

CHAPTER 1-1

AQUATIC AND WET

ANTHOCEROTOPHYTA

TABLE OF CONTENTS

Anthocerotaceae	1-1-2
<i>Anthoceros</i>	1-1-3
<i>Anthoceros agrestis</i>	1-1-3
<i>Anthoceros caucasicus</i>	1-1-4
<i>Anthoceros punctatus</i>	1-1-4
<i>Aspiromitus</i>	1-1-5
<i>Aspiromitus asper</i>	1-1-5
<i>Aspiromitus bulbosus</i>	1-1-5
<i>Aspiromitus lobatus</i>	1-1-5
<i>Aspiromitus squamulosus</i>	1-1-6
<i>Folioceros</i>	1-1-6
<i>Folioceros fuciformis</i>	1-1-6
<i>Folioceros glandulosus</i>	1-1-6
Dendrocerotaceae	1-1-6
<i>Megaceros</i>	1-1-6
<i>Megaceros flagellaris</i>	1-1-6
<i>Megaceros tjibodensis</i>	1-1-7
Phymatocerotaceae	1-1-7
<i>Phymatoceros</i>	1-1-7
<i>Phymatoceros bulbiculosus</i>	1-1-7
Notothyladaceae	1-1-8
<i>Phaeoceros</i>	1-1-8
<i>Phaeoceros carolinianus</i>	1-1-8
<i>Phaeoceros laevis</i>	1-1-9
Summary	1-1-10
Acknowledgments	1-1-10
Literature Cited	1-1-10

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Figure 1. *Phymatoceros bulbiculosus* with capsules, a species that can occur in European streams and rivers. Photo by Ken Kellman, through Creative Commons.

Nomenclature for this chapter is based primarily on Söderström *et al.* (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species. Listed synonyms are those I encountered in the aquatic literature and are not complete with all possible synonyms.

To develop this list, I used my own bibliography, collected over the past 56 years, and Google Scholar. These papers soon led me to others. I do not pretend that this is complete. It concentrates on streams, but includes lakes and other wetlands. It deliberately ignores bogs and mostly ignores fens, but nevertheless includes a few of these species because they were found in a wetland study. Bogs and poor fens have been treated in whole books and provide an extensive literature; fens seem somewhat less studied. They would require considerably more review and time. Thus I felt that less-reviewed topics, particularly the aquatic habitats with which I am most familiar, should be

given priority. Nevertheless, some of the citations took me into that literature.

Many of the species on this list are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study. Their relative frequency can be suggested based on the number of references cited.

The **Anthocerotophyta** (hornworts) is a small group when compared to the other two bryophyte phyla. Few of these occur in wet habitats, although some have been reported from mountain streams. Four of the five families have appeared among the studies cited herein.

Anthocerotaceae

Most systematic treatments include only *Anthoceros* and *Folioceros* in this family, but a number of studies use the name *Aspiromitus*, a genus that is considered a synonym of *Anthoceros* by Söderström *et al.* (2016), but some species have not been studied sufficiently to determine their affinities. These are listed here in *Aspiromitus* until their affinities are better understood.

Anthoceros (Figure 2, Figure 5, Figure 6, Figure 7)

The genus *Anthoceros* (Figure 2, Figure 5, Figure 6, Figure 7) occurs mostly on **arable** (suitable or used for growing crops) fields (Porley 2020). My own limited experience suggests that it is a non-competitor that benefits from the disturbance and reduction of "weeds" as competitors in such situations. It is perhaps these same factors that permit it to occasionally live in wet habitats.

***Anthoceros agrestis* (Figure 2)**

(syn. = *Anthoceros punctatus* var. *cavernosus*)

Distribution

Anthoceros agrestis (Figure 2) occurs primarily in the temperate zone in central Europe, ranging in northern and eastern Europe as well (Paton 1979), but is rather rare in the Mediterranean-Atlantic parts (www.iucnredlist.org). It grows in arable fields and gardens, or in ditches in open habitats or woodlands (www.iucnredlist.org).



Figure 2. *Anthoceros agrestis* with capsules in an area that becomes muddy. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

The only wetland/aquatic study that I found including this species reported it in mountainous streams on Madeira Island, Portugal (Luis *et al.* 2015). *Anthoceros agrestis* (Figure 2) is not uncommon, but difficult to find, because both the thallus and sporophytes are short-lived, and tend to occupy ephemeral habitats, such as the still-wet soils of receding rivers and lakes in the spring. In New Brunswick, Canada, it is found on wet soil and humus in boggy habitats (Haughian 2019). Kresáňová (2002) reported it from Slovakia, where it has been under-recorded. Paton (1979) considered it to have a more restricted distribution and ecology than that of *Anthoceros punctatus* (Figure 6-Figure 7).

Reproduction

Anthoceros agrestis (Figure 2) is **monoicous** (having male and female reproductive organs on same plant) (Paton (1979). The antheridia may number up to 45 in a chamber. Archegonia are embedded in the thallus and the egg is enclosed within that thallus. Szövényi *et al.* (2015) demonstrated its advantages as a model organism,

demonstrating that the plants grew faster when provided with continuous light than when given long-day photoperiods when the light was at or below $300 \mu\text{E m}^{-2} \text{s}^{-1}$. In the British Isles, it is a summer annual. Sporophytes (Figure 2) mature July to December. Colonies of *Nostoc* sp. (Figure 4) occur in mucilage cavities scattered in the ventral tissue.

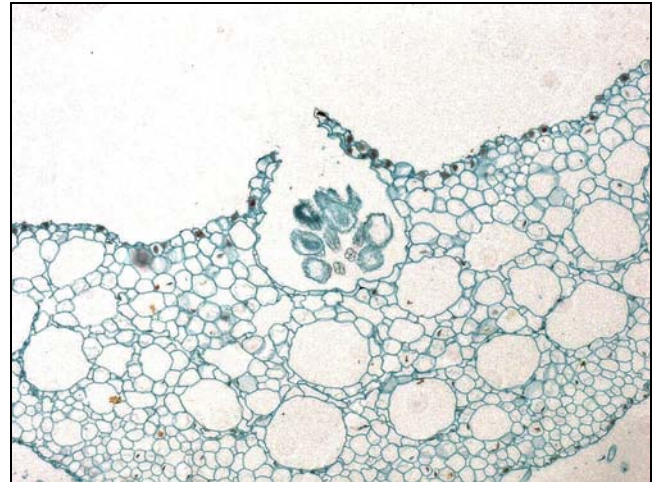


Figure 3. *Anthoceros* thallus cs showing large parenchyma cells and pore with *Nostoc*. Photo from Botany Website, UBC, with permission.

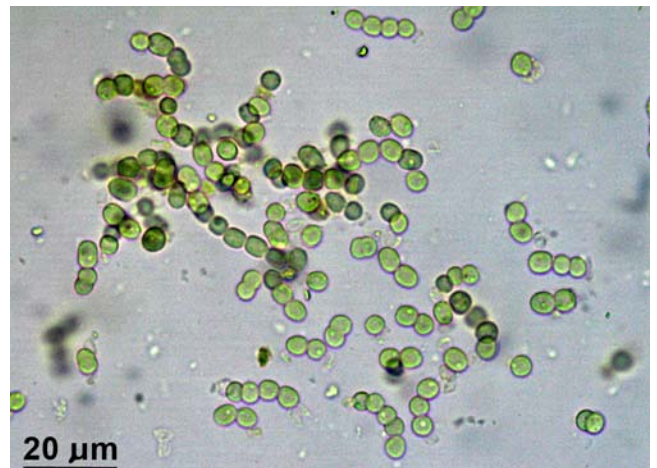


Figure 4. *Nostoc* from *Anthoceros agrestis*. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Biochemistry

Several biochemical studies have used this hornwort as a model organism. These have revealed alkaloids, a number of glutamic acids (Trennheuser *et al.* 1994), and cinnamic acid (accumulated as rosmarinic acid) (Peterson 2003). Soriano *et al.* (2018) considered that rosmarinic acid might aid in UV filtering, but none of the variables they measured seemed to respond significantly to the UV exposures used in the experiments. However, all of them had an increasing trend under the combination of PAR UV-A UV-B radiation.

***Anthoceros caucasicus* (Figure 5)**

Distribution

Anthoceros caucasicus (Figure 5) is European (GBIF 2019), occurring mostly in Macaronesia, with a few localities in the Azores, Portugal, Italy, southern Spain, and the Caucasus (During *et al.* 1996). The only wetland study in which I found this species is that of Luis *et al.* (2015) in mountainous streams on Madeira Island, Portugal. In a broader search on the species, I found that in 1994, it was discovered along a rivulet in The Netherlands (During *et al.* 1996).

Reproduction

It is **dioicous** (having separate male and female plants) in The Netherlands, but **monoicous** elsewhere (During *et al.* 1996). These plants in The Netherlands apparently originated from the large spores that were buried when the site was covered by sand 35 years earlier. The land was unfertilized at the time of discovery. Its general habitat includes rural mosaics with forest, hedges, pastures, and crops, as well as sublittoral sediment (GBIF (2019). In addition, GBIF (2019) reports it from sublittoral sediment, in addition to its presence in rural mosaic habits of woods, hedges, pastures, and cropland.



Figure 5. *Anthoceros caucasicus*, a stream that sometimes includes streams and rivulets among its habitats. Photo by Rosalina Gabriel, with permission.

***Anthoceros punctatus* (Figure 6-Figure 7)**

Distribution

Anthoceros punctatus (Figure 6-Figure 7) occurs in Europe, Asia, and North and South America (MBG 2020).

Aquatic and Wet Habitats

Anthoceros punctatus (Figure 6-Figure 7) presents near absence in wetland studies; like the previous species, only one of the wetland studies I have reviewed reports this species, likewise from mountainous streams on Madeira Island, Portugal (Luis *et al.* 2015). By contrast, Wagner (2011) reports that in Oregon, USA, it occurs mostly on recently disturbed soil in urban areas and is not common away from towns.



Figure 6. *Anthoceros punctatus* with sporophytes, in Madeira, Portugal. Photo by Michael Lüth, with permission.



Figure 7. *Anthoceros punctatus* with maturing sporophytes beginning to dehisce. Photo by Malcolm Storey, with online permission.

Role

A well-known symbiosis occurs between members of the **Anthocerotophyta** and **Cyanobacteria**. Campbell and Meeks (1989) found that all *Nostoc* (Figure 4) species that

were able to become symbionts in association with *Anthoceros punctatus* (Figure 6) formed **hormogonial filaments** (gliding filaments; Figure 8) in great frequency in its presence. The production of hormogonia was induced when *A. punctatus* grew in nitrogen-limited culture conditions. These symbiotic filaments lacked **heterocysts** (Figure 6), were mobile, and were comprised of "distinctly" smaller cells than those of "vegetative" filaments. These small cells were the result of continued cell division without biomass increase. During this time of rapid division, nitrogen fixation disappeared and CO₂ fixation decreased by 30%, accompanied by a 40% reduction in NH₄⁺ assimilation. These, however, returned to normal rates within 72 to 96 hours after hormogonia induction. Likewise, the hormogonia reverted to their vegetative growth state and differentiated heterocysts. One mutant was able to form chill-resistant akinetes.



Figure 8. *Nostoc punctiforme*, a *Cyanobacterium* that can be a symbiont in cells of *Anthoceros punctatus*. The colorless round cell at the lower left is a **heterocyst**. Photo from UTEX, through Creative Commons.

Wong and Meeks (2002) examined the ability of non-heterocystic strains of the *Cyanobacterium Nostoc punctiforme* (Figure 8) to form a symbiotic relationship with *Anthoceros punctatus*. With ammonium deprivation, vegetative cells of another *N. punctiforme* mutant randomly lysed, thus forming short filaments (**hormogonia**). These mutants were equally able to infect the hornwort compared to the wild type, but the association did not support the growth of the hornwort.

Fungal Interactions

The symbioses of this species are of interest regarding both its ecology and its evolution. When spores of the *Glomales* fungus *Claroideoglomus claroideum* (syn. = *Glomus claroideum*) (*Basidiomycota*; Figure 9) contact the thalli of *Anthoceros punctatus* (Figure 6-Figure 7), they develop hyphae that appear within the thallus as branched hyphae (Schüßler 2000). By 45 days in culture, these have formed arbuscules and vesicles. This is the first record of an identified Glomalean arbuscular mycorrhiza-like symbiosis with a bryophyte.

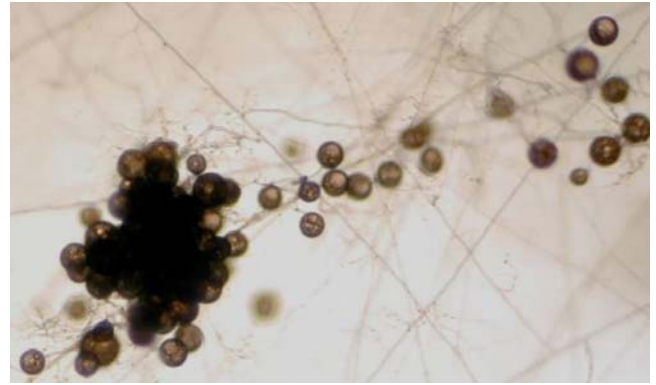


Figure 9. *Claroideoglomus claroideum*, an endophytic fungus that can occur within cells of *Anthoceros punctatus*. Photo by V. A. Silvani, M. Pérgola, and S. Fracchia, through Creative Commons.

Aspiromitus (Figure 10)

Most of the members of the genus *Aspiromitus* (Figure 10) have been included in the genus *Anthoceros* (Figure 2, Figure 5, Figure 6, Figure 7) (Söderström *et al.* 2016). The four listed here have not yet been transferred or synonymized and must therefore still be treated in the genus *Aspiromitus*. Their apparent limited distribution has left them as neglected taxa. All of them are reported in only one paper on wetlands, that by Ruttner (1955).

Aspiromitus asper

Aspiromitus asper can occur in wetland areas in the tropics (Ruttner 1955). It is reported from Java (Söderström *et al.* 2010). I have been unable to find additional information on its distribution or ecology.

Aspiromitus bullosus

Aspiromitus bullosus can occur in wetlands in the tropics (Ruttner 1955). It likewise has been reported from Java (Söderström *et al.* 2010)

Aspiromitus lobatus (Figure 10)

For *Aspiromitus lobatus* (Figure 10) Ruttner (1955) gave the most information, indicating that it occurs above water level, in water spray in the tropics. Söderström *et al.* (2010) reported the species from Java.



Figure 10. *Aspiromitus lobatus*, a species that can grow in waterfall spray in the tropics. Photo through Creative Commons.

Aspiromitus squamulosus

Ruttner (1955) indicated that *Aspiromitus squamulosus* occurs over water in the tropics. Information on this species is so scarce that I am unable to determine where it is known to occur.

***Folioceros* (Figure 11, Figure 12)**

Folioceros (Figure 11, Figure 12) is a tropical and subtropical genus in and near Asia, where it grows on moist rocks, in fallow fields, and near waterfalls (Wikipedia 2019).

***Folioceros fuciformis* (Figure 11)**

(syn. = *Aspiromitus falsinervius*)

Folioceros fuciformis (Figure 11) is often reported in checklists from various tropical locations and countries in Asia (TROPICOS 2020a), but its habitat is not included.



Figure 11. Wet *Folioceros fuciformis* with capsules, a species that lives in the zone above the water level in the tropics. Photo by Li Zhang, with permission.

Aquatic and Wet Habitats

The only wetland record I could find was that of Ruttner (1955), indicating that it occurs up to about 30 cm above water level in the tropics. The only labels in the online Consortium of North American Bryophyte Herbaria are from Hawaii, Micronesia (on steep clay and sand bank, associated with *Philonotis revoluta* and *Selaginella* sp.), Guam (abundant on moist clay bank), and India (in dense jungle beside a stream on a moist cliff and in wet soil of marshy area in jungle).

***Folioceros glandulosus* (Figure 12)**

(syn. = *Aspiromitus glandulosus*)

Folioceros glandulosus (Figure 12) is known from waterfalls in the Asian tropics (Ruttner 1955; TROPICOS 2020b). Like *Folioceros fuciformis* (Figure 11), little information seems to be published about it.



Figure 12. *Folioceros cf. glandulosus*, a species that occurs in waterfalls of the Asian tropics. Photo by Li Zhang, with permission.

Dendrocerotaceae

***Megaceros* (Figure 13)**

Of the nine species of *Megaceros* (Figure 13) listed by Söderström *et al.* (2016), only two occurred in the wetland studies I reviewed. Both are primarily tropical.

***Megaceros flagellaris* (Figure 13)**

(syn. = *Megaceros salakensis*)

Distribution

Megaceros flagellaris (Figure 13) is widely distributed in the Eastern Hemisphere, especially the tropics, including Angola, China, Japan, India, Sri Lanka, Thailand, Philippines, Borneo, Indonesia, Papua New Guinea, New Caledonia, Samoa, Society Islands, Tahiti, Hawaii, Vanuatu, Australia, New Zealand, and Tanzania (Chantanaorrapint 2014; Ruklani *et al.* 2016).



Figure 13. *Megaceros flagellaris* with sporophytes, a species of waterfalls and permanently wet habitats, among others. Photo by Scott Zona, through Creative Commons.

Aquatic and Wet Habitats

Ruttner (1955) reported *Megaceros flagellaris* (Figure 13) from waterfalls in the tropics. Cargill *et al.* (2013) considered its typical habitat to be shaded soil, over pebbles, rocks, and boulders, on fallen logs, and at the bases of tree ferns. It is usually in permanently wet habitats such as streambanks or in creeks and streams. In Thailand, Chantanaorrapint (2014) found it on wet rocks and tree logs in shady areas inside the forest. Ruklani *et al.* (2016) found this species on wet rocks and tree logs, in shady areas inside the forest of Sri Lanka.

Reproduction

The species is **monoicous** (Chantanaorrapint 2014). Desirò *et al.* (2013) did not find any colonization of this species by fungi, although some other **Anthocerotophyta** are known to serve as suitable substrates.

Megaceros tjibodensis

The only wetland or aquatic report for *Megaceros tjibodensis* is in the listing of Ruttner (1955) for the tropics. None of the online label publications by the Consortium of North American Bryophyte Herbaria includes habitat information except an occasional mention of forest. From these labels, we learn that the species occurs in montane forest in Micronesia and *Myristica* forest of the Caroline Islands. Other locations include Indonesia and Java.

Phymatocerotaceae

Phymatoceros (Figure 1, Figure 14-Figure 16)

Phymatoceros (Figure 1, Figure 14-Figure 16) is the only genus in this family (Söderström *et al.* 2016) and only one of its two species occurred in the aquatic/wetland studies reviewed here.

Phymatoceros bulbiculosus (Figure 1, Figure 14)

(syn. = *Phaeoceros bulbiculosus*)

Distribution

Proskauer (1957) reports *Phymatoceros bulbiculosus* (Figure 1, Figure 14) as widespread in the Mediterranean region of Europe and Africa, and it is also present in North and South America.

Aquatic and Wetland Habitats

Phymatoceros bulbiculosus (Figure 1, Figure 14) is the only member of this small family of two species (Söderström 2016) that seems to be reported from any wetland or aquatic habitat. Ferreira *et al.* (2008) reported it from rivers. Luis *et al.* (2015) found it in mountain streams on Madeira Island, Portugal.

Distribution and Wet Habitats

It occurs on shaded soils in slow-to-dry or summer-dry habitats (Doyle & Stotler 2006). These include hillsides, creek banks, road and trail banks, and margins of sloping meadows. Kresáňová (2002) reported the species as *agricolous* in Slovakia, but protected (red-listed), suggesting that it might be under-recorded.



Figure 14. *Phymatoceros bulbiculosus*, a species that can occur in rivers and mountain streams. Photo by David Wagner, with permission.

Reproduction

The species is **ephemeral** (short-lived), appearing in open sites during the rainy season and producing abundant tubers (Figure 15-Figure 16) (Stotler *et al.* 2005) that presumably permit its survival when in a dormant state resulting from insufficient water.

This perennial species is distinguished from the other species of *Phymatoceros* by the presence of stalked tubers on the ventral thallus surface (Figure 15-Figure 16) (Doyle & Stotler 2006). In some cases, the population consists entirely of only males or only females, persisting through these tubers.



Figure 15. *Phymatoceros bulbiculosus* showing numerous ventral tubers. Photo by Donna Pomeroy, through Creative Commons.



Figure 16. *Phymatoceros bulbiculosus* with young tubers. Photo by David Wagner, with permission.

Notothyladaceae

Phaeoceros (Figure 18-Figure 21)

This genus has 34 species recognized by Söderström *et al.* (2016). Of these, only two have been reported among the aquatic/wetland species reported here.

Ridgeway (1967a) described the *Nostoc* (Figure 17) relationship in the genus *Phaeoceros*. The *Nostoc* enters the thalloid cavities and produces typical globose **endophytic** (occurring within plant tissues) colonies. In this event, or when the *Nostoc* is cultured on a nitrogen-free substrate, but in intimate contact with the *Phaeoceros* thalli, **chlorosis** (abnormal reduction of green color in plant tissues) did not occur to the degree that it occurred in control cultures. Ridgeway considered this evidence that the *Nostoc* fixed nitrogen that was available to the hornworts. He also suggested that *Nostoc* might benefit if it could catabolize the carbohydrate components of the mucilaginous thalloid cavity.

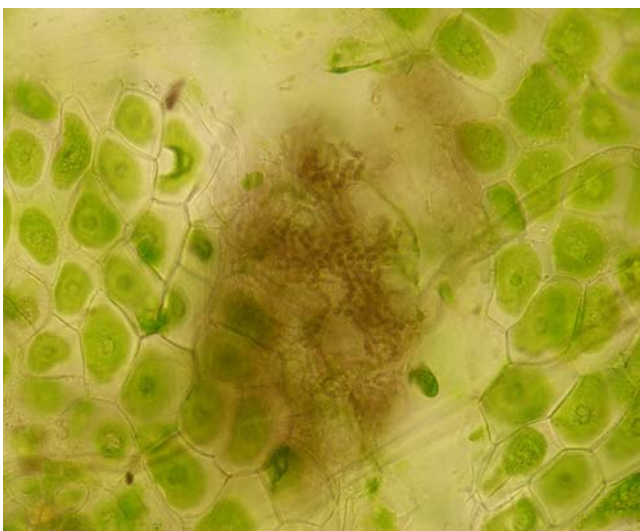


Figure 17. *Nostoc* (brown) in hornwort. Note the strings of round cells that form the hormogonia. Photo by Chris Lobban, with permission.

Phaeoceros carolinianus (Figure 18)

(syn. = *Anthoceros carolinianus*, *Anthoceros laevis* var. *carolinianus*, *Phaeoceros laevis* var. *carolinianus*)

Phaeoceros carolinianus (Figure 18) is a worldwide, ubiquitous species (Campbell & Outred 1995; Cargill & Fuhrer 2008). It was reported in only one wetland aquatic study included here; Ferreira *et al.* (2008) reported it from rivers. It is known in Australia from banks of waterways, as well as more terrestrial locations. This is the most common of the *Phaeoceros* species in New Zealand (Campbell & Outred 1995).



Figure 18. *Phaeoceros carolinianus* with capsules, a species for which wet habitats include rivers and stream banks. Photo by Hermann Schachner, through Creative Commons.

Reproduction

This is a **monoicous** species (Cargill & Fuhrer 2008). Penjor *et al.* (2016) reported that no tubers were present on this species at Coi Suthep, Chiang Mai, Thailand, despite their widespread occurrence among hornworts as a means of surviving unfavorable conditions. They suggested that the habitat might not be suitable for their formation. The **antheridia** (Figure 19) follow the typical pattern of green when young, turning yellow-orange at maturity. This color change results from the loss of green chlorophyll due to conversion of chloroplasts to chromoplasts in the antheridial cells. The genus is characterized by yellow spores with spines (Figure 20). In their study in Thailand, Penjor *et al.* (2016) found that the sporophyte tissue can continue spore production throughout the growing season.

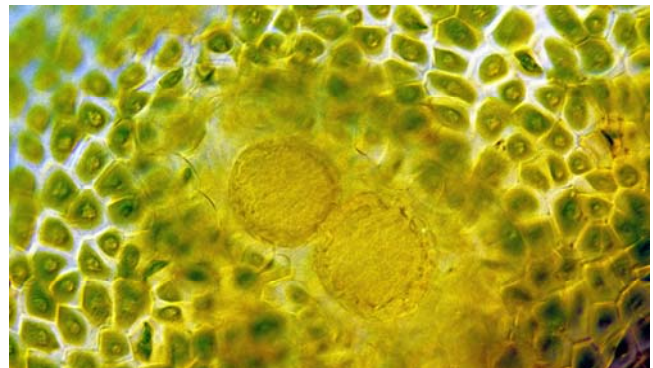


Figure 19. *Phaeoceros* antheridia in their yellow-orange mature stage. Photo by George Shepherd, through Creative Commons.

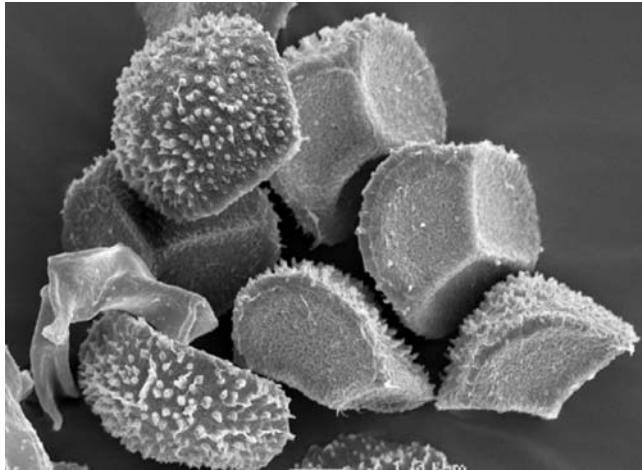


Figure 20. *Phaeoceros carolinianus* spores SEM. Photo by Christine Cargill, through Creative Commons.

Phaeoceros laevis (Figure 21)

Distribution

(syn. = *Anthoceros laevis*)

Phaeoceros laevis (Figure 21) is cosmopolitan, occurring in North America, South America, Europe, and Asia, but avoiding more northern locations above 60° N latitude (Schuster 1992). It has been reported from South Island, New Zealand, but the Southern Hemisphere records should be viewed with caution, as they are probably all misidentified *Phaeoceros carolinianus* (Figure 18) (Cargill & Fuhrer 2008).

Aquatic and Wet Habitats

Phaeoceros laevis (Figure 21) occurs on moist rock surfaces or springy banks of ravines in Connecticut, USA (Nichols 1916). Watson (1919) reported that it occurs on ground associated with fast water. In South Island, New Zealand, plants so-named are positively correlated with bankfull discharge in 48 streams (Suran & Duncan 1999). It survives in steep streams in the high rainfall area of South Island, New Zealand (Lepp 2012). For *Phaeoceros laevis* there was little or no difference in drag forces between bare rocks and hornwort-bearing rocks (Lepp 2012). *Phaeoceros laevis* can be found in rivers (Ferreira *et al.* 2008); and occurs in mountainous streams in Madeira Island, Portugal (Luis *et al.* 2015).



Figure 21. *Phaeoceros laevis* with sporophytes, a Northern Hemisphere hornwort that occurs in rivers, streams, and on wet soil. Photo by David Holyoak, with permission.

This species is common in areas that have abundant moisture, including moist soil in fields, sides of ditches and streams, and is sometimes even submerged (Isaac 1941).

Reproduction

One of the earliest reports of *Phaeoceros laevis* (Figure 21) is that it can be **aposporous** (producing $2n$ gametophytes from sporophyte tissue with no meiosis) (Lang 1901). It is dioicous (Cargill & Fuhrer 2008) and behaves as a short-day plant for antheridial initiation, but requires no critical temperature for initiation (Ridgeway 1967b). It grows well and forms gametangia at both 10°C and 21°C under **short-day** (occurring only after being exposed to light periods shorter than a critical length, as in early spring or fall) conditions, whereas liverworts and mosses in the same experiment were more specific in their requirements (Benson-Evans 1964).

Fungal Interactions

In addition to *Nostoc* (Figure 17) symbionts, Ligrone (1988) identified an aseptate fungus living as an endophyte in *Phaeoceros laevis* (Figure 21). This fungus forms **extracellular** (on outside of cell) thick-walled hyphae, **intercellular** (between cells) thin-walled hyphae, and **intracellular** (within cells) **arbuscules** (treelike growth of filaments in certain mycorrhizal fungi). **Vesicles** (swollen end cells, thought to be storage organs for food reserves in fungi) can be formed by either inter or intracellular hyphae that swell. These are common in summer. The fungus colonizes the host parenchyma, but is absent at the growing apices and epidermal cells. The infected cells of the hornwort increase their cytoplasmic contents while the chloroplast loses starch and its **pyrenoid** (protein body in chloroplasts of algae and hornworts, involved in carbon fixation and starch formation and storage). The arbuscule forms numerous convoluted branches intermingled with the **arbuscular hyphae** (Figure 22-Figure 23). Eventually the arbuscule degenerates, leaving intracellular clumps of collapsed hyphae. These hornwort cells can become re-infected. Ligrone and Lopes (1989) reported that in some strains of this hornwort **sessile** (unstaked) or shortly stalked tubers can form near the growing points or on the ventral surface.

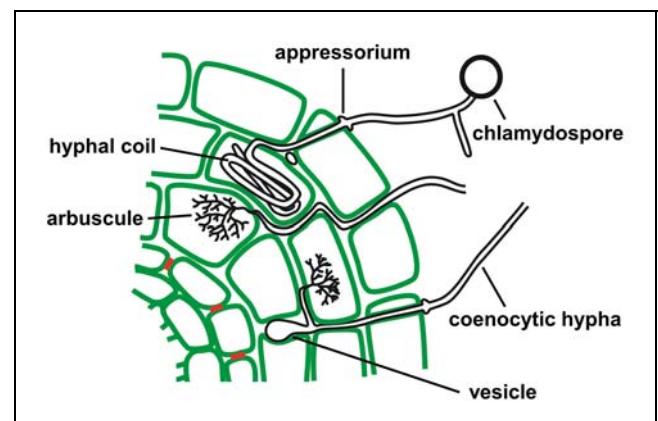


Figure 22. Diagram of arbuscular mycorrhiza, **Glomeromycota**, in a root. Diagram by M. Piepenbring, through Creative Commons.

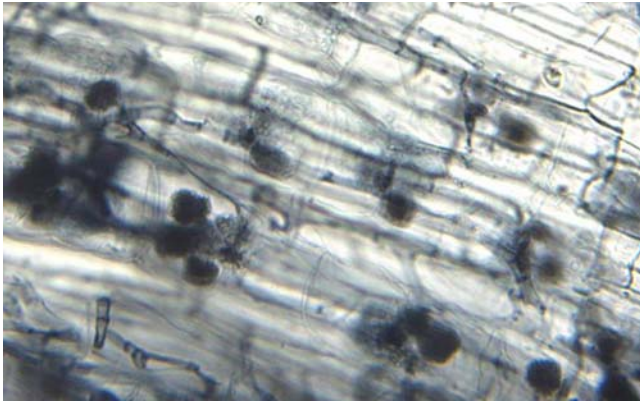


Figure 23. Arbuscular mycorrhizae in root cells. Photo by M. S. Turmel, through public domain.

Summary

Four families of hornworts have members that are associated with aquatic or wetland habitats. These representatives are rarely submersed. Some have Cyanobacteria partners that aid by producing usable nitrogen through nitrogen fixation. Others have associated fungi, but their role requires further investigation.

Anthoceros agrestis, *Anthoceros caucasicus*, *Anthoceros punctatus*, *Megaceros flagellaris*, *Phymatoceros bulbiculosus*, and *Phaeoceros laevis* occur in streams, especially mountain streams.

Acknowledgments

I appreciate Lars Söderström, who helped me find the current acceptable names for a number of older taxa. Thank you to all those who have put their images in Creative Commons or given me permission to use them. Llo Stark has contributed by noting minor errors in the chapter.

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CHAPTER 1-2

AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: CEPHALOZIINEAE 1

TABLE OF CONTENTS

Adelanthaceae.....	1-2-3
<i>Cuspidatula flexicaulis</i>	1-2-3
<i>Syzygiella sonderi</i>	1-2-3
Anastrophyllaceae.....	1-2-4
<i>Anastrophyllum assimile</i>	1-2-4
<i>Anastrophyllum michauxii</i>	1-2-5
<i>Barbilophozia barbata</i>	1-2-5
<i>Barbilophozia sudetica</i>	1-2-6
<i>Gymnocolea inflata</i>	1-2-7
<i>Isopaches bichenatus</i>	1-2-9
<i>Rivulariella gemmipara</i>	1-2-9
<i>Schljakovia kunzeana</i>	1-2-11
<i>Sphenobolus minutus</i>	1-2-12
<i>Tetralophozia filiformis</i>	1-2-14
Cephaloziaceae	1-2-14
<i>Cephalozia</i>	1-2-14
<i>Cephalozia ambigua</i>	1-2-14
<i>Cephalozia bicuspidata</i>	1-2-16
<i>Fuscocephaloziopsis albescens</i>	1-2-20
<i>Fuscocephaloziopsis connivens</i>	1-2-21
<i>Fuscocephaloziopsis lunulifolia</i>	1-2-22
<i>Odontoschisma elongatum</i>	1-2-24
<i>Odontoschisma fluitans</i>	1-2-25
<i>Odontoschisma sphagni</i>	1-2-26
Cephaloziellaceae	1-2-27
<i>Cephaloziella</i>	1-2-27
<i>Cephaloziella hampeana</i>	1-2-27
<i>Cephaloziella rubella</i>	1-2-28
<i>Kymatocalyx</i>	1-2-29
<i>Kymatocalyx africanus</i>	1-2-29
<i>Kymatocalyx cubensis</i>	1-2-29
<i>Kymatocalyx dominicensis</i>	1-2-29
<i>Kymatocalyx madagascariensis</i>	1-2-30
<i>Kymatocalyx rhizomatica</i>	1-2-30
Lophoziaceae	1-2-31
<i>Lophozia</i>	1-2-31
<i>Lophozia ventricosa</i>	1-2-31
<i>Lophozia wenzelii</i>	1-2-33
<i>Lophoziopsis excisa</i>	1-2-34
<i>Trilophozia quinqueidentata</i>	1-2-35
<i>Tritomaria exsecta</i>	1-2-36
<i>Tritomaria exsectiformis</i>	1-2-37
Summary.....	1-2-39
Acknowledgments	1-2-39
Literature Cited	1-2-39

CHAPTER 1-2

AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER JUNGERMANNIALES: CEPHALOZIINEAE 1



Figure 1. Alpine tundra lake, late snowbeds, and small streams where some members of the **Cephaloziineae** may take advantage of the longer availability of moisture. Photo courtesy of Bob Janke.

Nomenclature for the liverwort subchapters is based on Söderström *et al.* (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species.

As in the subchapter on **Anthocerotophyta**, I used my own bibliography, collected over the past 56 years, and Google Scholar. These papers soon led me to others. I searched in Google Scholar for additional information on the species in that constructed list. I do not pretend that this is complete. It concentrates on streams, but includes lakes and other wetlands. It deliberately ignores bogs and mostly ignores fens, but nevertheless includes a few of these species because they were found in one or more other wetland studies. Bogs and poor fens have been treated in

whole books and provide an extensive literature; fens seem somewhat less studied. They would require considerably more review and time. Thus I felt that less-reviewed topics, particularly the stream habitats with which I am most familiar, should be given priority.

I have thus far found no records of **Haplomitriopsida** in these studies. Hence I have not included that class in this chapter. Söderström *et al.* (2016) list 5 suborders in the order **Jungermanniales** of the **Jungermanniopsida**. This subchapter includes the suborder **Cephaloziineae**. In that suborder, most of the species outside the **Scapaniaceae** are only marginally associated with water. Although many of the species in the **Cephaloziineae** are not typical wetland or aquatic species, those included here were, nevertheless, found in a wetland or aquatic study. Their relative frequency can be noted based on the number of references cited.

The human propensity for trying to pigeon-hole members of a continuum is no more obvious anywhere than it is among "aquatic" bryophytes. Not only do they not pigeon-hole into neat habitat categories, the species tend to have wide physiological and at least some morphological variance, causing them to be named as multiple species when they are in fact environmental variations of one species. I have included the synonyms that I found in the aquatic literature, but many additional ones often exist.

Adelanthaceae

Only two members of this family appeared in my search for wetland and aquatic studies. These both occur in tropical regions where few studies are available regarding their ecology.

Cuspidatula flexicaulis (see Figure 3)

(syn. = *Jamesoniella balansae*, *Jamesoniella flexicaulis*, *Jamesoniella affinis* fo. *minor*)

Distribution and Wet Habitats

Cuspidatula flexicaulis (see Figure 2-Figure 3) is distributed in Malaysia, Indonesia, Papua New Guinea, and New Caledonia (GBIF 2020a). Ruttner (1955) listed it among the wetland and aquatic species in the tropics. In New Zealand it is an abundant species in subalpine forests (Scott 1970).



Figure 2. *Cuspidatula monodon*; *Cuspidatula flexicaulis* is a species that sometimes occurs in wetlands. Photo by David Tng, with permission



Figure 3. *Cuspidatula monodon*; *Cuspidatula flexicaulis* is a species that sometimes occurs in wetlands. Photo by David Tng, with permission.

Syzygiella sonderi (Figure 4)

(syn. = *Cryptochila grandiflora*)

Distribution

Syzygiella sonderi (Figure 4) is a widespread species, occurring in the Southern Hemisphere, including high elevations in the Neotropics (southeastern Brazil, tropical Andes, and Central America) (Gradstein & da Costa 2016). In the Eastern hemisphere it occurs on Réunion Island in the Mascarenes and in New Guinea and Borneo (Vána *et al.* 2014).



Figure 4. *Syzygiella sonderi*, a Southern Hemisphere species that benefits from high water levels of mountain streams. Photo by Juan Larrain, through Creative Commons.

Aquatic and Wet Habitats

In the Andes, Gradstein *et al.* (2018) listed *Syzygiella sonderi* (Figure 4) as a submerged liverwort from higher elevation lakes. In the northern maritime Antarctic it occurs on heated ground on volcanic islands. It is positively correlated with bankfull discharge in 48 streams on South Island, New Zealand (Suren & Duncan 1999); Lepp (2012) found it associated with steep streams in high rainfall areas on South Island. Nevertheless, on sub-Antarctic Marion Island this species occurs in **feldmark** (plant community characteristic of sites where plant growth is severely restricted by extremes of cold and exposure to wind, typical of alpine tundra and sub-Antarctic environments) in dry situations, typically associated with other bryophytes. In the Antarctic region, *Syzygiella sonderi* occurs on volcanic ash and debris, on rock ledges, and on gravel in protected moist areas (Bednarek-Ochyra *et al.* 2000).

On Marion and Prince Edward Islands, the mire drainage line peats are less acidic, and with higher Ca and Mg concentrations than peats of other mire habitats (Chown & Froneman 2008). On the more mineral soils, *Syzygiella sonderi* (Figure 4) is restricted to mire drainage lines, where it is one of the dominant species.

Adaptations

Syzygiella sonderi (Figure 4) has a moderate or low optimum for photosynthetically active radiation (PAR) and low photoinhibition, while also having high photoprotective capability when desiccated, characteristics that are beneficial at high elevations (Tonkie 2016). Nevertheless, it has only moderate photosynthetic capacity with low effective quantum yield and relatively low photoprotective capability. This species achieves its moderate photosynthetic rate at a moderate optimal PAR and has low to moderate response to light at low levels. Photochemistry ceases at moderate to very high **relative water content** [RWC; $RWC = ((\text{fresh mass-dry mass})/(\text{saturated mass-dry mass})) \times 100$]. Nevertheless, it has high ability to recover its photochemistry upon rehydration.

Anastrophyllaceae

Anastrophyllum assimile (Figure 5)

Distribution

Anastrophyllum assimile (Figure 5) is widespread in Asia, Europe, and North America, and extends to Malesia. Known locations include Austria, Switzerland, Italy, Norway, Alaska, Yukon, British Columbia, Labrador, Greenland, Japan, Korea, Borneo, and Papua New Guinea (Schill & Long 2003). It is an alpine species, extending down into the montane *Abies-Rhododendron* forests. In the Upper Bureya River (Russian Far East), where it is rare, it occurs on wet cliffs (Konstantinova *et al.* 2002). In Arctic and alpine areas of North America, this species is associated with **siliceous** (containing or consisting of silica) substrates (Horton 1977).

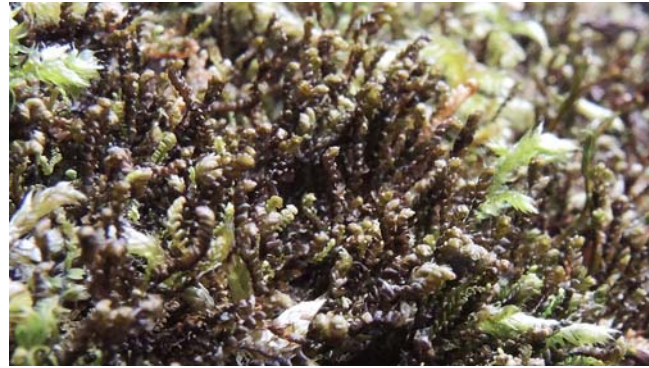


Figure 5. *Anastrophyllum assimile*, a Northern Hemisphere species that can occur on wet cliffs and submergence areas around lakes and other wet areas. Photo by Kristian Hassel, through Creative Commons.

Aquatic and Wet Habitats

Anastrophyllum assimile (Figure 5) occurs in wet cliff crevices along the shoreline of Takakia Lake, Queen Charlotte Islands, British Columbia, Canada (Hong 2007). It is among the numerous rare species that are vulnerable to changes in lake water level, including also the rare and unusual *Takakia lepidozoides* (Figure 6).

In higher altitudes in China and the Himalayas In higher altitudes in China and the Himalayas *Anastrophyllum assimile* (Figure 5) occurs on both soil and rocks, including both acidic and calcareous rocks, on open rocky slopes below cliffs, in block screes and boulder fields, on cliffs, on mossy banks, and in wetter habitats including boulders by streams and wet rocks by waterfalls (Schill & Long 2003). In the forest it is usually mixed with other bryophytes and does not grow as an epiphyte. Schill and Long considered it to be tolerant of wetter substrates at high altitudes.

Adaptations

Schofield (1985) describes this species as one that can be quite large, growing in **tall turfs** of more or less erect shoots. These occur predominantly in open sites, forming **mats** of creeping shoots and firmly attached by rhizoids. Mägdefrau (1982) notes that these life forms have good capillary action that permits them to hold "considerable" amounts of water.



Figure 6. *Takakia lepidozoides* in wet habitat, a species that occurs in habitats similar to those of *Anastrophyllum assimile* along the shoreline of Takakia Lake on the Queen Charlotte Islands. Photo from Botany Website, UBC, with permission.

The leaf color is variable when the liverwort is moist, but when it is dry it is very dark brown, purplish brown, or blackish (Figure 5) (Schill & Long 2003). Herzog (1926) observed that liverworts with dark coloration usually occur in open habitats at higher altitudes where the light is very intense. The dark color is able to protect against these high light levels. In colder seasons, the dark pigments absorb more heat, maintaining a higher temperature in the mat. Capsules are unknown.

***Anastrophyllum michauxii* (Figure 7)**

(syn. = *Sphenobolus michauxii*)

Distribution

Anastrophyllum michauxii (Figure 7) is widely distributed in the Holarctic region (Vána 1996). It is a montane species that occurs in Europe (Austria, Bulgaria, France, the Czech Republic and Slovakia, Germany, Hungary, the former Yugoslavia, Italy, Romania, Poland, Finland, Sweden, Norway), in Asia (China, Japan), and in a few sites in North America (Dulin & Philippov 2012).



Figure 7. *Anastrophyllum michauxii*, a Holarctic species that prefers rotten logs, especially near streams and other wet areas. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

On the Soyda River bank in the Russian Federation, Dulin and Philippov (2012) found *Anastrophyllum michauxii* (Figure 7) in the fern and herb spruce forest on a rotten spruce log. Choi *et al.* (2012) reported it as occurring near streams on Mt. Jiri-san in Korea. Nichols (1918) found it on wet rock cliffs on Cape Breton Island, Canada. Despite its occasional associations with water, the species seems most commonly to appear on rotten wood (Schuster & Patterson 1957; Dulin & Philippov 2012; Sofronova 2014).

