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CHAPTER 2-4
STREAMS: STRUCTURAL MODIFICATIONS – RHIZOIDS, SPOROPHYTES, AND PLASTICITY

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Figure 1. *Thamnobryum cataractarum* habitat at The Dales, UK. Photo by Nick Hodgetts, with permission.

Rhizoids and Attachment

Rhizoids on bryophytes are primarily used for attachment. In flowing water, this would seem to be the only function, whereas in terrestrial habitats they may help in forming capillary spaces and moving water from substrate to moss. Thus, in stream habitats the rhizoids are often a necessity for staying in place.

Effects of Submersion

Odu (1978) concluded that production of rhizoids is related to the habitat. Floating and submersed wetland plants often lack rhizoids (Watson 1919; Odu 1978). But when plants grow on the edges of lakes or in flowing streams, they require rhizoids for anchorage (Vitt & Glime 1984). Earlier, Watson (1919) concluded that for bryophytes to live in flowing water they need strong and numerous rhizoids to affix them firmly to the substrate.

Higuchi and Imura (1987) tested the effects of submersion on rhizoid characters, using ***Bryum*** (Figure 2-Figure 3), ***Pohlia*** (Figure 4-Figure 5), ***Macromitrium*** (Figure 6), and ***Trachycystis*** (Figure 7). He was unable to detect any difference between aerial and submersed rhizoids in the species tested, except that ***Macromitrium gymnostomum*** lost its mucilage in water culture.

Figure 2. *Bryum pseudotriquetrum* in a typical habitat. Photo by Michael Lüth, with permission.
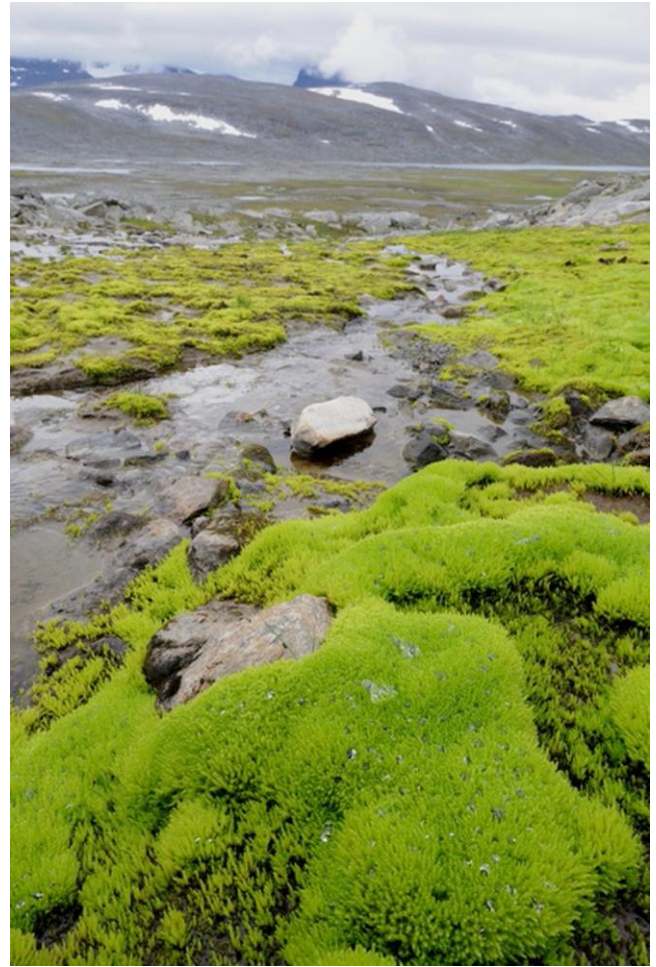

Figure 4. *Pohlia wahlenbergii* habitat. Photo by J. C. Schou, with permission.

Figure 3. *Bryum pseudotriquetrum* stem with rhizoids. Photo by Bob Klips, with permission.

Figure 5. *Pohlia wahlenbergii*, in a genus in which at least some species do not change rhizoid production depending on submersion. Photo by Betsy St. Pierre, with permission.

Figure 6. *Macromitrium* sp., typically a terrestrial moss. Tested species in this genus did not change rhizoid production depending on submersion. Photo by Niels Klazenga, with permission.

Figure 7. *Trachycystis flagellaris*, in a genus in which at least some species do not change rhizoid production depending on submersion. Photo by Misha Ignatov, with permission.

But other researchers have found that rhizoid production can differ between terrestrial and aquatic habitats. Odu (1978) found that pleurocarpous mosses produce more rhizoids on hard substrates. Acrocarpous mosses have more attachment problems because all the rhizoids are at the base of the stem, contributing to their lack of success on steep slopes and tree trunks. Auxins are known to stimulate rhizoid formation in diverse mosses and liverworts; auxins produced by microbes in the soil or sediments may promote the growth of rhizoids, but that hypothesis needs experimental exploration.

Effects of Flow on Rhizoid Production

Plants in quiet water have fewer rhizoids than those in fast water. Thus, the floating *Scorpidium* (Figure 8) lacks rhizoids, but the anchored *Fontinalis* requires them (Figure 9-Figure 10) (Vitt & Glime 1984). *Drepanocladus s.l.* species (Figure 11) typically lack rhizoids, but when *Warnstorfia fluitans* (=*Drepanocladus fluitans*; Figure 12) is cultured on agar it produces them. In mountain streams, *Fontinalis gigantea* (Figure 13), a species of quiet water, rarely produces rhizoids, but *Fontinalis hypnoides* (Figure 14) from streams produces abundant rhizoids (Glime

1980). Bruggeman-Nannenga (2013) similarly reported masses of rhizoids on *Fissidens bessouensis*, including those firmly attaching the stems, on axillary perigonia and perichaetia, and on infertile branches.

Figure 8. *Scorpidium revolvens*, typically a floating species with no rhizoids. Photo by David T. Holyoak, with permission.
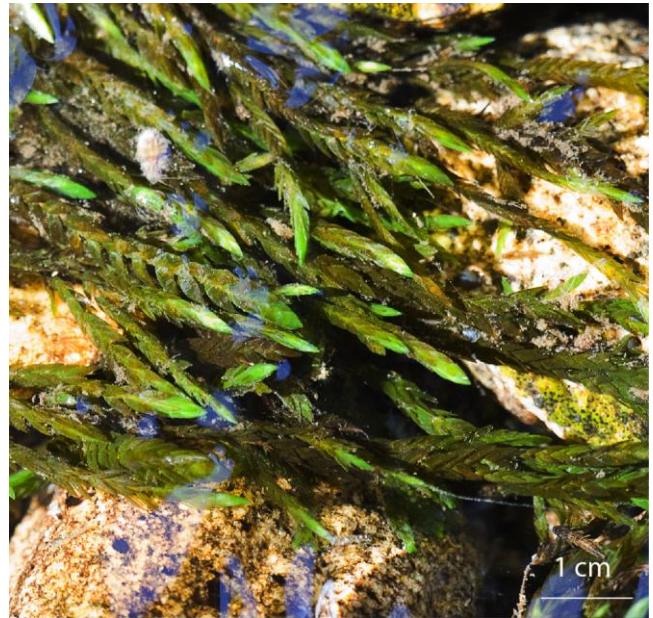

Figure 9. *Fontinalis antipyretica* attached to rock in flowing water. Photo from Projecto Musgo, through Creative Commons.

Figure 10. *Fontinalis antipyretica* wound rhizoids. Photo by Janice Glime.
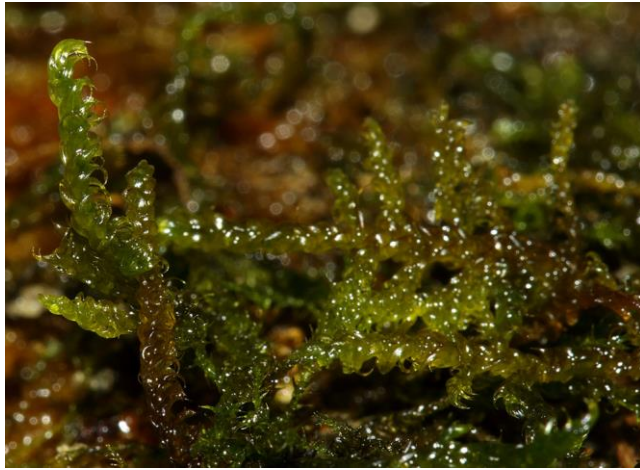
Figure 11. *Drepanocladus aduncus*, a species that typically lacks rhizoids. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University (permission from Russ Kleinman & Karen Blisard).

Figure 14. *Fontinalis hypnoides* with collected detritus in the Manganese River Gorge, MI, USA. Photo by Janice Glime.

Figure 12. *Warnstorfia fluitans*, a species that produces rhizoids when cultured on agar, but not in water. Photo by Michael Lüth, with permission.

