

CHAPTER 7-4b

WATER RELATIONS: LEAF STRATEGIES – CUTICLES AND WAXES

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Figure 1. *Pohlia wahlenbergii* var. *glacialis* in Norway. The drops of water on the surface are being repelled by hydrophobic surface waxes, preventing water logging. Photo by Michael Lüth, with permission.

Bryophytes Do Have Cuticles

Anyone who has observed the speed with which many mosses and leafy liverworts absorb water would assume that they lack waxes. But as we examine these bryophytes with chemical and SEM methods, we find that this assumption is not reliable (Buda *et al.* 2013). For example, the simple moss *Physcomitrella patens* (Figure 2) has a cuticle with a chemical composition and structure similar to that of flowering plants. It is likely that the cuticle was a necessary factor in the evolution to land, regulating water status and providing protection from biotic and abiotic stresses. Using knockout genes to create mutant plants that were "severely deficient in cuticular wax accumulation" Buda *et al.* found that these plants also had reduced desiccation tolerance. The gene responsible for the cuticle wax formation in *Physcomitrella patens* is the same one as that in *Arabidopsis thaliana*, indicating its evolution early in the invasion of land.



Figure 2. *Physcomitrella patens*, a moss from which the cuticular wax gene has been isolated. Photo by Janice Glime.

Although thickened waxy cuticles seem to be rare in moss gametophytes, various mosses have some sort of cuticular covering. In some mosses, this is expressed as granules, platelets, or ribbons that are soluble in chloroform (Proctor 1982), satisfying the test for cuticular wax in tracheophytes. This type of cuticle endows *Pohlia cruda* (Figure 3), *P. wahlenbergii* (= *P. albicans*; Figure 4), *Saelania glaucescens* (Figure 55), *Schistostega pennata* (Figure 5), *Pogonatum urnigerum* (Figure 6), and many **Bartramiaceae** with their **glaucous** (whitish) appearance (Proctor 1982). We shouldn't be surprised that *Pogonatum urnigerum* has surface waxes similar to those of tracheophytes, but even primitive mosses such as *Andreaea rupestris* (Figure 7) have surface waxes that are similar to the epicuticular waxes of tracheophytes (Haas 1982).



Figure 3. *Pohlia cruda*, a whitish moss due to cuticular waxes. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 4. *Pohlia wahlenbergii* with drops of water, presumably repelled by the surface waxes. Photo by J. C. Schou, with permission.



Figure 5. *Schistostega pennata* showing whitish cast of the cuticle. Photo courtesy of Martine Lapointe.



Figure 6. *Pogonatum urnigerum* wet, showing the waxy (glaucous) appearance of the leaves. Photo by Janice Glime.



Figure 7. *Andreaea rupestris* showing slightly glaucous appearance. Photo by Janice Glime.

In addition to most of the species already named, Stránský *et al.* 1967) found n-alkanes (19-33 carbon atom chains) in *Leucobryum glaucum* (Figure 8), *Rhytidadelphus triquetrus* (Figure 9), *Conocephalum conicum* (Figure 10), *Porella platyphylla* (Figure 11), *Pellia fabbroniana* (Figure 12), and *Pellia epiphylla* (Figure 13). Even *Sphagnum* is known to have waxes (lignoceryl alcohol) in *S. capillaceum* (*S. nemoreum*; Figure 59), *S. fuscum* (Figure 60), and *S. magellanicum* (Figure 61) (Ives & Neill 1958).



Figure 8. *Leucobryum glaucum* showing appearance of waxes on a moss with hyaline cells. Photo by Janice Glime.



Figure 9. *Rhytidiadelphus triquetrus*, a moss expressing waxes that are n-alkanes. Photo by Michael Lüth, with permission.



Figure 12. *Peltia fabbroniana* with waxy epidermis and propagules. Photo by Eugenia Ron Alvarez and Tomas Sobota at Plant Actions, with permission.



Figure 10. *Conocephalum conicum* showing a waxy surface. Photo by Jan-Peter Frahm, with permission.



Figure 13. *Peltia epiphylla* showing slightly waxy appearance due to wax on its surface. Photo by Kristian Peters, through Creative Commons.



Figure 11. *Porella platyphylla* on bark, showing slightly glaucous appearance due to wax. Photo by Michael Lüth, with permission.

The documentation of cuticle in bryophyte leaves is somewhat scant. Nevertheless, Proctor (1979b) examined 43 species of mosses and determined that 12 of these have a well developed surface wax on the leaves that is comparable to that of flowering plants. Eight more have traces of wax. Not surprisingly, all of these species are **endohydric** (have internal conduction). If a moss has a waxy or glaucous look, it most likely has surface wax. A good example of this is the leaves of *Polytrichum* (Figure 14-Figure 18) On the other hand, *Atrichum undulatum* (Figure 19-Figure 21), in the same family (**Polytrichaceae**), has no discernable wax and lacks the waxy appearance. Instead of having leaves that curl inward and wrap around the stem upon drying, members of *Atrichum* have wavy leaf surfaces and become contorted when they dry (Figure 22-Figure 23).



Figure 14. *Polytrichum commune* leaves showing waxy surface. Photo by James K. Lindsey, with permission.

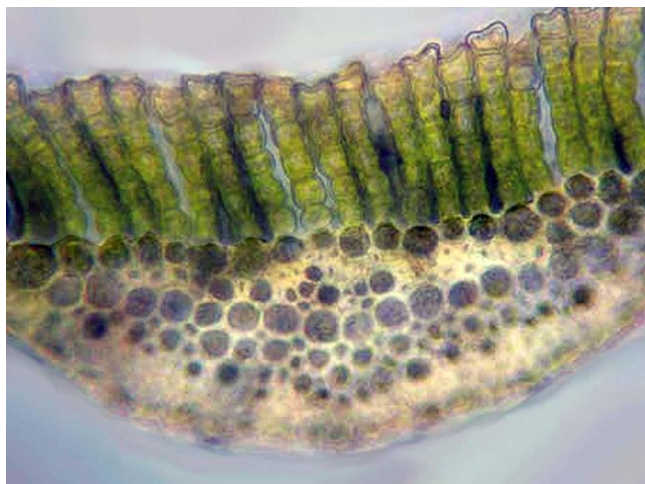


Figure 15. *Polytrichum commune* leaf lamellae where waxes are present on the terminal cells. Photo from Botany Department, University of British Columbia, with permission.

