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CHAPTER 4-12

ADAPTIVE STRATEGIES: SPECULATION ON GAMETOPHYTE STRUCTURES

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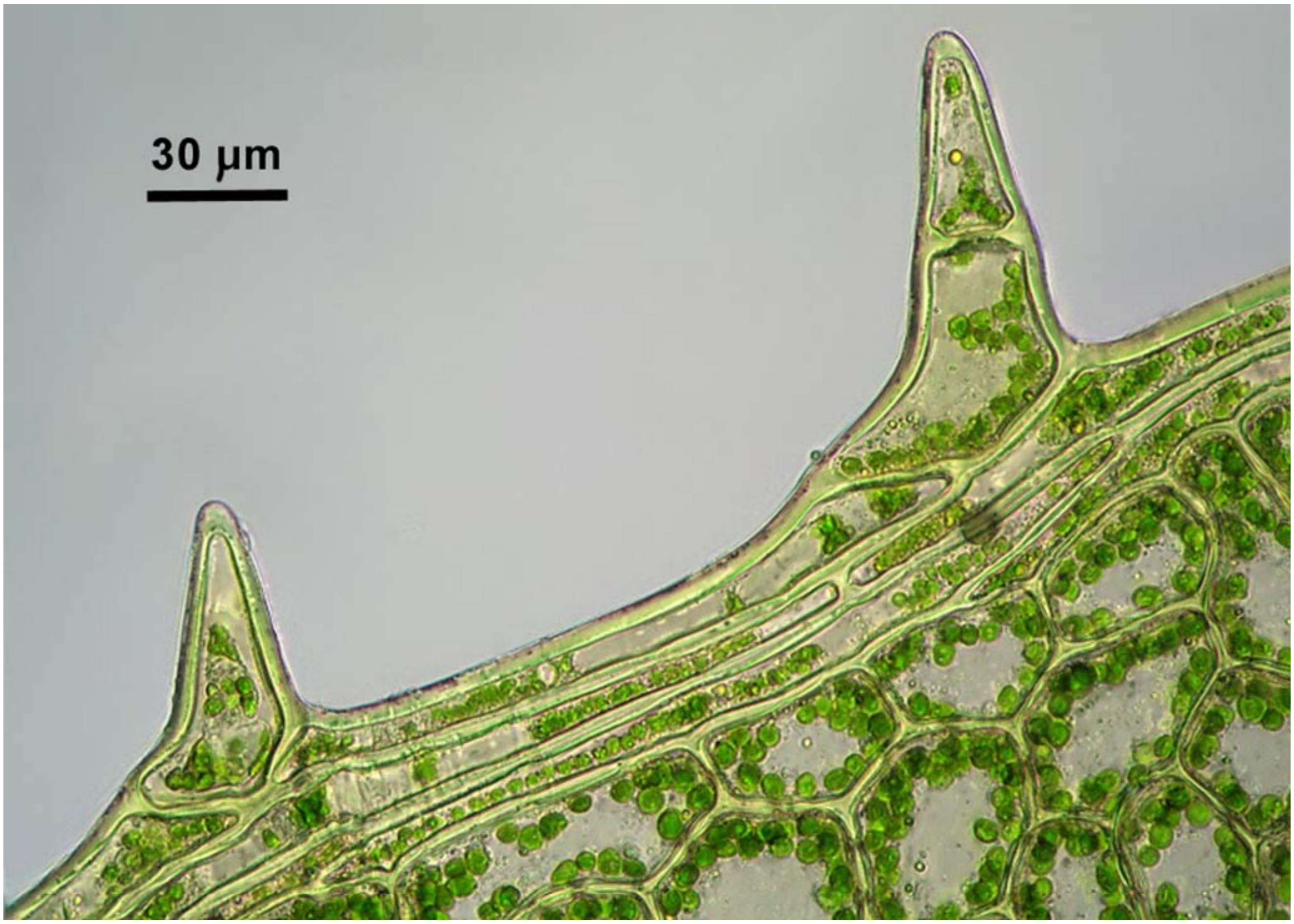

Figure 1. ***Plagiomnium affine*** leaf border with teeth. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Prologue

As I begin this chapter, I am reminded of a conversation I had with Louis Anderson. It was similar to the one relayed by Brent Mishler on Bryonet (8 May 2012) on the position of Lewis Anderson. When asked about the function of something like a hairy surface, he would point out that it had to have some kind of surface. We must keep this admonition in our minds constantly as we question functions of bryophyte parts, forcing us to ask more precise questions and to **test** our hypotheses.

Not all structures have adaptive value. With this caution in mind, we need to be aware if something is really adaptive or it is simply not an encumbrance. If it persists through more than one taxonomic group, is it more likely it has some adaptive significance than if its presence is rare? And if it occurs in all, might it be a necessity? But I dare not go farther in defining adaptive value. Hence, this chapter is necessarily speculative. Do keep that in mind as you read.

The descriptions of structural adaptations are largely the product of the human mind to seek explanations for things. Hence, we seek to learn why a certain structure persists in a bryophyte by trying to find a function for that structure. This teleological approach is not all bad. It can form the basis or our alternative hypotheses, the null hypothesis being that there is no special function.

The next step after identifying a hypothesis is attempting to test it, and this is often quite difficult. It often becomes necessary to ask the question, "What would happen if this structure were absent, as for example the teeth shown in Figure 1?" Modern genetic techniques are permitting us to identify the functions of genes that way, using knock-out genes to disable or remove a gene. Some structures are suitable for removing or disabling as well and can help us test our hypotheses.

Even with such testing, we must also keep in mind that not all structures have functions, and that structures and genes may not work alone. For selection to work against them, there must be some cost for their presence. If there is no cost, a structure may remain, seemingly with no purpose.

Often this cost is expenditure of energy, whereas when we look for adaptive value we tend to look for things like moisture conservation, herbivory protection, or increased dispersal. All of these relate to survival, so testing of adaptations often is a testing of survival value.

In this regard, we need to consider that Lamarckian evolution suggested that giraffes have long necks so they could reach higher branches where there was less competition for food. But there is no genetic mechanism that can cause a gene to arise due to need. Genes arise randomly through mutations or get lost through deletions. Combinations of genes change due to both mutations and recombinations. The recombinations can occur through mixing in meiosis or through mating with an individual with genotypic differences.

Medina *et al.* (2015) explored phenotypic variation in three Antarctic moss populations as a response to local environments. All three species of mosses studied revealed significant differences among populations for all evaluated morphometric characters. They concluded that in the Antarctic, local variation on a small geographic scale behaved in the same way as variation on a large geographic scale in geographic regions where the climate is more homogeneous. This is an example that may reflect random arrival of propagules, followed by selection by the environmental conditions at the site of arrival. But this is a my hypothesis for which the researchers urged the need for common garden studies and further investigation on many more species.

Linked Genes

A second complicating factor in our search for function is that genes may be kept because of their nearness to another important gene. If gene B resides on a chromosome with gene A, it will go where gene A goes unless it gets moved during a crossover event (a common occurrence during meiosis) or other type of rearrangement. The closer it is to gene A, the lower the chances of gene B becoming separated during a crossover event. If gene A is an important adaptive gene, and gene B does little or no harm, then it will be kept as it travels along with gene A, even if it codes for something that offers no adaptive value. But if gene B is harmful, and gene A is not essential or is unable to provide more benefit than the harm caused by gene B, then gene B will be begin to disappear from the gene pool – and gene A with it. I could explain this further, but you should be able to see my point – not all structures or physiological mechanisms are necessarily advantageous. They may be non-adaptive. They may even remain from a time when they were adaptive to conditions that no longer exist. Thus, we must keep in mind that not all structures or other phenotypic expressions are adaptive. The evolutionary model would, in fact, predict that some are not adaptive. And those that are maladaptive may take hundreds of years or even eons to disappear from the population. In the meantime, they may offer us taxonomic characters that are useful to systematists!

It is not easy to associate a given character with a particular gene. Vanderpoorten and Jacquemart (2004) found that most of the morphological variation in the aquatic moss genus ***Amblystegium*** (***Hygroamblystegium***; Figure 2) result not from genetic differences, but in plasticity of expression. They also found that the evolution of most characters in these aquatic taxa was often independent from phylogeny of the taxon. Rather, the morphological characters in this genus lack independence and stability, making them less useful for distinguishing species.

Figure 2. ***Hygroamblystegium fluviatile***. Photo by Hermann Schachner, through Creative Commons.

Evolutionary Drivers

Kürschner (2004) found common adaptive trends among the bryophytes from the Near and Middle East. These represented independent traits that arose in unrelated taxa evolving under similar habitat conditions. Such convergence suggests relationships of evolution with site ecology and niche differentiation.

Hence, this chapter will present more hypotheses than facts with the challenge to our young (and older) bryologists to test these.

GAMETOPHYTE

Schofield (1981) reviewed the literature and concluded that spore germination patterns, protonemal structure, life span, and methods of vegetative propagation are all related to nature of the habitat. Large, multicellular spores and swollen protonemal cells are more common in habitats that frequently experience desiccation. Protonemata are more specialized in deeply shaded environments. More typical types with strongly elongate cells are more frequent in mesic sites or terrestrial sites with favorable moisture conditions during at least part of the day during most of the growing season. Growth forms may be correlated genetically, or they may be "molded" by the environment. Energy conservation is often accomplished by having production of gemmae at different times from sexual reproduction.

In **ectohydric** (external) conduction systems, water movement is facilitated by leaf shape, arrangement, orientation (Figure 3), and detailed anatomy; branch arrangement, stem cortical cells; and the presence of rhizoids or paraphyllia (Schofield 1981). Surface ornamentation of leaves, stems, and rhizoids also may contribute. In **endohydric** (internal; Figure 12-Figure 13) conduction, the hydrome and leptome facilitate water movement and may be habitat specific, especially in the **Polytrichidae**. Again, there is little experimental evidence to support the conclusions that currently rest on habitat correlations.

Figure 3. ***Pohlia*** sp. with raindrops large and small, illustrating the way ectohydric water becomes trapped in the leaf axils. Photo by John Game, through Creative Commons.

Wetlands vs Non-wetland Trends

Hedenäs (2001) took compiled data that supports much of the tendencies noted by Schofield (1981) by examining frequencies of 86 character states in 439 species of pleurocarpous mosses on a worldwide scale. These were compared across climatic zones, general habitat, and wetland to non-wetland gradient. He found that 44% of the characters are indeed influenced by climatic zone – the largest sphere of influence in the study. General habitat accounted for 35% and wetland to non-wetland gradient 23%.

In the Hedenäs (2001) study, two complex functions emerged. Water conduction and retention can be measured by differences in stem central strand morphology, leaf orientation, leaf costa type, alar cells, paraphyllia, pseudoparaphyllia, inner perichaetial leaf plications, vaginular paraphyses, capsule stomatal pore, operculum type, and possibly seta length. The second important function is spore dispersal, facilitated by capsule shape and orientation, annulus, exostome and endostome appearance, spore size and maturation time, and possibly seta length. the importance of phylogenetic history cannot be ignored as a limiting factor on adaptive characters, but other drivers include water availability and exposure to wind.

As seen in Chapter 2, bryophytes have a leafy **gametophyte** generation with one set of chromosomes (**haploid**) and a **sporophyte** generation that produces a capsule atop a short or long stalk and having two sets of chromosomes (**diploid**). The morphology of these two generations is strikingly different, so it is expedient to divide our discussion into these two generations.

Proctor (2010), a very astute bryologist who is familiar with both bryophyte physiology and structure, has summarized his perspective, supported by literature, on bryophyte adaptations.

Without considering how traits got that way, or which bryophytes are their ancestors, let us consider the traits themselves and their possible adaptive roles. Proctor (2010) compares the wide diversity of leaf shape, proportions of costa (see below under Costae) and lamina, and cell shape (Figure 4) in the **Dicranaceae** to the essentially uniform structure of the ecologically diverse **Fissidentaceae** (Figure 5; Figure 107). Such comparisons testify to the complexity of such adaptive considerations.

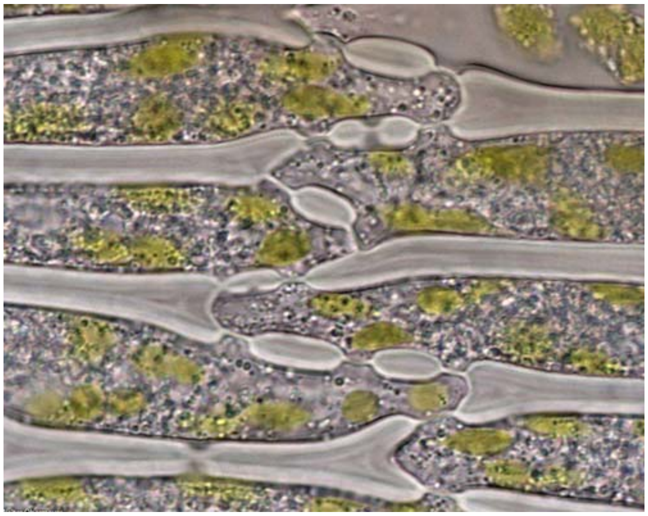

Figure 4. ***Dicranum polysetum*** leaf cells showing porose walls. Photo by Walter Obermayer, with permission.

Figure 5. ***Fissidens rivularis***, showing the costa, 2-ranked leaves, and flattened appearance that are present in all members of the genus. Photo by Des Callaghan, with permission.

Other families seem to have structures that adapt the family to narrower environmental circumstances. For example, the **Orthotrichaceae** live in the xeric locations of rocks and tree bark, supported by desiccation tolerance, cushion growth forms (Figure 6), and small isodiametric leaf cells (Figure 7), all of which help them to survive drying. **Hookeriaceae**, by contrast, have large, thin-walled cells (Figure 8-Figure 9) and survive only in moist, shady locations (Figure 10).

Figure 6. ***Orthotrichum obtusifolium*** forming a cushion on a tree trunk. Photo by Michael Lüth, with permission.

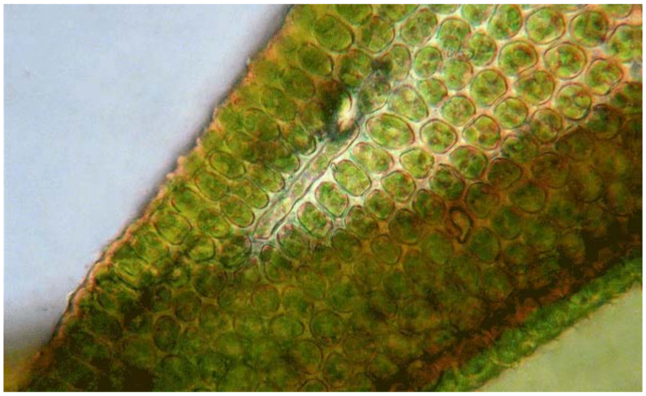

Figure 7. ***Orthotrichum pusillum*** showing isodiametric leaf cells. Photo by Bob Klips, with permission.

Figure 8. ***Hookeria lucens*** leaf showing thin-walled cells. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Stem

The bryophyte stem offers both support and a way of scavenging into a wider space. Pleurocarpous mosses extend across the ground surface, taking advantage of sunflecks on part of the moss while other parts are in the shade, a phenomenon that has been termed **foraging** (Figure 11). In some mosses, a central strand with specialized elongated **hydroids** and **leptoids** (Figure 12-Figure 13) contribute to transport of water, nutrients, and other substances, whereas in others these must travel from unspecialized cell to cell. Are there habitat conditions when ordinary cells are a better means of providing transport?

Figure 9. ***Hookeria lucens*** thin-walled leaf cells. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Figure 10. ***Hookeria lucens*** near Swallow Falls, Wales, where this whitish moss is kept moist by other mosses on a damp log in a stream valley. Photo by Janice Glime.

Richard Zander (Bryonet 8 May 2012) suggested that it might help to demonstrate a biophysical principle when one is unable to demonstrate an adaptation experimentally. As an example, he suggests that the cross section of a stem of ***Aloina hamulus*** (Figure 14) shows no central strand or sclerodermis. Rather, only a crowded set of cells is present. Zander compares that crowded set (see *e.g.* Figure 15) to the crowded bubbles of soap froth (Figure

16). And soap films assume the least area or least distance solution to their arrangement. He suggests that a stem with this arrangement therefore uses the least amount of photosynthate to create a plant axis. This would seem to be the simplest unspecialized case.

Figure 11. ***Brachythecium buchananii*** partly in sun and partly in shade. Connected plant parts can transfer photosynthate, and nutrients, from one part to the other through **foraging**. Photo by Michael Lüth, with permission.

Figure 12. ***Bryoxiphium*** stem ls showing long hydroids (green on left) and leptoids (reddish brown) compared to ordinary cortex cells (green or right). Photo courtesy of Izawa Kawai.

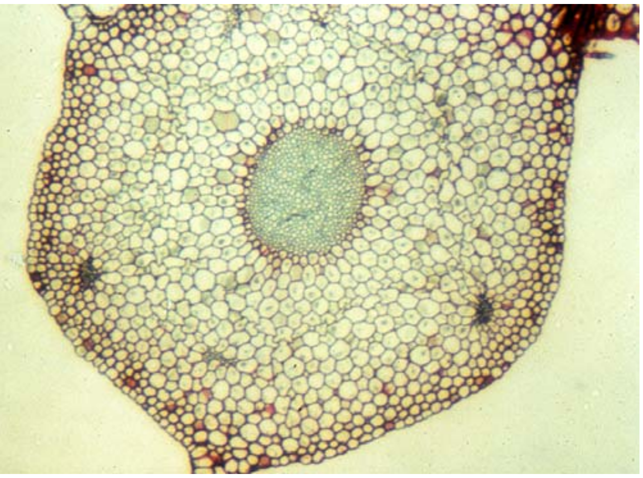

Figure 13. Stem cross section of the moss ***Mnium***. Blue-stained cells in center are **hydroids**; red-stained cells immediately around them are **leptoids**. Photo by Janice Glime.

Figure 14. ***Aloina hamulus***, a xerophytic moss with no central strand in its stem. Photo by Claudio Delgadillo Moya, with permission.