***Barbilophozia barbata* (Figure 8)**

Distribution

Barbilophozia barbata (Figure 8) is widespread in the Northern Hemisphere, especially in the boreal and mountain regions (Düll 2004; Wagner 2009).

Aquatic and Wet Habitats

Wagner described it as a species of terrestrial peaty substrates over rock where it usually occurs with other mosses and liverworts. In the West Carpathians, Mameczarz (1970) found it in rock communities associated with streams near Lacko. Papp *et al.* (2006) reported it

from the Iskur River, Bulgaria, and its main tributaries. Düll (2004) reported it from siliceous rocks in Sicily and Erzberger (2002) from Hungary. Cain and Fulford (1948) found it to be common on moist igneous rock cliffs and boulders in Ontario, Canada, where it was often associated with other species of moist habitats, including *Scapania nemorea* (Figure 9), *Lepidozia reptans* (Figure 9), and *Ptilidium ciliare* (Figure 10).



Figure 8. *Barbilophozia barbata*, a widespread Northern Hemisphere leafy liverwort from boreal and mountain regions, mostly in terrestrial habitats, but sometimes associated with streams. Photo by Hermann Schachner, through Creative Commons.

But it can also be found in wetter habitats. Lee (1944) reported it from a collection near a "little pool" in the low, partially grass-covered, tundra-like valleys of Greenland. Yamada and Iwatsuki (2006) reported it from fine-grained soil along a stream on the western slope of Chamga Mt. in Sakhalin Province, Japan, at 1406 m asl. In mountainous regions and the tundra, *Barbilophozia barbata* (Figure 8, Figure 11-Figure 12) can have an important role in ground cover **coenosis** (community of living beings belonging to different species and associated by way of inter-species interdependence or mutualism such as a food chain) (Troeva *et al.* 2010).



Figure 9. *Lepidozia reptans* (small, pinnate liverwort) and *Scapania nemorea* (several larger leafy branches in lower left quadrant), species that may accompany *Barbilophozia barbata*. Photo by Bernd Haynold, through Creative Commons.



Figure 10. *Ptilidium ciliare*, a species that may accompany *Barbilophozia barbata* on moist igneous cliffs. Photo by Hermann Schachner, through Creative Commons.



Figure 11. *Barbilophozia barbata* in a patch on a boulder (see arrow). Photo by Sture Hermansson, with online permission.

Reproduction

In their study of propagule banks in boreal old-growth spruce forest in SE Norway, Rydgren and Hestmark (1997) found it among the living vegetation and as propagules in the soil. However, they only achieved ~5% germination from the soil bank propagules. On the other hand, Ross-Davis and Frego (2004) found that the similarity between aerial propagules and the extant flora of bryophytes in New Brunswick, Canada, was greater than the similarity of the buried propagules with the extant flora.



Figure 12. *Barbilophozia barbata* ventral side showing rhizoids that help it adhere to rocks. Photo by Hermann Schachner, through Creative Commons.

Biochemistry

There have been a number of biochemical studies on this genus, particularly indicating sesquiterpenes (Anderson *et al.* 1973; König *et al.* 1994; Nagashima *et al.* 1996, 1999; Asakawa 2001). Despite these sesquiterpenes and other substances that can serve as antibiotics, Bidartondo and Duckett (2010) reported the presence of the **Basidiomycota** fungus *Sebacina* (Figure 13) in association with *Barbilophozia barbata* (Figure 8, Figure 11-Figure 12) collected from Switzerland and the UK.



Figure 13. *Sebacina incrustans* on moss, a genus known to occur in association with *Barbilophozia barbata*. Photo through Creative Commons.

Barbilophozia sudetica (Figure 14-Figure 15)

(syn. = *Lophozia sudetica*)



Figure 14. *Barbilophozia sudetica*, an arctomontane species sometimes found on wet cliffs and stream banks. Photo by Hugues Tinguay, with permission.

Distribution

Barbilophozia sudetica (Figure 14-Figure 15). *Barbilophozia sudetica* is an **arctomontane** (occurring in Arctic habitats and mountain habitats farther south) species that is common in the northern Holarctic, but distribution extends to mountain ranges in East Asia, Spain, and Portugal and even to subtropical islands in Madeira at 32°N (Bakalín 2004). In North America, Rahill (2018) found it among the tundra vegetation on Mount Washington, NH, USA.



Figure 15. *Barbilophozia sudetica* showing a color variant. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Konstantinova *et al.* (2002) found this species on a wet cliff and soil banks of a small creek of the Upper Bureya River in the Russian Far East. In Iceland, this species occurs on lava fields where the temperature does not exceed 39°C (Buda *et al.* 2018). In the Aleutian Islands, Alaska, USA, the species is common, forming dark strands overgrowing the tundra *Sphagnum* (like Figure 78) and *Sphagnum* at the edge of a pond (Talbot *et al.* 2018). It also occurs on the bank of a streamlet, on the slope of a late snow area, on an outcrop face with *Pohlia* (Figure 16), in an alpine fellfield, on a old pier, and on damp humus on a cliff shelf.



Figure 16. *Pohlia wahlenbergii* with water beads, in a habitat suitable for *Barbilophozia sudetica*. Photo by Michael Lüth, with permission.

Fungal Interactions

Like *Barbilophozia barbata* (Figure 8, Figure 11-Figure 12), *B. sudetica* (Figure 14-Figure 15) is known to form symbiotic mycorrhizal fungal associations (Wang & Qiu 2006) with the **Sebacinaceae** (Figure 13) (Kottke *et al.* 2003).

Gymnocolea inflata (Figure 17-Figure 18, Figure 20, Figure 22)

Distribution

Gymnocolea inflata (Figure 17-Figure 18, Figure 20, Figure 22) is distributed in Africa, Europe, northern and southern Asia, and North America (Alaska, Canada, USA) (ITIS 2020a).

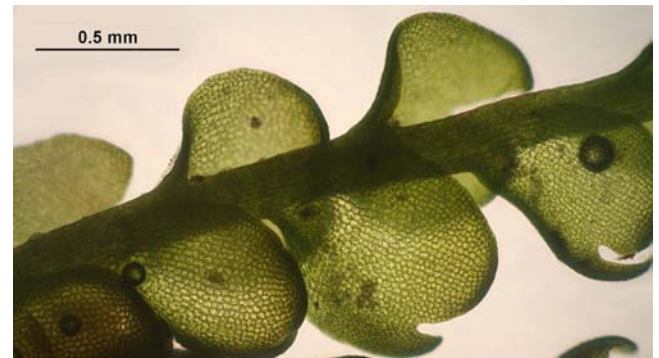


Figure 17. *Gymnocolea inflata*, a species with widespread distribution that can occur in or out of water. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Gymnocolea inflata (Figure 17-Figure 18, Figure 20, Figure 22) is a **hydroamphibiont** (living in transition zone between water and land, depending on water level; compare to euhydrobiont and geoamphibiont) (Figure 18), occurring in acid water (pH 3.5-4.2) in streams of Gory Stolowe Mountains, Poland (Szwejkowski 1951). In Europe it often occurs with *Carex goodenoughii*, but is uncommon with *Eleocharis quinqueflora* (Figure 76) and *Paludella squarrosa* (Figure 19) (Geissler & Selldorf 1986). In streams of the Harz Mountains of Germany it occurs in the upstream reaches (Bley 1987). It also occurs in small lakes in southern Finland (Toivonen & Huttunen 1995).



Figure 18. *Gymnocolea inflata* growing in a wet habitat. Photo by Michael Lüth, with permission.



Figure 19. *Paludella squarrosa* habitat where *Gymnocolea inflata* avoids cohabiting with *Paludella squarrosa* and *Eleocharis quinqueflora*. Photo by J. C. Schou, through Creative Commons.

In the Azores of Portugal, *Gymnocolea inflata* (Figure 20) occurs at 860-990 m asl (Schumacker & Gabriel 2002). Its habitat is permanently wet **pseudogley** (gley resulting from temporary or seasonal waterlogging due to poor drainage, rather than from permanent existence of high water table) soil overlain by a thin layer of **moor** (poor soil covered mainly with grass and heather; common in high latitudes and altitudes). The species is relatively common in wet heaths and bogs in Europe. Tyler *et al.* (1973) reported it from the *Rhynchospora fusca* (Figure 21) community where it covered the bottom of shallow depressions in heathland between bars.



Figure 20. *Gymnocolea inflata* showing one of its dark color forms. Photo by Michael Lüth, with permission.

Watson (1919) reported *Gymnocolea inflata* (Figure 17-Figure 18, Figure 20, Figure 22) as form *laxa* on peaty

sides of fast water streams, on banks with frequent submergence, and submerged in slow water with poor mineral salts.



Figure 21. *Rhynchospora fusca*, a community that often has *Gymnocolea inflata* in heathland low areas. Photo by Peter M. Dziuk, with online permission for educational use.

In Westfalens, northwestern Germany, *Gymnocolea inflata* (Figure 17-Figure 18, Figure 20, Figure 22) occurs between *Sphagnum* (Figure 22) (Koppe 1945). Tori *et al.* (1993) sampled peat profiles and found *Gymnocolea inflata* as part of the liverwort dominance with sparse *Sphagnum* cover. In the bare peat layer, only a few sedges occurred – no notable bryophytes. In Cataracts Provincial Park, Newfoundland, Canada, Weber (1976) found *Gymnocolea inflata* as a typical bog bryophyte, occupying open areas with a pH 3-4. Albinsson (1997) found that *Gymnocolea inflata* is among the liverworts that have narrow ecological amplitudes in mire habitats. Other smaller species tend to have wider amplitudes. Albinsson referred to those liverworts that required a habitat formed by other living bryophytes as using a **compromise strategy**. Those liverworts that prefer peat or litter as their substrate are included in the **avoidance strategy**. Albinsson found that those species that occur predominantly with *Sphagnum* (Figure 22) include those that are typically sterile, *i.e.*, not forming sexual reproductive structures. Frequently fertile species (*e.g.*, *Cephalozia* spp.; Figure 45-Figure 60) tend to occur on peat or litter, rather than on living *Sphagnum*.



Figure 22. *Gymnocolea inflata* in Perrault Fen, Houghton Co., MI, USA, with *Sphagnum*. Photo by Janice Glime.

Gough *et al.* (2006) found that *Gymnocolea inflata* (Figure 17-Figure 18, Figure 20, Figure 22) colonized and covered **ferricrete**-cemented (hard, erosion-resistant layer of sedimentary rock, usually conglomerate or breccia, cemented together by iron oxides) silty alluvial sediments within seeps and streams in undisturbed, highly acidic, metal-rich habitats in east-central Alaska. These liverwort-covered sediments have high concentrations of metals, including Al, As, Cu, Fe, Hg, La, Mn, Pb, and Zn. The *G. inflata* thalli here are very small and compact, forming intimate associations with the iron-rich sediments of the seeps and streams. When the liverworts become covered by silt, the thalli grow upward, creating a dense fibrous ferricrete sediment below them. The dominance of *G. inflata* causes these areas to appear black. This species dominates both in very damp sites and in areas with flowing water.

Basile and Basile (1980) examined the effects of ammonium ions on form and hydroxyproline content of cell wall proteins in *Gymnocolea inflata* (Figure 17-Figure 18, Figure 20, Figure 22). The presence of ammonium ions causes ventral leaves to develop, and the form of lateral leaves and branching pattern change due to a morphoregulatory role. This type of reaction might alter the appearance of this and other liverworts in the field as a result of the available nutrients.

Isopaches bicrenatus (Figure 23-Figure 24)

(syn. = *Lophozia bicrenata*)

Distribution

Isopaches bicrenatus ; Figure 23-Figure 24) is a widespread species in the temperate regions of the Northern Hemisphere (Gradstein *et al.* 2018). But it has appeared in a few widely separated areas, including southeastern Brazil, New Zealand, high elevations (>4000 m asl) in the Andes, Colombia (Gradstein *et al.* 2018), and the Dominican Republic in Central America (Bakalin 2008).



Figure 23. *Isopaches bicrenatus*, a widespread species in temperate regions where it can occur on river banks, but is often on wood or in wet depressions. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

The habitat of this species includes earthy and gravelly substrates on river banks in the Haute Ardenne rivers of Belgium (Leclercq 1977). It is predominantly a terrestrial liverwort, often in association with other leafy liverworts, often on wood, but can also occur on wet soil in hollows or inundated shrublet-moss spruce forest, making pure patches or occurring with other liverworts (Dulin 2014).

Reproduction

Fulford (1955) described development of *Isopaches bicrenatus* (Figure 23-Figure 24). Like the typical liverworts, the spore germinates to produce a thalloid protonema. But under adverse conditions, it can produce a filamentous protonema instead, a phenomenon that has been observed in a number of liverworts. The mature plants produce a number of reddish gemmae (Figure 24) in clusters. These, and leaf fragments that regenerate easily, make reproduction and spread easy for this species.

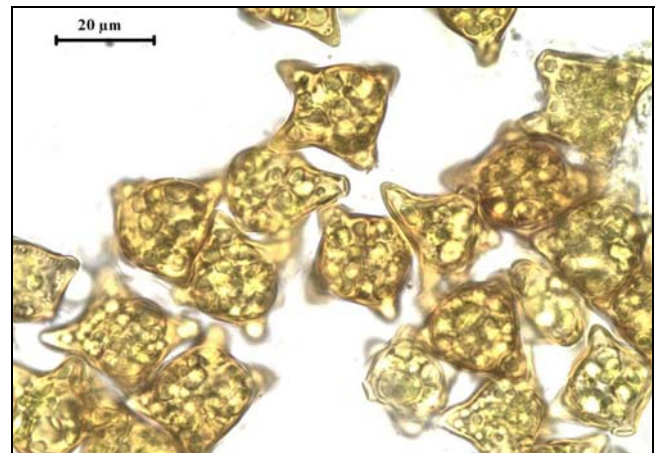


Figure 24. *Isopaches bicrenatus* gemmae; these become reddish at maturity. Photo by Hugues Tinguy, with permission.

Rivulariella gemmipara (Figure 25)

(syn. = *Chiloscyphus gemmiparus*)

Rivulariella gemmipara (Figure 25) seems to be a liverwort without a home – or with many homes. Whereas Wagner (2013) moved it from *Chiloscyphus* in the *Lophocoleaceae* to *Rivulariella* in the *Jungermanniaceae*, Patzak *et al.* (2016) consider its alignment to be with the *Scapaniaceae* s.l. Stotler and Crandall-Stotler (2017) argue for its placement in the *Anastrophyllaceae*, a family formerly included within the *Scapaniaceae*.

Distribution

Rivulariella gemmipara (Figure 25) is a subalpine or alpine species that is endemic to western North America (Wagner 2013). It is a species of concern, with only six known locations, those in Alaska, Oregon, California, and Utah, all in the USA.



Figure 25. *Rivulariella gemmipara* leaves from upward-growing stem. Photo courtesy of David Wagner.

Aquatic and Wet Habitats

Rivulariella gemmipara (Figure 25) grows in moderately fast water where there are small rocks (small pebbles to fist-sized cobbles) and gravel (Figure 26-Figure 31), avoiding areas with organic debris or muck over the substrate (Wagner 2013). It also avoids areas where the water surface is smooth or where the flow is very rapid. The suitable areas are typically permanent springs that keep the streambed submerged at all times, and that are exposed to sun most of the day, but that seldom have rapid flow due to any runoff. Rocks are its only known substrate. It is often associated with *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 27), *Chiloscyphus polyanthos* (Figure 28), and *Scapania undulata* (Figure 29).



Figure 26. *Rivulariella gemmipara* habitat in springfed stream. Photo courtesy of David Wagner.

Adaptations

Rivulariella gemmipara (Figure 25) lacks rhizoids in adults, but these are produced in germinating gemmae (Evans 1928). Perhaps this is enough to enable attachment, but it is an unusual characteristic for a bryophyte that grows on rocks in flowing water. Its slightly flattened stems are more in line with its habitat.

The species has horizontal, flattened stems (Figure 30) and upright, leafy stems (Wagner 2013). These flattened stems adhere closely to the substrate and lack rhizoids (David Wagner, pers. comm. 3 June 2020). The erect

shoots differ distinctly from these pioneering horizontal stems. The latter lack underleaves, but the upright stems produce them, these eventually being as large as the lateral shoot leaves and transversely inserted. When the stone gets overturned, as it does sporadically, the upright leafy stems die and disappear, probably due to abrasion or decomposition, but the flat stems remain tightly adhered to the rocks, leaving blackish tracks (Figure 30, Figure 32). This method of gluing to the substrate seems to be a unique adaptation of this species.



Figure 27. *Jungermannia exsertifolia* subsp. *cordifolia* from a wet habitat. Photo by Des Callaghan, with permission.



Figure 28. *Chiloscyphus polyanthos*, a frequent species in siliceous mountain brooks where *Jungermannia atrovirens* is able to grow. Photo by Hermann Schachner, through Creative Commons.



Figure 29. *Scapania undulata*, a species that associates with *Marsupella aquatica* on rocks in Maine, USA. Photo by Jan-Peter Frahm, with permission.



Figure 30. *Rivulariella gemmipara* flat horizontal stems on rock that was overturned. Photo courtesy of David Wagner.



Figure 32. *Rivulariella gemmipara* on rock showing the upright plants on one side and the tracks of stems on a side that has been buried. Photo courtesy of David Wagner.



Figure 31. *Rivulariella gemmipara* on pebbles in springfed stream. Photo courtesy of David Wagner.

Reproduction

Rivulariella gemmipara (Figure 25) is **monoicous**, thus facilitating sexual reproduction (Wagner 2013). It has marginal gemmae (Figure 33) on its leaves and these develop rhizoids as they germinate.



Figure 33. *Rivulariella gemmipara* leaf with gemmae. Photo courtesy of David Wagner.

Schljakovia kunzeana (Figure 34)

(syn. = *Lophozia kunzeana*, *Orthocaulis kunzeanus*)

Distribution

Schljakovia kunzeana (Figure 34) is widespread as an Arctic-alpine, circumboreal tundra species. It extends southward into the coniferous forest of the Great Lakes and alpine areas of Europe (Schuster 1969).



Figure 34. *Schljakovia kunzeana* is a widespread circumboreal species that can be found on some river banks and other wet habitats. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) described *Schljakovia kunzeana* (Figure 34) as a liverwort of alpine wet ground associated with fast water. Konstantinova *et al.* (2002) reported it from a boggy valley of a small creek of Upper Bureya River in the Russian Far East. In the Komi Republic of northwestern Russia, it occurs with other leafy liverworts on soil among sedges along the bank of the Ugum River (Dulin 2014). In the Russian Arctic National Park, Fedosov *et al.* (2018) reported that it occurs in willow and moss-dominated communities on smooth terraces, typically accompanied by other leafy liverworts.

Sphenolobus minutus (Figure 35, Figure 38-Figure 41)

(syn. = *Anastrophyllum minutum*)

Distribution

Sphenolobus minutus (Figure 35, Figure 38-Figure 41) is widely distributed in the Holarctic region (Schuster 1969), as well as Madagascar, Mexico, and the Russian Federation (TROPICOS 2020). Other reported locations include Norway, Czech Republic, Nova Scotia, Gaspé Peninsula, and Yukon in Canada, and Japan (Consortium of North American Bryophyte Herbarium 2020).



Figure 35. *Sphenolobus minutus*, a widely distributed Holarctic liverwort that is less common further south except on the mountains; it lives on peaty soil and areas of high moisture, but can become submerged in montane streams. Photo by Jouko Rikkinen, through Creative Commons.

Aquatic and Wet Habitats

In western Canada *Sphenolobus minutus* (Figure 35, Figure 38-Figure 41) occurs submerged as a hemicalciphilous species in montane streams and on stream banks (Figure 36) (Vitt *et al.* 1986; Glime & Vitt 1987). In these habitats, it forms mats (Figure 38). It is especially common on peaty soil, but it can also occur on north-facing cliffs where there is little or no seepage but high atmospheric moisture (Schuster 1969). In the flume (Figure 37) at Franconia Notch, New Hampshire, USA it occurred on the flume wall (Glime 1982).



Figure 36. Calcareous stream in BC, Canada, where one might find *Sphenolobus minutus*. Photo by Janice Glime.



Figure 37. Flume, Franconia Notch, NH, site where one can find *Sphenolobus minutus* on the walls. Photo by Janice Glime.



Figure 38. *Sphenolobus minutus* forming a mat. Photo by Jouko Rikkinen, through Creative Commons.

Reproduction

Like most of the leafy liverworts, *Sphenolobus minutus* (Figure 38) produces gemmae (Figure 39-Figure 41). These provide a means of surviving unfavorable conditions as well as dispersal.



Figure 39. *Sphenolobus minutus* with gemmae. Photo by Jouko Rikkinen, through Creative Commons.

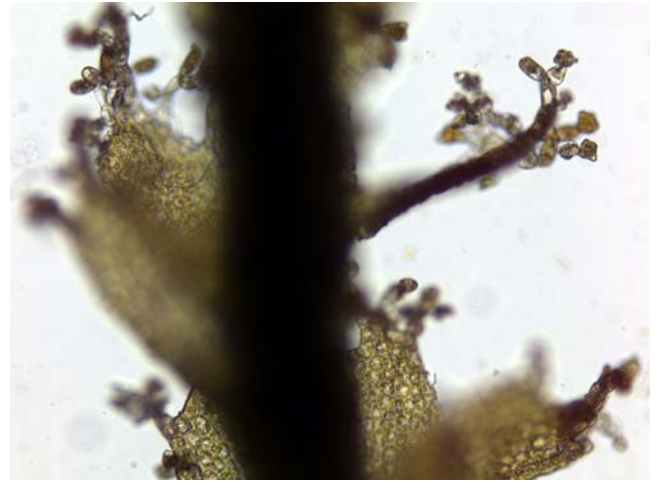


Figure 40. *Sphenolobus minutus* with gemmae on leaf tips. Photo by Jouko Rikkinen, through Creative Commons.

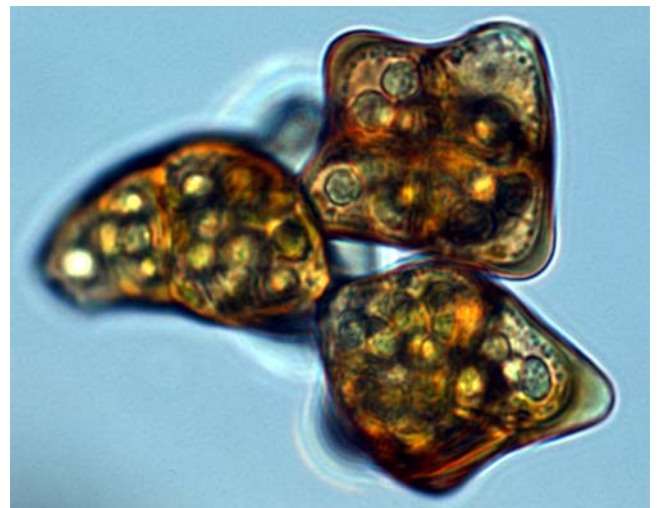


Figure 41. *Sphenolobus minutus* gemmae, showing their angular construction. Photo by Jouko Rikkinen, through Creative Commons.

Role

Kitagawa (1974) reported nematode galls (Figure 43-Figure 42) on *Sphenolobus minutus* (Figure 35, Figure 38-Figure 41) from Nepal. But other more common interactions seem to be lacking. For example, in their study on mycorrhizae in liverworts, Wang and Qiu (2006) could find no records of mycorrhizae for this species.



Figure 42. Nematode similar to the ones that can form galls on *Sphenolobus minutus*. Photo by courtesy of Andi Cairns.

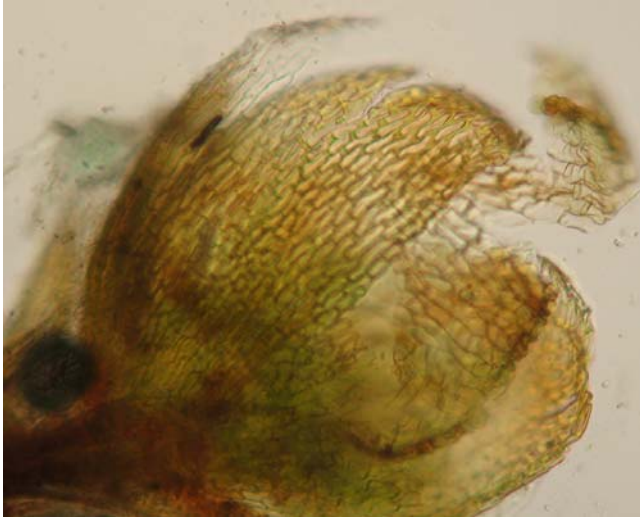


Figure 43. *Bryum argenteum* nematode galls, a parasitic attack that also occurs in *Sphenolobus minutus*. Photo courtesy of Claudio Delgadillo Moya.

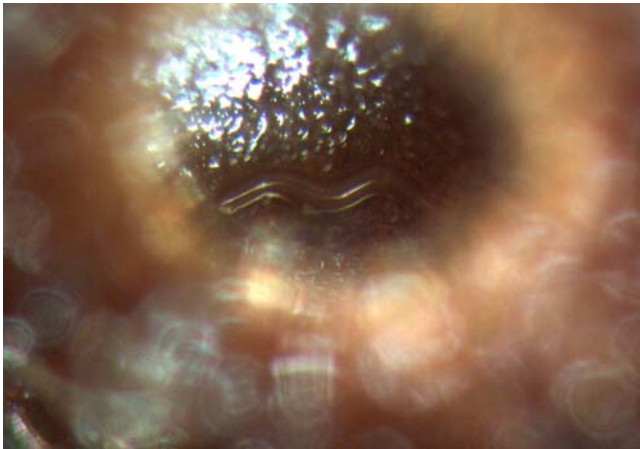


Figure 44. *Buxbaumia aphylla* nematode in gall showing nematode. Photo by Misha Ignatov, with permission.

Tetralophozia filiformis

(syn. = *Chandonanthus filiformis*, *Chandonanthus pusillus*)

Distribution

Tetralophozia filiformis has a very disjunctive distribution in Asia, Europe, and North America (Urmi 1983, 2015). Because its collections are widely separated (Japan, Himalayas, and Canada) and more recently in Russia (Konstantinova 2002b), it was originally treated as several species that have since been combined (Laine 1970).

Aquatic and Wet Habitats

In the Cantabrian Mountains of Spain it occurs on sheltered siliceous rocks with oceanic conditions (Urmi 1983). The records seem to be rather limited, but at least one record indicates that it occupies a dripping cliff near a waterfall of the Upper Bureya River in the Russian Far East (Konstantinova *et al.* 2002).

Cephaloziaceae

Cephalozia (Figure 45-Figure 59)

Cephalozia (Figure 45-Figure 59) occurs in small ponds of coastal barrens, Cape Breton Island, Canada (Nichols 1918). Albinsson (1997) found that *Cephalozia* species tended to have wider ecological amplitudes in Swedish mires than did the larger liverworts. The *Cephalozia* species are frequently fertile and seem to prefer peat and litter rather than living *Sphagnum* (like Figure 78) as a substrate, using an **avoidance strategy**.

Cephalozia ambigua (Figure 45-Figure 46)

Distribution

Cephalozia ambigua (Figure 45-Figure 46) is listed for China and Russia in TROPICOS (TROPICOS 2020). Geissler (1976) reported it from the Swiss Alps. Lorenz (1915) listed it for Scandinavia and Ellesmere Island in the Arctic Archipelago. Potemkin and Sofronova (2013) considered *Cephalozia ambigua* to be circumpolar, occurring in Arctic, alpine, and subalpine areas. In Europe it extends southward to the French Pyrenees, Spain, and Bulgaria. It extends from southern Polar Deserts to northern Taiga, mountain tundras, and elfin wood areas in the Far East.



Figure 45. *Cephalozia bicuspidata* complex; *C. ambigua* is a species from China and Russia and high elevations elsewhere in the Northern Hemisphere where it can occur on wet cliffs and lakeshore rocks or peaty soil. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

In the Swiss Alps, *Cephalozia ambigua* (Figure 45-Figure 46) occurs in alpine streams (Geissler 1976). In the Upper Bureya River of the Russian Far East, the species occurs on wet cliffs and rocks at the lake shore, often accompanied by other leafy liverworts (Konstantinova *et al.* 2002). It occurs on acid to neutral soil (incl. peaty soil and soil over the rocks) (Potemkin & Sofronova 2013).



Figure 46. Leaf from *Cephalozia bicuspidata* complex. Note the thickened walls of the terminal cells compared to those at the base. Photo by Hugues Tinguy, with permission.

Adaptations

Potemkin and Sofronova (2013) noted that most species of *Cephalozia* never develop any secondary pigmentation, thus always occurring as green or whitish green (Figure 45). However, members of the *Cephalozia bicuspidata* complex [*C. ambigua* (Figure 45-Figure 46), *C. bicuspidata* (Figure 47, Figure 53-Figure 56, Figure 59, Figure 60), *C. hamatiloba* (Figure 48)] from sunlit habitats are typically brown and/or purple. Furthermore, *C. catenulata* (Figure 49), *C. macrostachya* (Figure 50), *C. loitlesbergeri* (Figure 51) and *Nowellia curvifolia* (syn. = *Cephalozia curvifolia*; Figure 52) often develop brown pigmentation.



Figure 47. *Cephalozia bicuspidata* exhibiting reddish-brown color from exposure to direct sunlight. Photo by Hermann Schachner, through Creative Commons.

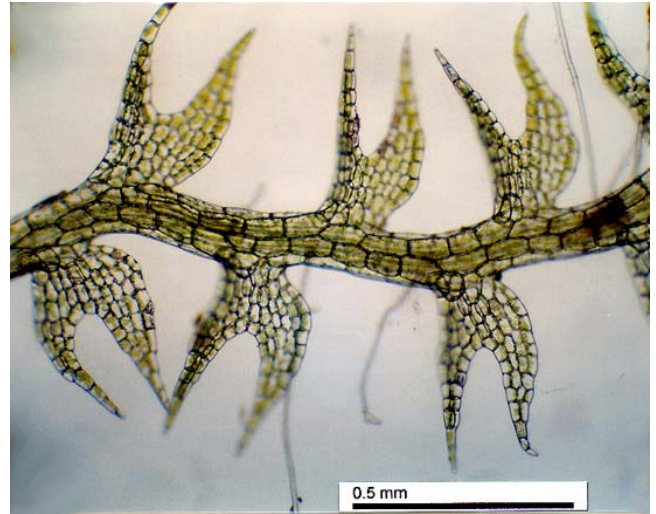


Figure 48. *Cephalozia hamatiloba*, from the *C. bicuspidata* complex, is usually brown or purple in sunlit habitats. Photo by David H. Wagner, with permission.



Figure 49. *Cephalozia catenulata*, a species that can develop brown pigmentation in direct sunlight. Photo by Michael Lüth, with permission.



Figure 50. *Cephalozia macrostachya*, a species that can develop brown pigmentation in direct sunlight. Photo by Michael Lüth, with permission.



Figure 51. *Cephalozia loitlesbergeri*, a species that can develop brown pigmentation in direct sunlight. Photo by Des Callaghan, with permission.



Figure 52. *Nowellia curvifolia*, formerly in the genus *Cephalozia*, red form from sunlit area. Photo by Hugues Tinguy, with permission.

Potemkin and Sofronova (2013) found that in *Cephalozia ambigua* (Figure 45-Figure 46) the extra thickenings of the apical wall of the terminal cells (Figure 46) is flexible, with the thickenings usually absent on soil, but present in populations growing on logs where humidity conditions are intermittent.

***Cephalozia bicuspidata* (Figure 47, Figure 53-Figure 56, Figure 59, Figure 60)**

Distribution

Cephalozia bicuspidata (Figure 47, Figure 53-Figure 56, Figure 59, Figure 60) has a widespread distribution in the Northern Hemisphere, with scattered reports from South America and Africa (DiscoverLife 2020a). *Cephalozia bicuspidata* occurs mostly in northern and temperate Eurasia (not known in Asia south of Taiwan), Azores, North America, northern South America, Macaronesia, Africa (central African mountains, South Africa), and from remote islands of southern Indian (Reunion, Marion I., Crozet Is.) and Atlantic (Tristan da Cunha group) oceans, Chile, South Georgia, and Tasmania (Schuster 1974; Piippo 1990; Vána 1993; Damsholt 2002).



Figure 53. *Cephalozia bicuspidata*. Photo by Jay Avery, through Creative Commons.

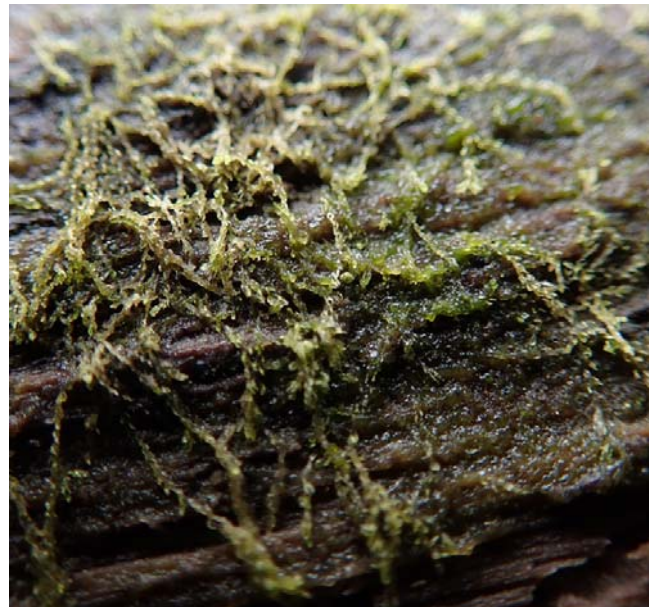


Figure 54. *Cephalozia bicuspidata* on a wet log. Photo by Rambryo, through Creative Commons.

Aquatic and Wet Habitats

In his early summary of aquatic bryophytes, Watson (1919) described *Cephalozia bicuspidata* (Figure 53-Figure 56, Figure 59, Figure 60) as a species to be found on stream banks of streams with slow water and that provided frequent submergence. Light (1975) reported it from small lakes with low ion concentrations in Scottish mountains where ice cover lasted 4-7 months. Geissler (1976) found the species in alpine streams of the Swiss Alps. Similar habitats around Europe and North America support the species – earthy and gravelly substrates of river banks in Haute Ardenne rivers, Belgium (Leclercq 1977); as calciphilous emergents of montane streams and streambanks in western Canada (Vitt *et al.* 1986; Glimme & Vitt 1987), contrasting with Schuster's (1953) statement of

intolerance of lime; upper and middle stream reaches in the Harz Mountains of Germany (Bley 1987); irrigation ditches (Beaucourt *et al.* 1987); in the *Platyhypnidium-Fontinalis antipyretica* association (Figure 55) of Thuringia, Germany (Marstaller 1987); in small lakes in southern Finland (Toivonen & Huttunen 1995); soil bank of a small creek of Upper Bureya River in the Russian Far East (Konstantinova *et al.* 2002); on the Southern Kuril Islands in the Goryachyee Lake area on fine-grained ground in crevices of a tufa cliff where they were splashed by water from the lake Bakalin 2007); in and along rivers (Ferreira *et al.* 2008). The most common sites for this species are sunny sites where the species uses decorticated rotting wood, rock, or bare mineral soil as substrate (Botany Website 2020).



Figure 55. *Fontinalis antipyretica*, a species that, along with *Platyhypnidium*, can be found in association with *Cephalozia bicuspidata*. Photo by Michael Lüth, with permission.

Potemkin and Sofronova (2013) reported *Cephalozia bicuspidata* (Figure 53-Figure 56, Figure 59, Figure 60) on acid and occasionally more or less neutral substrata – bare soil, rocks, rotten wood (Figure 54), among mosses and among *Sphagnum* (like Figure 78), particularly, at bases of trees. Schuster (1953, p. 507) considered the *C. bicuspidata* complex to have no tolerance for even tiny amounts of lime.

One of the more unusual occurrences of *Cephalozia bicuspidata* (Figure 53-Figure 56, Figure 59, Figure 60) is in the Kootenay Paint Pots (Figure 57), British Columbia, Canada (Wehr & Whitton 1983). These are natural springs enriched with heavy metals and a pH range of 3.2-4.0. The springs have high levels of iron and zinc. These springs are home to 14 species of algae, but only one liverwort (*Cephalozia bicuspidata*) and one moss (*Dicranella heteromalla*; Figure 58). The latter occurred only as protonemata.



Figure 56. *Cephalozia bicuspidata*, showing its mat growth form and a perianth in the upper right. Photo by Malcolm Storey, DiscoverLife.com, with online permission.



Figure 57. Kootenay National Park Paint Pots, where *Cephalozia bicuspidata* and *Dicranella heteromalla* are the only bryophytes able to grow in the iron-laden springs. Photo by Marek Slusarczyk, through Creative Commons.



Figure 58. *Dicranella heteromalla* with young capsules, one of two bryophyte species able to grow at the Kootenay Paint Pots on the iron-rich mud. Photo by Janice Glime.

Adaptations

Potemkin and Sofronova (2013) observed that *C. bicuspidata* (Figure 53-Figure 56, Figure 59, Figure 60), like *C. ambigua* (Figure 45-Figure 46), has flexible cell

wall thickenings (Figure 59) that seem to respond to intermittent humidity by developing stronger thickenings.

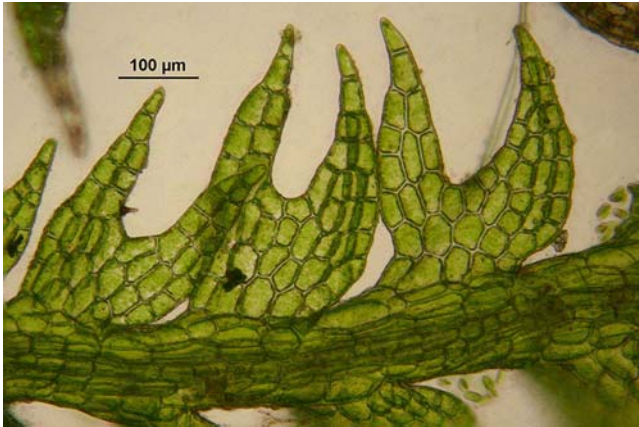


Figure 59. *Cephalozia bicuspidata* showing cell walls, in this case with no obvious thickening. Photo by Hermann Schachner through Creative Commons.

Proctor (1982) determined that the photosynthetic activity of the sporophytes of *Cephalozia bicuspidata* (Figure 53-Figure 56, Figure 59, Figure 60) is very low when compared with that of the gametophyte structures [perianth (Figure 60), bracts and uppermost leaves] associated with the sporophyte. In fact, the CO₂ uptake by the sporophyte is only a small percent of that translocated to it from the gametophyte. The greatest transport to the sporophyte seems to occur when the sporophyte has reached full size but is still green.



Figure 60. *Cephalozia bicuspidata* with numerous gametophyte perianths that dominate what you see. Photo by Michael Lüth, with permission.

The subspecies *Cephalozia bicuspidata* subsp. *lammersiana* (syn. = *Cephalozia lammersiana*, *Jungermannia lammerisiana*) occurs submerged in slow water with poor mineral salts (Watson 1919).

Role

At Tuckerman Ravine on Mt. Washington, New Hampshire, USA (1300 m asl), Duckett and Slack (2013) found *Cephalozia bicuspidata* (Figure 53-Figure 56, Figure 59) on wet vertical rocks where it was associated with *Scapania undulata* (Figure 61), *Solenostoma hyalinum* (Figure 62), *Blindia acuta* (Figure 63), *Philonotis fontana* (Figure 64), *Pohlia nutans* (Figure 65), *Racomitrium fasciculare* (Figure 66), and *R. heterosticum* (Figure 67). *Cephalozia bicuspidata* on the mountain had no sexual reproductive structures, but they displayed extensive subterranean shoots that were leafless and contained fungi, most likely *Mucoromycotina*.



Figure 61. *Scapania undulata* (red with green edges) with the moss *Philonotis fontana*, two species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by David T. Holyoak, with permission.



Figure 62. *Solenostoma hyalinum* with capsule, a species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by Michael Lüth, with permission.



Figure 63. *Blindia acuta*, a species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by David Holyoak, with permission.



Figure 66. *Racomitrium fasciculare*, a species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by Janice Glime.



Figure 64. *Philonotis fontana*, a species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by Janice Glime.



Figure 67. *Racomitrium heterostichum*, a species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by Jan-Peter Frahm, with permission.

Reproduction

Duckett and Clymo (1988) found that many leafy liverworts regenerate from slabs cut from various depths of peat cores. They found that species that lack underground axes regenerate most abundantly at the surface, but not below 9 cm depth. Species like *Cephalozia bicuspidata* (Figure 53-Figure 56, Figure 59, Figure 60) that have such underground structures often have poor regeneration from the surface, but have much more regeneration down to 12 cm and even grow from samples down to 24-30 cm. This relationship proved to be true for both the cores from live *Sphagnum*-covered surface (like Figure 78) and from the much older cut peat surface that had been recently colonized by liverworts. The researchers interpreted this to mean that most of the regeneration of *C. bicuspidata* is from underground axes rather than from spores or gemmae. The underground axes typically have a large biomass. All the axes had fungal associates that could be partially saprophytic or parasitic.



Figure 65. *Pohlia nutans* a species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by Michael Lüth, with permission.

Fungal Interactions

Pressel and Duckett (2006) found that *Mniaecia jungermanniae* (Figure 68), a parasitic **Ascomycota**, associated with *Cephalozia bicuspidata* (Figure 53-Figure 56, Figure 59, Figure 60). They hypothesized that the fungus could form a symbiotic relationship, producing swollen rhizoids on the liverwort. However, when cultured with *Cephalozia bicuspidata*, the *Mniaecia* remained extracellular. Rather, it induced the formation of giant perichaetia that contained supernumerary archegonia followed by **parthenogenetic** (reproduction from egg without fertilization) and **apogamous** (reproduction in which sporophyte develops from gametophyte without fusion of gametes). They also observed similar giant perichaetia and abnormal perianths in the field.

Mniaecia jungermanniae (Figure 68) is known from 17 species of liverworts, including *Cephalozia bicuspidata* (Figure 53-Figure 56, Figure 59, Figure 60) as one of the most frequently inhabited liverwort species (Egertová *et al.* 2016). In the Czech Republic all the substrata of this liverwort were acidic and included soil, rocks, and boulders. The liverworts and their symbionts were typically located in the shade of both coniferous and broad-leaved forests. The fungus produces turquoise apothecia (Figure 68) on the liverworts (Duckett *et al.* 2004). In *Cephalozia bicuspidata*, these occur on the shoots from January to March. This fungus does not colonize the rhizoids of *C. bicuspidata*.



Figure 68. *Mniaecia jungermanniae*, an **Ascomycota** fungus growing on *Cephalozia bicuspidata*. Photo courtesy of Jan Gaisler.

Liepina (2012) reported the occurrence of fungal structures in the cell walls of *Cephalozia bicuspidata* (Figure 59) from a swamp. Kowal *et al.* (2018) noted that the rhizoids of leafy liverworts are often colonized by the **Ascomycota** fungus *Pezoloma ericae* (see Figure 69), forming associations that might carry out the same functions as mycorrhizae from members of the heath family **Ericaceae** in which there is bi-directional phosphorus for carbon exchange. These researchers measured exchanges of P and CO₂ in the liverwort-fungal association using tracers. They demonstrated the transfer

of P from the fungus to the liverwort and transfer of carbon fixed by the liverwort to the fungus. The mycorrhizal liverworts also exhibited increased growth compared to those with no fungal partner.



Figure 69. *Pezoloma ciliifera*; *Pezoloma ericae* occurs on *Cephalozia bicuspidata*. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Hasselbring (1911) provided an early report of fungi in the rhizoids of liverworts. When the fungal hypha makes contact with the rhizoid, a thickening appears on the inside of the opposite wall. As the hypha grows into the cell, cellulose is deposited ahead of the growing point, surrounding the hypha with a sheath of cellulose. Hasselbring isolated *Mucor rhizophilus* (Figure 70) in the **Zygomycota** from nine liverwort species and successfully cultured it with *Gymnocolea inflata* (Figure 17-Figure 18, Figure 20, Figure 22), *Cephalozia bicuspidata* (Figure 53-Figure 56, Figure 59, Figure 60), *Cephaloziella* sp. (Figure 100-Figure 105), and *Lophozia ventricosa* (Figure 112-Figure 116). This association appears to be neither mycorrhizal nor parasitic, although when the liverworts become strongly infected the plants experience an unfavorable reaction.



Figure 70. *Mucor mucedo*; *Mucor rhizophilus* is known from nine liverwort species, including *Gymnocolea inflata*. Photo by Lena Wild, through Creative Commons.