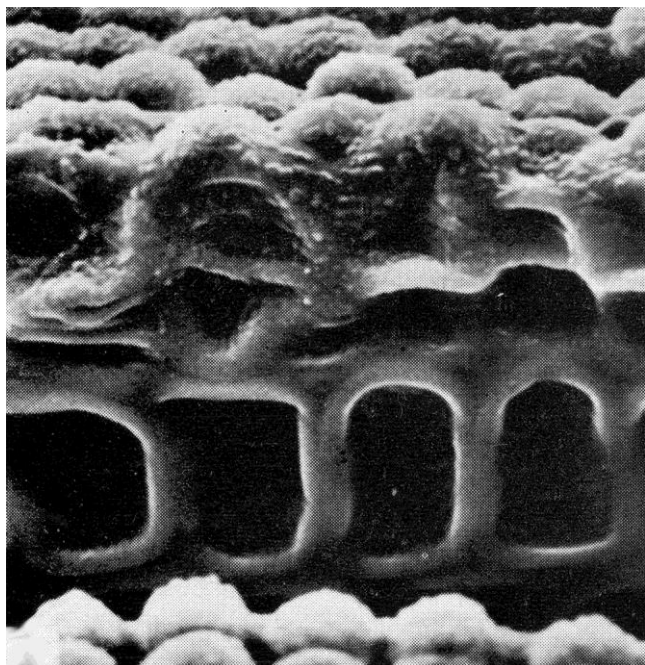


Figure 16. SEM of *Polytrichum commune* leaf cuticle. Photo by Michael Proctor, with permission.



Figure 17. *Polytrichum juniperinum* showing leaves with lamina rolled over lamellae and waxy appearance. Photo by Michael Lüth, with permission.



Figure 18. *Polytrichum juniperinum* side view of lamella with thick waxy layer on top. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 19. *Atrichum undulatum* showing lack of glaucous coloring and presence of wavy leaves that curl and twist when drying. Photo by Janice Glime.

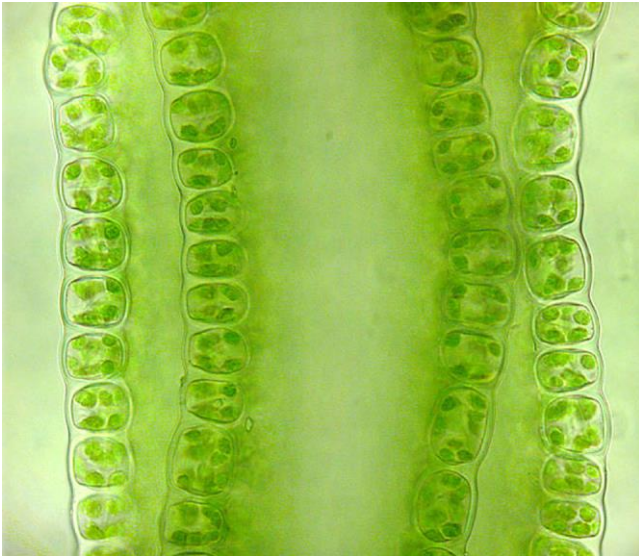


Figure 20. *Atrichum undulatum* leaf showing tips of lamellae. Photo by Walter Obermayer, with permission.

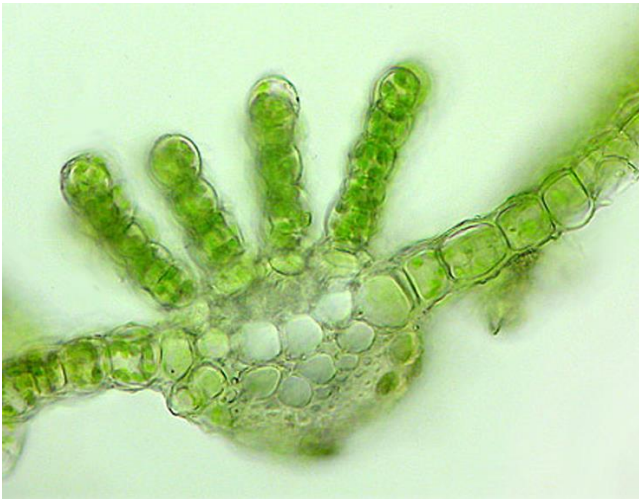


Figure 21. *Atrichum undulatum* leaf cross section showing lamellae. This moss has little or no wax on its leaves. Photo by Walter Obermayer, with permission.



Figure 22. *Atrichum altecristatum* drying (lower part of image). Photo by Eric Schneider, with permission.



Figure 23. *Atrichum undulatum* leaf lamellae and out of focus areas that indicate undulations. Photo by Walter Obermayer, with permission.

The array of species with demonstrated waxes is a mixed group of xerophytes and hydrophytes (Proctor 1979b, 1982). *Pohlia wahlenbergii* (Figure 24-Figure 26), a glaucous moss of wet habitats, has a high content of wax, whereas *Pohlia nutans* (Figure 27-Figure 28), a ubiquitous moss often found in dry habitats, has little wax. *Pohlia cruda* (Figure 29-Figure 31), a species of moist places, has a high content like that of *P. wahlenbergii*. It appears that the wax in these species is important to prevent water logging, allowing for gas exchange for photosynthesis.



Figure 24. *Pohlia wahlenbergii* showing a wet habitat that is typical for it. Photo by Michael Lüth, with permission.



Figure 25. *Pohlia wahlenbergii* showing water droplets that are repelled by the waxy surface. Photo by Michael Lüth, with permission.

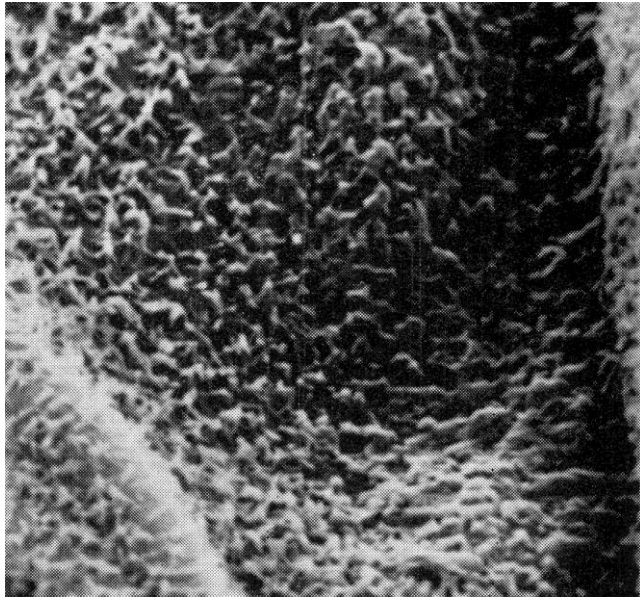


Figure 26. SEM of *Pohlia wahlenbergii* cuticle. Photo by Michael Proctor, with permission.