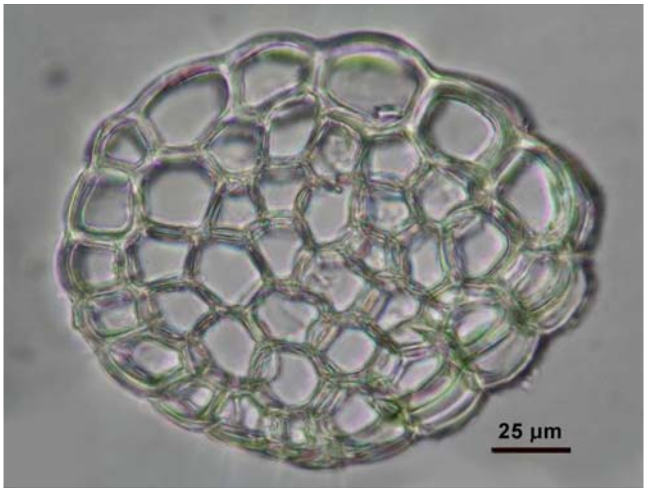

Figure 15. Leafy liverwort ***Telaranea pallescens*** stem cross section showing the "bubble" arrangement of cells described by Richard Zander. Photo by Tom Thekathyil, with permission.

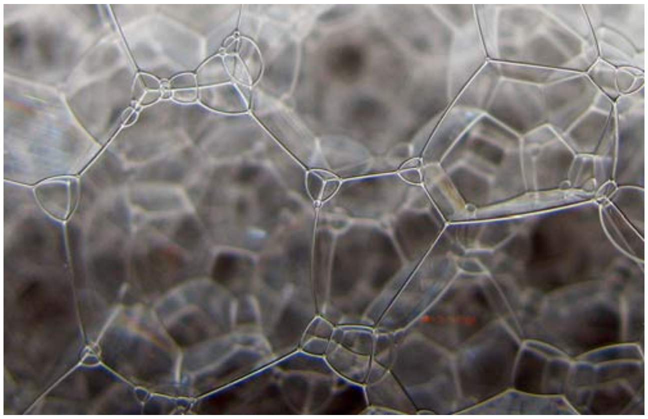

Figure 16. Soap bubble arrangement maximizing contact. Note pyramidal cells at the corners – reminiscent of trigones. Photo by Janice Glime.

Elumeeva *et al*. (2011) screened 22 abundant subarctic bryophytes from diverse habitats. They found that colony water retention did not correlate with individual shoot properties of leaf cell wall properties, water retention capacity, and desiccation rate. Instead, the colony desiccation rate was dependent on the density of water-saturated colonies of bryophytes. Colony desiccation rate was only marginally related to individual shoot desiccation rate, and was negatively correlated with it, suggesting that shoots with higher desiccation rates benefit from the protection of a colony.

Elumeeva and coworkers (2011) identified six distinct species groups based on habitat choice and phylogenetic relationships. ***Sphagnum*** (Figure 20-Figure 21) formed a unique group. **Forest mosses** were characterized by relatively big shoots with rather thick cell walls and loose colonies - tall turfs as well as wefts). **Moist to wet open habitats** had two groups: 1) those growing on stones, open soil patches, and somewhat drier parts of fens and characterized by thick cell walls and smaller amounts of internal and external water; 2) those growing in streams and wet fens and characterized by thinner cell walls but with more internal and external water. **Polytrichaceae** (Figure 17), like **Sphagnaceae**, formed its own group due to the small amount of external water. Similarly, ***Racomitrium lanuginosum*** (Figure 18) stood by itself as a group due in part to its low amount of external water and its unusual cells with thick, sinuose walls (Figure 19) and narrow cell lumen.

Figure 17. ***Polytrichum*** sp.; the ***Polytrichum*** species form a separate structural group due to their poor ability to hold external water. Photo by Annie Martin, with permission.

Figure 18. ***Racomitrium lanuginosum*** showing loose colony that does not hold much external water. Photo by Hermann Schachner, through Creative Commons.

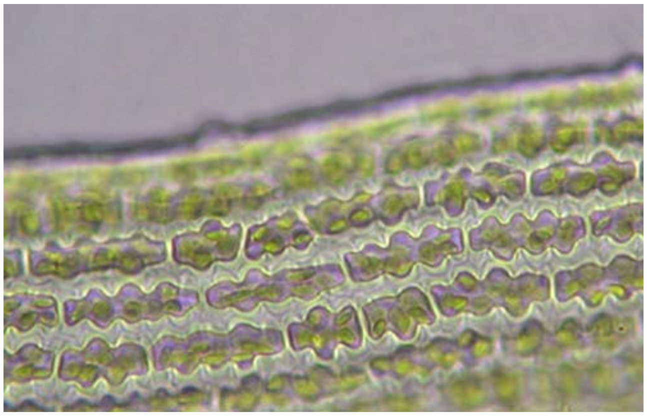

Figure 19. ***Racomitrium lanuginosum*** leaf cells showing sinuose walls and narrow lumen. Photo from Botany Website, UBC, with permission.

They (Elumeeva *et al*. 2011) found the lowest desiccation rate in species of ***Sphagnum*** [varying from 208 ± 15 min in ***S. fuscum*** (Figure 20) to 879 ± 51 min in ***S. lindbergii*** (Figure 21); mean ± SE, w=10]. The highest rates were in species with small shoots: ***Paludella squarrosa*** (Figure 22), ***Codriophorus fascicularis*** (=*Racomitrium fasciculare*; Figure 23), and ***Warnstorfia pseudostraminea*** (Figure 24) (17±2, 15±2, and 20±2 min).

Figure 20. ***Sphagnum fuscum*** hummock, a colony arrangement that holds large amounts of external water. Photo by Peter J. Foss, with permission.

Figure 21. ***Sphagnum lindbergii*** hummock, a colony arrangement that holds large amounts of external water. Photo by Allan Harris, through Creative Commons.

Figure 22. ***Paludella squarrosa***, a species among those with the highest rates of water loss. Photo by Michael Lüth, with permission.

Figure 23. ***Codriophorus fasciculare***, a species among those with the highest rates of water loss. Photo by Janice Glime.

They (Elumeeva *et al*. 2011) suggested that the relationships between the shoot and colony traits could help to predict changes in the hydrological function in bryophyte-dominated peatlands that are experiencing climate-induced shifts in species abundance. These relationships may also be useful in evaluating feedbacks of species shifts as they affect permafrost insulation and carbon sequestration functions.

Figure 24. ***Warnstorfia pseudostraminea***, a species among those with the highest rates of water loss. Photo by Stefan Gey, through Creative Commons.

Stem Structure

Stems are usually circular (Figure 25), but some are triangular in cross section (Figure 26); others are somewhat flattened (Figure 27). They can have layers of cells that differ in wall thickness and coloration. Some of these differences are expressed by cells in the central strand (Figure 25-Figure 26, Figure 30-Figure 31), but not all bryophytes have a central strand (Figure 15, Figure 27-Figure 29). Others are expressed in the outer cells and can contribute to reduction in water loss and strengthening of stems. But little testing has been done to determine how these outer cells really help. Are they hydrophobic? Do any help in the absorption of water? Do the strengthening cells correlate with habitats where stem strength is an advantage? Do the colors and thickness of the outer layer respond to the environment?

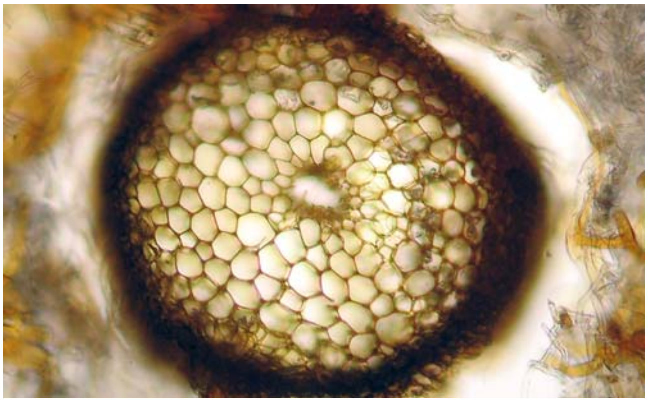

Figure 25. ***Dicranum scoparium*** stem cross section with outer cells having thick, darkly colored walls, thin-walled cortical cells, and rudimentary central strand. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Figure 26. ***Dendroligotrichum dendroides*** stem cross section showing triangular shape. Image on right shows details of the central strand. Photo by Juan Larrain, with permission.

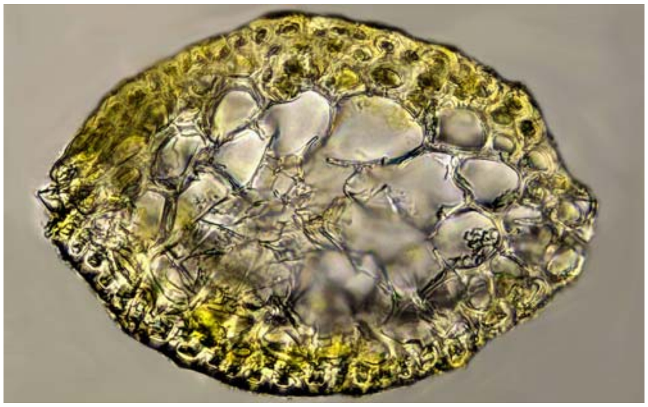

Figure 27. ***Fissidens bryoides*** stem cross section showing thick-walled outer cells and thin-walled central cells with no central strand. Photo by Dick Haaksma, with permission.

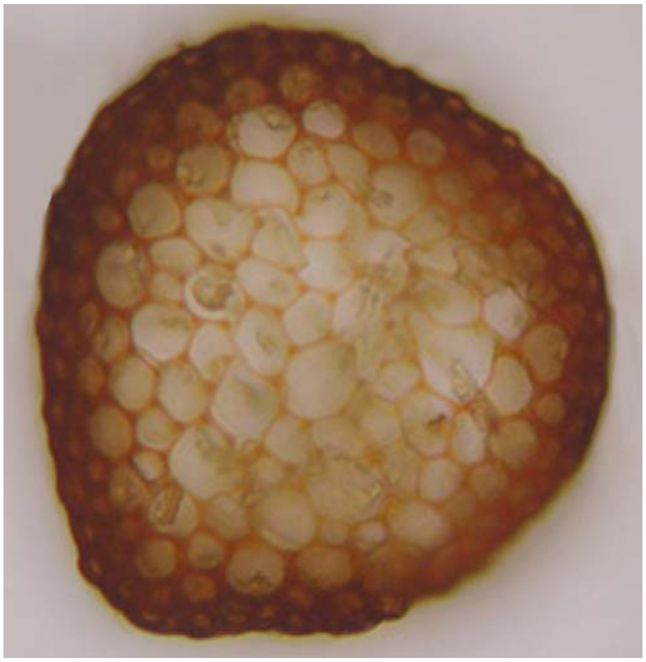

Figure 28. ***Andreaea*** stem with no central strand but with color in all the cell walls, suggesting phenolic pigments. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Figure 29. ***Hylocomium splendens*** stem cross section showing thick-walled, colored outer cells and thin-walled cortex with no central strand. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

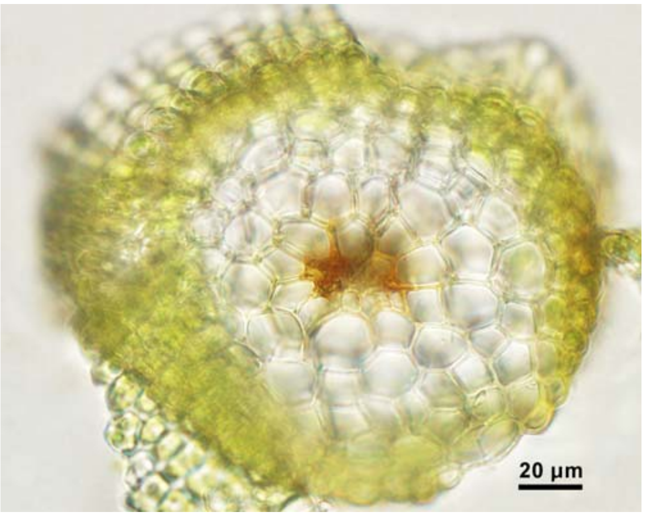

Figure 30. ***Molendoa sendtneriana*** stem cross section showing outer photosynthetic cells, translucent cortex, and central strand. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Several studies have addressed the thickness of the stem and the thickness of the outer layer under different environmental influences. See and Glime (1984) compared the stem thickness and stem wall thickness in ***Fontinalis flaccida*** (quiet water; Figure 32-Figure 33) and ***F. dalecarlica*** (fast water; Figure 34-Figure 35) after growing them in a common garden artificial stream. The new growth on both species retained their distinctness, with ***F. dalecarlica*** having both thicker stems and more thickened outer cells (Figure 36). Furthermore, even the central cortex cells of ***F. dalecarlica*** were thickened, whereas they were not in ***F. flaccida***.

Figure 31. ***Polytrichastrum formosum*** stem cross section showing thick-wall, colored outer cells, colored walls of cortex cells, thin-walled leptoids (food-conducting cells) and thick-walled, colored hydroid cells, the latter two cell groups forming the central strand. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Figure 32. ***Fontinalis flaccida*** showing thin stems for this quiet-water species. Photo by Lance Biechele, permission pending.

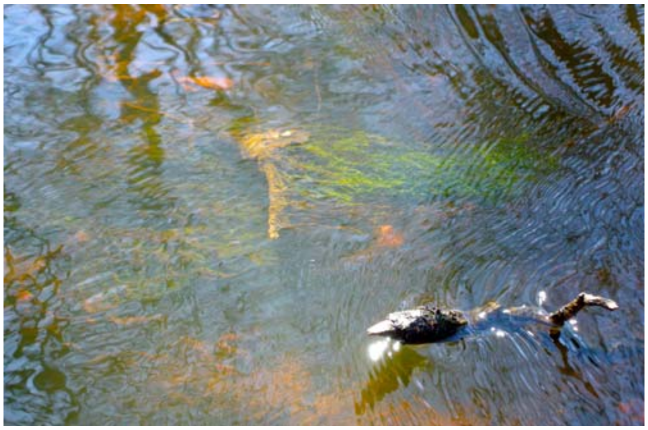

Figure 33. ***Fontinalis flaccida*** in relatively quiet stream water. Photo by Lance Biechele, permission pending.

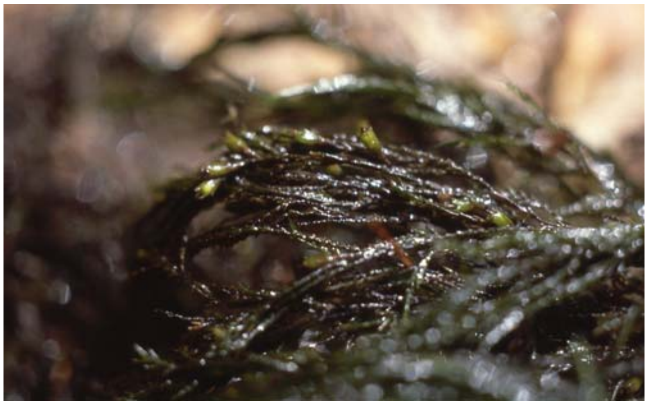

Figure 34. ***Fontinalis dalecarlica*** showing thick, strong stems. Photo by Janice Glime.

Figure 35. ***Fontinalis dalecarlica*** in a fast mountain stream. Photo by Janice Glime.

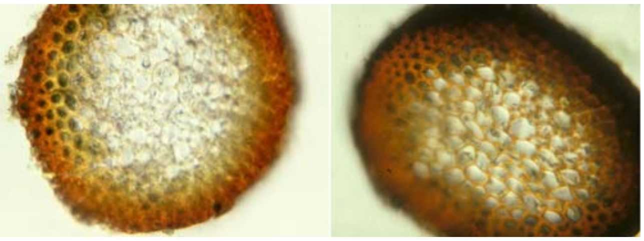

Figure 36. ***Fontinalis flaccida*** (**left**) and ***F. dalecarlica*** (**right**) stem cross sections showing the thickened (and colored) cortex cells and thicker outer layer of ***F. dalecarlica*** (**right**). Photos by Janice Glime.

Li *et al.* (1992) found that stem width in two ***Sphagnum*** species was plastic and differed significantly within species between those grown in water and those grown above water (Figure 37). Those above water developed 1-2 additional rows of hyaline cells in the outer layer of the stem (Figure 38). It is interesting that the less drought-resistant ***S. papillosum*** (Figure 39) had the greater difference in stem width between the two conditions. Despite that difference, ***Sphagnum magellanicum*** (Figure 40) is better at moving water than is ***S. papillosum*** and when grown in mixed clumps or alone it remains wet longer, whereas ***S. papillosum*** dries out quickly when it is in a hummock alone, but retains water as long as ***S. magellanicum*** when it grows mixed with it in about equal numbers (see Chapter 7-3).

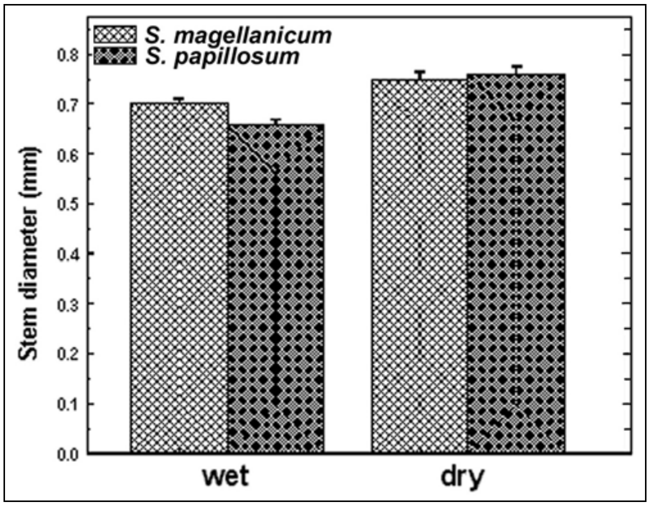

Figure 37. ***Sphagnum magellanicum*** and ***S. papillosum*** stem diameter when grown in wet vs dry (above water level) conditions. Graph by Yenhung Li, with permission.

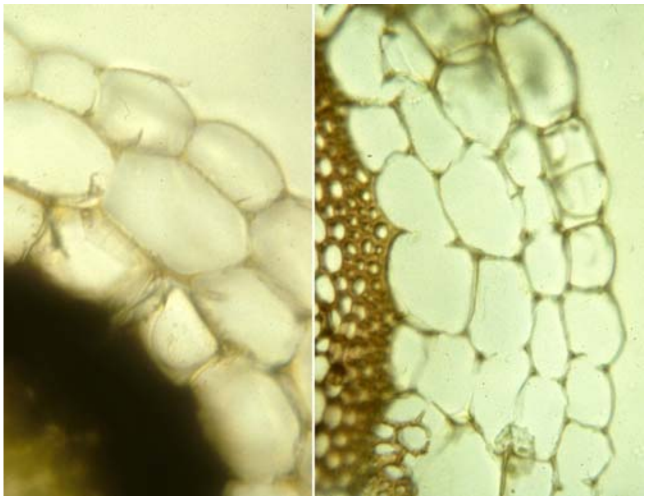

Figure 38. ***Sphagnum magellanicum*** stem cross sections showing outer hyaline layers. **Left:** stem grown in water; **right:** stem grown above water. Photos by Yenhung Li, with permission.

