CHAPTER 4-12
ADAPTIVE STRATEGIES: SPECULATION ON GAMETOPHYTE STRUCTURES

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CHAPTER 4-12
ADAPTIVE STRATEGIES: SPECULATIONS ON GAMETOPHYTE STRUCTURES

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 of 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.

**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.

**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.
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 82). Such comparisons testify to the complexity of such adaptive considerations.
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?
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 sclerodermin. 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.

**Stem Structure**

Stems are usually circular (Figure 17), but some are triangular in cross section (Figure 18); others are somewhat...
flattened (Figure 19). 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 17-Figure 18, Figure 22-Figure 23), but not all bryophytes have a central strand (Figure 15, Figure 19-Figure 21). 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 17. *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 18. *Dendroligotrichum dendroides* stem cross section showing triangular shape. Image on right shows details of the central strand. Photo by Juan Larrain, with permission.

Figure 19. *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 20. *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 21. *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 22. *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.
Figure 23. *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.

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 24-Figure 25) and *F. dalecarlica* (fast water; Figure 26-Figure 27) 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 28). Furthermore, even the central cortex cells of *F. dalecarlica* were thickened, whereas they were not in *F. flaccida*.

Figure 24. *Fontinalis flaccida* showing thin stems for this quiet-water species. Photo by Lance Biechele, permission pending.

Figure 25. *Fontinalis flaccida* in relatively quiet stream water. Photo by Lance Biechele, permission pending.

Figure 26. *Fontinalis dalecarlica* showing thick, strong stems. Photo by Janice Glime.

Figure 27. *Fontinalis dalecarlica* in a fast mountain stream. Photo by Janice Glime.

Figure 28. *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 29). Those above water developed 1-2 additional rows of hyaline cells in the outer layer of the stem (Figure 30). It is interesting that the less drought-resistant *S. papillosum* (Figure 31) had the greater difference in stem width between the two conditions. Despite that difference, *Sphagnum magellanicum* (Figure 32) 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 29.** *Sphagnum magellanicum* and *S. papillosum* stem diameter when grown in wet vs dry (above water level) conditions. Graph by Yenhung Li, with permission.

**Figure 30.** *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 31.** *Sphagnum papillosum*, a drought-resistant species that develops additional rows of cells when above water. Photo by David T. Holyoak, with permission.

**Figure 32.** *Sphagnum magellanicum*, a drought-tolerant species that develops additional rows of cells when above water. Photo by Michael Lüth, with permission.

**Paraphyllia**

Paraphyllia (Figure 33) are small green outgrowths on stems of some pleurocarpous mosses. They are useful taxonomic characters, permitting us to separate the sometimes lookalikes of *Pleurozium schreberi* (lacking paraphyllia; Figure 34) from *Hylocomium splendens* (having paraphyllia; Figure 35-Figure 36). 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 33.** Stem of *Thuidium* sp. showing paraphyllia. Photo by Paul Davison, with permission.
Figure 34. *Pleurozium schreberi*, a moss that lacks paraphyllia. Photo by Janice Glime.

Figure 35. *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 36. *Hylocomium splendens* paraphyllia. Photo from Botany Department website, University of British Columbia, BC, Canada, with permission.

**Leaf Margins**

Margins of leaves can be flat, **involute** (rolled upward (Figure 37), **revolute** (rolled under; Figure 38-Figure 39), and **bordered** or **unbordered**. The borders can be one cell thick or multiple cells thick. The whole leaf can be **inrolled** (rolled upward; Figure 40-Figure 41), 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 37. *Weissia controversa* leaf cross section showing involute margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 38. *Bryoerythrophyllum recurvirostre* leaf cross section showing revolute leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 39. *Ceratodon purpureus* showing revolute leaf margins. Photo by Malcolm Storey, through Creative Commons.

Figure 40. *Dicranum muehlenbeckii* showing the curled, inrolled leaves. 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 42), 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 49). And those with borders typically have elongate cells (Figure 43-Figure 44) that differ from lamina cells. These specialized border cells may have teeth or lack them.

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 45-Figure 46) and Grimmiaaceae (Figure 47-Figure 49). 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).
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 leaved, 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 50-Figure 52)?
Chapter 4-12: Adaptive Strategies: Speculations on Gametophyte Structures

Figure 51. *Plagiochloa 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 50) or doubly (Figure 52)], but also occasionally projecting from the leaf lamina (Figure 53-Figure 55) or costa (Figure 55-Figure 56).

Figure 52. * Mnium spinosum* leaf showing double teeth on leaf margin. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 53. *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 54. *Atrichum undulatum* leaf showing teeth in diagonal rows on dorsal side. Photo by Jutta Kapfer, with permission.

