the border is like the party toy that you blow into and it extends straight out, but when it is relaxed, it forms a coil. Species of **Mniaceae** (Figure 58) with borders seem to have similar responses, with the borders causing the leaf margins to curl



Figure 58. *Plagiomnium* branch with contorted leaves due to drying. Although this moss has been rewet, it is slow to hydrate and regain its shape. Photo source unknown.

A similar adaptation appears in **Lejeuneaceae** and *Porella*, where a hyaline row of marginal leaf cells function in water storage (Daniels 1998). Perhaps the same function occurs in some of the mosses such as some *Fissidens* (Figure 59-Figure 60) or *Plagiomnium* (Figure 56) with well-developed borders. Because of their elongate structure, water can be expected to move more quickly along the border because of fewer end walls to traverse. Yet there seems to be little experimentation to demonstrate that these cells are of any advantage in gaining or moving water to vital parts, or holding water.

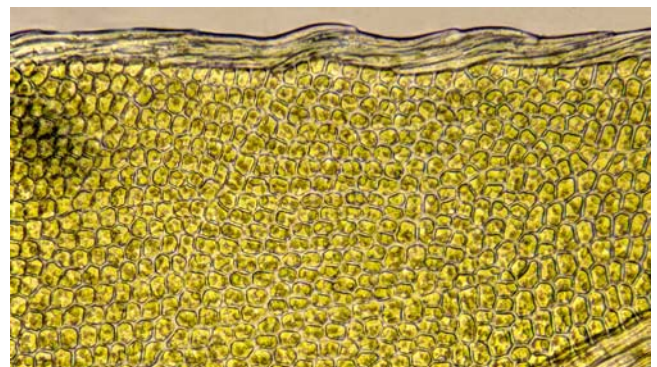


Figure 59. *Fissidens bryoides* leaf cells and border, showing elongate border cells. Photo by Dick Haaksma, with permission.



Figure 60. *Fissidens bryoides* showing leaves being constricted by their borders. Photo by Michael Lüth, with permission.

Leaf Teeth

Lots of ideas have been presented to suggest the evolutionary significance of teeth in tracheophytes, from deterrents to insects (making the leaf look like something has eaten it, stimulating production of antiherbivore compounds or being spiny) to dripping points for water to help reduce growth of fungi and epiphytes. But what might their value be to bryophytes (Figure 61-Figure 62)?

One interesting observation is that teeth and lobed leaves of deciduous trees are more common in deciduous forests, but they are rare in tropical forests (Baker-Brosh & Peet 1997). Baker-Brosh and Peet hypothesized that they might provide sites for early season photosynthesis. They found that eight species with prominent teeth or lobes did indeed have early season photosynthesis on the margins of the leaves, but not in seven others and none in the four entire-leafed species in the experiments.



Figure 61. *Mnium spinosum* leaf showing small, nearly rounded lamina cells compared to the elongate border cells and prominent paired teeth. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Royer and Wilf (2006) noted that toothed leaves of tracheophytes were common in cold climates and that the percentage of toothed leaves correlated negatively with temperature in **mesic** (containing a moderate amount of moisture) environments. They conducted experiments in Pennsylvania and North Carolina, USA, to determine the

advantages of the teeth. They found that the physiological activity at the leaf margins was greatest early in the first 30 days of the growing season. And toothed margins were more active in photosynthesis and transpiration than were those of untoothed leaves. They supported the observations of Baker-Brosh and Peet 1997, showing that the leaf margins were more active in leaves from Pennsylvania, which was colder, than those of the California leaves. This strategy maximizes carbon gain during the season when the temperature is limiting but moisture and nutrients are not limiting.

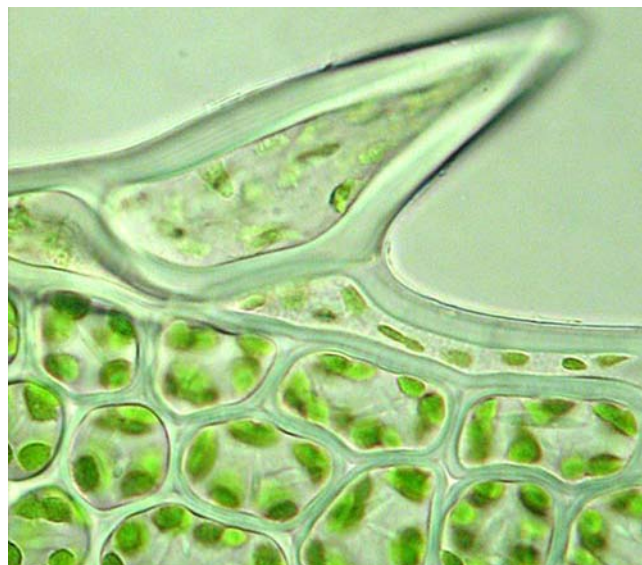


Figure 62. *Atrichum undulatum* leaf cells and border showing enlarged tooth with chlorophyll. Photo by Walter Obermayer, with permission.

Obeso (1997) found that spines on the European holly (*Ilex aquifolium*) deterred browsing by ungulates, and that the spines were inducible, decreasing significantly when browsing was prevented for one year.

Another possibility for the adaptive value of teeth is their bearing on water relations. Royer *et al.* (2009) found that among the 227 sites they studied in the Australian subtropical rainforest, both the percentage of species and abundance of toothed species declined from **riparian** (wetlands adjacent to rivers or streams) habitats to ridge-top habitats. Hence, we can rule out any protective value that teeth might have against desiccation. On the contrary, this correlation suggests that teeth could have a role in reducing water in saturated leaves.

Do these tracheophyte models help us to suggest roles for teeth in bryophytes, or are they simply not a detriment to the mosses and liverworts that have them? Do leaf teeth suggest that something has eaten the leaves? We don't know if antiherbivore compounds are inducible in bryophytes, so there may be no disadvantage to having teeth as a warning unless most of the leaves with teeth do have antiherbivore compounds, inducible or not. It seems unlikely that the teeth have any painful effect to deter browsers. And we don't even understand how deciduous tree leaves benefit from teeth in more moist climates.

It is possible that the bryophyte teeth do have a photosynthetic role in spring when new leaves are forming. The apex, especially of acrocarpous mosses, has the most exposure to light, and the marginal parts of the leaves will have the most exposure, so it is possible that they have such a role. But experiments to demonstrate such a benefit are lacking.

Teniolae

The **teniola** is a border-like row of differentiated cells (Figure 63), differing from a true border by being intramarginal (*i.e.* not at the margin). They are more than one cell thick and this condition may extend also throughout the blade portion. These are found in *Calymperes* (Figure 64) and function for support, but may also provide water transport (Reese 1993).

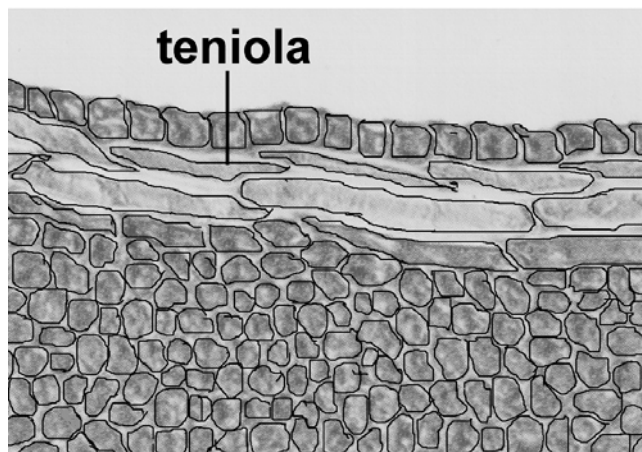


Figure 63. Portion of leaf showing the intramarginal border, the **teniola**. Drawing by Janice Glime.



Figure 64. *Calymperes motleyi*, member of a genus that has **teniolae**. Photo by Jan-Peter Frahm, with permission.

Costa

The **costa** is the supporting structure for many moss leaves, often also providing an avenue of water transport (Frahm 1985) (Figure 65-Figure 66). It resembles a midrib both in appearance and function (Figure 67). Habitat

seems to play some role in its development, although its predisposition to presence or absence is usually genetically determined.



Figure 65. *Mnium hornum* showing distinct costa and teeth. Photo by Bob Klips, with permission.

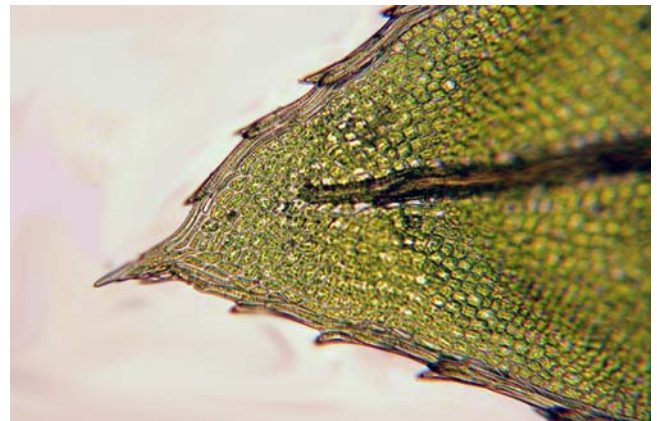


Figure 66. *Mnium hornum* leaf showing elongate cells of costa and border. Photo by Bob Klips, with permission.



Figure 67. Cross section of *Trichodon cylindricus* showing costa. Photo by Janice Glime.

The costa of some species may be shorter, thinner, and even disappear when it develops in water (Zastrow 1934). For example, the submerged forms of *Warnstorfia exannulata* (= *Drepanocladus exannulatus*) (Figure 68-Figure 69) have a costa that only reaches midleaf, whereas the terrestrial forms have a strong costa; similarly, *Cinclidium stygium* (Figure 70) normally has a strong costa above water, but when grown submerged it becomes thin and small (Zastrow 1934). When cultured in artificial streams where the leaves were exposed to air, *Fontinalis novae-angliae* developed short double costae, although

these are normally absent when it grows submersed (Glime, unpubl.). The broad costa in *Campylopus* (Figure 71-Figure 72) not only serves as the photosynthetic organ, but as a water reservoir as well, adding to the possible advantages of growing a costa above water.



Figure 68. *Warnstorfia exannulata* branch. Photo from Proyecto Musgo, through Creative Commons.

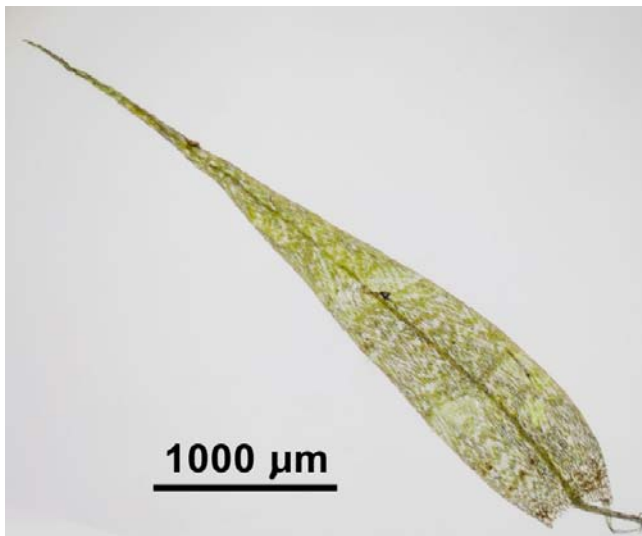


Figure 69. *Warnstorfia exannulata* leaf showing costa typical of emergent leaves. Photo by Kristian Peters, with permission.

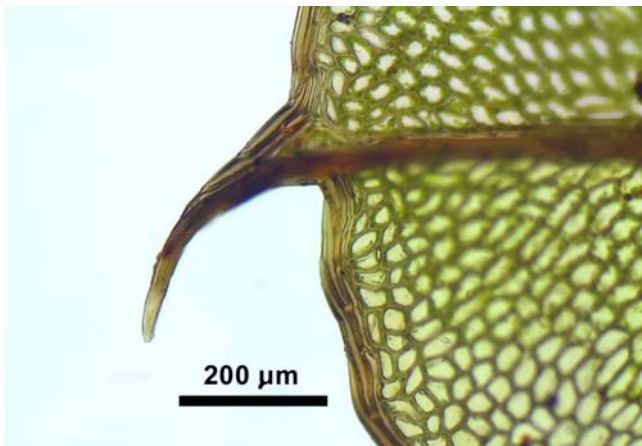


Figure 70. *Cinclidium stygium* with leaf tip, costa, and border. Its strong costa indicates that it was grown above water. Photo by Kristian Peters, through Wikimedia Commons.



Figure 71. *Campylopus lamellinervis* showing the broad, thickened costa and a tomentum on the stem that absorbs moisture. Photo by Michael Lüth, with permission.



Figure 72. Leaf cross section of *Campylopus flexuosus* showing broad costa with cells that have water-holding capacity as well as photosynthetic capacity. Photo by Michael Lüth, with permission.

Guerra *et al.* (1992) considered **nerve enlargement** to be an adaptation to the xeric environment, providing stiffening that supports the leaf during desiccation. Bell (1982) suggested that it also might retain water.

Stereids

In the stem, **stereids** are thick-walled cells that contain living protoplasm and have been compared to xylem parenchyma cells (Héban 1970). In leaves, they form ribs on one or both sides of the costa (Figure 73) and may function as protection against desiccation (Frahm 1985). They occur in a variety of families, including **Dicranaceae** (Figure 74) and **Pottiaceae** (Figure 75-Figure 76).

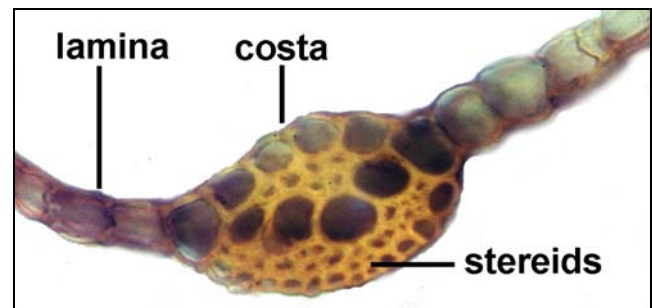


Figure 73. *Trichostomum tenuirostre* (moss) leaf cross section showing stereids. Photo by Janice Glime.



Figure 74. *Dicranum scoparium* (Dicranaceae) leaf cross section. This leaf has few sclereids but has relatively large conducting cells, in this case smaller than the leaf lamina cells. Photo from Botany website, University of British Columbia, Canada.



Figure 75. *Syntrichia inermis* (Pottiaceae) leaf cross section. Note the enlarged costa with stereid cells on the bottom and conducting cells near the top. In this case, the lamina cells are covered with papillae that may help in water intake, a function thus far demonstrated for only one species. More likely they channel the water. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 76. *Syntrichia princeps* (Pottiaceae) leaf cross section showing costa with stereids (pinkish color on lower portion) and large leptoids. Photo by Paul S. Wilson.