Fuscocephaloziopsis albescens (Figure 71-Figure 72)

(syn. = *Pleurocladula albescens*)

Distribution

Fuscocephaloziopsis albescens (Figure 71-Figure 72) is reported by GBIF (2020b) from Canada, USA, Iceland, Greenland, Russian Federation, Norway, Sweden, Switzerland, UK, and Japan. The species is also known from the Tatra Mountains of Poland and Slovakia (Górski 2015, 2016).



Figure 71. *Fuscocephaloziopsis albescens*, a mostly Arctic and alpine species from Europe and North America, plus Japan, a species occasionally found in mires, seepage streamlets, and snowbeds. Photo by Des Callaghan, through Creative Commons.

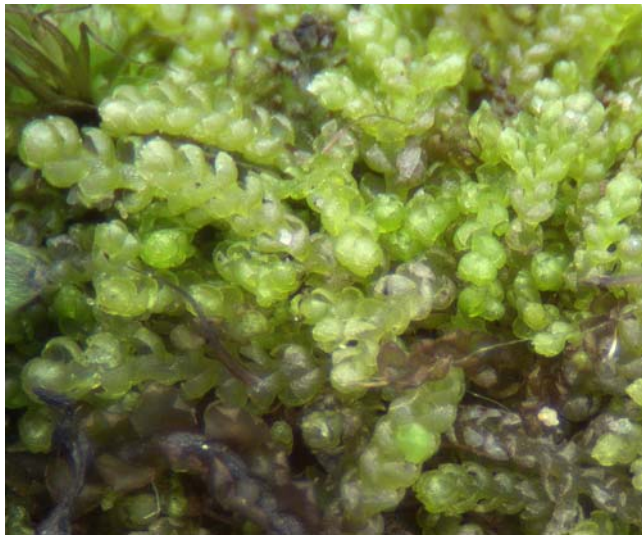


Figure 72. *Fuscocephaloziopsis albescens* forming a mat. Photo by Tomas Hallingbäck, with permission.

Aquatic and Wet Habitats

This is not a frequent wetland species. Konstantinova *et al.* (2002) reported it from wet rocks of the Upper Bureya River in the Russian Far East. Górski (2015) reports it from snowbeds in the Tatra Mountains of Poland and Slovakia. There it occurred in an association with *Pohlia nutans* (Figure 65) (Górski 2016). Talbot *et al.* (2018) found it on Attu Island of the Aleutian Islands, again rare, on rock cliff outcrops, late snowbeds, cliff crevices, mesic mires, and seepage streamlets. It was sometimes mixed with other leafy liverworts.

Fuscocephaloziopsis connivens (Figure 73-Figure 78)

(syn. = *Cephalozia connivens*)

Distribution

Fuscocephaloziopsis connivens (Figure 73-Figure 78) is a Holarctic species, mostly occurring in boreal and temperate areas with a more or less humid microclimate (Potemkin & Sofronova 2013). This distribution includes records from Africa, the Caribbean, Europe, northern Asia, Middle America, Alaska, Canada, continental USA, Mexico, Oceania, and South America, even occurring on the Hawaiian Islands (ITISb).



Figure 73. *Fuscocephaloziopsis connivens*, a holarctic species on streambanks and in wetlands. Photo by Paul Davison, with permission



Figure 74. *Fuscocephaloziopsis connivens*, the smaller liverwort mixed here with a larger liverwort. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

Watson (1919) included this species in his list of aquatic and wetland species. It occurs on banks with frequent submergence and slow water (Figure 75). Geissler and Selldorf (1986) considered it to be uncommon in association with *Eleocharis quinqueflora* (Figure 76). Henriques *et al.* (2017) considered *Fuscocephaloziopsis connivens* (Figure 73-Figure 78) to be a **humicolous** (thriving on humus) specialist.

Reproduction

Cores in peatlands demonstrate the regeneration capacity of *Fuscocephaloziopsis connivens* (Figure 77-Figure 78). Duckett and Clymo (1988) found it remarkable that this species was nearly absent at the surface where there were actively growing *Sphagnum* capitula (like Figure 78), but that it was able to regenerate from lower layers in the cores (3-12 cm depth). Nevertheless, Michael Lüth has photographed it growing well with *Sphagnum* (Figure 78).



Figure 75. *Fuscocephaloziopsis connivens* growing in a wetland habitat near water. Photo by Michael Lüth, with permission.



Figure 78. *Fuscocephaloziopsis connivens* growing with *Sphagnum* and other bog/poor fen vegetation. Photo by Michael Lüth, with permission.



Figure 76. *Eleocharis quinqueflora*, sometimes an associate of *Fuscocephaloziopsis* in alpine regions. Photo by Max Licher, through Creative Commons.



Figure 77. *Fuscocephaloziopsis connivens* with young capsule and perianth and demonstrating the light green leaf color. The spores have the potential to join the upper layers of peat in the spore bank. Photo by Des Callaghan, with permission.

Fuscocephaloziopsis lunulifolia (Figure 79, Figure 81-Figure 82)

(syn. = *Cephalozia lunulifolia*, *Cephalozia media*)

Distribution

Fuscocephaloziopsis lunulifolia (Figure 79, Figure 81-Figure 82) is widespread in the Northern Hemisphere (Hong 2007). TROPICOS specifically lists it for China, Japan, the Russian Federation, and the USA. Potemkin and Sofronova (2013) list it as a Holarctic boreal species, extending in the Eastern Hemisphere to Japan and SW China (Yunnan) but having a disjunct location in Cuba, as well as Guatemala (Gradstein & Vána 1994).

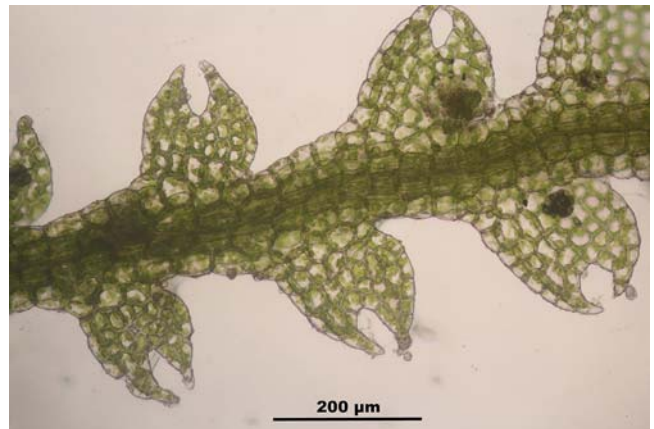


Figure 79. *Fuscocephaloziopsis lunulifolia*, a widespread species in the Northern Hemisphere, occurring on rotten wood, soil, rocks, or among other mosses. It is associated with lakes, stream banks, and bare peat in subalpine zones and the taiga. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Potemkin and Sofronova (2013), from their experience in Russia, describe this species as one found among *Sphagnum* (like Figure 78), on rotten wood, more rare among other mosses, on humus soil, rocks, or fine sandy soil. The *Fuscocephaloziopsis lunulifolia* plants are medium-sized, whitish green, and lack secondary pigmentation (Figure 79, Figure 81).

Nichols (1918) reported this species from moist hollows between *Sphagnum* hummocks (Figure 80) on

Cape Breton Island, Canada. In the Altai Mountains of Russia, Vána and Ignatov (1995) considered it rare in the upper taiga and subalpine zones, where it occurred on sides of hummocks, lake shores just above the water level, and on bare peat of bogs. In the Takakia Lake area of the Queen Charlotte Islands, western Canada, Hong (2007) found it on shaded decayed wood, wet rocks, and stream banks. Jonsson (1996) reported *Fuscocephaloziopsis lunulifolia* (Figure 79, Figure 81-Figure 82) from the riparian zone of the H. J. Andrews Experimental Forest in the western Cascades, Oregon, USA.



Figure 80. *Sphagnum* hummocks and hollows, similar to the ones where *Fuscocephaloziopsis lunulifolia* can occur. Photo by Nicholas A. Tonelli, through Creative Commons.



Figure 81. *Fuscocephaloziopsis lunulifolia* forming a mat on its substrate. Photo by Michael Lüth, with permission.

Adaptations

Fuscocephaloziopsis lunulifolia (Figure 79, Figure 81-Figure 82) presents evenly thickened leaf cell walls (Figure 82) that are unable to develop extra thickenings in the apical wall of the terminal cells in **xylicolous** (living on wood that has lost its bark) habitats, making it less flexible

in these adaptations compared to *Cephalozia bicuspidata* (Figure 53-Figure 56, Figure 59, Figure 60) (Potemkin & Sofronova 2013).



Figure 82. *Fuscocephaloziopsis lunulifolia* cells showing walls that are evenly thickened. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Fuscocephaloziopsis lunulifolia (Figure 79, Figure 81-Figure 82) can be dioicous or autoicous. The propagule bank seems to be rather inconsequential for this species. In their study in a boreal old-growth spruce forest in SE Norway, Rydgren and Hestmark (1997) observed germination in fewer than 5% of the samples. However, it likewise was poorly represented in the extant flora sampled, occurring in only 1 of 50 samples.

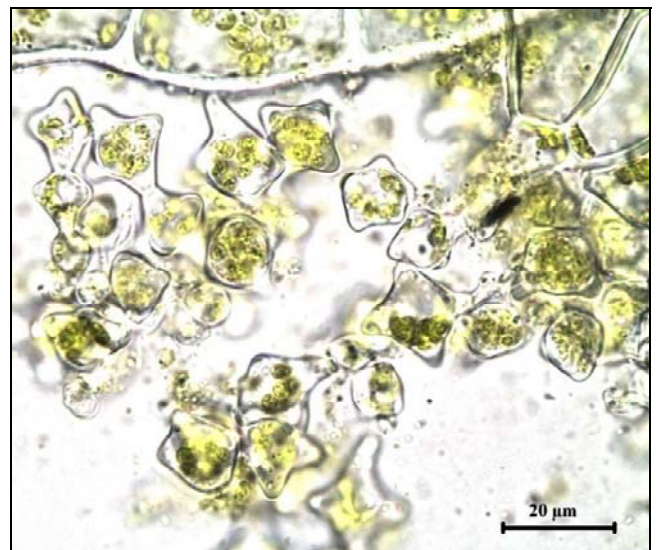


Figure 83. *Fuscocephaloziopsis lunulifolia* gemmae, potential members of the sporebank in upper layers of peat. Photo by Hugues Tinguy, with permission.

Fungal Interactions

Wang and Qiu (2006) reported mycorrhizal relationships with *Fuscocephaloziopsis lunulifolia* (Figure 79, Figure 81-Figure 82).

Odontoschisma elongatum (Figure 84, Figure 89-Figure 90)

(syn. = *Odontoschisma denudatum* subsp. *elongatum*)

Distribution

Odontoschisma elongatum (Figure 84, Figure 89-Figure 90) presents a distribution in the Caribbean, Europe, Northern Asia, Alaska, Canada, and the continental USA (ITIS 2020c).



Figure 84. *Odontoschisma elongatum*, a Northern Hemisphere species that can occur in mires. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

This species likewise is not a common member of wetland communities. Geissler and Selldorf (1986) found it with *Trichophorum cespitosum* (Figure 85) and *Carex chillanensis*, and uncommonly with *Eleocharis quinqueflora* (Figure 76) and *Paludella squarrosa* (Figure 19). Albinsson (1997) reported this species from *Sphagnum* associations (like Figure 78) in mires, noting that liverworts were encountered more often among species of *Sphagnum* in the subgenera *Sphagnum* (Figure 86) and *Acutifolia* (Figure 87) than in subgenus *Cuspidata* (Figure 88).



Figure 85. *Trichophorum cespitosum*, a sedge species that sometimes contributes to making a suitable habitat for *Odontoschisma elongatum*. Photo by Peter M. Dziuk, with online permission for educational use.



Figure 86. *Sphagnum magellanicum*, a member of the subgenus *Sphagnum*. Photo by Michael Lüth, with permission.



Figure 87. *Sphagnum capillifolium*, a member of the subgenus *Acutifolia*. Photo by Blanka Shaw, with permission.



Figure 88. *Sphagnum tenellum*, a member of the subgenus *Cuspidata*. Photo by David Holyoak, with permission.

Adaptations

Odontoschisma elongatum (Figure 84, Figure 89-Figure 90) can be a bright green (Figure 89), but more commonly has a yellowish or brownish pigment (Figure

90) (Evans 1912). Even a deep blackish purple color is relatively common. Shoots initially produce branches very sparingly, producing unbranched ascending axes. As the stems become longer, they become prostrate and produce the typical intercalary branches, some lateral and some ventral. A few of these are flagelliform (Figure 89) and grow downward, holding the plant in place, especially in its *Sphagnum* habitat, and rhizoids are scarce.



Figure 89. *Odontoschisma elongatum* with flagelliform stolon (arrow) and green color. Photo by Norbert Schnyder, with permission.



Figure 90. *Odontoschisma elongatum* from a wetland community, exhibiting brownish and golden coloration. Photo by Andrew Hodgson, with permission.

Role

Cyanobacteria (Figure 91) can be involved in symbiotic relationships with leafy liverworts (Rikkinen 2017). These can be important sources of fixed nitrogen that is available to the liverworts. Although Rikkinen investigated terrestrial populations, this relationship might as well occur in wetland species. In *Odontoschisma elongatum* (Figure 84, Figure 89-Figure 90) the slime papillae at the margins and surface of reduced underleaves near the growing tip were uninfected with any symbiont. But contrary to earlier observations, Rikkinen found that both bacteria and fungal hyphae could attach to the surface of the young slime papillae. The fungus would eventually infect the papilla with its haustoria. In later stages one can observe heavy fungal infections of the slime papillae, and these papillae are eventually shed from the plant.



Figure 91. *Nostoc linckia*, a Cyanobacterium; some species of *Nostoc* are common on leafy liverworts as symbionts. Photo from Proyecto Agua, through Creative Commons.

Reproduction

The species is dioicous and male plants are apparently rare (Evans 1912). Despite the difficulty of sexual reproduction, gemmae are also rather rare. This suggests that fragments may be an important means of reproduction and spreading.

Fungal Interactions

Pocock and Duckett (1985) found no mycorrhizal fungi in *Odontoschisma elongatum* (Figure 84, Figure 89-Figure 90) among British liverworts. Likewise, Wang and Qiu (2006) found no records of mycorrhizae in *Odontoschisma elongatum*. Nevertheless, Duckett *et al.* (1991) reported not only flagelliform branches, but also rhizoidal fungi from British *O. elongatum*.

Odontoschisma fluitans (Figure 92-Figure 93)

(syn. = *Cephalozia fluitans*, *Cladopodiella fluitans*)

Distribution

Odontoschisma fluitans (Figure 92-Figure 93) is distributed in temperate regions of the northern hemisphere and occurs in Europe and eastern North America (Gradstein & Ilkiu-Borges 2015).



Figure 92. *Odontoschisma fluitans*, a species of Northern Hemisphere temperate regions, known from stream banks, heathlands, peat bogs, and small lakes. Photo by Jean Faubert, with permission.

Aquatic and Wet Habitats

Few records seem to exist for this species in wetlands. Nevertheless, Watson (1919) included it in his treatment of aquatic and wetland species, attributing it to banks with frequent submergence and slow water (Figure 93). Koppe (1945) reported it from *Sphagnum* moors in Westfalens, northwestern Germany. It is typically associated with *Sphagnum* in heathlands and peat bogs (Gradstein & Ilkiu-Borges 2015). But Toivonen and Huttunen (1995) reported it from small lakes in southern Finland.



Figure 93. *Odontoschisma fluitans* forming mats. Photo by David T. Holyoak, with permission.

Reproduction

Unlike some members of the genus, *Odontoschisma fluitans* lacks gemmae (Figure 92-Figure 93) (Gradstein & Ilkiu-Borges 2015).

Odontoschisma sphagni (Figure 94-Figure 97, Figure 99)

(syn. = *Jungermannia sphagni*, *Odontoschisma prostratum*)

In North America, this species has been widely known as *Odontoschisma prostratum*, but based on molecular data, Gradstein and Ilkiu-Borges (2015) considered it to belong to the same species as the European *O. sphagni* (Figure 94-Figure 95). *Odontoschisma sphagni* is exceptional in the genus in being autoicous; other members are dioicous (Gradstein & Ilkiu-Borges 2015).



Figure 94. *Odontoschisma sphagni*, a species that is both Holarctic and tropical, especially occurring in bogs and other peatlands. Note the whitish underground shoots. Photo by Des Callahan, with permission.



Figure 95. *Odontoschisma sphagni*. Photo by Michael Lüth, with permission.

Distribution

Odontoschisma sphagni (Figure 94-Figure 97, Figure 99) occurs in tropical America as well as the Holarctic region, including records from Europe, North America, Mexico, and the Greater Antilles (Gradstein & Ilkiu-Borges 2015).

Aquatic and Wet Habitats

Bley (1987) legitimizes *Odontoschisma sphagni* (Figure 94-Figure 97, Figure 99) as an aquatic species (Figure 96-Figure 97), reporting it from the upper reaches of streams in the Harz Mountains of Germany. Gradstein and Ilkiu-Borges (2015) summarize its habitats to include "raised bogs between *Sphagnum*, on moist, often somewhat peaty soil, on rotten or dead wood, or on thin soil over moist sandstone rock in evergreen or deciduous forests. Sometimes the species grows over *Leucobryum* (Figure 98) or among other mosses" (Figure 99).



Figure 96. *Odontoschisma sphagni* well hydrated, showing its (mostly) green form. Photo by Michael Lüth, with permission.



Figure 97. *Odontoschisma sphagni* in a dry state, showing its reddish color form. Photo by Michael Lüth, with permission.



Figure 98. *Leucobryum glaucum*; *Odontoschisma sphagni* will sometimes grow over members of this moss genus. Photo by Amadej Trnkoczy, through Creative Commons.



Figure 99. *Odontoschisma sphagni*, growing here with the moss *Polytrichum*. Photo by Michael Lüth, with permission.

Reproduction

Duckett and Clymo (1988) found that *Odontoschisma sphagni* (Figure 94-Figure 97, Figure 99) occurred in core samples from 12-23 cm depth, but was absent from the

surface. Because this species does not produce gemmae, but exhibits the same regeneration patterns as species that do, Duckett and Clymo considered the regeneration of liverworts in these habitats not to be the result of gemmae. It is more likely that they are underground shoots (Figure 94). It is also possible that in *Odontoschisma sphagni* they result from spores because this species is **autoicous** (having male and female organs on same plant but on separate branches) (Gradstein & Ilkiu-Borges 2015).

Cephaloziellaceae

Cephaloziella (Figure 100-Figure 105)

Cephaloziella (Figure 100-Figure 105) is a widespread genus in a variety of habitats. In the maritime Antarctic, it forms bryophyte carpets in wet areas and depressions around melt pools and streams (Gimingham & Birse 1957). In southern Finland, it occurs in small lakes (Toivonen & Huttunen 1995).

Cephaloziella hampeana (Figure 100-Figure 101)

Distribution

Cephaloziella hampeana (Figure 100-Figure 101) has a scattered distribution that may include disjunct locations or just missing collection areas. When Flores *et al.* (2017) discovered it in Argentina, they raised the question of its disjunct distribution, noting the importance of high elevation locations for species like this. It is widely distributed in the Northern Hemisphere, with its most southern localities previously known from Vera Cruz in Mexico and El Quiche in Guatemala.

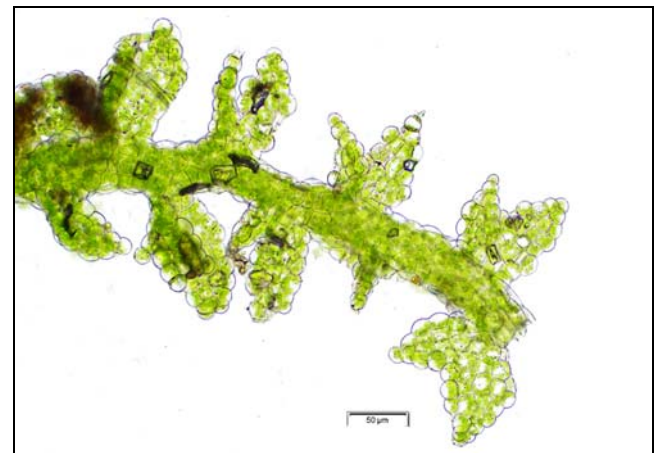


Figure 100. *Cephaloziella hampeana*, a species widely distributed in the Northern Hemisphere, but also at high elevations in the Southern Hemisphere, where it can be found in fens and mires and similar wetlands. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

Aquatic and Wet Habitats

Cephaloziella hampeana (Figure 100-Figure 101) appears to be mostly terrestrial, but its tolerance of moisture permits it to live in wetland habitats. Ingerpuu *et al.* (2014) report it from fens and mires in Estonia. In Argentina, as with a number of other Neotropical liverworts, *C. hampeana* occurs on soil, associated with

wetlands (Flores *et al.* 2017). In Tennessee, USA, at Abrams Falls Trails, it occurs on moist soil. In Connecticut, USA, the liverwort occupies crevices or the surface of drier cliffs in a ravine (Nichols 1916). In Turkey Run State Park, Indiana, USA, Ellis (1973) found *Cephaloziella hampeana* on moist ground on peat mosses, on the sides of ditches, and on sandy and turfy ground. Sass-Gyarmati *et al.* (2015) found *Cephaloziella hampeana* on one of the control plots in their experiments on temperature increase and drought. In that heathland vegetation, the species typically grows on acidic or neutral substrates, requiring a somewhat colder temperature range that might not be available as the climate warms, but it has a wide tolerance for moisture levels.



Figure 101. *Cephaloziella hampeana* with both gemmae and sporophytes. Photo by David T. Holyoak, with permission.

Fungal Interactions

As for many liverwort species, Wang and Qiu (2006) list it among the species that have fungal associations. The nature of this association needs to be explored.

Cephaloziella rubella (Figure 102-Figure 105)

Distribution

Cephaloziella rubella (Figure 102-Figure 105) occurs in the Northern Hemisphere, mostly in the Temperate Zone: Europe, Asia, North America (ITIS 2020d)



Figure 102. *Cephaloziella rubella*, a species of the temperate Northern Hemisphere that occurs occasionally on montane stream banks. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

This species occurs as a submerged hemicalciphilous species in montane streams and on stream banks in western Canada (Figure 103) (Vitt *et al.* 1986; Glime & Vitt 1987). But elsewhere, reports of its wetland presence are rare. Strout (1976) found it in Larks Lake, Michigan, USA, where it hosted an apparent symbiont in the **Cyanobacteria** (see Figure 91). In addition to its cyanobacterial symbiont, *Cephaloziella rubella* (Figure 102-Figure 105) has fungal associations (Wang & Qiu 2006).



Figure 103. Glacial melt stream where *Cephaloziella rubella* grows in BC, Canada. Photo by Janice Glime.



Figure 104. *Cephaloziella rubella* showing its growth pattern in mats. Photo by Michael Lüth, with permission.



Figure 105. *Cephaloziella rubella* showing the large, dense mats it can form. Photo by Michael Lüth, with permission.

Kymatocalyx (Figure 106-Figure 111)

(syn. = *Ruttnerella*, *Stenorhipis*)

Kymatocalyx (Figure 106-Figure 111) is a leafy liverwort known from Andean streambeds (S. Robbert Gradstein pers. comm. 3 November 2011). This is a pantropical rheophytic genus that grows in or near running water, on periodically submersed rocks, in waterfalls, on wet cliffs, and similarly wet habitats. Members of this genus produce very small erect leafy shoots from creeping, stoloniform axes.

Kymatocalyx africanus (Figure 106)**Distribution**

Kymatocalyx africanus (Figure 106) occurs in the Uluguru Mts. (1600-2350 m asl) of Tanzania, and Mt. Mulanje (1200-2220 m asl), Malawi.



Figure 106. *Kymatocalyx africanus*, a species of limited known distribution in eastern Africa where it can grow partially submerged in streams and wet places. Photo courtesy of Tamás Pócs.

Aquatic and Wet Habitats

The species occurs in montane forest areas on shady granitic rocks and boulders, on soil banks or on thin peat over rocks in streams or wet places, partially submerged in water (Gradstein & Vána 1999). The type was found on Mt. Mulanje in the bed of a seasonal stream on thin gritty soil over a granite boulder at 1740 m asl.

Reproduction

Kymatocalyx africanus (Figure 106) is **cladautoicous** (having male sexual organs on special branch separate from female organs) (Gradstein & Vána 1999).

Kymatocalyx cubensis (Figure 107)

In Madagascar, *Kymatocalyx cubensis* (Figure 107) can occur 0.3-1 m above the tidal surface, suggesting that it is salt-tolerant (Pócs 1998). Its only claim to being hydrophilic is its nearness to the ocean water.



Figure 107. *Kymatocalyx cubensis*, a species that occurs within a meter of the tidal surface in Madagascar. Photo courtesy of Tamás Pócs.

Kymatocalyx dominicensis (Figure 108)**Distribution**

Kymatocalyx dominicensis (Figure 108) is known from Cuba (1210 m asl), Puerto Rico (900 m asl), Dominica (800 m asl), St. Vincent Is., Guyana (150-1200 m asl), Venezuela (500 m asl), Colombia (1800 m asl), Bolivia (850 m asl), and Brazil (10-1850 m asl) in the Western Hemisphere and in Madagascar (1 m asl) in the Eastern Hemisphere (Gradstein & Vána 1999).



Figure 108. *Kymatocalyx dominicensis*, a species known from the Neotropics and Madagascar where it can occur on shaded rocks along rivers, in waterfalls, and at times be partly submerged. Photo courtesy of Tamás Pócs.

Aquatic and Wet Habitats

Like other taxa of the genus, *Kymatocalyx dominicensis* (Figure 108) grows on shaded rocks along rivers, in waterfalls, etc., often partly submerged, in moist tropical lowland and lower montane areas (Gradstein & Váňa 1999). It was very common as dark green mats on volcanic stones along the trail in Dominica (Gradstein 1989).

Kymatocalyx madagascariensis (Figure 109-Figure 110)

Distribution

Kymatocalyx madagascariensis (Figure 109-Figure 110) seems to be restricted to the East African islands: Madagascar (0.3-1380 m asl), Mauritius (700 m asl), Reunion (200-1800 m asl), and Comoro Archipelago (500-1580 m asl). Material from mainland Africa belongs to *K. africanus* (Figure 106) (Gradstein & Váňa 1999).

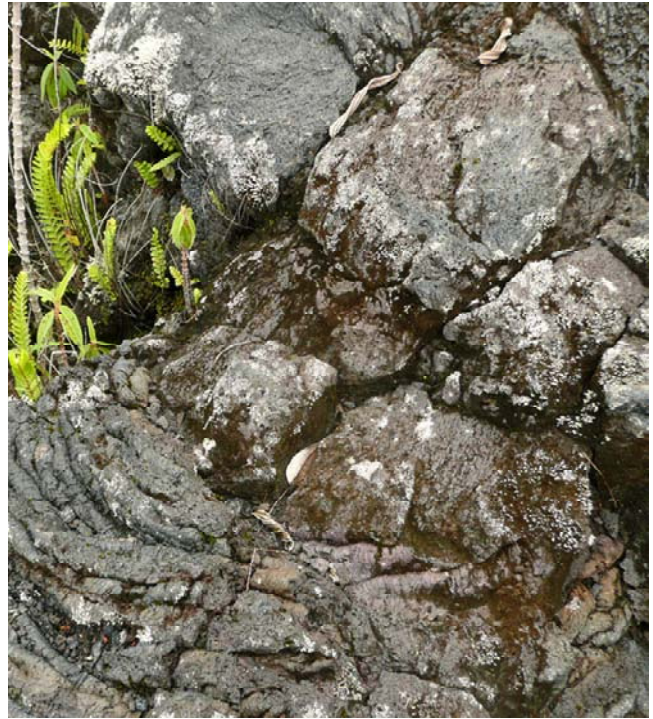


Figure 110. *Kymatocalyx madagascariensis* in crevices on old lava flow, Reunion Island. Photo courtesy of Tamás Pócs.



Figure 109. *Kymatocalyx madagascariensis*, a species endemic to east African islands, occupying lava rocks where they may be submerged at times of high rainfall. Photo courtesy of Tamás Pócs.

Aquatic and Wet Habitats

Kymatocalyx madagascariensis (Figure 109-Figure 110) grows on shaded granite and basaltic lava rocks, on cliffs and boulders near waterfalls, partly submerged or irrigated, in moist tropical lowland and montane rainforest areas (Gradstein & Váňa 1999). In Madagascar, Comores, and the Mascarenes it occurs mostly on volcanic rocks of temporary water flows (see Figure 111), but also occurs on wet soil on roadsides. On Réunion Island it occurs in shady cracks in 5-20-year-old lava flows (Figure 110) (Tamás Pócs, pers. comm. 3 March 2020).



Figure 111. *Kymatocalyx madagascariensis* temporary water flow habitat on old lava flow, Reunion Island. Photo courtesy of Tamás Pócs.

Kymatocalyx rhizomatica

(syn. = *Ruttnerella rhizocaula*)

Distribution

Kymatocalyx rhizomatica was reported from tropical wet areas by Ruttner (1955). It is a pantropical species from Malaysia, Sarawak (300 m asl), Sumatra, Costa Rica (150-600 m asl), Panama (150-300 m asl), and Colombia (700 m asl) (Gradstein & Váňa 1999).

Aquatic and Wet Habitats

Kymatocalyx rhizomatica grows on volcanic rock, stones, or moist earth in and along rivulets, in waterfalls and on trails in lowland and submontane rainforest areas (Gradstein & Vána 1999).

Reproduction

Kymatocalyx rhizomatica is cladautoicous and gemmae observations are rare (Gradstein & Vána 1999).

Lophoziaceae

Lophozia (Figure 112-Figure 121)

In western Canada, Glime and Vitt (1987) considered members of *Lophozia* in their stream study to be a restricted terrestrial of montane streams and streambanks. These are not submersed species.

Lophozia ventricosa (Figure 112-Figure 116)

Distribution

Records of *Lophozia ventricosa* (Figure 112-Figure 116) are almost entirely restricted to the Northern Hemisphere, from the Arctic to the subtropics (DiscoverLife 2020b). It occurs in the Antarctic/Southern Ocean region on an island off the southern coast of Australia, Europe, Asia, and North America (Alaska, Canada, Continental USA) (ITIS 2020e).



Figure 112. *Lophozia ventricosa* occurs from the Arctic to the subtropics in the Northern Hemisphere. Its wet habitats include being submerged in small lakes, on river banks, and in fens. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Lophozia ventricosa (Figure 112-Figure 116) can be truly aquatic in small lakes in the Scottish mountains where the ice cover lasts 4-7 months and the water is low in ions (Light 1975). In Belgium, Leclercq (1977) reported it on earthy and gravelly substrates of river banks (Figure 113) in the Haute Ardenne rivers. Lenz (2011) reported this species from fens in the Bighorn National Forest, Wyoming, USA.



Figure 113. *Lophozia ventricosa*, appearing here with other bryophytes on a gravelly substrate. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Lophozia ventricosa (Figure 112-Figure 116) produces gemmiferous shoots (Figure 114-Figure 116). Algar-Hedderston *et al.* (2013) found little difference in the gemma production between a boreal population in central Norway and one in the Arctic tundra on Svalbard. There was a significant difference in that shoots in the boreal site tended to produce somewhat more gemmae and form larger, denser colonies. This combination results in a somewhat higher colony level output in the boreal site.



Figure 114. *Lophozia ventricosa* with gemmiferous branches. Photo by Jan-Peter Frahm, with permission.

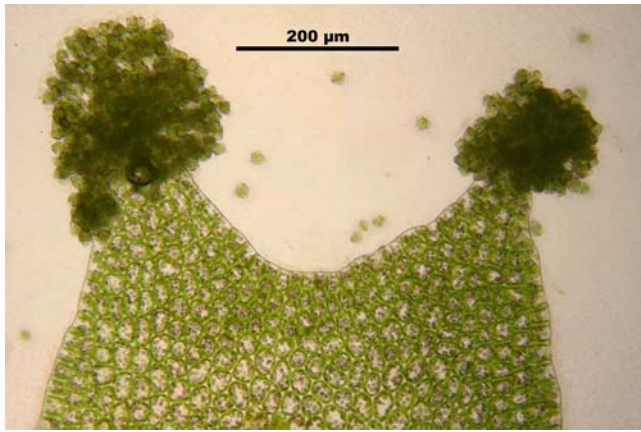


Figure 115. *Lophozia ventricosa* leaf showing gemmae at the tips of the leaf lobes. Photo by Hermann Schachner, through Creative Commons.



Figure 117. *Lophozia ascendens* with gemmae, a species that produces gemmae later than do *L. ventricosa* and *L. longifolia*. Photo by Michael Lüth, with permission.

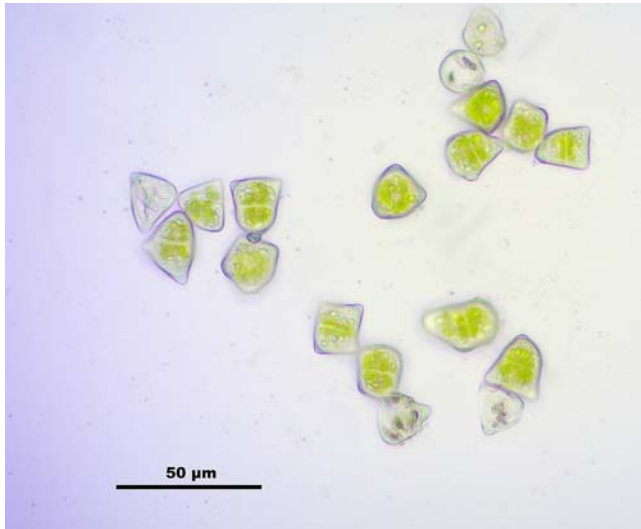


Figure 116. *Lophozia ventricosa* gemmae. Photo by Hermann Schachner, through Creative Commons.

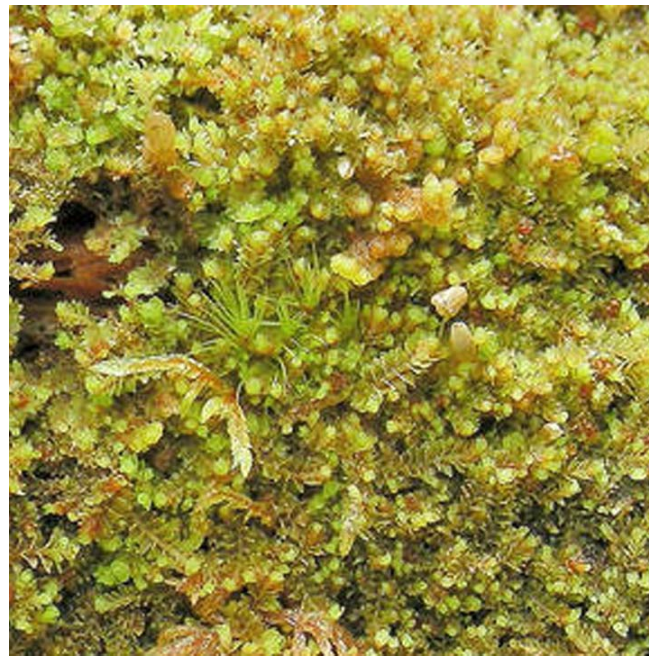


Figure 118. *Lophozia longiflora*, a species that has earlier gemma production compared to *L. ventricosa*. Photo by Earth.com, with permission.

Lophozia ventricosa (Figure 112-Figure 116) is a common liverwort in the National Nature Reserve in the Sumava Mountains, Bohemian Forest, Czech Republic. Holá *et al.* (2011) found that gemma production of the rare *L. ascendens* (Figure 117) was delayed in the growing season when compared to the more common *Lophozia ventricosa* and *L. longiflora* (Figure 118). The researchers concluded that air humidity was an important factor in the germinability of these gemmae. Gemma germination was low in early spring, reaching its highest level in August and September, and decreasing slightly in October. The researchers suggested that the rather mild winters of the Czech Republic assure a lower mortality of shoots in winter, thus decreasing selection pressure toward production of dormant gemmae of these species.

Fungal Interactions

Like many liverworts, *Lophozia ventricosa* (Figure 112-Figure 116) associates with members of the Ascomycota fungus *Sebacina vermifera* (see Figure 13) species complex (Bidartondo & Duckett 2010). It is known to share identical *Sebacina vermifera* DNA with the fungus on the leafy liverwort *Nardia scalaris* (Figure 119).

Biochemistry

Lophozia ventricosa (Figure 112-Figure 116) most likely benefits from its antimicrobial activity (Bukvicki *et al.* 2015). This species proved to have a number of compounds that are active against a variety of bacteria and fungi.



Figure 119. *Nardia scalaris*, a leafy liverwort species that shares the fungus *Sebacina vermifera* having the same DNA as that fungus occurring on *Lophozia ventricosa*. Photo by Hermann Schachner, through Creative Commons.

Lophozia ventricosa (Figure 112-Figure 116) possesses a variety of secondary compounds (Lu *et al.* 2005). The essential oils include sesquiterpenoids (Lu *et al.* 2005; Song *et al.* 2007) and terpenoids (Tori *et al.* 1993). Thus far, we have little information on the advantage these compounds give to specific liverworts, but it is likely that at least some of them serve as antiherbivore compounds. This is beneficial for organisms with slow growth rates, where the rate of herbivory could be greater than the growth rate. These antifeedant compounds could help the liverwort win the race.

Lophozia wenzelii (Figure 120-Figure 121)

Distribution

Lophozia wenzelii (Figure 120-Figure 121) is an arctomontane species (Bakalin 2004) distributed in Europe, Asia, and North America from Alaska, through the continental USA (ITIS 2020f). It extends from Greenland to India, China, and Japan in the Eastern Hemisphere, and to New Mexico, USA, in the Western Hemisphere (GBIF 2020c). It is unknown in the high Arctic except for Greenland (Bakalin 2004).



Figure 120. *Lophozia wenzelii*, an arctomontane species that can occur in alpine streams, mountain bogs, and marshy areas. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Vána (2005) considers that this species occurs mostly in mountain bogs and marshy areas. It occurs more rarely on wet rocks or rock debris. But in the Swiss Alps, Geissler (1976) found it in alpine streams, occurring uncommonly with *Carex goodenoughii* and *Eleocharis quinqueflora* (Figure 76) (Geissler & Selldorf 1986). In Russia at the Ushkovskii Volcano, Bakalin (2005) *Lophozia wenzelii* (Figure 120-Figure 121) occurs in glacial areas on stones of stream banks as well as on light soil between hummocks. This hummock soil is mixed yearly by freezing and thawing dynamics.



Figure 121. *Lophozia wenzelii* showing its growth habit. Photo by Štěpán Koval, with permission.

Bakalin (2005) reports that *Lophozia wenzelii* (Figure 120-Figure 121) grows among mosses and liverworts, but rarely forms pure **mats**. In moss tundra and oligotrophic bogs it is interspread within the boreal forest zone. In rare circumstances it grows along the peaty banks of streams on fine-granulated soil or on somewhat dry rocks. In the tundra it is able to grow in microdepressions between heath-lichen or moss patches. Frequently it occurs in wet (var. *wenzelii*) or dry (var. *groenlandica*) crevices of gravelly barrens and rocks (including seacoast cliffs). The main habitats, however, are oligotrophic bogs, where *L. wenzelii* sometimes grows in pure mats or mixed with *Gymnocolea inflata* (Figure 17-Figure 22), *Scapania* spp. (most frequently with *S. paludicola* – Figure 122), *Cephalozia* spp. (Figure 45-Figure 60), and *Odontoschisma fluitans* (Figure 92-Figure 93) (Bakalin 2004).



Figure 122. *Scapania paludicola*, a species that often accompanies *Lophozia wenzelii*. Photo by Michael Lüth, with permission.

In the Upper Puiva River in the Urals of Russia, Konstantinova and Lapshina (2017) found *Lophozia wenzelii* (Figure 120-Figure 121) on soil and bare loamy soil of the tundra, in snowbed communities, between boulders in rock fields, in dwarf shrub-sedge-*Sphagnum* bogs, in seepages, on banks of brooks, and on road sides. Here they occur in pure mats or mixed with a variety of other leafy liverworts and mosses.

Adaptations

In Europe and northern Asia, var. *litoralis* exhibits rusty brown to red-brown plants. These live in places with disturbed vegetation cover, on soil near brook banks, or in the subalpine belt on mountains. Where vegetation is disturbed they occur on finely granulated soil or among mosses in lax mats. The occurrence on wet cliffs is rare.

Lophozia wenzelii (Figure 120-Figure 121) is a critically endangered species in the Czech Republic (Čihál & Kaláb 2017). In a model to determine the most important habitat characters for their presence, several factors emerged. The probability of presence is lower when the temperatures are higher in the warmest month. Higher precipitation values in the driest month also favor habitation. Since the least precipitation in the Czech Republic occurs in winter (January or February), the winter precipitation is important.

Lophoziopsis excisa (Figure 123-Figure 124)

(syn. = *Lophozia excisa*)

Distribution

Lophoziopsis excisa (Figure 123-Figure 124) is a highly variable and wide-ranging species (Schuster 1969). Its distribution is bipolar, ranging from Greenland southward to Italy and Spain in the Eastern Hemisphere and to some of the mountain forests in the southern Appalachian Mountains in eastern USA and to California in western USA. It has been found on Antarctica, in New

Zealand, southern Chile, and southern Argentina. GBIF (2020d) includes it in Northern Asia as well, probably in alpine regions of Japan (Kitagawa 1965).



Figure 123. *Lophoziopsis excisa* with gemmae, a bipolar species extending south into mountains of the temperate zone. It most commonly occurs with other bryophytes on cliffs along streams and in bogs. Photo by Štěpán Koval, with permission.



Figure 124. *Lophoziopsis excisa* with gemmae. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

The habitats of this species suggest that it is indifferent to pH within most of the normal range (Schuster 1969). It occurs primarily on mineral substrata, but is also able to live on exposed loamy, acid soil. It is always mixed with other bryophytes, especially other leafy liverworts, in the Upper Puiva River basin of the Ural Mountains in Russia (Konstantinova & Lapshina 2017). Geissler and Selldorf (1986) found it was uncommon with *Carex goodenoughii* in bogs in Ticino, Switzerland. In *Rhododendron lapponicum* (syn. = *Ledum groenlandicum*; Figure 125) bogs of the glacial relict lake areas of the Komi Republic of northwestern Russia, it occurs on decaying wood and slightly matted soil, and on soil in a *Menyanthes-Comarum Sphagnum* mixed forest (Dulin 2015). In the

Timpton River Basin, South Yakutia, Russia, Sofronova (2017) found *Lophozia excisa* (Figure 123-Figure 124) mixed with other liverworts on soil of moist south-facing cliffs along the river bank as well as on fine soil in cliff cracks. But it is also found on soil in between stones of the stone field on south-facing slopes, where it can occur in pure mats or mixed with other liverworts.



Figure 125. *Rhododendron groenlandicum* bog, a habitat where it occurs on decaying wood and slightly matted soil in northwestern Russia. Photo by Wynn Anderson, through Creative Commons.

Reproduction

Lophozia excisa (Figure 123-Figure 124) is **paroicous** with red gemmae (Konstantinova & Savchenko 2018).

Fungal Interactions

Newsham and Bridge (2010) noted the presence of fungi belonging to **Sebacinales** (Figure 13) in *Lophozia excisa* (Figure 123-Figure 124) at Léonie Island in the southern maritime Antarctic. Newsham *et al.* (2014) reported the occurrence of *Cladophialophora* (Figure 126) and related fungi in the tissues of *Lophozia excisa* from Léonie Island. Fungal partners are fairly well known among bog plants (Thormann 2006), including liverworts (Duckett & Clymo 1988) so the presence of fungi with this liverwort species on peaty soils is not surprising.



Figure 126. *Cladophialophora* sp.; some species of this fungal genus are found in tissues of *Lophozia excisa*. Photo by Medmyco, through Creative Commons.

Trilophozia quinquedentata (Figure 127-Figure 128)

(syn. = *Tritomaria quinquedentata*)

Distribution

Trilophozia quinquedentata (Figure 127-Figure 128) is widely distributed in the Northern Hemisphere from the Arctic to northern USA and to at least one location each in China and Japan (TROPICOS 2020).