Figure 55. *Atrichum undulatum* leaf showing teeth (arrow) on dorsal side. Note also the teeth on the costa. Photo by Jutta Kapfer, 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 antitherbivore 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 antitherbivore 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 53-Figure 55).

**Liverworts**

And what about the lobes and teeth of *leafy liverworts* (Figure 57)? Do they have any adaptive value? Could they also have antitherbivore 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 58-Figure 59) 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 60). 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?
Presumably, size affects the utility of teeth and lobes. If one compares the large size of the leaf and its lobes in *Lophocolea* (Figure 63) with those in *Cephalozia* (Figure 64), 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 CO₂ to enter the cells, behaving like the drip tips of some tropical leaves?

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 65), *Porella* (Figure 66), and *Radula* (Figure 67). In the tropics, *Plagiochila* (Figure 68) 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 65. *Frullania dilatata* showing lobules and entire margins (no teeth or lobes). Photo by Walter Obermayer, with permission.

Figure 66. *Porella cordacana* showing entire leaf margin. Photo by Jan-Peter Frahm, with permission.

Figure 67. *Radula* from the Neotropics showing entire leaf margins. Photo by Michael Lüth, with permission.

Figure 68. *Plagiochila adiantoides* from the Neotropics showing toothed leaf margins. Photo by Michael Lüth, with permission.

One might argue that in liverworts like *Nowellia curvifolia* (Figure 69), 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 69. *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 70-Figure 71). 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 72).
A second function has been suggested – that the hair points may help to absorb condensed water vapor from fog and dew (Figure 73–Figure 75) (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.
If we examine the picture of *Grimmia* from Scotland (Figure 77), 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.

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 78), 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 79).

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 80).

The *costae* are the moss versions of midribs (Figure 81). 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 82) 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.
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 83) and Brachelyma (Figure 84), both occurring in inundated areas but living mostly above water, from the ecostate genus Fontinalis (Figure 85), 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.
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 CO₂ 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 86-Figure 87) 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.

Selkirk 1984) observed that the costae of *Bryum pseudotriquetrum* (Figure 88-Figure 89) 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 90) 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?

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 &
In the genus *Dicranum* (Figure 91-Figure 96), the costa varies widely, with almost no differentiation in *Dicranum rhabdocarpum* (Figure 91) to phalanges along the costa in *Dicranum scoparium* (Figure 96). In other members of the *Dicranaceae*, for example *Pilopogon peruvianus*, the costa can occupy most of the leaf width (Figure 97).

**Figure 91.** *Dicranum rhabdocarpum* leaf cross section showing absence of papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

**Figure 92.** *Dicranum muehlenbeckii* leaf cross section showing relatively smooth cell surface. Photo by Michael Lüth, with permission.

**Figure 93.** *Dicranum brevifolium* leaf cross section showing costa and mammillate cells. Photo by Michael Lüth, with permission.

**Figure 94.** *Dicranum dispersum* leaf cross section showing costa and thickened margins. Photo by Michael Lüth, with permission.

**Figure 95.** *Dicranum fuscescens* leaf cross sections showing costa and papillose leaf cells. Photo by Michael Lüth, with permission.

**Figure 96.** *Dicranum scoparium* teeth on back of leaf costa. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.
Glenn Shelton (Bryonet 15 June 2012) contended that mosses tend to evolve from having multiple costae (Figure 98) 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.

Perhaps Kürschner (2004) has the right idea for some species. He notes that the costa is often shiny (Figure 99-Figure 100) 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 99-Figure 100), suggesting they might absorb more heat than the lamina.

Lamellae

Lamellae (Figure 101-Figure 113) can greatly increase the surface area of a leaf. They provide numerous surfaces, exposed on both sides for absorption of light and especially CO₂ and provide capillary spaces for taking up and holding water.
Members of the family *Polytrichaceae* are defined by the presence of lamellae (Figure 101-Figure 106), but other genera in scattered families have them as well. These include *Aloina* (Figure 107), *Crossidium* (Figure 108-Figure 109), *Pterygoneurum* (Figure 110-Figure 112), and some *Syntrichia* (Figure 113).

Figure 101. *Atrichum undulatum* leaf lamellae. Photo by Walter Obermayer, with permission.

Figure 102. *Atrichum undulatum* leaf cross section showing lamellae. Photo by Walter Obermayer, with permission.

Figure 103. *Polytrichastrum formosum* leaf cross section showing lamellae. Photo by Michael Lüth, with permission.

Figure 104. *Polytrichum commune* leaf cross section showing lamellae. Photo by Michael Lüth, with permission.

Figure 105. *Polytrichum hyperboreum* showing leaf lamina rolled over the lamellae. Photo by Michael Lüth, with permission.