Figure 39. ***Sphagnum papillosum***, a drought-resistant species that develops additional rows of cells when above water. Photo by David T. Holyoak, with permission.

Figure 40. ***Sphagnum magellanicum***, a drought-tolerant species that develops additional rows of cells when above water. Photo by Michael Lüth, with permission.

One of the fascinating aspects of plants is their ability to change their structure in response to their environmental conditions. In at least some mosses, the stem diameter is able to increase in diameter in response to added ABA (Figure 41) (Spirina *et al*. 2020). ABA is known as a stress hormone, and one of its roles is to increase in response to drought, causing dehydration stress tolerance (Takezawa *et al*. 2011). Enlargement of the stem can provide strength, as seen by the response of tracheophytes to physical stress such as high wind (Telewski 2021). Already present in bacteria, ABA was of critical importance in adapting plants to land through added strength and adaptation to drought (Takezawa *et al*. 2011; Telewski 2021).

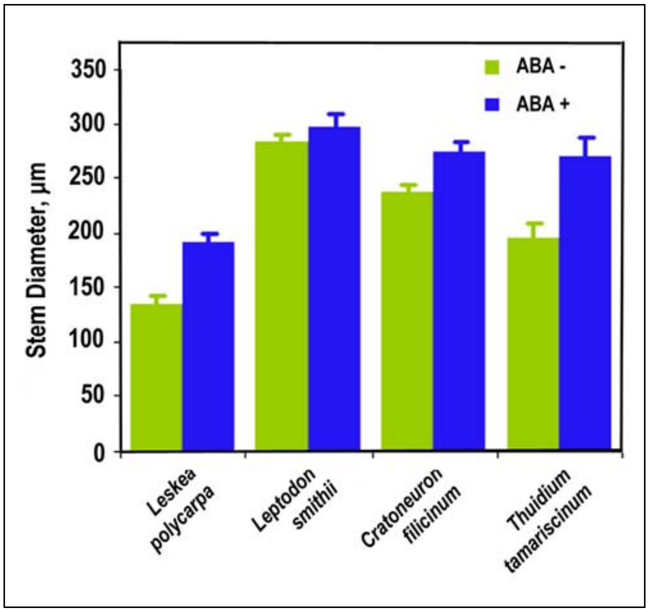

Figure 41. Effects of ABA on moss stem diameter. Modified from Spirina *et al*. 2011, through Creative Commons.

The **thigmomorphogenetic response** is the response to such stresses as mechanical bending or flexing in trees (Jaffe 1973; Telewski 2021). It is caused primarily by wind stress. Typically the trees respond to such bending by a reduction in extension or height growth and an increase in radial growth. A dose-dependent response to ABA contributes to these responses in trees and other plants, and now we know it can happen in bryophytes (Spirina *et al*. 2020).

Paraphyllia

Paraphyllia (Figure 42) are small green outgrowths on stems of some pleurocarpous mosses. They are useful taxonomic characters, permitting us to separate the sometimes look-alikes of ***Pleurozium schreberi*** (lacking paraphyllia; Figure 43) from ***Hylocomium splendens*** (having paraphyllia; Figure 44-Figure 45). But what is their function? The most logical is that of increasing water transport and reducing evaporation. There have been no tests to determine the value of their photosynthetic ability. And how often do they function as propagules, easily broken from the stems when dry? Do they form new plants under those conditions?

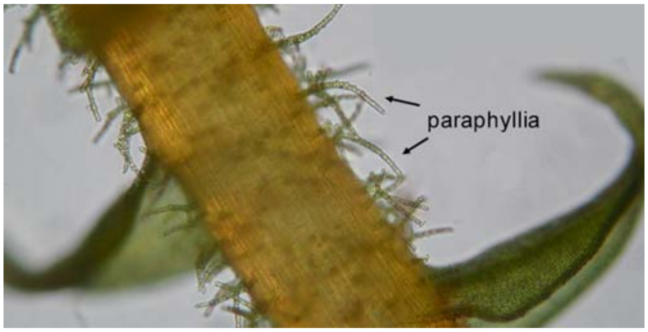

Figure 42. Stem of ***Thuidium*** sp. showing paraphyllia. Photo by Paul Davison, with permission.

Figure 43. ***Pleurozium schreberi***, a moss that lacks paraphyllia. Photo by Janice Glime.

Figure 44. ***Hylocomium splendens***. If you look carefully at the lowest visible part of the red stem in the center, you can see small bits of green paraphyllia. Photo by Rosalina Gabriel, with permission.

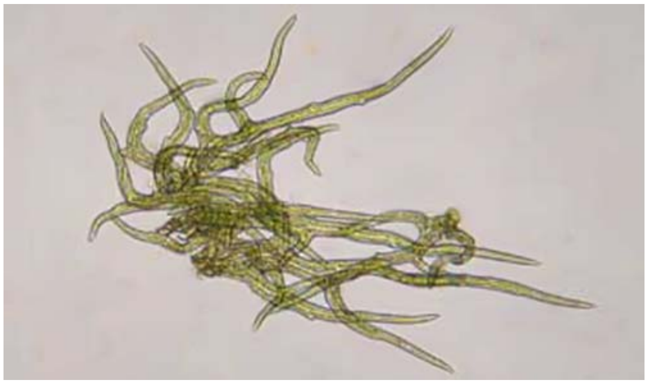

Figure 45. ***Hylocomium splendens*** paraphyllia. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Spirina *et al*. (2020) compared paraphyllia in various species of mosses. They found that in the **Leskeaceae** (Figure 46-Figure 47), **Neckeraceae** (Figure 48-Figure 49), and **Amblystegiaceae** (Figure 50-Figure 51) these were distributed along the stem near the branch primordia. In these families, abscisic acid (ABA) stimulates increased production of the paraphyllia. On the other hand, they occur all along the stem in **Climaciaceae** (Figure 52-Figure 53), **Hylocomiaceae** (Figure 54-Figure 56), and **Pseudoleskeaceae** (Figure 57-Figure 58). In the **Thuidiaceae** (Figure 42; Figure 59-Figure 61), both types occur.

Figure 46. ***Leskea polycarpa*** (**Leskeaceae**), a species with paraphyllia near the branch buds. Photo by Hugues Tinguy, with permission.

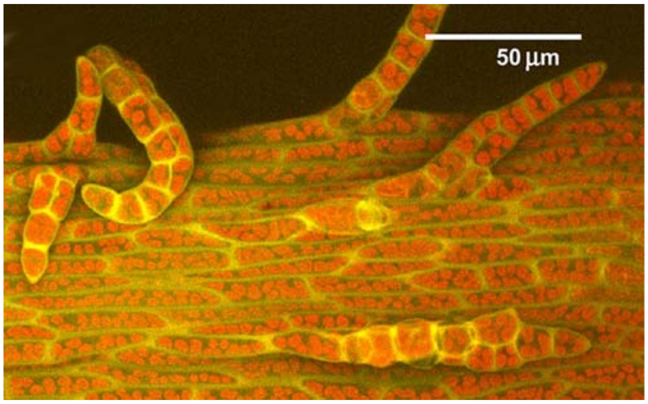

Figure 47. Paraphyllia on stem of ***Leskea polycarpa***. Photo modified from Spirina *et al*., through Creative Commons.

Figure 48. ***Metaneckera menziesii*** (**Neckeraceae**), a species with paraphyllia near branch buds. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

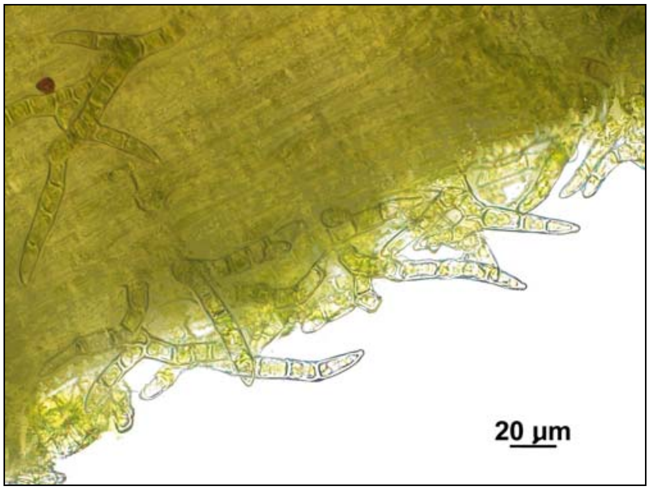

Figure 49. ***Metaneckera menziesii*** paraphyllia on stem near bud. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

Figure 50. ***Cratoneuron filicinum*** (**Amblystegiaceae**) in water, a species with paraphyllia near branch buds. Photo by Hugues Tinguy, with permission.

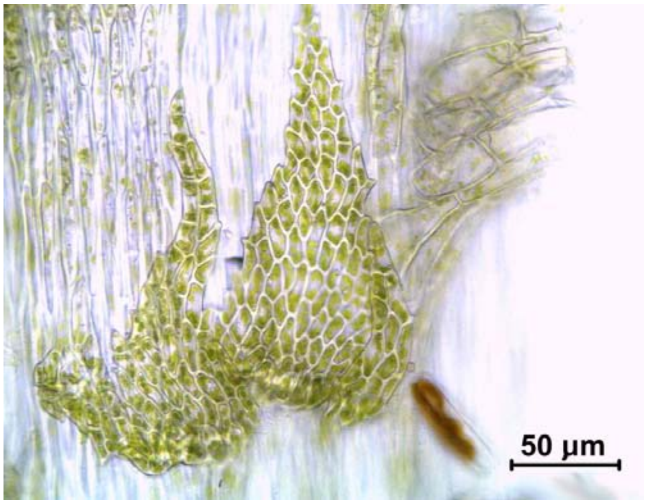

Figure 51. ***Cratoneuron filicinum*** paraphyllia near bud. Photo by Hugues Tinguy, modified, with permission.

Figure 52. ***Climacium dendroides*** (**Climaciaceae**), a species with paraphyllia along the stem. Photo by Vladimir Bryukhov, through Creative Commons.

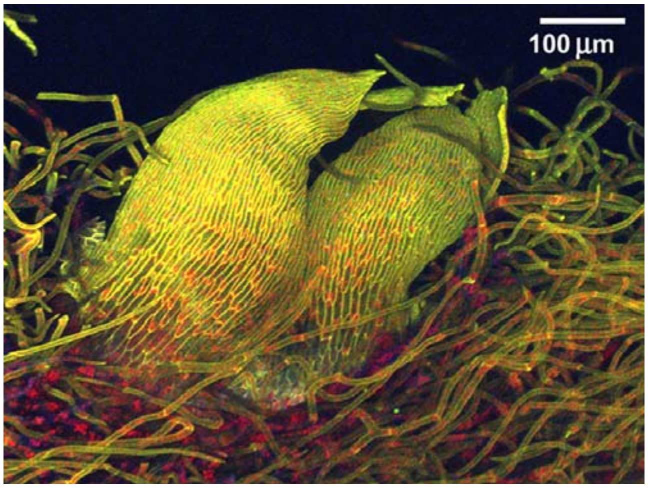

Figure 53. ***Climacium dendroides*** paraphyllia on stem. Photo modified from Spirina *et al*. 2011, through Creative Commons.

Figure 54. ***Hylocomium splendens*** (**Hylocomiaceae**), a species that produces paraphyllia along the stem. Photo by Claire Halpin, with permission.

Figure 55. ***Hylocomium splendens*** showing paraphyllia along stem. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

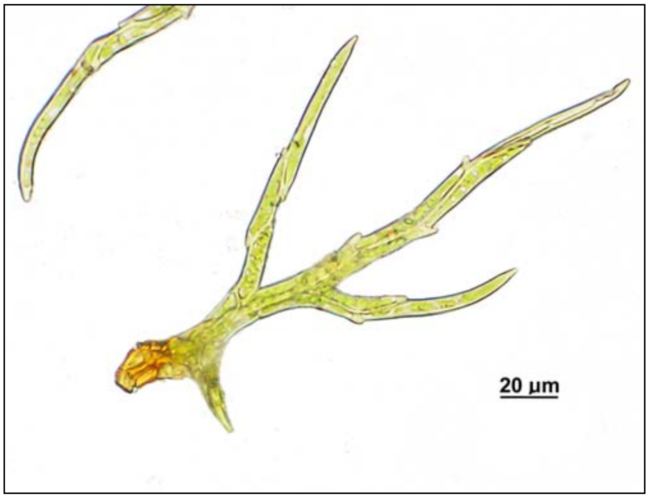

Figure 56. ***Hylocomium splendens*** paraphyllia. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

Figure 57. ***Pseudoleskea radicosa*** (**Pseudoleskeaceae**), a species with paraphyllia spread along the stem. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

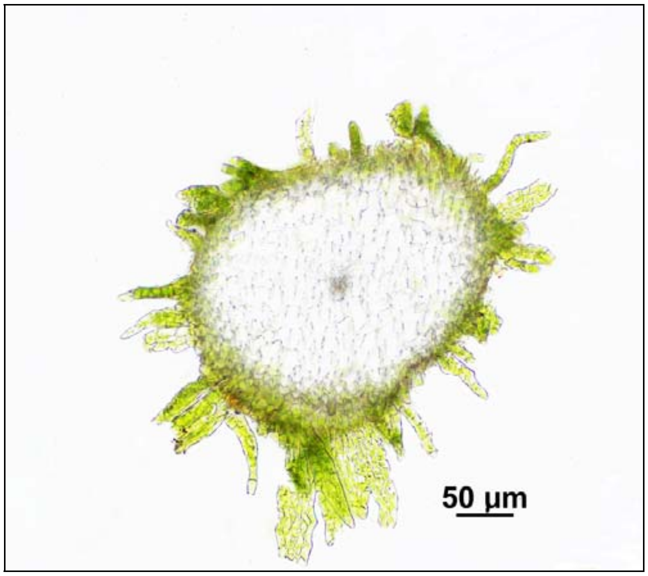

Figure 58. ***Pseudoleskea radicosa*** with paraphyllia on stem cross section. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

Figure 59. ***Thuidium delicatulum*** (**Thuidiaceae**), a species with paraphyllia along the stem and surrounding the branch buds. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

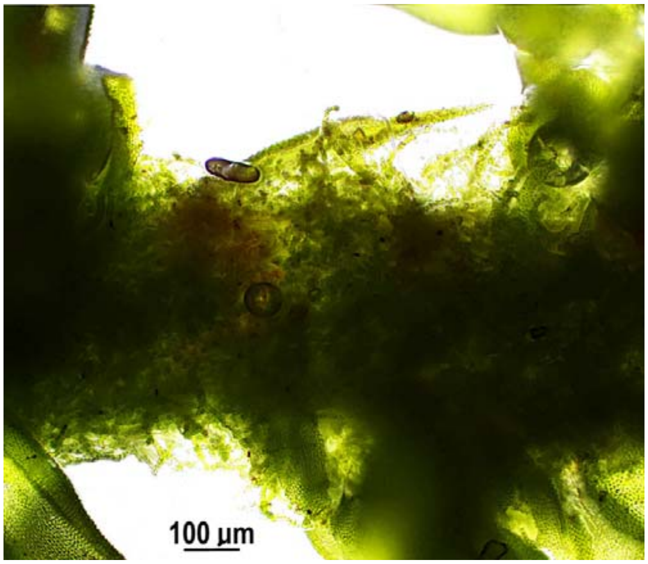

Figure 60. ***Thuidium delicatulum*** paraphyllia showing their density on the stem. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

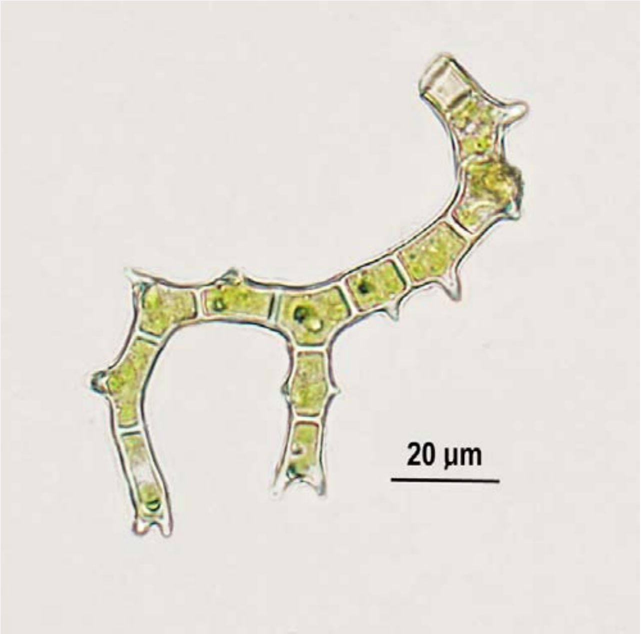

Figure 61. ***Thuidium delicatulum*** paraphyllium. Photo from Dale A. Zimmerman Herbarium, WNMU, with permission from Russ Kleinman & Karen Blisard.

Leaf Margins

Margins of leaves can be flat, **involute** (rolled upward (Figure 62), **revolute** (rolled under; Figure 63-Figure 64), and **bordered** or **unbordered**. The borders can be one cell thick or multiple cells thick. The whole leaf can be **inrolled** (rolled upward; Figure 65-Figure 66), folded (see Keels below), or flattened. And the borders can have teeth or be smooth. Some functions for these will be discussed in the chapter on Water Relations (Chapter 7-4, Vol. 1), but this chapter would not be complete without some consideration of them.