Figure 127. *Trilophozia quinquedentata*, a Northern Hemisphere mostly terrestrial species that can occur on wet cliffs, dripping rock surfaces, and associated with waterfalls. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

This mostly terrestrial species is at least tolerant of water, occurring on wet cliffs of the Upper Bureya River in the Russian Far East (Konstantinova *et al.* 2002). It also occurs on dripping steep rock surfaces of granite at the margins of shaded permanent waterfalls, where it is only loosely attached (Figure 128) (Vieira *et al.* 2005). It is also typically associated with *Chiloscyphus polyanthos* (Figure 129) and *Aneura pinguis* (Figure 130) in mountain streams of northwest Portugal.



Figure 128. *Trilophozia quinquedentata* loosely attached to its substrate. Photo by Hugues Tinguy, with permission.



Figure 129. *Chiloscyphus polyanthos*, a common associate of *Trilophozia quinquedentata*. Photo by Štěpán Koval, with permission.



Figure 130. *Aneura pinguis*, a common associate of *Trilophozia quinquedentata*. Photo by Hermann Schachner, through Creative Commons.

***Tritomaria exsecta* (Figure 131-Figure 136)**

(syn. = *Sphenolobus exsectus*)

Distribution

Tritomaria exsecta (Figure 131-Figure 136) extends in a wide range including Australia, Asia, Europe, and North America from Mexico to Alaska (ITIS 2020g). It has also been reported from eastern Africa (BFNA 2020) and New Zealand (Engel 2006).

Aquatic and Wet Habitats

Its inclusion in aquatic and wetland studies seems to be rare. Nichols (1916) reported it as a **calciphobic** (avoiding calcium) species along rivers in Connecticut, USA. Glime (1982) reported it from the wall of the humid flume (Figure 37) at Franconia Notch, New Hampshire, USA.



Figure 131. *Tritomaria exsecta*, a wide-ranging mostly terrestrial species, occurring as a calciphobe along rivers and on humid canyon walls. Photo by Hermann Schachner, through Creative Commons.



Figure 132. *Tritomaria exsecta*. Photo by Michael Lüth, with permission.

Reproduction

It forms mats and can produce apical gemmae (Figure 133-Figure 136).



Figure 133. *Tritomaria exsecta* in a mat with gemmae at the apex of shoots. Photo by Hermann Schachner, through Creative Commons.



Figure 134. *Tritomaria exsecta* with apical gemmae. Photo by Michael Lüth, with permission.



Figure 135. *Tritomaria exsecta* with gemmae. Photo by Michael Lüth, with permission.

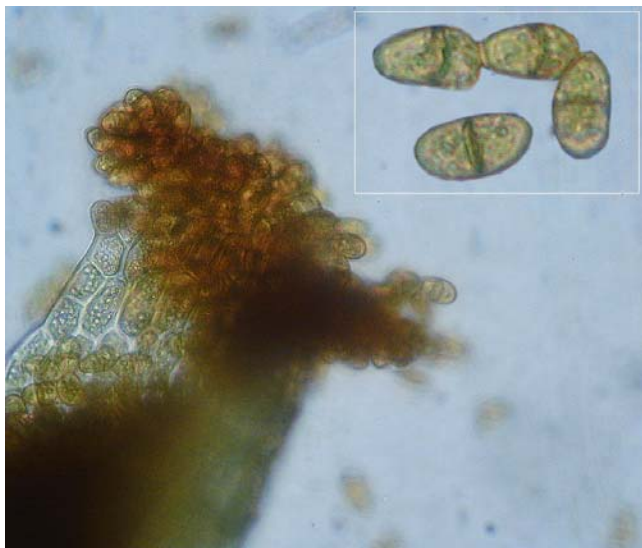


Figure 136. *Tritomaria exsecta* gemmae. Photo by Michael Lüth, with permission.

Tritomaria exsectiformis (Figure 137, Figure 141-Figure 143)

Distribution

Tritomaria exsectiformis (Figure 137, Figure 141-Figure 143) is an Arctic-alpine, circumboreal species (Harpel & Dewey 2005). It is distributed in North America from Greenland and Alaska southward to Colorado, Iowa, Michigan, and Pennsylvania in the USA. It is also present in Europe, Asia, and Africa (Hong 2002).



Figure 137. *Tritomaria exsectiformis*, a species distributed from the Arctic to the temperate region in the Northern Hemisphere, occurring mostly at high elevations where it often occurs in areas of perennial flow at or near springs and seeps. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

In Greenland, Hassel *et al.* (2014) found *Tritomaria exsectiformis* (Figure 137, Figure 141-Figure 143) growing on rocks in a heathland of *Vaccinium uliginosum* (Figure 138) with the mosses *Saelania glaucescens* (Figure 139), *Bartramia ithyphylla* (Figure 140), and liverwort *Scapania* sp. (e.g. Figure 122).



Figure 138. *Vaccinium uliginosum* with fruit, the dominant species in heathland where one can find *Tritomaria exsectiformis*. Photo by David Gaya, through Creative Commons.



Figure 139. *Saelania glaucescens*, a species growing with *Tritomaria exsectiformis* on rocks in blueberry heathlands. Photo by Michael Lüth, with permission.



Figure 140. *Bartramia ithyphylla*, a species growing with *Tritomaria exsectiformis* on rocks in blueberry heathlands. Photo by J. C. Schou, with permission.

In western USA, Harpel and Dewey (2005) found *Tritomaria exsectiformis* (Figure 137, Figure 141-Figure 143) to be typical of open to shaded coniferous forest where it is associated with low volume, perennial water flow at or near springs and seeps. These typically occur on very gentle topographic gradients. Its substrate is usually decaying wood (Figure 141) in stage four decay and having direct contact with water. It is never present where there is high volume flow.



Figure 141. *Tritomaria exsectiformis* on wet, decaying wood. Photo by Stan Phillips, through public domain.

Reproduction

This perennial species occurs mostly at high elevations where snow remains a long time into spring and summer, usually at elevations above 1500 m (Harpel & Dewey 2005). This gives it a short growing season with a late summer and fall. Reproduction occurs only by gemmae (Figure 142-Figure 143) and other vegetative means. The species is a restricted terrestrial associated with the montane streams and streambanks of western Canada (Figure 103) (Vitt *et al.* 1986; Glime & Vitt 1987). Hong (1994) reported it from creek banks, decayed wood, and humus over decayed wood in forests ranging from 0 to 2300 m asl.

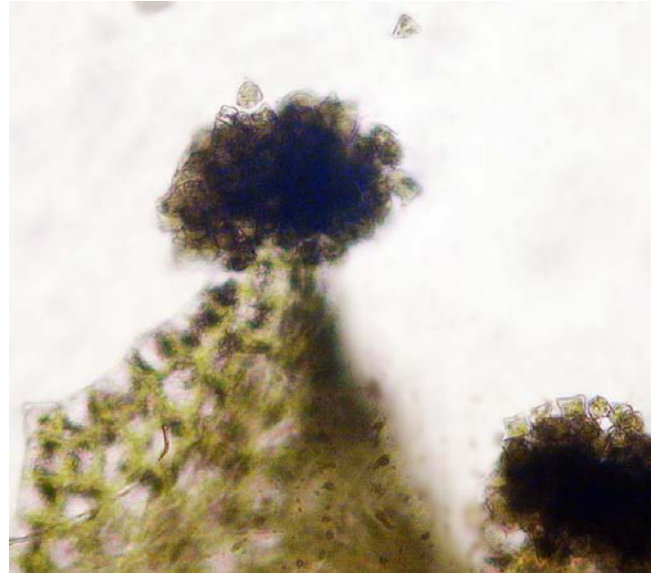


Figure 142. *Tritomaria exsectiformis* with clusters of gemmae on leaf tips. Photo by Michael Lüth, with permission.

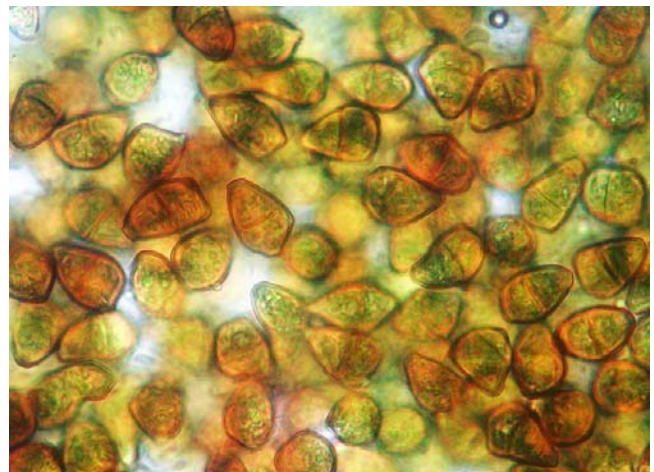


Figure 143. *Tritomaria exsectiformis* gemmae. Photo by Michael Lüth, with permission.

Tritomaria exsectiformis (Figure 137, Figure 141-Figure 143) is dioicous, thus rarely producing sporophytes. Harpel and Dewey (2005) suggested that dispersal is most likely accomplished by moving water and possibly invertebrates. It requires a substrate that provides a constant water supply without the dangers of scouring.

Summary

The **Cephaloziineae**, except for **Scapaniaceae**, are not common in wet habitats, and especially rare in the water. The **Adelanthaceae** has only 2 species in 2 genera that have appeared in wetland habitats, with *Syzygiella sonderi* being submerged in high elevation lakes in the Andes. The **Anastrophyllaceae** is predominantly terrestrial, but may appear on wet cliffs and wet rocks of stream banks and waterfalls. I have identified only 9 species (7 genera) in such wet habitats. The mostly tiny **Cephaloziaceae** seem somewhat more aquatic, occurring in small ponds and mires as well as wet cliffs and rocks of lake shores and stream banks, but with only 9 species (3 genera) included in the literature surveyed. They often occur among other bryophytes, thus protecting them from frequent desiccation. Some become submerged. Some species regenerate from buried stolons. The **Ascomycota** *Mniaecia jungermanniae* can inhabit members of *Cephalozia*, and *Pezoloma ericae* can occur on the rhizoids. The **Zygomycota** species *Mucor rhizophilus* occurs on rhizoids in several genera of **Cephaloziaceae**. The **Cephaloziellaceae** is represented by 8 species (2 genera) in carpets of wet areas in the Antarctic and lakes of Finland, but it is mostly terrestrial. The **Lophoziaceae** is represented by 6 species (2 genera) here, again by species that grow mostly terrestrially. Nevertheless, some occur in mountain lakes and others in bogs and marshy areas. Seeps and dripping rock surfaces are suitable for some. Some take advantage of the water from late snow melt.

Acknowledgments

Lars Söderström helped me find the current acceptable names for a number of older taxa. David Wagner alerted me to *Rivulariella* and provided me with references and images.

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CHAPTER 1-3

AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: CEPHALOZIINEAE 2

TABLE OF CONTENTS

Scapaniaceae	1-3-2
<i>Diplophyllum</i>	1-3-2
<i>Diplophyllum albicans</i>	1-3-2
<i>Diplophyllum taxifolium</i>	1-3-7
<i>Douinia ovata</i>	1-3-9
<i>Saccobasis polita</i>	1-3-9
<i>Scapania</i>	1-3-10
<i>Scapania aspera</i>	1-3-10
<i>Scapania crassiretis</i>	1-3-11
<i>Scapania cuspiduligera</i>	1-3-11
<i>Scapania hyperborea</i>	1-3-13
<i>Scapania irrigua</i>	1-3-15
<i>Scapania microdonta</i>	1-3-18
<i>Scapania nemorea</i>	1-3-19
<i>Scapania paludicola</i>	1-3-22
<i>Scapania paludosa</i>	1-3-23
<i>Scapania ridiga</i>	1-3-24
<i>Scapania rufidula</i>	1-3-25
<i>Scapania subalpina</i>	1-3-25
<i>Scapania uliginosa</i>	1-3-26
<i>Scapania umbrosa</i>	1-3-29
<i>Scapania undulata</i>	1-3-30
Distribution	1-3-30
Aquatic and Wet Habitats	1-3-31
Streams.....	1-3-32
Lakes	1-3-33
Associations	1-3-34
pH	1-3-35
Water Relations.....	1-3-36
Temperature	1-3-37
Photosynthetic Products	1-3-37
Reproduction.....	1-3-37
Biochemistry	1-3-38
Pigments.....	1-3-38
Nutrient Relations	1-3-39
Heavy Metals	1-3-40
Other Pollutants.....	1-3-41
Disturbance	1-3-41
Role	1-3-41
Habitat Summary	1-3-41
Summary.....	1-3-42
Acknowledgments	1-3-42
Literature Cited	1-3-42

CHAPTER 1-3

AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER JUNGERMANNIALES: CEPHALOZIINEAE 2



Figure 1. *Scapania undulata* and habitat, showing its close adherence to water without necessarily being submerged. Many of the leafy liverworts treated in this chapter occupy niches that maintain moisture without submergence. Photo by Jean Faubert, with permission.

Scapaniaceae

It is interesting that very similar mosaic infection patterns in **Lophoziaceae** and **Scapaniaceae** add strength to the molecular link between the two families (Duckett *et al.* 2006). Both are in Cephaloziineae.

Diplophyllum albicans (Figure 2, Figure 12, Figure 14-Figure 15)

Distribution

Diplophyllum albicans (Figure 2, Figure 12, Figure 14-Figure 15) is an amphi-oceanic species, but rarely penetrates away from the oceanic climate (Bakalin & Vilnet 2018).



Figure 2. *Diplophyllum albicans*, an amphi-oceanic species of wet cliffs and lake shores as well as fast streams. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

In Scotland, this species sometimes covers the hill lake shore rocks (West 1910). Nichols (1918) reported *Diplophyllum albicans* (Figure 2, Figure 12, Figure 14-Figure 15) from wet rock cliffs on Cape Breton Island, Canada. But by contrast, Watson (1919) considered the species to be associated with fast water. This is more consistent with their habitat on moist stones and rocks in the stream beds of the Gory Stolowe Mountains in Poland (Szweykowski 1951), on rocks in streams near Lacko in the Western Carpathians (Mamczarz 1970), upper and middle stream reaches in Harz Mountains of Germany (Bley 1987), in aquatic habitats of eastern Odenwald and southern Spessart with *Heterocladium heteropterum* (Figure 3) (Philippi 1987), and in rivers (Ferreira *et al.* 2008).



Figure 3. *Heterocladium heteropterum*, a species that may accompany *Diplophyllum albicans* on gravelly river banks. Photo by Štěpán Koval, with permission.

Other habitats are wet, but not submersed. In the Haute Ardenne rivers in Belgium, Leclercq (1977) found *Diplophyllum albicans* (Figure 2, Figure 12, Figure 14-Figure 15) on earthy and gravelly substrates of river banks. In the British Isles, Orange (2001) found the species on a shaded damp rock face by a wooded stream. In the Upper Bureya River of the Russian Far East, Konstantinova *et al.* (2002) reported it from a wet cliff and rocks at the lake shore, occurring with *Blepharostoma trichophyllum* (Figure 4), *Cephalozia ambigua* (Figure 5), *Gymnomitrium concinnatum* (Figure 6), *Barbilophozia sudetica* (Figure 7), *Marsupella boeckii* (Figure 8), *M. emarginata* subsp. *tubulosa* (Figure 9), and *Fuscocephaloziopsis albescens* (Figure 10).



Figure 4. *Blepharostoma trichophyllum*, a species that may accompany *Diplophyllum albicans* on wet cliffs and lake shore rocks. Photo by Hermann Schachner, through Creative Commons.

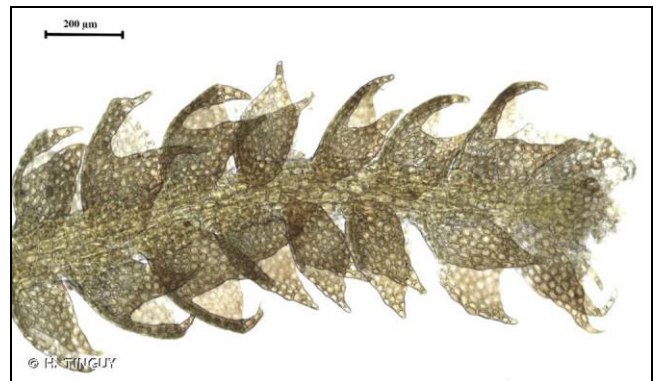


Figure 5. *Cephalozia ambigua*, a species that may accompany *Diplophyllum albicans* on wet cliffs and lake shore rocks. Photo by Hugues Tinguy, with permission.



Figure 6. *Gymnomitrium concinnatum*, a species that may accompany *Diplophyllum albicans* on wet cliffs and lake shore rocks. Photo by Michael Lüth, with permission.



Figure 7. *Barbilophozia sudetica*, a species that may accompany *Diplophyllum albicans* on wet cliffs and lake shore rocks. Photo by Hugues Tinguy, with permission.



Figure 8. *Marsupella boeckii*, a species that may accompany *Diplophyllum albicans* on wet cliffs and lake shore rocks. Photo by Earth.com, with permission.



Figure 9. *Marsupella emarginata* subsp. *tubulosa*, a species that may accompany *Diplophyllum albicans* on wet cliffs and lake shore rocks. Photo from Taiwan Moss Color Book, through Creative Commons.

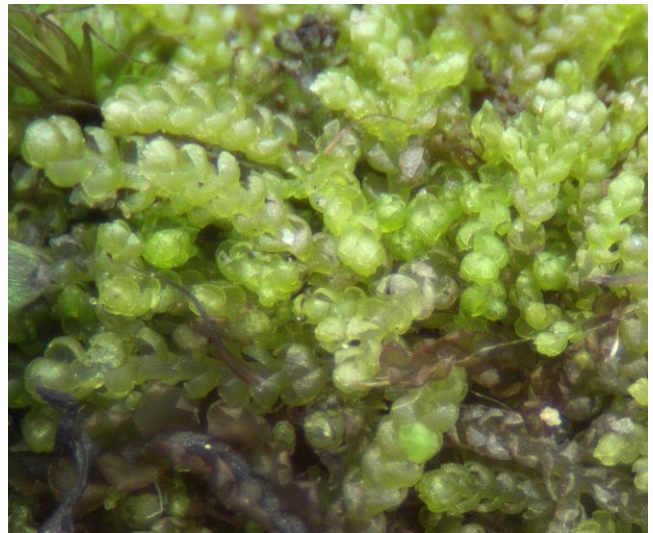


Figure 10. *Fuscocephaloziopsis albescens*, a species that may accompany *Diplophyllum albicans* on wet cliffs and lake shore rocks. Photo by Tomas Hallingbäck, with permission.

Not all of the reported habitats are associated with water. Leach (1930) found them on non-calcareous British scree, associated with *Racomitrium* (Figure 11) species. In southern Chile, *Diplophyllum albicans* (Figure 2, Figure 12, Figure 14-Figure 15) occurs on sea cliffs where they are subject to seawater spray (Engel & Schuster 1973). The researchers suggest that bryophytes are able to survive the salt spray on these cliffs because of high rainfall and forest drainage that provide fresh water. In the humid Queen Charlotte Islands, Glime and Hong (2002) found *Diplophyllum albicans* as epiphytes.

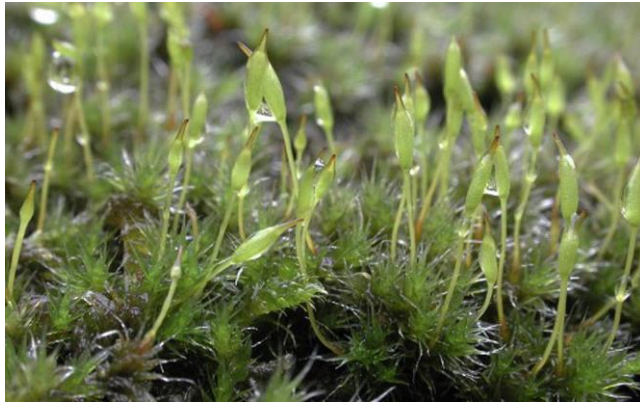


Figure 11. *Racomitrium heterostichum*; members of this genus accompany *Diplophyllum albicans* on non-calcareous British scree. Photo by Jan-Peter Frahm, with permission.

Physiology

Clausen (1964) demonstrated the need for water by *Diplophyllum albicans* (Figure 2, Figure 12, Figure 14-Figure 15). In experiments, most cells of this species died at humidities less than 63% at 20°C. Most stream environments where this species occurs would rarely reach these conditions at this low humidity and this degree of heat. Nevertheless, its tolerance is greater than that of *Calypogeia arguta* (Figure 13).



Figure 12. *Diplophyllum albicans* in a hydrated state, showing the overlapping shoots. Photo by Hermann Schachner, through Creative Commons.



Figure 13. *Calypogeia arguta*, a species with poor tolerance of low humidity. Photo by Des Callaghan, with permission.

Reproduction

This species is dioicous, limiting its ability to reproduce sexually (Schuster 1974). However, it can produce abundant gemmae (Figure 14-Figure 15).

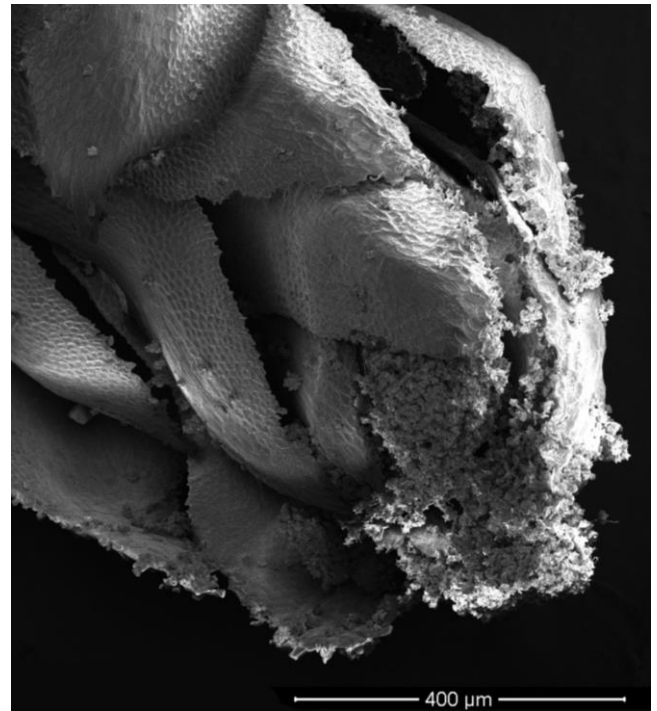


Figure 14. SEM of *Diplophyllum albicans* leaves with gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

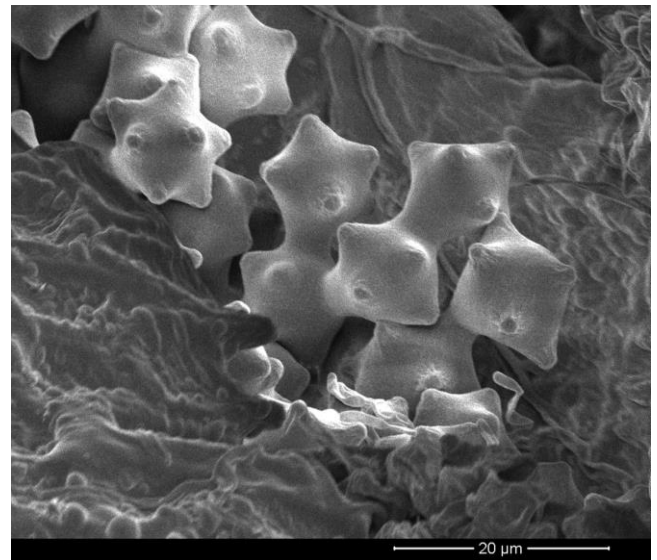


Figure 15. SEM of *Diplophyllum albicans* gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

Interactions

That *Diplophyllum albicans* (Figure 2, Figure 12, Figure 14-Figure 15) is a poor competitor has been demonstrated in high altitude blanket bogs (Rawes 1983). When sheep grazing ceased, this species declined, suggesting that the ability of other plant species, especially *Calluna vulgaris* (Figure 16), to increase may have created competition against the *D. albicans*.



Figure 16. *Calluna vulgaris*, a species that increases when sheep grazing ceases. Photo by Willow, through Creative Commons.

Diplophyllum albicans (Figure 2, Figure 12, Figure 14-Figure 15) occurring in mossy ravines is frequently a substrate for *Myxomycetes* (slime molds) (Ing 1983). The nature of this relationship is not known.

Fungal Interactions

Like many of the leafy liverworts, *Diplophyllum albicans* (Figure 2, Figure 12, Figure 14-Figure 15) can serve as host for the parasitic Ascomycota fungus *Mniaecia jungermanniae* (Figure 17) (Pressel & Duckett 2006). Although the fungus does not seem to penetrate the cells, its colonization coincides with the formation of giant perichaetia and abnormal perianths, conditions that were also present in wild populations of *Diplophyllum* and other species. The association does not appear to cause long-term damage, although it can cause a local reduction of perianth development. Henderson (1972) concluded that this fungus favors **moribund** (at point of death) *Diplophyllum albicans* as its substrate.



Figure 17. *Mniaecia jungermanniae* on *Cephalozia bicuspidata*; *M. jungermanniae* causes enlarged perianths on *Diplophyllum albicans*. Photo courtesy of Jan Gaisler.

Biochemistry

This raises the question of its ability to survive and thrive within some plant communities, but not others. Like other liverworts, *Diplophyllum albicans* (Figure 2, Figure 12, Figure 14-Figure 15) produces sesquiterpenoids. Their

abundance and diversity are evidenced by the discovery of six new sesquiterpenoids and two new norsesquiterpenoids from three liverworts (Adio & König 2007; see also Benešová *et al.* 1975), with one from *Diplophyllum albicans*. Asakawa *et al.* (1979) had already named "pungent sesquiterpene lactones" from this species. All of these exhibited inhibitory activity toward germination and root elongation in rice husks, suggesting a competitive advantage for the slower-growing liverworts.

Tadesse (2002) found natural plant products in *Diplophyllum albicans* (Figure 2, Figure 12, Figure 14-Figure 15) that exhibited antifungal activity, but these were not tested on *Mniaecia jungermanniae* (Figure 17). They are known to act against the common fungi *Botrytis cinerea* (Figure 18-Figure 19) and *Alternaria solani* (Figure 20-Figure 21) (Mekuria *et al.* 1999; Tadesse 2002). Saxena and Harinder (2004; Olofin *et al.* 2013) noted the presence of diplophyllin from *Diplophyllum albicans*. This compound is active against human epidermoid carcinoma (Ohta *et al.* 1977).



Figure 18. *Botrytis cinerea* on tomato; this is a fungus that is inhibited by extracts from *Diplophyllum albicans*. Photo by Paul Bachi, USDA, through Creative Commons.



Figure 19. *Botrytis cinerea* a fungus that is inhibited by extracts of *Diplophyllum albicans*. Photo by Paul Bachi, USDA, through Creative Commons.



Figure 20. *Alternaria solani* causing stem lesions; this fungus is inhibited by extracts from the liverwort *Diplophyllum albicans*. Photo from Clemson University USDA, through Creative Commons.



Figure 21. *Alternaria solani* spore. Photo by Paul Bachi, through Creative Commons.

***Diplophyllum taxifolium* (Figure 22-Figure 23, Figure 29)**

Distribution

Diplophyllum taxifolium (Figure 22-Figure 23, Figure 29) is a Northern Hemisphere taxon, mostly from temperate and boreal zones in Europe, Asia, Oceania, Alaska, Canada, USA (ITIS 2020a). It extends from Greenland in the East southward to Newfoundland, Labrador, Nova Scotia, Ontario, Maine, south as far as North Carolina and Tennessee and in the west from Alaska, USA, to British Columbia and New Brunswick in Canada, southward to Washington state in the USA (Redfearn 2008).



Figure 22. *Diplophyllum taxifolium*, a Northern Hemisphere species that extends southward into the mountains. It occurs on humid and wet rock cliffs, rocky stream banks, and on alder hummocks. Photo by Michael Lüth, with permission.



Figure 23. *Diplophyllum taxifolium* showing its growth habit. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

On Cape Breton Island, Canada, Nichols (1918) reported *Diplophyllum taxifolium* (Figure 22-Figure 23, Figure 29) from rock cliffs associated with streams. Choi *et al.* (2013) found it on wet cliffs along a stream in a mixed conifer-broadleaf forest of Mt. Deogyu National Park at 680-1160 m asl in the Republic of Korea. Here it was often in association with *Bazzania denudata* (Figure 24) and *Calypogeia tosana* (Figure 25). In the Endybal River Basin, Yakutia, in Russia, *Diplophyllum taxifolium* occurs on soil of rocky outcrops along stream banks (Sofronova & Kopyrina 2016). It is typically mixed with *Cephaloziella varians* (Figure 26), *Marsupella emarginata* (Figure 27), *Scapania crassiretis* (Figure 36), and *Sphenobolus minutus* (Figure 28). In a different region of Yakutia (Indigirka River), *Diplophyllum taxifolium* likewise occurred on wet cliffs, but forming less cover than some of the other liverwort species (Sofronova 2018). At the Ushkovskii Volcano in Kamchatka, Russia, Bakalin (2006) found this species growing between the hummocks and on spots of light soil shaded by alder. In North America, Redfearn (2008) found that it occurs at 0-1950 m asl on shaded rocks, cliffs, soil banks, humus, and frequently along streams.



Figure 24. *Bazzania denudata*, a species in association with *Diplophyllum taxifolium* on rock cliffs by streams. Photo by Kent Brothers, with permission through UBC Botany website.



Figure 27. *Marsupella emarginata*, a species in association with *Diplophyllum taxifolium* on rock cliffs by streams. Photo by Hermann Schachner, through Creative Commons.



Figure 25. *Calypogeia tosana*, a species in association with *Diplophyllum taxifolium* on rock cliffs by streams. Photo from Digital Museum, Hiroshima University, with permission.



Figure 28. *Sphenolobus minutus*, a species in association with *Diplophyllum taxifolium* on rock cliffs by streams. Photo by Jan-Peter Frahm, with permission.



Figure 26. *Cephaloziella varians*, a species in association with *Diplophyllum taxifolium* on rock cliffs by streams. Photo by Kristian Peters, with permission.

Terrestrial

Diplophyllum taxifolium (Figure 22-Figure 23, Figure 29) does occur in habitats that one would expect to get dry (Figure 29). Růžicka *et al.* (2012) reported it from periglacial areas in low-altitude scree slopes. The air circulation through these talus slopes creates microclimates that have lower temperatures, often experiencing temperatures $<0^{\circ}\text{C}$ during snow-free periods. These allow ice to accumulate year-round, as seen on Kamenec Hill in North Bohemia, Czech Republic at only 330 m asl. These habitats serve as refugia for boreal and Arctic bryophytes. The slow melt may keep the atmosphere near the ice sufficiently moist to provide for the needs of the liverworts.



Figure 29. *Diplophyllum taxifolium* in a terrestrial habitat. Photo by Michael Lüth, with permission.

Reproduction

Diplophyllum taxifolium (Figure 22-Figure 23, Figure 29) is dioicous (Redfearn 2008). The male and female plants typically are in separate patches, resulting in little fertilization. The male plants are smaller. Hong (1980) states that gemmae are abundant, but none of the pictures I found showed any.

Biochemistry

Diplophyllum taxifolium (Figure 22-Figure 23, Figure 29) exhibits ent-eudesmanolides and entprenylaromadendrones, compounds that provide biological activities that may increase its competitive ability (Wang *et al.* 2016). This species of *Diplophyllum* seems to avoid colonization by fungi (Bidartondo & Duckett 2010). We need to test the effectiveness of these secondary compounds in deterring the colonization of common liverwort-inhabiting fungi. These secondary compounds do not seem to prevent at least some fungi from colonizing this species

Douinia ovata (Figure 30)

(syn. = *Harpalejeunea ovata*)

Distribution

Douinia ovata (Figure 30) is a subarctic species, distributed on the Pacific coast of North America from Alaska, USA, to British Columbia, Canada (Váňa 1996). It also is known from the Atlantic side of Europe and from Japan.



Figure 30. *Douinia ovata*, a species distributed along the Pacific coast of North America, the Atlantic side of Europe, and Japan. It is only occasionally submerged. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Douinia ovata (Figure 30) is not usually an aquatic species, but Watson (1919) reported it as being occasionally submerged. It is among the most common species of the **Lophoziaceae-Scapaniaceae** complex north of the tropics (Söderström *et al.* 2007). Its occurrence is oceanic, suggesting it may be intolerant of a climate with a wide variation.

Adaptations and Reproduction

Douinia ovata (Figure 30) has a **mat** life form and is a perennial stayer (Miyashita 2013). It lacks specialized asexual reproductive structures.

Fungal Interactions

Like *Diplophyllum taxifolium* (Figure 22-Figure 23, Figure 29), Wang and Qiu (2006) found no records of fungal associations for this species.

Saccobasis polita (Figure 31)

(syn. = *Sphenolobus politus*)

Distribution

Saccobasis polita (Figure 31) occurs in Austria, Russian Federation (TROPICOS 2020), North America from Alaska to Washington and Colorado, USA (Hong 1994), the Swiss Alps (Geissler 1976), and Norway (Zander 1983).



Figure 31. *Saccobasis polita*, a species from North America and northern Europe where it occurs in alpine streams. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) reported *Saccobasis polita* (Figure 31) in alpine areas on wet ground associated with *Harpanthus flotovianus* (Figure 32) and *Mesoptychia bantriensis* (Figure 33). Geissler (1976) similarly reported it from alpine streams. Bakalin (2008) found this species in the Nabil'sky Range at 1406 m asl in Russia, where it occurred on fine-grained soil along a stream.

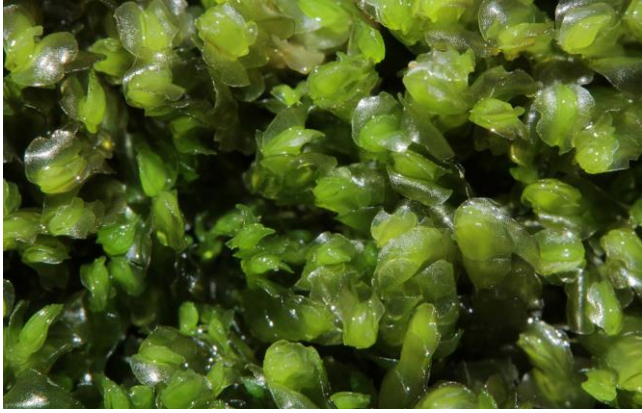


Figure 32. *Harpanthus flotvianus*, a species associated with *Saccobasis polita* in alpine areas on wet ground. Photo by Hermann Schachner, through Creative Commons.



Figure 33. *Mesoptychia badensis*, a species associated with *Saccobasis polita* in alpine areas on wet ground. Photo by Štěpán Koval, with permission.

Reproduction

In Norway, *Saccobasis polita* (Figure 31) plants produce gemmae, but these appear to be different from those reported elsewhere for the species and appear to represent at least a different variety (Damsholdt 1983). Jóhannsson (1984) found that ssp. *polita* is widely distributed, but that in Iceland one can find ssp. *polymorpha* as well. This latter purported subspecies produces prolific gemmae there on the sandy lava, differing from ssp. *polita* that prefers stream banks, bogs, and otherwise very wet habitats. But Jóhannsson argues that the taxonomic character of gemmae used to separate the subspecies does not separate them at all.

Scapania (Figure 34-Figure 158)

Scapania (Figure 34-Figure 158) presents a number of species that occur in or near water. Vuori *et al.* (1999) noted a number of these in small, pristine streams of the Tolvajärvi region in the Russian Karelia.

Scapania aspera (Figure 34-Figure 35)

Distribution

Scapania aspera (Figure 34-Figure 35) is distributed throughout Europe, but is also known from subarctic eastern Siberia (Borovichev *et al.* 2016).



Figure 34. *Scapania aspera*, a European calcicole. Photo by Hermann Schachner, through Creative Commons.



Figure 35. *Scapania aspera* showing its mat habit. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Scapania aspera (Figure 34-Figure 35) occurred at a spring in Tara River canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).

Reproduction

Harrington (1966a, b) experimented with *Scapania aspera* (Figure 34-Figure 35) and determined that neither spores nor gemmae would germinate in the absence of calcium. Spore germination was even reduced at 10 mg L⁻¹ calcium. Borovichev *et al.* (2016) supported this preference for calcareous rock by their discovery of the species in Siberia at least 3000 km from the nearest known location of the species. The area is known for its calcareous rock outcrops. It is interesting that the molecular distances between these populations and the European populations are extremely low.

Biochemistry

When Bukvicki *et al.* (2013) extracted the chemical constituents from this species using solid phase micro extraction gas chromatography-mass spectrometry, they

were able to identify 96 compounds. These demonstrated inhibitory activity against yeast and bacterial strains, with a higher zone of inhibition for yeast than for bacteria. The activity against fungi needs ecological investigation. It is possible that these liverworts could interfere with mycorrhizal relationships needed by rooted plants near them.

***Scapania crassiretis* (Figure 36)**

(syn. = *Scapania nemorea* subsp. *crassiretis*)

Distribution

Scapania crassiretis (Figure 36) is a Northern Hemisphere species known from Greenland to Colorado, USA (EOL 2020). It occurs in Europe and Asia as well (ITIS 2020b).



Figure 36. *Scapania crassiretis*, a species in association with *Diplophyllum taxifolium* on rock cliffs by streams. Photo from Earth.com, with permission.

Aquatic and Wet Habitats

Vitt and Horton (1979) found *Scapania crassiretis* (Figure 36) on an east-facing shale cliff in the Olgive Mountains in the Yukon, Canada. Konstantinova and Vasiljev (1994) found the species in the Malaya Golaya River mouth of southern Siberia, where it occurred on the river bank, or rocks at 1100 m asl and was associated with *Scapania rufidula* and *Tritomaria exsecta* (Figure 37). In the Lower Golaya River Konstantinova and Vasiljev found it on a cliff associated with *Sphenolobus minutus* (Figure 28) and *Diplophyllum obtusifolium* (Figure 38). Konstantinova *et al.* (2002) found the species on the soil bank of a small creek and on alpine wet cliffs of the Upper Bureya River in the Russian Far East.



Figure 37. *Tritomaria exsecta*, a species associated with *Scapania crassiretis* on river banks in southern Siberia. Photo by Michael Lüth, with permission.



Figure 38. *Diplophyllum obtusifolium*, a species associated with *Scapania crassiretis* on river banks in southern Siberia. Photo by Hermann Schachner, through Creative Commons.

***Scapania cuspiduligera* (Figure 39, Figure 43-Figure 44)**

Distribution

Scapania cuspiduligera (Figure 39, Figure 43-Figure 44) occurs in the mountains of China (Cao *et al.* 2003) and the Chichibu Mountains of Japan (Inoue 1958). It is known from the Russian Federation (TROPICOS 2020), Europe, North America, and South America (ITIS 2020c), but it is absent in the tropics (DiscoverLife 2020). In western North America it is Arctic-alpine (Hong 1980). Puglisi *et al.* (2013) described the species as a circumpolar boreo-Arctic montane species, but it is very rare in the Mediterranean area where it only occurs in Spain, France, and Italy.

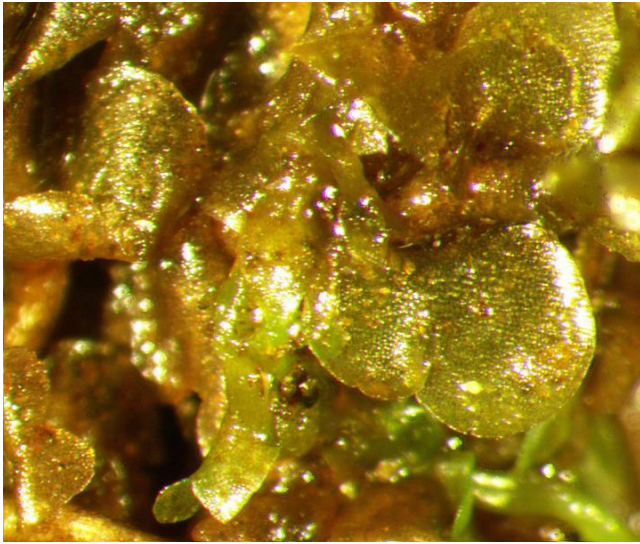


Figure 39. *Scapania cuspiduligera*, a boreo-Arctic circumpolar montane species that extends to the Mediterranean area. It can be aquatic, but also prefers calcareous terrestrial habitats. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

Aquatic and Wet Habitats

In Finland, Koponen *et al.* (1995) considered this species to be aquatic. Bosanquet (2020), based on his experience in the British Isles, described this as a species mostly from upland habitats. It creeps over *Gymnostomum aeruginosum* (Figure 40) and other mosses that occur in crevices in damp, base-rich crags. Its habitats in Wales include drier habitats such as calcareous turf on spoil heaps of limestone quarries. In Scotland, it occurs at sea level on the damp ground found in calcareous dunes. In the Machtum-Kelsbaach of Luxembourg, *Scapania cuspiduligera* (Figure 39, Figure 43-Figure 44) occurs in a calcareous ravine (Werner & Caspari 2002). In the Sayan Mountains of southern Siberia it occurs in cliff crevices of the high mountains, often associated with *Blepharostoma trichophyllum* (Figure 4), but also with *Mesoptychia gillmanii* (Figure 41) and *Preissia quadrata* (Figure 42) at 1050 m asl on rocks at the river bank (Konstantinova & Vasiljev 1994).



Figure 40. *Gymnostomum aeruginosum*; *Scapania cuspiduligera* creeps over this and other species in crevices in damp, base-rich crags. Photo by Bob Klips, with permission.



Figure 41. *Mesoptychia cf. gillmanii*, a species that occurs with *Scapania cuspiduligera* in cliff crevices of the high mountains. Photo by Michael Lüth, with permission.



Figure 42. *Preissia quadrata*, a species that occurs with *Scapania cuspiduligera* in cliff crevices of the high mountains. Photo by Andy Hodgson, with permission.

In western Canadian montane streams, this species can be classified as a restricted terrestrial species (Vitt *et al.* 1986), occurring in montane streams and on stream banks (Glime & Vitt 1987).

Reproduction

Gemmae are common in the genus *Scapania*, including reddish to brownish gemmae in *Scapania cuspiduligera* (Figure 43-Figure 44).



Figure 43. *Scapania cuspiduligera* with patches of brown gemmae on leaves near the tips. Photo by Hugues Tinguy, with permission.

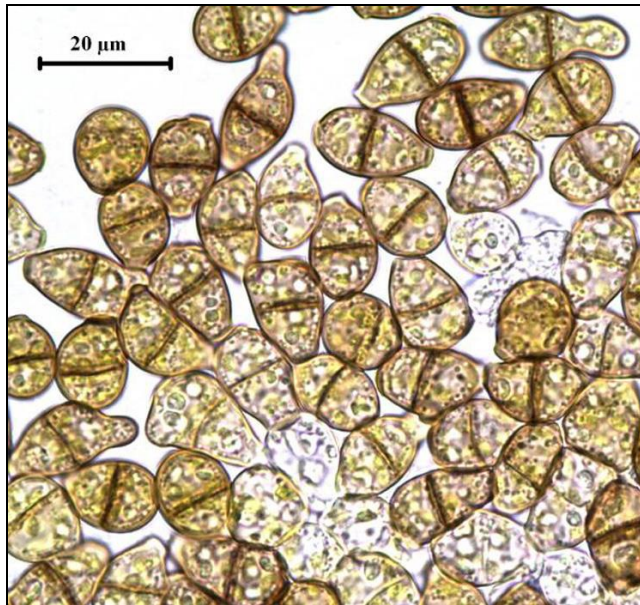


Figure 44. *Scapania cuspiduligera* gemmae showing their 2-celled structure. Photo by Hugues Tinguy, with permission.

Fungal Interactions

Wang and Qiu (2006) found no records of mycorrhizae on *Scapania cuspiduligera* (Figure 39, Figure 43-Figure 44). But in 2010, Bidartondo and Duckett found UK populations in association with *Sebacina* (Figure 45). It is of interest that they found identical fungal DNA from two locations; they suggested that this might result from long-distance dispersal of either the liverwort or the fungus, perhaps together.



Figure 45. *Sebacina sparassoidea* on moss, in a fungus genus that forms associations with *Scapania cuspiduligera*. Photo by Dave W., through Creative Commons.

Scapania hyperborea (Figure 46, Figure 50)

Distribution

Scapania hyperborea (Figure 46, Figure 50) is almost exclusively Arctic, but it does extend into some alpine

areas in North America (3900 m in Colorado, USA), but is not known from European alpine areas (Schuster 1974).