Figure 106. *Dendroligotrichum squamosum* SEM showing tops of lamellae. Photo courtesy of Jeff Duckett and Silvia Pressel.
Figure 107. *Aloina rigida* with lamellae within the inrolled leaf margins. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 108. *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 109. *Crossidium aberrans* leaf showing lamellae along costa. Photo by Michael Lüth, with permission.

Figure 110. *Pterygoneurum ovatum* showing fleshy, inrolled leaves that partially cover the lamellae. Photo by Kristian Peters, with permission.

Figure 111. *Pterygoneurum ovatum* leaf showing lamellae in upper half. Photo by Hermann Schachner, through Creative Commons.

Figure 112. *Pterygoneurum ovatum* leaf cross section showing leaf lamellae. Photo by Hermann Schachner, through Creative Commons.
Kürschner (2004) suggests that the lamellae facilitate water conduction as well as storing water. These roles are in addition to their photosynthetic role. Proctor (2005) demonstrated that the lamellae in *Polytrichaceae* (Figure 101-Figure 106) are important for the absorption of CO₂, increasing typical uptake by six times that of the projected leaf area, whereas in unistratose leaves of most other bryophytes, CO₂ uptake is limiting. This permits the *Polytrichaceae* to take advantage of high light intensity in open areas. Furthermore, these lamellate species experienced high non-saturation light levels, permitting them to take advantage of high intensity light. In a number of these species, including some of *Polytrichum* (Figure 105), the leaf margins fold over the lamellae, affording protection from excess UV light and preserving moisture and space for CO₂ exchange.

**Keels**

Most leaves are slightly concave, some are flat, and some are folded over, forming a keel (Figure 114). 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 115). 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.

**Leaf Plications**

Some genera are characterized by leaf plications (). 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?
Leaf Cells

Cell shape varies considerably, from small isodiametric cells (Figure 82) to large, nearly hexagonal ones (Figure 119) to elongate ones (Figure 120). Some cells have wall invaginations or wavy walls (Figure 121). 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 121). 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.

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 122-Figure 124), 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 123. *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 124. *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 125). 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 126). 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 126. *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 macrosorum* (Figure 127), 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 127. *Andreaeobryum macrosorum*, 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.

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 128) – well, the chloroplasts didn't really surprise me, but they certainly made a beautiful image.

Figure 128. *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 129) 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 130) 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.

Figure 129. *Coleochaete*, the only alga known to produce fluorescent tissues at the placental junction. Photo by Yuuji Tsukii, with permission.

Figure 130. *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 131-Figure 132) 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 131-Figure 132), Riccia (Figure 133), and Oxymitra (Figure 134) species undoubtedly serve to reduce desiccation and provide capillary spaces to facilitate water uptake upon wetting.

Figure 131. Mannia androgyna in hydrated condition with reddish edges that characterize the color of anthocyanins on the ventral side. Photo by Michael Lüth, with permission.

Figure 132. 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 133. 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 134. 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 135) 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 135-Figure 136), 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 135. *Exormotheca welwitschii* in southern Portugal, showing "windows" in the thalli. Photo by Michael Lüth, with permission.

Figure 136. *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 137) 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.

Thallus pores may 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 138-Figure 140) 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 138. *Marchantia polymorpha* section of thallus showing pore opening with ridge extending from apical cells of pore. Photo by Wilhelm Barthlott, with permission.

Figure 139. *Marchantia polymorpha* thallus pore opening with ridge. Photo by Wilhelm Barthlott, with permission.

Figure 140. *Marchantia polymorpha* thallus pore opening with ridge that is heavily endowed with wax. Photo by Wilhelm Barthlott, with permission.

Once inside the thallus, we must look for adaptations to obtain sufficient CO₂ 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 138) (Proctor 2010).

**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 141) and *Fontinalis* (Figure 142-Figure 143) may protect the chlorophyll from high light intensity.

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 144-Figure 145) illustrate the green and red color expressions in this species.

Figure 141. *Sphagnum* showing the red colors that develop in some species when they grow in the sun. Photo by Janice Glime.

Figure 142. *Fontinalis antipyretica* with red pigments responding to cold spring water and full sun. Photo by Janice Glime.

Figure 143. *Fontinalis antipyretica* with red pigments, responding to being out of water, but moist, in bright light. Photo by Janice Glime.

Figure 144. *Grimmia elongata* showing its green form. Photo by Michael Lüth, with permission.

Figure 145. *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 146) or stem rigidity (Figure 147), but they also occur in many leaf borders (Figure 43).

Figure 146. Syntrichia inermis leaf showing dark color in costa. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

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 148), 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.

Figure 148. 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.

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 149) produces highly volatile 8-carbon compounds including \((R)-1\text{-octen-3-ol}\) 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 149. 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.
Crosier 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.

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**Literature Cited**