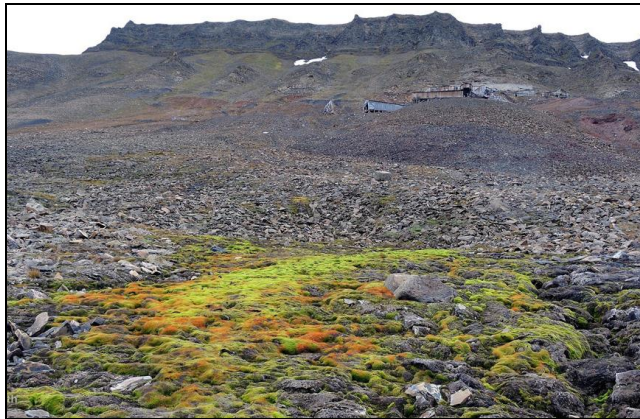


Figure 27. *Pohlia nutans* showing a typical dry, exposed habitat for the species. Photo by Michael Lüth, with permission.



Figure 28. *Pohlia nutans* showing the lack of a glaucous or waxy appearance. Photo by Michael Lüth, with permission.



Figure 29. *Pohlia cruda* in a crevice where moisture can be maintained, showing a waxy appearance. Photo by Michael Lüth, with permission.



Figure 30. *Pohlia cruda*, a glaucous moss with a high leaf wax content. Photo by Michael Lüth, with permission.

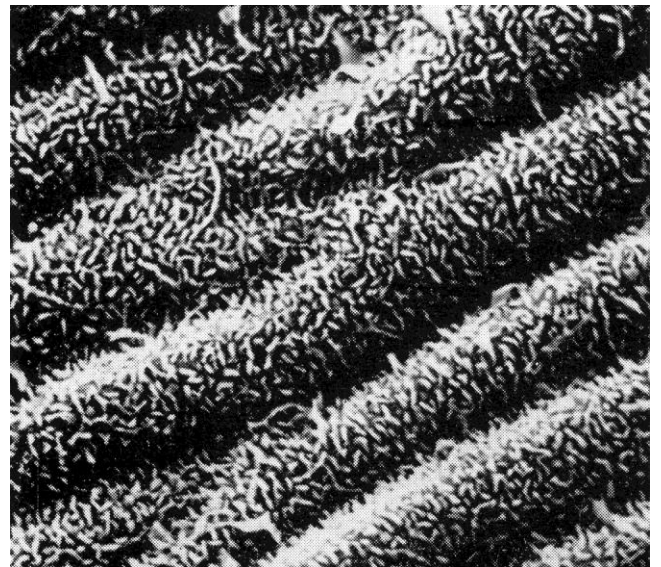


Figure 31. SEM of *Pohlia cruda* cuticle. Photo by Michael Proctor, with permission.

Bartramia pomiformis (Figure 32-Figure 34) has a whitish appearance and has a high degree of wax covering (Figure 34) (Proctor 1979b). In the same family, *Conostomum tetragonum* (Figure 35) has an intriguing 3-d mesh of wax (Figure 36).



Figure 32. *Bartramia pomiformis* in its typical rock crag habitat. Photo by Janice Glime.



Figure 33. *Bartramia pomiformis* showing glaucous leaves. Photo by Michael Lüth, with permission.

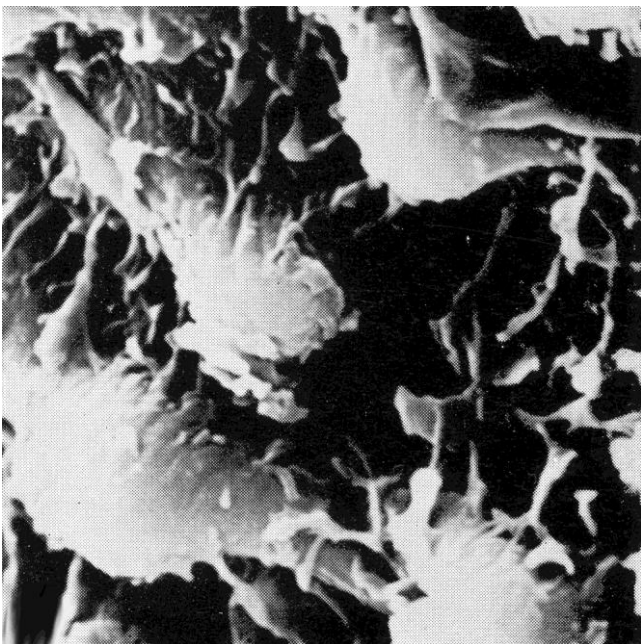


Figure 34. SEM of *Bartramia pomiformis* leaf cuticle. Photo by Michael Proctor, with permission.

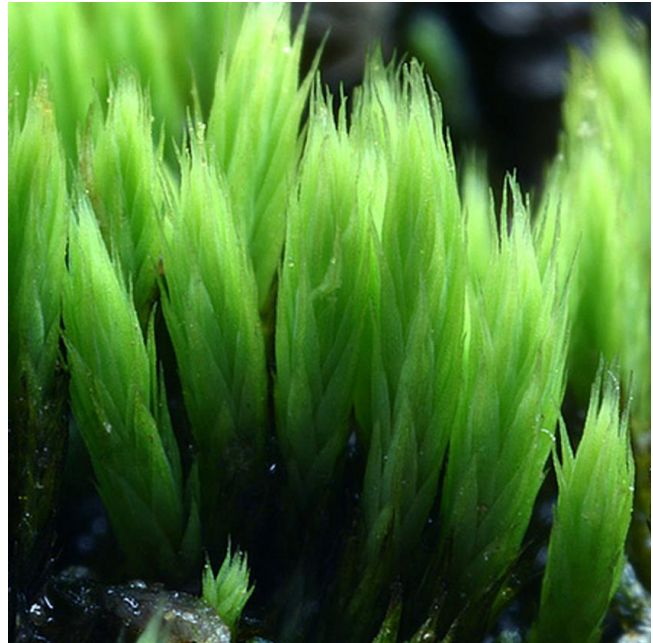


Figure 35. *Conostomum tetragonum* showing the glaucous appearance of the leaves. Photo by Des Callaghan, with permission.