Temperature and flow conditions are both important in the production of rhizoids in *Fontinalis* species, a pleurocarpous genus (Glime 1980). Both *F. hypnoides* (Figure 14) and *F. novae-angliae* (Figure 15-Figure 26) produced significantly more rhizoids in flowing water than in pool conditions in laboratory experiments, except for *F. novae-angliae* at 20ºC (Figure 17). *Fontinalis hypnoides* produced significantly more rhizoids than did *F. novae-angliae* at temperatures below 15ºC, both species increased their rhizoid production with increasing temperatures up to 20ºC (see Figure 16), and *F. novae-angliae* greatly exceeded rhizoid production of all other species at that temperature (Figure 17). This response should be adaptive in many streams where flow is low when the temperature is as high as 20ºC, permitting attachment while the flow is less able to detach them. Furthermore, the plant growth rate is very slow at this higher temperature (Figure 18). This combination of behaviors would permit the mosses to remain on a rock without high flows to wash them away while they grow their rhizoids and attach.

Figure 13. *Fontinalis gigantea*, a species of quiet water that rarely produces rhizoids. Photo by Paul Wilson, with permission.

Figure 15. *Fontinalis novae-angliae*, a species of rapid water. Photo by Janice Glime.
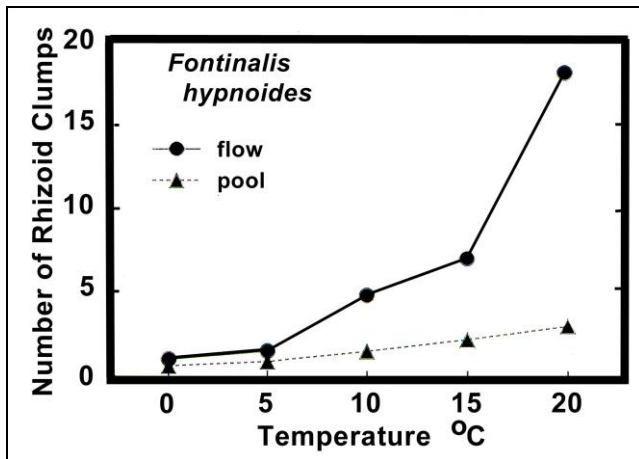
Figure 16. Comparison of rhizoid clumps per moss stem (5 cm starting length) produced by *Fontinalis hypnoides* after 15 weeks of growth in artificial streams with flowing water and pool conditions. Modified from Glime and Raeymaekers 1987.
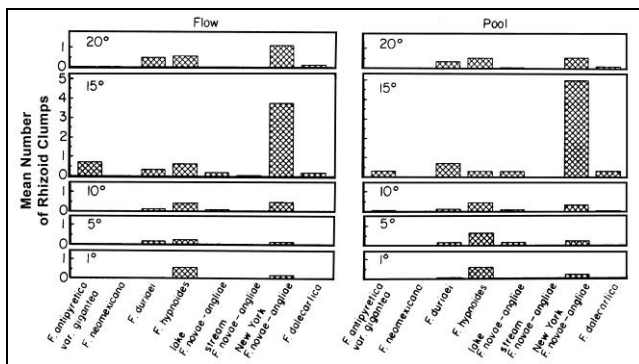

Figure 17. Comparison of *Fontinalis* species and their production of rhizoids at temperatures of 1-20ºC in flow and pool conditions.

Since rhizoids are very important in anchoring *Fontinalis* and other mosses to the rocks and wood in streams, it is predictable that species living in faster water would have higher rhizoid production. Glime (1980) showed that *Fontinalis hypnoides* (Figure 14) produced significantly more rhizoid clumps than did *F. novae-angliae* (Figure 15). Glime and Raeymaekers (1987) also found that the most rhizoids in *Fontinalis hypnoides* were produced at 20ºC compared to plants at lower temperatures, contrasting with the best growth at 15ºC, and those plants in flowing water conditions produced considerably more rhizoid clumps than did plants in pool conditions.

The pleurocarpous stream moss *Fontinalis dalecarlica* (Figure 19) in axenic culture produced rhizoids on all sides of the stem (Figure 20) (Glime 1980), a trait mostly restricted to acrocarpous mosses (Odu 1979). Such a growth pattern would facilitate attachment wherever the stem made contact with a substrate. More rhizoids were produced at 15-20ºC (Figure 17), depending on the species, than at lower temperatures (Glime 1980, 2015; Glime & Raeymaekers 1987). This would encourage rhizoid growth when stream water was low during the summer, making it easier for attachment to occur without the danger of being dislodged by heavy flows. When heavier rains return in the autumn, the mosses would already be well attached.
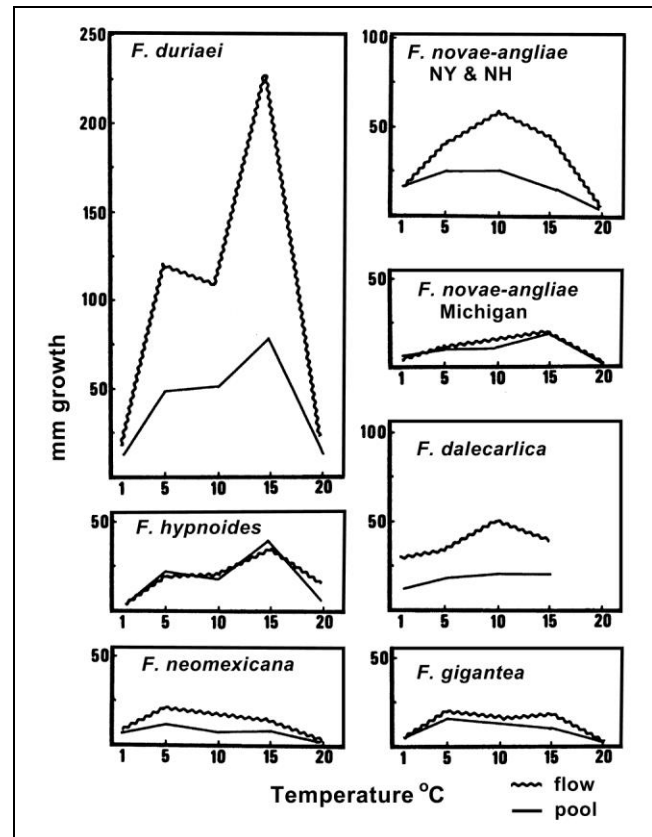

Figure 18. Growth rates of six *Fontinalis* species at five temperatures in flowing water and pool conditions in artificial streams. From Glime 1987b.

Figure 19. *Fontinalis dalecarlica* habitat in Tolliver Run, Garrett County, MD, USA. Photo by Janice Glime.

Finding and Recognizing the Substrate

In flowing water, rapid flow and ice flows can easily dislodge fragile bryophytes. I found two strategies of attachment in members of *Fontinalis* that grow in rapid water. In *F. dalecarlica* (Figure 19) rhizoids appear along the stem at points of contact. These can arise on any side of the stem (Figure 20) (Glime 1980). When fragments of the plant are developing new rhizoids, these rhizoids spiral (Figure 21) in growth until they make contact with a substrate (Figure 22) (Glime 1987a). Schuepp (1928) noted the frequent presence of spirals in nature, including

Fontinalis. Once the rhizoids contact a substrate, they branch at the tips and attach to the substrate with an adhesive (Glime 1987a).

Figure 20. *Fontinalis dalecarlica* rhizoidal branch in liquid culture. Culture courtesy of Dominic Basile; photo by Janice Glime.

Figure 21. *Fontinalis squamosa* rhizoid spirals from a broken stem. Photo by Janice Glime.

Figure 22. *Fontinalis squamosa* rhizoid tips branching where they contact the filter paper. Photo by Janice Glime.

Using the bryophytes *Hypnum* (Figure 23), *Rhynchostegium* (*Platyhypnidium*? – Figure 24), and *Lophocolea* (Figure 25), Odu (1989) demonstrated that their rhizoids produce extra-wall materials when they contact a solid object. These are sulfated mucopolysaccharides that are highly viscous and sticky.

These compounds are also involved in adhesion of microorganisms and algae. Odu also noted that pleurocarpous mosses, such as those typical of rapid water, have flattened parts toward the rhizoid tips, but in acrocarpous mosses the flattenings extended far behind the tips.
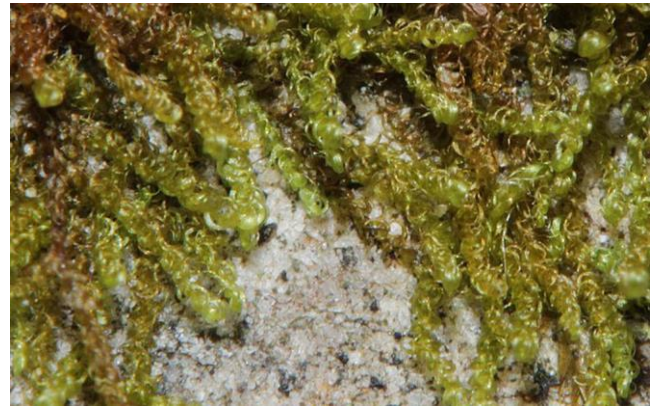

Figure 23. *Hypnum sauteri* with rhizoid attachments to its substrate; rhizoids in tested members of this genus produce extra-wall materials when they contact a solid object. Photo by Hermann Schachner, through Creative Commons.