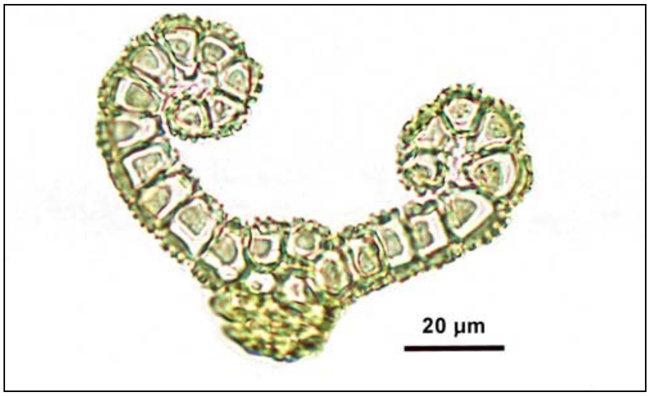

Figure 62. ***Weissia controversa*** leaf cross section showing involute margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

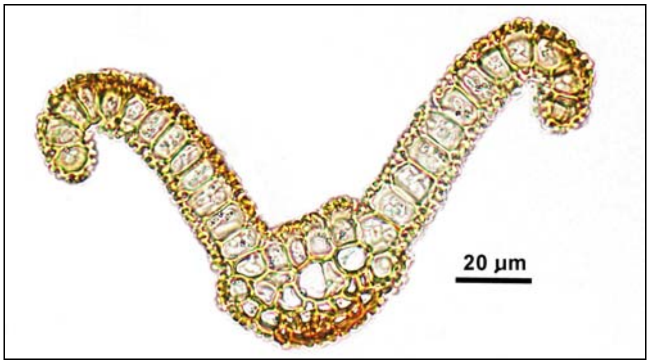

Figure 63. ***Bryoerythrophyllum recurvirostre*** leaf cross section showing revolute leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 64. ***Ceratodon purpureus*** showing revolute leaf margins. Photo by Malcolm Storey, through Creative Commons.

Figure 65. ***Dicranum muehlenbeckii*** showing the curled, inrolled leaves. Photo by Michael Lüth, with permission.

Figure 66. ***Dicranum muehlenbeckii*** leaf cross section showing inrolled leaf. Photo by Michael Lüth, with permission.

Borders or Not

Bryophytes distinguish their leaf borders in a number of ways. While many lack special border cells (Figure 67), they may still have teeth on the border, as discussed below. Others may lack specialized cells but have margins that are more than one cell thick (Figure 74). And those with borders typically have elongate cells (Figure 68-Figure 69) that differ from lamina cells. These specialized border cells may have teeth or lack them.

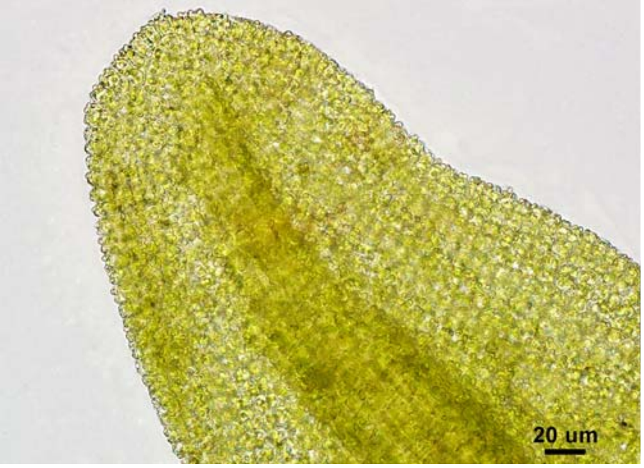

Figure 67. ***Barbula convoluta*** leaf with no border and with papillose cells and a costa. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 68. ***Mnium spinosum*** leaf showing border with colored elongate cells contrasting with nearly isodiametric leaf lamina cells. Photo by Michael Lüth, with permission.

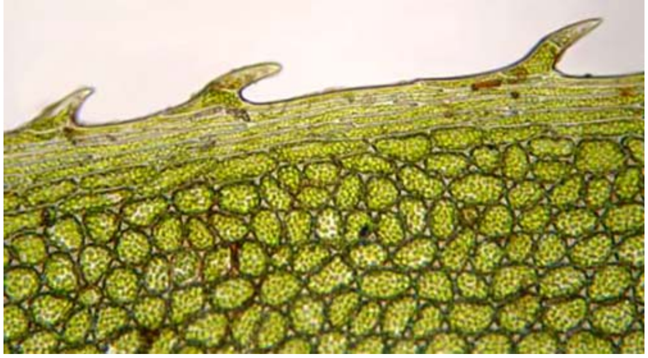

Figure 69. ***Plagiomnium insigne*** showing border that is several cells wide with elongate cells that contrast with the isodiametric lamina cells. Photo from Botany website, University of British Columbia, BC, Canada, with permission.

Special border cells are rare among tracheophytes, so this suggests that their presence may indicate a function in bryophytes that is not useful in tracheophytes. In fact, it is likely that this is true. Kürschner (2004) described the contortions and shrinkage of the leaf lamina in **Pottiaceae** (Figure 70-Figure 71) and **Grimmiaceae** (Figure 72-Figure 74). These contortions are typically dependent on the leaf border. As the lamina shrinks while drying, the border remains firm and does not shrink. Hence, the shrinking lamina cells pull and tug on the borders and a twisted leaf results. These leaves wind around the stem helically, benefitting from protection by the stem and reducing further desiccation and protecting against solar radiation. In desert habitats, the adhering sand grains are removed as the twisting leaves respond to water uptake and straighten during a rainfall (Scott 1982).

Figure 70. ***Tortula intermedia*** (**Pottiaceae**) hydrated. Photo by Michael Lüth, with permission.

Figure 71. ***Tortula intermedia*** (**Pottiaceae**) dry with leaves twisted around the stem. Photo by Michael Lüth, with permission.

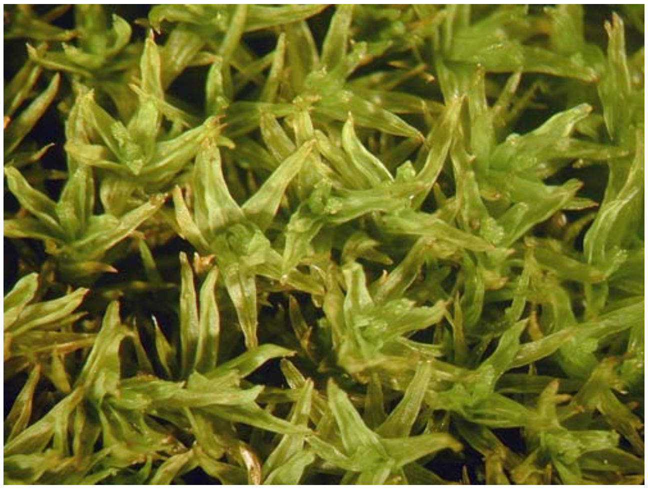

Figure 72. ***Grimmia anomala*** (**Grimmiaceae**) showing hydrated leaves that spread widely around the stem. Photo by Michael Lüth, with permission.

Figure 73. Dry ***Grimmia anomala*** (**Grimmiaceae**) showing leaves twisted around the stem. Photo by Jan-Peter Frahm, with permission.

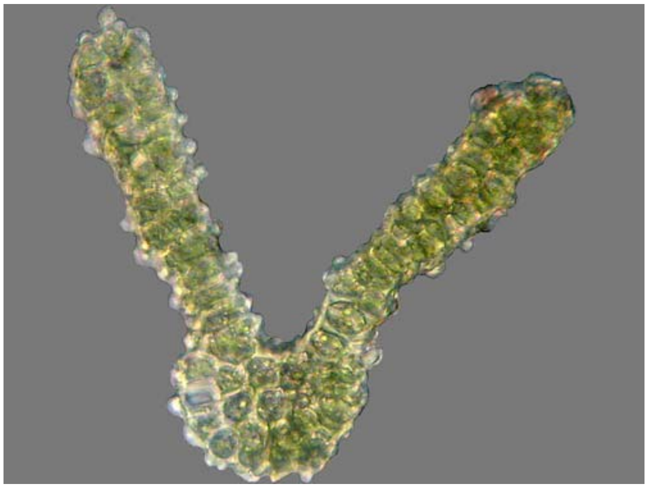

Figure 74. ***Grimmia anomala*** (**Grimmiaceae**) leaf cross section showing areas that are more than one cell thick, especially at the margin. The thickenings may contribute to the way it twists around the stem when dry. Note that the margin consists of a double layer of cells, giving the margin rigidity. Photo by Michael Lüth, with permission.

Marginal Teeth

Marginal teeth in tracheophytes seem to have multiple functions. In tracheophytes, marginal teeth are responsive to temperature (Royer & Wilf 2006; Royer *et al*. 2012). Using 3549 tracheophyte species from six continents, they determined toothed species are more likely to be deciduous, thin leafed, of low leaf mass per area, with ring-porous wood, and have a high leaf nitrogen content. Trees in the canopy are most likely to be sensitive to temperature as a determinant of leaf-margin state compared to shrubs and herbs. Hence, leaf thinness and deciduousness as well as temperature are linked to having teeth. Royer *et al*. argue that by being thin and having thin tissues in teeth along the margins, these deciduous leaves can return their contents to the ecosystem quickly. Perhaps the thin margins permit fungal and bacterial colonies to get established quickly?

Yet another hypothesis was tested by Baker-Brosh and Peet (1997). They observed that teeth were rare in tropical moist forests but frequent in temperate deciduous forests. They hypothesized that in those forests where leaves had to grow anew each year the teeth and lobes served as the site of early season photosynthesis in new leaves. Using $^{14}CO_2$ and autoradiography, they determined that eight species with prominent teeth or lobes did indeed exhibit early season photosynthesis on the margins, whereas in those with entire margins (no teeth; 4 species) there was no early season photosynthesis on the margins. However, seven species that were toothed or lobed likewise lacked early season photosynthesis on the margins. Royer and Wilf (2006) demonstrated that teeth were advantageous for early season photosynthesis in temperate climates. Could there be similar early season photosynthetic behavior to aid growth of new leaves in some mosses, particularly if margins at that stage are predominantly green (Figure 75-Figure 77)?

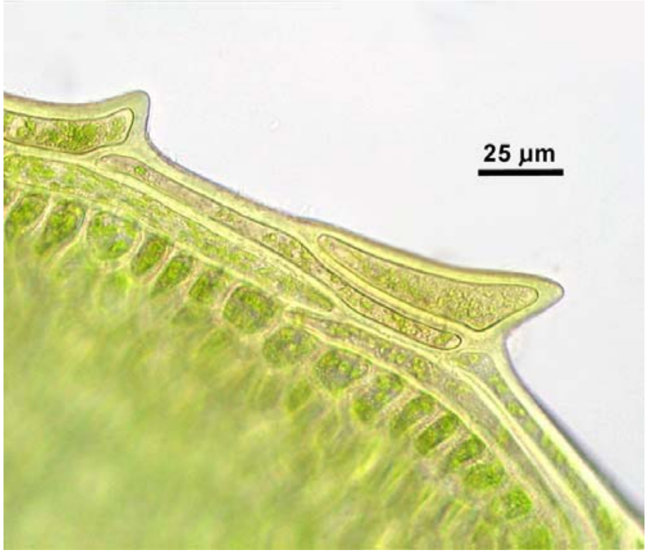

Figure 75. ***Plagiomnium undulatum*** leaf border showing photosynthetic marginal teeth. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 76. ***Plagiomnium undulatum*** showing small leaves at apex where teeth may help in photosynthesis in early development. Photo from <www.aphotofauna.com>, with permission.

Royer *et al*. (2009) further explored the role of teeth in the Australian subtropical rainforest trees. Using 227 sites, they found a correlation between humidity and number of toothed species, with the greatest occurrence of toothed species in the riparian zone and the fewest at the drier ridge tops. They attribute the relationship to the availability of water. Could it be that toothed species of these large leaves lose water more easily due to the increased surface area, negating the early spring advantage in dry sites? Would this incur the same problem in bryophytes, or might the teeth actually confer a water advantage – a site for collecting and absorbing water much like the hair tips discussed below? I am aware of no quantitative study to test this hypothesis in bryophytes.

Applying these tracheophyte principles to bryophytes could bring interesting insights, but I am unaware of any attempt to test the correlations.

In bryophytes, teeth can occur along the margins [singly (Figure 75) or doubly (Figure 77)], but also occasionally projecting from the leaf lamina (Figure 78-Figure 80) or costa (Figure 80-Figure 81).

Figure 77. ***Mnium spinosum*** leaf showing double teeth on leaf margin. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 78. ***Atrichum selwynii*** leaf showing teeth projecting from the dorsal side of the leaf lamina. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 79. ***Atrichum undulatum*** leaf showing teeth in diagonal rows on dorsal side. Photo by Jutta Kapfer, with permission.

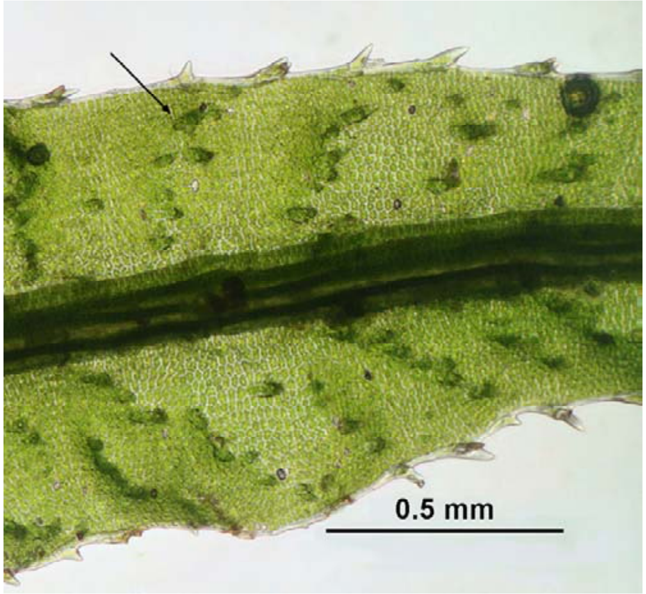

Figure 80. ***Atrichum undulatum*** leaf showing teeth (arrow) on dorsal side on undulations. Photo by Hermann Schachner, through Creative Commons.

Figure 81. ***Mnium spinosum*** back of costa showing tooth on costa. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Among tracheophytes, leaf teeth are postulated to mimic effects of herbivory and thus to discourage additional herbivores on a leaf that has already been eaten. This proposed deterrent may have credence in the fact that antiherbivore compounds often are inducible (Karban & Baldwin 1997; Karban *et al*. 1997; Ceh *et al*. 2005), so a herbivore might recognize that the leaf (or alga) has been eaten and will taste bad without the herbivore having to take a sample. The argument is that the teeth give the appearance that the leaf has been nibbled before.

Could this tracheophyte herbivore deterrent of teeth have a role in bryophytes? Might herbivores consider it a signal that the leaves will taste bad? We don't even know if antiherbivore compounds in bryophytes are inducible. But then, perhaps the insects don't know either and assume the bryophytes behave like tracheophytes. And do these bryophyte teeth really look like evidence of herbivore browsing? Or do they possibly have the deterrent effects that hairs and spines have on browsing by large herbivores? Might they deter such soft-bodied herbivores as snails? It would be easy to see if snails choose to crawl over bryophyte leaves without such teeth in preference to those with them. ***Atrichum undulatum*** would be a good test subject with its teeth on the lamina (Figure 78-Figure 80).

Liverworts

And what about the lobes and teeth of **leafy liverworts** (Figure 82)? Do they have any adaptive value? Could they also have antiherbivore functions? Do they serve to hold water on the leaf surface? Or are they just useful tools for bryophyte taxonomists?

In the leafy liverwort genus ***Plagiochila***, habitats in North America differ from those in the tropics and so do the teeth. In North America, ***P. porelloides*** (Figure 83-Figure 84) lives next to or in water and has small or almost no teeth. In the tropics, where there are many species in the genus, this genus lives on tree trunks and sides of boulders where conditions may be almost xeric. Most of these species have large teeth (Figure 85). When it rains, these liverworts can become quite saturated. Do the teeth help the leaves to hold droplets of water? Could their added surface area provide evaporative cooling? Or is this again an early season adaptation to enhance photosynthesis?

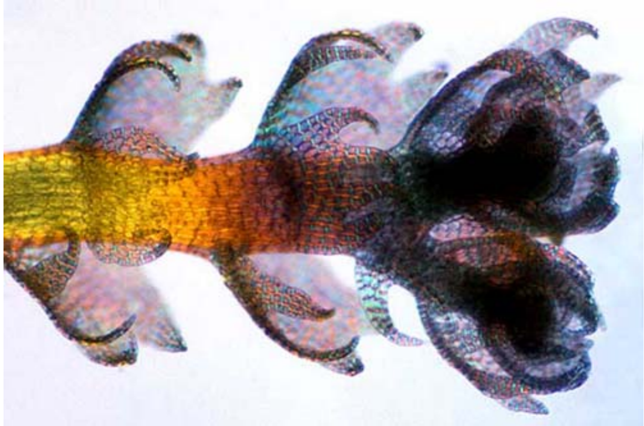

Figure 82. Leafy liverwort showing lobes that curl toward the stem. One can easily imagine these leaves trapping a cohesive drop of water, then slowly bending inward as that dater droplet shrinks. Photo by Bill Malcolm, through Creative Commons.

Figure 83. ***Plagiochila porelloides***, a species that grows in moist areas like stream banks in the Northern Hemisphere. Note that the teeth are much smaller than in most tropical species. Could teeth provide evaporative cooling? Photo by Dick Haaksma, with permission.

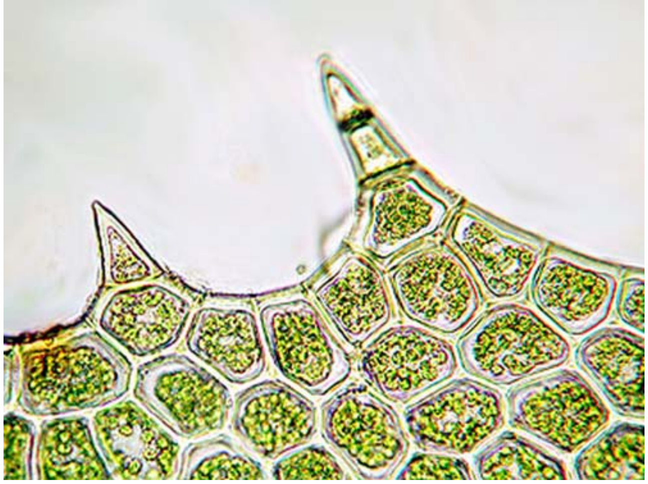

Figure 84. ***Plagiochila porelloides*** leaf teeth showing the smaller size in this streamside and wet habitat species compared to tropical epiphytes and epiliths. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Figure 85. ***Plagiochila raddiana*** from the Neotropics. How do these teeth function for the tropical epiphytic and epilithic species? Photo by Michael Lüth, with permission.