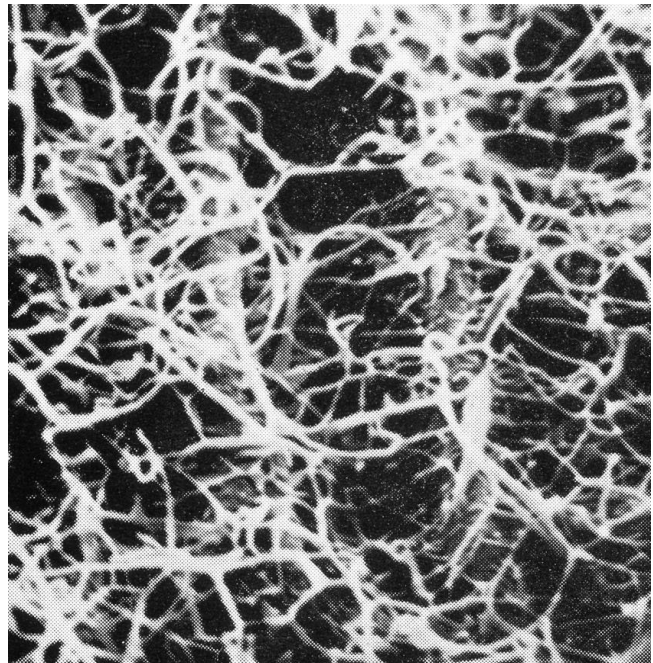


Figure 36. SEM of *Conostomum tetragonum* leaf cuticle. Photo by Michael Proctor, with permission.

Xu *et al.* (2009) found surface wax on the leaves of the desert moss *Syntrichia caninervis* (Figure 37). These waxes were comprised of fatty acids, alcohols and alkanes. In this species, the wax crystals shift as the leaf ages, increasing the percentage and weight (13.6%; 1150 $\mu\text{g g}^{-1}$ DW) of very long-chain components in young leaves to 37.2% and 2640 $\mu\text{g g}^{-1}$ in older leaves. Furthermore, when juvenile leaves experienced dehydration followed by rehydration the wax content of juvenile leaves increased by 35.17%. In lab-cultivated leaves subjected to three wet/dry cycles, the wax content increased by 1900%.

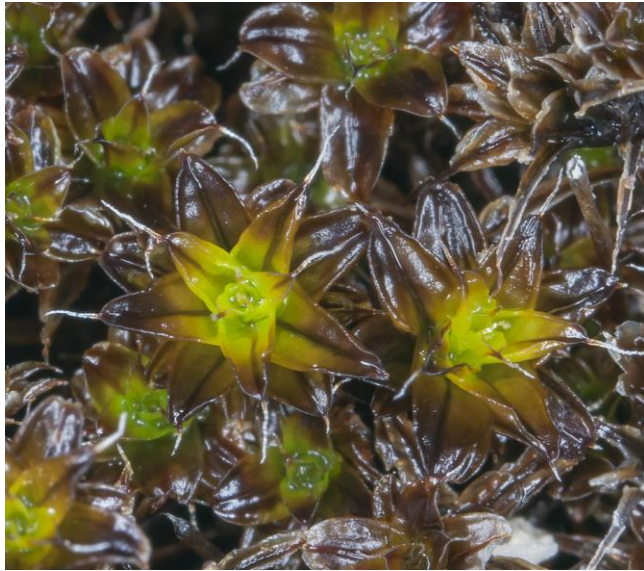


Figure 37. *Syntrichia caninervis*, a desert moss with a cuticle comprised of fatty acids, alcohols, and alkanes. Photo by John Game, with permission.

Some bryophytes are puzzling at first glance. For example, *Hedwigia* (Figure 38-Figure 40) species appear to be waxy, yet absorb water rapidly. But members of the **Hedwigiales** lack waxes (Pressel & Duckett 2011). This puzzle unravels when we understand the role of the papillae (which typically make leaves look whitish) on the leaves of **Andreaeales**, **Grimmiales** (Figure 41-Figure 42), **Pottiales** (Figure 43-Figure 46), **Hedwigiales**, and **Orthotrichales**. Based on experiments by Proctor (1979a) and confirmed by Pressel and Duckett (2011), the water enters these leaves by flowing within channels in the **striated** (having linear marks, slight ridges, or grooves on surface, often one of number of similar parallel features) cell walls and between the papillae, causing rapid uptake of water through the leaf surface between the papillae. These taxa lack waxes.



Figure 38. *Hedwigia ciliata ciliata* dry, showing whitish leaves resulting from numerous papillae. Photo by Des Callaghan, with permission.



Figure 39. *Hedwigia ciliata* wet, showing ability to spread when hydrated. Photo by Hermann Schachner, through Creative Commons.

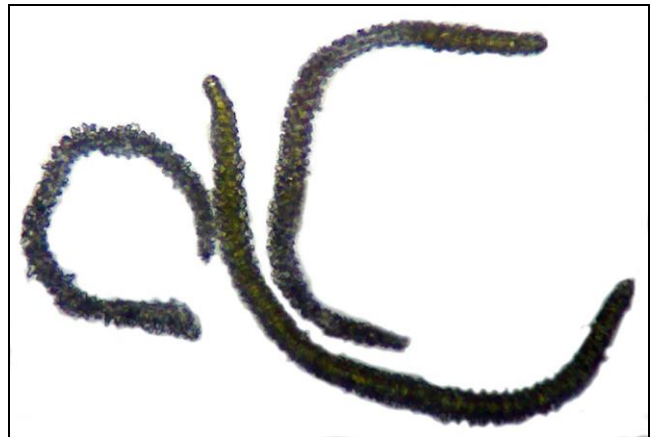


Figure 40. *Hedwigia ciliata* leaf cross sections showing dense papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 41. *Racomitrium lanuginosum* (Grimmiales) showing awns on leaves. These leaves lack waxes. Photo from Botany Department website, University of British Columbia, with permission.