Figure 24. *Platyhypnidium riparioides*, a common species on emergent rocks in rapid streams. Photo by Michael Lüth, with permission.

Figure 25. *Lophocolea heterophylla*, in a genus that produces extra-wall materials when the rhizoids contact a substrate. Photo by Janice Glime.

In *Fontinalis dalecarlica* (Figure 19) and *F. novae-angliae* (Figure 15, Figure 26), both species of relatively rapid water, the moss spreads by producing **stolons** (horizontal stem that typically lacks leaves or has reduced leaves; Figure 26), and rhizoids are restricted to these stolons in the latter species (Glime 1980). This may actually be a better strategy than normal branching because the stolon grows along the substrate and its leaf reduction would save energy over producing a leafy branch. Experiments are needed to determine if the stolon truly has a faster growth rate than a normal branch. This would appear to be beneficial for a species that branches and rebranches while dangling in rapidly flowing water.

Figure 26. *Fontinalis novae-angliae* stolon, where rhizoids are produced. Photo by Janice Glime.

Growing the Right Direction

Fontinalis also uses **tropisms** (turning responses to a stimulus) to orient the rhizoids. The rhizoids are **negatively phototropic**, *i.e.*, they grow away from light, but seem to lack **gravitropism** (growth toward the Earth's gravity), or it is not as strong as the **phototropism** (Figure 27) (Glime 1987a). In *Fontinalis squamosa* (Figure 27), once the substrate is located, the moss expands the tips of the rhizoids by their branching, and attaches. The negative phototropism can prevent the rhizoids from "exploring" locations closer to the water surface and may be adaptive in helping them find suitable locations on the rocks. It would be interesting to track where the moss first attaches and follow its development on the rock.

Figure 27. *Fontinalis squamosa* rhizoid negative phototropism. Based on Glime 1987a.

Rate of Attachment

Rhizoids serve primarily for attachment, and the ability of *Fontinalis* fragments to attach to rocks takes advantage of the ability to produce rhizoids on all sides of the stem and all along the stem. This is necessary for even small fragments to stay in place (Figure 28). Glime *et al.* (1979) attached *Fontinalis duriaei* (Figure 29-Figure 30) and *Hygroamblystegium fluviatile* (Figure 31) to rocks in artificial streams to follow the rate of attachment. It required at least 9 weeks for the mosses to attach (Figure 32). But these mosses were held in place artificially, whereas mosses in nature must remain in place by natural mean for this attachment to occur. Following that initial attachment, the rhizoid proliferates rapidly, resulting in a network of rhizoids. This rapid rhizoid growth diminishes after 12-13 weeks from the initial introduction of the moss stem to the rock.
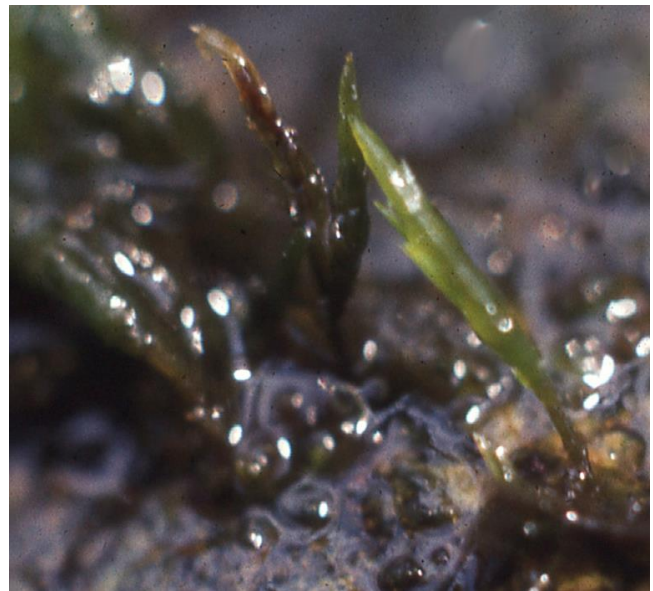

Figure 28. Young shoots of *Fontinalis novae-angliae* in Fox Run, Grafton Co., New Hampshire, USA, showing that even these young shoots are attached. Photo by Janice Glime.
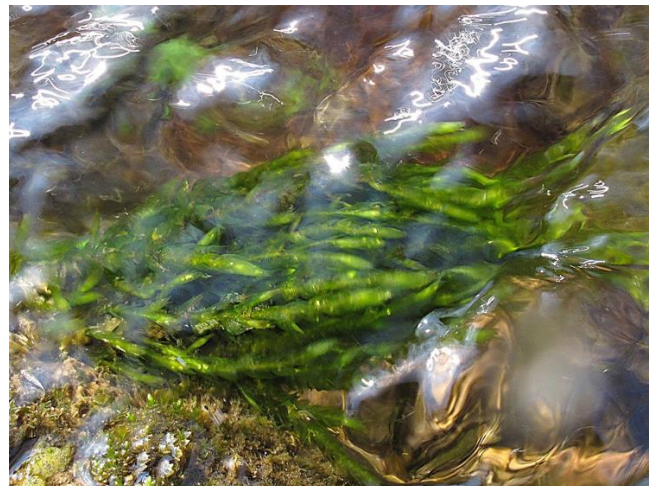

Figure 29. *Fontinalis duriaei*, a species of streams with moderate flow. Photo by Jan-Peter Frahm, with permission.
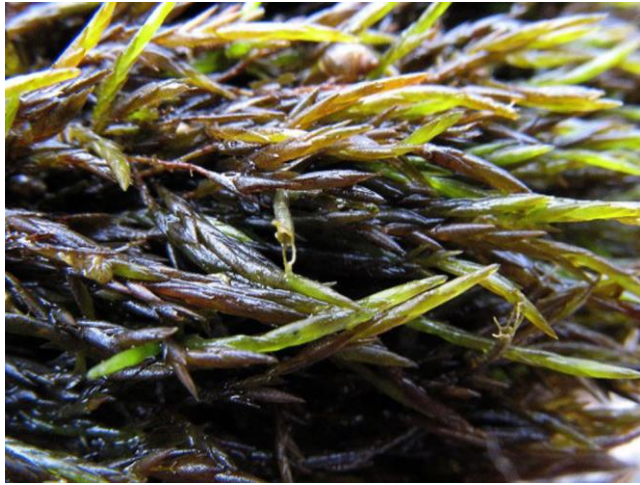
Figure 30. *Fontinalis duriaei*, a species that attaches to rocks in ~9 weeks after establishing contact. Photo by Michael Lüth, with permission.

Figure 31. *Hygroamblystegium fluviatile*, a species that can begin attachment in 9 weeks when in contact with a substrate. Photo by Hermann Schachner, through Creative Commons.
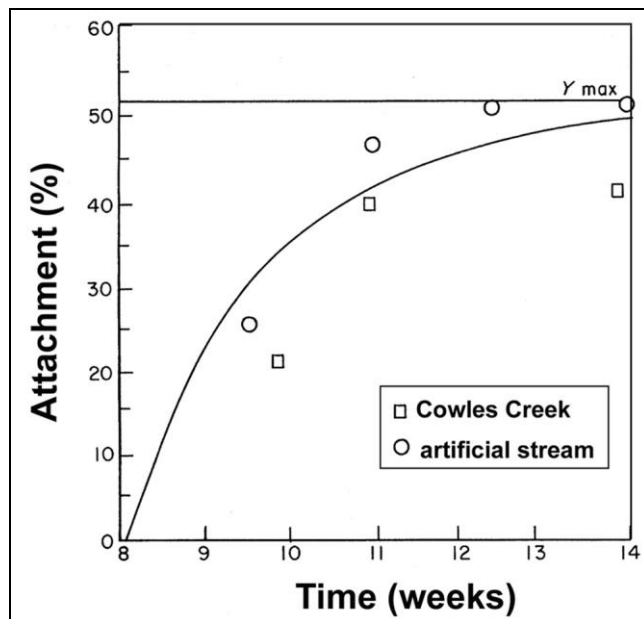

Figure 32. Attachment time for *Fontinalis duriaei* and *Hygroamblystegium fluviatile* in artificial streams. From Glime *et al.* 1979.

If you examine a stream during autumn leaf fall, you would notice that a collection of leaves is impinged against the rocks on the upstream side of the rock. For mosses like *Fontinalis*, one might imagine that the drifting moss fragments can be trapped behind rocks (Figure 33) and debris when the higher temperatures of summer cause the water levels to drop. With little or no rapid flow during summer, the moss could remain in place. At the same time, the higher temperatures of summer would stimulate rhizoid growth (Glime 1980; Figure 17). This combination of events could permit the mosses to attach to the rocks by time the heavier rainfall occurs in autumn.