Some species of liverworts have deep lobes. In some cases these are curved toward the stem (Figure 86) and one can imagine that they help to hold drops of water, clinging to them and curving further inward as the drop decreases in size (Figure 87). Such structure could provide a water reservoir for the leaf, permitting photosynthesis for a longer period of time. If the convex surface faces the light, the water reservoir could permit photosynthesis to continue for a longer period of time without interfering with light capture, while permitting CO_2 to enter from the surface opposing the water drop.

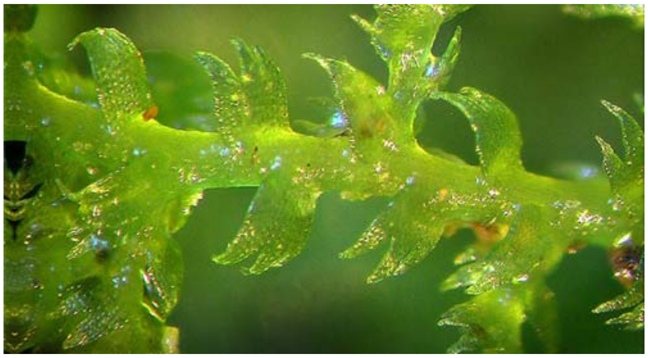

Figure 86. ***Lepidozia reptans***, a relative small species with leaves in a size range where they could trap a cohesive water drop. Teeth may aid in holding that water next to the leaf. Photo by Walter Obermayer, with permission.

Figure 87. Wet ***Ptilidium ciliare*** showing teeth clinging to the leaf beneath, presumably aiding in water retention. Photo by Des Callaghan, with permission.

Presumably, size affects the utility of teeth and lobes. If one compares the large size of the leaf and its lobes in ***Lophocolea*** (Figure 88) with those in ***Cephalozia*** (Figure 89), it appears their functionality should work differently. Small droplets of water are harder to break up than large ones. Does this have any bearing on utility, size, and location of the lobes? Would long, thin lobes on large leaves direct water off the leaf, permitting CO_2 to enter the cells, behaving like the drip tips of some tropical leaves?

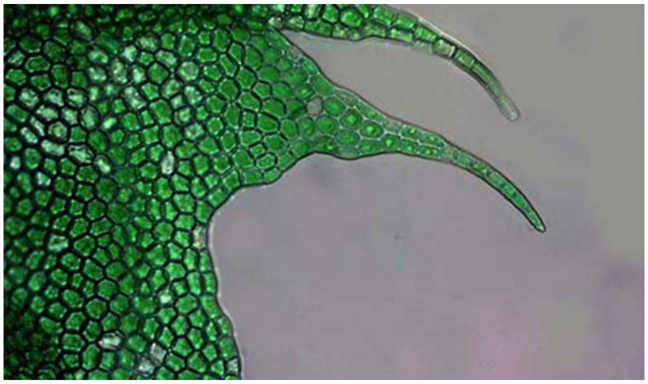

Figure 88. ***Lophocolea bidentata***, a relatively large species showing leaf lobes. Might these aid in holding drops of water? Photo by Aimon Niklasson, with permission.

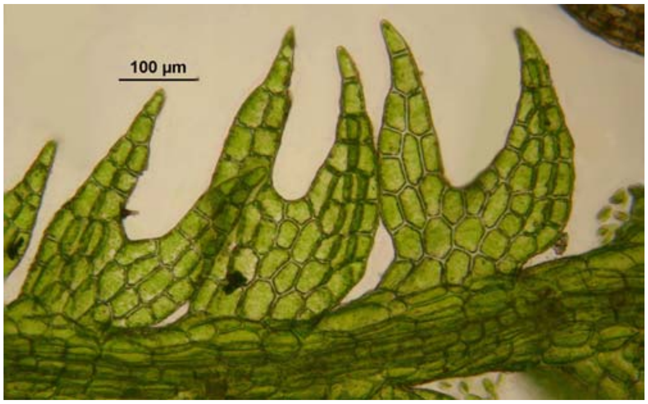

Figure 89. ***Cephalozia bicuspidata***, a much smaller species than ***Lophocolea bidentata***, showing leaf with deep lobes. Could these lobes provide a means of holding onto a drop of water, much as a diving beetle holds onto a bubble of air? Photo by Hermann Schachner through Wikimedia Commons, with permission.

Let's return to the consideration of moisture relationships and number of species with teeth. This might be simplest to demonstrate with epiphytes. In the temperate zone, where epiphytic positions can impose long drought periods, most of the large leafy liverworts have entire leaf margins, *e.g.* ***Frullania*** (Figure 90), ***Porella*** (Figure 91), and ***Radula*** (Figure 92). In the tropics, ***Plagiochila*** (Figure 93) is very common, with many species, and most of these have rather large teeth. Tropical rain forests have long seasons of rainy weather that can maintain the moisture among these liverworts, followed by a long season of drought when the liverworts can remain dormant. Temperate species, on the other hand have the risk of drying before they have repaired the damage from the last drought. Which strategy – teeth or no teeth – permits them to hold water longer? What fun for experimentation!

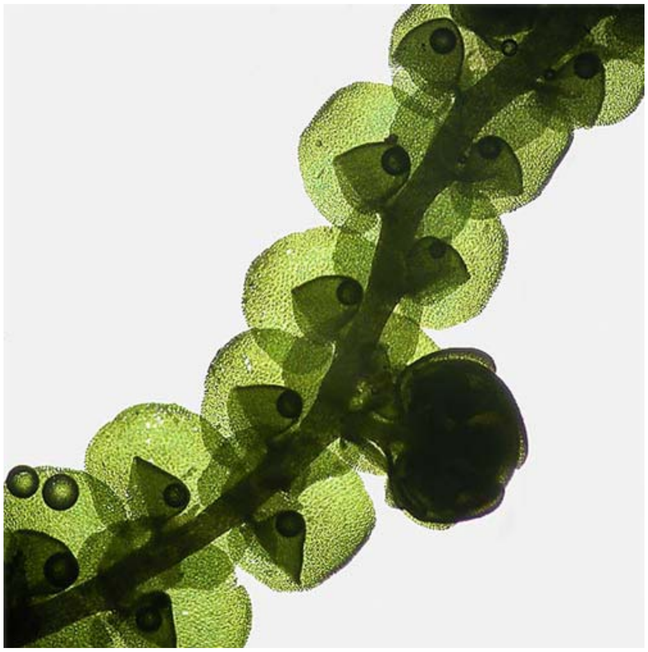

Figure 90. ***Frullania dilatata*** showing lobules and entire margins (no teeth or lobes). Photo by Walter Obermayer, with permission.

Figure 91. ***Porella cordaeana*** showing entire leaf margin. Photo by Jan-Peter Frahm, with permission.

Figure 92. ***Radula*** from the Neotropics showing entire leaf margins. Photo by Michael Lüth, with permission.

Figure 93. ***Plagiochila adianthoides*** from the Neotropics showing toothed leaf margins. Photo by Michael Lüth, with permission.

One might argue that in liverworts like ***Nowellia curvifolia*** (Figure 94), the long lobes provide a stalk for the clusters of gemmae produced at their tips. Such positioning for the gemmae might make it easier for them to escape the plant and travel a greater distance.

Figure 94. ***Nowellia curvifolia*** showing gemmae positioned at the ends of narrow leaf lobes. Photo by Paul G. Davison, with permission.

Hair Tips

Many bryophytes in dry habitats have hair tips on the leaves (Figure 95-Figure 96). One suggestion for their role is that they are able to reflect sunlight (Kürschner 2004). This can protect the underlying cells from sun damage when they are dry and the leaves are compressed against the stem. And in many species, when the plants are dry the leaves twist around the stems so that each hair overlaps the leaf above it (Figure 97).

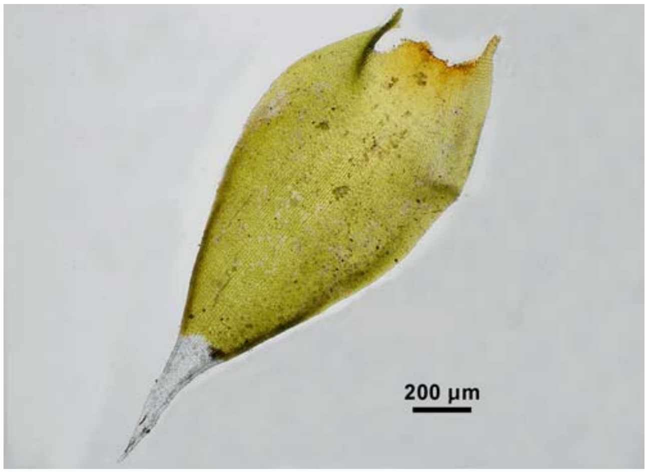

Figure 95. ***Hedwigia ciliata*** leaf showing translucent hair point. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 96. ***Hedwigia ciliata*** with wet plants on the upper left and dry ones on the edge of the colony (lower right). Note how the dry leaves cling to the stem compared to the spreading wet leaves. Photo by Janice Glime.

Figure 97. ***Grimmia decipiens*** showing array of hairs that help fill in spaces between stems. Photo by Des Callaghan, with permission.

A second function has been suggested – that the hair points may help to absorb condensed water vapor from fog and dew (Figure 98-Figure 100) (Kürschner 2004). This phenomenon is well known from physics – small droplets accumulate around thin wires – and on fine hairs. To this role, I would add that the hairs may provide additional capillary spaces that gain water in rain as well and hold it there for longer periods of time, preventing evaporation from the leaves.

Figure 98. ***Grimmia*** cf ***pulvinata***, lightly covered with dew, on churchyard wall. This picture supports the notion that the hairs can act to collect dew that can eventually drip down into the moss mat. In areas with low precipitation and frequent fog, this can be the only source of water for some mosses. Photo by Brian Eversham, with permission.

Figure 99. ***Grimmia horrida*** habitat at edge of fog in northern Portugal. Photo by Michael Lüth, with permission.

Figure 100. ***Campylopus introflexus*** collecting water drops on the fine hairs. Photo by Michael Lüth, with permission.

Figure 101. ***Tortula muralis*** with hair tips trapping water droplets. Photo by Christophe Quintin, through Creative Commons.

If we examine the picture of ***Grimmia*** from Scotland (Figure 102), we can see a third possible function. Note that the frost is held away from the leaves. Frost and ice crystals are very hygroscopic and can draw water out of the leaves as they do from the foods in your freezer. The hairs seem to function, at least in this case, to keep the frost from contacting the leaves, thus avoiding their potential desiccating effect. The same is often seen in leaves of early spring perennial flowers.

Figure 102. ***Grimmia*** capsules and frost at Dunkeld, Scotland. Photo by Allan Water.

As I sorted through images, I was struck by another potential purpose for some hairs. As you will learn in Chapter 7, bryophytes survive desiccation much better than their tracheophyte counterparts. But when they are rehydrated, they must repair damaged membranes, and this seems to take about 24 hours. A short misting or very light rain that evaporates right away may not provide enough hours for repair before the bryophyte is once again desiccated, hence wasting the energy expended in its failed attempt. Hairs can fill in spaces between apices (Figure 103), trapping water droplets and keeping them from entering the moss mat, thus preventing a hydrated period that is too short, or perhaps keeping the water at the tip to be absorbed slowly over time (Figure 104).

Figure 103. ***Grimmia*** at Goudini Spa, South Africa. With hairs in this position, they can capture the cohesive water drops (Figure 104) and prevent them from entering the moss mat during a light shower. When the storm lasts longer, the weight and size of the droplets will finally force them through the hairs. Photo by Janice Glime.

Figure 104. ***Pohlia wahlenbergii*** with cohesive water drops. Note that these drops are mostly too large to penetrate the mat and hence remain at the surface, held together by their own cohesive forces. Photo by J. C. Schou, through Creative Commons.

Finally, I suggest that hair points, at least in some species, can deter some kinds of herbivores. We know that invertebrate herbivores are deterred by hairy leaves of tracheophytes (Karban & Agrawal (2002) and that spiny leaves deter ungulates (Obeso 1997). It is not unreasonable to assume that they can confer similar advantage to bryophytes, particularly when hair points overlap extensively as in ***Grimmia arenaria*** (Figure 105).

Figure 105. ***Grimmia arenaria***, demonstrating long hairs that might protect from bright sun or prevent desiccation. Photo by Des Callaghan, with permission.

Costae

The **costae** are the moss versions of midribs (Figure 106). They are absent in liverworts. Their functions may include movement of water from base to tip of the leaf, or perhaps from tip to base. This can be surmised by the elongate structure of the cells (Figure 107) compared to the shortness of leaf lamina cells in many species. I have referred to base to tip transport because it is the base where water can accumulate in the leaf axil and receive water from the stem through its external movement of water. But in some plants, water might move into the leaf at the tip, possibly absorbed through the apical leaf hair, but empirical data to demonstrate this seems to be lacking.

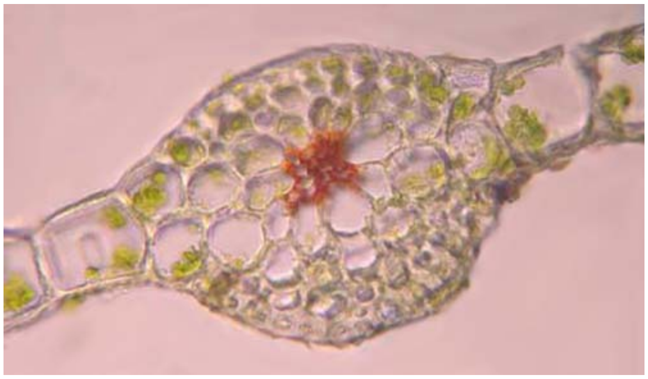

Figure 106. ***Rhizomnium glabrescens*** leaf cross section showing costa. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

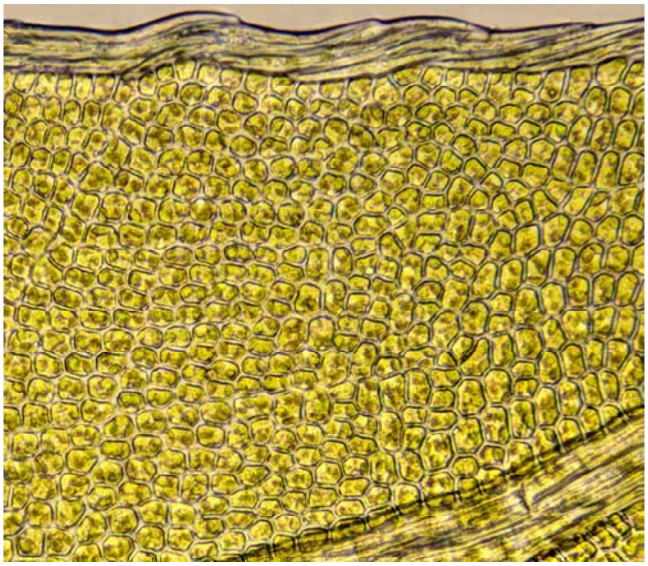

Figure 107. ***Fissidens bryoides*** leaf cells showing elongate cells of costa in lower right. Photo by Dick Haaksma, with permission.

I have constantly been struck by the attempts of ecologists to find a single explanation or advantage for a particular strategy for plants or animals. I am convinced that many of these strategies/structures persist because they provide small advantages for multiple functions. And certainly some are advantageous in some situations or years, but not in others. They may at times even be disadvantageous.

Proctor (2010) points out that in **Sematophyllaceae**, some members have a costa and others do not. The same is true in the **Fontinalaceae**. In the latter family, the costa separates the costate genera ***Dichelyma*** (Figure 108) and ***Brachelyma*** (Figure 109), both occurring in inundated areas but living mostly above water, from the ecostate genus ***Fontinalis*** (Figure 110), a genus that spends most of the year under water. Olsson *et al.* (2009) have shown that in the **Neckeraceae** reduction of the costa has recurred in all three main clades. Proctor (1979) concludes that the presence or absence of a costa, as well as the shape of leaf cells, must have functional consequences, but we are uncertain how important these are for mechanical support vs conduction within the leaf, not to mention simply chance occurrence relating more to ancestry than to (current) function.

Figure 108. ***Dichelyma falcata***, a member of the **Fontinalaceae** with a costa. Photo by Michael Lüth, with permission.

Figure 109. ***Brachelyma subulatum***, a member of the **Fontinalaceae** with a costa and keeled leaves. Photo by Janice Glime.

Figure 110. ***Fontinalis hypnoides*** showing absence of costa. Photo by John Game, with permission.

I was surprised to find that when grown in my artificial stream with considerable air exposure, ***Fontinalis*** produced short costae. Bruce Allen once told me he had also sometimes found ***Fontinalis*** leaves from nature that had short costae. To me this suggests that something suppresses the development of the costa and that under certain conditions that suppression doesn't function. That would imply that the costa came first and that a suppressor developed later. That suppressor is most likely water, which not only affects hydration, but also affects CO_2 uptake, oxygen concentration, and escape of gases such as the developmental hormone **ethylene**.

Costae can provide strength for a leaf. It can represent a tough tissue not eaten by herbivores. It is the structure that remains on leaves of aquatic species such as those of ***Hygroamblystegium*** (Figure 111-Figure 112) when exposed to rapid flow and suspended solids. But is any of these adaptive in any way? Possibly. If the costa is capable of growth into a new plant, it could become a dispersal agent. It could also provide photosynthetic tissue when leaf lamina tissue has been eaten or eroded. But there is no empirical proof that these things occur or if so, are they of any consequence.

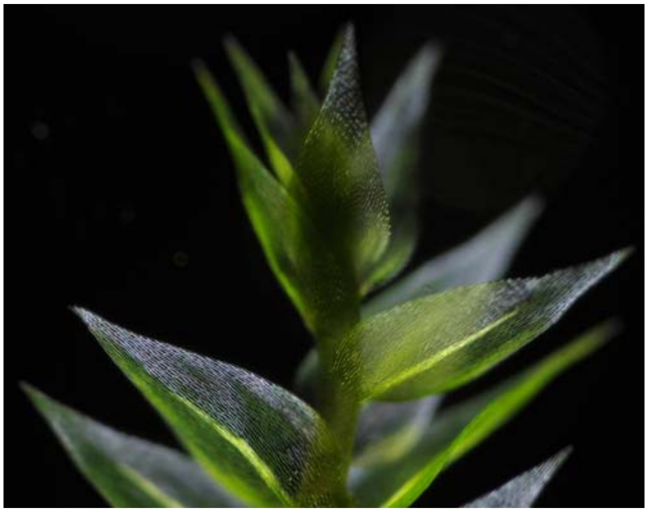

Figure 111. ***Hygroamblystegium tenax*** showing thick costa in leaves. Photo by Martha Cook, with permission.