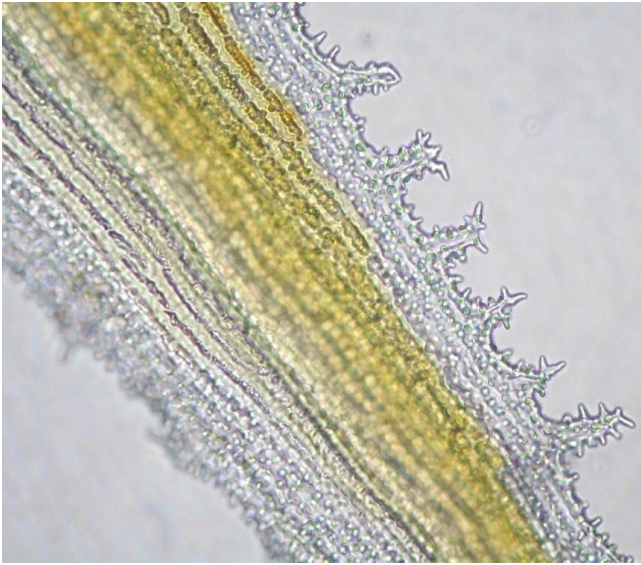


Figure 42. *Racomitrium lanuginosum* (Grimmiales) leaf awn and cell papillae. Photo from Botany Department website, University of British Columbia, with permission.

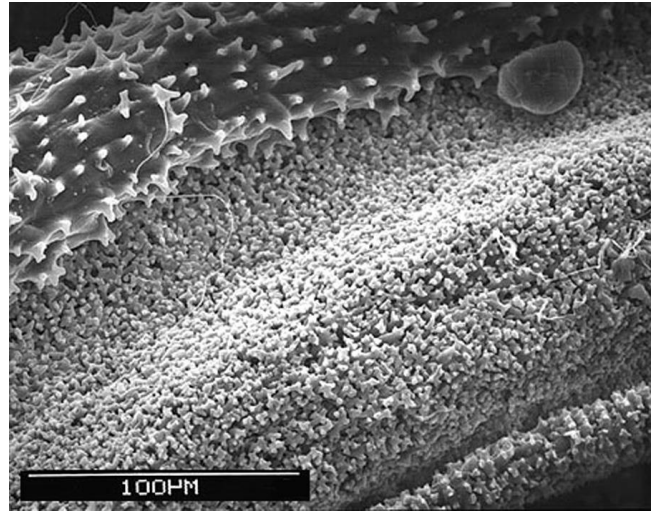


Figure 45. SEM of *Tortula muralis* (Pottiales) papillae showing their density and channels where water moves and enters the leaf. Photo from Botany Department website, University of British Columbia, with permission.



Figure 43. *Tortula muralis* in its dry state. Photo by Christophe Quintin, through Creative Commons.

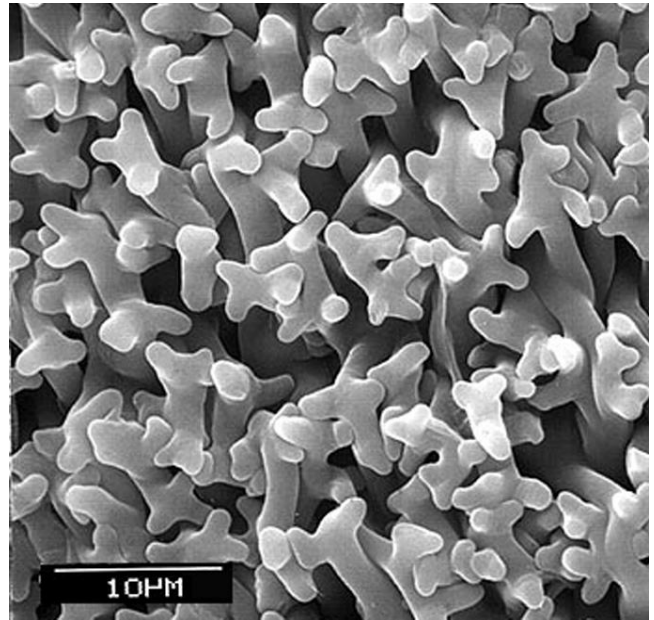


Figure 46. SEM of *Tortula muralis* (Pottiales) papillae showing the spaces between them where channels are provided for water transport and entry to the leaf cells. Photo from Botany Department website, University of British Columbia, with permission.



Figure 44. *Tortula muralis* in its wet state. Note the water collected on the awns. Photo by Christophe, Quintin through Creative Commons.

In genera such as *Aloina* (Figure 47), *Crossidium* (Figure 48-Figure 49), and *Pterygoneurum*, (Figure 50-Figure 52) the water enters between the leaf lamellae (Figure 51-Figure 52) (Proctor 1979a; Pressel & Duckett 2011). All these taxa grow in habitats where intermittent dehydration/rehydration, often in rapid sequence, is common. However, in the **Polytrichaceae** (Figure 14-Figure 18), water logging between the lamellae is an issue, depressing gas exchange needed for photosynthesis (Proctor 1979a, 1982, 1984). These leaves are protected by abundant waxes that prevent water from entering the spaces between the leaf lamellae. Instead, air bubbles are trapped in these spaces.



Figure 47. *Aloina rigida* showing waxy leaves. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 48. *Crossidium aberrans* leaves with lamellae. Photo by Michael Lüth, with permission.



Figure 49. *Crossidium aberrans* leaf cells showing lamellae in center where water is easily absorbed. Photo by Michael Lüth, with permission.



Figure 50. *Pterygoneurum papillosum* showing succulent appearance of leaves due to lamellae. Photo by Michael Lüth, with permission.



Figure 51. *Pterygoneurum ovatum* leaf showing lamellae where water enters the leaf. Photo by Hermann Schachner, through Creative Commons.



Figure 52. *Pterygoneurum ovatum* leaf cross section showing lamellae where water enters leaf. Photo by Hermann Schachner, through Creative Commons.

One of the problems that bryophytes must face is having ice or ice crystals on their surfaces (Figure 53- Figure 54). These crystals are very hygroscopic, potentially causing the kind of dehydration that can occur to your meat in the freezer. A waxy cuticle could serve like a plastic freezer bag, in this case preventing the water from being drawn from the cells. This role for the wax, if present, remains to be tested.



Figure 53. *Polytrichum* sp. with frost, a condition that could draw water out of unprotected cells. Photo by Allan Water.