Figure 33. *Fontinalis squamosa* on rock above water near Swallow Falls, Wales. At this time, rhizoids can grow more prolifically in the warmer temperatures. Photo by Janice Glime.

Reductions and Other Modifications

Reduction is helpful to some species in water (Watson 1919). *Marchantia* (Figure 34) species have fewer pores (Figure 35); *Dumortiera* (Figure 36-Figure 37) has fewer ventral scales or none; *Sphagnum* (Figure 38-Figure 39) has fewer hyaline cells. *Sphagnum* in pools may have fewer strengthening fibers in the hyaline cells, but those living in rapid streams display no such reduction. *Atrichum crispum* (Figure 40) has fewer and lower leaf lamellae than other members of the genus that occur on drier ground, with similar differences also in *Polytrichum s.l.* (Figure 41-Figure 42). Species in streams are often robust and very elongated, *e.g.* the leafy liverwort *Nardia compressa* (Figure 43. Species with pinnate branches often lose that character and the branches become long (*e.g. Platyhypnidium alopecuroides* – Figure 44). In other species, the leaves are large and may be lengthened. In the thallose liverwort *Pellia epiphylla* (Figure 45) the number of strengthening bands is typically more pronounced in rapid streams than in moist habitats along streams.

Figure 34. *Marchantia polymorpha*, a species that survives a wide range of habitats. Photo from Botany Website, UBC, with permission.

Figure 35. *Marchantia polymorpha* air pores that become less dense under water. Photo by Des Callaghan, through Creative Commons.

Figure 36. *Dumortiera hirsuta* in a typical habitat in the splash. Photo by Michael Lüth, with permission.

Figure 37. *Dumortiera hirsuta* has fewer ventral scales or none in water. Photo by Li Zhang, with permission.

Figure 38. *Sphagnum cuspidatum*, a species that can be submersed or emergent from water. Photo by Michael Lüth, with permission.
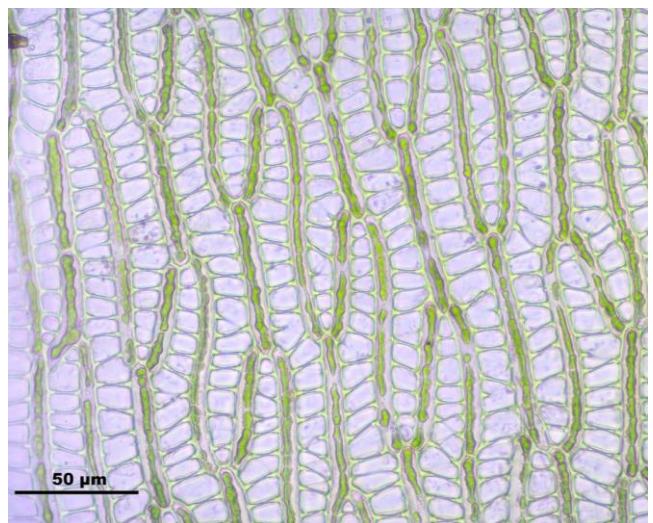

Figure 39. *Sphagnum cuspidatum* leaf cells showing fibrils; these become fewer in submersed *Sphagnum*. Photo by Hermann Schachner, through Creative Commons.

Figure 40. *Atrichum crispum* showing leaf lamellae; these are lower and have fewer cells when grown in water. Photo from Northern Forest Atlas, with permission through Jerry Jenkins.

Figure 41. *Polytrichum commune*, a wetland and bog species. Photo by Alan J. Silverside, with permission.
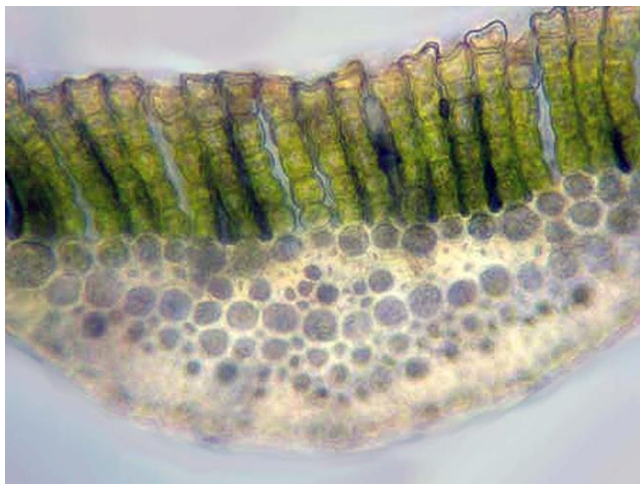
Figure 42. *Polytrichum commune* leaf lamellae; these are shorter when the moss is grown in water. Photo from Botany Website, UBC, with permission.

Figure 43. *Nardia compressa* representing a leafy liverwort species that is robust and very elongated. Photo by Hermann Schachner, through Creative Commons.

Figure 44. *Platyhypnidium alopecuroides*, a species that loses its pinnate branching in water. Photo by David T. Holyoak, with permission.

Figure 45. *Pellia epiphylla*, a common streamside species that develops more strengthening in fast water. Photo by Kristian Peters, through Creative Commons.

Duckett (1994) described yet another modification that would be helpful in some aquatic environments. In *Straminergon stramineum* (Figure 46-Figure 47) rhizoids develop below the apex of each leaf (Figure 48). Damaged apices regrow, providing a means of reproduction. These

rhizoids are more frequent further down the stem. They become highly branched on peaty substrata or on dead *Molinia* leaves. He found that rhizoid branches would coil around other rhizoids of both ***S*. stramineum** and ***Aulacomnium palustre*** (Figure 49), whereas others were unbranched and wove their way through ***Sphagnum*** hyaline cell pores (Figure 50). When the rhizoids occur in water cultures, the new parts branch and adhere upon contact. When new leaves form in culture, they produce numerous rhizoids upon contact; those that grow unobstructed do not. This is similar to the behavior of ***Fontinalis*** rhizoids (Figure 22) described above.

Figure 46. *Straminergon stramineum* habitat. Photo by Michael Lüth, with permission.
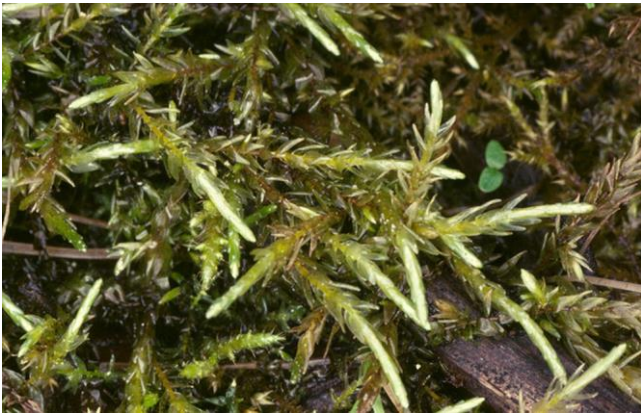
Figure 47. *Straminergon stramineum*, a species that produces rhizoids on the leaf tips. Photo by Malcolm Storey, with online permission.

Figure 48. *Straminergon stramineum* showing rhizoids at leaf tips. Photo by Hermann Schachner, through Creative Commons.

Figure 49. *Aulacomnium palustre* showing rhizoidal tomentum. Photo by J. C. Schou, through Creative Commons.

Figure 50. *Sphagnum* leaf hyaline cell with pore. Photo from Botany website, UBC, with permission.

When these ***Straminergon stramineum*** leaves (Figure 48) are detached, they produce numerous branched chloronemal filaments not only at their apices, but also at the margins and bases (Duckett 1994). At the bases of these filaments, gametophores develop, making these leaves highly likely propagules.

Sporophyte Characters

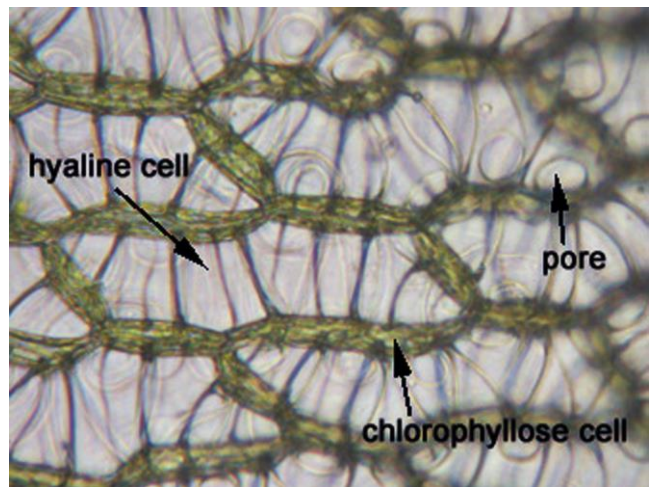Most of the stream mosses produce their capsules above the water and therefore these capsules resemble terrestrial capsules (Vitt 1981; Vitt & Glime 1984). But several produce capsules under water. These include *Blindia* (Figure 51), *Cinclidotus* (Figure 52), *Fontinalis* (Figure 53), *Hydropogon*, *Hydropogonella* (Figure 54), *Rhabdodontium*, and *Wardia* (Figure 55). These underwater capsules are characterized by immersed, smooth, ovate-oblong capsules, short, thick setae (Figure 53), somewhat reduced peristome, and capsule surrounded by enlarged, sheathing perichaetial leaves.