Figure 112. ***Hygroamblystegium fluviatile*** showing dark costae left from eroded leaves. Photo by Michael Lüth, with permission.

Some amphibious bryophytes actually have reduced or lost costae when they have grown in the water. For example, Rod Seppelt (Bryonet 24 June 2012; Seppelt & Selkirk 1984) observed that the costae of ***Bryum pseudotriquetrum*** (Figure 113-Figure 114) were shorter and weaker on aquatic specimens from lakes in Antarctica compared to those growing out of water. He also reported inducing absence of costae and change in leaf shape in ***Bryum argenteum*** (Figure 115) in culture, with temperature playing a major role in inducing leaf changes; lower temperatures resulted in wider leaves. Furthermore, at 4°C the costa was absent. Clearly in some species the environment can affect how the costa develops. But what does it mean for the plant?

Figure 113. ***Bryum pseudotriquetrum*** showing strong costa of the terrestrial form. Photo by Des Callaghan, with permission.

Figure 114. ***Bryum pseudotriquetrum*** leaf showing costa that becomes shorter and weaker in Antarctic lakes. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

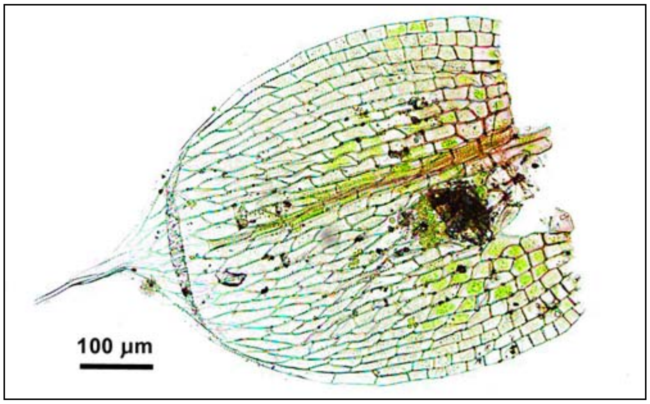

Figure 115. ***Bryum argenteum*** leaf showing well developed costa of a terrestrial form. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

In the genus ***Dicranum*** (Figure 116-Figure 121), the costa varies widely, with almost no differentiation in ***Dicranum rhabdocarpum*** (Figure 116) to phalanges along the costa in ***Dicranum scoparium*** (Figure 121). In other members of the **Dicranaceae**, for example ***Pilopogon peruvianus***, the costa can occupy most of the leaf width (Figure 122).

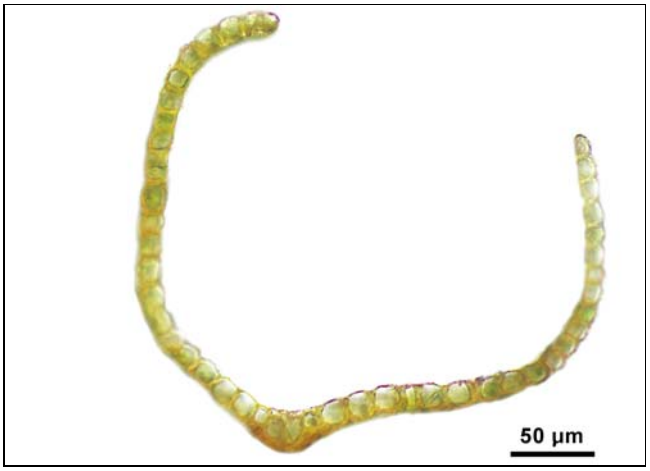

Figure 116. ***Dicranum rhabdocarpum*** leaf cross section showing absence of papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 117. ***Dicranum muehlenbeckii*** leaf cross section showing relatively smooth cell surface. Photo by Michael Lüth, with permission.

Figure 118. ***Dicranum brevifolium*** leaf cross section showing costa and mammillate cells. Photo by Michael Lüth, with permission.

Figure 119. ***Dicranum dispersum*** leaf cross section showing costa and thickened margins. Photo by Michael Lüth, with permission.

Figure 120. ***Dicranum fuscescens*** leaf cross sections showing costa and papillose leaf cells. Photo by Michael Lüth, with permission.

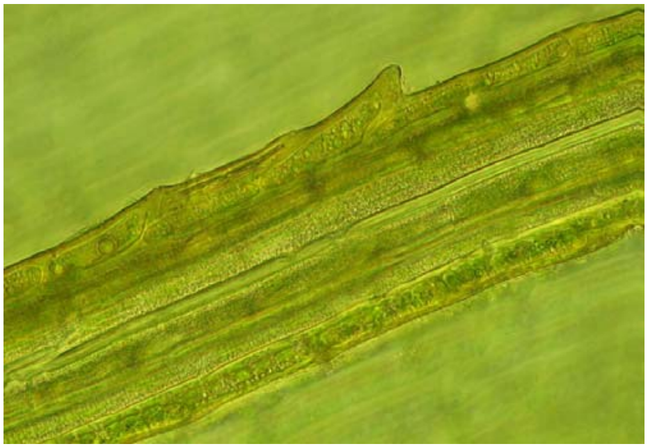

Figure 121. ***Dicranum scoparium*** teeth on back of leaf costa. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 122. ***Pilopogon peruvianus*** showing a costa that occupies most of the leaf. Photo by Michael Lüth, with permission.

Glenn Shelton (Bryonet 15 June 2012) contended that mosses tend to evolve from having multiple costae (Figure 123) to few (single or none). He and colleagues have found a number of tricostate mosses from the Early Cretaceous of Vancouver Island, B.C., Canada, some apparently pleurocarpous, as evidenced by a high degree of branching (including pinnate) and cell morphology. On the other hand, it appears that costa number is quite plastic among major moss lineages – and even within species (see above). And Ben Tan (Bryonet 30 June 2012) enters a word of caution – that folds or plicae at the leaf base can look like short costae, so one must be careful in interpreting fossil costae.

Shelton (Bryonet 15 June 2012) explains that one theory is based on the premise that the costa gives rigidity to the leaf and that multiple costae provide more rigidity. This assumes, then, that the need for this rigidity has been lost in some species. The theory also considers evolution from complex leaf structure to a simpler structure – **reduction**.

Figure 123. ***Vesicularia montagnei*** showing short, double costa. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>, with permission.

Perhaps Kürschner (2004) has the right idea for some species. He notes that the costa is often shiny (Figure 124-Figure 125) in mosses growing in xeric sites. Hence, he suggests that the costa may reflect the solar radiation and thus reduce both evaporation and heat stress. I would need proof to see how a narrow costa could have much impact, and it seems that xeric costae are often darker than the leaf (Figure 124-Figure 125), suggesting they might absorb more heat than the lamina.

Figure 124. ***Syntrichia andicola*** showing shiny costa. Photo by Michael Lüth, with permission.

Figure 125. ***Syntrichia andicola*** showing costa of leaf. Photo by Michael Lüth, with permission.

Zander (Bryonet 25 June 2012) reminded us of the perspective of Gould (2002) that there are minimum constraints on size – a developmental wall to small size for particular organisms. He considers that the elimination of superfluous costal material might depend on size. As leaves get smaller, the costa necessarily gets smaller, and it might no longer serve the same function or advantage it did in larger leaves. Zander points out that acrocarpous mosses usually have costae, but that pleurocarpous mosses may or may not. Is this a size difference, or a difference in phylogenetic history? And perhaps costae persist, or not, because some other linked trait is affected by some selection pressure that has changed over time.

Lamellae

Lamellae (Figure 126-Figure 138) can greatly increase the surface area of a leaf. They provide numerous surfaces, exposed on both sides for absorption of light and especially CO_2 and provide capillary spaces for taking up and holding water.

Members of the family **Polytrichaceae** are defined by the presence of lamellae (Figure 126-Figure 131), but other genera in scattered families have them as well. These include ***Aloina*** (Figure 132), ***Crossidium*** (Figure 133-Figure 134), ***Pterygoneurum*** (Figure 135-Figure 137), and some ***Syntrichia*** (Figure 138).

Figure 126. ***Atrichum undulatum*** leaf lamellae. Photo by Walter Obermayer, with permission.

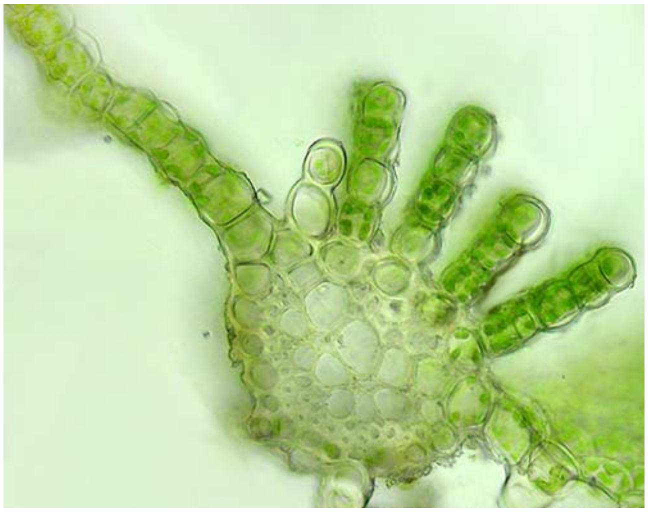

Figure 127. ***Atrichum undulatum*** leaf cross section showing lamellae. Photo by Walter Obermayer, with permission.

Figure 128. ***Polytrichastrum formosum*** leaf cross section showing lamellae. Photo by Michael Lüth, with permission.

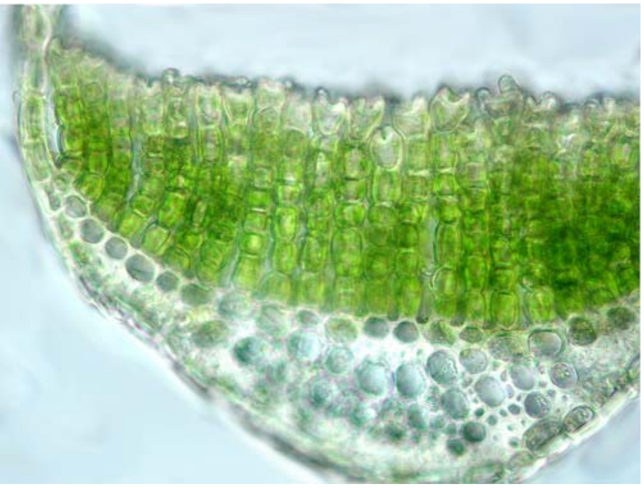

Figure 129. ***Polytrichum commune*** leaf cross section showing lamellae. Photo by Michael Lüth, with permission.

Figure 130. ***Polytrichum hyperboreum*** showing leaf lamina rolled over the lamellae. Photo by Michael Lüth, with permission.

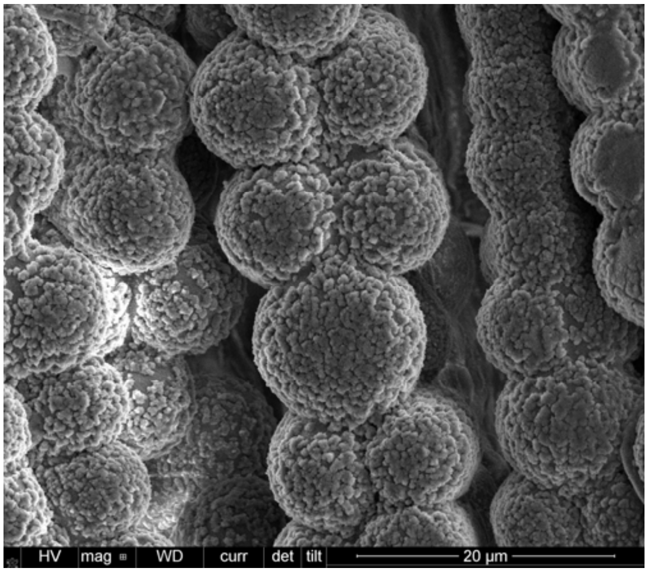

Figure 131. ***Dendroligotrichum squamosum*** SEM showing tops of lamellae. Photo courtesy of Jeff Duckett and Silvia Pressel.

Figure 132. ***Aloina rigida*** with lamellae within the inrolled leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 133. ***Crossidium squamiferum*** showing leaves that appear to be succulent due to lamellae. Note how the leaf curves inward in this species. Photo by Jan-Peter Frahm, with permission.

Figure 134. ***Crossidium aberrans*** leaf showing lamellae along costa. Photo by Michael Lüth, with permission.

Figure 135. ***Pterygoneurum ovatum*** showing fleshy, inrolled leaves that partially cover the lamellae. Photo by Kristian Peters, with permission.

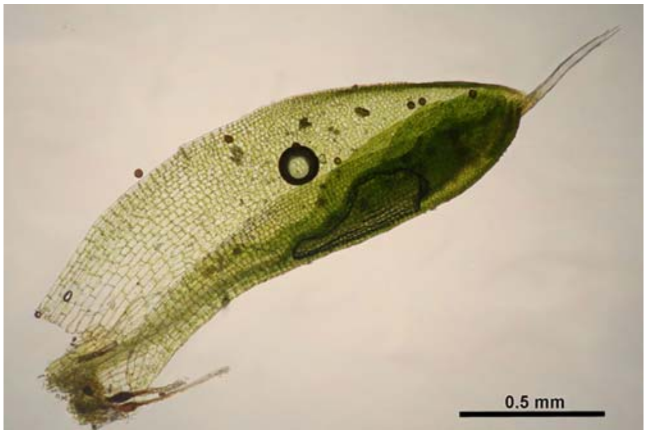

Figure 136. ***Pterygoneurum ovatum*** leaf showing lamellae in upper half. Photo by Hermann Schachner, through Creative Commons.

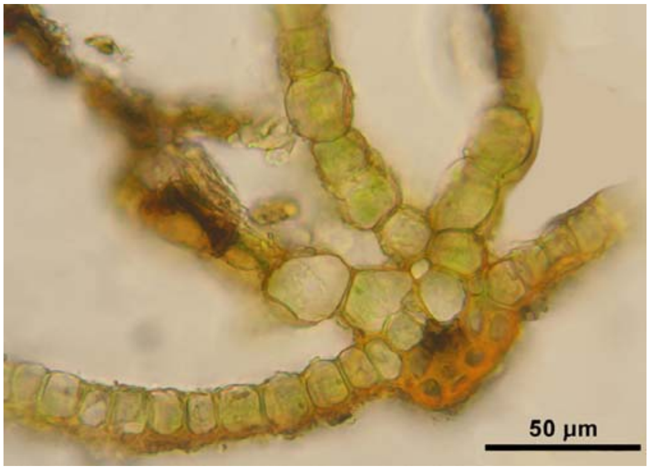

Figure 137. ***Pterygoneurum ovatum*** leaf cross section showing leaf lamellae. Photo by Hermann Schachner, through Creative Commons.

Figure 138. ***Syntrichia papillosa*** leaf showing tips of lamellae. Photo by Des Callaghan, with permission.

Kürschner (2004) suggests that the lamellae facilitate water conduction as well as storing water. These roles are in addition to their photosynthetic role. But this role seems to be incorrect. The surface of cells surrounded by water presents a barrier to CO_2 absorption (Budke 2010). Instead, the waxy cuticle repels the water. The lamellae in ***Polytrichum commune*** (Figure 129) increase the leaf surface area 2.4 fold (Thomas *et al*. 1996). Even the lamellae margins are coated with a waxy cuticle that restricts external capillary water. Thus they serve as photosynthetic tissue rich in chlorophyll.

Proctor (2005) demonstrated that the lamellae in **Polytrichaceae** (Figure 126-Figure 131) are important for the absorption of CO_2, increasing typical uptake by six times that of the projected leaf area, whereas in unistratose leaves of most other bryophytes, CO_2 uptake is limiting. This permits the **Polytrichaceae** to take advantage of high light intensity in open areas by increasing available absorptive surface area. In a number of these species, including some of ***Polytrichum*** (Figure 130), the leaf margins fold over the lamellae, affording protection from excess UV light, preserving moisture, and providing space for CO_2 exchange.

Air Chambers

Air Chambers are present in some of the thallose liverworts, such as species of ***Marchantia*** (Figure 139-Figure 142) (Ishizaki *et al*. 2013) and others (Figure 143-Figure 148). These facilitate the exchange of gasses within the thallus (Ishizaki *et al*. 2013). The small pores at the surface of the thallus in these chambered species permit the exchange of these gasses, providing an entry for CO_2 and exit of O_2.

Figure 139. ***Marchantia polymorpha***, a species with internal air chambers. Photo by Walter Obermayer, with permission.

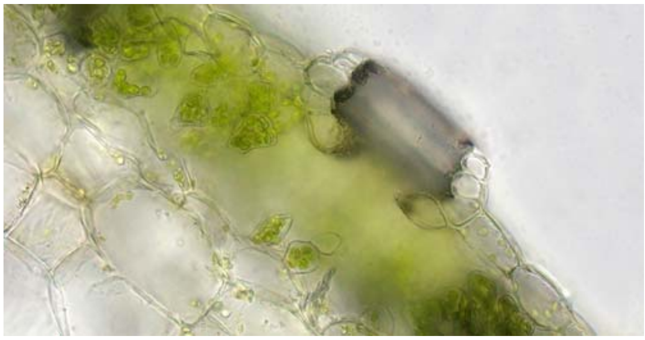

Figure 140. ***Marchantia polymorpha*** pore cs, above air chamber. Photo by Walter Obermayer, with permission.

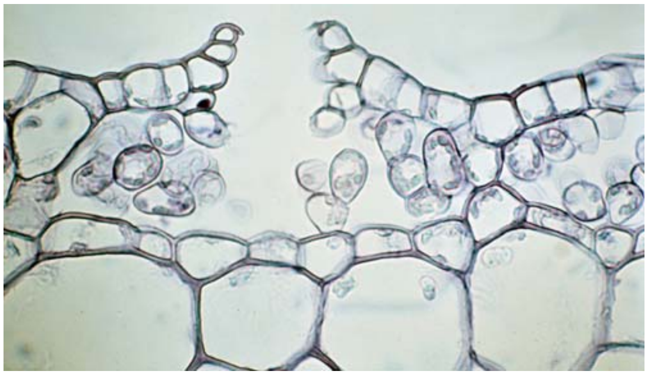

Figure 141. ***Marchantia polymorpha*** thallus cs showing pore and air chamber. Photo ©Wilhelm Barthlott, with permission.