Figure 55. *Saelania glaucescens* showing waxy appearance. Photo by Michael Lüth, with permission.



Figure 54. *Hedwigia ciliata* in ice, a frequent condition for this rock dweller. The ice, like freezer ice, draws water out of plant cells. Photo by Michael Lüth, with permission.

The presence of a white flocculent material on the moss *Saelania glaucescens* (Figure 55-Figure 57) is widely known. *Saelania glaucescens* has been a puzzle to bryologists and biochemists. Its whitish covering is predominantly on the backs of the leaves and takes the form of a hoary appearance, not a smooth or shiny surface. Although this material has been identified as kauranol plus several minor waxes (Nilsson & Mårtensson 1971), the reason for the peculiar arrangement that looks like a thin layer of minute angel hair remains a mystery. Bryologists have suggested that it might be caused by parasitic fungi or bacteria, but there is no evidence to support these ideas (Mårtensson & Nilsson 1974). Likewise, it does not seem to be the result of any normal metabolic product. Proctor's (1979b) analysis demonstrates that this is a heavy coating of waxes with weblike ridges covered by a fine, cobwebby matrix of wax.



Figure 56. *Saelania glaucescens*, a moss in which the waxy extrusions are so large that they are visible to the naked eye. Photo by Jan-Peter Frahm, with permission.

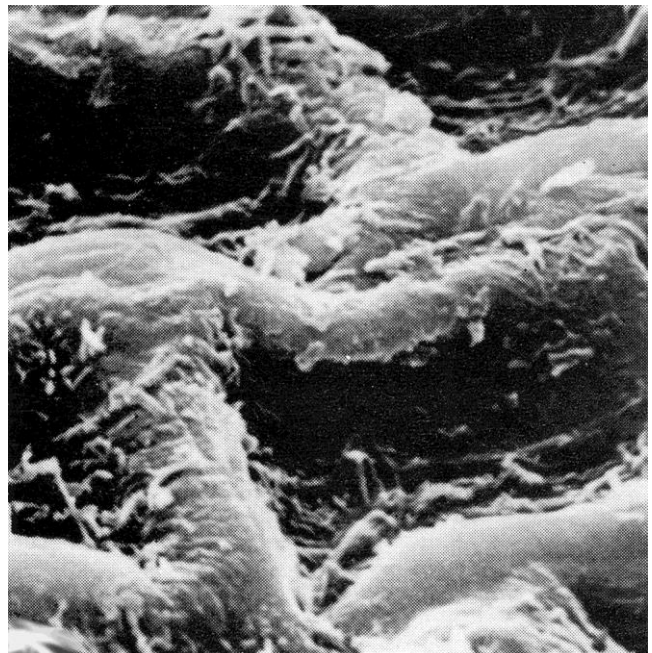


Figure 57. SEM of *Saelania glaucescens* cuticle. Photo by Michael Proctor, with permission.

Sphagnum

Sphagnum fimbriatum (Figure 58-Figure 62), a peatmoss of wet habitats, has an osmiophilic layer (one that stains with osmium tetroxide, indicating wax) that resembles the early developmental stage of tracheophyte cuticle (Cook & Graham 1998). One might think that a wet habitat moss would not need such protection, but in summer these peatmosses can become quite dry, so such a layer may help to reduce desiccation. On the other hand, this layer may prevent water logging at times when this moss is submersed (*cf.* Pressel & Duckett 2011). The cuticle in *S. fimbriatum* is sheetlike with regular ridges that run parallel to the edges of the "thalli." Our next question is how can a leaf with a cuticle use it for protection from desiccation and yet be able to absorb water. In *Sphagnum*, this may be facilitated by the pores, but might the structure of the cuticle play a role?



Figure 58. Dry *Sphagnum fimbriatum*, a moss with a known osmiophilic layer resembling an early developmental cuticle of tracheophytes. Photo by Michael Lüth, with permission.



Figure 59. *Sphagnum capillaceum* (= *S. nemoreum*), a *Sphagnum* species known to have waxes (lignoceryl alcohol). Photo by Michael Lüth, with permission.



Figure 60. *Sphagnum fuscum*, a *Sphagnum* species known to have waxes (lignoceryl alcohol). Photo by Michael Lüth, with permission.



Figure 61. *Sphagnum magellanicum*, a species known to have waxes. Photo by Michael Lüth, with permission.



Figure 62. *Sphagnum fimbriatum* leaf cross section, a moss that has an osmiophilic (waxy) layer on the outside of the leaf cells. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Leafy Liverworts

Even the leafy liverworts can have waxes. Heinrichs *et al.* (2000) support the contention of Cook and Graham (1998) that this innovation occurred prior to the evolution of bryophytes from their algal ancestor. Although only six (5 of *Plagiochila* plus *Plagiochilium mayebarae*) of the 81 species of **Plagiochilaceae** in the study had surface waxes on their leaves (Heinrichs *et al.* 2000), this is a family with

many members in damp or wet, even submersed, habitats. They found that *P. tabinensis* contains 1.4% of its dry weight as surface waxes. These are comprised of steryl esters, triacylglycerols, and free fatty acids.

By using the electron microscope, Heinrichs and Reiner-Drehwald (2012) found surface wax in the leafy liverworts *Lejeunea flava* (Figure 63), *Mytilopsis albifrons*, *Dinckleria pleurata*, and *D. fruticella*, representing the families **Lejeuneaceae**, **Lepidoziaceae**, and **Plagiochilaceae**, respectively.



Figure 63. *Lejeunea flava*, a leafy liverwort known to have a cuticle with surface wax. Photo by Jonathan Sleath, with permission.

Admissibility of Water

If leaves of bryophytes are covered with waxes, how does water enter these largely ectohydric plants? One suggestion is that the bases of the leaves may lack a cuticle, but that would seem to slow down water entry and be maladaptive for gathering dew or taking advantage of short desert rainfall events. But the structure of the wax itself may solve this problem. Shepherd and Wynne Griffiths (2006) describe the layered sheets of wax as probably discontinuous and surrounded by further solid amorphous regions. The crystalline regions are considered impermeable, but water and solutes are able to diffuse through the cuticular wax by way of the amorphous zones. This requires a greater travel distance than a straight path through the surface, but it seems a better route than travelling to the leaf base, then travelling internally through cell contents and cell walls to reach the tip of the leaf.