It appears that the structure of the costa can have adaptive value relating to moisture conditions. Those *Campylopus* taxa surviving habitats with changeable conditions have well-developed costal stereids (Frahm 1985). Frahm found that dorsal costal **lamellae** (Figure 95) aid in water uptake, whereas the ventral costal stereids (Figure 77) common among *Campylopus* species help to reduce desiccation. *Campylopus savannarum* survives its savannah habitat with the aid of such stereids, whereas *Campylopus* taxa occurring on wet cliffs, dripping rocks, and swamps lack stereids (Figure 78).



Figure 77. *Campylopus flexuosus* leaf cross section showing ventral (lower) stereids. Photo by Amelia Merced, Duke Herbarium.



Figure 78. *Campylopus tallulensis* leaf cross section showing thin-walled ventral costal cells typical of the more humid mountainous regions. Photo by Amelia Merced, with permission.

Lamellae

The term **lamella** shares the same root word as laminate and refers to layers, in this case vertical stacks of cells that form rows, often reaching the length of the leaf (Figure 82, Figure 83). They may cover the costa, the blade, or a liverwort thallus. These rows are arranged in such a way that they somewhat resemble a book that has just been opened and laid to rest, with its pages still parting and standing upward from the middle. Some of the most **xerophytic** (referring to plants of dry habitats) mosses, such as *Aloina* (Figure 79), have branched filaments over the costa, giving it a **succulent** (fleshy) appearance; *Crossidium* (Figure 80-Figure 81) achieves a similar effect with dense filamentous outgrowths from the costa in the upper half of the leaf.

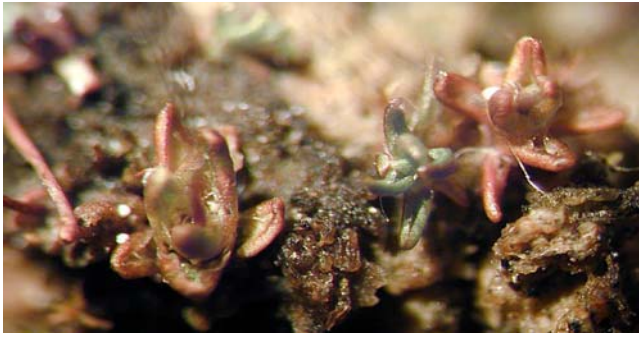


Figure 79. *Aloiina brevirostris*, illustrating the succulent appearance caused by the numerous filaments on the costa. Photo by Michael Lüth, with permission.



Figure 80. *Crossidium crassinerve* with filaments on leaf costae. Photo by Michael Lüth, with permission.



Figure 81. *Crossidium aberrans* leaf showing filaments on costa. Photo by Michael Lüth, with permission.

Members of the **Polytrichaceae**, such as *Polytrichum* and *Dawsonia*, which are all **endohydric** (having internal water transport), have vertical lamellae (Figure 82, on their leaves that provide capillary spaces and create dead air spaces that can reduce water loss across the broad surface of these atypically large moss leaves (Figure 82-Figure 85). In addition, some species [*Polytrichum hyperboreum* (Figure 86-Figure 87), *P. piliferum* (Figure 88-Figure 89), *P. juniperinum* (Figure 90-Figure 91)] have the edge of the

leaf **lamina** (flattened part of leaf not including costa or border) rolled over the lamellae, creating an internal structure somewhat like the **palisade mesophyll** (columnar cells of inner leaf tissue) of a flowering plant, with the lamina behaving in some ways like an epidermis. The leaves have the additional ability to flex like a hinge when water fills the thin-walled leaf base cells (van Zanten 1975), causing the leaves to be spread lengthwise away from the stem under moist conditions but be straight or curved around the stem when dry (Figure 2). Such behavior retards water loss and protects the chlorophyll during dry periods, while permitting maximum use of light during wet periods.

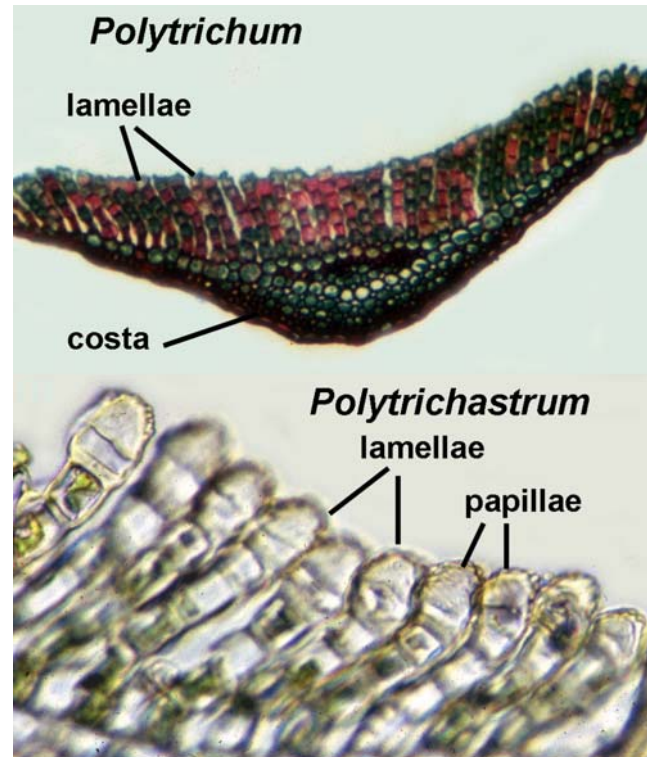


Figure 82. Cross sections of lamellae of **Polytrichaceae**. **Top:** stained section of *Polytrichum*. **Bottom:** *Polytrichastrum alpinum* with papillose terminal cells on the lamellae. Photos by Janice Glime.

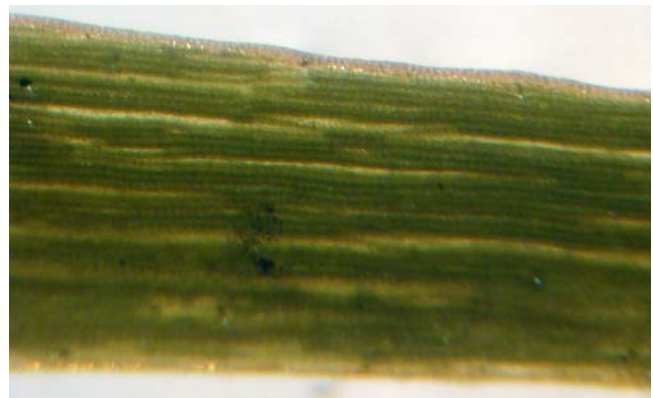


Figure 83. Lamellae on leaf of *Polytrichum ohioense*, viewed down onto leaf surface at 100X. Photo courtesy of John Hribljan.

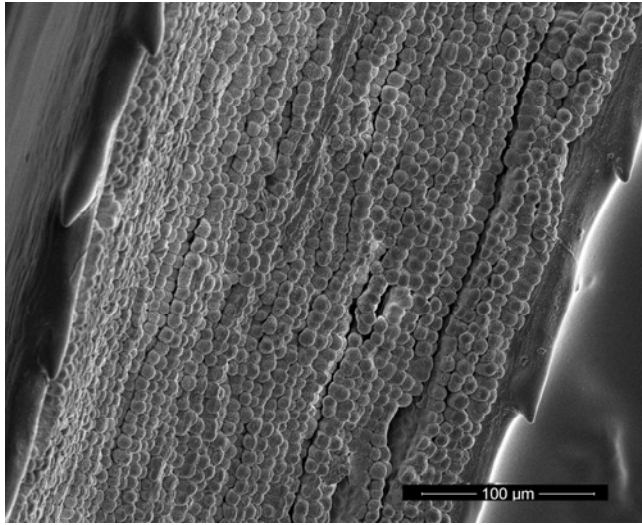


Figure 84. SEM of *Dendroligotrichum squamosum* (Polytrichaceae) showing tops of lamellae. Photo courtesy of Jeff Duckett and Silvia Pressel.

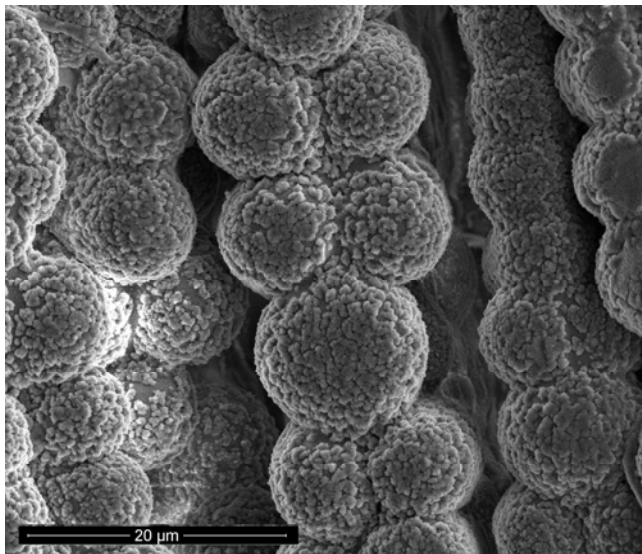


Figure 85. SEM of *Dendroligotrichum squamosum* leaf showing terminal cells of lamellae. Photo courtesy of Jeff Duckett and Silvia Pressel.



Figure 86. *Polytrichum hyperboreum* showing leaf lamina rolled over the lamellae. Photo by Michael Lüth, with permission.

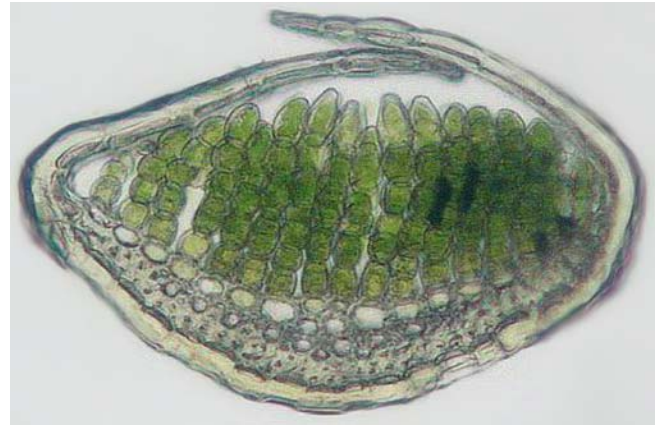


Figure 87. *Polytrichum hyperboreum* leaf cross section showing lamina folded over lamellae. Photo by Michael Lüth, with permission.



Figure 88. *Polytrichum piliferum* showing leaf lamina rolled over the lamellae. Photo from Botany Department website, University of British Columbia, Canada, with permission.



Figure 89. *Polytrichum piliferum* leaf cross section showing leaf lamina rolled over the lamellae. Photo from Botany website, University of British Columbia, Canada, with permission.

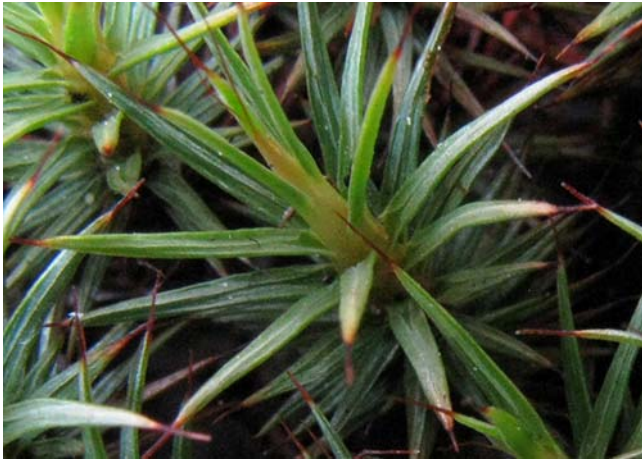


Figure 90. *Polytrichum juniperinum* showing leaf lamina rolled over leaf lamellae. Overlap can be seen easily near leaf bases where the overlap is incomplete, permitting water to enter the basal cells. Photo by Janice Glime.



Figure 91. *Polytrichum juniperinum* leaf cross section showing leaf lamina rolled over leaf lamellae. Photo by John Hribljan, with permission.

In *Pilopogon laevis* (Figure 92) the costa is ribbed on the back of the leaf; in *P. peruvianus* (Figure 93-Figure 94) it has 3-4-cell-high lamellae on the back of the leaf, adapting this species to its dry coastal desert habitat. Likewise, *Campylopus pilifer* (Figure 95) has similar lamellae and prefers such dry habitats as rocks, soil-covered boulders, and gravel. On the other hand, *C. introflexus* (Figure 96) has only 1-2-cell-high lamellae and lives on humus, wet sand, and peat.

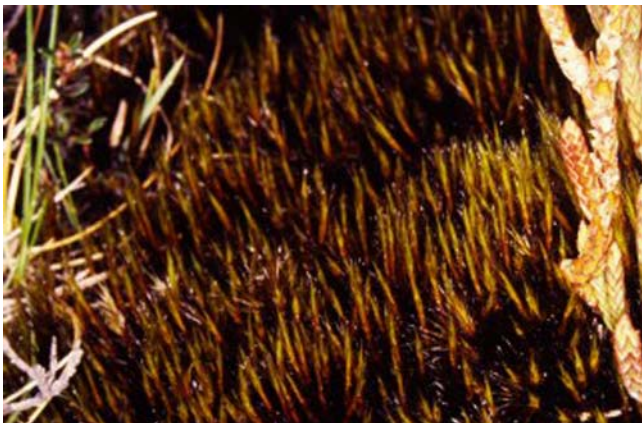


Figure 92. *Pilopogon laevis*, a species with a ribbed costa. Photo by Jan-Peter Frahm, with permission.



Figure 93. *Pilopogon peruvianus* in its desert habitat. Photo by Michael Lüth, with permission.



Figure 94. *Pilopogon peruvianus* leaf cross section showing 3-4 cell high lamellae. Photo by Michael Lüth, with permission.

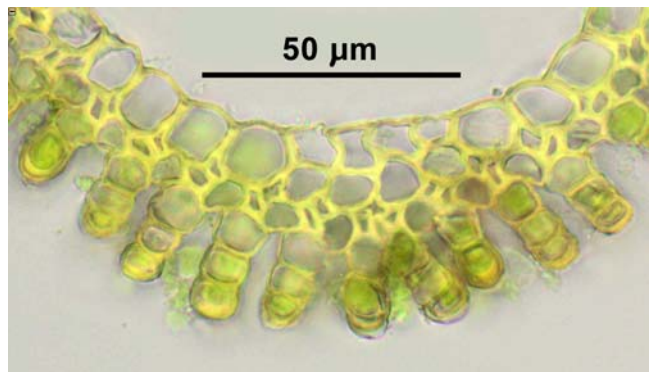


Figure 95. *Campylopus pilifer*, a plant of rocks and gravel, leaf cross section showing deep lamellae. Photo by Amelia Merced, Duke Herbarium, with permission.