Figure 46. *Scapania hyperborea*, an Arctic-alpine species that inhabits sunny areas of wetlands. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Scapania hyperborea (Figure 46, Figure 50) forms golden brown to reddish brown patches or dense mats (Figure 46) (Schuster 1974). In the Arctic it is often associated with other wetland bryophytes [*Paludella squarrosa* (Figure 47), *Drepanocladus s.l.* (Figure 48), *Gymnocolea inflata* (Figure 49), *Fuscocephaloziopsis albescens* (Figure 10), and others] in sunny areas with seepage or around rock pools and tarns. In low-lying swales and marshy areas it exhibits vigorous growth, but when growing over dead peat the creeping growth can be very small, typically under 2 mm wide.



Figure 47. *Paludella squarrosa*, an associate of *Scapania hyperborea* in wetlands. Photo by Hermann Schachner, through Creative Commons.



Figure 48. *Drepanocladus aduncus*; some species of *Drepanocladus* are associates of *Scapania hyperborea* in wetlands. Photo by Hermann Schachner, through Creative Commons.



Figure 50. *Scapania hyperborea*, growing here on a dry rock. Photo by Michael Lüth, with permission.



Figure 49. *Gymnocolea inflata*, an associate of *Scapania hyperborea* in wetlands. Photo by Michael Lüth, with permission.



Figure 51. *Lophozipsopsis excisa*, a species that grows with *Scapania hyperborea* at high elevations and in boreal regions. Photo from Earth.com, with permission.

Koponen *et al.* (1995) reported *Scapania hyperborea* (Figure 46) as aquatic in Finland. Choi *et al.* (2012) report it from Russia in hummocky sedge-moss communities and wet, peaty roadsides in the tundra zone, ranging from 14 to 1300 m asl. Sofronova and Potemkin (2018) report it from 700-1859 m asl in Russia, growing typically on acid rocks in sheltered niches with other leafy liverworts. In the tundra belt it occurs on moist soil on rocky outcrops, also associated with other leafy liverworts. In Sweden, Ohlson *et al.* (1997) found it in old-growth swamp forests.

Terrestrial

In the forest and tundra belt of Yakutia, Russia, *Scapania hyperborea* (Figure 46, Figure 50) occurs at 700-1859 m asl, typically growing on acid rocks (Figure 50) and in sheltered niches (Sofronova & Potemkin 2018). It frequently associates with *Lophozipsopsis excisa* (Figure 51), *Scapania microdonta* (Figure 70), *Scapania sphaerifera*, *Scapania spitsbergensis*, *Sphenobolus saxicola* (Figure 52), *Sphenobolus minutus* (Figure 28), *Tetralophozia setiformis* (Figure 53), and *Trilophozia quinquedentata* (Figure 54).



Figure 52. *Sphenobolus saxicola*, a species that grows on acid rocks with *Scapania hyperborea* at high elevations and in boreal regions. Photo by Jean Faubert, with permission.



Figure 53. *Tetralophozia setiformis*, a species that grows on acid rocks with *Scapania hyperborea* at high elevations and in boreal regions. Photo by Michael Lüth, with permission.



Figure 55. *Scapania irrigua*, a widely distributed Holarctic species that occurs in standing and running water and in bogs and in other wet habitats. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.



Figure 54. *Trilophozia quinquedentata*, a species that grows on acid rocks with *Scapania hyperborea* at high elevations and in boreal regions. Photo by Hugues Tinguy, with permission.



Figure 56. *Scapania irrigua* growing in a mat with mosses. Photo by David T. Holyoak, with permission.

Scapania irrigua (Figure 55-Figure 56)

Distribution

Scapania irrigua (Figure 55-Figure 56) is a widely distributed Holarctic species that extends southward to the Coniferous Forest Biome and the northernmost edge of the Deciduous Forest Biome (Schuster 1974). It occurs throughout Europe, south to England, and is recorded from Japan.

Aquatic and Wet Habitats

Scapania irrigua (Figure 55-Figure 56) is considered by Watson (1919) as occasionally submerged (Watson 1919). Geissler (1976) reported it from alpine streams in the Swiss Alps; Geissler and Selldorf (1986) noted that it occurred with the sedge *Baeothryon cespitosum* (Figure 57), but was uncommon with *Eleocharis quinqueflora* (Figure 58) and the moss *Paludella squarrosa* (Figure 47). Koponen *et al.* (1995) considered it to be aquatic in Finland. Schuster (1974) stated that it is usually associated with standing water, although the later observations of Geissler would seem to broaden that habitat to running water. It is often in bogs with *Sphagnum* and *Polytrichum* (Figure 59), occurs on peat at lake margins (Figure 60), can withstand pH below 4, and seems to be most frequently associated with sunny rock pools (Schuster 1974). By contrast, it also occurs in wet, springy depressions of calcareous *Thuja* swamps (Figure 61) and on moist, loamy soil (Schuster 1974). On the Isle of Arran off the coast of

Scotland, Travis (1917) reported this species from wet soil on the shore.



Figure 57. *Baeothryon cespitosum*, a species that accompanies *Scapania irrigua* in the Swiss Alps. Photo by Hermann Schachner, through Creative Commons.



Figure 58. *Eleocharis quinqueflora*, a species where *Scapania irrigua* is an uncommon companion in the Swiss Alps. Photo by Max Licher, through Creative Commons.



Figure 59. *Polytrichum commune* and *Sphagnum* habitat suitable for *Scapania irrigua*. Photo with online permission.



Figure 60. Perrault Fen peat surrounding small lake in the Keweenaw Peninsula of Michigan, USA. Photo by Janice Glime.

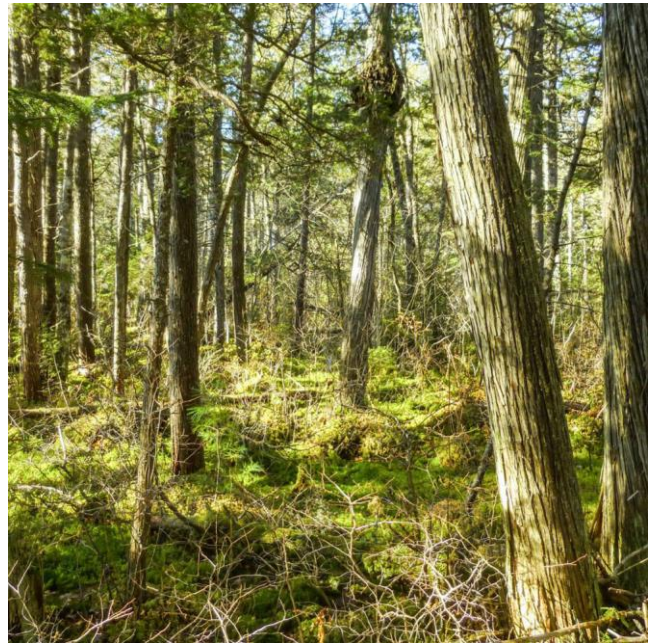


Figure 61. *Thuja* swamp habitat suitable for *Scapania irrigua*. Photo by Allen Norcross, with permission.

In central Europe, *Scapania irrigua* (Figure 55-Figure 56) forms part of the *Cardamino-Montention* suballiance (Zechmeister & Mucina 1994). This alliance is comprised of *Scapania irrigua*, *Carex frigida* (Figure 62), and *Luzula*

alpinopilosa (Figure 63). These species all have an alpine distribution in spring communities.



Figure 62. *Carex frigida*, a member of the alliance with *Scapania irrigua* in central Europe. Photo by Michael Kesl, through Creative Commons.



Figure 63. *Luzula alpinopilosa*, a member of the alliance with *Scapania irrigua* in central Europe. Photo by Hugues Tinguy, through Creative Commons.

In the Algama River Basin of southeastern Yakutia, Russia, *Scapania irrigua* (Figure 55-Figure 56), occurs on sand between rocks, where it often occurs with *Blasia pusilla* (Figure 64) and *Solenostoma confertissimum* (Figure 65) (Sofronova 2013). It also occurs on river banks, on rotting wood, and in habitats with *Gymnocolea inflata* (Figure 49) and *Scapania paludicola* (Figure 84-Figure 88). In the Franconia Mountains of New Hampshire, USA, *S. irrigua* occurs on the shores of Eagle Lake where it is associated with *Mylia anomala* (Figure 66), *Gymnocolea inflata*, and *Calypogeia sphagnifolia* (Figure 67) on the *Sphagnum* (Figure 59) (Lorenz 1908).



Figure 64. *Blasia pusilla*, a species that often occurs with *Scapania irrigua* on sand between rocks. Photo by Hermann Schachner, through Creative Commons.



Figure 65. *Solenostoma confertissimum*, a species that often occurs with *Scapania irrigua* on sand between rocks. Photo by Hermann Schachner, through Creative Commons.



Figure 66. *Mylia anomala* with *Sphagnum*, two taxa that often occur with *Scapania irrigua*. Photo by Blanka Agüero, with permission.

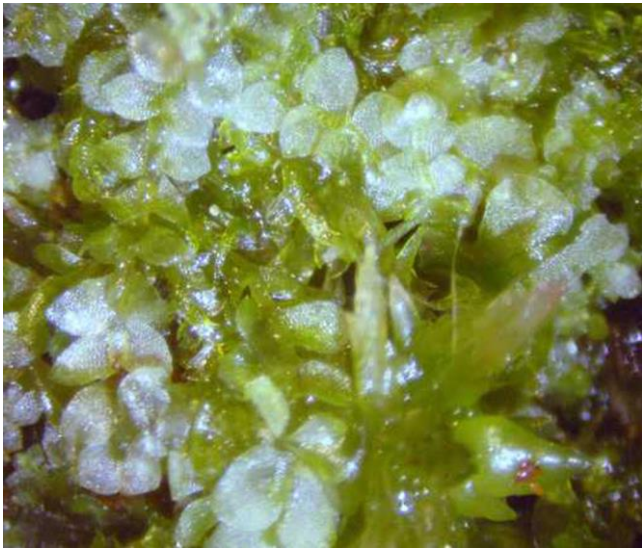


Figure 67. *Calypogeia sphagnifolia*. Photo by Scot Loring, through Creative Commons.

Adaptations

In bright light, *Scapania irrigua* can develop brown protective pigments (Figure 68). The gemmae (Figure 69) in this species are not as protected as in some species.



Figure 68. *Scapania irrigua* showing a brown form. Photo by J. C. Schou, with permission.

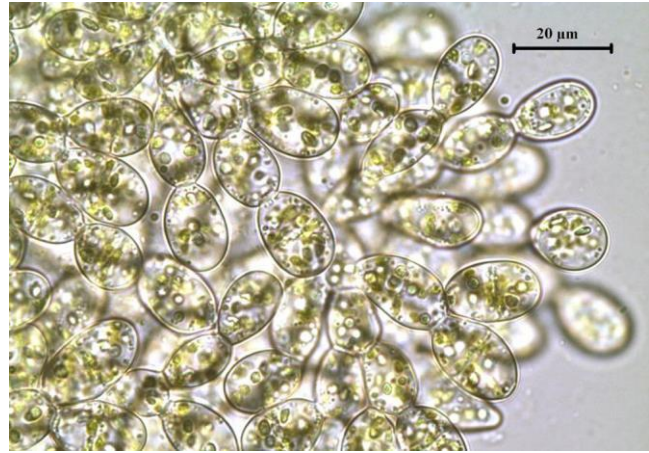


Figure 69. *Scapania irrigua* gemmae showing thin walls. Photo by Hugues Tinguy, with permission.

Biochemistry

Scapania irrigua (Figure 55-Figure 69) is among the many bryophytes that have been tested for secondary compounds. Zhang *et al.* (2015) have identified diterpenoids that are active against some human cancer cell lines. Although many liverworts have exhibited anti-cancer properties, the medical and pharmaceutical professions have done little to pursue this ability as an actual treatment.

Scapania microdonta (Figure 70)

Distribution

Scapania microdonta (Figure 70) has an amphipacific distribution (Kuznetsova *et al.* 2010) in the Arctic and subarctic of North America and Asia (Wagner 2017).

Aquatic and Wet Habitats

Scapania microdonta (Figure 70) occurs on shaded rocks, cliffs, and crevices in gravelly barrens (Wagner 2017). Konstantinova *et al.* (2002) reported it from a wet cliff on the south-facing slopes and rocks on the lake shore of the Upper Bureya River in the Russian Far East.



Figure 70. *Scapania microdonta* (herbarium specimen), a species that can occur on wet cliffs and lake shores. Photo by CBG Photography Group, through Creative Commons.

In the forest and tundra belt of Yakutia, Russia, *Scapania microdonta* (Figure 70) occurs at 700-1859 m asl, typically growing on acid rocks and in sheltered niches (Sofronova & Potemkin 2018). It frequently associates with *Lophozipsis excisa* (Figure 51), *Scapania hyperborea* (Figure 46-Figure 50), *Scapania sphaerifera*, *Scapania spitsbergensis*, *Sphenolobus saxicola* (Figure 52), *Sphenolobus minutus* (Figure 28), *Tetralophozia setiformis* (Figure 53), and *Trilophozia quinquedentata* (Figure 54). It seems to rarely be in wet habitats.

***Scapania nemorea* (Figure 71-Figure 79)**

(syn. = *Scapania nemorosa*, *Scapania nemorosa* var. *uliginosa*)

Distribution

Scapania nemorea (Figure 71-Figure 79) occurs from Europe to Asia, south to Oceania, and in North America from Alaska to the continental USA to Hawaii (UNB 2020). This seems inconsistent with the amphi-Atlantic distribution given by Kuznetsova *et al.* (2010). In fact, Schuster (1974) puts it mostly in temperate regions, but extending northward in Europe to Sweden, Norway, and Finland and in North America as far south and inland as Louisiana. In much of its range it is the most ubiquitous species of *Scapania* (Schuster 1974).



Figure 71. *Scapania nemorea*, a Northern Hemisphere species, south to Hawaii, but mostly temperate. It is typical in moist habitats in a zone above *Scapania undulata* (Figure 125-Figure 136). Photo by Hermann Schachner, through Creative Commons.



Figure 72. *Scapania nemorea* showing a lighter color form. Photo by Rick Ballard, through Creative Commons.



Figure 73. *Scapania nemorea* with apical gemmae. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Koponen *et al.* (1995) found *Scapania nemorea* (Figure 71-Figure 79) to be aquatic in Finland. It occurs along rivers (Figure 74) and on wet or moist cliffs of ravines in Connecticut, USA. On Cape Breton Island, Canada (Nichols 1918) and in the Appalachian Mountains, USA (Glime 1968), it is likewise associated with streams. In New Hampshire, USA, it occurs on rocks that are normally above the water level in a headwater stream (Glime 1970). In the Haute Ardenne rivers of Belgium it occurs on earthy and gravelly substrates on river banks (Leclercq 1977). It is rare in upstream reaches in the Harz Mountains of Germany (Bley 11987). In marshes it is usually associated with fast water (Watson 1919). Coroi *et al.* (2004) considered to be a diagnostic streamside species in southern Ireland.



Figure 74. *Scapania nemorea* growing just above the water level. Photo by Bernd Haynold, through Creative Commons.

But it can also occur in less aquatic habitats. At the Flume of Franconia Notch, New Hampshire, USA, it occurs on bedrock near the stream edge, on the flume wall, and on ledges in the flume (Glime 1982). Cleavitt (1996) likewise found it to be common growing on moist rock ledges in the White Mountain National Forest, New Hampshire, as well as on rocks in streams.

In the northwestern European region of Russia, Potemkin (2018) found it with *Calypogeia fissa* (Figure 75) both in a rock crevice with seepage and on soil in a rock fissure with seepage. In the alder swamps of southern Sweden, Darell and Cronberg (2011) found it only close to the ground on "stools" and stones where it was both humid and shaded; they did not find it in streams, but only on their banks, as well in flooded black alder stools. Thus, it occurs not only on rocks in streams, but also in moist habitats such as on moist rocks, moist rotting logs, and loam or clay on stream banks (UNB 2020).



Figure 75. *Calypogeia fissa*, a species that occurs with *Scapania nemorea* in a rock crevice with seepage and on soil in a rock fissure with seepage. Photo by Hermann Schachner, through Creative Commons.

In my own experience, this species occurred in association with Appalachian Mountain streams, but it was always in less wet locations than was *Scapania undulata* (Figure 125-Figure 136), especially when it was only centimeters away. Weber (1976) reported similar moisture relationships, with *S. undulata* in Cataracts Provincial Park, Newfoundland, Canada, being confined to submerged or emergent rocks and *S. nemorea* (Figure 71-Figure 79) growing optimally in the inundation zone – a narrow strip along the river that is submerged only periodically (Figure 76). There *S. nemorea* is also part of the rich bryophyte flora on dripping rock faces and other seepage areas.



Figure 76. *Scapania nemorea* on rock, near Swallow Falls Park, Maryland, growing just above water level. Photo by Janice Glime.

Scapania nemorea (Figure 71-Figure 79) is calciphobic (Nichols 1916). Dulin (2008) described it as a rare **nemoral** (inhabiting woods or groves) amphi-oceanic species that was confined to rare substrates on the bank of the Bolshaja Khozja River in the Komi Republic of Russia. Adlassnig *et al.* (2013) found that this species formed lush carpets in a metal-contaminated site in Salzburg, Austria, where the substrate was the acidic soil of a spoil heaps on both banks of Brown Creek.

Reproduction

Reproduction by gemmae (Figure 77) is likely to be important in this species. Laaka-Lindberg *et al.* (2003) considered size of propagules to be important in determining the number produced. *Scapania nemorea* (Figure 71-Figure 79) typically produces up to 500-700 one-celled gemmae per leaf (Figure 77-Figure 79), whereas *Radula complanata* (Figure 80) produces multicellular gemmae that number only 15-45 per leaf (Figure 80-Figure 81).



Figure 77. *Scapania nemorea* with gemmae at the shoot tips. Photo by William Schachner, through Creative Commons.

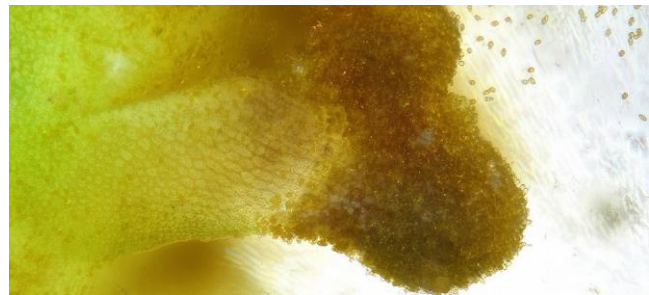


Figure 78. *Scapania nemorea* gemmae, showing how numerous they are. Photo by Dick Haaksma, with permission.



Figure 79. *Scapania nemorea* gemmae. Photo by Dick Haaksma, with permission.



Figure 80. *Radula complanata* with multicellular gemmae on leaf margin. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

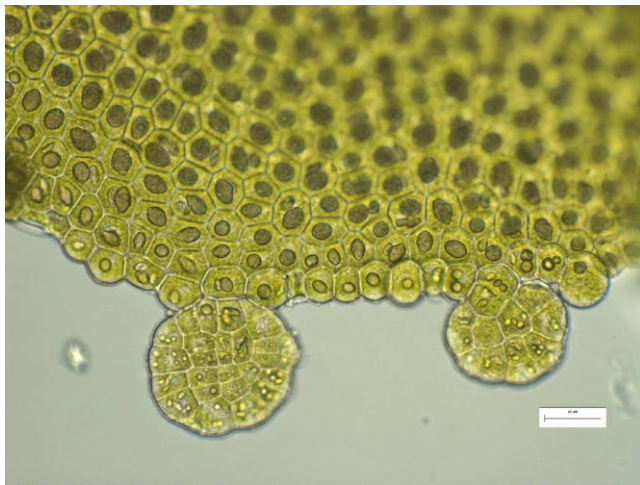


Figure 81. *Radula complanata* multicellular gemmae. Photo by Blanka Aguero, with permission.

Nevertheless, this species produces sporophytes (Figure 82), indicating successful sexual reproduction, as seen here from a population near Swallow Falls Park, Maryland, USA.

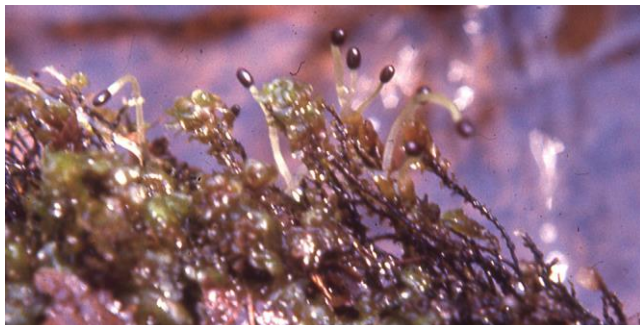


Figure 82. *Scapania nemorea*, near Swallow Falls Park, Maryland, USA, showing capsules with water nearby.

Fungal Interactions

We know from the work of Egertová *et al.* (2016) that *Mniaecia jungermanniae* (Figure 17) is a bryophyte-loving ascomycetous fungus that occurs on *Scapania nemorea* (Figure 71-Figure 74, Figure 76), although this fungus is more common on another member of the Scapaniaceae, *Diplophyllum albicans* (Figure 2, Figure 12, Figure 14-Figure 15). All of the locations where the association occurred had acidic bedrock and included sandstone, granite, and phyllite. These were typically in the shade of coniferous or broad-leafed forests where there was a rich liverwort cover.

Biochemistry

Knowledge of biochemistry can help us to separate difficult taxa. In 1981, Zehr undertook the investigation of variation in *Scapania nemorea* (Figure 71-Figure 79). He found that variation of terpenes correlated with the substrate, suggesting a potential plastic adaptation to the habitat. These results also indicate that terpene constituents are not suitable for demarcating species or lower levels of classification in *Scapania*.

Scapania nemorea (Figure 71-Figure 79) produces volatile compounds such as sesquiterpenes that exhibit antimicrobial activity against the common yeast, *Saccharomyces cerevisiae* (Figure 83) (Bukvicki *et al.* 2014). Whereas these studies were conducted to consider the potential for preservation of foods, we need to examine their importance in determining the ability of these liverworts to survive in wet habitats that could be otherwise suitable for fungi.

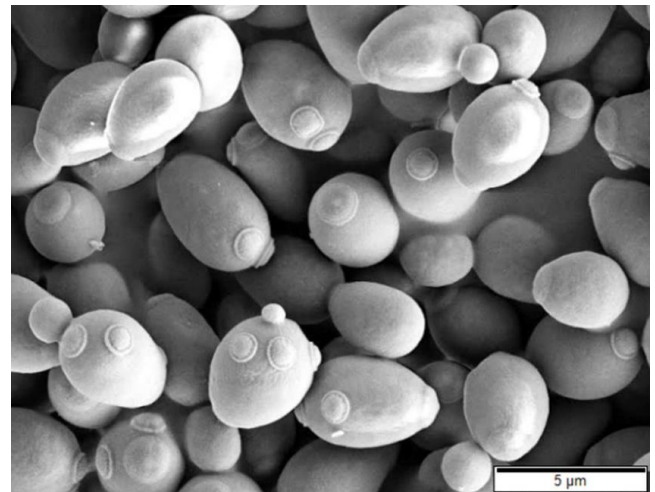


Figure 83. *Saccharomyces cerevisiae* (yeast) SEM. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

On the one hand, it is good news that bryophytes may help us to solve both cancer problems and food preservation, but this can be bad news for the bryophytes. Studlar and Peck (2007) considered not only the harvesting of the bryophytes for various uses, especially horticultural, but also the incidental species that often are harvested with them, to be detrimental to their success. They considered *Scapania nemorea* (Figure 71-Figure 74, Figure 76) to be only a facultative aquatic and expressed concern regarding its incidental harvesting in mesic habitats.

***Scapania paludicola* (Figure 84-Figure 88)**

Distribution

Scapania paludicola (Figure 84-Figure 88) is circumboreal and circumpolar (Schuster 1974). In North America, it extends southward to New York and Michigan in the eastern USA and from Alaska, USA, through the Northwest Territories, Yukon, and Alberta in Canada, south to Montana, USA (Hong 1980). In Eurasia it extends from central Europe northward to Scandinavia and eastward to Russia and Siberia, reaching Japan in the south and Iceland in the north.



Figure 84. *Scapania paludicola*, a species that is circumboreal and circumpolar, extending southward into the mountains. Photo by Jan-Peter Frahm, with permission.



Figure 85. *Scapania paludicola* in a common upright growing position. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Scapania paludicola (Figure 84-Figure 88) is almost completely restricted to bogs (or poor fens; Figure 88), but in the tundra it can occur on wet granite rocks, especially at the margins of pools and shallow lakes (Schuster 1974). In these habitats it typically occurs with other liverworts. In peat bogs it is sometimes submerged, but it also grows among *Sphagnum* (Figure 59) where it is barely above the water level. In shaded spots, it is green, but in sunny spots it is purplish black to copper red. It seems to prefer a pH of 5.5 or lower, occurring widely in granitic mountain areas. Geissler and Selldorf (1986) found it associated with *Carex goodenoughii* and uncommonly with *Eleocharis*

quinqueflora (Figure 58) in moors of Switzerland. *Scapania paludicola* (Figure 84-Figure 88) occurs in the Upper Karasu River, Turkey, at 1850 m and in a swampy meadow near a pool (Konstantinova & Vasiljev 1994). Sofronova (2018) reported *S. paludicola* from 500 to 1200 m asl along the upper course of the Indigirka River, eastern Yakutia, Russia, where it was present on the soil of grass mires and on brook and river banks. Color forms vary (Figure 87-Figure 88).

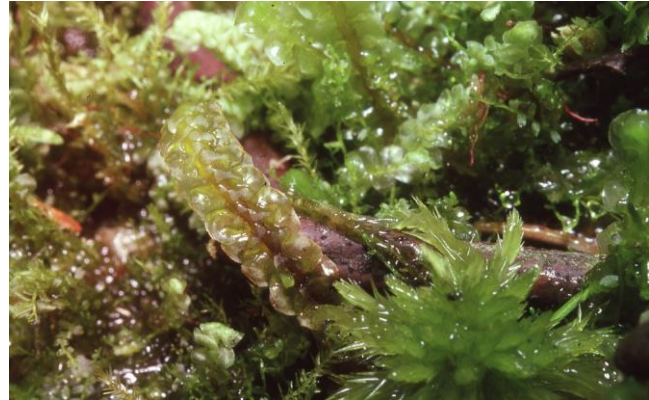


Figure 86. *Scapania paludicola*, Perrault Fen (poor fen), Michigan, USA. Photo by Janice Glime.



Figure 87. *Scapania paludicola* illustrating green color and growth habit. Photo by David T. Holyoak, with permission.



Figure 88. *Scapania paludicola* showing a dark brown form. Photo by Michael Lüth, with permission.

***Scapania paludosa* (Figure 89-Figure 92)**

Based on his studies on the isozymes of a number of *Scapania* species, Zehr (1981) concluded that *Scapania paludosa* (Figure 89-Figure 92) should be combined with *Scapania uliginosa* (Figure 103-Figure 109). Söderström *et al.* (2016) have not recognized this combination, so I shall maintain separate discussions for these two species.

Distribution

Scapania paludosa (Figure 89-Figure 92) seems to be either rare or infrequent in alpine and subalpine areas and has a restricted distribution (Schuster 1974). It is Holarctic, mostly in the Spruce-Fir Biome and southern tundra. In Europe it occurs in the Alps, north to Scandinavia and east to Siberia; it also occurs in Iceland, Greenland, and Japan. In North America it extends from Alaska south to Oregon in the west and in the east on Isle Royale, Michigan, USA, reaching as far south as Massachusetts along the eastern coast.



Figure 89. *Scapania paludosa*, a Holarctic species that is mostly restricted to alpine rills and springs. Photo by Hermann Schachner, through Creative Commons.



Figure 90. *Scapania paludosa* in a wet habitat such as a spring. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Koponen *et al.* (1995) listed *Scapania paludosa* (Figure 89-Figure 92) as an aquatic species in Finland. The habitat differs from that of *Scapania paludicola* (Figure 84-Figure 88) by the occurrence of *S. paludosa* restricted to alpine rills and springs (Figure 91-Figure 92), but not swift streams (Schuster 1974). It attaches to rocks, sticks, or stones and may be submerged or submersed in the spring. But it can also occur in alpine bogs. It frequently associates with other members of the genus. It can also occupy stones in snow-water brooks.



Figure 91. *Scapania paludosa* growing at the side of a spring or rill with tracheophytes encroaching into the mounds of liverworts. Photo by Hermann Schachner, through Creative Commons.



Figure 92. *Scapania paludosa* showing the density its mats can form. Photo by Hermann Schachner, through Creative Commons.

Shacklette (1965) found that the stems of *Scapania paludosa* (Figure 89-Figure 92) on Yakobi Island, Alaska, USA, could become intertwined to a degree that could dam the swift mountain rivulet, causing a series of terraced pools. The liverworts are able to close the pool surface, permitting tracheophytes to invade the mat. Lepp (2012)

reported it from the edges of a small stream through a steep ravine in Alaska. Sjörs and Een (2000) found *Scapania paludosa* in numerous springs in Muddus National Park in northern Sweden. Likewise, Smieja (2014) reported 51 taxa of liverworts at springs in the Polish Tatra Mountains. Among these, *Scapania paludosa* finds its optimum ecology in the **crenic** (referring to a spring and brook water flowing immediately from it) habitats. Figure 95-Figure 96 show the preferred temperatures, altitude, and water pH that make these alpine habitats suitable for the species, where it is entirely restricted to bryophyte-dominated springs, forming extensive, swollen turfs.

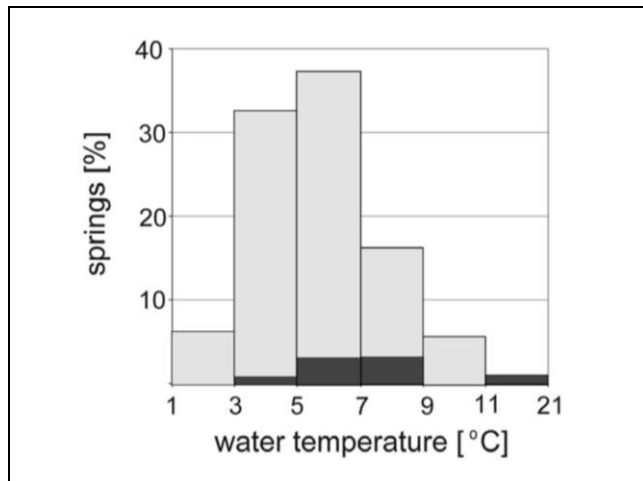


Figure 93. The temperature range of *Scapania paludosa* in the Tatra National Park springs, where it occurs in the upper montane zone. Black bars represent bryophytes; gray bars represent tracheophytes. Modified from Smieja 2014.

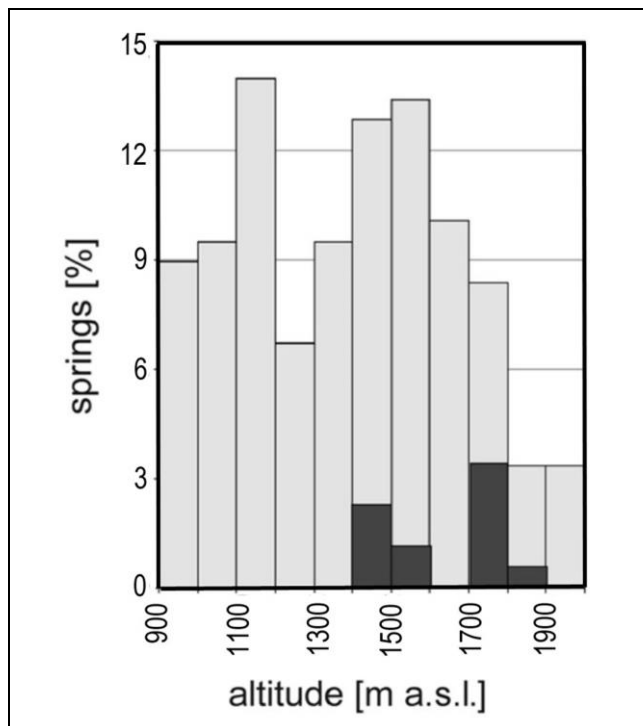


Figure 94. The distribution and temperature range of *Scapania paludosa* in the Tatra National Park springs. Black bars represent bryophytes; gray bars represent tracheophytes. Modified from Smieja 2014.

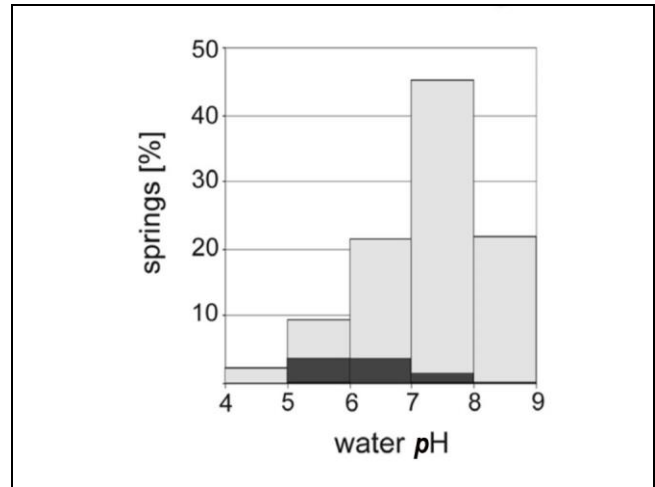


Figure 95. The distribution and habitat range of *Scapania paludosa* in the Tatra National Park springs, where it occurs in the upper montane zone. Black bars represent bryophytes; gray bars represent tracheophytes. Modified from Smieja 2014.

Scapania rigida (Figure 97-Figure 96)

(syn. = *Scapania rigida* fo. *minor*)

Scapania rigida (Figure 97-Figure 96) seems to be a little-known species with almost no published information. The only information I have found is that of Ruttnier (1955), who considered it to be among aquatic liverworts and reported it from the wall of a bay in the tropics.



Figure 96. *Scapania rigida* growing on a branch. Photo by Naufalurf, through Creative Commons.



Figure 97. *Scapania rigida* growing as an epiphyte. This is a little-known tropical species known from the wall of a bay. Photo by Naufalurfi, through Creative Commons.

Scapania rufidula

Distribution

Scapania rufidula is a species with the narrow distribution of Europe and northern Asia, *i.e.* in Siberia (Steere 1954; ITIS 2020d).

Aquatic and Wet Habitats

Scapania rufidula occurs on soil banks of small creeks and rivers of Upper Bureya River (Russian Far East) (Konstantinova *et al.* 2002). In the Indigirka River of eastern Yakutia, Russia, *S. rufidula* is the most frequently occurring liverwort and occurs on the banks of small brooks, on numerous rock outcrops, and in rock fields (Sofronova 2018). In southern Siberia in the Sayan Mountains, *S. rufidula* occurs at the Malaya Golaya River mouth at 1100 m asl on rocks of the stream bank (Konstantinova & Vasiljev 1994). Here it is associated with *Scapania crassiretis* (Figure 36). In the Lower Malaya Golaya River, it occupies soil deposits on river bank rocks, as well as occurring in rock fields and on rocks covered with humus. In the latter habitat it is often mixed with *Trilophozia quinqueidentata* (Figure 54).

***Scapania subalpina* (Figure 98-Figure 102)**

Distribution

Scapania subalpina (Figure 98-Figure 102) is a montane and alpine species with a circumboreal distribution (Gesierich & Rott 2004). It occurs from California and Colorado, USA, northward to Alaska (Schuster 1974). In Europe it occurs from the Alps and Pyrenees northward to Scandinavia, Siberia, and Iceland. It also occurs in alpine areas of Japan.



Figure 98. *Scapania subalpina*, a circumboreal alpine and montane species that is facultatively aquatic in streams, springs, cascades, and other wet areas. Photo by Michael Lüth, with permission.



Figure 99. *Scapania subalpina* showing its growth habit. Photo by Andy Hodgson, with permission.



Figure 100. *Scapania subalpina* showing various color forms. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Koponen *et al.* (1995) reported *Scapania subalpina* (Figure 98-Figure 102) as aquatic in Finland, although

Virtanen (1995) considered it to be a facultative aquatic liverwort in Finland. Ferreira *et al.* (2008) reported it from rivers. Gesierich and Rott (2004) considered it to be a montane species on moist and wet earth (Figure 101) in the catchment of a glacial stream in Austria. There they considered it to be potentially endangered in the perialpine area where it is one of two dominating liverwort species in the fen.



Figure 101. *Scapania subalpina* growing with a variety of other species. Photo by Michael Lüth, with permission.

The ecology of *Scapania subalpina* (Figure 98-Figure 102) is similar to that of *Scapania undulata* (Figure 125-Figure 136) (Schuster 1974). This restricts it mostly to wet ledges, borders of rocky springs, cold streams, and cascades. It lives where it is kept wet at all times either by high humidity or by spray. However, it avoids locations where it is permanently submerged. It seems to prefer shaded, acid rocks (Figure 102), although it can occur on weakly basic rocks. Watson (1919) ascribed to it a habitat of gravelly detritus associated with fast water.



Figure 102. *Scapania subalpina* growing in a habitat that can dry out. Photo by Jean Faubert, with permission.

Physiology

In experiments, *Scapania subalpina* (Figure 98-Figure 102) from Greenland tolerated temperatures down to -10°C

in ice for 34 days (Clausen 1964). In the same set of experiments, it withstood 1 day in ice at -40°C, likewise with no cellular damage. It was among the most cold-tolerant species in the experiments on the 32 liverwort species tested.

Reproduction

Schuster (1974) reports that *Scapania subalpina* (Figure 98-Figure 102) commonly produces gemmae but rarely produces capsules.

Scapania uliginosa (Figure 103-Figure 109)

(syn. = *Scapania obliqua*)

Distribution

Scapania uliginosa (Figure 103-Figure 109) has a restricted range in Arctic-alpine areas, extending from the European Alps to northern Scandinavia (Schuster 1974). Although it is frequent in Iceland and Greenland, it is not known from Spitzbergen. In North America it extends from Alaska southward to high mountains in Colorado, USA.



Figure 103. *Scapania uliginosa* is restricted to Arctic-alpine areas where it grows in streams and small lakes. Photo by Jan-Peter Frahm, with permission.



Figure 104. *Scapania uliginosa* showing its upright growth habit. Photo by Michael Lüth, with permission.



Figure 105. *Scapania uliginosa* showing a brown form with fist-like branch apices. Photo by Dick Haaksma, with permission.

Aquatic and Wet Habitats

Watson (1919) reported *Scapania uliginosa* (Figure 103-Figure 109) from alpine or subalpine areas where it grows submersed in fast water. Geissler (1975, 1976) supported this description by reporting it from European alpine streams. Kozłowski *et al.* (2017) reported that *Scapania uliginosa* was among the bryophytes covering stream bottoms in streams of Tatra National Park in Poland. Likewise, other researchers reported that *Scapania uliginosa* grows in streams (Dohnal 1950; Sykora & Hadac 1984).

But this species, while apparently needing a steady water supply [Koponen *et al.* (1995) considered it to be aquatic in Finland], does not always grow in streams. Light (1975) found it in small lakes in the Scottish mountains, where the lakes are covered with ice 4-7 months a year and the ion concentration is low.

In high mountains *Scapania uliginosa* (Figure 103-Figure 109) is restricted to seepage-moistened rocks or cold springs and streams (Figure 106-Figure 108) (Schuster 1974). It sometimes occurs on stony, marshy ground in cold regions of high altitude or latitude (Figure 109). Schuster describes the species as occurring in large, swelling tufts at the sides of alpine rills, the types of sites where one might find *Scapania undulata* (Figure 125-Figure 136), *S. paludosa* (Figure 89-Figure 92), *Marsupella aquatica* (Figure 110), and *M. sphacelata* (Figure 111). *Scapania uliginosa* (Figure 103-Figure 109) occurs in sites that remain submerged for at least part of the year and apparently avoids calcareous rocks. Cantonati and Lange-Bertalot (2011) reported that *S. uliginosa* was the dominant substrate for diatoms from springs in Nature Parks of the south-eastern Alps.



Figure 106. *Scapania uliginosa* in an alpine seepage. Photo by Michael Lüth, with permission.



Figure 107. *Scapania uliginosa*, shown here in the middle, joins other bryophytes and a saxifrage in a seepage area. Photo by Michael Lüth, with permission.



Figure 108. *Scapania uliginosa* in a seepage area. Photo by Michael Lüth, with permission.



Figure 109. *Scapania uliginosa* in a marshy habitat. Photo by Michael Lüth, with permission.



Figure 110. *Marsupella aquatica*, a species that occurs on the sides of alpine rills similar to the ones to occupied by *Scapania uliginosa*. Photo by Barry Stewart, with permission.



Figure 111. *Marsupella sphacelata*, a species that occurs on the sides of alpine rills similar to the ones to be occupied by *Scapania uliginosa*. Photo by Hermann Schachner, through Creative Commons.

In Sweden, Sjörs and Een (2000) found this species in springs. In the Upper Tissa River of southern Siberia, Konstantinova and Vasiljev (1994) found *S. uliginosa* (Figure 103-Figure 109) on the stream bank in a *Larix* forest (Figure 112). Here it occurred with the leafy liverworts *Blepharostoma trichophyllum* subsp. *brevirete* (Figure 113), *Mesoptychia heterocolpos* (Figure 114), *Lophozia excisa* (Figure 51), *Scapania subalpina* (Figure 98-Figure 102), and *Trilophozia quinquedentata* (Figure 54). Geissler (1982) reported *Scapania uliginosa* growing in deep and sometimes overflowing spring fens. In an alpine catchment in Austria, Gesierich and Rott (2004) considered it to be potentially endangered, a case where extinction would greatly alter the fens where it is one of two dominant liverworts. They surmised that it avoids calcareous habitats.



Figure 112. *Larix* forest, a suitable habitat for *Scapania uliginosa* on a stream bank. Photo through public domain.

Reproduction

Although this plant apparently produces gemmae in Scotland, gemmae appear to be rare throughout the Arctic-alpine range (Aleffi 1992).



Figure 113. *Blepharostoma trichophyllum* subsp. *brevirete*, a species that occurs with *Scapania uliginosa* on stream banks. Photo by Hugues Tinguy, with permission.



Figure 114. *Mesoptychia heterocolpos*, a species that occurs with *Scapania uliginosa* on stream banks. Photo by Blanka Aguero, with permission.

Physiology

Scapania uliginosa (Figure 103-Figure 109) exhibits a degree of tolerance to a variety of heavy metals. Samecka-Cymerman *et al.* (1991) found this species to contain up to a maximum in mg kg⁻¹ dry plant weight of 518 B, 418 Ba, 16 Cd, 180 Co, 119 Cr, 292 Cu, 11 Li, 10,700 Mn, 694 Mo, 243 Ni, 464 Pb, 955 Sr, 123 V, and 2067 Zn in Sudetan streams of Poland and Ardennes streams in Belgium and western Germany. Whitton (2003) likewise chose this liverwort for monitoring heavy metals in fresh water.

Role

Egorov (2007) examined the ability of associated *Cyanobacteria* (Figure 115) to fix nitrogen. The biological assimilation of atmospheric nitrogen by such microorganisms associated with *Scapania uliginosa* (Figure 103-Figure 109) during the growing period was 0, compared to 0.09 mg cm⁻² on a species of the moss *Bryum* (Figure 116). This is somewhat surprising to me due to the wet habitats where this liverwort is found.



Figure 115. *Nostoc*, one of the **Cyanobacteria** that occur on bryophytes and can fix nitrogen. Photo by Proyecto Agua, through Creative Commons.



Figure 116. *Bryum capillare*; some members of the genus *Bryum* support nitrogen-fixing **Cyanobacteria**. Photo by Michael Becker, through Creative Commons.

***Scapania umbrosa* (Figure 117-Figure 124)**

Distribution

Scapania umbrosa (Figure 117-Figure 124) ranges from Lapland southward to the Azores, Russia, and Scotland, but it is unknown in Asia (Schuster 1974). In North America it occurs on both coasts but is rare further inland. It extends from Alaska south to California and from Newfoundland and Labrador to New York.



Figure 117. *Scapania umbrosa*, a species from coastal regions of the Northern Hemisphere where it occurs in moist habitats, but only occasionally submerged. Photo by Michael Lüth, with permission.