Multiple Forms – Multiple Roles

The cuticle, like many plant features, can serve multiple advantages for plants. In tracheophytes it is able to reduce water loss, prevent water logging, protect against high light intensity, reduce the temperature, reduce osmotic stress, prevent physical damage, protect against altitudinal stresses (light, extreme temperatures, wind), and protect against pollution (Shepherd & Wynne Griffiths 2006).

In tracheophytes, waxes exist in several forms, including rods, ribbons, filaments, tubes, and plates (Shepherd & Wynne Griffiths 2006). Among the bryophytes, for five *Plagiochila* (leafy liverwort) species studied, two exhibited wax platelets and three exhibited wax rodlets (Heinrichs *et al.* 2000). Proctor (1979b)

demonstrated several forms among mosses (Figure 31, Figure 34, Figure 36, Figure 57).

Among the tracheophyte forms, wax tubes are associated with mid-chain oxy-substituents, such as β -diketones, hydroxy- β -diketones, diols, and secondary alcohols (Shepherd & Wynne Griffiths 2006). Platelets are associated with primary alcohols with a terminal oxy-substituent. Are these same factors influential in bryophyte wax morphology? If so, is there any adaptive significance for these differences?

Temperature

We know that in tracheophytes temperature, light intensity, and humidity influence the wax morphology, but since these three factors typically act together, it is often difficult to tease out cause and effect (Shepherd & Wynne Griffiths 2006). For example, in *Citrus aurantium*, a higher daytime temperature during leaf development reduces the quantities of alkanes, primary alcohols, fatty acids, and alkyl esters per unit area (Riederer & Schneider 1990). But except for the esters, the amounts of these same compounds increase with higher night-time temperatures.

At higher temperatures, the waxes are more likely to form plates and flakes, whereas at lower temperatures they are more likely to form vertical structures such as rods and tubes (Shepherd & Wynne Griffiths 2006). But waxes at higher temperatures also often form complex dendritic shapes. Tubular forms of waxes are thermodynamically unstable due to their high surface area to volume ratio, so an input of energy, typically heat, can transform them into compact planar forms that are thermodynamically more stable. And tubes can turn into dendrites when the temperature is raised. On the other hand, rapid cooling can also favor dendrite formation. Furthermore, more waxes are produced at lower temperatures.

Light

Shorter, less elaborate wax structures are often associated with greater illumination (Shepherd & Wynne Griffiths 2006). Thick waxes such as those in *Eucalyptus* leaves increase reflectance and reduce photosynthesis, but in "non-waxy" leaves (*i.e.* not appearing waxy or glaucous), there is no effect. In wheat, reflectance is proportional to the amount of wax present, with higher reflectance reducing light transmission to underlying mesophyll cells (Johnson *et al.* 1983). Higher radiation levels can cause an increase in wax thickness in many plants, suggesting an inducible mechanism to protect the cells (Baker 1974; Giese 1975; Reed & Tukey 1982; Shepherd *et al.* 1995).

But it seems unlikely that the thin cuticle of bryophytes has much of an effect on reflectance or photosynthesis. Nevertheless, as will be seen in the chapter on light relations, many bryophyte leaves transmit more light when wet than when dry, suggesting that papillae or other surface features may screen light, thus protecting the DNA and chlorophyll, but that when water fills in the spaces, light is transmitted rather than scattered. Are these waxes protective agents against UV radiation when the

bryophytes are dry? But UV reflectance is an uncommon adaptation among tracheophytes. It can range from <10% in most plant species, to 70% in only a few others (Caldwell *et al.* 1983; Barnes *et al.* 1996).

Waxes may play yet another role for the light-limited bryophytes. Droplets held on wettable tracheophyte leaves can focus solar radiation up to 20 times (Brewer *et al.* 1991). We might imagine that bryophyte leaves or multiple plant tips might trap water droplets that likewise focus the light in some low-light habitats. This focussing would occur at the actively growing tips in most acrocarpous mosses.

Salt Stress

Waxes also protect leaf cells from salt stress (Shepherd & Wynne Griffiths 2006). Examples from tracheophytes suggest that an increase in wax production may be an inducible response to increased salt exposure. Fujiwara *et al.* (2002) found that pre-treating cabbage seedlings with NaCl induced hardening, improving drought resistance. It would be interesting to compare wax content among bryophytes that grow within areas affected by salt spray to the same species grown away from its influence.

Contact Angles and Entry

Contact angles are important for water entry. Brewer *et al.* (1991) found that changes in the contact angle and wettability are also associated with changes in wax composition and morphology in tracheophytes. These observations present interesting questions for bryophytes. If leaves have waxes over the leaf lamina, but lack waxes at the base, water will roll to the leaf base where uptake is easy. This movement to the leaf base would further facilitate the solution of deposited nutrients and carry them to the base for absorption (Cape 1996 for tracheophytes). Because of the mode of water uptake in bryophytes, this feature is likely to be more important than it is in tracheophytes. Hence, we should expect the angle of the leaf to be important in this nutrient and water gathering. At the same time, it presents dangers for collecting deposited pollutants.

Combined Role and Water Relations

Let's continue under the assumption that at least in some cases the waxes on bryophytes may play a role in reflectance and scattering of light to a degree that can lower the temperature of the bryophyte cells they cover. This will, in turn, reduce the vapor pressure difference between the leaf tissue and the air, reducing the loss of water through transpiration. But all these assumptions remain to be tested in bryophytes.

Altitude Protection

High altitude imposes stresses that include weathering, dehydration, low temperatures, and greater UV light intensity. In conifers, a thicker wax coverage is characteristic of high altitude growth (Günthardt 1984; Riolo 1999). We need to look for a similar relationship in bryophytes.

Pollution Protection

Ozone

In tracheophytes, ozone causes a severe reduction in the formation of new wax, but it does not seem to affect existing wax (Carlsson *et al.* 1994; Hellgren *et al.* 1995). Its effect on bryophyte cuticles remains unknown, but failure to replace cuticle could have severe consequences in prevention of water logging and protection from UV radiation.

CO₂

The effects of CO₂ on tracheophytes are varied, in some cases causing an increase in waxes and in others a decrease (Shepherd & Wynne Griffiths 2006). The effect on bryophyte cuticles remains to be demonstrated.