Figure 96. *Campylopus introflexus*, a plant of humus, wet sand, and peat, leaf cross section showing shallow lamellae. Photo by Gilles Bailly, through Creative Commons.

Although Frey and Kürschner (1991) found a correlation between costal lamellae and increasing aridity, the lamellae of *Polytrichum* seem not to be so much an adaptation to prevent water loss as to provide for additional surface area [2.4-fold in *Polytrichum commune* (Figure 97-Figure 98)] and gas exchange during photosynthesis (Thomas *et al.* 1996). Proctor (1979a, b) and Thomas *et al.* (1996) described wax on the terminal cells of the lamellae of *Polytrichum* and attributed to this wax the repulsion of water, preventing it from entering between the lamellae. Perhaps lamellae are adapted to increasing gas exchange and are more important in water retention or repulsion than in absorption, at least in some species.



Figure 97. *Polytrichum commune* leaves with waxy surface that keeps water out of the lamellae. Photo by James K. Lindsey, with permission.

The genus *Atrichum* (Polytrichaceae) also has shallow to deep lamellae, and these have been used to justify separation into different species. The lamellae shown in Figure 99-Figure 101 fall within *Atrichum undulatum* var. *undulatum*, but any lamellae more than 4 cells high would indicate a different variety (Crum 1983), or species (The Plant List 2010).

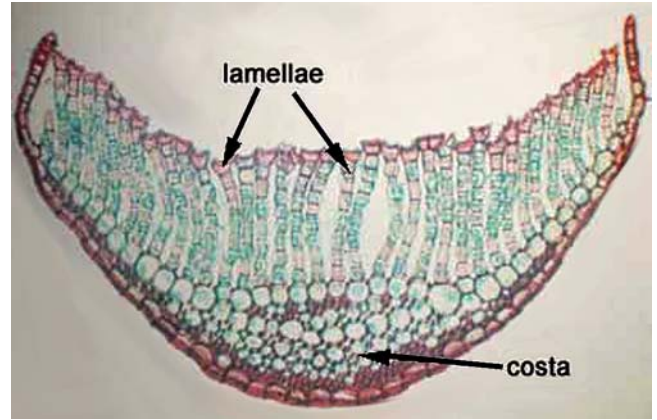


Figure 98. *Polytrichum commune* leaf cross section with lamellae showing terminal cell with different stain from other lamellae cells, perhaps due to the presence of wax. Photo from Botany website, UBC, with permission.



Figure 99. *Atrichum undulatum* leaf showing leaf lamellae and border with teeth. Photo by Walter Obermayer, with permission.



Figure 100. *Atrichum undulatum* leaf (costa) cross section showing small, thick-walled stereids, large transparent conducting cells, and lamellae 3-4 cells high. Photo by Walter Obermayer, with permission.

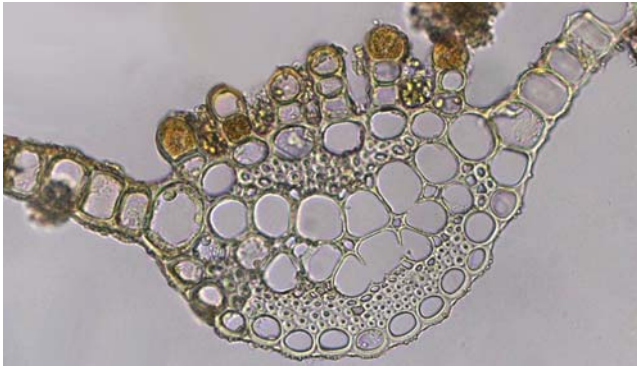


Figure 101. *Atrichum undulatum* leaf (costa) cross section showing small, thick-walled stereids above and below the large, transparent conducting cells. Lamellae are on top of the costa and are only 2-3 cells high. Photo by Walter Obermayer, with permission.

Lobules and Storage Organs

Liverworts have an evolutionary history that separates some of the major groups by their water relations (Heinrichs *et al.* 2005). In the **Jungermannniidae**, two clades split. The **Porellales** are predominantly epiphytes that have specialized **lobules** (Figure 102) or water sacs and **endosporous** protonemata. The **Jungermanniales** (Figure 103) are frequently terrestrial, lack water sacs, and normally develop **exosporous** protonemata.



Figure 102. Ventral side of *Porella platyphylla* showing underleaves along stem and lobules on each side of them. Photo by Paul Davison, with permission.



Figure 103. *Lophozia wenzelii*, a member of the **Jungermanniales**, showing the absence of lobules. Photo by Des Callaghan, with permission.

Daniels (1998) has compared leafy liverworts growing in a variety of habitats. **Xerophytic** (dry habitat adapted) taxa such as *Frullania* (Figure 104) have helmet-shaped leaf **lobules** and *Radula* (Figure 105) has a saccate lobule, both functioning for water storage. *Porella* (Figure 102), capable of both an **epiphytic** (living on plants) and a **saxicolous** (living on rock) habit, has leaf folds underneath (lobules) and large underleaves. Liverwort plants in the humid rainforests such as those in the **Lejeuneaceae** (Figure 106-Figure 108) have smaller lobules than those growing in drier, more exposed habitats (Cornelissen & ter Steege 1989; Gradstein 1995). Such structures help to hold water in capillary spaces in the absence of multiple rows of leaves. Some aquatic invertebrates, especially rotifers, live in these watery lobules (see Volume 2, Chapter 4-5 on Rotifers). It is likely that the pockets of *Fissidens* (Figure 21-Figure 24, Figure 37) may have similar water-holding functions.

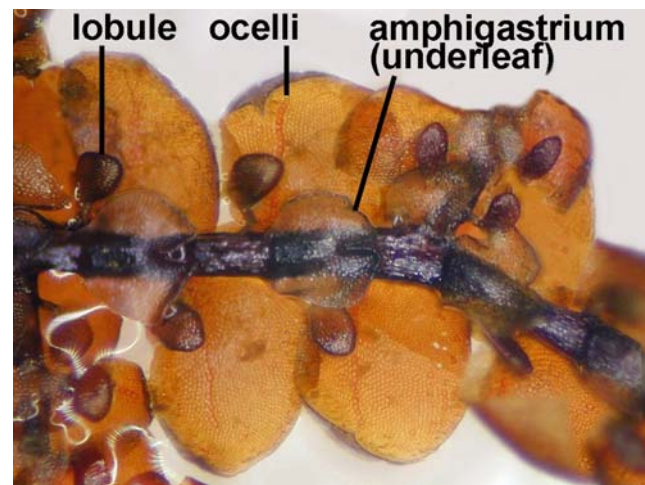


Figure 104. *Frullania tamarisci* showing lobules. Photo by Michael Lüth, with permission.



Figure 105. *Radula* from the tropics with saccate lobules (arrows). Photo by Michael Lüth, with permission.



Figure 106. *Lejeuneaceae* epiphylls from Panama. Photo by Janice Glimme.



Figure 107. *Lejeunea patens* showing small lobules. The upper three have air bubbles trapped in them. Photo by Jan-Peter Frahm, with permission.

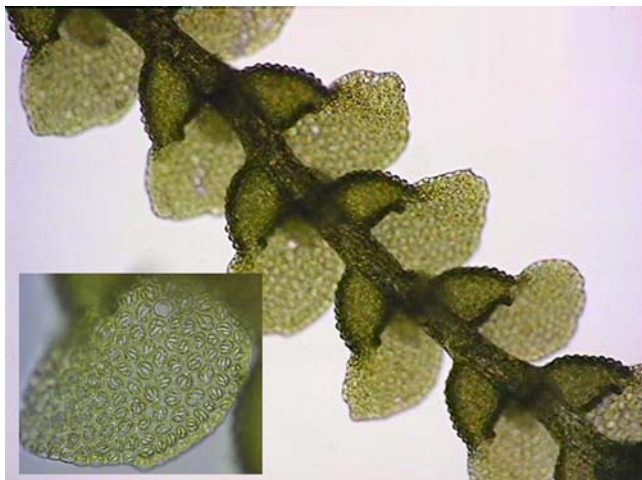


Figure 108. *Cheilolejeunea evansii* branch showing ventral lobules. Photo by Paul Davison, with permission.

Hair Points

Hair points are common on leaves of xerophytic mosses, including species of *Campylopus* (Figure 109- Figure 110), *Grimmia* (Figure 111), *Schistidium* (Figure

112-Figure 113), *Hedwigia* (Figure 134), and *Syntrichia* (Figure 114). As discussed earlier, Loeske, in 1930, demonstrated that in *Schistidium apocarpum* (Figure 112-Figure 113) hair points are actually lost when the mosses are kept in damp air or deep shade. Proctor (1979a) and Kürschner (2004) consider these hairs to be organs that reflect some of the solar radiation, thus reducing energy absorption, temperature, and evaporation. But they reduce water loss more directly as well; hair points on *Syntrichia intermedia* (Figure 114) and *Grimmia pulvinata* (Figure 111) reduce the boundary layer conductance by about 20-35% in experiments (Proctor 1980). Not only does this thicker boundary layer trap stagnant air, thus reducing evaporation loss, but it increases the distance from the leaf surface to the surrounding air, thus decreasing the diffusion gradient (Proctor 1982).



Figure 109. *Campylopus introflexus* showing dry hair tips. Compare to Figure 110. Photo by Michael Lüth, with permission.



Figure 110. *Campylopus introflexus* showing hair tips that have collected moisture from the atmosphere. Photo by Michael Lüth, with permission.



Figure 111. *Grimmia pulvinata* showing the long hairs that reduce the boundary layer conductance and trap atmospheric moisture. Photo by Michael Lüth, with permission.



Figure 112. *Schistidium apocarpum* exhibiting the lack of hair points typical of this species when it is grown in wet or shaded habitats. Photo by Christophe Quintin, through Creative Commons.



Figure 113. *Schistidium apocarpum* exhibiting the leaf hair points that develop when the plants are in dry areas. Photo by Christophe Quintin, through Creative Commons.

Hair points may also help in trapping and absorption of water vapor from fog and dew (Figure 109-Figure 110). Dry tips can reflect sunlight (Figure 109), reducing water loss (Kürschner 2004).



Figure 114. *Syntrichia intermedia* demonstrating prominent hair points. Photo by Jan-Peter Frahm, with permission.

As suggested by the example of *Campylopus introflexus* (Figure 109-Figure 110), hair points can help in collecting moisture from the air as well (Figure 110). Shaun Russell has described to me that in African highlands the mosses act as tiny collectors that trap moisture from the fog. This is often their only source of water for an entire year. Chang and coworkers (2002) have measured the water available to epiphytes in fog (Table 2) and in precipitation in a subtropical montane forest in Taiwan. In a one-year study, they found that the fog endured for a mean of 4.7 hours per day at its low in the summer to 11 hours per day the rest of the year, reaching nearly 15 hours per day in November. Furthermore, it contributed more than 50% of the nutrient ions reaching the bryophytes.

Table 2. Absorption rate of fog in dominant epiphytes during a single dense fog event on 24 February 2001 at Yuanyang Lake, Taiwan. From Chang *et al.* (2002).

Species	absorption rate g H ₂ O gdw ⁻¹ h ⁻¹
<i>Bazzania fauriana</i>	1.28
<i>Bazzania</i> sp. 2	0.90
<i>Pleurozia acinosa</i>	0.67
<i>Mastigophora diclados</i>	0.59
<i>Schistochila acuminata</i>	0.58
<i>Dicranoloma blumii</i>	0.42
<i>Scapania</i> sp. 1	0.38
<i>Bazzania</i> sp. 1	0.23

Zhang *et al.* (2009) considered the effect of dew as an important moisture source in the Gurbantunggut Desert, Northwestern China. They measured dew quantities with micro-lysimeters and demonstrated the increase in dew deposition as the crust grew larger. Mosses had the highest deposition compared to that of lichen crusts, cyanobacterial crusts, and bare sand ($p < 0.05$). Interestingly, the retention time for the moisture gained from dew did not follow this pattern. Instead, it was held longest by sand, followed by the cyanobacterial crust, moss crust, and lichen crust, in that order.

Tao and Zhang (2012) further examined the function of hair points in the desert moss *Syntrichia caninervis* (Figure 115). The hair points in this case comprised only about 4.8% of the shoot weight, but they were able to increase the absolute water content by 24.9%. And, during dehydration, those moss samples with hair points always

had a higher water content than did those without. Furthermore, the shoots with hair points took 20 minutes longer to become completely dehydrated. And of course there was greater dew accumulation on the shoots with leaf hair points, increasing the dew on the crusts by 10.3%. Following short simulated rainfall events, the evaporation of water from the crusts was always slower when the leaves had hair points in contrast to the rapid loss of water trapped from dew (Zhang *et al.* 2009).

Yuan Ming Zhang's research team filmed the events following application of a drop of water on the hair points of *Syntrichia caninervis* (Figure 115). The water moved quickly down the hair point and was absorbed by the leaves within seconds. Like a fine wire, the hair tips serve as a conduit for the water. This mechanism permits these mosses to extract water from dew or fog, and to benefit from rapid absorption of the first few drops of rain, maximizing its period of hydration. Zhang *et al.* (2011) supported the significance of this rapid rewetting. In lab experiments they showed that within the first minute the photosynthetic yield (F_v/F_m) recovered to 90% of its rate after 30 minutes. Cytological changes occurred rapidly, indicating no damage to membranes or organelles. This rapid recovery makes it possible for it to use the water collected by the hair points from fog, dew, rain, and melting snow for immediate recovery, making it possible to attain positive photosynthetic gain in its desert ecosystem.



Figure 115. *Syntrichia caninervis*, a desert crust moss with hair points that are important to the hydration of the crust. Photo by John Game, through Creative Commons.



Figure 116. *Syntrichia caninervis* leaf showing awn. Photo by Yuan Ming Zhang.

Duration of the rainfall or dew fall event is important. Proctor (2004) found that in *Grimmia pulvinata* (Figure 111), dew fall did not enter the moss sufficiently to rehydrate it. Could these hair points prevent wetting and drying cycles that are too frequent for adequate repair of dehydration damage in mosses regularly subjected to hot, dry days? Is this a mechanism to prevent the leaf from becoming hydrated at a time when it will dehydrate again within hours? This is reminiscent of the dormancy mechanism in desert seeds wherein a chemical must be washed off before the seed will germinate. This keeps the seed from germinating unless there is enough rainfall to sustain the young seedling until it reaches a size where it can survive. In these mosses, it requires a rainfall that will hydrate the moss long enough for it to repair the damage of desiccation and make a positive photosynthetic gain before becoming dehydrated again.