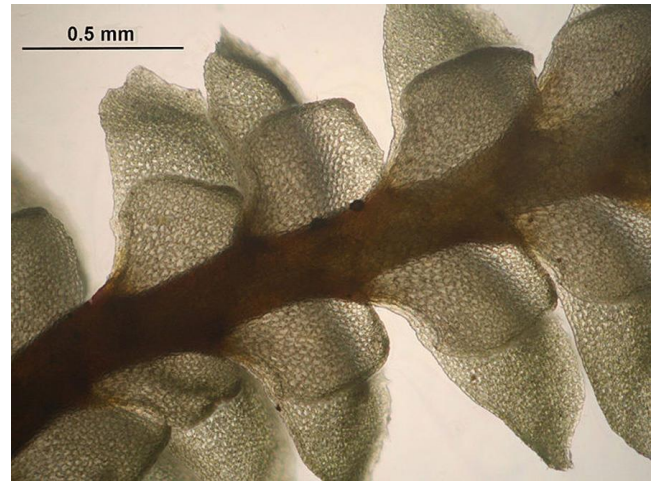


Figure 118. *Scapania umbrosa* showing leaf folds. Photo by Hermann Schachner through Creative Commons.



Figure 119. *Scapania umbrosa* showing a moist, pale color form. Photo by Hermann Schachner, through Creative Commons.



Figure 120. *Scapania umbrosa* showing the upright habit and claw-like tips. Photo by Hugues Tinguy, with permission.



Figure 121. *Scapania umbrosa* showing a drier and darker appearance. Photo by Hermann Schachner, through Creative Commons.



Figure 123. *Scapania umbrosa* with apical gemmae. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Schuster (1974) considers *Scapania umbrosa* (Figure 117-Figure 124) to be restricted to locations where it is continually moist. These can include decaying, damp, shaded logs (Figure 122) or moist rocks. It is known from both igneous rock and calcareous or noncalcareous sandstone. Watson (1919) noted that it was occasionally submerged.



Figure 122. *Scapania umbrosa* on decaying wood. Photo by Hermann Schachner, through Creative Commons.

In Russia, Choi *et al.* (2012) reported *Scapania umbrosa* (Figure 117-Figure 122) from fine-grained soil on wet roadsides in the dark coniferous forest belt, ranging 60-1400 m alt. At Eagle Lake in the Franconia Mountains, New Hampshire, USA, *Scapania umbrosa* similarly occurred along the trail above 915 m, in this case on wet rocks (Lorenz 1908).

Reproduction

Gemmae in this species are apical and 2-celled (Figure 123-Figure 124).

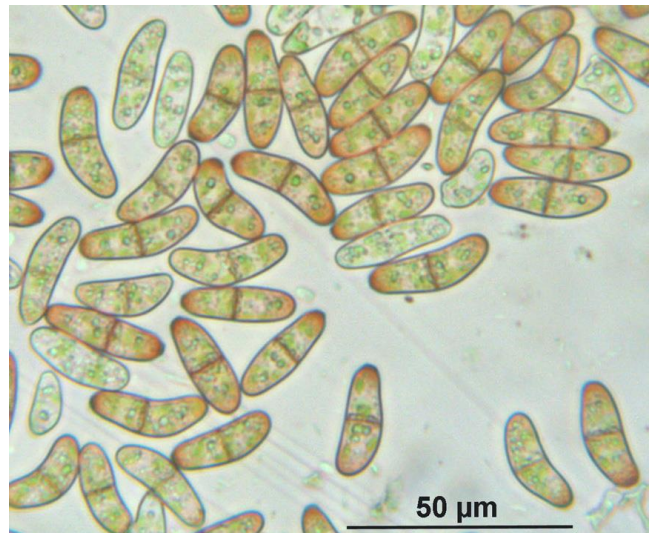


Figure 124. *Scapania umbrosa* gemmae. Photo by Hermann Schachner, through Creative Commons.

Fungal Interactions

Bidartondo and Duckett (2010) reported that the fungus *Sebacina* (Figure 45) associates with this species.

Scapania undulata (Figure 125-Figure 136)

(syn. = *Martinellius undulata*, *Plagiochila undulatum*, *Pleurozia cochleariformis*, *Scapania dentata*, *Scapania intermedia*)

Distribution

Scapania undulata (Figure 125-Figure 136) is distributed widely throughout the Arctic, southward on high mountains (Schuster 1974). In eastern North America it extends southward in the Appalachian Mountains into the Mixed Mesophytic Forest and the Hemlock-Hardwoods Forest. In western North America it extends from Alaska and the Yukon southward to California. In the Rocky Mountains it extends southward to New Mexico. In the Eastern Hemisphere it extends from Europe to North Africa, Korea, and Japan.



Figure 125. *Scapania undulata*, a species widely distributed throughout the Arctic, southward on high mountains. This species is predominantly aquatic, occurring in both streams and lakes, but also on banks where it is usually wet. Photo by Florent Beck, through Creative Commons.



Figure 126. *Scapania undulata* showing its growth habit. Photo by Hermann Schachner, through Creative Commons.



Figure 127. *Scapania undulata* showing shoot apices. Photo by David T. Holyoak, with permission.



Figure 128. *Scapania undulata* with only the shoot apices emergent. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Of all the aquatic liverworts, *Scapania undulata* (Figure 125-Figure 136) seems to be the most widespread and abundant. Because of its widespread importance, I will provide more detail on its ecology. *Scapania undulata* ranges from hydric to almost xeric (Schuster 1974). In the Haute Ardenne rivers of Belgium, it is strictly aquatic (Leclercq 1977). Satake (1983) likewise reported it as aquatic from Kyushu, Japan. Koponen *et al.* (1995) considered it aquatic in Finland, whereas Virtanen (1995) reported it to be common in both Finnish streams and other wet habitats. Koppe (1945) reported it in water in Westfalens, northwestern Germany. Ferreira *et al.* (2008) simply reported it from rivers. Weber (1976) found *S. undulata* to be confined to submerged or emergent rocks (Figure 129-Figure 130) in the Cataracts Provincial Park, Newfoundland, Canada. Its wide-ranging moisture requirements permit it to also occupy the narrow riverbank strip that is periodically submerged and exposed as the stream level changes, a zone in which it achieves its optimum growth in these streams. It is even at least somewhat salt-tolerant, living where it becomes submersed in seawater at high tide, leading Shacklette (1961) to consider it to be a facultative halophyte.



Figure 129. *Scapania undulata* and habitat on rock just above the water. Photo by Jean Faubert, with permission.



Figure 130. *Scapania undulata* on rock in stream. Photo by Bernd Haynold, through Creative Commons.

Streams

This species typically prefers upstream habitats. It occurs in fast water of the River Rheidol, but it can't compete with flowering plants in slow water downstream (Jones 1955). Holmes and Whitton (1975) found it to be among the most common bryophytes in the extreme upper reaches and tributaries of the River Tweed in the UK. Holmes and Whitton (1977) found it in the upper upstream of the River Swale in Yorkshire, UK, but in the River Tyne, UK, it was more scattered (Holmes & Whitton 1981). In northern England, it occurs in streams and rivers (Wehr 1983). Weekes *et al.* (2014) reported *Scapania undulata* (Figure 125-Figure 136) to be the most common bryophyte in small streams in Ireland, where it forms turfs (Figure 131). It is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006).



Figure 131. *Scapania undulata* in a dry montane stream bed, showing how abundant it can become. Photo by Michael Lüth, with permission.



Figure 132. *Scapania undulata* habitat on a dripping cliff. Photo by Dick Haaksma, with permission.

Scapania undulata (Figure 125-Figure 136) has been well-known from other parts of Europe as well. It occurs in European alpine streams (Figure 133), also generally being fast-flowing headwaters (Geissler 1975, 1976). It has been reported from streams in Polish and Czech Sudety Mountains (Samecka-Cymerman & Kempers 1998) and Szoszkiewicz *et al.* (2018) found that *Scapania undulata* was among the three most abundant leafy liverworts in Tatra and Sudeten streams, with bryophytes being especially important to macroinvertebrates in the siliceous rivers of Tatra. In the Maritsa River, Bulgaria, it is a hygrophyte in the upper course of the river where conductivity and sulfates had low values (Gecheva *et al.* 2011) and is likewise reported from other Bulgarian rivers (Gecheva *et al.* 2010, 2013). It occurs in streams in northeastern Finland (Heino & Virtanen 2006). Virtanen (1995) found *S. undulata* to be "rather common" in the 8 streams in his study in Lohja parish in southern Finland. Vieira *et al.* (2005) reported it from mountain streams of northwest Portugal, and it is common in mountain fluvial microhabitats of northwest and center-west Portugal (Vieira *et al.* 2012a), with *Scapania undulata* being among the most common species in 187 streams in Portugal (Vieira *et al.* 2012b). This species also occurs in upstream areas in mountainous streams in Madeira Island off the northwest coast of Africa (Luis *et al.* 2015).



Figure 133. Alpine stream, northwestern Georgia, southeastern Europe. Photo by Lodian, through Creative Commons.

In the streams I have studied in eastern North America, *Scapania undulata* (Figure 125-Figure 136) was certainly the most common of the submersed liverworts. In North

America, it occurs in fast-flowing streams in the Adirondack Mountains, USA, streams (Slack & Glime 1985; Glime *et al.* 1987). Glime (1970) likewise found it to be the dominant bryophyte at upstream locations with fast water and an absence of tracheophytic macrophytes in the headwaters of a New Hampshire, USA, stream. In Quaker Run, a stream originating at 700 m asl near the Pennsylvania-New York border, *S. undulata* covers many of the small rocks that are submerged in the stream, forming luxurious mats (Matthews 1932). Lanfear (1933) reported it as submerged in deep, swift, clear water in Pennsylvania, USA. Knapp and Lowe (2009) found it in streams in the Great Smoky Mountains National Park, Kentucky, USA. Porter (1933) reported it submerged in a small stream in Albany County, Wyoming, USA, attached to rocks.

On the other hand, it is dominant not only in middle and upstream reaches, but also in lower stream reaches in the Harz Mountains of Germany (Bley 1987) and midstream in the unpolluted upper and middle parts of streams of eastern Odenwald and southern Spessart (Philippi 1987).

It can survive permanent submergence (Schuster 1974). But it can also survive in the constant spray of water near a waterfall of Upper Bureya River in the Russian Far East (Konstantinova *et al.* 2002). Hence, one can frequently find it on emergent rocks where it remains wet even when above water (Figure 134-Figure 136).



Figure 134. *Scapania undulata* on rock in stream. Photo by Michael Kestl, through Creative Commons.



Figure 135. *Scapania undulata* on the sides of a rock, partly in and partly out of water, at Cranberry Lake, New York, USA. Photo by Janice Glime.



Figure 136. *Scapania undulata* partially submerged at Cranberry Lake, New York, USA. Photo by Janice Glime.

While *Scapania undulata* (Figure 125-Figure 136) is often the most common or abundant liverwort in streams, in upland Welsh streams it was surpassed by *Nardia compressa* (Figure 137) (71% cover) compared to its 23% cover (Wilkinson & Ormerod 1994). The researchers found that acidification and subsequent liming changed the bryophyte community composition, with *N. compressa* decreasing. However, in the five years following liming, no other species replaced the *Nardia*.



Figure 137. *Nardia compressa* a species that can surpass *Scapania undulata* in upland Welsh streams. Photo by Barry Stewart, with permission.

Hall *et al.* (2001) used TWINSpan to assess the important parameters determining the suitable streams for plants, including bryophytes. For *Scapania undulata* (Figure 125-Figure 136), these include an area of medium percent open water, lowest pH, and lowest mean height above water table. As noted earlier, *S. undulata* occupied a lower mean height above water table than did *S. nemorea* (Figure 71-Figure 79).

Lakes

Although it is almost always associated with running water, this species is not restricted to streams. It occurs to 5 m depth in a Yorkshire, UK, reservoir, and in small lakes with low ion concentration in Scottish mountains with ice cover 4-7 months of the year (Light 1975). At the margins of large lakes wave action seems to replace running water

(Schuster 1974). It is particularly common at the water's edge where spray from the water keeps it constantly wet.

Nygaard (1965) reported *Scapania undulata* var. *purpurascens* as rare in the deepwater of a lake at 11.5 m deep. This variety no longer has taxonomic status. Nygaard commented that the clear lake was disappointing for fishing, with perch being the only fish present.

Scapania undulata (Figure 125-Figure 136) is abundant in and out of water on rocks and stones at lake margins and on boggy shores (Figure 138) in Scotland (West 1910). Tremp (2003) reported it forming turfs in oligotrophic water.



Figure 138. *Scapania undulata* as it could appear on boggy shores or lake margins. Photo by Michael Lüth, with permission.

Associations

Marstaller (1987) found it as part of the *Platyhypnidium* (Figure 139)-*Fontinalis antipyretica* (Figure 161) association in streams in Thuringia, Germany. Gregor and Wolf (2001) likewise found it in locations where these two species also occurred. I have frequently found it in Appalachian Mountain streams, USA, where *Fontinalis dalecarlica* (Figure 140) occurred.



Figure 139. *Platyhypnidium riparioides*; *Scapania undulata* frequents streams with this species and *Fontinalis antipyretica*. Photo by David T. Holyoak, with permission.

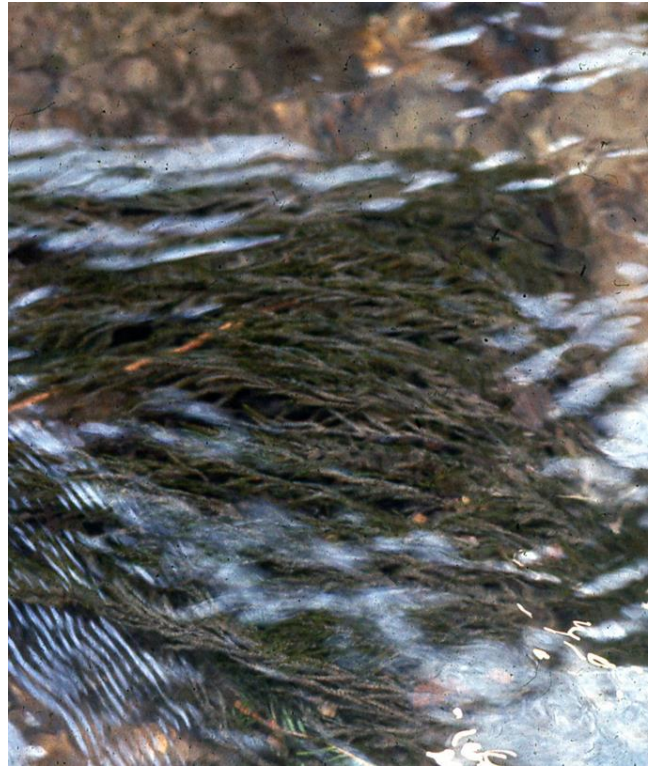


Figure 140. *Fontinalis dalecarlica*, a species characteristic of streams that also have *Scapania undulata*. Photo by Janice Glime.

Because of their ubiquity and ability to become relatively abundant, the plants of *Scapania undulata* (Figure 125-Figure 136) have been useful accumulator plants for inorganic **xenobiotics** (substances foreign to body or to ecological system) in the Tatra streams, Poland (Samecka-Cymerman *et al.* 2007). In Portugal, Vieira *et al.* (2012a) used it, along with *Platyhypnidium lusitanicum* (Figure 141), *Fissidens polyphyllus* (Figure 142), and *Fontinalis* (Figure 140), as characteristic bryophytes to assess the fluvial status of mountain streams. Lang and Murphy (2012) considered *S. undulata* to be an indicator of upland **oligotrophic** (relatively low in plant nutrients) acidic streams with base-poor waters.



Figure 141. *Platyhypnidium lusitanicum*, one of the species used to assess fluvial status in Portuguese streams. Photo by Barry Stewart, with permission.



Figure 142. *Fissidens polyphyllus*, one of the species used to assess fluvial status in Portuguese streams. Photo by David T. Holyoak, with permission.

Spitale (2009) found that seasons affect the competition vs facilitation of bryophyte community members. As seasons change, so does the water level. Spitale tested the effects of these changes on two species adjacent to the moss *Warnstorfia exannulata* (Figure 143): *Sphagnum warnstorffii* (Figure 144) and *Scapania undulata* (Figure 125-Figure 136). However, he was unable to show that the seasonal water gradient affected the competition vs facilitation relationships. Nevertheless, climatic fluctuations that affected the length of the water gradient also changed the competitive hierarchies of these species on a seasonal scale.



Figure 143. *Warnstorfia exannulata*, a species subjected to water level fluctuations. Photo by Michael Lüth, with permission.

pH

Scapania undulata (Figure 125-Figure 136) is almost entirely restricted to acidic rocks, but in the Lake Superior region it may be closely adjacent to basaltic, neutral to basic rock outcrops. Tremp and Kohler (1991) found it submersed in low-buffered water of streams. It occurs in waters affected by mineralization zones in the Sudeten Mts, Poland (Samecka-Cymerman & Kempers 1993) and its preferred pH range is 3.89-6.6 in West Virginia, USA, mountain streams (Stephenson *et al.* 1995). It can also

occur in acid waters in Japan (Satake *et al.* 1989a). Shilland and Monteith (2010) found that *Scapania undulata* increased in cover of the stream bed during their acid waters monitoring.



Figure 144. *Sphagnum warnstorffii*, a species, along with *Scapania undulata*, that occurs in locations with water level fluctuations. Photo by Michael Lüth, with permission.

In Denmark it occurs in streaming water at pH 7.2 (Sørensen 1948), whereas it is an acidophilic (pH 4.0-6.0) hydroamphibiont in streams of Gory Stolowe Mountains, Poland (Szweykowski 1951). Hübschmann (1957) reported it from acid water in the mountains, and Glime (1968) reported it from acid springs and brooks in the Appalachian Mountains, USA. Papp *et al.* (2006) likewise found that it prefers waters with low concentrations of dissolved minerals in the Iskur River, and its main tributaries, in Bulgaria. Weekes *et al.* (2014) found it to be a strong indicator species of non-calcareous conditions.

Scapania undulata (Figure 125-Figure 136) had the highest constancy value of the macrophytes identified to species in the study by Weekes *et al.* (2014). The species was typically associated with *Racomitrium aciculare* (Figure 145) and *Hyocomium armoricum* (Figure 146), all common in fast-flowing acidic streams.



Figure 145. *Racomitrium aciculare*, a species often associated with *Scapania undulata*. Photo by Michael Lüth, with permission.



Figure 146. *Hyocomium armoricum*, a species often associated with *Scapania undulata*. Photo by Dick Haaksma, with permission.

Scarlett and O'Hare (2006) found that *Scapania undulata* (Figure 125-Figure 136) distribution is correlated with low cation concentrations in the Bosge and Black Forest mountains. It is capable of regulating proton levels within the protoplasts and thus might serve as an indicator species for acidic geology.

The pH of the water affects the sensitivity of the bryophyte to heavy metals. Thiébaud *et al.* (2008) examined the cellular distribution of heavy metals in *Scapania undulata* (Figure 125-Figure 136) in two streams with different acidity (pH 5.20 & 6.57) in the Vosges Mountains in eastern France. Little difference was observed in the apparent health of the liverwort, and it remained green in both streams. However, in the most acidic stream lipid droplets accumulated in some of the leaf cells. This acid-tolerant species accumulated more Fe and less toxic Al when compared to the non-acid-tolerant *Platyhypnidium riparioides* (Figure 139), where the relationship was reversed. The researchers suggested that the ability to control metal uptake may help to explain the acid tolerance of some species of bryophytes.

Stephenson *et al.* (1995) found that when the streams in their West Virginia mountain stream study had sandstone beds, the species diversity declined as the pH declined. At pH 3.15, no bryophytes were present. In the highly acidic streams, *Scapania undulata* (Figure 125-Figure 136) predominated. When transplanted from a stream with pH 5.97 to one with pH 3.15, ultrastructural damage was present within three months. These streams also had a heavy load of SO₄ and Al that most likely contributed to the damage.

In upland Welsh streams, Ormerod *et al.* (1987) likewise found that the bryophyte community composition related most strongly to pH and aluminium concentration. *Scapania undulata* (Figure 125-Figure 136) was characteristic of streams with a mean pH of 5.2-5.8. Streams with *S. undulata* generally had impoverished macroinvertebrate populations. Since at least some of these invertebrates can feed successfully on the acid-tolerant plants such as *S. undulata*, the researchers postulated that it was the pH, and not the liverworts, that kept the invertebrates out of these streams.

Water Relations

Gupta (1977a) suggested that in *Scapania undulata* (Figure 125-Figure 136), the ability of reabsorbing solutes from damaged cells upon rewetting may help in survival. Gupta (1977b) also found that *S. undulata* exhibited a peak in photosynthesis after 6 hours of desiccation at 96.5% RH, whereas the more drought-resistant xerophytic *Porella platyphylla* (Figure 147) reached its peak after 2 hours. Both species continued to lose water up to 50 hours at that humidity. Furthermore, at 84% relative humidity, *S. undulata* had few living cells remaining, but at 93% it had ~3/4 of the cells still living (Clausen 1964). Thus, it can be out of water, but only if the humidity is still high (Figure 148-Figure 149).



Figure 147. *Porella platyphylla*, an epiphytic species that has good drought resistance. Photo by Hugues Tinguy, with permission.



Figure 148. *Scapania undulata* habitat, in this case, emergent but wet. Photo by Dick Haaksma, with permission.



Figure 149. *Scapania undulata* in Roaring Creek, West Virginia, USA, where it is only slightly above water and fully hydrated. Photo by Janice Glime.

Temperature

The streams where *Scapania undulata* (Figure 125-Figure 136) occurs demonstrate its ability to tolerate cold temperatures, at least down to 0°C (Figure 150).



Figure 150. *Scapania undulata* in an Appalachian stream with snow, showing its ability to tolerate low temperatures. Photo by Janice Glime.

Temperature affects the kinetics of nutrients and heavy metals. Duncker (1976) found that the rate of uptake of zinc by dead *Scapania undulata* at 32°C at zinc concentrations of 2 mg L⁻¹ was greater than that of live material at 14°C. There was some indication that uptake was also greater at 24°C than at 14°C in live material. Such temperature differences can affect the rate at which the liverwort obtains nutrients in different seasons, but this needs to be explored.

Photosynthetic Products

We have little understanding of the role played by the various photosynthetic products produced by leafy liverworts. Suleiman *et al.* (1980) noted the possibility that these products could be used taxonomically, identifying **mannitol** in *Scapania undulata* and **volemitol** and **sedoheptulose** in some other leafy liverworts. These products are formed in addition to sucrose and fructans. But how do they relate to habitat adaptations, or do they?

Reproduction

We know somewhat more about the role of reproduction in permitting a species to live and prosper where it does. Grainger (1947) discovered that *Scapania undulata* (Figure 125-Figure 136) produces its gametangia in the cold months of December to April in a stream near Huddersfield, England, with fertilization occurring near the air-water interface. Production of capsules follows (Figure 151).



Figure 151. *Scapania undulata* with capsules. Photo by Michael Lüth, with permission.

Scapania undulata (Figure 125-Figure 136) is a dioicous species (Holá *et al.* 2014), making its fertilization difficult in its flowing water habitats. Based on 100 plots in ten streams in southern Finland, the sex ratio was male biased, contrasting with the female-biased sex ratio of most dioicous bryophytes (Holá *et al.* 2014). It was not unusual for plots to have only one sex. Females produced only one sexual branch per shoot, and no sex-expressing branches also had gemmae. The researchers interpreted this to indicate presence of a trade-off between sexual and asexual reproductive structures. Nevertheless, sporophytes can be produced (Figure 152).



Figure 152. *Scapania undulata* with capsules. Photo by Malcolm Storey, with online permission through DiscoverLife.

The gemmae in this species are small, having only 1, or mostly 2, cells (Figure 153) (Potemkin 1998). Their walls are thin and they vary from green to red (Figure 154).

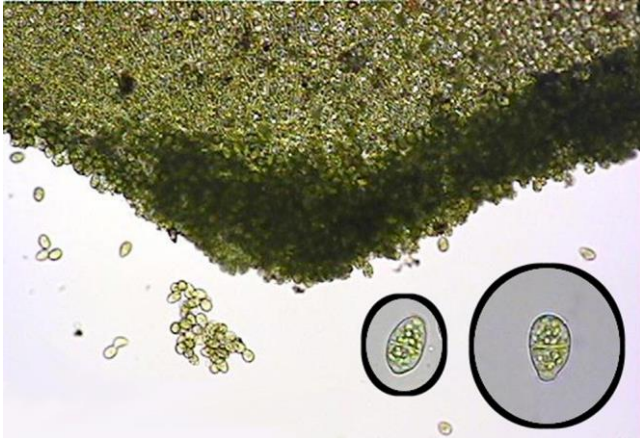


Figure 153. *Scapania undulata* gemmae on leaf. Photo by Paul Davison, with permission.

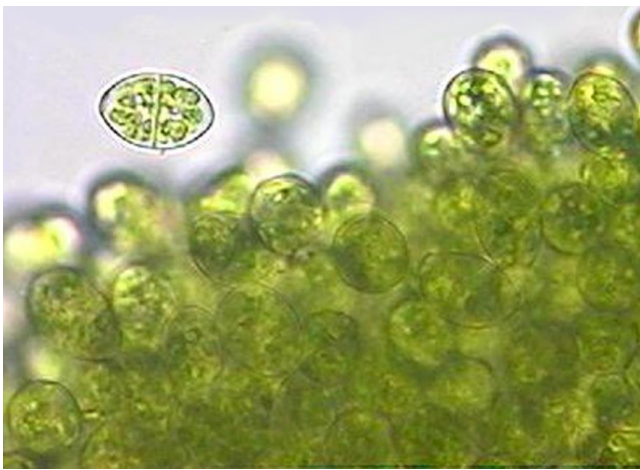


Figure 154. *Scapania undulata* gemmae. Photo by Paul Davison, with permission.

But this species may have another, possibly more successful, means of reproduction. Its detached leaves can germinate to produce new plants (Figure 155) (Glime 1970). This mechanism can permit wide dispersal in the stream and provide more surface area to help it attach in a new location. It is also possible, but not yet demonstrated, that it has access to the nutrients remaining in the leaf.

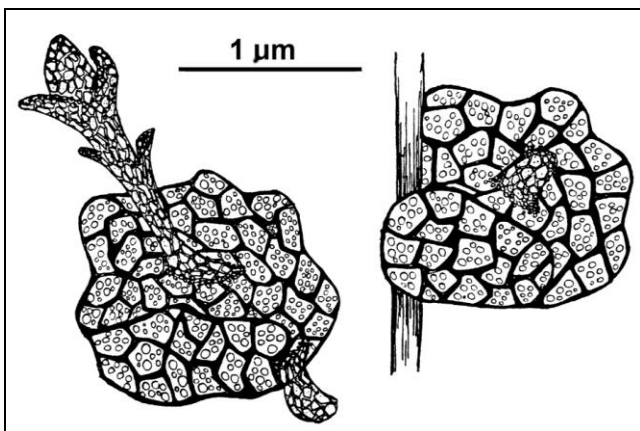


Figure 155. *Scapania undulata* plantlets on leaves from a stream in New Hampshire, USA. Drawings by Flora Mace.

Biochemistry

Like so many liverworts, *Scapania undulata* (Figure 125-Figure 136) has a variety of secondary compounds, including terpenoids (Huneck *et al.* 1986; Mues *et al.* 1988; Nagashima *et al.* 1993, 1994; Adio *et al.* 2004). What we lack is an understanding of the biological importance of these compounds to the liverwort. It is eaten by some caddisflies (Ito 1991), suggesting these compounds are at least not always effective as antiherbivore compounds.

Pigments

Pigments can be important to bryophytes to trap more light energy in low light and to protect the chlorophyll (Figure 156) and DNA in high light environments. In direct sunlight, there is a dentate, pigmented form of *Scapania undulata* (Figure 157-Figure 158), but this expression seems to occur only north of the Southern Appalachians, USA (Schuster 1974). This suggests that it is at least partly genetically controlled.



Figure 156. *Scapania undulata* showing non-red form. Photo by Michael Lüth, with permission.



Figure 157. *Scapania undulata* showing red pigments in a European population. Photo by Michael Lüth, with permission.



Figure 158. *Scapania undulata*, a pigmented form from Europe. Photo by Michael Lüth, with permission.

López and Carballeira (1989; see also Martínez-Abaigar *et al.* 1994) found that the aquatic bryophytes they studied, including *Scapania undulata* (Figure 125-Figure 136), exhibited higher chlorophyll concentrations than did terrestrial bryophytes. Pigment ratios were indicators of stress from organic and metal pollution, with *Scapania undulata* being the most sensitive of the five bryophytes tested (although no other liverworts were included). On the other hand, its chlorophyll *a* and *b* as a percent of dry weight did not decrease as a result of increasingly poor water quality.

Martínez-Abaigar *et al.* (1994), in addition to supporting the higher concentration of chlorophyll in aquatic bryophytes compared to terrestrial ones, also demonstrated that concentrations in aquatic bryophytes, including *Scapania undulata* (Figure 125-Figure 136), were similar to those of epilithic river algae. Chlorophyll *a:b* ratios and the carotenoid index were lower than in terrestrial bryophytes. Of the 14 species of aquatic bryophytes tested, they found that *S. undulata* had a total chlorophyll content of 150 ± 7 mg m² within a range of 97–351 mg m² per shoot area. In this species, the chlorophyll concentration increased in spring when shade developed and light decreased. At the same time, the *a/b* ratio decreased due to an increase in chlorophyll *b*. Chlorophyll *b* serves as an antenna pigment to capture more light energy.

Martínez-Abaigar *et al.* (2009) attempted to show the effects of UV-B on six aquatic bryophytes, including *Scapania undulata* (Figure 125-Figure 136). They found a greater response to the culture conditions than to the enhanced UV-B conditions. However, the culture conditions did not impede growth. UV-B affected some pigment variables, but did not affect photosynthetic performance or growth. They attributed the muted response to the fact that these bryophytes were collected from high elevations where they were already acclimated to high light intensities.

Kunz *et al.* (1993) reported the presence of riccionidin A in *Scapania undulata* (Figure 125-Figure 136), a pigment it shares with the floating liverwort *Ricciocarpus natans* (Figure 159) and the streambank liverwort *Marchantia polymorpha* (Figure 160).



Figure 159. *Ricciocarpus natans*, a species with the pigment riccionidin A. Photo by Murray Fagg, Australian National Botanic Gardens, with online permission.



Figure 160. *Marchantia polymorpha* with gemmae, a species with the pigment riccionidin A. Photo by Hermann Schachner, through Creative Commons.

Nutrient Relations

Nitrogen is often a limiting nutrient in streams. In the Hubbard Brook Experimental Forest in New Hampshire, USA, Yakubik *et al.* (2000) tested the effect of nitrate releases on *Scapania undulata* (Figure 125-Figure 136) and its rate of nitrate uptake. In low discharge releases there is more contact between the liverwort and the nitrate than in high discharge releases, thus affecting the ability of the liverwort to absorb and store the nitrate. Thus, through removal the bryophytes had a greater effect on stream nitrate concentrations in low discharges.

In addition to nitrogen experiments at the Hubbard Brook Experimental Forest, Meyer and Likens (1979) conducted similar experiments within the forest in the stream system. They found that *Scapania undulata* (Figure 125-Figure 136) that occurred in first and second order streams readily absorbed P, another limiting nutrient in streams, from the water, even when it occurred in relatively low concentrations. Inputs to these *S. undulata* streams were essentially balanced with outputs, resulting in no annual net retention of P in the stream.

Vanderpoorten and Klein (1999) showed the importance of pH on the ability of bryophytes to tolerate minerals in the water. *Scapania undulata* (Figure 125-

Figure 136) can tolerate a neutral pH if the mineral concentration is low. Such waters have low buffering capacity, causing greater responses to slight changes in the chemical balance. This is consistent with its use as a bioindicator of oligotrophic, acidified to weakly acidified, and poorly buffered streams (Thiébaud & Muller 1999). Effluent from villages or trout hatcheries cause an increase of dissolved Mg^{++} , K^{+} , and NO_3^{+} , causing species like *Scapania undulata* to disappear (Vanderpoorten & Klein 1999). Hence, Grasmück *et al.* (1995) considered that *S. undulata* served as an indicator for weakly mineralized, oligotrophic water.

Samecka-Cymerman *et al.* (2007) compared the effects of various substrates (granites/gneisses, limestones/dolomites, and sandstones) on absorption levels of an array of elements, including both nutrients and heavy metals. The bryophytes from the Tatra mountains streams in Poland, including *Scapania undulata* (Figure 125-Figure 136), varied in their behavior depending on the substrate. Those from granites/gneisses had higher concentrations of Cd and Pb. Those from sandstones had higher concentrations of Cr. And those from limestones/dolomites had higher concentrations of Ca and Mg.

Heavy Metals

Nutrients become toxic at higher levels. Heavy metal pollutants typically exceed those levels. Bryophytes are great accumulators, and in some cases they are able to sequester the heavy metals and survive. In other cases, they die from the exposure. For this reason, they can be used as bioindicators of heavy metals, or of clean water, and *Scapania undulata* (Figure 125-Figure 136) is a species that has been used in a number of bioindicator studies (Samecka-Cymerman 1989).

When compared to *Fissidens polyphyllus* (Figure 142), *Fontinalis antipyretica* (Figure 161), *Platyhypnidium riparioides* (Figure 139), and *Brachythecium rivulare* (Figure 162), *Scapania undulata* (Figure 125-Figure 136) had the highest accumulation capacity for heavy metals (López & Carballeira 1993). Metal accumulation is affected by the concentration of the metal in the water, pH, sulfate concentration, nitrite and ammonia, and filtrable reactive phosphate. In their study, they found the relationship between concentration in the water and that in *S. undulata* to be statistically significant except for Cd, Pb, and Co.

Vázquez *et al.* (1999) examined the distribution of a variety of heavy metals in the plants of *Scapania undulata* (Figure 125-Figure 136). They found that for most metals, more was taken up by the extracellular compartment than the intracellular compartment; the particulate fraction was negligible. The relationship between the metal concentration of the water and that of the liverwort followed Michaelis-Menten kinetics for enzymes, an asymptotic curve that increases with the concentration gradient. They also found that heavy metal uptake caused considerable loss of intracellular K, probably due to membrane damage. It also caused loss of extracellular Mg, most likely due to displacement on cation binding sites. Of the species tested, loss of intracellular K was greatest in *S. undulata*. By contrast, this species had the least loss of extracellular Mg.



Figure 161. *Fontinalis antipyretica*, a species that has less capacity for heavy metal accumulation than *Scapania undulata*. Photo by Dick Haaksma, with permission.



Figure 162. *Brachythecium rivulare*, a species that has less capacity for heavy metal accumulation than does *Scapania undulata*. Photo by Michael Lüth, with permission.

Satake *et al.* (1990) explored the effects of mercury sulfide crystals in *Scapania undulata* (Figure 125-Figure 136). In transplant studies, they found that mercury compounds accumulated in the cell walls. Likewise, this species accumulated Pb in the cell wall, but not in the nucleus or other cell components (Satake *et al.* 1989b). They found that PbS was undetectable in the liverwort, but the insoluble $PbSO_4$ accounted for ~3% of the total Pb in the shoots.

Vincent *et al.* (2001) examined the effects of pH on accumulation of Al, Mn, Fe, Cu, Zn, Cd, and Pb in *Scapania undulata* (Figure 125-Figure 136) in the English Lake District. They found that the metals had accumulated more in older parts of the plants, whereas the studies noted previously here used apical portions only. They found that there was greater aluminium accumulation in the two more acidic streams (pH 5.35 and 5.81). Fe showed no preference. Cu, Zn, and Cd accumulated mostly in the liverworts from the highest pH (7.26). Pb accumulated most at the middle and highest pH. The **accumulation enrichment factor** (amount of metal in plants divided by stream water concentration) followed the

sequence of $Zn < Cd < Cu < Mn < Pb < Al < Fe$, making Fe the most enriched.

As in other studies, Duncker (1976) found that zinc uptake was correlated with concentration, reaching a saturation at 60 mg L^{-1} . This was essentially constant after half an hour or two days. Light affected the uptake rate at low concentrations, with a 15% greater rate in the light with a 1 mg L^{-1} concentration. Temperature seemed to affect the rate, but it was not definitive. Duncker was unable to demonstrate any genetic differences in plants from high vs. low concentrations of zinc.

Other Pollutants

Scapania undulata (Figure 125-Figure 136) has also been used to assess fluoride in streams (Samecka-Cymerman & Kempers 1990). It has the ability to accumulate fluoride, dependent on the concentration in the water. In water with a concentration of 250 ppm, the concentration in the plants increased by 21-67%.

López and Carballeira (1989) found that, based on pigment contents among the five aquatic bryophytes they tested, *Scapania undulata* was the most sensitive to pollution. On the other hand, Stephenson *et al.* (1995) found this species to have an exceptionally high tolerance to both acidity and toxic metals in their North American sites. Could these be differences in physiological races?

Disturbance

Rudolf *et al.* (2012) noted that lower parts of streams in the Tatra Mountains of Slovakia are typically characterized by disturbance events, including road construction and use, clearings, buildings, avalanches, insect infestation (especially bark beetles), windthrows, and ski resorts. *Scapania undulata* (Figure 125-Figure 136) was among the bryophytes that was present more than three times in their survey of 78 sites spread across 28 streams, with altitudes ranging 639-2002 m asl. They also noted that nutrient relationships of stream bryophytes are poorly known, and that these disturbances often increase the nutrients in the streams.

Role

Scapania undulata (Figure 125-Figure 136) serves in a variety of roles in streams, lakes, and other wetlands. In streams, they are typically home to many insects and other aquatic invertebrates. In my own experience, if the stream was suitable for *S. undulata*, the liverwort was suitable as a home for a variety of insects (Glime 1968, 1978).

Some studies have demonstrated the use of *Scapania undulata* (Figure 125-Figure 136) as food for caddisflies (Cairns & Wells 2008). A more interesting documentation is that several caddisflies use this species to make their cases (Glime 1968). The species of liverwort depends on availability, with cases of *Paleagapetus celsus* from the eastern USA known from *Scapania nemorea* (Figure 71-Figure 79) (Flint 1962; Glime 1978) and several other leafy liverworts, including *S. undulata*. Ito (1998) found that all four species of *Paleagapetus* that he reviewed used *Scapania undulata* (and *Chiloscyphus polyanthos* – Figure 163) for their cases. Ito (1991) found that *Paleagapetus rotundatus* feeds on the leaves and lives among the plants, preferentially. It appears that all known members of the genus have this same strong dependence on leafy liverworts, including those in the eastern part of the

former Soviet Union (Botosaneanu & Levanidova 1987), Japan (Ito & Hattori 1986; Ito 1988, 1991), and North America (Flint 1962; Glime 1978).



Figure 163. *Chiloscyphus polyanthos*, a leafy liverwort found in the cases of the caddisfly *Paleagapetus* spp. Photo by Bernd Haynold, through Creative Commons.

In Japan, the caddisfly *Ptilocolepus granulatus* (Figure 164) uses *Scapania undulata* (Figure 125-Figure 136) (and *Chiloscyphus polyanthos* – Figure 163) to make its cases https://www.youtube.com/watch?v=7uZBMz_Qyuk, to serve as its substrate, and to become food (Ito 1998; Waringer & Graf 2002). Depisch (1999) and Ito and Higler (1993) also found that this caddisfly species commonly lives among and feeds on the liverwort *Scapania undulata*.



Figure 164. Larva of the caddisfly *Ptilocolepus granulatus* carrying its case made with leafy liverworts. Photo by Michel-Marie Solito de Solis, YouTube - permission needed.

Habitat Summary

It is difficult to describe the habitat of this species because of its variability. In Connecticut, USA, it is hydrophytic in rock ravines and calciphobic along rivers (Nichols 1916). On Cape Breton Island, Canada, it occurs in ravines (Nichols 1918). Watson (1919) summarized the information known to him to describe the species as submerged in slow or fast water with poor mineral salts,

often in marshy places, on wet rocks or soil associated with fast water, occasionally submerged. To these habitats, Verdoorn (1932) added that it occurs in water on emergent basket-ball-sized rocks in shallow water, an observation supported by Glime (1970) for occurrences on rocks just above and below the water surface of a headwater stream in New Hampshire, USA.

Summary

The **Scapaniaceae** has four genera with members that occur in wet or aquatic habitats. Of these, *Scapania* has the most aquatic members. Among these, *Scapania undulata* is usually submersed and has been the subject of a variety of studies.

The wetland and aquatic species of the **Scapaniaceae** can be found from the tropics to the Arctic, but in the tropics they are mostly confined to the high altitudes in the mountains. They are relatively common at the interface of water and air, occurring on emergent rocks and stream banks. Some are common in bogs, where they grow over or among the *Sphagnum*. They can often develop red and brown pigments in response to prolonged bright sunlight. They mostly occur in cool or cold water and some can withstand temperatures down to -10°C in ice for at least 34 days. Many produce abundant gemmae. Some are associated with *Mniaecia jungermanniae* and other fungi.

Some caddisflies use leaves of several species of *Scapania* to make their cases. And some eat the leaves, despite the presence of antibiotics and potential antifeedants. The aquatic species are usually good accumulators, often with a high tolerance to both acidity and toxic metals. Their nutrient requirement is low.

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CHAPTER 1-4

AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: JUNGERMANNIINEAE

TABLE OF CONTENTS

Antheliaceae	1-4-3
<i>Anthelia julacea</i>	1-4-3
<i>Anthelia juratzkana</i>	1-4-5
Balantiopsidaceae	1-4-6
<i>Balantiopsis convesiuscula</i>	1-4-6
Calypogeiaceae	1-4-7
<i>Calypogeia</i>	1-4-7
<i>Calypogeia arguta</i>	1-4-7
<i>Calypogeia azurea</i>	1-4-8
<i>Calypogeia fissa</i>	1-4-10
<i>Calypogeia goebelii</i>	1-4-12
<i>Calypogeia muelleriana</i>	1-4-12
<i>Calypogeia sphagnicola</i>	1-4-14
<i>Calypogeia sullivantii</i>	1-4-16
Geocalycaceae	1-4-16
<i>Geocalyx graveolens</i>	1-4-16
Gymnomitriaceae	1-4-18
<i>Gymnomitrium commutatum</i>	1-4-18
<i>Gymnomitrium crenulatum</i>	1-4-18
<i>Marsupella</i>	1-4-19
<i>Marsupella aquatica</i>	1-4-19
<i>Marsupella boeckii</i>	1-4-20
<i>Marsupella emarginata</i>	1-4-21
<i>Marsupella emarginata</i> subsp. <i>tubulosa</i>	1-4-22
<i>Marsupella koreana</i>	1-4-23
<i>Marsupella pseudofunkii</i>	1-4-24
<i>Marsupella sparsifolia</i>	1-4-23
<i>Marsupella sphacelata</i>	1-4-26
<i>Marsupella subemarginata</i>	1-4-28
<i>Marsupella vietnamica</i>	1-4-28
<i>Marsupella yakushimensis</i>	1-4-29
<i>Nardia assamica</i>	1-4-30
<i>Nardia compressa</i>	1-4-30
<i>Nardia geoscyphus</i>	1-4-32
<i>Nardia scalaris</i>	1-4-32
Harpanthaceae	1-4-34
<i>Harpanthus flotovianus</i>	1-4-34
Hygrobilaceae	1-4-36
<i>Hygrobilla laxifolia</i>	1-4-36
Jungermanniaceae	1-4-37
<i>Eremontus myriocarpus</i>	1-4-37
<i>Jungermannia</i>	1-4-38
<i>Jungermannia atrovirens</i>	1-4-38
<i>Jungermannia borealis</i>	1-4-39
<i>Jungermannia callithrix</i>	1-4-39
<i>Jungermannia exsertifolia</i>	1-4-40

<i>Jungermannia exsertifolia</i> subsp. <i>cordifolia</i>	1-4-40
<i>Jungermannia pumila</i>	1-4-44
<i>Jungermannia quadridigitata</i>	1-4-45
<i>Mesoptychia badensis</i>	1-4-45
<i>Mesoptychia bantriensis</i>	1-4-46
<i>Mesoptychia collaris</i>	1-4-46
<i>Mesoptychia gillmanii</i>	1-4-47
<i>Mesoptychia turbinata</i>	1-4-47
Notoscyphaceae.....	1-4-48
<i>Notoscyphus lutescens</i>	1-4-48
Saccogynaceae.....	1-4-49
<i>Saccogyna viticulosa</i>	1-4-49
Solenostomataceae.....	1-4-51
<i>Solenostoma</i>	1-4-51
<i>Solenostoma ariadne</i>	1-4-51
<i>Solenostoma gracillimum</i>	1-4-51
<i>Solenostoma hyalinum</i>	1-4-53
<i>Solenostoma javanicum</i>	1-4-54
<i>Solenostoma obovatum</i>	1-4-55
<i>Solenostoma sphaerocarpum</i>	1-4-56
<i>Solenostoma stephanii</i>	1-4-57
<i>Solenostoma tetragonum</i>	1-4-57
<i>Solenostoma truncatum</i>	1-4-57
<i>Solenostoma vulcanicola</i>	1-4-58
Summary.....	1-4-59
Acknowledgments.....	1-4-59
Literature Cited.....	1-4-59

CHAPTER 1-4

AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: JUNGERMANNINEAE



Figure 1. A sulfur stream in Japan where the dominant vegetation is *Solenostoma vulcanicola*. Photo by Juuyoh Tanaka, through Creative Commons.