Figure 53. *Fontinalis dalecarlica* capsules that are produced under water. Although it has a well-developed peristome, that peristome is quickly damaged and broken off in the water, as in the lower capsule. Photo by Janice Glime.

Figure 51. *Blindia acuta* with capsules that can be produced under water. Photo by Hermann Schachner, through Creative Commons.

Figure 54. *Hydropogonella gymnostoma*, a species that produces capsules under water. Photo from <aqvium.ru> through public access.
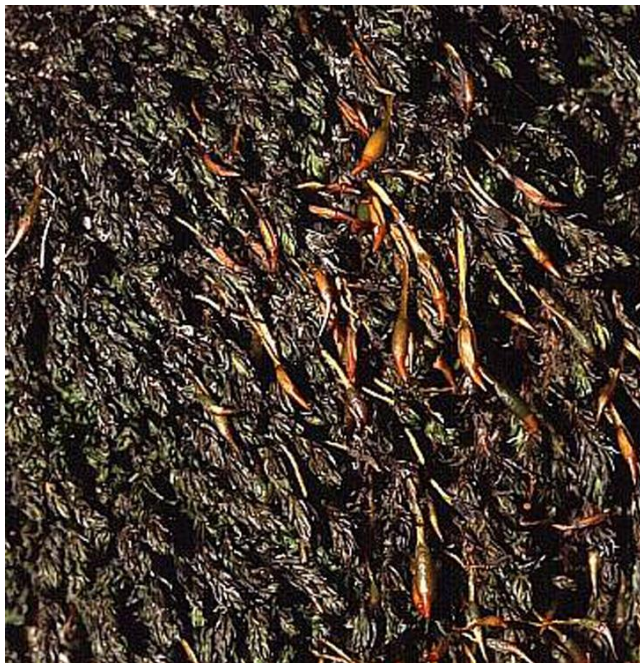

Figure 52. *Cinclidotus confertus* with capsules that can be produced under water. Photo by Michael Lüth, with permission.

Figure 55. *Wardia hygrometrica* with capsules that can be produced under water. Photo by Jonathan Sleath, Sanbi.

Fissidens fontanus likewise has a reduced peristome (Figure 56) (Bruggeman-Nannenga 2013) and *F. bessouensis* has a very short seta (Figure 57), the latter also seen above in *Fontinalis* (Figure 53). To these sporophyte characters, Ida Bruggeman-Nannenga (Bruggeman-Nannenga 2013; pers. comm. 10 April 2020) adds loss of stomata in the capsule, a character often omitted in moss species descriptions.
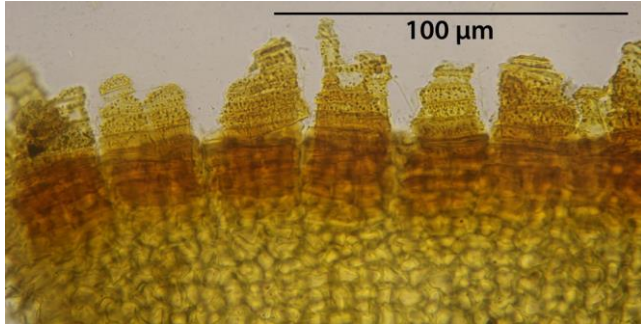

Figure 56. *Fissidens fontanus* with reduced peristome, a common character of submersed species. Photo by courtesy of Ida Bruggeman-Nannenga.

Figure 57. *Fissidens bessouensis* sporophyte showing short seta. Photo courtesy of Ida Bruggeman-Nannenga.

Pursell (1987) noted that in the *Octodiceras* subgenus of *Fissidens* the capsules tend to break off in the herbarium. Kortselius *et al.* (2018) reported that the calyptrae of *Fissidens* (*Octodiceras*) *fontanus* (Figure 58) frequently develops new plants from the calyptra (Figure 59). If the breakage also occurs in the field, it would provide these species with an additional dispersal mechanism in the water.

Figure 58. *Fissidens fontanus*, a species that can grow new plants from the calyptra. Photo by Matt Keevil, through Creative Commons.

Figure 59. *Fissidens fontanus* calyptrae with germination. Photo courtesy of Hans Kruijer.

The recently described *Ochyraea tatrensis* (Váňa 1986) was collected from granite rocks in a stream in Nízké Tatry in Slovakia. It has since then been found with sporophytes (Bednarek-Ochyra & Váňa 2014). These sporophytes showed no morphological differences from their more familiar terrestrial relatives.

Spores

Some of the aquatic species have multicellular spores (Bruggeman-Nannenga 2013). One such species with multicellular spores is *Fissidens bessouensis*, a potential advantage in permitting the protonema to develop quickly before it can be washed away.

Character Plasticity

Berthier (1965) concluded that the environment intervenes in the development of *Fontinalis antipyretica* (Figure 9-Figure 10). In support of Berthier's conclusion, Frahm (2006) concluded that *Fontinalis antipyretica* var. *gracilis* (Figure 60) was only a modification of *Fontinalis antipyretica*. On the other hand, he (Frahm 2013) concluded that *F. antipyretica* var. *rotundifolia* (Figure 61) is a valid separate species (*F. rotundifolia*). These forms can be modified by flow rate, submersion vs emergent, nutrient levels, light penetration, and probably other factors.

Figure 60. *Fontinalis antipyretica* var. *gracilis*, a more conservative classification of *Fontinalis gracilis*. Photo by David T. Holyoak, with permission.

Figure 61. *Fontinalis antipyretica* var. *rotundifolia* holotype, a distinct variety. Photo by Jan-Peter Frahm, with permission.

Vanderpoorten and Jacquemart (2004) demonstrated, using culture experiments, that most of the morphological variation exhibited by the aquatic moss genus *Amblystegium* (*Hygroamblystegium*?; Figure 31) occurred as a result of plasticity. Furthermore, those genetic characters that resulted in morphological evolution tended to occur in consort; constraining the characters to be independent from each other produced less likely results

than in models that permitted them to evolve as correlated traits. This has made it difficult to describe distinguishing characters for separating species.

Philonotis fontana (Figure 62), sometimes a stream edge species in quiet, shallow water, exhibits phenotypic plasticity (Buryová & Shaw 2005). When grown under two light and two water regimes, both habitat characters affected growth. Light treatments had greater effects and affected more characters. Several traits indicated genetic variation, with the plasticity varying among plants from six populations in the common garden experiments. Leaf dimensions seemed to have a strong genetic component, but the cell dimensions showed little genetic variation.

Figure 62. *Philonotis fontana* from a stream edge habitat. Photo by J. C. Schou, with permission.

Resultant Identification Problems

Morphological plasticity complicates identification of aquatic bryophytes, but permits the species to live in a greater range of habitats. We have demonstrations that some of these differences result from the environmental factors, but others are apparently genetic. For example, Huttunen and Ignatov (2010) considered the genetics of the genus *Rhynchostegium s.l.* (Figure 63). *Platyhypnidium* (Figure 24), an aquatic member of the *Rhynchostegium* complex, proved to be polyphyletic (having more than one ancestor for the genus). Huttunen and Ignatov found that phylogeny of *Rhynchostegium* and *Platyhypnidium* indicates there have been numerous habitat shifts between terrestrial and aquatic habitats, as well as between different terrestrial (epiphytic and epigeic) habitats, which may have affected taxonomic complexity in *Rhynchostegium*.

Figure 63. *Rhynchostegium confertum*, member of a genus that has had many shifts between terrestrial and aquatic habitats. Photo by Michael Lüth, with permission.

Species can even mimic other species. De Mey and During (1972) found that *Fontinalis squamosa* (Figure 21-Figure 22, Figure 27, Figure 33) in the Netherlands sometimes had keeled leaves like those of *F. antipyretica*. I have seen a similar keeling occasionally in *F. duriaei* (Figure 64), a trait also observed by Zastrow (1934), but only among some of the leaves of the plant. But any adaptive value for keeled leaves is elusive. Glime and Trynoski (1977) suggested that in *Fontinalis neomexicana* (Figure 65) the trait might provide rigidity and keep the leaves tightly together, providing a smooth surface in deep water. *Fontinalis antipyretica* (Figure 9-Figure 10), on the other hand, often has its leaves torn along the keel (Figure 66), suggesting that it is not really adaptive against abrasion. *Fontinalis gigantea* (Figure 13) occurs in quiet water, and thus its keeled leaves do not suffer the tearing of abrasion and rapid flow. One explanation for the presence of keeled leaves has been revealed by experiments conducted on *Fontinalis antipyretica* (Zastrow 1934). Zastrow found that in acid waters, the leaves were strongly keeled, in neutral water they were less keeled, and in alkaline water they were the least keeled and most narrow. It seems to be a consequence, but not necessarily an adaptation.