Nucleation

It appears that bryophytes are good nucleators. This is a phenomenon in which a small object, known best from bacteria and proteins, causes the formation of ice around itself. Moffett *et al.* (2009) suggest that this phenomenon is widespread among bryophytes. Nucleation occurs when the difference in vapor pressure over ice and water is at or close to the maximum. At these temperatures, typically -8 to -18°C, ice grows at the expense of supercooled water. Moffett *et al.* suggest that the nucleation ability permits the bryophytes to collect water from fog, dew, and cloud water. It is interesting to note that airborne bryophytes may use this nucleation to initiate precipitation.

Papillae

Papillae in bryophytes are small projections from cells, especially common in the **Pottiaceae** (Figure 117-Figure 118). Kou *et al.* (2014) attempted to limit the confusion of many terms in their descriptions by providing four terms to describe them: simple, forked, branched, and pedicellate.

Papillae can both facilitate rapid water uptake (Proctor 1979a; Longton 1988; Kürschner 2004) and accelerate water loss (Pressel *et al.* 2010). Species that benefit from these papillae must, as a consequence, shut down under drying conditions. This is consistent with the role of surface waxes (discussed in Chapter 7-4b of this volume). The thick surface waxes of tracheophytes are usually associated with conditions of drying. In bryophytes, however, they are often characteristic of species from constantly flowing aerated water or other places where water logging depresses gas exchange (Pressel *et al.* 2010). In other words, often they are important for their **hydrophobic** (water-repelling) nature.

The role of papillae, those little bumps and extensions on cell walls (Figure 118), has been controversial for a long time, but their common appearance on bryophytes of dry habitats cannot be ignored. Nevertheless, Loeske (1926) points out that papillae are also found in a number of wetland and aquatic taxa, including *Dichodontium pellucidum* (Figure 119-Figure 120), *Philonotis* (actually **prostrate** cells – end walls overlap and protrude; Figure 121-Figure 122), *Aulacomnium palustre* (Figure 123-Figure 124), *Helodium blandowii* (Figure 125-Figure 126), and *Paludella* (Figure 127). Loeske observed that the papillae

are maintained in a number of species through a wide range of wet to dry habitats. On the other hand, these taxa are common in wet meadows, lake shores, and other wet habitats where they may periodically be dry while being exposed to high sunlight, suggesting that the papillae may be of value under those exposed conditions.

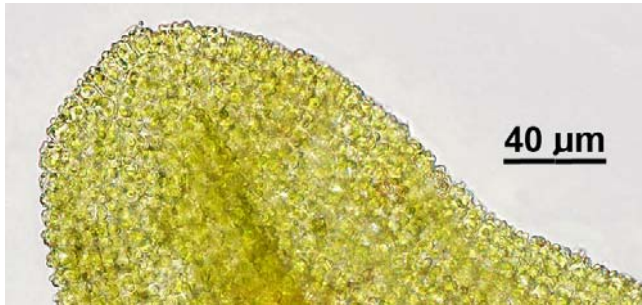


Figure 117. *Barbula convoluta* leaf cells showing papillae (especially visible as tiny projections along the margins). Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 118. *Chrysoblastella chilensis* leaf cross section showing papillae. This leaf is well endowed with stereids in the costa. Photo by Juan Larrain, with permission.



Figure 119. *Dichodontium pellucidum* showing dull, waxy look that results from surface papillae. Photo by Jan-Peter Frahm, with permission.



Figure 120. *Dichodontium pellucidum* leaf cells in cross section showing papillae. Photo by Amelia Merced through Duke University Plant Biology website, with permission.



Figure 121. *Philonotis fontana* exhibiting dull appearance resulting from **prorate** cells. Photo by Malcolm Storey, through Creative Commons.

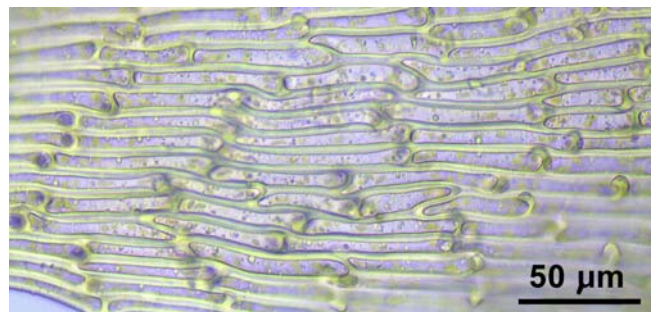


Figure 122. *Philonotis fontana* leaf lamina showing **prorate** cells that have an appearance similar to papillae. Photo by Kristian Peters, through Creative Commons.



Figure 123. *Aulacomnium palustre*, wetland moss with papillae. Photo by David T. Holyoak, with permission.

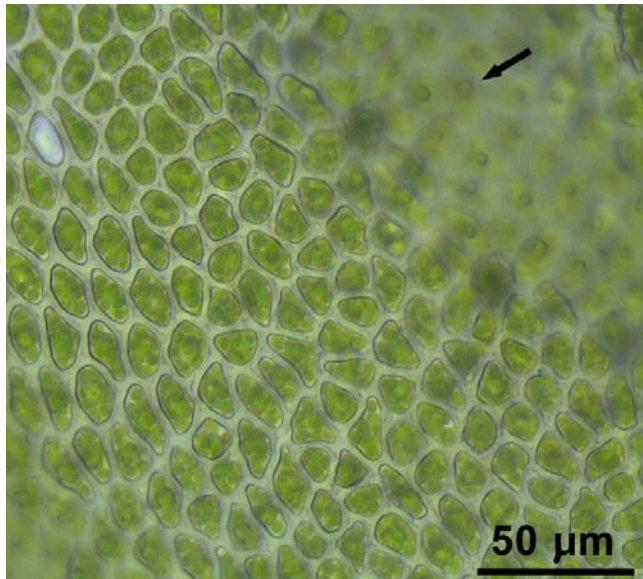


Figure 124. *Aulacomnium palustre* leaf lamina showing papillae, best seen in the upper right corner at arrow. Photo by Kristian Peters, through Creative Commons.



Figure 125. *Helodium blandowii*, a moss that feels "crunchy" due to papillae. Photo by J. C. Schou, through Creative Commons.



Figure 126. *Helodium blandowii* leaf with **prorate** cells. Photo by Kristian Peters, with permission.



Figure 127. *Paludella squarrosa*, emergent in full sun. Photo by Michael Lüth, with permission.

Some papillae are quite decorative, adorning species that typically live on limestone rocks or other highly desiccating habitats. *Encalypta ciliata* (Figure 128-Figure 130) has branched papillae and lives on limestone rocks and other dry locations.



Figure 128. *Encalypta ciliata* in a hydrated state, showing the nearly translucent appearance of the leaves. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 129. *Encalypta ciliata* in a dry state, showing the dull surface of the contorted leaves. Photo by Li Zhang, with permission.

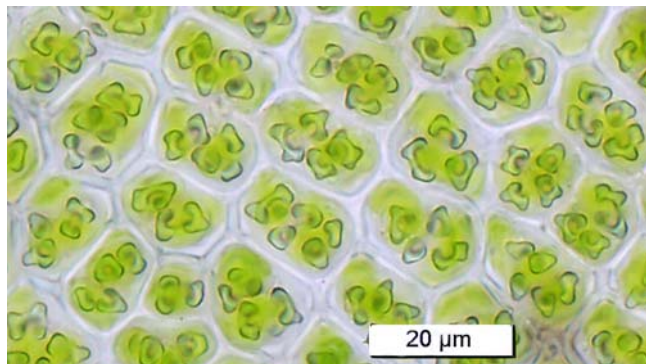


Figure 130. *Encalypta ciliata* leaf cells with multiple papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Proctor (1979a, 1984, also Longton 1988) described the interstitial spaces between papillae as forming a capillary conducting system that is capable of rapid water movement, as we might expect in *Tortula muralis* (Figure 131-Figure 132). (See also the chapter on Leaf Strategies – Cuticles and Waxes in this volume.) But papillae may be most important in altering the boundary layer and creating a dead space that reduces water loss. Both of these ideas, as well as their role in deflecting UV light, remain to be tested.



Figure 131. *Tortula muralis* leaf cross section showing the multiple papillae on each cell. Photo from Botany Department website, University of British Columbia, with permission.

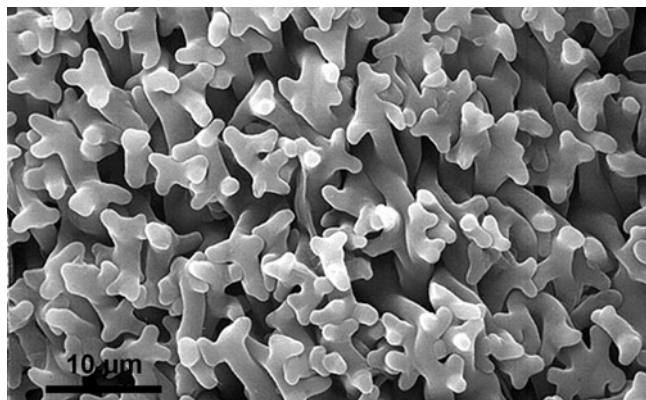


Figure 132. SEM of papillae on *Tortula muralis*, illustrating the type of channelling described by Proctor (1984). Photo with permission from Botany 321 website, <www.botany.ubc.ca/bryophyte/LAB8.htm>, with permission.

Hedwigia ciliata (Figure 133-Figure 134) is a moss that has white tips on its leaves, presumably protecting the underlying leaves from sun damage. But we need to examine the role of these tips in water uptake as well. The leaf and awn cells are heavily endowed with papillae that give the leaves a waxy appearance despite the absence of waxes.



Figure 133. *Hedwigia ciliata* with hyaline tips and awns on leaves. Photo by Michael Lüth, with permission.



Figure 134. Hyaline hair tip on the leaf of *Hedwigia ciliata*. Note the numerous papillae on these awn (hair tip) cells as well as on the lamina cells. Photo by Janice Glime.

At least some leaf papillae (*Andreaeobryum macrosporum*, Figure 135) are constructed in such a way that they provide a channel for the uptake of water (Crandall-Stotler & Bozzola 1990, 1991). This channel is within each papilla and is different from the channels formed between the papillae (*cf.* Proctor 1984). SEM observations indicate the channel within the papilla facilitates the rapid uptake of water during rehydration (Crandall-Stotler & Bozzola 1990, 1991). So far, this channel has not been demonstrated in any other species.

So how can papillae function both for water absorption and water loss, and why would evolution tolerate such a seeming contradiction? Pressel *et al.* (2010) may have answered this question. They found that in *Rhacocarpus purpurascens* (Figure 136), the trilemmate (having 3 layers) walls have a porous outer layer that permits rapid uptake of water, whereas its cuticle-like layer is highly hydrophobic and prevents water-logging. Could it be that the papillae of bryophytes create that space needed to prevent water-logging? But Pressel and coworkers contend that papillae in *R. purpurascens* accelerate water loss,

resulting in a metabolic shutdown when the plants are water-stressed. With the wide variety of shapes, sizes, and density of papillae among the bryophytes, it is still possible that some have the ability to prevent water-logging during the critical periods when the plants are wet in normally dry habitats. If this ability exists, it may be of considerable importance in at least some cases.



Figure 135. *Andreaeobryum macrosporum*, a moss for which papillae are known to aid in uptake of water through a channel in the papilla. Photo from Botany website, University of British Columbia, Canada, with permission.



Figure 136. *Rhacocarpus purpurascens* showing shiny leaves. Photo by Michael Lüth, with permission.

One such species is the desert moss, *Syntrichia caninervis* (Figure 115, Figure 137-Figure 139). When Wu *et al.* (2014) compared absorption of rhizoids to that of leaves, the leaves were clearly the greater absorptive organs. They tested absorption by dropping water onto the upper and lower leaf surfaces, both of which have C-shaped papillae (Figure 137) (Zheng *et al.* 2010). Wu and coworkers found that the adsorption by the papillae is so rapid that they could not determine the leaf angles. They concluded that in this case the papillae are **superhydrophilic** (having a highly efficient water absorption mechanism). The spaces between the papillae form microcapillary spaces that serve as an efficient conducting system (see also Koch *et al.* 2008).

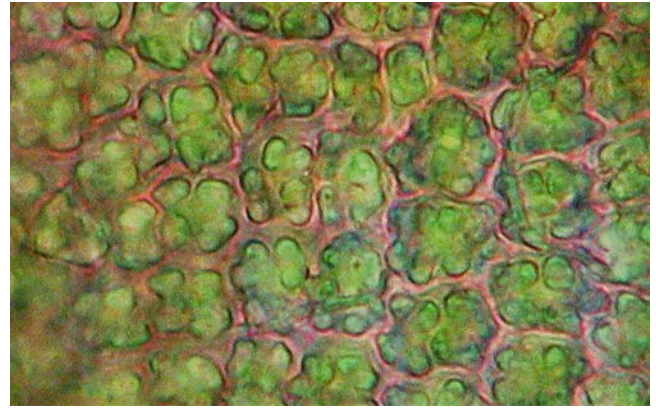


Figure 137. *Syntrichia caninervis* leaf papillae. Photo by Michael Lüth, with permission.

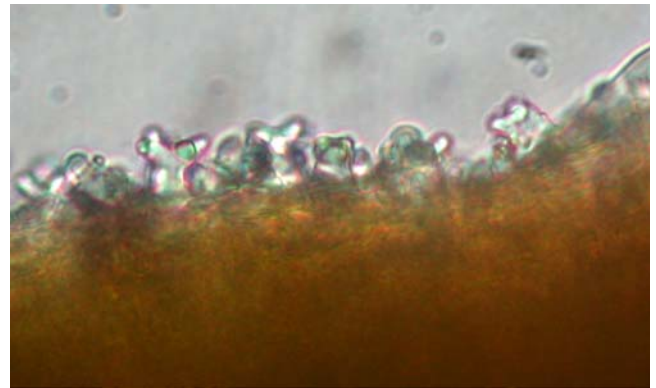


Figure 138. *Syntrichia caninervis* side view of leaf papillae that appear C-shaped from above. Photo by Terry McIntosh, with permission.