Repelling Water

Despite all of these reports on waxes on the cuticle of bryophytes, we know little of their role. Mårtensson and Nilsson (1974) comment that not all of the aforementioned waxy species are shiny, including *Rhytidiadelphus triquetrus* (Figure 9), although I would consider it to be shiny. Others, such as *Sphagnum subnitens* (Figure 64-Figure 65) and *S. subfulvum* (Figure 66) are shiny when dry, but lose their shine when moist, suggesting that the relationship is complex and is not a matter of simple reflection. It would be interesting to determine their role in repelling water to avoid water logging vs retaining water in times of drought.



Figure 64. *Sphagnum subnitens* dry with a waxy shine. Photo by Michael Lüth, with permission.



Figure 65. *Sphagnum subnitens* wet with a less waxy look than dry plants. Photo by Barry Stewart, with permission.



Figure 66. *Sphagnum subfulvum*, a species that is shiny when dry due to waxes. Photo by Michael Lüth, with permission.

The role of repelling water may be more important than that of retaining water. I have mentioned a potential role of repelling water, as seen in Figure 1. Gas exchange works poorly through a wet surface. Waxy or oily surfaces help to repel the water, yet allow a higher rate of gas exchange than does water. Hence it is not uncommon to find such surfaces among aquatic bryophyte taxa (Proctor 1984).

Proctor (1984) contends that the ability to shed surface water is important to bryophytes in their low-light habitats of crevices and caves or in waterside habitats of waterfalls. He cites the waxy surfaces of the tops of photosynthetic lamellae of the **Polytrichaceae** (Figure 6, Figure 14-Figure 18) as support for this contention. This might also be supported by the waxy surface of *Pohlia cruda* (Figure 29-Figure 31), a common species in crevices.

As discussed in Chapter 7-3 of this volume, the pores of *Marchantia* (Figure 67), as in the stomata of tracheophytes, have strongly water-repellent ledges (Schönherr & Ziegler 1975; Figure 68), like the waxy ridges of tracheophytes, preventing water from entering and interfering with the photosynthetic interior.



Figure 67. *Marchantia polymorpha* with gemmae cups and tiny white dots that indicate pores. Photo by Jan-Peter Frahm, with permission.

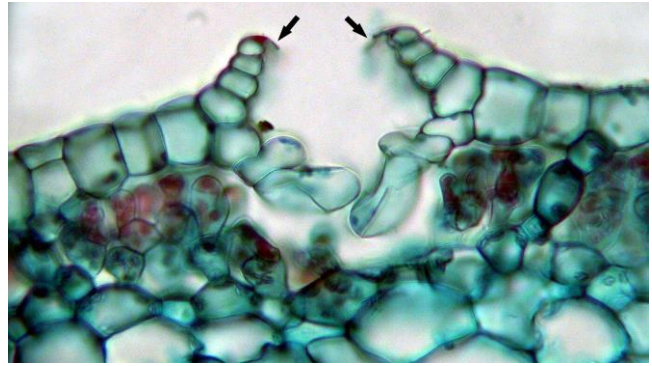


Figure 68. Section through pore of *Marchantia polymorpha*, with waxy ledge indicated by arrows. Photo by George Shepherd, through Creative Commons.

Mosses like *Plagiomnium* (Figure 69) have both upright and horizontal stems. But this genus has a different problem from most mosses in obtaining water. Its leaves repel water, as known by anyone who has tried to wet them to make a slide. It has perhaps solved this problem by its well-developed hydroids and leptoids, and even false leaf traces (Figure 70).



Figure 69. *Plagiomnium ellipticum* with drops of water on its water-repellent (waxy) surface. Photo by Des Callaghan, with permission.

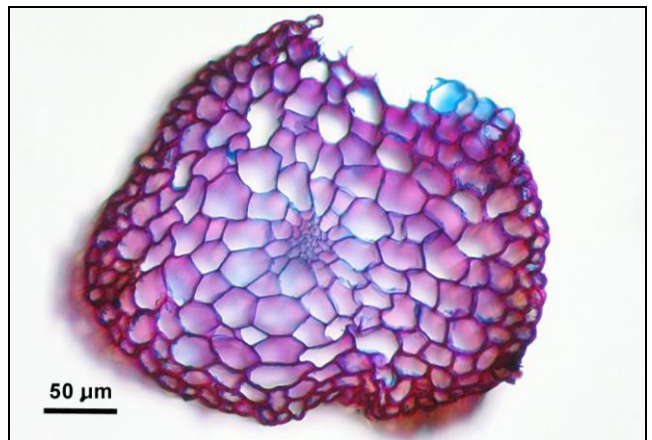


Figure 70. *Plagiomnium ellipticum* stem cross section. This is a moss with both upright and horizontal (plagiotropic) stems. It most likely benefits from having both hydroids and leptoids to transport substances because its leaves are very resistant to getting wet and typically repel water. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

In some cases, there are special adaptations for bringing water into the leaves while at the same time being able to prevent water loss. In *Rhacocarpus purpurascens* (Figure 71), a moss of exposed habitats that experience frequent alternation of drought and heavy precipitation, the cell walls are trilamellate (Pressel *et al.* 2010). The outer layer is porous and ensures rapid uptake of water and retention. At the same time its very hydrophobic cuticle-like layer prevents waterlogging. The middle lamellar stratum permits extension of protoplast hydration, allowing the metabolism to remain active under drying conditions. *Sphagnum*, on the other hand, can become waterlogged and experience depressed metabolism as a result.



Figure 71. *Rhacocarpus purpurascens*, a moss that repels water. Photo by Michael Lüth, 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, cuticles, hair points, papillae, costae, stereids, borders, cancellinae, teniolae, alar cells, hyaline cells, pores, oil bodies, 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.

Waxes are known from all the major groups of bryophytes, including such aquatic taxa as *Sphagnum*, and occur in a wide range of habitat moisture, but many species seem to lack them. Glaucous species may be so because of waxes or because of dense papillae. The water repellent nature of waxes keeps water from entering pores of a thallus and prevents water from remaining on plants in a way that blocks gas exchange. The presence of waxes may relate to endohydry or to living in places where water lingers on the plants. The role may be more to keep water away than to hold water in.

Waxes need to be arranged on a leaf to admit water, at least at the base, but they may have an amorphous layer that transmits water. Multiple forms

of waxes seem to be correlated with various environmental parameters such as UV light, temperature, salt stress, contact angle, and altitude, but these correlations have not been explored in bryophytes. Cuticles can offer protection from such pollutants as ozone and CO₂ and may play a role in preventing absorption of airborne pollutants that land on the surfaces of the leaves.

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