Figure 64. *Fontinalis duriaei*, a species that can have some keeled leaves among the typically concave ones. Photo by Michael Lüth, with permission.

Figure 65. *Fontinalis neomexicana*, a species with keeled leaves that might provide a smooth surface. Photo by Amy Gibson, through Creative Commons.

Figure 66. *Fontinalis antipyretica* split leaf, a common occurrence when the plant is in rapid flow. Photo by Malcolm Storey, with online permission.

Differences are often so great between terrestrial and aquatic habitats that the plants are described as different species. For example, Beever and Fife (2008) determined that the aquatic moss *Hypnobartlettia fontana* (Figure 67) from Te Waikoropupuu (Pupu Springs), New Zealand, is but an environmental expression of *Cratoneuropsis relaxa* (Figure 68). *Hypnobartlettia fontana* had been placed not only in a different species, but in a different family. *Cratoneuropsis relaxa* varies widely throughout its wide range of habitats in New Zealand. Among these are waterfalls, irrigated and shaded rocks, stream beds, and seepages. It likewise occupies a wide range of substrates. The Pupu Springs version differs in having bistratose laminae, a very stout, excurrent costa, and linear-flexuose lamina cells that are 40-100 µm long, all features that are common among submersed species. It also has paraphyllia on its stems (Ochyra 1985), a feature not usually seen in submersed taxa. Beever and Fife concluded that the environmental form erroneously named as *H. fontana* is a form induced by the unusual conditions at Te Waikoropupuu. It is known only from this type locality,

where the water is nearly perfectly clear, high in calcium, and cold (11.7ºC).

Figure 67.   *Cratoneuropsis relaxa*, previously treated as *Hypnobartlettia fontana*, from Pupu Springs, TePapa. Photo by John Bartlett, through Creative Commons.

Figure 68. *Cratoneuropsis relaxa*; one form is so different it was named to a different family and genus as *Hypnobartlettia fontana*. Photo by Tom Thekathyil, with permission.

Further evidence of the variability of *Cratoneuropsis relaxa* (Figure 68) is that *Sciaromium bellii* (Figure 69) likewise is now considered to be a variant of this variable

species (Sainsbury 1948, 1955; Beever & Fife 2008). It differs in having laminal cells that are unistratose except occasionally a few bistratose marginal cells. They also have only a weak laminal border of thicker-walled cells in the lower part of the leaf. This form is widespread on both of the main islands of New Zealand. In Pupu Springs, the leaves have bistratose margins and nearly equal areas of unistratose and bistratose mid-leaf laminal cells.

Figure 69.   *Cratoneuropsis relaxa*, previously treated as *Sciuromium bellii* from Te Papa. Photo from TePapa, through Creative Commons.

Plastic Characters

Flow rate is one cause of polymorphisms in *Fontinalis antipyretica* (Figure 9-Figure 10). These differences include stem thickening and branching angle of the leaves, as already noted in subchapter 2-3 of this volume.

Plications (folds like a Japanese fan; Figure 71, Figure 73) also seem to have no value in the water. *Tomentypnum nitens* (Figure 70-Figure 71) and *Climacium dendroides* (Figure 72-Figure 73) both lose their plications when grown submersed (Zastrow 1934).
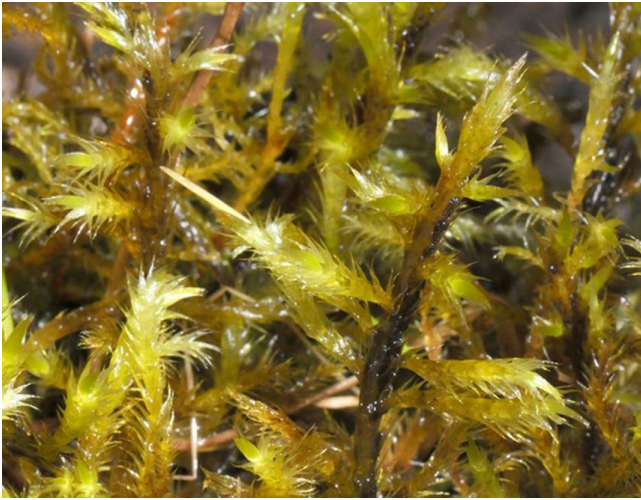
Figure 70. *Tomentypnum nitens*, a species that loses its plication when grown in water. Photo by J. C. Schou, with permission.

Figure 71. *Tomentypnum nitens* plicate leaf. Photo by Hermann Schachner, through Creative Commons.

Figure 72. *Climacium dendroides*, a moss often found on stream banks and other moist habitats. Photo by Jeremy Baker, through Creative Commons.
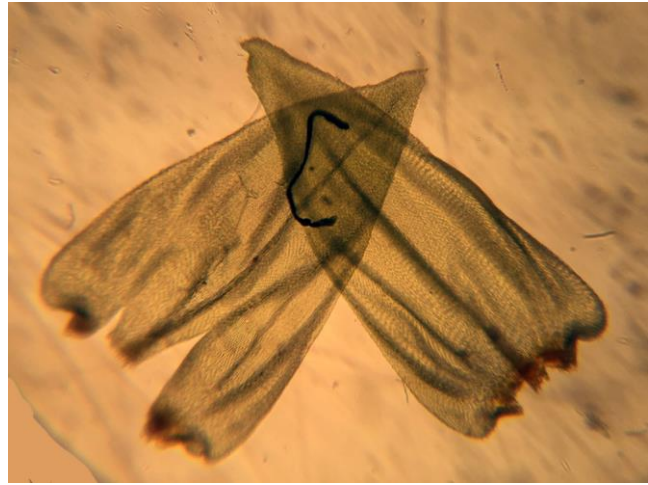

Figure 73. *Climacium dendroides* plicate leaves; plications are lost when the species grows under water. Photo by Matt Keevil, through Creative Commons.

Warnstorfia exannulata (Figure 74), when grown submersed, has stems four times as long as those grown out of water (Zastrow 1934). This results from longer internodes (Lodge 1959). Lodge suggested that the elongation may result from the lower light levels, *i.e.* an **etiolation** (characterized by long, weak stems, smaller leaves, longer internodes, and pale yellow color) response, a response I have seen by terrestrial bryophytes in a terrarium.
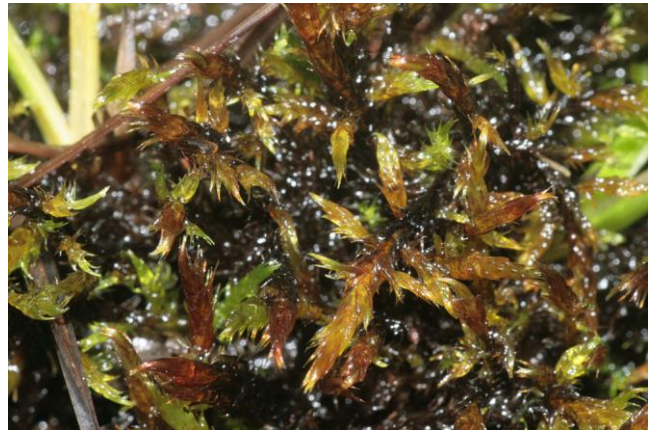

Figure 74. *Warnstorfia exannulata*, a species that can grow four times as long in the water. Photo by Hermann Schachner, through Creative Commons.

Falcations are typically lost in the water. This is clearly visible in *Warnstorfia exannulata* (Figure 74). It can be very falcate when it is emergent (Figure 75), but have completely straight leaves (Figure 76) when it grows submerged. Likewise, *Fontinalis novae-angliae* has straight leaves (Figure 77) in nature when it grows in water but when I grew it in an artificial stream where it was exposed to air, but constantly wet, it grew falcate leaves! (Figure 78). This is interesting because the mostly terrestrial genus *Dichelyma* in the same family typically has falcate leaves. The monotypic *Brachelyma* in that family is often inundated but has straight leaves, but they are keeled, like some species of *Fontinalis*.

Figure 75. *Warnstorfia exannulata* emergent, showing falcate leaves. Photo courtesy of Michael Lüth.

Figure 76. *Warnstorfia exannulata* submersed, showing straight leaves. Photo courtesy of Michael Lüth.

Figure 77. *Fontinalis novae-angliae* growing submersed, showing straight leaves. Photo by Matt Keevil, through Creative Commons.