Antheliaceae

Anthelia julacea (Figure 2-Figure 3)

Distribution

Anthelia julacea (Figure 2-Figure 3) is somewhat Holarctic, being absent in the northernmost part of the tundra (Schuster 1974). In Europe it extends southward

from Iceland to Austria and the Czech Republic in alpine regions. It is present in eastern Siberia, but not in European Russia. It also extends into China, India, and Japan. Its North American distribution is more scattered and rare, with records often proving to be *Anthelia juratzkana* (Figure 7-Figure 10). *Anthelia julacea* seems to be concentrated on the west coast, from the Aleutian Islands and Alaska southward to Oregon and possibly California. But it is also known from Quebec (Kucyniak 1949).



Figure 2. *Anthelia julacea*, a holarctic and alpine species common in springs and *Sphagnum* hummocks, mixed here with other bryophytes. Photo by Michael Lüth, with permission.



Figure 4. *Sphagnum auriculatum*, a species that occurs with *Anthelia julacea* on flushed slabs of granite. Photo by Bernd Haynold, through Creative Commons.

Aquatic And Wet Habitats

West (1910) described this as a species of wet sandy or peaty shores of mountain lakes in Scotland. This liverwort seems to be rather consistently present in the damp tundra (Schuster 1974). In the damp tundra Shimwell (1972) named the *Anthelion julaceae* alliance for the sub-alpine spring vegetation dominated by this species. The masses of these liverworts resemble polsters of *Sphagnum* hummocks of **ombrogenous** (dependent on rain for its formation) bogs (Figure 3). Jerram (2003) found it in a spring **flush** (area where water from underground flows out onto surface to create area of saturated ground, rather than well-defined channel; piece of boggy ground, especially where water frequently lies on surface; swampy place; pool of water in field) in Cumbria, UK. *Anthelia julacea* (Figure 2) occurred with *Sphagnum auriculatum* (Figure 4) on flushed slabs of granite. Bajzak and Roberts (2011) found it in tundra-like meadows where *Sphagnum lindbergii* (Figure 5) and *Paludella squarrosa* (Figure 6) dominated. It covered the ground in some places that were open, forming a dense crust.



Figure 5. *Sphagnum lindbergii*, a species that occurs with *Anthelia julacea* in tundra-like meadows. Photo by J. C. Schou, with permission.



Figure 3. *Anthelia julacea* forming hummocky mats. Photo by Jean Faubert, with permission.



Figure 6. *Paludella squarrosa*, a species that occurs with *Anthelia julacea* in tundra-like meadows. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Anthelia julacea (Figure 2) is a relatively robust plant that occurs in patches or mats (Figure 3). It is typically dark green to deep yellowish green to brown, often is crowded, forming shrub-like mounds.

I have found little information on its photosynthesis and productivity. Dilks and Proctor (1975) found that the photosynthetic response to temperature in *Anthelia julacea* (Figure 2) did not differ significantly from that of most lowland species. The species seem to be protected from intracellular freezing to at least -5°C.

Reproduction

The species is **dioicous** (Jessup 2019), accounting for the fact it is usually lacking sporophytes.

Anthelia juratzkana (Figure 7-Figure 10)

Distribution

Anthelia juratzkana (Figure 7-Figure 10) is mostly Arctic-alpine and bipolar (Schuster 1974). In the Southern Hemisphere it is present in New Zealand, Bolivia, at Tierra del Fuego, Argentina, South Georgia, and Livingston Island, Antarctica. In the Northern Hemisphere, it extends as far northward as the exposed land. It extends southward from there in high alpine summits, extending from Spitsbergen through Scandinavia to England and the central European Alps. In North America it extends southward to Quebec, Canada, and Maine, USA.

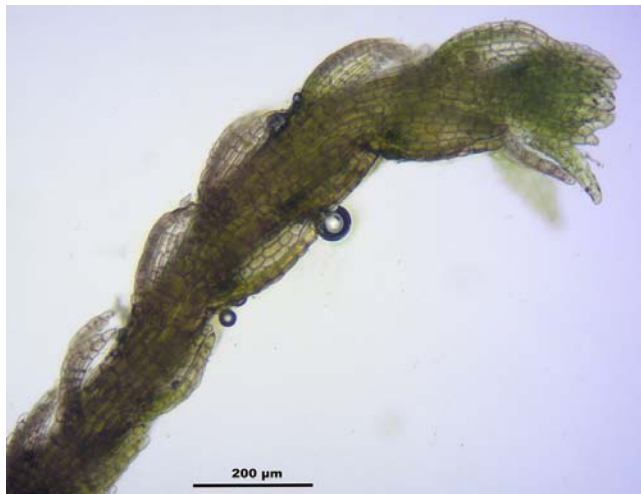


Figure 7. *Anthelia juratzkana*, an Arctic-alpine and bipolar species that occurs in streams, on the banks of streams and lakes, and on wet cliffs. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Anthelia juratzkana (Figure 7-Figure 10) is typical of perennially wet microhabitats (Jessup 2019). Bakalin (2005) found *Anthelia juratzkana* (Figure 7-Figure 10) in a sedge-moss mire on Bering Island in northwestern Russia. It also occurred on peaty banks of small lakes with several other leafy liverworts, and on hummocks or hollows in moss-shrub or moss-sedge mires and is also relatively common on the island on peaty banks of lakes, on fine-grained soil in wet crevices, on rocks near small waterfalls, and along streams. It is not common elsewhere in northwestern Asia.

The species is typical of cold, damp sites exposed to full sun for at least part of the growing season (Schuster 1974). It frequently occupies moist, snow-fed slopes (Figure 10) in the Far North. It occurs in alpine streams in the Swiss Alps (Geissler 1976) and on wet cliff and rocks

at the lake shore of the Upper Bureya River in the Russian Far East (Konstantinova *et al.* 2002).



Figure 8. *Anthelia juratzkana* habitat showing silvery mats. Photo by Michael Lüth, with permission.



Figure 9. *Anthelia juratzkana* mats showing closer view with hummocky appearance. Photo by Michael Lüth, with permission.



Figure 10. *Anthelia juratzkana* habitat at receding snow bank. Photo by Michael Lüth, with permission.

Role

Anthelia juratzkana (Figure 7) forms thin, silvery gray or decolorate patches on bare ground, sometimes forming dense mounds and appearing bluish gray to gray-green (Schuster 1974). The individual branches are minute.

The bluish coloring is often due to the presence of **Cyanobacteria**. *Anthelia juratzkana* (Figure 7-Figure 10) has the blue-green bacterium *Gloeocapsa montana* (see Figure 11) associated with it (Riedl 1977). These bacterial colonies give it a gelatinous sheath that causes a waxy, whitish appearance, with a fungus growing in the sheath and another forming a mycorrhiza-like symbiosis with the liverwort.

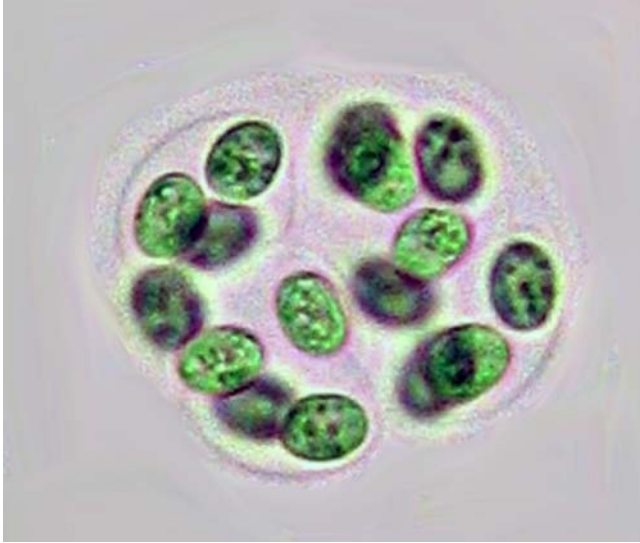


Figure 11. *Gloeocapsa* sp.; *Gloeocapsa montana* is a **Cyanobacterium** that associates with *Anthelia juratzkana*. Photo by John, through Creative Commons.

Adaptations

Both species of *Anthelia* expresses a variety of phenotypes in response to light, moisture, temperature, and substrate. Both species form lax patches, sods, mounds and **turfs** of elongate stems (2–4 cm) in perennially wet microhabitats.

Lösch *et al.* (1983) found that only the uppermost 4 mm layer of *Anthelia juratzkana* (Figure 7-Figure 10) had enough pigment concentration to accomplish photosynthesis. At light saturation, its optimum temperatures were 6–11°C. In those conditions, maximum CO₂ uptake was 0.7 mg CO₂ g⁻¹ dw h⁻¹, compared to 1.5 mg for *Polytrichastrum sexangulare* (Figure 12). *Anthelia juratzkana* has its low temperature **compensation point** at -4°C (compensation point is level at which photosynthesis gain is offset by respiration loss). On the other end of the scale, this species cannot sustain photosynthesis at 30°C. The photosynthetic rate is not damaged by nine months of storage in dark, cold, wet conditions, securing its ability to survive in Arctic and alpine areas.

Reproduction

Anthelia juratzkana is **paroicous** and produces sporophytes frequently (Jessup 2019). It is abundant in the Arctic in midsummer; spore dispersal there occurs as bird migrations begin, increasing opportunities for spores and miniscule stem fragments to be dispersed in the dusted feathers of these birds.



Figure 12. *Polytrichastrum sexangulare*, a species with a maximum CO₂ uptake of 1.5 mg compared to only 0.7 mg CO₂ g⁻¹ dw h⁻¹ for *Anthelia juratzkana*. Photo by Štěpán Koval, with permission.

Balantiopsidaceae

Balantiopsis convexiuscula (Figure 13-Figure 14)

Distribution

Balantiopsis convexiuscula (Figure 13-Figure 14) seems to be restricted to New Zealand and Australia (Simpson 1977; GBIF 2020a).



Figure 13. *Balantiopsis convexiuscula*, a species of New Zealand and Australia, where it occurs on stream banks, logs, and near waterfalls. Photo by Shirley Kerr, with permission.

Aquatic and Wet Habitats

Balantiopsis convexiuscula (Figure 13-Figure 14) occurs on streambanks in New Zealand (Fineran). Simpson (1971) found it on a bank near a waterfall in Nelson Lakes National Park, New Zealand. Referring to it as **hygrophilic**, Mark *et al.* (1989) noted that it was absent in stands of the Fiord Ecological Region of New Zealand that lacked flowing water. Instead, they are typical in watercourses.



Figure 14. *Balantiopsis convexiuscula* forming a vertical mat as one might find on a stream bank. Photo by Shirley Kerr, with permission.

Suren and Duncan (1999) found that *Balantiopsis convexiuscula* (Figure 13-Figure 14) is positively correlated with bankfull discharge in their study of 48 streams in South Island, New Zealand. Simpson (1977) found it on logs and on a bank near a waterfall of Coldwater Creek, New Zealand.

Reproduction

Female stems of *Balantiopsis convexiuscula* (Figure 13-Figure 14) form an archegonium (Allison & Child 1975). After fertilization, a marsupium forms around the archegonium, from which the capsule emerges. However, capsules are relatively rare. Spores are small.

Calypogeiaceae

Calypogeia (Figure 15-Figure 21, Figure 23-Figure 46)

Geissler (1976) reported *Calypogeia* (Figure 15-Figure 21, Figure 23-Figure 46) as *C. trichomanis* in alpine streams of the Swiss Alps. Unfortunately, this name has been used for a variety of species and I cannot be sure which one she found. The name is no longer in use.

Stephenson *et al.* (1995) reported *Calypogeia* (Figure 15-Figure 21, Figure 23-Figure 46) species from West Virginia, USA, mountain streams. The preferred pH was around 5.95.

Calypogeia arguta (Figure 15-Figure 16)

Distribution

Calypogeia arguta (Figure 15-Figure 16) is widely distributed, from the Faeroe Islands and Scandinavia through India, Korea, Japan, and many provinces of China, to South Africa, and New Caledonia (GBIF 2020b). In the Western Hemisphere, it seems to be unknown farther north than Nova Scotia or farther south than Cuba.



Figure 15. *Calypogeia arguta*, a widely distributed species in the Northern Hemisphere, of moist soil and wet sites. Photo by Bat Whittler, through Creative Commons.

Aquatic and Wet Habitats

Ferreira *et al.* (2008) reported *Calypogeia arguta* (Figure 15) from rivers. *Calypogeia arguta* is relatively common on moist soil (Figure 16) in Hong Kong (So & Zhu 1996). It occurs there along with *Kurzia gonyotricha*, *Heteroscyphus argutus* (Figure 17), *Pallavicinia subciliata* (Figure 18), and *Notoscyphus lutescens* (Figure 19). Those populations vary considerably in size and color. Alam (2011) reports that the species forms smooth mats in the Nilgiri Hills, Tamil Nadu, India. In the Azores, Gabriel and Bates (2005) reported this as a species characteristic of the wettest sites, although it also was most commonly found on rocks.



Figure 16. *Calypogeia arguta* habitat at a stream edge on moist soil. Photo by George G., through Creative Commons.



Figure 17. *Heteroscyphus argutus*, an associate of *Calypogeia arguta* in some habitats. Photo by Lin Shanxiong, through Creative Commons.



Figure 18. *Pallavicinia subciliata*, an associate of *Calypogeia arguta* in some habitats. Photo by Lin Shanxiong, through Creative Commons.



Figure 19. *Notoscyphus lutescens*, an associate of *Calypogeia arguta* in some habitats. Photo by David Tng, with permission.

Kitagawa (1978a) considered *Calypogeia arguta* (Figure 15-Figure 16) to be a pioneer on the sterile soil of a roadside bank in Mts. Hakkôda, Japan, but also was abundant on soil along sulfur-rich streams.

Adaptations

Its need for water was demonstrated by Clausen (1964). She found that few cells were alive after 12 hours at 20°C and 93% humidity. At 96% humidity, only about half the cells were alive. But low temperatures are also detrimental; few cells were alive from plants from the Faeroe Islands when subjected to two days on ice at -10°C.

Reproduction

One possible explanation for the widespread distribution of this species is its ability to survive in diaspore banks. Bisang *et al.* (2003) found that this species germinated from a turf diaspore bank in the Malaysian rainforest.

Fungal Interactions

Calypogeia arguta (Figure 15-Figure 16) is among the liverwort species that apparently inhibit the parasitic ascomycete *Mniaecia jungermanniae* (Figure 24-Figure 26) (Pressel & Duckett 2006). Two other liverwort species in the bryophyte association were infected and produced apothecia. Benkert and Otte (2006), on the other hand, observed *M. jungermanniae* using *Calypogeia arguta* as host. The fungus is most common in the colder periods of the year (March to May) in the Liberec Region of the Czech Republic (Egertová *et al.* 2016).

Calypogeia azurea (Figure 20-Figure 21)

Distribution

Calypogeia azurea (Figure 20-Figure 21) is a widespread, subboreal-montane species (Buczkowska *et al.* 2016), being widely distributed through the northern hemisphere, including North America (rare; in Pacific Northwest), Europe, and eastern Asia (Buczkowska *et al.* 2018).



Figure 20. *Calypogeia azurea*, a species widely distributed in the Northern Hemisphere. Photo by Hermann Schachner, through Creative Commons.



Figure 21. *Calypogeia azurea* showing gemmae. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

It occurs on loamy soil, humus, peat, wet stones and rocks, to rotten logs (Buczkowska *et al.* 2018). Watson (1919) considered it (as *Calypogeia trichomanis*) to be a

species of stream or river banks that experienced frequent submergence and slow water. Thus, the populations would occasionally become submerged. Geissler and Selldorf (1986) reported it occurring with *Carex goodenoughii* and uncommonly with *Eleocharis quinqueflora* (Figure 22) in European mountains.



Figure 22. *Eleocharis quinqueflora*, a sedge species that sometimes has *Calypogeia azurea* at its base. Photo by Max Licher, through Creative Commons.

In the *Calypogeia azurea* complex, *C. sinensis* prefers wet open cliffs and partly shaded cliff caves in the waterfall spray zone, or mesic tree trunk bases and decaying wood in broad-leaved, evergreen, subtropical to southern subtropical montane forests (Buczkowska *et al.* 2018). It has only two known localities. The first is subtropical montane forest near Xiniu Waterfall in the Chinese province of Guizhou at about 1300 m asl. The second locality is a subtropical montane forest in southern North Vietnam, at about 2000 m asl.

Adaptations and Variations

Calypogeia azurea (Figure 20-Figure 21) is one of the few members of *Calypogeia* that has blue oil bodies (Figure 23) (Buczkowska *et al.* 2016), giving it a bluish color and accounting for the epithet *azurea*. The species presents a variety of environmentally induced morphological differences.

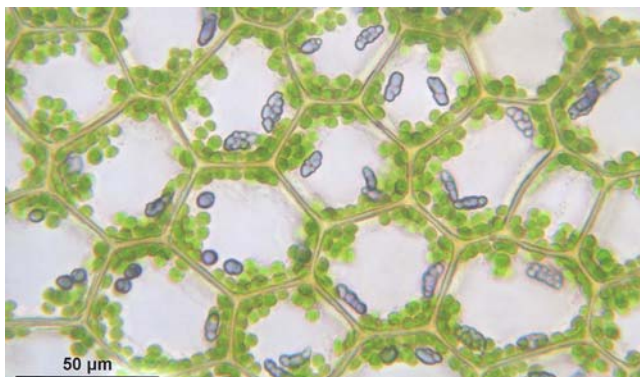


Figure 23. *Calypogeia azurea* leaf cells showing bluish oil bodies. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Calypogeia azurea (Figure 20-Figure 21) is **autoicous** (Paton 1999; Damsholt 2002), although Damsholt also questions the possibility it is sometimes **paroicous**.

Fungal Interactions

Calypogeia azurea (Figure 20-Figure 21) is a species where the fungal parasite *Mniaecia jungermanniae* (Figure 24-Figure 26) finds suitable habitat and host (Egertová *et al.* 2016). These occurrences include liverworts growing on wet soil.

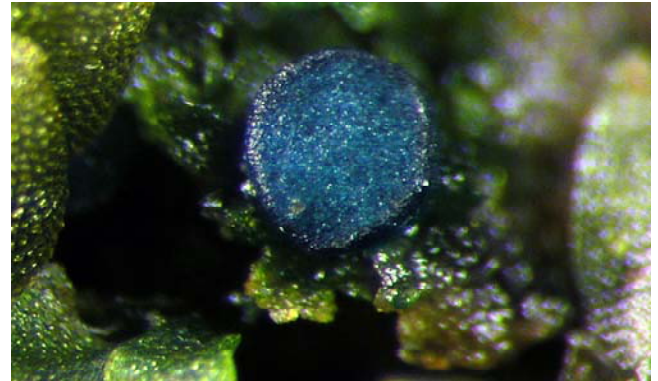


Figure 24. *Calypogeia azurea* with fungal parasite *Mniaecia jungermanniae*. Photo by Walter Obermayer, with permission.

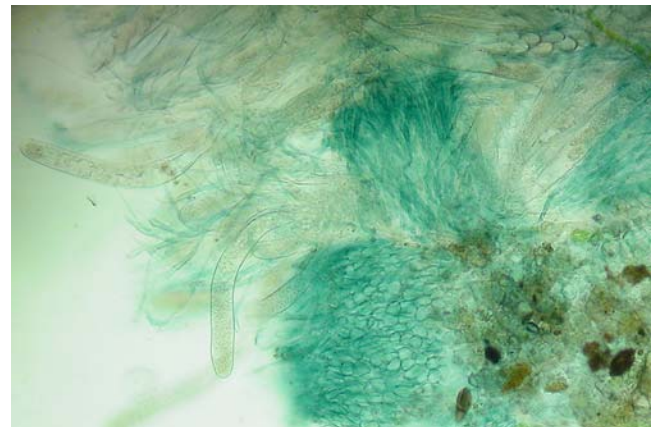


Figure 25. *Calypogeia azurea* with fungal parasite *Mniaecia jungermanniae* asci in the upper right corner of the image. Photo by Walter Obermayer, with permission.



Figure 26. *Calypogeia azurea* with asci of the fungal parasite *Mniaecia jungermanniae*. Photo by Walter Obermayer, with permission.

Biochemistry

A number of studies have examined the secondary compounds in *Calypogeia azurea* (Figure 20-Figure 21). Among these, Nakagawara *et al.* (1992) looked at the azulenes in their study of sesquiterpenoids. One of these azulenes exhibits anti-inflammatory and anti-ulcer activity. Tazaki *et al.* (1998) likewise isolated a new sesquiterpenoid from the species.

Calypogeia fissa (Figure 27-Figure 29, Figure 33-Figure 34)

Distribution

Calypogeia fissa (Figure 27-Figure 29, Figure 33-Figure 34) has a suboceanic distribution pattern in North America, Europe, Asia, and North Africa (Potemkin 2018).



Figure 27. *Calypogeia fissa*, a species with a suboceanic distribution in the Northern Hemisphere, occurring in a variety of wet habitats. Photo by Hermann Schachner, through Creative Commons.



Figure 28. *Calypogeia fissa*. Photo by Štěpán Koval, with permission.



Figure 29. *Calypogeia fissa* ventral side showing under leaves. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) attributed this species to peaty ground, associated with fast water. Clapham (1940) reported it from the sides and tops of tussocks in calcareous fens in the Oxford District, UK. Its occurrence in the River Tweed, UK, was not common (Holmes & Whitton 1975a). It can occur in irrigation ditches (Beaucourt *et al.* 1987). In southern Finland it occurs in small lakes (Toivonen & Huttunen 1995). *Calypogeia fissa* (Figure 27-Figure 29, Figure 33-Figure 34) in the study area in northwestern European Russia grows on more or less wet humus as well as sandy soils and rotten wood near temporary water courses in coastal communities (Potemkin 2018). It also occurs in rock crevices with seepage where one might also find *Scapania nemorea* (Figure 30). *Calypogeia fissa* frequently forms rather extensive mats resulting from frequent production of gemmae (Figure 33) and probably regular spore production (Figure 34).



Figure 30. *Scapania nemorea*, a species that can occur in rock crevices with *Calypogeia fissa*. Photo by Michael Lüth, with permission.

Genetic and Physiological Differences

Buczkowska *et al.* (2011) identified two morphologically distinct groups of the *Calypogeia fissa* (Figure 27-Figure 29, Figure 33-Figure 34) complex in Europe. These were supported by statistical analysis of 34 morphological characters as well as by genetic distance. Furthermore, PCR indicates that the European and North American populations represent two subspecies of *Calypogeia fissa* (Buczkowska *et al.* 2012a): *Calypogeia fissa* subsp. *fissa* (Figure 31) in Europe and *C. fissa* subsp. *neogaea* (Figure 32) in North America (Buczkowska *et al.* 2015). These could be distinguished by both genetic and molecular markers. In Europe, there is a haploid group and a diploid group, with an isozyme pattern that suggests an **allopolyploid** (having two haploid sets of chromosomes that are dissimilar and derived from different species; *i.e.*, a hybrid which has a functional set of chromosomes from each parent of two species) origin of the diploid group. Such differences can express themselves in physiological differences without necessarily showing morphological differences. This can account for finding the species in different habitats on different continents.

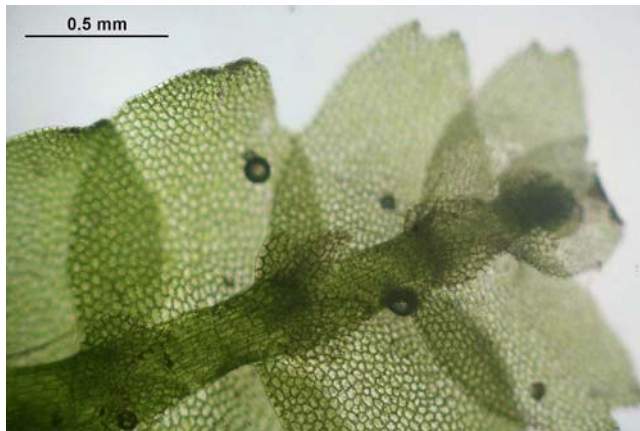


Figure 31. *Calypogeia fissa* subsp. *fissa*, the subspecies typical in Europe, showing underleaves. Photo by Hermann Schachner, through Creative Commons.

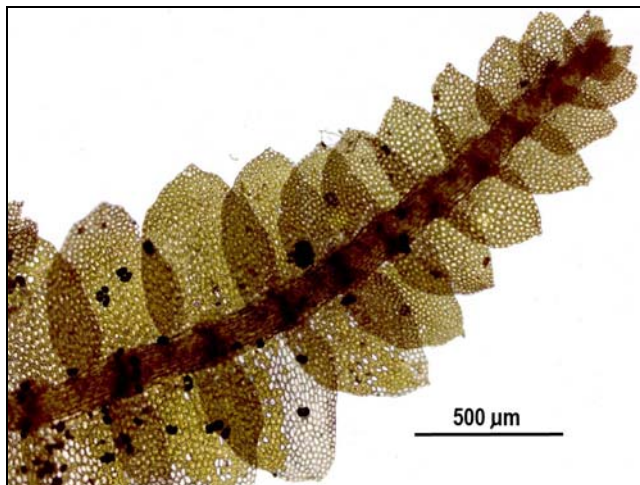


Figure 32. *Calypogeia fissa* subsp. *neogaea*, the subspecies typical in North America; ventral leaves in the photo are the darkened areas across the stem. Photo by Blanka Agüero, with permission.

Reproduction

Calypogeia fissa frequently forms rather extensive **mats** resulting from frequent production of gemmae (Figure 33) and probably regular spore production (Figure 34) (Schuster 1969; Potemkin 2018). *Calypogeia fissa* (Figure 27-Figure 29, Figure 33-Figure 34) is **autoicous** or **paroicous** (Schuster 1969).



Figure 33. *Calypogeia fissa* with gemmae. Photo by Štěpán Koval, with permission.



Figure 34. *Calypogeia fissa* with nearly mature capsule. Photo by Malcolm Storey, through Creative Commons.

It is able to regenerate from peat slabs (Duckett & Clymo 1988). Unlike some leafy liverworts, *Calypogeia fissa* lacks underground shoots (Figure 29). Therefore, it regenerates most abundantly at the surface, failing to have regenerative parts below 9 cm depth in the peat.

Fungal Interaction

Wang and Qiu (2006) found a report of fungal association with *Calypogeia fissa* (Figure 27-Figure 29, Figure 33-Figure 34), but I have not found details of this record.

Biochemistry

Warmers and König (1999) found four new sesquiterpenes in *Calypogeia fissa* (Figure 27-Figure 29, Figure 33-Figure 34). Their role remains unknown, but they are likely to play a role in antiherbivory. The oil bodies (Figure 35) typically house such secondary compounds.



Figure 35. *Calypogeia fissa* leaf cells showing colorless oil bodies. Photo by Hermann Schachner, through Creative Commons.

Calypogeia goebelii (Figure 36)

(syn. = *Kantia goebelii* fo. *thermarum*)

Distribution

Calypogeia goebelii (Figure 36) is distributed in Australia, Oceania, and southern Asia (Guala & Döring 2019).



Figure 36. *Calypogeia goebelii*, a species that lives in thermal acidic sprays, from Australia, Oceania, and southern Asia. Photo through Creative Commons.

Aquatic and Wet Habitats

Ruttner (1955) reported this species from areas with thermal acidic spray in the tropics. Elsewhere, Kitagawa (1978b) reported *Calypogeia goebelii* (Figure 36) from 1550-1600 m asl in the evergreen forest of Thailand as terrestrial and listed its distribution as Java, Sumatra, New Guinea, and Micronesia.

Calypogeia muelleriana (Figure 37-Figure 40)

Like many of the liverworts, the taxonomy has been confusing for *Calypogeia muelleriana* (Figure 37-Figure 40). Buczkowska (2010) found that among 52 samples from Poland that resembled *Calypogeia muelleriana*, 21 belonged to a new taxon, as identified with isozyme markers. Based on Chloroplast DNA sequences, this new taxon more closely resembles *C. azurea* (Figure 20-Figure 21) than it does *C. muelleriana* and this unnamed new species has also been identified in the USA (Buczkowska *et al.* 2013)

Distribution

Calypogeia muelleriana (Figure 37-Figure 40) is widespread in Europe, but was poorly known in North America (Stotler & Vitt 1972). It is circumpolar and bipolar (Emerson & Loring 2010). Hong (1990) added a number of locations in western USA and Canada, including shaded decaying logs, moist loam, and shaded damp stream banks. He described two new forms (fo. *schofieldii* and fo. *shieldsii*) in this western North American region. It is also known in eastern North America from Manitoulin Island, Ontario, Canada (Williams & Cain 1959), in North and South Carolina, USA (Raczka 2014), and in Pickle Springs, Missouri, USA (Stotler & Vitt 1972).



Figure 37. *Calypogeia muelleriana*, a species widespread in Europe on stream and river banks and in lakes. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

In the Pickle Springs, Missouri, USA, *Calypogeia muelleriana* (Figure 37-Figure 40) occurred on sandy soil of stream banks (Stotler & Vitt 1972) and in North and South Carolina, USA, along the Waccamaw River (Raczka 2014). Leclercq (1977) also reported it from earthy and gravelly substrates of river banks in Haute Ardenne rivers, Belgium. In Germany, it occurs in upper and middle

stream reaches in the Harz Mountains (Bley 1987). In southern Finland it occurs in small lakes (Toivonen & Huttunen 1995). These latter two suggest that it is facultatively aquatic.

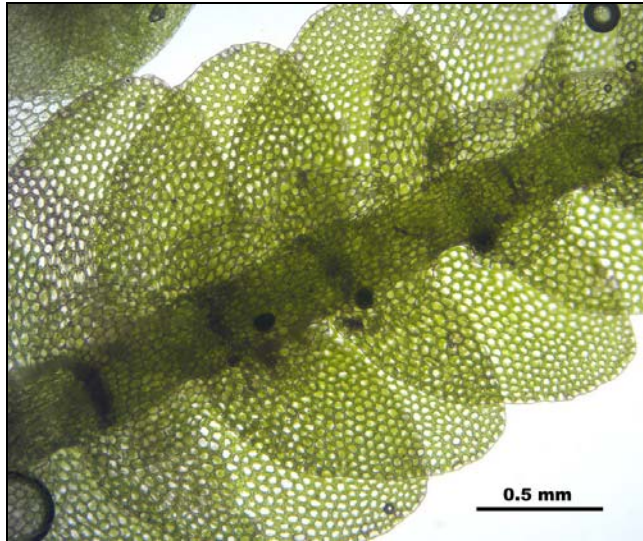


Figure 38. *Calypogeia muelleriana* ventral side with underleaves. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Calypogeia muelleriana (Figure 37-Figure 40) is **monoicous**, with both male and female reproductive organs developing from short lateral branches (Schuster 1969). After fertilization, a spore-bearing capsule develops, splits, and releases spores to the wind. Sometimes gemmae develop near the tips of its leafy stems (Figure 39-Figure 42) or around the leaf margins. These gemmae eventually detach, after which they can form new clonal plants under favorable conditions.



Figure 39. *Calypogeia muelleriana* habitat showing plants with gemmae. Photo by Michael Lüth, with permission.



Figure 40. *Calypogeia muelleriana* with gemmae. Photo by David T. Holyoak, with permission.



Figure 41. *Calypogeia muelleriana* with terminal gemmae. Photo by Des Callaghan, with permission.

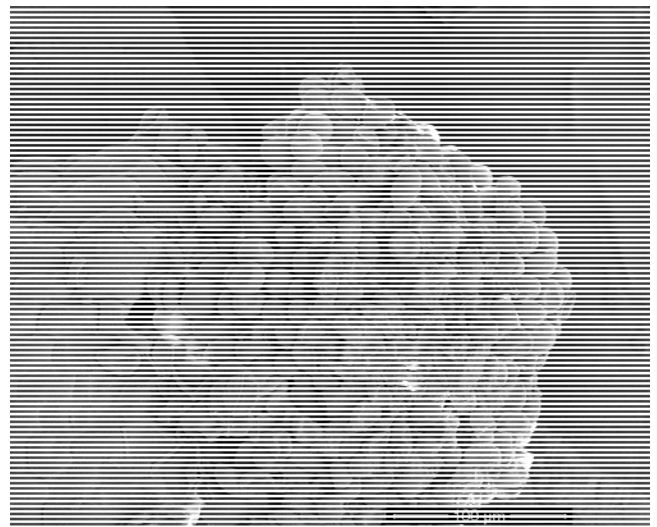


Figure 42. SEM of *Calypogeia muelleriana* leaf with gemmae. Photo by Jeff Duckett and Silvia Pressel, with permission.

Biochemistry

Some of its secondary compounds have been identified. Warners *et al.* (1998) investigated the lipophilic constituents and reported three new sesquiterpene compounds. Such compounds often occur in the oil bodies (Figure 43).



Figure 43. *Calypogeia muelleriana* showing oil bodies in leaf cells. Photo from Botany Website, UBC, with permission.



Figure 45. *Calypogeia sphagnicola* showing underleaf. Photo by Scot Loring, through Creative Commons.

***Calypogeia sphagnicola* (Figure 44-Figure 46)**

(syn. = *Calypogeia muelleriana* fo. *sphagnicola*)

Distribution

Calypogeia sphagnicola (Figure 44-Figure 46) is widely distributed, occurring in the subarctic and alpine areas in northern and central Europe, from Greenland southward, and North America, with a report from Japan (Schuster 1969). In North America it extends from Alaska southward to Alberta and British Columbia in the west and from Newfoundland (Weber 1976), Quebec, and Ontario to West Virginia in the east (Schuster 1969). In the southern extensions it is primarily in spruce and tamarack bogs – habitats that are often considered **refugia** (locations which support isolated or relict population of once more widespread species) and suggest it may have had a wider distribution at one time.

Aquatic and Wet Habitat

Of the many references I found documenting the presence of this species, all but one indicated it was associated with *Sphagnum* (Figure 46). Thus, I question the record from North Carolina, USA, indicating that it was found on moist soil (Blomquist 1936) and suggest it may have been a misidentification – or incomplete habitat information.



Figure 44. *Calypogeia sphagnicola*, a species from sub-Arctic and alpine areas in the Northern Hemisphere. Photo by Erika Mitchell, through Creative Commons.



Figure 46. *Calypogeia sphagnicola* with *Sphagnum*. Photo by David T. Holyoak, with permission.

Calypogeia sphagnicola (Figure 44-Figure 46) has earned its name because it occurs almost exclusively in *Sphagnum* bogs, but also on *Sphagnum*-capped crests of cliffs (Schuster 1969; Emerson & Loring 2010). *Calypogeia sphagnicola* occurs at the summits of *Sphagnum* hummocks in southern France (Hugonnot 2011). They are able to colonize degenerating mats in communities with other leafy liverworts. It is one of the species that has high conservation value because of its restriction to specific microhabitats, especially dying *Sphagnum*. Kitagawa (1978a) likewise reported this species from oligotrophic moors where it grows among *Sphagnum* in the alpine zone of Ödake, Japan, but its primary distribution is in the Arctic, with only three locations in Japan in Japan's northern mountains. Near Gladkovskaya Bay in Russia, Bakalin (2005) found it to occur on the peaty banks of ponds in a peat moss-sedge mire, typically occurring with other liverworts. Bakalin *et al.* (2016) reported it from bare peat of peat moss tussocks in mires in the Putorana Plateau of eastern Siberia, where it grew with other liverworts.

Albisson (1997) considered *Calypogeia sphagnicola* (Figure 44-Figure 46) to have a somewhat wider ecological

amplitude than some of the mire specialists. They also found that these liverworts occur more frequently with *Sphagnum* species in subgenera *Sphagnum* (Figure 47) and *Acutifolia* (Figure 48) than in subgenus *Cuspidatum* (Figure 49). This is consistent with the observations of Souto *et al.* (2015) who found that *C. sphagnicola* was associated with dense carpets of *Sphagnum magellanicum* (Figure 47), a moss in subgenus *Sphagnum*.



Figure 47. *Sphagnum magellanicum*, subgenus *Sphagnum*, showing a dense carpet that can serve as substrate for *Calypogeia sphagnicola*. Photo by Dale Vitt, with permission.

Despite its relative rarity, *Calypogeia sphagnicola* (Figure 44-Figure 46) is able to successfully compete with other liverworts by over-growing the *Sphagnum* capitula in the hummocks, but this is further supported by other liverworts that overgrow the *Sphagnum* and reduce its growth rate (Nordbakken 1996). Hugonnot *et al.* (2015) suggest that *C. sphagnicola* grows over actively growing *Sphagnum* capitula (Figure 46), whereas some leafy liverwort species avoid the *Sphagnum* competition by growing on bare peat as well as among *Sphagnum*.



Figure 48. *Sphagnum girgensohnii*, subgenus *Acutifolia*, representing the more preferred substrate group for *Calypogeia sphagnicola*. Photo by Kari Pihlaviita, through Creative Commons.

In the Alaskan black spruce forest, *Calypogeia sphagnicola* (Figure 44-Figure 46) forms small patches or even isolated shoots (Seppelt *et al.* 2008). These are green to pale green to yellowish-green, but older parts are frequently yellowish-brown.

Reproduction

Calypogeia sphagnicola (Figure 44-Figure 46) is **monoicous** (Schuster 1969). Gemmae are common (Bosanquet 2021).



Figure 49. *Sphagnum cuspidatum* (subgenus *Cuspidatum*) submersed; this species prefers wetter habitats than most *Sphagnum* species and is not a preferred substrate for *Calypogeia sphagnicola*. Photo by Bernd Haynold, through Creative Commons.

Biochemistry

Buczowska *et al.* (2012b) used isozymes to determine that two forms of *Calypogeia sphagnicola* (fo. *sphagnicola* and fo. *paludosa*) represent genetically distinct species. The former is haploid and the latter is diploid. They likewise differ distributionally in Poland. "*Calypogeia sphagnicola* fo. *sphagnicola* occurs exclusively in the lowlands of the northern part of the country on raised peat bogs; *C. sphagnicola* fo. *paludosa* is found only in the mountains of southern Poland, mainly in the subalpine zone, where it grows on *Sphagnum-Polytrichum* hummocks (Figure 50) on the upper part of north-facing slopes."



Figure 50. *Sphagnum capillifolium* and *Polytrichum commune* forming a hummock where *C. sphagnicola* fo. *paludosa* is able to grow. Photo by Sheila, through Creative Commons.

Fungal Interactions

Wang and Qiu (2006) reported that *Calypogeia sphagnicola* (Figure 44-Figure 46) has fungi associated with it.

Calypogeia sullivanii (Figure 51)

Distribution

Calypogeia sullivanii (Figure 51) occurs from Maine to Florida and Puerto Rico and west to Ohio, Missouri, Mississippi, Kentucky, and Louisiana, all in the eastern half of the USA (Pagán 1939; Schuster 1969). In the eastern states, Schuster and Patterson (1957) considered it to be a mostly mountain species.

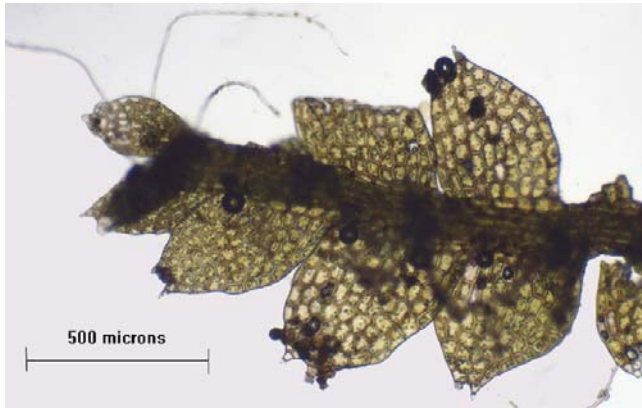


Figure 51. *Calypogeia sullivanii*, a species previously considered a variety of *C. arguta*, occurs around springs. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Wittlake (1950) found that *Calypogeia sullivanii* (formerly placed in *C. arguta* as a variety; Figure 51) occurred around springs at Spy Rock Hollow, Arkansas, USA, in association with other mosses and liverworts. Guerke (1971) reported this species from moist ditch banks in Louisiana, USA. In West Virginia, it lives in a sandstone cave where there is a constant drip from the ceiling of the cave, along with seepage, that keeps the cave continuously wet (Ammons 1933). In southern Illinois, Skorepa (1968) found it on wet clay and rocks and under a sandstone ledge. Pagán (1939) found it on wet banks and on rocks in Puerto Rico.

But its habitat is not always wet. Vitt (1967) reported it from sandy soil in the forest above and below a cliff area at Pickle Springs, Missouri, USA. Fulford (1934) found it on moist, sandy soil in Kentucky, USA. Evans (1907) found that it usually grows scattered among other plants or in loose thin tufts. Schuster (1969) lists a variety of habitats, including stream banks, along cascading brooks, and on moist or damp soil in deep shade.

Reproduction

Calypogeia sullivanii (Figure 51) is **autoicous** (having separate male and female branches but on same plant) (Schuster 1969). They reproduce asexually by gemmae.

Geocalycaceae

Geocalyx graveolens (Figure 52-Figure 54)

Distribution

Geocalyx graveolens (Figure 52-Figure 54) is a widespread species in oceanic Holarctic regions (Szweykowski & Kozlicka 1974; Schäfer-Verwimp & Vána 2011; Hugonnot 2014). In North America, it is abundant from Alaska to California and from Labrador to North Carolina and Tennessee (Hugonnot 2014). Nevertheless, it does not reach the tundra (Schuster 1980). It is much less common in Europe, and Asia exhibits only local occurrences.



Figure 52. *Geocalyx graveolens*, a Holarctic species that extends southward into the mountains, occurring in such wet habitats as humus, peat, and mires. Photo by Hugues Tinguy, with permission.



Figure 53. *Geocalyx graveolens* ventral side showing underleaf at the red star. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Its most common habitats seem to be on humus, peaty soil, or decayed forest litter in mires, often on banks or sides of ledges (Simó *et al.* 1978; Schuster 1980; Damsholt 2002; Nebel & Philippi 2005). Gabriel and Bates (2005) considered it to be indicative of the wettest sites in the Azores.

In Germany *Geocalyx graveolens* (Figure 52-Figure 54) is very rare, occurring in calcareous alder breaks with "brisk" water (Rätzl *et al.* 2004). In western Canada, Vitt *et al.* (1986) found that it fell in the restricted terrestrial category when associated with montane streams. In eastern Canada, in Ontario, Cain and Fulford (1948) reported it from wet rotten logs, humus, and peat in deep shade, being very common throughout the province. Similarly, Evans and Nichols (1935) reported it on logs in swampy woods in the Upper Peninsula of Michigan, USA, and Steere (1934) likewise found it on rotten wood and humus in swamps and wet woods on Sugar Island, Michigan. Sharp (1944) made a similar habitat observation at Mountain Lake, Virginia, USA. Järvinen (1976) reported similar habitats in eastern Fennoscandia.

In the Himalayas, Long (2005) found it in mossy carpets under dripping cliffs. Several researchers have found it on the banks of brooks and rivers (*e.g.* Figure 54) (Plitt 1908 in Maryland, USA; Greenwood 1910 in Massachusetts, USA; Burnham 1919 in the Lake George area of New York, USA). In Massachusetts, these habitats also include damp soil on the edge of streams (Greenwood 1915). Darlington (1938) found it on moist ground near Glen Lake in Michigan, USA. Clee (1937) found it on shaded hedge banks that had an abundance of water. Mogensen and Damsholt (1981) found it in habitats with percolating water. Further attesting to its broad ecological amplitude, Váňa and Ignatov (1996) found it in the Altai Mountains in eastern Asia on a sand bar that was temporarily flooded in a stream running through a narrow canyon. Fulford (1934) found it growing over moist, shaded sandstone cliffs in Kentucky, USA. Ingerpuu *et al.* (2014) considered it to be a facultative fen species in Estonian mires.



Figure 54. *Geocalyx graveolens* on stream bank. Photo by Michael Lüth, with permission.