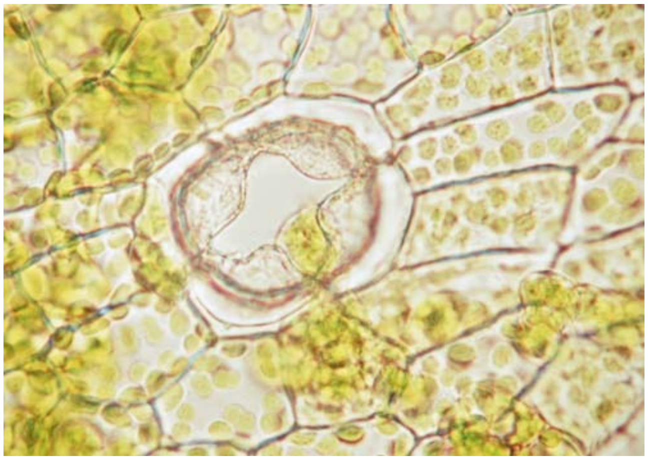

Figure 142. ***Marchantia polymorpha*** pore opening showing surrounding ridge. Photo ©Wilhelm Barthlott, with permission.

Figure 143. ***Mannia androgyna***, in a genus with air chambers in the thallus. Photo by Michael Lüth, with permission.

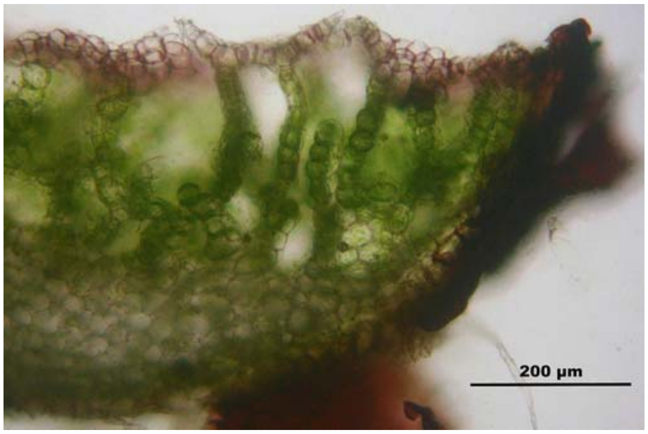

Figure 144. ***Mannia triandra*** thallus section showing air chambers. Photo by Hermann Schachner, through Creative Commons.

Figure 145. ***Conocephalum conicum*** showing pores on the surface and polygonal areas that mark the internal air chambers. Photo by Hermann Schachner, through Creative Commons.

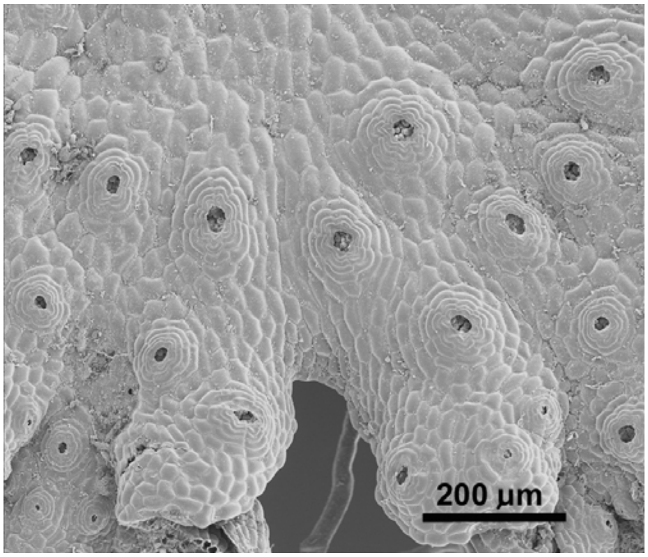

Figure 146. SEM of ***Conocephalum supradecompositum*** thallus with pores. Photo by Jeff Duckett & Silvia Pressel, with permission.

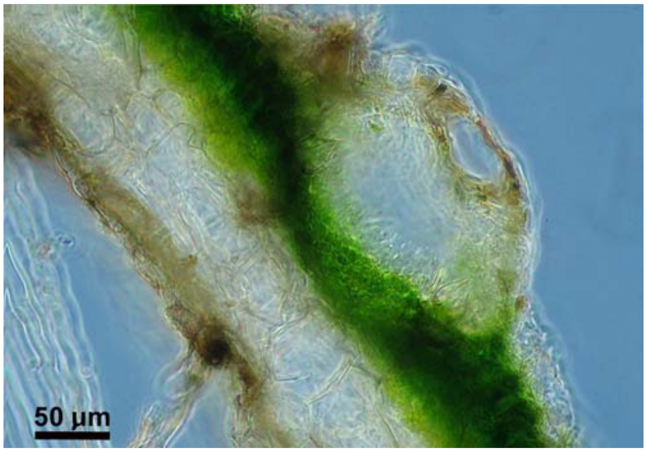

Figure 147. ***Conocephalum conicum*** pore section showing photosynthetic cells in the chamber beneath it. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.

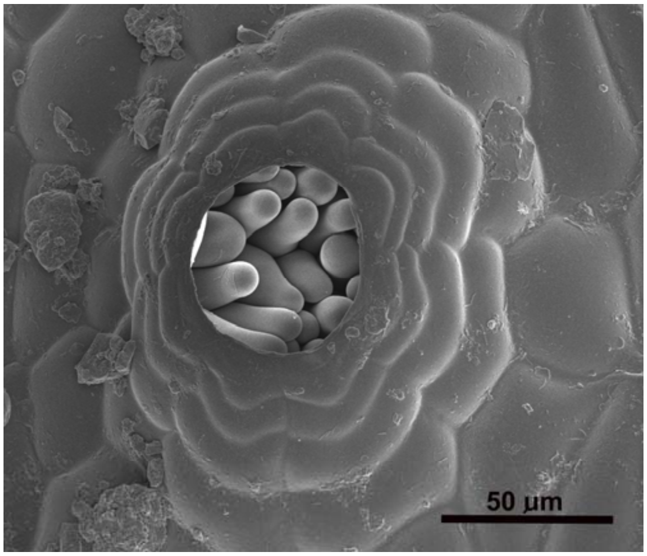

Figure 148. SEM of ***Conocephalum supradecompositum*** pore showing chambers and finger-like photosynthetic cells inside. Photo by Jeff Duckett and Silvia Pressel, with permission.

Keels

Most leaves are slightly concave, some are flat, and some are folded over, forming a **keel** (Figure 149). The most striking of these is the keel in several species of the aquatic moss ***Fontinalis***. The keel appears to give rigidity to the leaf, but when this species occurs in flowing water the keel often is abraded, leaving the leaf in nearly two pieces.

A modification of the keel occurs in the **Fissidentaceae** (Figure 150). This unique structure forms a pocket on the apical edge of the leaf into which the succeeding leaf can partially fit. The double area of each leaf adds rigidity and provides capillary space that presumably holds water for a longer time. When the leaves overlap into the pockets, they can help to make the entire plant more rigid.

Figure 149. ***Fontinalis antipyretica*** showing keeled leaves. Photo by Li Zhang, with permission.

Figure 150. ***Fissidens curvatus*** showing pockets with succeeding leaves fitting into them in some cases. Photo by Tom Thekathyil, with permission.

Leaf Plications

Some genera are characterized by leaf plications (Figure 151-Figure 153). These are typically folded like a Japanese fan. But what is the value of these plications? In tracheophytes, they can add strength. Consider lifting something with a sheet of paper. Then consider lifting the same thing with that same paper after it is fan folded. But is that kind of strength needed by a bryophyte leaf? Does it give a thin leaf a better ability to hold a drop of water?

Figure 151. ***Coscinodon cribrosus*** leaf with plications. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 152. ***Coscinodon cribrosus*** leaf cross section showing plications. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 153. ***Cratoneuron decipiens*** leaf with plications. Photo by Michael Lüth, with permission.

Leaf Cells

Cell shape varies considerably, from small isodiametric cells (Figure 107) to large, nearly hexagonal ones (Figure 154) to elongate ones (Figure 155). Some cells have wall invaginations or wavy walls (Figure 156). Little mention has been made of the advantages of various cell types. One can imagine that elongate, narrow cells might move water more quickly with fewer walls to cross and formation of capillary space within the cell. I can't even imagine an advantage for the irregular wall shapes in ***Racomitrium*** (Figure 156). Bill Buck once asked me what I thought was the significance of the elongate cells in many pleurocarpous mosses. I couldn't give a good answer then, and now, several decades later, I still can't.

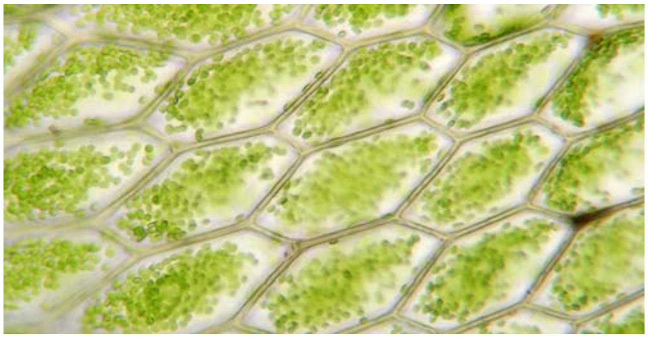

Figure 154. ***Hookeria lucens*** hexagonal leaf cells. Photo by Malcolm Storey <www.discoverlife.org>, through Creative Commons.

Figure 155. ***Hygroamblystegium tenax*** showing elongate cells. Photo by Martha Cook, with permission.

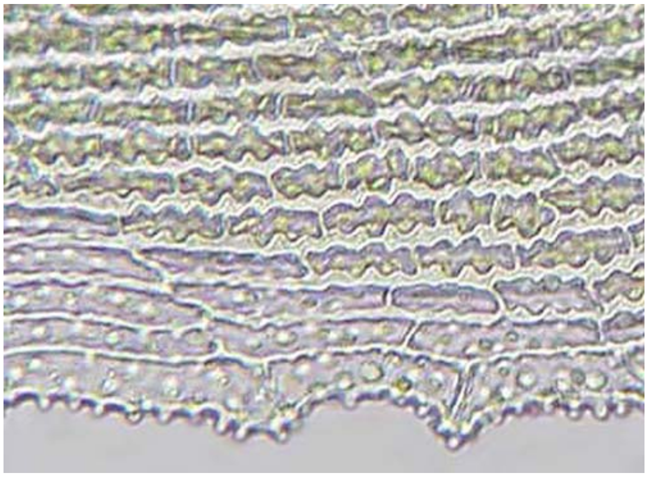

Figure 156. ***Racomitrium canescens*** cells showing wavy walls with invaginations. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Papillae

Many theories have been proposed for papillae, but little is available as experimental evidence to support them. The papillae have a number of shapes and forms (Figure 157-Figure 159), while varying in size and density. Based on this variability, it seems to me that their functions may not be the same in all species or under all conditions.

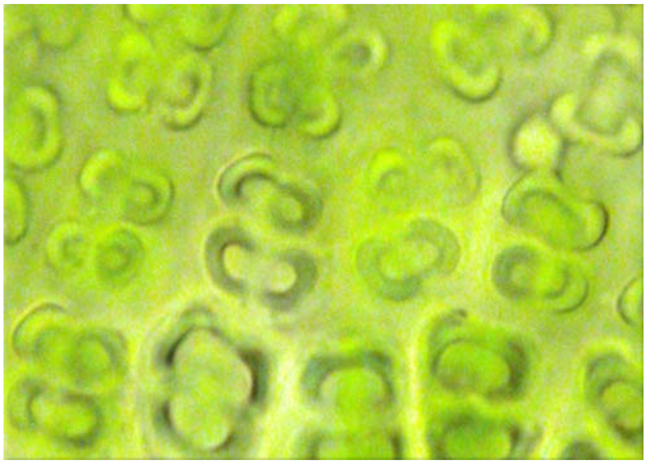

Figure 157. ***Tortula muralis*** leaf cells with C-shaped papillae. Photo by Walter Obermayer, with permission.

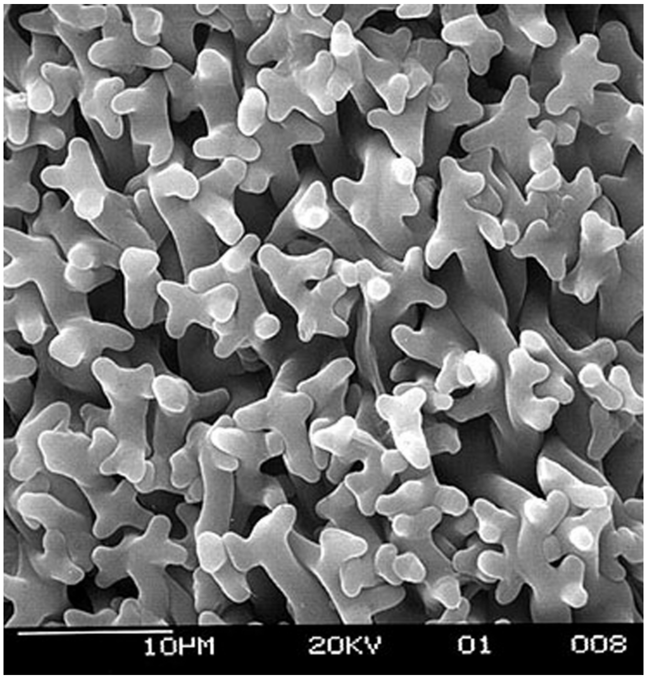

Figure 158. ***Tortula muralis*** SEM of branched papillae. It is easy to see how these papillae could scatter light and protect the chlorophyll during dry periods. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

Figure 159. ***Chrysoblastella chilensis*** leaf cross section showing papillae and capillary spaces between them. Photo by Juan Larrain, with permission.

When lamina papillae are dense, they give the leaf a waxy, often succulent look (Figure 160). The dull surface most likely does the same to the sunlight as it does to our eyes – it bends the light rays, preventing them from making straight entry into the leaf cells and thereby reducing damage to the chlorophyll when the leaf is dry. When the leaf is wet, the capillary spaces fill with water and the leaf surface behaves more like a uniform translucent surface (Figure 161). At least that is how some of us have interpreted the behavior. In experiments in my lab with papillose leaves under the microscope, we found that wet leaves transmitted about twice as much light as dry leaves, supporting that hypothesis.

Figure 160. ***Encalypta streptocarpa*** illustrating the waxy appearance when dry caused by numerous papillae. Photo by Michael Lüth, with permission.

Figure 161. ***Encalypta streptocarpa*** showing translucent appearance of the leaf when wet. Photo by Jan-Peter Frahm, with permission.

In some, perhaps all, the papillae facilitate water uptake by providing capillary spaces (Proctor 1979; Longton 1988; Pressel *et al*. 2010; see Chapter 7-4), but they can also facilitate water loss (Pressel *et al*. 2010). The uptake is usually accomplished by the small channels between the papillae, but in ***Andreaeobryum macrosporum*** (Figure 162), a small capillary channel goes through the papillae toward the cell and facilitates the rapid uptake of water during rehydration (Crandall-Stotler & Bozzola 1990, 1991).

Figure 162. ***Andreaeobryum macrosporum***, a moss for which papillae are known to aid in uptake of water. Photo from Botany website, University of British Columbia, Canada, with permission.

An Alternative to Papillae?

In the moss ***Rhacocarpus purpurascens***, the leaf cell wall has an unusual structure. The wall has three layers that Pressel *et al*. (2010) interpret as "a supreme adaptation to exposed habitats." This moss lives where there are frequent alternations between drought and heavy precipitation. We know that ***Sphagnum*** experiences water logging that prevents photosynthesis, and Pressel *et al*. reasoned that this special wall structure in ***R. purpurascens*** prevents water logging. Its outer cell wall layer is porous, ensuring rapid water uptake and retention. The hydrophobic cuticle-like layer simultaneously prevents water logging. The middle layer serves to extend the period of cell hydration, permitting active metabolism under drying conditions. The ***R. purpurascens*** cell wall differs in function from cells with papillae in that papillae not only accelerate water uptake, but also accelerate water loss. Pressel *et al*. surmise that unlike the alternating conditions experienced by ***R. purpurascens***, constantly flowing aerated water or underhangs where water logging can depress gas exchange select for mosses that are protected from water logging by surface waxes – a condition seemingly quite different from that seen in tracheophytes.

Stomata

True stomata do not exist in the gametophytes of bryophytes. However, as in tracheophytes, they do occur in many sporophytes. These are well-documented in the sporophytes of hornworts, but are not universal in mosses. They seem to be absent in leafy liverwort capsules, but evidence of potential evolutionary precursors is present in capsules of the genus ***Haplomitrium*** (Figure 163-Figure 164) (Duckett & Pressel 2019).

Figure 163. ***Haplomitrium hookeri***, in a genus that exhibits precursors to stomata in the capsule. Photo by Janice Glime.

Figure 164. ***Haplomitrium hookeri*** with capsules. Photo by Norbert Schnyder, with permission.

Egunyomi (1982) reported sporophyte stomata in 29 tropical African moss species, distributed in 12 families. These mostly have round pores with two guard cells. Capsules he examined ranged in number of stomata from 2 to >200 (***Wijkia trichocoleoides*** - Figure 165). Some stomata are raised above the level of the capsule epidermis [***Wijkia trichocoleoides***, ***Trichosteleum microcalyx*** (Figure 166), ***Stereophyllum radiculosum*** (Figure 167-Figure 168), and ***Stereophyllum reclinatum***]. Others are sunken [***Brachymenium leptophyllum*** (Figure 169) and ***Bryum coronatum*** (Figure 170)]. He found interesting correlations between stomata number and seta length, and between stoma size and epidermal cell size.

Figure 165. ***Wijkia trichocoleoides***, a species with more than 200 stomata in its capsule. Photo by John C. Brinda, through Creative Commons.

Figure 166. ***Trichosteleum*** sp. with capsules, a species with stomata raised above the capsule epidermis. Photo by Jan-Peter Frahm, with permission.

Figure 167. ***Stereophyllum radiculosum*** leaves, a species with stomata raised above the capsule epidermis. Photo by Juan David Parra, through Creative Commons.

Figure 168. ***Stereophyllum radiculosum*** capsule with raised stomata creating visible bumps in the lower part of the capsule. Photo by Juan David Parra, through Creative Commons.

Figure 169. ***Brachymenium leptophyllum*** with capsules that have sunken stomata. Photo from Earth.com, with permission.