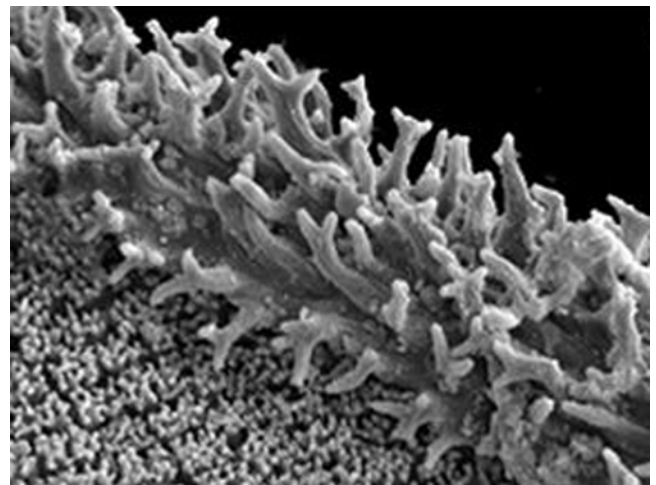


Figure 139. *Syntrichia caninervis* var. *caninervis* showing long papillae on costa and smaller ones on cells. Photo by M. T. Gallego.

The only thing that seems clear about papillae is that our understanding of them is not clear. It is likely that papillae cannot be lumped into one function, but that shapes, structure, and arrangement may create different capabilities, and these must coordinate in various ways with surface waxes, cell wall components, and other leaf surface features to optimize their role in the climates where the bryophytes live.

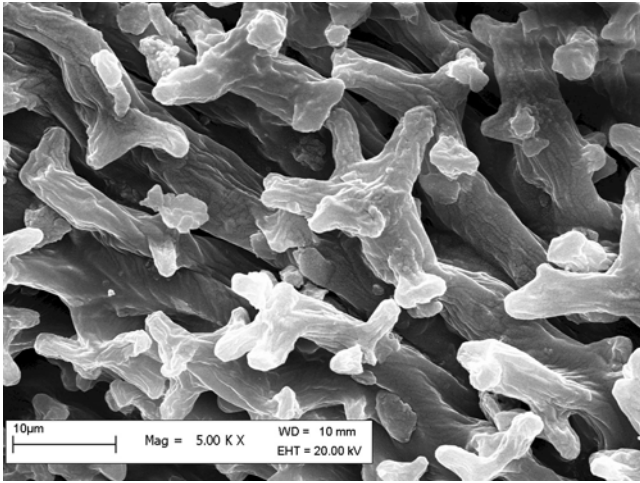


Figure 140. *Syntrichia caninervis* SEM of papillae on abaxial leaf surface. Photo by Zhang Yuan Ming.



Figure 142. Leaf of *Calliergon giganteum* showing costa and enlarged **alar cells** at leaf base. Photo by Michael Lüth, with permission.

Leaf Bases and Alar Cells

Many mosses have the advantage of enlarged, thin-walled cells at the base of the leaf (**alar cells**) (Figure 141- Figure 142). These serve as entry points for water into the leaf and stem, but in many species their enlargement when fully hydrated also forces the leaf away from the stem, exposing greater surface area for photosynthesis, and perhaps even for water capture.

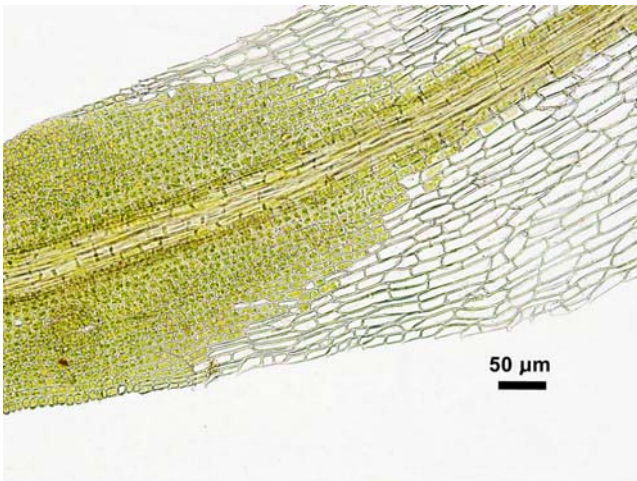


Figure 141. *Tortella tortuosa* leaf base showing enlarged hyaline cells where water can enter and cells can swell. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Those alar cells that are thin-walled shrink upon drying and readily gain water as it moves along external capillary spaces. Tucker and coworkers (1975) describe shrinkage of the basal cell cytoplasm during dehydration, creating gas pockets. Upon rehydration, the pockets of gas shrink and disappear within 10-30 seconds and the cytoplasm expands to fill the entire cell. This can explain the rapid unfolding of leaves upon rewetting in many taxa of bryophytes, with alar cells acting like the bulliform (expansion) cells of grasses.

Wu *et al.* (2014) demonstrated the importance of adjusting the leaf angle in the desert moss *Syntrichia caninervis* (Figure 115, Figure 144). Although this moss is extremely desiccation tolerant, it must balance the need for water conservation with the need for light for photosynthesis when it is hydrated. This is accomplished by the movement of the leaves in response to moisture changes. As leaves become hydrated, they can move from a steep angle of 69-84° with the horizontal axis (Figure 144) to one of only 30° (Figure 115) within 7 seconds of becoming hydrated, with the first leaves moving within 1 second. They are able to obtain maximum net photosynthetic gain at a shoot relative water content of only 60%. The hyaline cells at the leaf base facilitate the rapid absorption of water, but they also swell and force the leaf away from the stem mechanically. It is interesting that the loss of leaf hair retards the leaf angle adjustment. When water was added to the soil instead of being added as an aerial source of water, the absorption rate was reduced, indicating that most water absorption is through the leaves.



Figure 143. *Syntrichia caninervis* leaf showing hyaline cells at the base that force the leaf away from the stem when it is hydrated. Photo by Dorothy Allard.



Figure 144. *Syntrichia caninervis* dry showing leaves twisted about the stem. Photo by Misha Ignatov, with permission.

Leaf Cell Shape

Bill Buck once asked me what I thought about the elongate cells in mosses such as *Fontinalis* and what the significance of such elongate cells might be, predominant in pleurocarpous mosses but rare in acrocarpous ones. I don't know that either of us has a better answer than we did then, but long, narrow cells should have an advantage in water movement. Elongate cells mean that fewer end walls must be crossed for water and other substances to traverse the interior of the leaf from tip to base or vice versa. The split between acrocarpous and pleurocarpous mosses suggests to me that the innovation of elongate cells, perhaps unnecessary in aquatic ancestors, occurred early in the evolution of pleurocarpous mosses and was rarely achieved among the acrocarpous species.

In the acrocarpous moss *Bryum pseudotriquetrum*, this elongation is partially achieved (Figure 145). This is a moss of wet habitats that dries out. The leaves are usually out of the water, and having somewhat elongated cells should improve transport.



Figure 145. *Bryum pseudotriquetrum* leaf showing somewhat elongate cells, bordered by longer cells. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

It is interesting that many acrocarpous mosses have short leaf cells and tend to be more endohydric, whereas

the pleurocarpous mosses, largely lacking a central strand and endohydric conduction, have mostly elongate leaf cells. Although these elongate cells would seemingly facilitate conduction between cells and from the leaf surface to the stem, we lack experimental evidence to support this.

Porose Cells

Porose cells provide more cause for speculation. These cells, uncommon among bryophytes, would seem to provide linkages to adjoining cells while permitting the cells to have otherwise thick walls. Such porosity is easily seen in *Dicranum polysetum* (Figure 146). I am unaware of any experiments to demonstrate that this is actually true or to compare the rate of transport in leaves with such cells to those in leaves with non-porose cell walls.



Figure 146. *Dicranum polysetum* leaf cell wall structure. Photo by Walter Obermayer, with permission.

Hyalocysts

Colorless or **hyaline** cells (Figure 147) are typical of leaves of *Sphagnum* (Figure 148) and *Hedwigia* (Figure 134), and the awns of numerous xerophytes. Frahm (1985) examined the correlation between **hyalocysts** and habitat in *Campylopus* (Figure 149). *Campylopus shawii* occurs in wet swamps where it can obtain and store water easily; it has large ventral hyalocysts. *Campylopus setifolius*, on the other hand, grows on wet, dripping rocks that dry out occasionally; it has smaller hyalocysts, presumably to reduce the water loss to evaporation from these cells. The presence of ventral hyalocysts in *C. flagelliferus* (Figure 149) seem to adapt it to its life restricted to the bark of living trees where it needs a means of rapid water uptake.

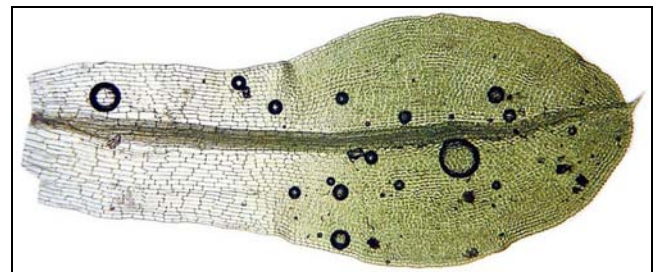


Figure 147. Leaf of *Tortula vahlana* showing hyalocysts in basal half of leaf. Photo by Michael Lüth, with permission.

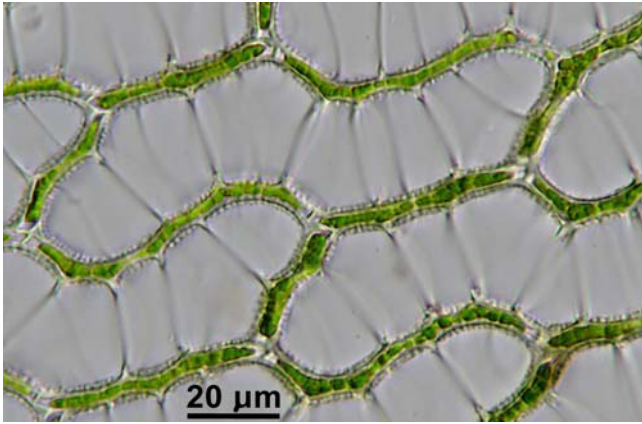


Figure 148. *Sphagnum papillosum* leaf cells showing large hyaline cells with fibrils and green photosynthetic cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 149. *Campylopus flagelliferus*, an epiphyte with ventral hyalocysts. Photo by Jan-Peter Frahm, with permission.

Species of the cushion moss, *Leucobryum* (Figure 18, Figure 150), appear very succulent because of the hyalocysts among the photosynthetic cells. In this case, the leaf is several cells thick and the hyalocysts give them a whitish appearance. *Leucophanes* (Figure 151-Figure 152) has two different types of hyalocysts. The base of the leaf has a V-shaped arrangement of hyaline cells and the leaf lamina has an upper and lower layer of hyaline cells surrounding the photosynthetic cells.



Figure 150. *Leucobryum juniperoideum*, showing the thick, whitish leaves. Photo by Michael Lüth, with permission.



Figure 151. *Leucophanes molleri* leaf showing v-shaped hyaline base. Photo courtesy of Noris Salazar Allen.

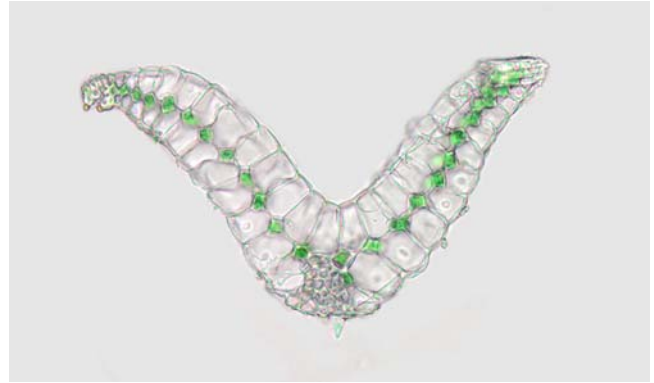


Figure 152. Cross section of *Leucophanes molleri* leaf showing hyaline cells surrounding the photosynthetic cells. Photo courtesy of Noris Salazar Allen.

Sphagnum species are considered xerophytic hydrophytes with many adaptations to deal with periodic drought (Andrus 1986). Living in a watery mire for most of the year, this genus has no internal conducting system and must face a severe threat of drying in the full sun of the summer when the water table is low. The ectohydric *Sphagnum* is a poor drought tolerator, but a relatively good drought avoider (Li *et al.* 1992). It has two types of leaf cells, small photosynthetic cells and large hyaline cells (Figure 153).

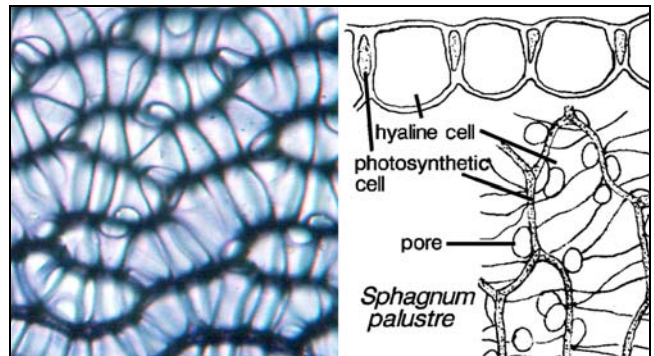


Figure 153. *Sphagnum* leaf cell types and pores. **Left:** *Sphagnum* leaf cells stained with crystal violet. Photo by Janice . Glime. **Right:** *Sphagnum palustre* photosynthetic and hyaline cells as seen in cross section (**upper**) and flat (**lower**). Drawings by Margaret Minahan.

Hyaline cells bathe the photosynthetic cells in water by providing a reservoir. Since the hyaline cell is a dead cell, its sole purpose seems to be to supply water to the photosynthetic portion of the leaf. These cells give some species of *Sphagnum* (Figure 153-Figure 154) the ability to hold up to 25 times their own mass in water (Andrus 1986).

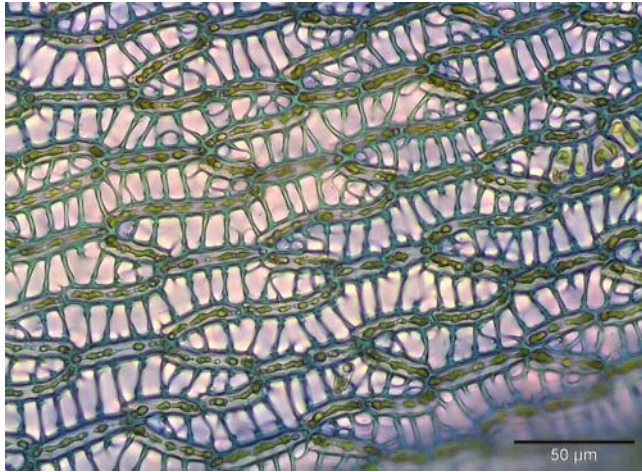


Figure 154. *Sphagnum fallax* leaf cells under normal nutrient conditions. Hyaline cells disappear under certain high N or low carbohydrate conditions in culture. Photo by Kristian Peters, with permission.