Figure 78. *Fontinalis novae-angliae* growing in artificial stream where its leaves are exposed to air but constantly wet, showing the resulting falcate leaves. Photo by Janice Glime.

Even thallose liverworts have thallus plasticity. The best known of these examples is *Riccia fluitans*. In water, the thallus is composed of narrow, ribbon-like branches (Figure 79), whereas on soil the thallus is broader (Figure 80), more similar to other *Riccia* species.

Figure 79. *Riccia fluitans* aquatic form showing narrow thalli. Photo courtesy of Michael Lüth.

Figure 80. *Riccia fluitans* terrestrial form showing broader thallus. Photo courtesy of Michael Lüth.

Zastrow (1934) also found that *p*H affects height growth in aquatic and semi-aquatic species. ***Aulacomnium palustre*** (Figure 81), ***Bryum pseudotriquetrum*** (Figure 2-Figure 3), ***Fissidens adianthoides*** (Figure 82), and ***Fontinalis antipyretica*** (Figure 9-Figure 10), all grow taller when in alkaline water than when in neutral or acid water.

Figure 81. ***Aulacomnium palustre***, a species known to grow taller in alkaline water. Photo by Michael Lüth, with permission.
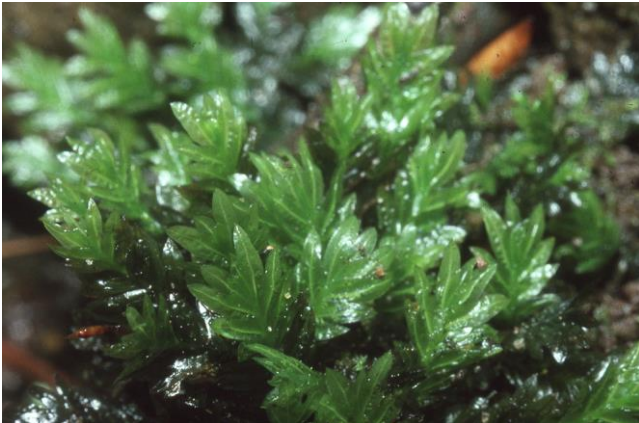

Figure 82. ***Fissidens adianthoides***, a species known to grow taller in alkaline water. Photo by Janice Glime.

Platyhypnidium riparioides (Figure 24), a species that frequently grows intermixed with ***Hygroamblystegium fluviatile*** (Figure 31), varies among populations (Wehr & Whitton 1986). In 105 sites in 71 streams and rivers, there was variation in size and robustness of the plants, dimensions and shape of leaves, degree of leaf denticulation, and relative length of the costa. The characters of less robustness, smaller leaves, and weaker denticulation correlated with the nutrient richness of the water.

Alterations of Terrestrial and Wetland Species in Water

Water culture can alter the anatomy and morphology of wet habitat species. For example, ***Aulacomnium palustre*** (Figure 81), ***Brachythecium rivulare*** (Figure 83),

Fissidens adianthoides (Figure 82), and ***Tomentypnum nitens*** (Figure 84) exhibit loss of central strand, loss of papillae, loss of border, reduction of costa, and loss of alar cells when grown submersed (Zastrow 1934). Furthermore, chlorophyll is often reduced, although that is more likely a response to reduced red light than it is an adaptation.

Figure 83. ***Brachythecium rivulare***, a species that loses its central strand in water. Photo by Snappy Goat, through public domain.

Figure 84. ***Tomentypnum nitens***, a species that exhibits character plasticity when submerged. Photo by Scot Loring, through Creative Commons.

It appears that even mosses that do not ever grow aquatically have the potential to change their morphology when grown submersed. Higuchi and Iwatsuki (1986) submersed two terrestrial mosses to discover what characters were plastic under these conditions. They found that ***Hypnum plumiforme*** (Figure 85) and ***Gollania japonica*** (Figure 86) produced smaller leaves that were scattered, *i.e.* longer internodes. The leaves had a more or less entire margin with thinner-walled lamina cells and less defined alar cells. The new shoots were more julaceous. Leaf shape and cell size showed little change.
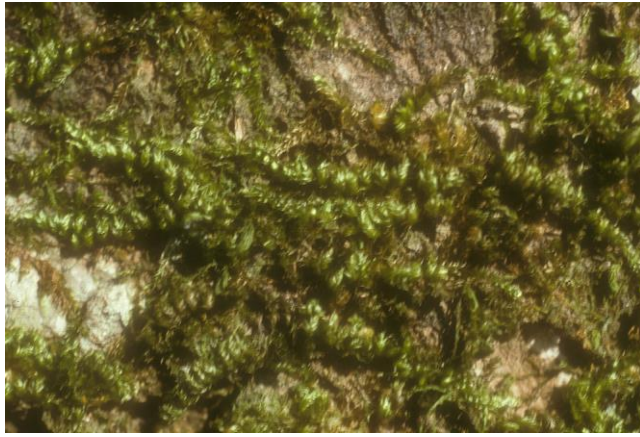
Figure 85. *Hypnum plumaeforme*, a terrestrial moss that produces smaller leaves with longer internodes if cultured under water. Photo by Janice Glime.

Figure 86. *Gollania japonica*, a terrestrial moss that produces smaller leaves with longer internodes if cultured under water. Photo from Taiwan Mosses, through Creative Commons.

Genetic Variation

In *Hygroamblystegium tenax* (Figure 87) the genetic variation within a species can be higher than that between this species and *H. fluviatile* (Figure 31) (Vanderpoorten & Tignon 2000). Such variability can explain the many forms found among some aquatic species, but it does not explain the variability expressed by one plant under different growing conditions.

Figure 87. *Hygroamblystegium tenax*, a species with high genetic variation. Photo by Štěpán Koval, with permission.

The Central American *Platyhypnidium pringlei* (Figure 88) is an aquatic montane species of Central Mexico and Guatemala (Wynns *et al*. 2009). But this species seems to be somewhat widespread, albeit uncommon. A morphologically different form occurs in sheltered coves of the Blue Ridge Mountains in SE USA. In both locations, the plants are sterile. A more robust form occurs in Arizona and California, USA, where all plants are females. In the Himalayas of India, the populations are fertile. Here there are several forms that intergrade, whereas those in North America appear to be geographically isolated. Genetically, this species seems to belong to *Oxyrrhynchium* (Figure 89). The aquatic species in that genus are characterized by their dark green color, frequent branching, loose leaf arrangement, short leaf laminal cells, and long costae, characters that seem to differ from those of *Platyhypnidium riparioides* (Figure 24).
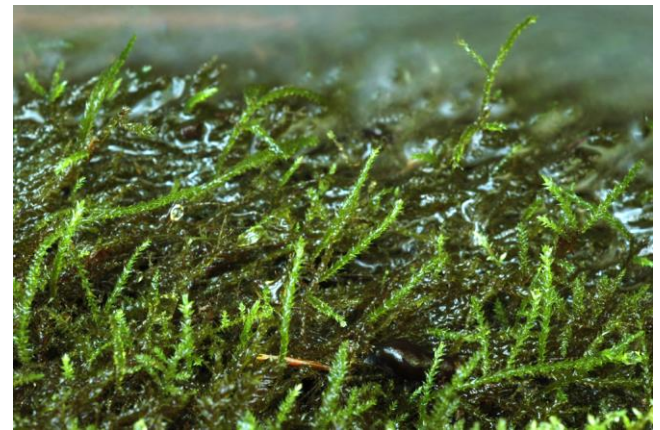

Figure 88. *Platyhypnidium pringlei*, a widespread species with many known forms. Photo by Ken McFarland and Paul Davison, with permission.

Figure 89. *Oxyrrhynchium hians*; genetically, *Platyhypnidium pringlei* seems to be in the genus *Oxyrrhynchium*. Photo by Hermann Schachner, through Creative Commons.

Zhu *et al*. (2007) found 67.2% of the *Brachythecium rivulare* (Figure 83) populations were polymorphic. Genetic variation reached 91.2% within populations, but only 8.8% among different populations. Genetic distance did not correlate with elevation gradient.

Mechanisms Facilitating Morphological Changes

Changes in light quality and intensity can account for such differences as stem elongation and greater internode differences. Rapid flow carrying siltation can cause abrasion, a possible selection pressure to cause genetic and morphological differences between pools and flowing water. But even with these physical factors as causes, there must be a physiological response. Few studies address these physiological responses and the biochemical differences that might facilitate them.