Figure 170. ***Bryum coronatum*** with capsules that have sunken stomata. Photo by Aruna Balasubrahmanya , through Creative Commons.

Their function, however, seems to differ from that of tracheophyte stomata, playing a role in dispersal by permitting the capsule to dehydrate and contract. Their function has been the subject of recent research and will be updated soon.

Fluorescence

Fluorescence is seldom mentioned in bryophyte studies. I can remember the excitement of Gisela Nordhorn-Richter when she relayed to me the use of a fluorescent microscope to see propagula in ***Pohlia***. It became a great tool for detecting these often obscure structures with UV light.

Following her enthusiasm, I had the opportunity to examine ***Fontinalis antipyretica*** with a fluorescent microscope and was surprised to find beautiful yellow cell walls and glowing red chloroplasts (Figure 171) – well, the chloroplasts didn't really surprise me, but they certainly made a beautiful image.

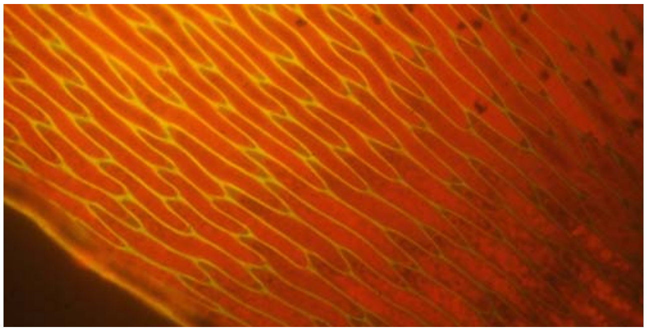

Figure 171. ***Fontinalis antipyretica*** wall fluorescence. Photo by Janice Glime.

Kroken *et al*. (1996) found that both charophytes and bryophytes have fluorescent cell walls. They suggested that the bryophytes inherited this fluorescence ability from the charophytes, citing evidence from time of production and location. A number of charophytes produce these resistant cell walls in response to desiccation stress. Furthermore, ***Coleochaete*** (Figure 172) is the only charophyte known to produce fluorescent tissues at the placental junction in hydrated tissues, induced by sexual reproduction. However, this characteristic is true of all bryophytes tested. Furthermore, in ***Sphagnum***, the maternal tissue in the apical portion of the **pseudopodium** (Figure 173) has fluorescent compounds similar to those in ***Coleochaete*** zygotes. Other known sites of autofluorescence in bryophytes include the sporangial epidermis, spiral thickenings of elaters, rhizoids, and leaves. Kroken and coworkers suggested that this fluorescence represents repeated exaptation. The regulation of deposition has been modified through time, "resulting in a sequence of functions: desiccation resistance and/or microbial resistance in lower charophytes, a role in embryogenesis in ***Coleochaete*** and embryophytes, and finally, decay resistance in innovative structures that characterize bryophytes, such as rhizoids, sporangial epidermis, and elaters.

Fluorescence is discussed in more detail in Chapter 9-5 of this volume.

Figure 172. ***Coleochaete***, the only alga known to produce fluorescent tissues at the placental junction. Photo by Yuuji Tsukii, with permission.

Figure 173. ***Sphagnum*** with capsule, showing the upper portion of the pseudopodium where fluorescent compounds are produced (**arrow**). Photo by Vita Plasek, with permission.

Thallus

Liverworts are of two types – thalloid and leafy. The thallus brings its own set of adaptations, with its thickness making possibilities that are not available to the leafy taxa with their one-cell-thick leaves. Among the **xerophytic** (of dry habitats) adaptations are the ability to roll up, shrivel, or fold the thalli, exposing the normally ventral side where red pigments (**anthocyanin**) or hyaline ventral scales (Figure 174-Figure 175) serve to protect the photosynthetic tissue from damage due to exposure to sunlight while dry (Kürschner 2004). The hyaline scales such as those in many ***Mannia*** (Figure 174-Figure 175), ***Riccia*** (Figure 176), and ***Oxymitra*** (Figure 177) species undoubtedly serve to reduce desiccation and provide capillary spaces to facilitate water uptake upon wetting.

Figure 174. ***Mannia androgyna*** in hydrated condition with reddish edges that characterize the color of anthocyanins on the ventral side. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman & Karen Blisard.

Figure 175. ***Mannia fragrans*** showing curling of the drying thallus; hyaline ventral scales and reddish under surface will soon protect the photosynthetic tissue. Photo by Michael Lüth, with permission.

Figure 176. ***Riccia trichocarpa*** showing hairs that can reduce water loss and protect the photosynthetic tissue from damage by UV rays. Photo by Jonathan Sleath, with permission.

Figure 177. ***Oxymitra incrassata*** showing marginal scales. Photo by Chris Cargill, with permission.

The raised cells of the epidermis and the chimney-like hyaline air chambers of some species in ***Exormotheca*** (Figure 178) may likewise serve as protection from solar radiation and protection from desiccation. Thalli of some species have "windows" (**Fensterthallus**), for example the chimney-like, hyaline air-chambers of ***Exormotheca*** (Figure 178-Figure 179), like those in the flowering plant family Aizoaceae (for example *Lithops*). These windows provide a covering that helps to reduce the light intensities that reach the photosynthetic layer (Kürschner 2004). The liverwort thallus is thick and nearly semi-circular in cross section. Internally, it has dense assimilatory columns in its air chambers. The column thickness in the liverworts frequently correlates with the degree of insolation.

Figure 178. ***Exormotheca welwitschii*** in southern Portugal, showing "windows" in the thalli. Photo by Michael Lüth, with permission.

Figure 179. ***Exormotheca*** sp. thallus showing columnar cells that form the windows to the photosynthetic tissue of the thallus. Photo © Wilhelm Barthlott <lotus-salvinia.de>, with permission.

Liverworts such as ***Plagiochasma rupestre*** (Figure 180) have hydrophobic wax globules on the thallus surface, making them unwettable. Such waxes keep xerophytic members of the **Marchantiales** from taking up water through the thallus surface, using their pegged rhizoids instead.

Figure 180. ***Plagiochasma rupestre***, a thallose liverwort with hydrophobic wax on its surface. Photo by Jan-Peter Frahm, with permission.

Thallus pores could serve as a site of water entry, but a ring of wax around the inner margin of the pore in species like ***Marchantia polymorpha*** (Figure 139-Figure 142, Figure 181) serves both to repel water and to make the opening smaller, making it difficult for cohesive water droplets to enter the air chambers of the thallus. Many thalloid species have hydrophobic cuticular ledges around these pores (Ziegler 1987). These waxes protect the air chambers from becoming water-logged (Schonherr & Ziegler 1975; Kürschner 2004).

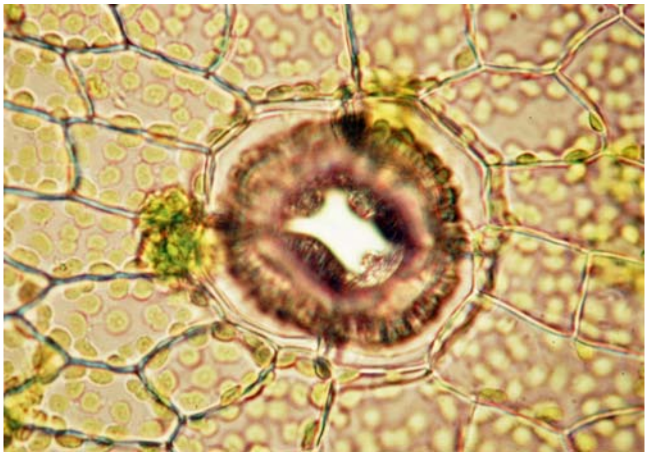

Figure 181. ***Marchantia polymorpha*** thallus pore opening with ridge that is heavily endowed with wax. Photo © Wilhelm Barthlott, with permission.

Once inside the thallus, we must look for adaptations to obtain sufficient CO_2 and to maintain moisture. For the thallose liverworts this problem seems to be solved in a manner similar to that of most flowering plants – a ventilated photosynthetic tissue that has stacks of cells one cell wide interspersed within air chambers (Figure 140-Figure 142) (Proctor 2010). See **Air Chambers** above

Pigmentation

In physiological studies on animals, it is clear that environmentally induced variation is often adaptive. More arachidonic acid makes membranes more pliable. Non-nucleating proteins prevent ice crystallization. Changes from glucose to glycogen prepare an animal for dormancy. Even physical changes, such as color of fur or feathers, can prepare an animal for a change in seasons. Development of red pigment in ***Sphagnum*** (Figure 182) and ***Fontinalis*** (Figure 183-Figure 184) may protect the chlorophyll from high light intensity.

Figure 182. ***Sphagnum*** showing the red colors that develop in some species when they grow in the sun. Photo by Janice Glime.

Figure 183. ***Fontinalis antipyretica*** with red pigments responding to cold spring water and full sun. Photo by Janice Glime.

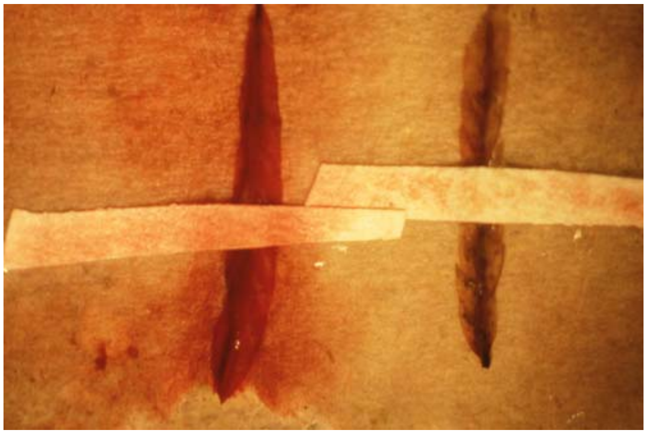

Figure 184. ***Fontinalis antipyretica*** with red pigments, responding to being out of water, but moist, in bright light. Photo by Janice Glime.

Red pigments in high elevations and alpine regions might serve dual purposes. The red color can protect the chlorophyll and DNA from UV damage, but it could also cause the mosses to absorb heat in their cool climate. The images of ***Grimmia elongata*** (Figure 185-Figure 186) illustrate the green and red color expressions in this species.

Figure 185. ***Grimmia elongata*** showing its green form. Photo by Michael Lüth, with permission.

Figure 186. ***Grimmia elongata*** in Norway, exhibiting its red pigments in the high UV light of the high elevation. Photo by Michael Lüth, with permission.

Some pigmentation may just come along for the ride. For example, phenolic compounds are typically colored, but their primary function can be support or antiherbivory. Such support functions are most likely for structures like the costa (Figure 187) or stem rigidity (Figure 188), but they also occur in many leaf borders (Figure 68).

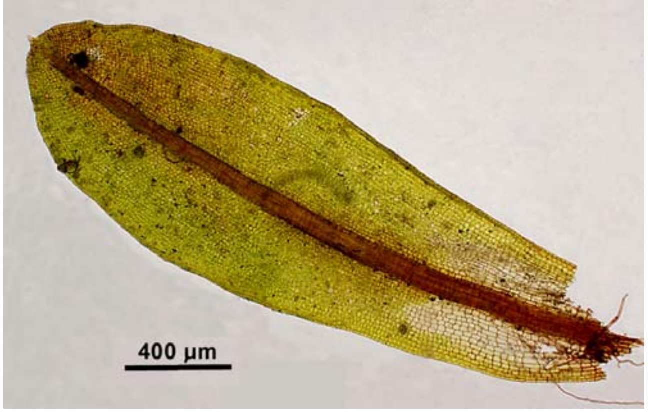

Figure 187. ***Syntrichia inermis*** leaf showing dark color in costa. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

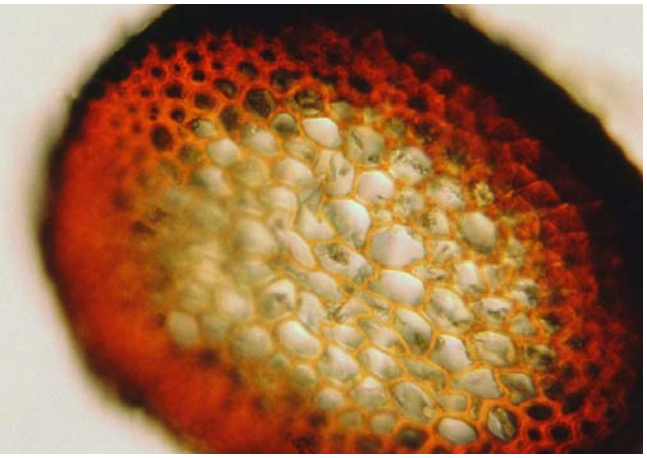

Figure 188. ***Fontinalis dalecarlica*** stem section showing dense coloration in the cell walls. Photo by Janice Glime.

Seta Colors

David Long (Bryonet 24 March 2023) asked why some moss setae are red. Questions like this bring out some of the lurkers because there is no known right answer. In fact, Jack Sharp used to respond to such questions with the admonishment that not al things are adaptive – they simply must not be maladaptive to persist.

This question can be divided into two parts: what biochemistry makes it red, and does it have an adaptive persistence.

Let's first examine possible adaptive significance. Here are my potential hypotheses:

1. In species like *Ceratodon purpureus* where the capsule is likewise red-purple, the pigmentation pathway starts early in development of the sporophyte.
2. Red is a warning color to animals, so the red color could deter herbivory.
3. Red absorbs heat, thus warming the developing sporophyte if that occurs in spring or autumn, possibly speeding up development.
4. Red protects against UV damage and could therefore be helpful in preventing damage to young sporohyte tissues.
5. Lignin-like compounds might provide structural support, and these can be red in color.

Gender

Zander (Bryonet 8 May 2012) suggested that the presence of only males in a population would have the adaptive advantage of conserving photosynthate by the lack of necessity for producing sporophytes. Thus dioicy in dry habitats might be an adaptation to conserve photosynthate. But Stark has reported that in many desert populations the males are absent. Nevertheless, this principle would operate whether the population was male or female. On the other hand, monoicy provides advantages in a moist or otherwise less stressful habitat where there is sufficient energy for producing sporophytes.

Adaptive value of gender expression was discussed in detail in Chapters 3 and will not be discussed further here.

Wound Response

If you are a plant, what you do when you get damaged may have important effects on the future of your species. And if you live in fast-flowing water (Figure 189), that damage is a certainty. Some species are adapted to take advantage of the wounds; others merely protect themselves; some (perhaps most bryophytes) do both. The advantage for bryophytes – a means for dispersing and making new colonies.

We have limited understanding of the means of protection. One study on the biochemical response is that for ***Marchantia polymorpha***. When wounded, ***Marchantia polymorpha*** (Figure 190) produces highly volatile 8-carbon compounds including (R)-1-octen-3-ol and octan-3-one (Kihara *et al*. 2014). These emissions occurred within 40 minutes of the wounding. The importance of arachidonic acid and/or eicosapentaenoic acid was demonstrated by the weak or absent response of the volatiles. In completely disrupted thalli, only minimal amounts of octan-3-one were produced, whereas the greatest amounts were produced in partially disrupted thalli, compared to undisturbed thalli. This suggests signalling from the disrupted cells that initiates the production of octan-3-one in the undisturbed cells.

Figure 189. ***Cinclidotus danubicus*** habitat, illustrating the power of the water. Damage to leaves can be significant during high-water events. Photo by Michael Lüth, with permission.

Figure 190. ***Marchantia polymorpha*** with an isopod – a potential herbivore. Herbivory and other wounds can stimulate production of highly volatile compounds in this liverwort. Photo by Walter Obermayer, with permission.

Croisier *et al.* (2010) found a variety of responses in the bryophytes they surveyed. Instead of the predominant C8 volatiles, they found a variety of C5, C6, C8, and C9 volatiles in 23 mosses tested. These are **oxylipins** – metabolites derived from oxidative fragmentation of polyunsaturated fatty acids. Both C18 and C20 fatty acids serve as the precursors for the volatile oxylipins that respond to mechanical wounding of mosses. These oxylipins are important hormonal regulators and defense compounds in plants. In liverworts and hornworts, oxylipin production was less pronounced than in the mosses.

This still leaves us with the ecological question of how these volatiles protect the species. Do they deter herbivores, as do many volatiles in tracheophytes? The ***Marchantia*** story suggests they are inducible. Do they protect against fungal and attack? (Fungal attack will be covered later in a chapter on fungal interactions.) Do they play any role in dedifferentiation and regrowth? Do they stimulate the production of rhizoids or protonemata often seen at wound sites? This would seem to be a fertile area of research for understanding hormonal interaction and control of development in bryophytes.

Summary

Bryophytes have a simple structure. That does not mean they have not advanced morphologically. Their stems may have conducting cells, have various phenolic compounds in the cell walls, or be covered with paraphyllia, rhizoids, or tomentum. The leaves may have borders, marginal teeth, lobes, hair tips, costae, lamellae, or keels. The leaf cells may be short and nearly isodiametric (often with thick walls), larger hexagonal cells with thin walls, or elongate narrow cells. These cells may have waxes, papillae, or be swollen. These structures seem to be adaptations to habitats ranging from aquatic to desert.

Aquatic bryophytes that do not spend much time out of water generally lack papillae, have elongate narrow cells, and lack conducting cells in the stems. They may have strong stems with colored cells walls from phenolic compounds, protecting them against moving water and suspended solids. At the other extreme, xerophytic bryophytes are often papillate, have thicker waxes, are reduced in size, and have mechanisms of curling up while dry and expanding when wet. Specialized cell walls, lamellae, and marginal teeth may provide mechanisms to increase photosynthesis while preventing water logging. Hair tips can scatter high light, absorb water, or reduce drying. Pigments can protect bryophytes from high light intensities, especially when low temperatures slow photosynthesis or the plant is dormant due to high temperatures.

Leafy liverworts may be able to hold water droplets with their lobes and teeth. These structures could also serve to deter herbivores. The thallus can have windows to direct light and protect the photosynthetic cells, be protected by waxes and scales, have thallus pores that open and close, permitting gas exchange while preventing internal water logging.

These adaptive value of bryophyte structures are largely speculation, hypotheses waiting to be tested.

Acknowledgments

This chapter is largely the product of discussions with other bryologists, especially on Bryonet. Thank you to Louis Anderson for his constant reminders that things do not always have an adaptive function. My appreciation always goes to the many people who have given me permission to use their images, including those who make them available online through Creative Commons. And thank you to Bryonetters who contributed to the discussion on seta colors.

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