Transplant studies indicate that species of *Sphagnum* differ in abilities to inhabit different heights above the water level, and these differences seem to correlate with the positions they occupy in the field (See Li *et al.* 1992, Rydin 1993, and discussion in competition chapter). Studies by Hintikka (1972) hint that the mechanism for some of these adaptive differences may not relate to water, but to other factors associated with submersion. When grown in sterile culture, *S. fallax* (Figure 154) produced no hyaline cells in the presence of high ammonium, high organic nitrogen, or low carbohydrates. In nature, ammonia from decomposing plant matter would be greater under water than around emergent plants, quickly diffusing away in the atmosphere. Likewise, amino acids from organic decomposition would be present only in submersion water, not in rainfall. Response to low carbohydrates may be a limit in carbon available for making additional cell wall tissue, a need for an energy source, or it could relate to CO₂ from decomposing plant material in interstitial bog or fen waters.

Sphagnum seems to require a tremendous water content to achieve its maximal net photosynthesis, probably supplied by the large reservoir of water in its non-photosynthetic hyaline cells. In *S. fuscum* (Figure 155), a hummock top species, 600-1000% saturation was optimal, whereas in *S. angustifolium* (Figure 156), which tends to occur somewhat closer to the water surface, 900-1300% was optimal (Silvola & Aaltonen 1984), indicating the greater need for water in species that live closer to the water level. The photosynthetic decrease with water reduction was steeper for *S. fuscum*, and plants in the field generally occurred where their water content was within this 600-1000% range. In *S. angustifolium*, however, plants often occurred where their water content was outside their optimum range, thus defining narrow and broad relative niches.

Sphagnum is well known for its morphological plasticity in response to water availability (Miller 1991). For example, *Sphagnum magellanicum* (Figure 157) and *S. papillosum* (Figure 158) in dry conditions produce leaves that are longer (Figure 159) with more pores per cell (Figure 160). Li and coworkers (1992) suggest that these modifications may promote water-holding and absorbing properties.



Figure 155. *Sphagnum fuscum* in its typical position atop a hummock. Photo by Michael Lüth, with permission.



Figure 156. *Sphagnum angustifolium*, a species that lives low on a hummock. Photo by Michael Lüth, with permission.



Figure 157. *Sphagnum magellanicum*, a species that makes longer leaves under dry conditions. Photo by Janice Glime.



Figure 158. *Sphagnum papillosum*, a species that makes longer leaves under dry conditions. Photo by Michael Lüth, with permission.

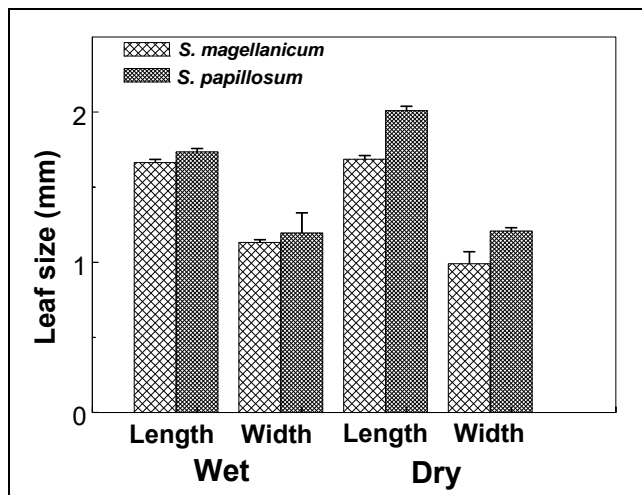


Figure 159. Comparison of leaf dimensions in *Sphagnum magellanicum*, a drought-resistant species, and *S. papillosum*, a more drought-tolerant species. Based on Li *et al.* (1992).

Yet, these two species also differ in their water relations (Li *et al.* 1992). *Sphagnum magellanicum* (Figure 157) seems to be a better competitor for water than is *S. papillosum* (Figure 158) under dry conditions. This is exhibited by its better water transport ability and greater water content under the same atmospheric moisture conditions (Figure 161). This greater ability may be facilitated by its greater stem diameter due to larger hyaline cells, greater pore number, and smaller leaf size. On the other hand, *S. papillosum* (Figure 158) seems to be a better drought tolerator, having a higher survivorship following severe drought conditions.

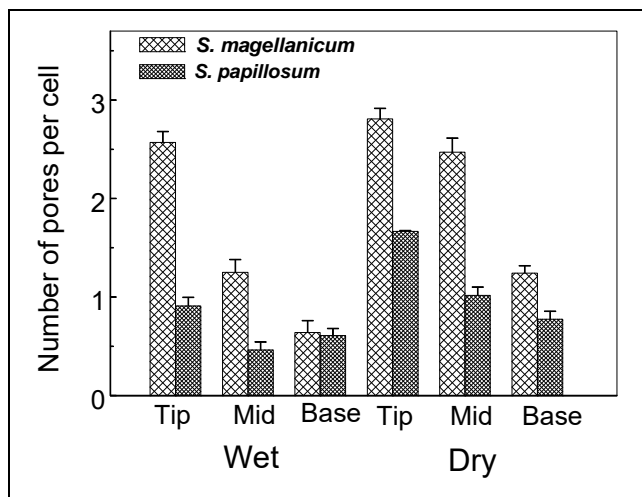


Figure 160. Comparison of number of pores per leaf cell in *Sphagnum magellanicum*, a more drought-resistant species, and *S. papillosum*, a more drought-tolerant species. Based on Li *et al.* 1992.

Superiority in water transport permits *S. magellanicum* (Figure 157) to occupy a higher position in the hummock than does *S. papillosum* (Figure 158). Li and coworkers (1992) found that when the two species grow intermixed in the higher hummock positions, both species grow better than if either is alone, provided at least half the plants are *S. magellanicum*. They suggest that lateral transport among stems may occur to facilitate this, with *S. magellanicum* providing water for both species. If

S. papillosum is dominant, even at somewhat lower positions in the hummock, both dry out more quickly.

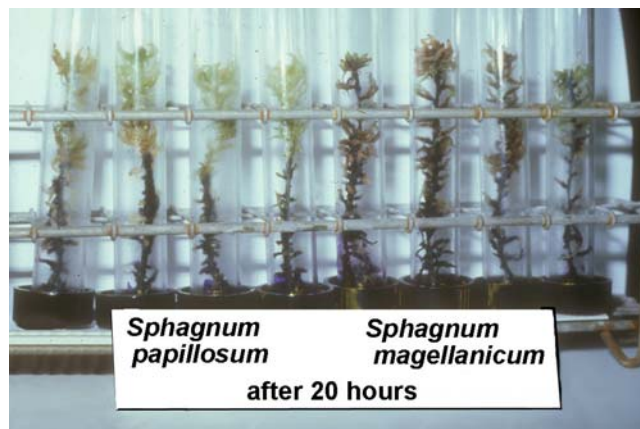


Figure 161. Comparison of distance a water-soluble dye has moved in 20 hours in *Sphagnum papillosum* and *Sphagnum magellanicum*. Photo courtesy of Yenhung Li.

Cancellinae

The **cancellinae** (sing. cancellina) occur in few bryophytes, but especially in the **Calymperaceae**, **Pottiaceae**, **Encalypta** (Figure 163-Figure 164), and some species of **Leptodontium** (Figure 162). They are large, empty basal leaf cells, usually hyaline, that form a lattice. In the **Calymperaceae**, these are porate (having pores), and may serve as water storage cells.

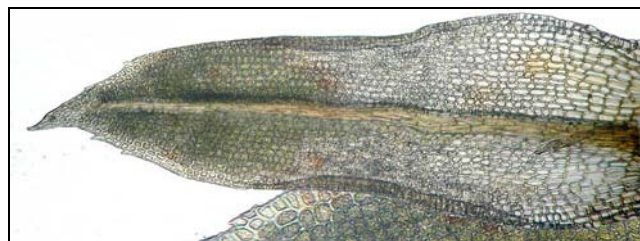


Figure 162. *Leptodontium* from the Neotropics showing cancellinae in the upper leaf. Photo by Michael Lüth, with permission.

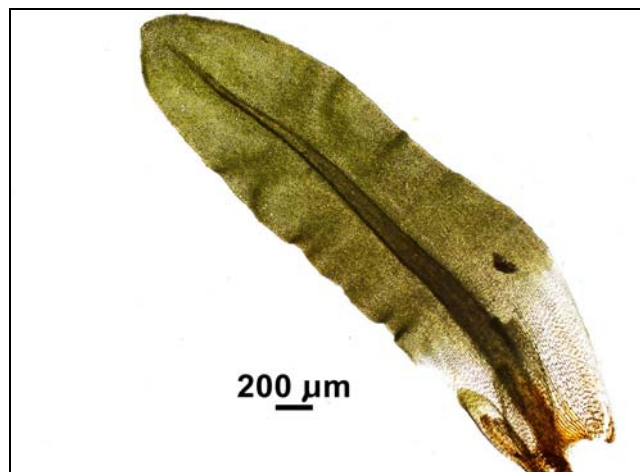


Figure 163. *Encalypta vulgaris* leaf showing lattice of cancellinae (gold walls) at base of leaf. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

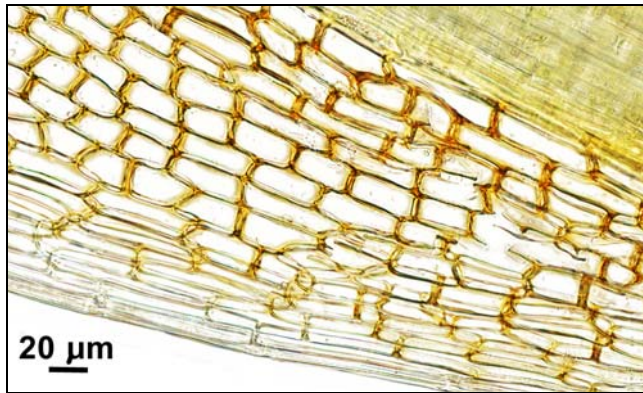


Figure 164. *Encalypta vulgaris* leaf showing lattice of cancellinae (cells with gold walls). Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Cell Structure

Cells structures can differ in a variety of ways that can affect water uptake, movement, and conservation. These differences include cell wall thickness, cell wall components, pores in the walls, internal papillae, presence of oil bodies, and vacuole size. These differences have the potential to alter the water relations of the leaves.

Cell Walls

Guerra *et al.* (1992) included **incrassate** cell walls among the adaptations of xerophytic mosses. Examples of these include *Aloina aloides* (Figure 165-Figure 166) and *Didymodon fallax*. (Figure 167-Figure 168).



Figure 165. *Aloina aloides*, a dry habitat moss with incrassate leaf cell walls. Photo by Michael Lüth, with permission.



Figure 166. *Aloina aloides* leaf cells showing incrassate cell walls. Photo by Heike Hofmann © swissbryophytes <www.swissbryophytes.ch>, with permission.



Figure 167. *Didymodon fallax*, a dry habitat species. Photo by David T. Holyoak, with permission.

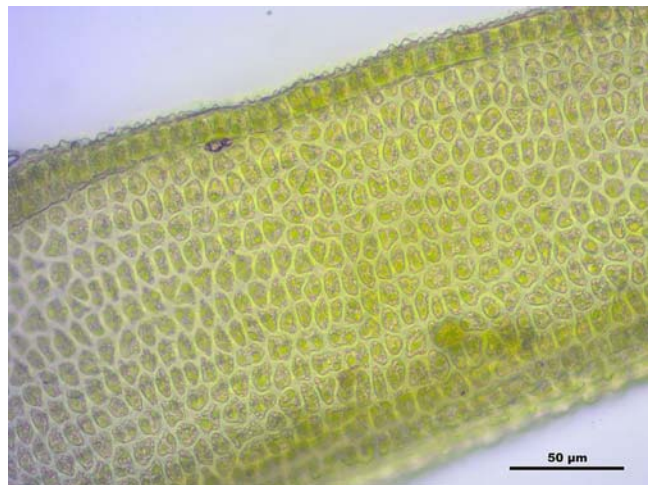


Figure 168. *Didymodon fallax* with incrassate leaf cell walls. Photo by Hermann Schachner, through Creative Commons.

Proctor (1979a) contends that coarse leaf cell walls (Figure 169) seem to aid water movement, possibly creating more internal capillary spaces among the fibrils of the cell wall (Proctor 1982). Proctor (1984) noted that mosses of dry habitats tend to have thick cell walls that can occupy more than half the cross section of the leaf. Fajuke (2010) further found that six mosses from Nigeria had thick cell walls that helped them survive desiccation.

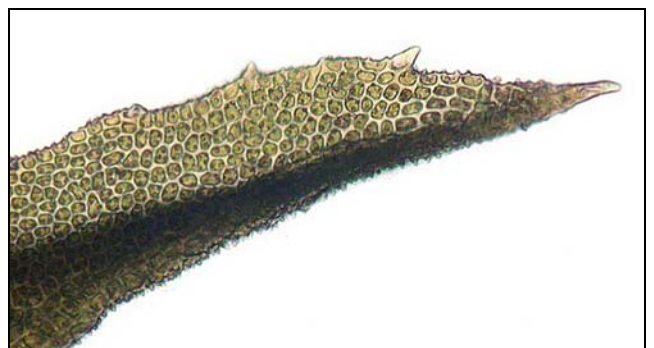


Figure 169. Leaf of *Zygodon dentatus* showing thick cell walls and papillae. Photo by Michael Lüth, with permission.

On the other hand, Frey and Kürschner (1991) could find no correlation between thickened cell walls and increasing aridity. Proctor (1982) also pointed out that such xerophytic mosses as *Syntrichia* (Figure 170-Figure 171), *Encalypta* (Figure 172-Figure 173), and *Anomodon viticulosus* (Figure 174-Figure 175) have quite thin walls and external conduction, suggesting that the thick walls are associated with species having internal conduction.



Figure 170. *Syntrichia ruralis*, a moss of xeric habitats. Photo by Michael Lüth, with permission.

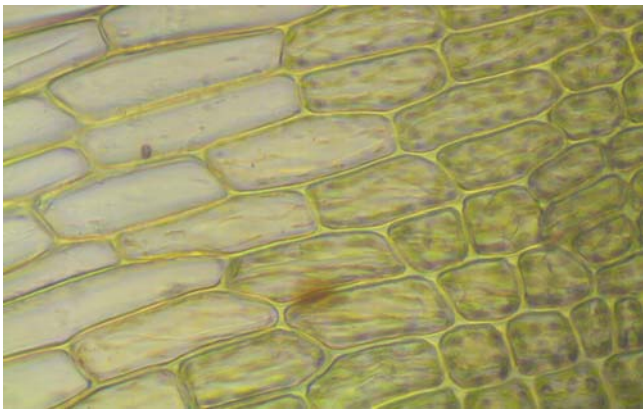


Figure 171. *Syntrichia ruralis* leaf lamina cells showing thin walls. Photo by Kristian Peters, with permission.