Ethylene may play a role in the morphological plasticity of *Fontinalis* (Glime & Rowher 1983). Ethylene is a stress hormone. In *Fontinalis squamosa* (Figure 21-Figure 22, Figure 27, Figure 33) and *F. antipyretica* (Figure 9-Figure 10) it causes color changes (Figure 90), leaf undulations (Figure 91), inhibition of rhizoid production, and crumpled branches and leaves (Figure 92). The stress of flow and contact with a substrate could alter the morphology by both affecting production of ethylene and by slowing its rate of dissipation. In these experiments, the two species responded somewhat differently. Changes in stem characters were not assessed.
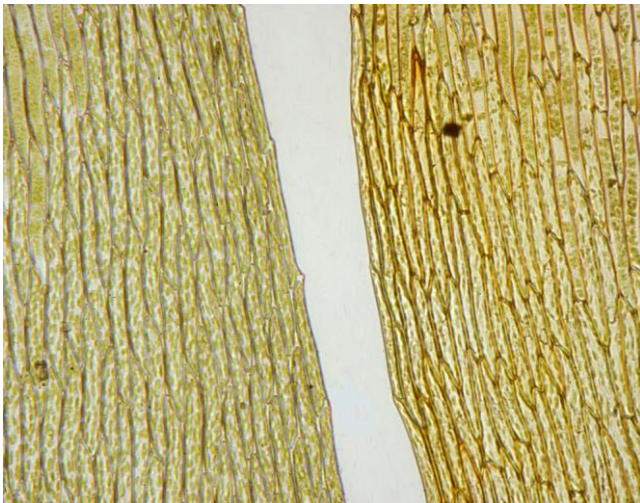

Figure 90. *Fontinalis antipyretica* leaf cells of control (**left**) and with ACC10^{-4} (**right**), showing color changes in presence of ACC, an ethylene precursor. Photo by Janice Glime.

Figure 91. *Fontinalis antipyretica* showing undulate leaf modifications due to ACC, an ethylene precursor. Photo by Janice Glime.
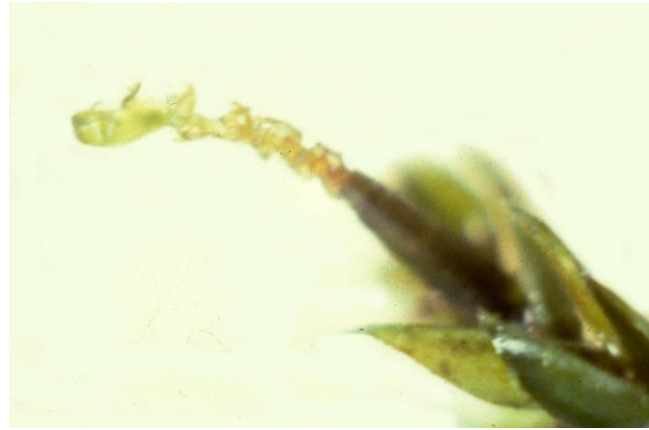

Figure 92. *Fontinalis squamosa* showing crumpled-leaf modifications due to ACC, an ethylene precursor. Photo by Janice Glime.

We also cannot ignore the potential role of **ABA** (hormone – abscisic acid) in the morphological differences within aquatic bryophyte species. Takezawa *et al*. (2011) noted the presence of ABA in all the living kingdoms and specifically demonstrated its role in drought tolerance in the terrestrial moss *Physcomitrella patens* (Figure 93). Wanke (2011) noted that ABA is a "key factor" in the expression of heterophylly in aquatic plants, making it possible for them to switch from submersed leaf forms to emergent ones. He surmised that such heterophylly is present in ferns and flowering plants, but that it is absent in aquatic bryophytes, citing studies by Hsu *et al*. (2001), Lin (2002), Villani and Etnier 2008), and Takezawa *et al*. (2011). But is this heterophylly really totally absent in bryophytes?

Figure 93. *Physcomitrella patens* with plant on right having 6 disrupted MADSbox genes (Koshimizu *et al*. 2018). The elongated internodes are similar to that seen if the species is grown in water and prevent the typical capillary movement of water upward. Photo by Koshimizu & Hasebe, with online permission.

Koshimizu *et al*. (2018) learned that the MADSbox genes regulate cell division and growth in the stems of *Physcomitrella patens* (Figure 93), thus controlling the appropriate internode distance for the water availability through external conduction. Could this control be important in the larger internode distance in aquatic

populations? Does water block these genes? How does the water interact with light intensity? Are the longer internodes adaptive in making the species more flexible?

Dimorphic Forms?

Welch (1948) reported that the leaves of *Fontinalis sphagnifolia* (Figure 94) exhibited dimorphism (Figure 95). Similarly, I have seen *Fontinalis duriaei* with both keeled leaves and rounded leaves on the same plant. Could it be that at different times they grew under different conditions? Are there other examples?
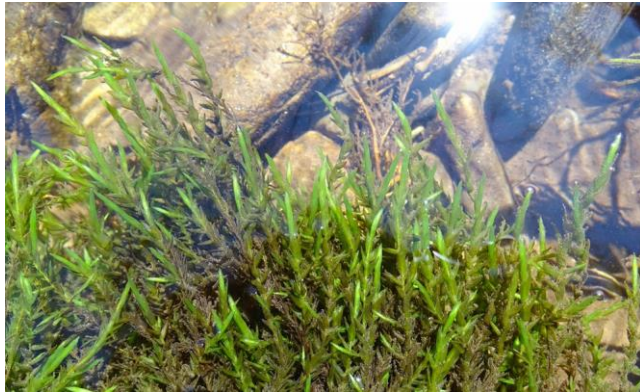

Figure 94. *Fontinalis sphagnifolia*, a species known for dimorphic leaves. Photo by Will Van Hemessen, through Creative Commons.
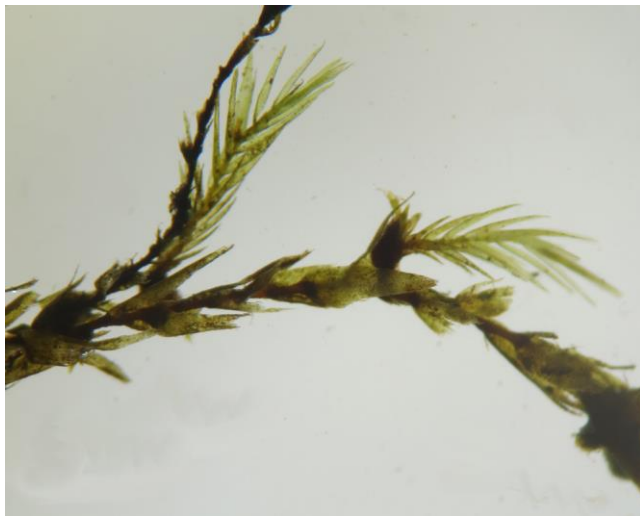

Figure 95. *Fontinalis sphagnifolia* leaf dimorphism between stem and branch leaves, Hudson Bay. Photo courtesy of Eric Snyder.

Among the liverworts, the semi-aquatic *Colura irrorata* (Figure 96) (= *Myriocolea irrorata*) from Ecuador has lobulate leaves on prostrate shoots and very different, elobulate leaves on erect (or pendent) shoots (pers. comm. S. Robbert Gradstein, 9 April 2020). These do not seem to relate to an aquatic environment, but perhaps to contact with a surface. Basile (1967, 1969) demonstrated that hydroxyproline could be responsible for controlling the size of underleaves in leafy liverworts, so it could play a role here. Differences in ethylene concentration might also provide an explanation.

Figure 96. *Colura calyptrifolia* on willow, showing lobules. Photo by Stan Phillips, through public domain.

Summary

Stream bryophytes tend to have more rhizoids than in other wetland types, and increased flow can cause that number to increase. The rhizoids of *Fontinalis* are negatively phototropic, thus growing toward the substrate. In *Fontinalis* and other species they produce an adhesive and branching at the rhizoid tips when they make contact.

In some groups, the standing water species are characterized by reductions, including of ventral scales or none, fewer hyaline cells, fewer strengthening fibers in the hyaline cells, and fewer and lower leaf lamellae, but those living in rapid streams display no such reduction. Submersed species can exhibit loss of central strand, loss of papillae, loss of leaf border, reduction of costa, and loss of alar cells.

Sporophytes are produced above water in many species, often taking advantage of low water levels. Submersed capsules are frequently characterized by being smooth and ovate-oblong, and having short setae, reduced peristome, and no stomata. Spores can be enlarged and may be multicellular.

Character plasticity is common, including stem elongation, modified leaf size and shape. Keels may disappear in alkaline water. Stems in fast water may thicken, plications and falcations disappear, branching angles may change. The thallus of thallose liverworts may be narrower in water, as in *Riccia fluitans*. Nutrients may also affect elongation and leaf size. Species with dimorphic leaf expressions on the same plant are rare.

Among the physiological responses, it is possible that ABA and ethylene may play a role in morphological differences. MADSbox genes may regulate cell elongation based on moisture conditions. Some species have more genetic variability than terrestrial species.

Acknowledgments

Many Bryonetters have contributed to these aquatic chapters, permitting me to expand my world view of the taxa. Jim Shevock alerted me to the story of **Hypnobartlettia**. Ida Bruggeman-Nannenga has been very helpful in sharing her experience with **Fissidens** and providing images and references and even taking photographs I needed.

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