Figure 172. *Encalypta rhabdocarpa* showing xeric habitat in Europe. Photo by Michael Lüth, with permission.

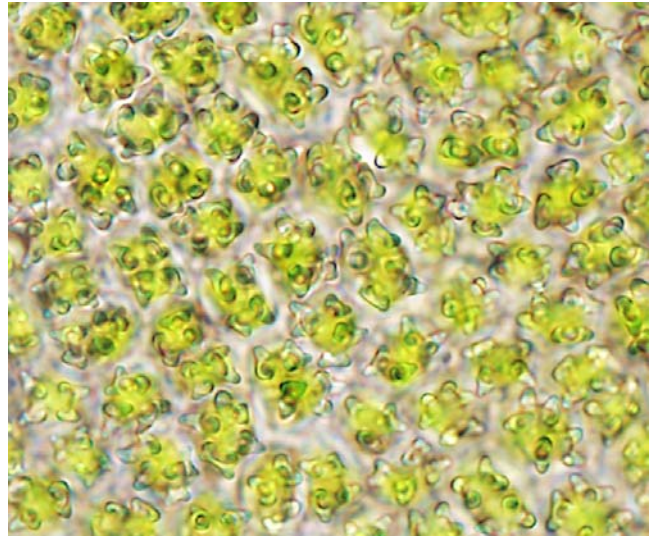


Figure 173. *Encalypta vulgaris* leaf cells with branched papillae and thin cell walls. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 174. *Anomodon viticulosus*, a xerophytic moss with thin cell walls and papillae. Photo by Janice Glime.

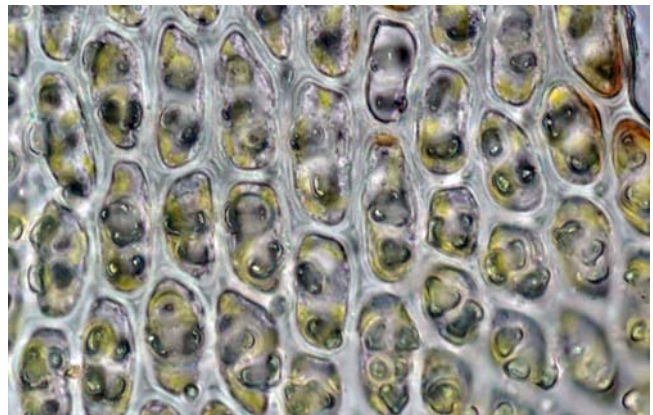


Figure 175. *Anomodon viticulosus* leaf cells and papillae. Proctor (1982) considered this species to have thin cell walls, but that does not appear to be the case in this example. Photo by Walter Obermayer, with permission.

The moss *Rhacocarpus purpurascens* (Figure 136) appears to have a unique means of facilitating rapid absorption of fog, dew, and rain (Barthlott & Schultze-Motel 1981; Edelmann *et al.* 1998). It has four layers of cell wall with a "peculiar architecture," forming cavities within the wall.

Flexibility of the cell wall is undoubtedly an aid to cell survival. This permits the cells to shrink upon dehydration, up to 50-70% in *Syntrichia ruralis* (Figure 176), without allowing for air to enter the drying cells (Moore *et al.* 1982).

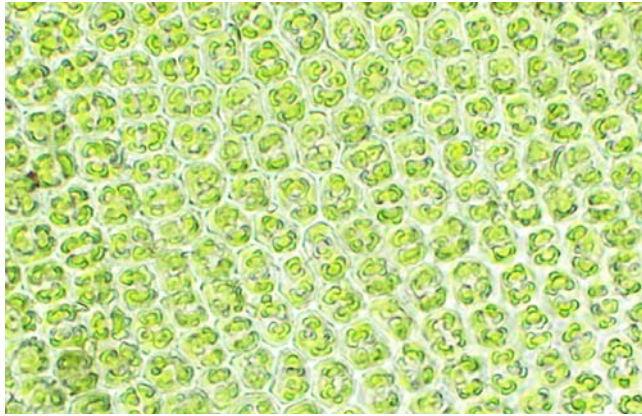


Figure 176. *Syntrichia ruralis* leaf cells with c-shaped papillae and thin walls. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Popper and Fry (2003) suggest that the addition of **xyloglucans** to the cell wall components may have been an important contribution to the ability of bryophytes to invade land. The presence of high concentrations of uronic acids would have permitted these plants to hold nutrient ions until such time as water was available for transport.

Cell walls seem like the first line of defense against desiccation. Autofluorescing compounds that can strengthen these walls are present in sporangial epidermis, spiral thickenings of elaters, and rhizoids, and leaf cells in the special case of *Sphagnum* (Figure 177) Krokken *et al.* (1996). In charophytes, these resistant compounds have multiple functions that include desiccation resistance and microbial resistance in lower charophytes, a role in embryogenesis in *Coleochaete* (Figure 178) and embryophytes, and decay resistance in structures that characterize bryophytes, such as rhizoids, sporangial epidermis, and elaters.



Figure 177. *Sphagnum palustre* cells showing the spiral thickenings on the hyaline cells. Photo by Malcolm Storey, through Creative Commons.



Figure 178. *Coleochaete*, an alga with slime papillae and other characters that are more common among bryophytes. Photo by Yuuji Tsukii <<http://protist.i.hosei.ac.jp/>>, with permission.

It appears that the resistance of cell walls to desiccation is an ancient trait, already present in the green alga *Coleochaete* (Figure 178) (Krokken *et al.* 1996). In fact, it seems to be unique to *Coleochaete* among the charophytes and the resistance is produced in response to desiccation stress.

But bryophytes also have this ability – sexual reproduction induces autofluorescence in the cell walls of well-hydrated tissues at the placental junction, suggesting that these cell walls are endowed with compounds (phenols?) that endow them with desiccation resistance (Krokken *et al.* 1996). A similar phenomenon occurs in the gametophyte tissue at the apical end of the **pseudopodium** (gametophyte stalk that suspends the *Sphagnum* capsule away from the plant; Figure 179), suggesting a similar role to that of other bryophytes and even *Coleochaete* (Figure 178).



Figure 179. *Sphagnum* pseudopodia supporting capsules. The swollen upper end is desiccation tolerant and houses the foot of the sporophyte. Photo by Joan Edwards, with permission.

Lignin: The presence of lignin in bryophytes has been a controversial topic for ages. Lignins are present in xylem and sclerenchyma cells of tracheophytes. To demonstrate whether these substances might be present in bryophyte and charophyte cell walls, Ligrone *et al.* (2008) examined the charophyte *Nitella* and a number of bryophytes. Using polyclonal antibodies that labelled lignified walls in tracheophytes, they found that these also bound to the cell walls of bryophytes. But rather than the specific locations found in tracheophytes, the locations in mosses and liverworts were not tissue-specific. Hornworts (*Megaceros flagellaris* and *M. fuegiensis*; Figure 180) differed somewhat in that labelling was stronger in pseudoelaters and spores than in other cell types. Cell walls were likewise labelled in the charophyte *Nitella*, but a lack of binding suggested that lignins or lignin-like substances were absent in *Coleochaete*.

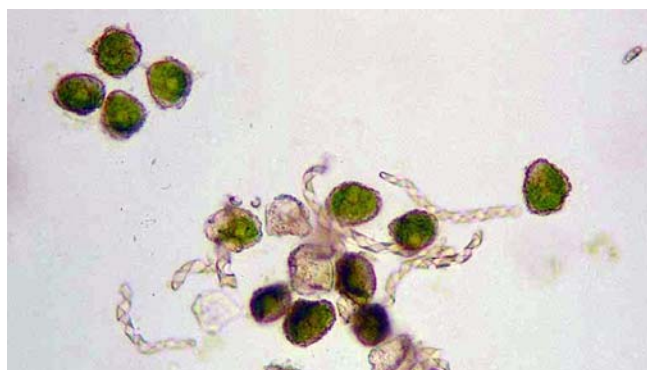


Figure 180. *Megaceros* spores and elaters, a genus in which lignin labelling is stronger in spores and elaters than in other cell types. Photo by Christine Cargill, with permission.

Oil Bodies

Oil bodies are common in the leaf cells of leafy liverworts (Pfeffer 1874; Garjeanne 1903; Müller 1905, 1939; Schuster & Hattori 1954; Pihakaski 1972a, b; Stewart 1978; Schuster 1992; Asakawa 2004), but similar structures are generally absent in mosses. Kronstedt (1983) found that they had seasonal variability in the nature of the matrix and the amount of lipophilic material in the floating liverwort *Ricciocarpus natans* (Figure 181). The globules can coalesce to form larger units. Their role has remained a mystery (He *et al.* 2013), but recently several researchers have provided evidence that they may have a crucial role in desiccation tolerance.

Oil bodies seem to have different developmental pathways in different species. Pihakaski (1966, 1968, 1972a) compared their development in two leafy liverworts – *Bazzania trilobata* (Figure 182-Figure 183) and *Lophozia ventricosa* (see Figure 184). The component parts are the same in both species: an outer membrane that envelops the whole oil body, a granular stroma layer that varies in size and thickness, specific globules enveloped by the stroma layer, and a thin inner membrane that surrounds the specific globules. But the oil bodies in these two species develop in different ways. In *B. trilobata*, they develop from vacuole-like formations in the shoot apex or in leaf primordia where certain substances segregate. In this species, granular dense bodies are visible in the cells of

the shoot apex, but these shrink in size as oil bodies develop and are absent in the mature leaf cells. In *L. ventricosa* they originate by aggregation and fusion of lipid bodies.



Figure 181. *Ricciocarpus natans*. Photo by Štěpán Koval, with permission.

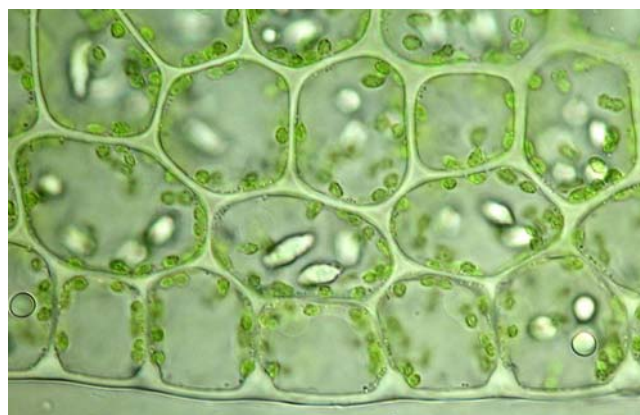


Figure 182. Oil bodies (transparent) in leaf cells of *Bazzania trilobata*. Photo by Walter Obermayer, with permission.

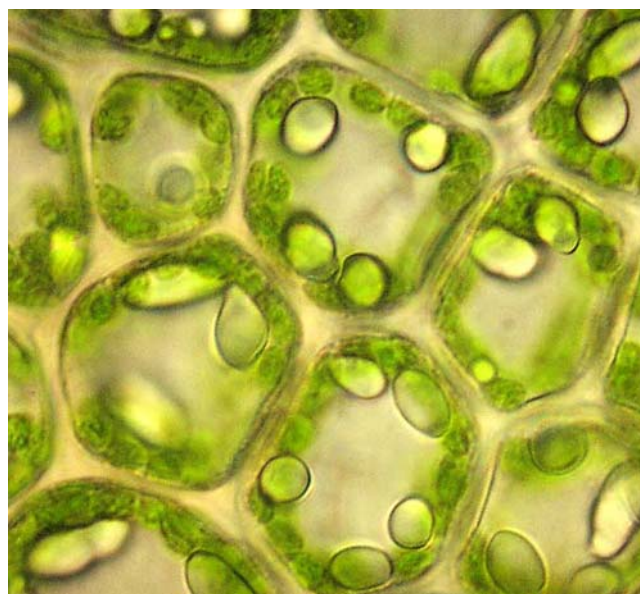


Figure 183. Oil bodies (transparent) in leaf cells of *Bazzania trilobata*. Photo by Walter Obermayer, with permission.

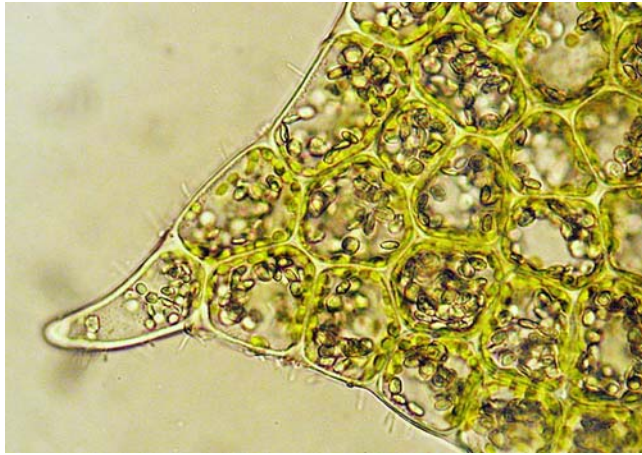


Figure 184. *Lophozia incisa* leaf cells with oil bodies. Photo by Walter Obermayer, with permission.

Duckett and Ligrone (1995) followed the development of oil bodies in gemmae of *Odontoschisma denudatum* (Figure 185). They appear suddenly early in development, forming flat structures associated with the endoplasmic reticulum. Suire (2000) provided evidence that liverwort oil bodies are secretory cell compartments that originate from the endoplasmic reticulum. The oil bodies remain closely associated with the cytoplasmic lipid bodies throughout development but do not fuse with them. Finally they take on their ultimate shape and become suspended by fine cytoplasmic bridges within the vacuoles.

Oil bodies are notorious for disappearing in herbarium specimens. Pressel *et al.* (2009) described this behavior for desiccation-tolerant liverworts. They found that while they are dry, they remain substantially unchanged, but when they are rewet, they initially change drastically, becoming flattened. It requires up to 48 hours for them to regain their normal shapes. However, if the liverworts are dried faster than would typically happen in nature, they, and other organelles, disintegrate when the liverwort is rewet. Pressel *et al.* suggested that loss of shape upon normal rewetting could be evidence of a shift in soluble carbohydrates or other substances into the cytosol, indicating that the oil bodies may be critical to the desiccation tolerance of liverworts.

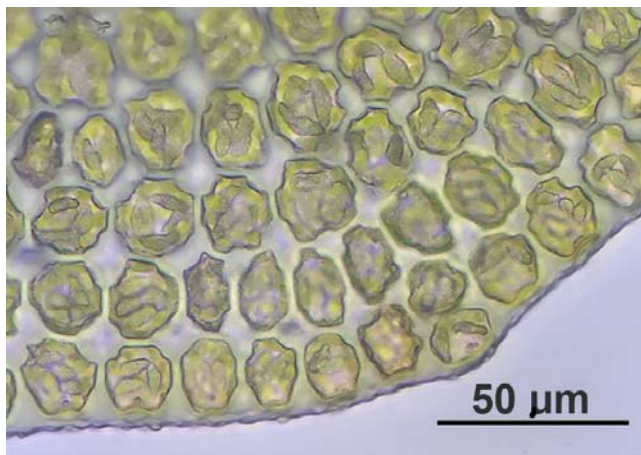


Figure 185. *Odontoschisma denudatum* "cuticular" papillae (see leaf edge), leaf cells, and oil bodies. Photo by Kristian Peters, with permission.

Galatis *et al.* (1978) found phenolic and "polysaccharidic" compounds but no protein in the oil bodies of *Marchantia palacea* (Figure 186). On the other hand, He *et al.* (2013) reported that in *Marchantia polymorpha* (Figure 187) the oil bodies (Figure 188) contain a protein complex that is immunologically related to plastid and cytoplasm enzymes of the **isoprenoid** synthesis (isoprenoids belong to a class of organic compounds composed of two or more units of hydrocarbons, with each unit consisting of five carbon atoms in a specific pattern; they have a wide range of roles in physiological processes of plants and animals). Suire *et al.* (2000) similarly found isoprenoid biosynthetic enzymes similar to those found in plastids and the cytosol of *Marchantia polymorpha*. The suggested paucity of protein in the oil droplets of liverworts (Galatis *et al.* 1978) is likewise in sharp contrast with that found in the green alga *Chlamydomonas reinhardtii* (Moellering & Benning 2010). In this alga, 259 proteins were associated with lipid droplets.



Figure 186. *Marchantia palacea* thallus with archegoniophores, a species with phenolic and "polysaccharidic" compounds but no protein in the oil bodies. Photo from Briofitas de Mexico, through Creative Commons.



Figure 187. *Marchantia polymorpha* with ice crystals. This species has oil bodies that contain a protein complex. Photo by David Taylor, with permission.

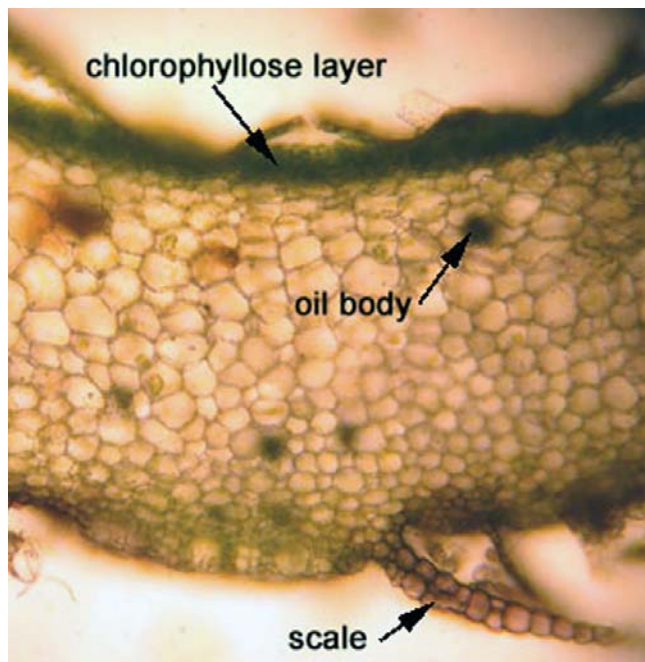


Figure 188. *Marchantia polymorpha* thallus vertical section showing oil bodies. Photo from Botany Department, University of British Columbia, with permission.

Oil bodies of liverworts produce mono-, sesqui-, and diterpenoids, aromatic compounds such as bibenzyl, bis-bibenzyls, and acetogenins (Asakawa 2008; Asakawa *et al.* 2013). These often aromatic compounds have such activities as causing allergenic contact dermatitis, antimicrobial action, antifungal and antiviral action, cytotoxicity, insecticidal action, insect antifeedant, superoxide anion radical release, 5-lipoxygenase, calmodulin, hyaluronidase, cyclooxygenase, DNA polymerase β , and α -glucosidase and NO production inhibition, antioxidant, piscicidal, neurotrophic, and muscle relaxation. But these are mostly uses of interest to humans and do little to tell us how the liverwort benefits from them.

It appears that mosses do have their own version of oil bodies. Huang *et al.* (2009) reported abundant oil bodies in the photosynthetic gametophyte and the spores of *Physcomitrella patens* (Figure 189-Figure 190). These researchers found that neutral lipids in these oil bodies in the gametophyte were largely steryl esters and triacylglycerols, and unlike some reports on the liverwort oil bodies, they had proteins. These proteins were programmed by three oleosin genes. The expression of these oleosin genes were tissue specific. Structural proteins cover the surfaces of the lipid droplets and prevent them from coalescing during desiccation (Huang *et al.* 2009; He *et al.* 2013).

The number of oil bodies in apical gametophyte tissue decreases during the production of sex organs in *Physcomitrella patens* (Figure 189-Figure 190) (Huang *et al.* 2009). In spores, the oil bodies serve as food reserves for **gluconeogenesis** (formation of glucose from smaller molecules) and are equivalent to those of seed oil bodies. It appears that these oil bodies have an energy function for reproduction, but could they be important in providing the energy needed during rehydration as well?



Figure 189. *Physcomitrella patens*, a species produces abundant oil bodies in its leafy gametophyte and spores, but the oil bodies decrease during sex organ production. Photo by Michael Lüth, with permission.



Figure 190. *Physcomitrella patens* sporophyte with spores that contain oil bodies. Photo by Ralf Reski Lab through Wikipedia Commons, with permission.

It seems surprising to me that we know so little about the functioning of oil bodies, especially in liverwort leaf cells. We cannot discount them as a non-functioning structure that happened and wasn't eliminated because they are so widespread. And they have tremendous variability, both in morphology and in chemical constituents. More than 1600 lipophilic compounds have been extracted from liverworts (Ludwiczuk & Asakawa 2019)!

Hieronymus (1892) suggested that oil bodies protected against UV light stress. Schuster (1966) suggested that they help maintain the liverworts through cold, drought, and osmotic stress.

Early experiments demonstrate a role in antiherbivory, with snails preferring species with fewer oil bodies (Stahl 1888). And when oil bodies were leached from some of the liverworts, those were preferred over the non-leached ones. Further support of the antiherbivory hypothesis was demonstrated by genetic manipulation of *Marchantia* (Figure 187-Figure 188). Those plants defective in oil bodies were more likely to be eaten than were the normal populations (Kanazawa *et al.* 2020; Romani *et al.* 2020). Likewise in *Marchantia*, Peñuelas *et al.* (2019) demonstrated that mutant plants with reduced sesquiterpenes experienced greater foraging by *Spodoptera littoralis* caterpillars (Figure 191).



Figure 191. *Spodoptera littoralis* larva, a species that responds to reduced sesquiterpenes in *Marchantia* by eating more of it. Photo by Ishbb, through Creative Commons.

We know that essential oils extracted from liverworts serve as antibiotics against a wide range of organisms (Asakawa & Ludwiczuk 2018). Furthermore, we know that extracts from plants that have reduced oil bodies also have reduced antibiotic activity against bacteria and fungi (Romani *et al.* 2020).

One of the functions of oil bodies is that they enclose vast quantities of sesquiterpenoids and other compounds, meanwhile protecting the cells from the toxicity of these chemicals (Tanaka *et al.* 2016; Romani *et al.* 2022). Mapping of oil body types suggests that they were present in the most recent common ancestor of liverworts and were probably the first secretory structure in land plants.

Tanaka *et al.* (2016) found that nutrient starvation and non-axenic growth in *Marchantia* greatly increases the number of oil bodies, suggesting a possible role in maintaining nutrient reserves. This notion is supported by the chemical properties of the carbohydrates present and the maintenance of turgidity after dehydration (Pressel *et al.* 2009).

To protect the cells from the toxic nature of the specialized compounds, the oil bodies not only compartmentalize the compounds, but also the enzymes needed to make them (Tissier 2018; Suire *et al.* 2000). Hence, the cells are completely protected from these toxic substances. Furthermore, the substances are typically volatile and the oil bodies prevent them from evaporating too quickly. This explains the various aromas one can smell when the tissues are crushed.

Vacuoles

Bryophytes, for some reason, were long thought to lack vacuoles. However, this is not the case, as demonstrated in the liverwort *Lunularia cruciata* (Figure 192) (Carginale *et al.* 2004), the mosses *Physcomitrella patens* (Figure 189) (Nagao *et al.* 2005), *Ephemerum cohaerens* (Figure 193) (Kwok & Rushing 1999), and *Fontinalis antipyretica* (Figure 194) (Bruns 1998). In fact, the vacuoles can be quite large, as witnessed by the chloroplasts crowded around the periphery of the cell in many species. But there has been no systematic study to indicate which bryophytes have vacuoles and which do not. We might ask if there is some correlation between the ability to withstand drought or to take up water, or even to hold on to cellular water as the environment dries and the presence of one or more vacuoles.

Vacuoles are known in plants to contain solutes that control the water uptake by the vacuole (Taiz & Zeiger

1991). In bryophytes, Nagao *et al.* (2005) have demonstrated that ABA affected the appearance of vacuoles during treatment with freezing. Since ABA is also involved in drought tolerance and has resulted in the increased osmotic concentration of protonemal cells, this mechanism of vacuolar preparation should be explored for possible relationships to drought tolerance in various bryophytes. Could presence of a vacuole help the cell take in water more quickly by storing solutes that create an osmotic gradient, yet are safely out of the way of cellular metabolism? Could it also have a role in the ability of the cells to shrink as they dry and expand when wet?



Figure 192. *Lunularia cruciata* thallus section through gemmae cup. This is a species of thallose liverwort with demonstrated vacuoles. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 193. *Ephemerum cohaerens* leaf, a species with demonstrated cell vacuoles in the leaves. Photo by Dick Haaksma, with permission.

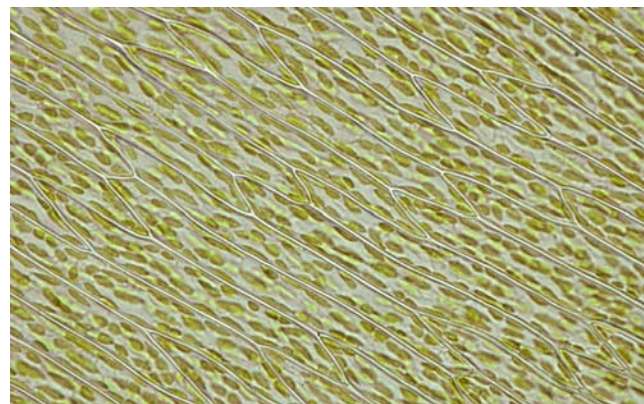


Figure 194. *Fontinalis antipyretica* leaf cells, a species with demonstrated cell vacuoles in the leaves. Photo by Janice Glime.

Slime Papillae

In leafy liverworts, **slime papillae** on marginal leaf cells can help to absorb and hold water, as in the leaf margins of *Porella* (Figure 195) and *Heteroscyphus* (Figure 196) (Daniels 1998). The presence of slime papillae in *Takakia* (Figure 197) was among the reasons why several bryologists originally considered that genus to be a liverwort, but capsule structure confirmed its similarity to mosses.



Figure 195. *Porella pinnata*, a species with slime papillae on the leaf margins. Note white margins at arrows on right. Photo by Des Callaghan, with permission.



Figure 196. *Heteroscyphus coalitus*, a leafy liverwort with slime papillae. Photo by Tom Thekathyl, with permission.

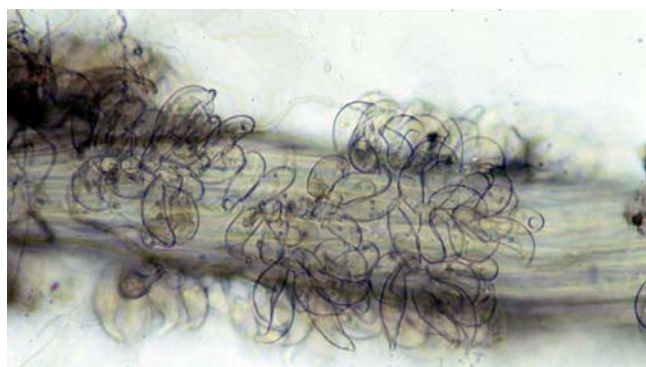


Figure 197. *Takakia lepidozoides* slime papillae. Photo from the Herbarium of Hiroshima University, with permission.

Summary

Bryophytes gain water in their cells both through external (**ectohydric**) capillary movement and internal (**endohydric**) transport. Structural adaptations such as **overlapping leaves**, **concave leaves**, **crispate leaves**, **plications**, **revolute** or **involute margins**, **lamellae**, **multi-layered leaves**, **lobules**, **hair points**, **papillae**, **costae**, **stereids**, **borders**, **leaf teeth**, **teniolae**, **alar cells**, **hyaline cells**, **cancellinae**, **resistant cell walls**, **oil bodies**, and **vacuoles**, aid in moving water, facilitating entry, or reducing loss. In areas with high fog occurrence and little or no rainfall, fog can be a major contributor to the bryophyte water budget.

Overlapping leaves, **concave leaves**, **revolute margins**, and **involute margins** help to hold water in capillary spaces. **Alar cells** provide a point of entry through thin walls that balloon up and mechanically spread the leaves. The **costa** and **border** cells may move water more quickly because the cells are long and have fewer end walls to be crossed. **Plications** permit leaf expansion in hydrated leaves and conserve moisture in drying conditions, as do **twisting** and **contorted** leaves. **Hair points** collect water from fog and dew and slow down drying by reducing exposed surface area of the leaf above. In leafy liverworts, **lobules** retain water for species of dry habitats. **Lamellae** may repel water and prevent water logging in some species, but hold water in capillary spaces in others.

Cell walls may contain **phenols** and other fluorescing materials similar to lignin to resist water loss. **Oil bodies** may provide rehydration energy, but their role in water relations is still poorly understood. **Vacuoles** hold water within the cell and permit expansion and contraction of the cell. **Slime Papillae** may contribute to absorption and holding of water.

Acknowledgments

An earlier version of this chapter benefitted from the help of Beth Scafone and Medora Burke-Scoll, who helped me tow the line in explaining things without leaving too much to one's imagination, but at the same time not repeating myself. Ron Gratz translated part of the work by Loeske. Linda Luster checked the literature citations, proofread, and made glossary suggestions from a layperson's perspective. I was fortunate to have Ken Kellman ask on Bryonet for examples of bryophytes with a demonstrated cuticle; he was kind enough to share his collected references with me. Thank you to Noris Salazar Allen for sending me the leaf images of *Leucophanes*.

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