In contrast to these wet habitats, it occurs on sandstones in Baden Wurtemberg (Nebel & Philippi 2005) and Vosges (Frahm 2002) in the oriental Pyrenees (Hugonnot 2014). Furthermore, in North America (Schuster 1953) and Nordic countries (Damsholt 2002) *Geocalyx graveolens* (Figure 52-Figure 54) seems to tolerate subcalcareous situations, but this is not the case in the British Isles (Paton 1999). Zübel (2009) found that in southeastern Poland, it occurs on rock, sandstone, mineral soil, and humus in the mountains, but in the lowlands it occurs on rotting wood, humus, and tree bases in wet and

very wet sites in alder forests and other wet forest types or boggy forests.

In North America, Schuster (1953) considered that the species showed a decided tolerance for subcalcareous conditions, and Damsholt (2002) for basic rocks in Nordic countries, which apparently is not the case in the British Isles (Paton, 1999).

Reproduction

Geocalyx graveolens (Figure 52-Figure 54) forms extensive creeping mats over *Sphagnum* species (Figure 47). Sharp (1944) described it as having a peculiar yellowish color (Figure 52). It typically produces numerous capsules. Ross-Davis and Frego (2004) found its diaspores in diaspore rain and buried propagule banks. Its rarity, particularly in Europe, would not seem to be caused by a limited number of suitable habitats or propagules.

Role

These mats can serve as home for the boreid beetle, *Caurinus decetes* (Figure 55), where the beetles feed on the liverwort on decaying logs (Russell 1979). Asakawa (1998) reported a turpentine-like odor in this liverwort species. It is possible that this odor discourages some of the potential insect herbivory, but it apparently has no negative effect on *Caurinus decetes*.



Figure 55. *Caurinus decetes*, a boreid beetle that feeds on *Geocalyx graveolens*. Photo by CBG Photography Group, through Creative Commons.

Fungal Interactions

In their study on liverwort-fungal symbioses, Bidartondo and Duckett (2010) were only able to find *Ascomycetes*. This was different from the previous reports of *Basidiomycetes* on this species.

Gymnomitriaceae

Gymnomitrium commutatum (Figure 56)

(syn. = *Marsupella commutata*)

Distribution

Gymnomitrium commutatum (Figure 56) occurs in Europe, Siberia, Russian Far East, China, eastern Asia, Indian Subcontinent, Malesia, subarctic America, western Canada, northwestern USA (Váňa *et al.* 2010), Iceland, and South Greenland (Konstantinova 2000).



Figure 56. *Gymnomitrium commutatum*, a Northern Hemisphere wet habitat liverwort. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Konstantinova *et al.* (2002) found *Gymnomitrium commutatum* (Figure 56) on wet cliffs and cliff crevices associated with the Upper Bureya River in the Russian Far East. Bakalin (2008) found it on cliffs near streams in the tundra belt in several locations in the Sakhalin Province, Russia. Choi *et al.* (2013) found it at elevations of 1400-1614 m asl in Mt. Deogyu National Park in the Republic of Korea, where it occurred on shaded cliffs and rocks. Its records are few, and it is included in the Red Data Book for Russia (Sofronova *et al.* 2015). *Marsupella commutata* grows on crystalline substrates in streams on the Ushkovskii Volcano, Kamchatka (Bakalin 2006).

Adaptations

This high altitude species is blackish-brown (Mamontov *et al.* 2018), a characteristic that most likely protects it from the high levels of UV radiation at those altitudes.

Reproduction

Gymnomitrium commutatum is only occasionally fertile and capsules are rare in the UK (Smith 1990).

Gymnomitrium crenulatum (Figure 57-Figure 58)

Distribution

The distribution of *Gymnomitrium crenulatum* (Figure 57-Figure 58) is in question because of misidentifications.

Váňa *et al.* (2010) consider it confined to northern and southwestern Europe, with other locations representing misidentifications. However, GBIF (2020c) still includes Norway, Finland, Britain, Ireland, France, Portugal, Spain, Yamal-Nenets, Tibet (Xizang), Sichuan, Yunnan, Japan, Alaska, Nunavut, British Columbia, Washington, and South Georgia.



Figure 57. *Gymnomitrium crenulatum*, a Northern Hemisphere species with a poorly understood distribution; it seems to prefer emergent rocks of streams, but can get submersed. Photo by Andrew Hodgson, with permission.

Aquatic and Wet Habitats

This species seems to do best above the low flow water level in exposed streambed conditions, preferring moderately stable boulders (Figure 58) that are easily submerged (Vieira *et al.* 2005). It is tolerant of acid water, perhaps preferring it, especially in mountain streams of northwest Portugal. Casas *et al.* (1999) reported it on rocks by a stream in shrubby heathland in Spain.



Figure 58. *Gymnomitrium crenulatum* habitat in rock crevices. Photo by Andrew Hodgson, with permission.

One of the populations studied was reduced considerably by a strong fire, causing rock sediments to erode the bryophyte communities in the streambed (Vieira *et al.* 2004). In more protected locations it typically forms dense patches.

Reproduction

When Rawat *et al.* (2016) reported *Gymnomitrium crenulatum* (Figure 57-Figure 58) from India for the first time, they reported that they found no fertile plants. Its rarity most likely contributes to lack of observations on reproduction, but conversely, the rarity of reproduction probably contributes to the rarity of plants. In the UK, the plant is only occasionally fertile and capsules are very rare (Smith 1990).

Marsupella (Figure 59-Figure 62, Figure 63-Figure 67, Figure 70-Figure 87, Figure 89)

Marsupella (Figure 59-Figure 62, Figure 63-Figure 67, Figure 70-Figure 87, Figure 89) has more than one species in aquatic habitats, and these have at times been registered as the genus only. These include a dominance in the upper and middle reaches in the Harz Mountains of Germany (Bley 1987) and occurrence in small, pristine streams of the Tolvajärvi region, Russian Karelia (Vuori *et al.* 1999).

Marsupella aquatica (Figure 59-Figure 62)

(syn. = *Marsupella emarginata* var. *aquatica*)

Marsupella aquatica (Figure 59-Figure 62) seems to be confined to alpine or subalpine regions (Evans 1904). *Marsupella emarginata*, on the other hand, extends downward into the plains, at least in eastern North America.

Distribution

Marsupella aquatica (Figure 59-Figure 62) has an **arctomontane** (in Arctic and in montane regions at lower latitudes) semi-circumpolar distribution with oceanic affinities (Konstantinova 2000). More specifically, Vána *et al.* (2010) list it for northern and southwestern Europe, Asia, including Macaronesia, Siberia, Russian Far East, Caucasus, subarctic America, Canada, and northwestern and northeastern USA. They consider other records in North America to be misidentifications.



Figure 59. *Marsupella aquatica*, an Arctic-montane semi-circumpolar species from wet and submerged rocks of streams and rivers. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Nichols (1918) reported *Marsupella aquatica* (Figure 59-Figure 62) from ravines on Cape Breton Island, Canada. Lorenz (1924) reported it on rocks in Deer Brook on Mt. Desert, Maine, whereas the more western species *M. emarginata* (Figure 65-Figure 66) was frequent on wet rocks. Watson (1919) considered *Marsupella aquatica* to be a species that grows submerged in slow water with poor mineral salts and to occupy more aquatic rocks than *Marsupella emarginata*. Dulin *et al.* (2009) likewise reported *M. aquatica* from streams with poor mineral salts in the Vologda Region of Russia, where it frequently occurred with *Scapania undulata* (Figure 60) and *Fontinalis dalecarlica* (Figure 61). Koppe (1945) reported it from stones in streams in the Westfalens of northwestern Germany. Koponen *et al.* (1995) merely listed it as aquatic in Finland. Vieira *et al.* (2005) reported it from mountain streams in northwest Portugal. By contrast, Lepp (2012) reported that it occurs to depths of 30 m in Australia, and Heggnes and Saltveit (2002) reported that it forms a carpet down to almost 40 m in the regulated River Suldalslågen in western Norway. This lake in the river is free of ice only from July to October.



Figure 60. *Scapania undulata*, a species that associates with *Marsupella aquatica* on rocks in Maine, USA. Photo by Jan-Peter Frahm, with permission.



Figure 61. *Fontinalis dalecarlica*, a species that associates with *Marsupella aquatica* on rocks in Maine, USA. Photo by J. C. Schou, with permission.

Bodin and Nauwerck (1968) studied the biology of the leafy liverwort *Marsupella aquatica* (Figure 59-Figure 62), the dominant member of the well-developed bryophyte vegetation of Latnajaure, a mountain lake (maximum depth 43.5 m) in the Abisko area of Sweden. *Marsupella aquatica* increases in size and robustness with depth in Latnajaure in Swedish Lappland.

Monteith (1996) reported that *Scapania undulata* (Figure 60) may be replacing *Marsupella aquatica* (Figure 59-Figure 62), a common inhabitant in acid streams, following an experimental burn.

Adaptations

Marsupella aquatica can reach 10 cm long and is dark green to almost black, not red-brown (Smith 1990; Wagner 2008). In contrast to Wagner, Evans (1904) describes the color as bright green to reddish. The latter dark coloration can protect it from the high UV radiation in its alpine habitat. The stems branch little and are very firm (Evans 1904). A cross-sectional view reveals that stem cells are all about the same size. Those in the middle have thin walls, grading to thicker walls toward the outer cells. The outermost layer has shorter cells than the interior.



Figure 62. *Marsupella aquatica*, exhibiting a red form. Photo by Barry Stewart, with permission.

Reproduction

Marsupella emarginata is dioicous (Smith 1990).

Biochemistry

Marsupella aquatica (Figure 59-Figure 62) has received less biochemical attention than some of the previously mentioned bryophytes. Huneck *et al.* (1982) identified an Ent-longipinane derivative from the species. Nagashima *et al.* (1994) identified a new gymnomitrane-type sesquiterpenoid from it, as well as others that were previously known. Adio *et al.* (2002) identified volatile compounds from *Marsupella aquatica*. Leong *et al.* (2002) identified amorphane sesquiterpenoids from the species in Scotland. Later Adio *et al.* (2007) determined nine amorphane sesquiterpenoid constituents of the species from Austria.

Marsupella boeckii (Figure 63)

Distribution

Marsupella boeckii (Figure 63) occurs in the Antarctic-Southern Ocean area, Europe, including Svalbard (Konstantinova & Savchenko 2008), Asia, and North America from Alaska to continental USA (ITIS 2020a).



Figure 63. *Marsupella boeckii*, a species of scattered locations worldwide, occurring in wet habitats such as the edges of springs and wet cliffs. Photo from Earth.com, with permission.

Aquatic and Wet Habitats

Koponen *et al.* (1995) reported it as aquatic in Finland. Konstantinova and Savchenko (2008) found it in Svalbard at the edge of a spring that was covered with mats of *Marsupella arctica* (Figure 64) where both occurred on shallow sandy soil (<1 cm) overlying rocks. Sofronova (2018) found that it created "minute" cover up to 1 cm square on wet cliffs, compared to carpets of more than 1 sq m of *Marsupella emarginata* (Figure 65-Figure 67) in the same habitat in eastern Yakutia, Russia.



Figure 64. *Marsupella arctica* herbarium specimen, a species that forms mats at the edges of springs. Photo by CBG Photography Group, through Creative Commons.

Reproduction

Marsupella boeckii is **dioicous** (Smith 1990; Konstantinova & Savchenko 2008).

Marsupella emarginata (Figure 65-Figure 67)

(syn. = *Nardia emarginata*)

Distribution

Marsupella emarginata (Figure 65-Figure 67) is a widespread Laurasian species that extends into the tropics in the high mountains (Váňa 1993). It occurs in Europe, Asia, North America from Alaska to Mexico, South America (ITIS 2020b), and Africa (Váňa 1993).



Figure 65. *Marsupella emarginata*, a widespread Northern Hemisphere species that extends into the high mountains of the tropics where it is common in streams and rivers and banks. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Marsupella emarginata (Figure 65-Figure 67) is the most common species in the genus, as noted by Scarlett and O'Hare (2006), in English and Welsh rivers. It is common and abundant in wet or damp acidic places, especially on rocks or gravel both in and beside streams and rivers. Its less wet habitats include humid woodland rocks in woods, wet crags, lake margins, wet gravel tracks, and near snowbeds. Sofronova (2018) similarly found it in places of late snow melt in East Yakutia, Russia. It often occurs in mountain streams (Vieira *et al.* 2005 – northwest Portugal; Knapp & Lowe 2009 – Great Smoky Mountains National Park, Kentucky, USA; Luis *et al.* 2015 – Madeira Island).

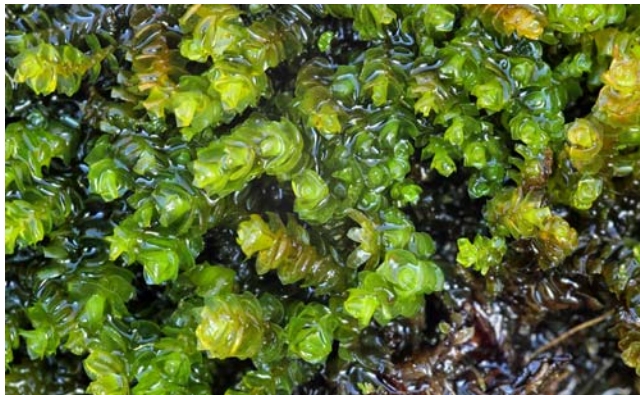


Figure 66. *Marsupella emarginata* in its green form, showing mat growth. Photo by Barry Stewart, with permission.

West (1910) reported this species from wet rocks and shores, often submersed, in Scotland. In Connecticut, USA, it occurs on wet or moist cliffs of ravines, but it is calciphobic along rivers (Nichols 1916). On Cape Breton Island, Canada, Nichols (1918) found it again on rocks of a ravine stream bank and on wet rock cliffs associated with streams. Sofronova (2018) found it on wet cliff habitats in carpets of more than 1 sq. m. Watson (1919) attributed its most common occurrence to rocks in fast water, on banks with frequent submergence in slow water that is low in mineral salts, in waterfalls, and on mostly submerged rocks in fast streams. Weber (1976) likewise found it in Newfoundland, Canada, in the narrow zone that is periodically submerged along the river (Figure 67).



Figure 67. *Marsupella emarginata* in its habitat, forming mats on a bank where it can be periodically submerged. Photo by Chris Wagner, through Creative Commons.

It also occurs in European springs, particularly in the Central Alps (Zechmeister & Mucina 1994). In the Altai Mountains, Váňa and Ignatov (1996) found it on wet rocks of deep canyons and near a waterfall in the lower forest zone, but also in the alpine zone among rocks in rock fields, and in the subalpine covering wet cliffs with extensive pure mats.

Koponen *et al.* (1995) considered it to be an aquatic species in Finland. Ferreira *et al.* (2008) reported it as growing in rivers. Szweykowski (1951) considered it to be an acidophile (pH 4.0-6.0) in streams of Gory Stolowe Mountains, Poland, terming it a **hydroamphibiont** in streams. Thiébaud *et al.* (1998) considered it to be an acidophilous stream species in the Vosges Mountains of northeastern France, being sensitive to high ion concentrations. Geissler (1975, 1976) termed it a **helokrene** (living in marsh spring communities) in European alpine areas. Vanderpoorten and Klein (1999a) found that it could tolerate neutral pH if it is in **oligomineral** (having few dissolved minerals) waters; sewage effluent causes populations to decrease. Light (1975) reported it from small lakes in the Scottish mountains, where it experienced ice cover 4-7 months of the year; again, it preferred low ion concentrations. Satake *et al.* (1989) reported it from the acid river Akagawa, Japan. Tremp and Kohler (1991) likewise reported it as

submersed in low-buffered streams and Bahuguna *et al.* (2013) reported that it grows only in water low in solutes. Kohler and Tremp (1996) found *Marsupella emarginata* (Figure 65-Figure 67) to be an indicator of silicate rock areas with acidic water. Birk and Willby (2010) likewise found it to be somewhat common in siliceous mountain streams. In view of these low-ion occurrences, Tremp (2003) classified the species as **oligotrophic** (preferring low nutrients). Vanderpoorten (2012) considered it to be an indicator species for acidic waters with low buffering capacity.

In West Virginia, USA, *Marsupella emarginata* (Figure 65-Figure 67) preferred a pH of around 4.17 in mountain streams (Stephenson *et al.* 1995). In the Haute Ardenne rivers of Belgium, it is known from earthy and gravelly substrates of river banks (Leclercq 1977). But it also occurs near water on the wall of the Flume at Franconia Notch, New Hampshire, USA (Glime 1982). In the Canary Islands, it is never dominant and occurs on moist, shaded, soft volcanic rocks of the laurel forest (Dirkse 1985). Wagner *et al.* (2000) reported it from 40 and 70 m depth in Waldo Lake, Oregon, USA.

It occurs in association with *Scapania undulata* (Figure 60) in aquatic habitats of eastern Odenwald and southern Spessart (Philippi 1987) and in the *Platyhypnidium* (Figure 68)-*Fontinalis antipyretica* (Figure 69) association in Thuringia, Germany (Marsteller 1987).



Figure 68. *Platyhypnidium riparioides*, a species that can occur in association with *Marsupella emarginata*. Photo by Hermann Schachner, through Creative Commons.



Figure 69. *Fontinalis antipyretica* in dried out small pool, a species that can occur in association with *Marsupella emarginata*. Photo by Matt Goff, with permission.

Janauer and Dokulil (2006) report that when the water flow is too fast or runoff is too irregular, tracheophytic macrophytes are unable to become established, but bryophytes can become dominant. *Marsupella emarginata* (Figure 65-Figure 67) is one of those bryophytes to take advantage of these conditions (Lottausch *et al.* 1980).

In the River Dee, Maitland (1985) found dense liverwort growth, *Marsupella emarginata* (Figure 65-Figure 67) on most rock surfaces, reaching about 3 m diameter, but only 20 cm in depth (*e.g.* Figure 67).

Adaptations

Thiebaut *et al.* (1998) considered *Marsupella emarginata* (Figure 65-Figure 67) to be acidophilous and sensitive to high concentrations of cations. It disappears when Mg is too high and pH reaches 7.0. But they found that it was the cation concentration, not the pH that discouraged its presence. They concluded that it must have a physiological mechanism to regulate the difference in H⁺ concentration between the cell and the surrounding water. They suggested that cations such as Mg and Ca limit the penetration of other elements needed by the plant cells.

Marsupella emarginata varies from bright green to reddish (Evans 1904). Reddish colors can help to protect the plants from damage by UV rays, particularly at high elevations, whereas green colors are more typical of bryophytes growing at lower light levels and lower elevations.

Reproduction

Marsupella emarginata (Figure 65-Figure 67) is **dioicous** with only occasional capsules that appear in late winter or spring in the UK (Smith 1990).

Fungal Interactions

Wang and Qiu (2006) report *Marsupella emarginata* (Figure 65-Figure 67) as having associations with fungi, but with no mycorrhizal relationships known. Egertová *et al.* (2016) found *Mniaecia jungermanniae* (Figure 24-Figure 26) in three samples of this species. Hopefully studies like that of Adio and König (2007) on sesquiterpenoids and other terpenes will help us to understand why some species have fungal partners or parasites and others do not.

Marsupella emarginata subsp. *tubulosa* (Figure 70)

(syn. = *Marsupella tubulosa*)

Distribution

Marsupella emarginata subsp. *tubulosa* (Figure 70) has been identified in several studies. It is a subspecies of the Northern Hemisphere, primarily in eastern Asia and nearby islands, but also reported from fewer known locations in Europe and North America (GBIF 2020d). However, in their revision of the **Gymnomitriaceae**, Bakalin *et al.* (2021) exclude it from these latter areas and from the Russian far East continental mainland as incorrect identifications, based on the absence of the biconcentric character of the oil bodies there, confining it to the insular and peninsular areas in Amphi-Pacific Boreal and Temperate Eastern Asia

Aquatic and Wet Habitats

Bakalin *et al.* (2021) considered *Marsupella emarginata* subsp. *tubulosa* (Figure 70) to be acidophilic and meso- to hygrophytic. The species occupies sandy soils and mineral substrates, over wet to moist, and sometimes mesic cliffs, being most common along streams near running water in the Korean Peninsula. Song and Yamada (2006) reported it from wet rocks on Jeju (Cheju) Island, Korea. It occurs on a soil bank of a small creek of the Upper Bureya River in the Russian Far East (Konstantinova *et al.* 2002). On Mts. Hakkôda in northern Japan, it occurs on moist rocks (Kitagawa 1978a). Records of this subspecies with habitat data are harder to find despite its recorded number of locations.



Figure 70. *Marsupella emarginata* subsp. *tubulosa* forming mats in a small creek. Photo from Taiwan Mosses, through Creative Commons.

Biochemistry

Despite the paucity of readily available ecological information, Matsuo *et al.* (1979) isolated three new sesquiterpenoids from this species.

Marsupella koreana (Figure 71-Figure 73)

Distribution

Marsupella koreana (Figure 71-Figure 73) is probably an endemic species of the montane-temperate (Bakalin *et al.* 2021) Korean Peninsula, but is quite common there and has a highly variable morphology (Bakalin *et al.* 2019b). As a result, it may occur elsewhere, hiding under different names.

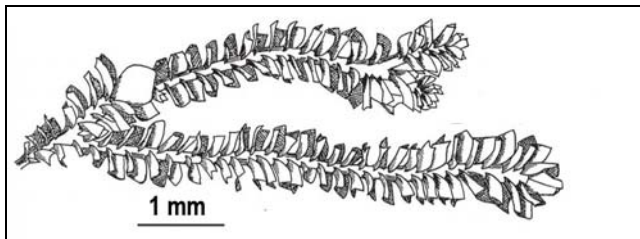


Figure 71. *Marsupella koreana*. Drawing modified from Bakalin *et al.* 2021.



Figure 72. *Marsupella koreana*, an apparent endemic of the Korean Peninsula. Photo modified from Bakalin *et al.* 2019; permission pending.



Figure 73. *Marsupella koreana*. Photo modified from Bakalin *et al.* 2019; permission pending.

Aquatic and Wet Habitats

Bakalin *et al.* (2019b) consider *Marsupella koreana* (Figure 71-Figure 73) to be acidophilic to neutro-tolerant and meso- to hygrophytic. It occupies mesic, rarer moist or dry substrata in open to partly shaded places.

Adaptations

The brownish green to deep green coloration of *Marsupella koreana* (Figure 71-Figure 73) (Bakalin *et al.* 2019b) suggest an adaptation to high light intensity. They form loose mats that are somewhat rigid (Bakalin *et al.* 2021). They have few or no rhizoids, but rhizoids are

common on geotropic stolons, a feature that should aid in their spread locally. Stems have hyaline epidermal cell with thick inner walls (Figure 74).

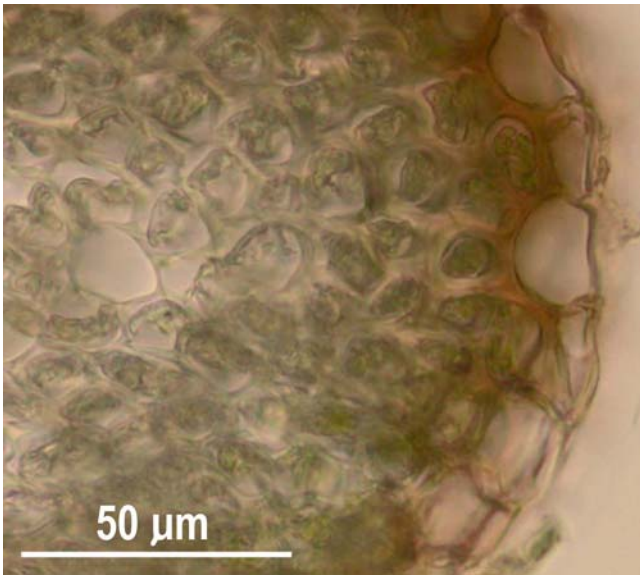


Figure 74. *Marsupella koreana* stem cross section showing thick inner walls of epidermal cells. Photo modified from Bakalin *et al.* 2019; permission pending.

Reproduction

Marsupella koreana (Figure 71-Figure 73) is **dioicous** (Bakalin *et al.* 2019b). Its spores are small (10-11 μm) and papillose.

Biochemistry

This rare endemic lacks biochemical studies, and it is not clear if it has oil bodies (Figure 75).

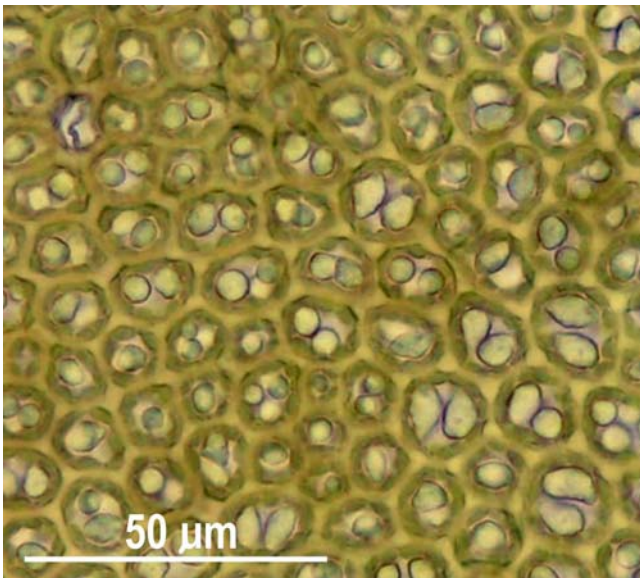


Figure 75. *Marsupella koreana* leaf cells with oil bodies? Photo modified from Bakalin *et al.* 2019; permission pending.

Marsupella pseudofunkii (Figure 76-Figure 77)

Distribution

Marsupella pseudofunkii (Figure 76-Figure 77) is a Temperate Montane East Asian species, known from Korea, China, Taiwan, the Russian Far East, and Japan (Bakalin *et al.* 2021).

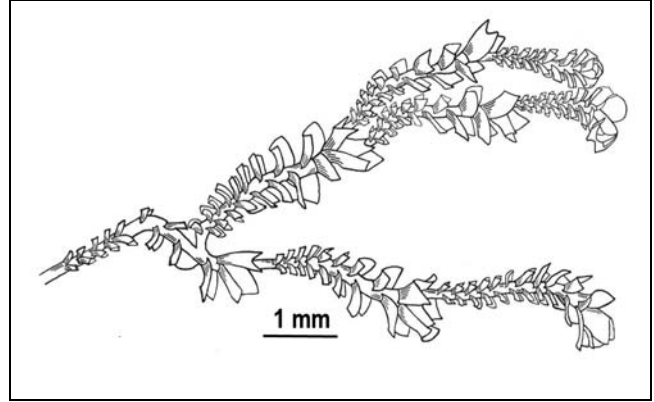


Figure 76. *Marsupella pseudofunkii* female plant. Drawing modified from Bakalin *et al.* 2021.



Figure 77. *Marsupella pseudofunkii*. Photo from Bakalin *et al.* 2019; permission pending.

Aquatic and Wet Habitats

Marsupella pseudofunkii (Figure 76-Figure 77) is acidophilic and occurs as a mesophyte to hygrophyte (Bakalin *et al.* 2021). It occurs on dry to moist cliffs, rarely on wet rocks or stones near streams, in open or, more commonly, partly shaded places. Choi *et al.* (2013) list cliffs along streams, sometimes accompanied by *Scapania undulata* (Figure 60).

Adaptations

The species can at least sometimes form mats (Figure 78). These should help it to conserve water when it is not in a wet location. Its leaves also fold, further conserving water.



Figure 78. *Marsupella pseudofunkii*, a montane east Asian species. Photo from Bakalin *et al.* 2019; permission pending.

Reproduction

Marsupella pseudofunkii (Figure 76-Figure 78) is **dioicous** (Bakalin *et al.* 2021).

Biochemistry

There seems to be nothing published on biochemistry of *Marsupella pseudofunkii* (Figure 76-Figure 78), and the oil bodies (Figure 79) are not described.

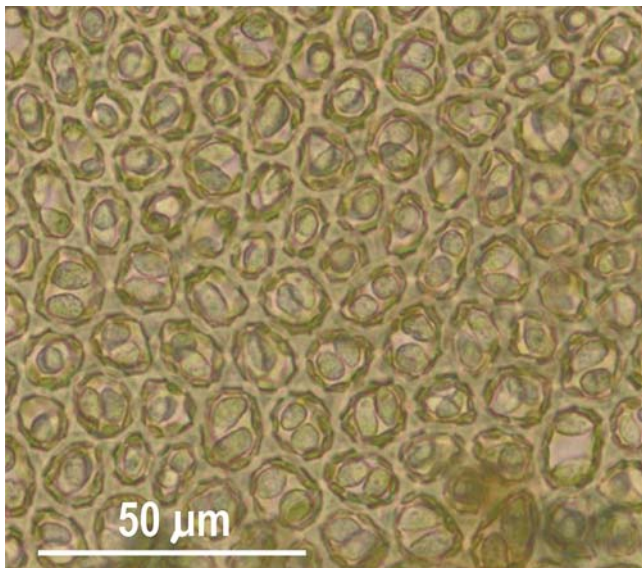


Figure 79. *Marsupella pseudofunkii* cells with oil bodies? Photo modified from Bakalin *et al.* 2019; permission pending.

Marsupella sparsifolia (Figure 80-Figure 81)

Distribution

Marsupella sparsifolia (Figure 80-Figure 81) is a bipolar species, mostly from Arctic-alpine and high subarctic areas (Schuster 1974). It occurs in Europe from Greenland and Scandinavia south to Great Britain and alpine central Europe. It also occurs in Uganda and the Cape of Good Hope, South Africa. In North America it occurs in the mountains of British Columbia and Alberta, Quebec, Canada, and in the USA on Mt. Washington, New Hampshire and in the Huron Mtns, Michigan. It also occurs in New Zealand.

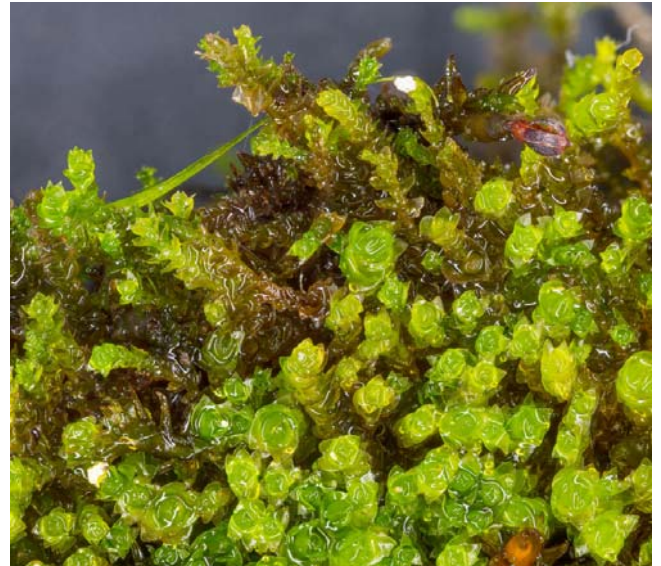


Figure 80. *Marsupella sparsifolia* in a wet habitat. Photo by Kristian Peters (Kersey Online; Sage bud), with permission.



Figure 81. *Marsupella sparsifolia*, is a bipolar Arctic-alpine species that occurs on stream banks and other wet habitats. Photo by Kristian Peters (Kersey Online; Sagebud), with permission.

Aquatic and Wet Habitats

Koponen *et al.* (1995) considered this species to be aquatic in Finland. Schuster (1974) attributes it to alluvial sand or sandy soil adjacent to streams, in acid late snow areas, on siliceous rock faces receiving water. Like *Marsupella emarginata* (Figure 65-Figure 67), it avoids calcareous sites but tolerates frequent inundation. Hong (1980) reported *Marsupella sparsifolia* (Figure 80-Figure 81) from soil in the North Cascades Range, Washington, USA. It also occurs on moist cliffs where it can form close mats, as seen along Cliff River in the Huron Mountains, Michigan, USA (Nichols 1935).



Figure 82. *Marsupella sparsifolia* habitat. Photo by Kristian Peters (Korseby Online; Sagebud), with permission.

Reproduction

Marsupella sparsifolia (Figure 80-Figure 81) is **paroicous** (Smith 1990). It is usually fertile and frequently produces capsules.

Marsupella sphacelata (Figure 83-Figure 86)

Distribution

Marsupella sphacelata (Figure 83-Figure 86) is Holarctic, occurring in boreal and low-Arctic regions (Schuster 1974). Its terrestrial form extends further south than does the aquatic form. This species is widespread in Europe, from Greenland southward to England, Spain, and the Azores. It is widespread in Japan, but is poorly known elsewhere in Asia. In North America it extends from Alaska south to California and in the east from Newfoundland to North Carolina.

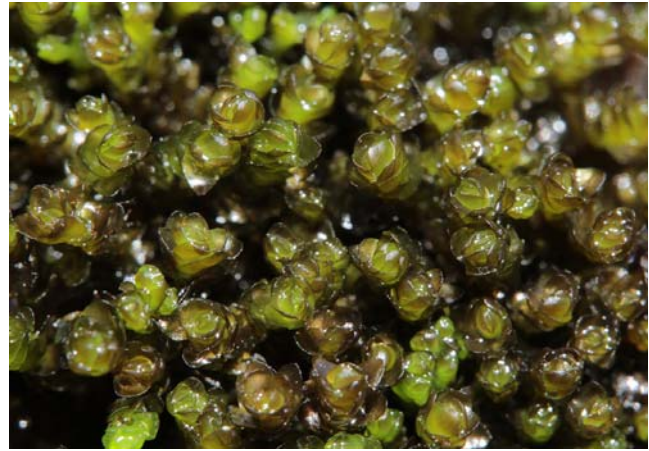


Figure 83. *Marsupella sphacelata* clone. Photo by Hermann Schachner, through Creative Commons.



Figure 84. *Marsupella sphacelata*, a boreal and low-Arctic species mostly of slow streams. Photo by Štěpán Koval, with permission.



Figure 85. *Marsupella sphacelata*. Photo by Giovanni Bergamo Decarli, through Creative Commons.



Figure 86. *Marsupella sphacelata* showing its mat growth habit and dark pigments. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Watson (1919) considered *Marsupella sphacelata* (Figure 83-Figure 86) to be an alpine species submerged in fast water. Geissler (1975) likewise found it in European alpine streams. At 1400 m in the Sayan Mountains of southern Siberia, Konstantinova and Vasiljev (1994) reported it submerged on rocks in brooks, mixed with other liverworts. But in the eastern USA, it occurs in mountain streams that are not alpine (Glime 1968), and Vieira *et al.* (2005) found it in mountain streams of northwest Portugal. Sharp (1939) reported it from boulders in brooks in Tennessee, USA, where it was rare. It also occurs on a rock cliff associated with Katrine Lake in Sudbury, Ontario, Canada and on wet rock of a small stream at Pinetree Lake in Algonquin Park at 600 m or less, also in Ontario (Williams & Cain 1959). At Cumberland Falls State Park (327 m) in Kentucky, USA, it occurred on moist rocks (Norris 1967).

Koponen *et al.* (1995) considered this species to be aquatic in Finland. The typical aquatic form grows attached to rocks and rock walls of mountain streams, usually in small pools and in slow water (Figure 87) (Schuster 1974). It seems to be absent from calcareous rocks. It can form pure patches, but also grows with *Marsupella emarginata* (Figure 65-Figure 67), *Scapania undulata* (Figure 60), and *S. subalpina* (Figure 88). Its lax tufts are typically dull green and brownish-tinged above (Figure 83-Figure 86, Figure 89).



Figure 87. *Marsupella sphacelata* in submersed habitat. Photo by Hermann Schachner, through Creative Commons.



Figure 88. *Scapania subalpina*, a species that often grows with *Marsupella sphacelata* in mountain streams. Photo by Andy Hodgson, with permission.

But *Marsupella sphacelata* (Figure 83-Figure 86) can also be found in wet areas not associated with streams. Kitagawa (1978a) found it to be locally abundant on damp soil at the edge of moors below the summit of Odaake, Japan.

Adaptations

The terrestrial forms of *Marsupella sphacelata* (Figure 83-Figure 86) are able to grow in direct sun, often with intermittent seepage (Figure 89) (Schuster 1974). They are able to endure long dry periods. Their life form is small to large tufts (Smith 1990). These forms create blackish patches. This attests to a wide physiological range for the species (Schuster 1974).

Marsupella sphacelata (Figure 83-Figure 86, Figure 89) can produce UV-B-absorbing compounds (Figure 86, Figure 89) in mountain streams where this radiation is high. Arróniz-Crespo *et al.* (2004) verified that these differed among populations, but we need to verify whether these are environmentally induced or genetically different.

Reproduction

Marsupella sphacelata (Figure 84-Figure 87, Figure 89) is **dioicous** (Smith 1990). Fertile plants are rare and capsules very rare.



Figure 89. *Marsupella sphacelata* habitat on wet substrate, showing dark pigments that absorb UV radiation. Photo by Hermann Schachner, through Creative Commons.

***Marsupella submarginata* (Figure 90)**

Distribution

Collections of *Marsupella submarginata* (Figure 90) thus far suggest that it is **oro-boreal** (boreal mountains and mountainous regions), with records from Switzerland, Russia, and Japan (Bakalin *et al.* 2019b).

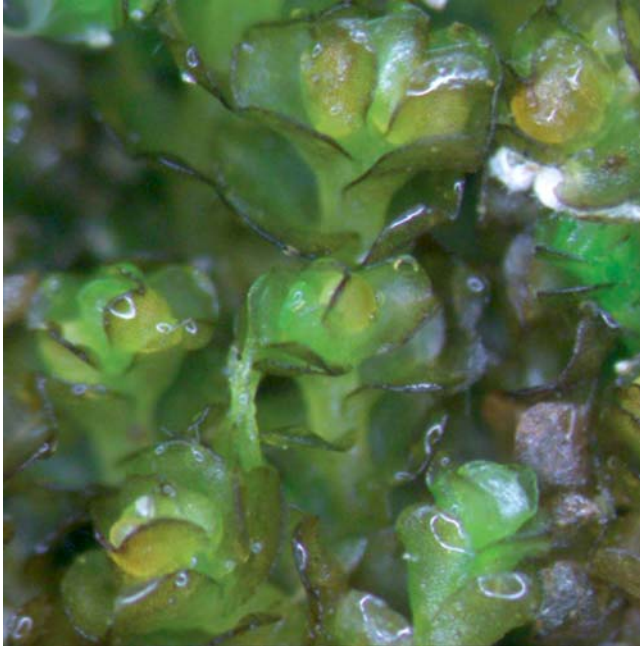


Figure 90. *Marsupella submarginata*, a species from an Eastern Hemisphere oro-boreal region. Photo modified from Bakalin *et al.* 2019; permission pending.

Aquatic and Wet Habitats

Marsupella submarginata (Figure 90) occurs on temporarily wet cliffs and boulders in areas with a mild climate and even distribution of precipitation around the year (Bakalin *et al.* 2019). In Kamchatka it occurs on moist boulders near temporary streams in mountain tundra.

Adaptations

Plants of *Marsupella submarginata* (Figure 90) are greenish brownish to rusty (Bakalin *et al.* 2019); the darker colors can filter out the high UV light one would expect in its mountain environments. Its stem has marginal cells of the hyaloderm with thickened walls on all sides (Figure 91), possibly protecting them from gushes of water when it rains or preventing water loss when it does not. Nevertheless it has few rhizoids.

Reproduction

Although *Marsupella submarginata* (Figure 90) is **dioicous**, Bakalin and coworkers (2019) reported it as freely producing spores that frequently germinate within the cushions.

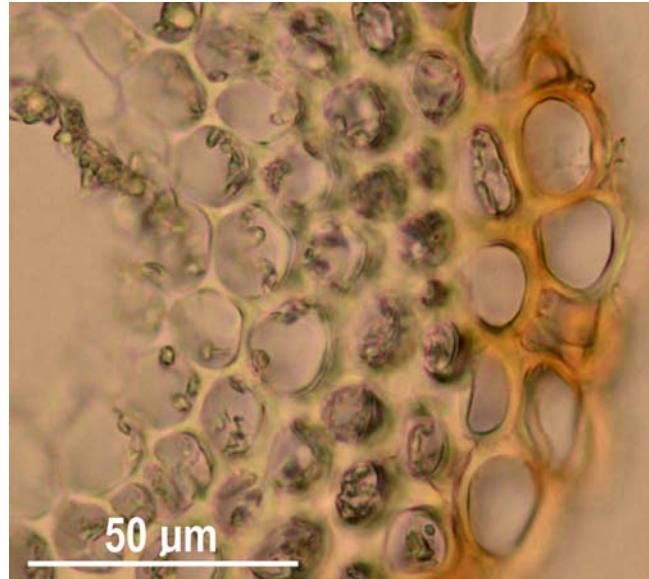


Figure 91. *Marsupella submarginata* stem cross section showing thickened walls on the epidermal cells. Photo modified from Bakalin *et al.* 2019; permission pending.

Biochemistry

There seem to be no studies on the biochemistry of *Marsupella submarginata* (Figure 90) and oil bodies are not described (Figure 92).

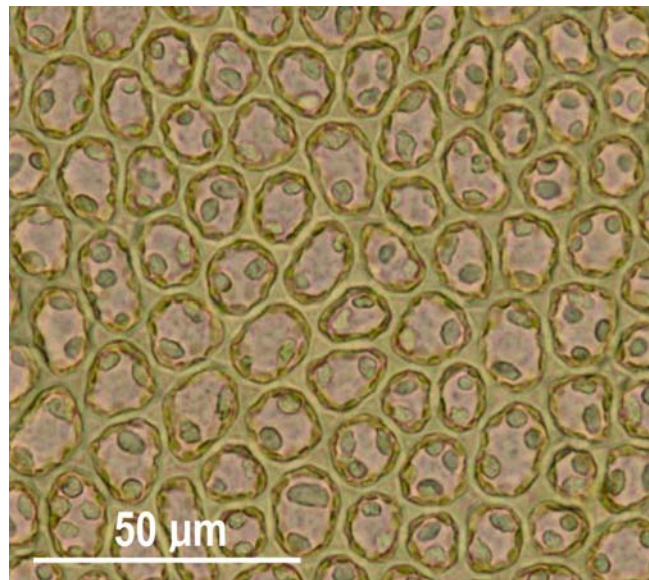


Figure 92. *Marsupella submarginata* leaf cells with oil bodies? Photo modified from Bakalin *et al.* 2019; permission pending.

***Marsupella vietnamica* (Figure 93)**

Distribution

So far, *Marsupella vietnamica* (Figure 93) is known only from North Vietnam, but Bakalin and coworkers suggest it should be found in Yunnan, China, as well (Bakalin *et al.* 2019b).



Figure 93. *Marsupella vietnamica*, a species from North Vietnam. Photo modified from Bakalin *et al.* 2019; permission pending.

Aquatic and Wet Habitats

Marsupella vietnamica (Figure 93) is thus far a meso-hygrophytic species and an acidophile. It prefers shaded to semi-open moist to wet cliffs near streams where there is sufficient water even during the so-called "dry season" in the tropical zone. The species occurs in middle mountain elevations.

Adaptations

No special adaptations seem to be described for *Marsupella vietnamica* (Figure 93). The stem appears to have somewhat thickened walls in the outer layers (Figure 94). The leaf cells have huge trigones and in the photo they have brown cell walls (Figure 95).

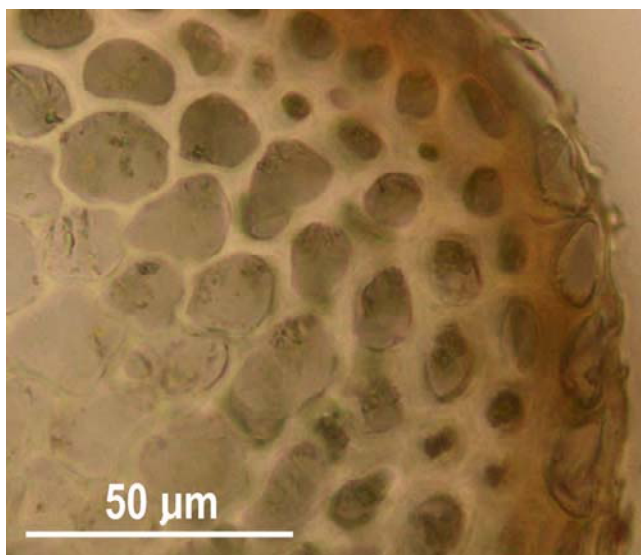


Figure 94. *Marsupella vietnamica* stem cross section. Photo modified from Bakalin *et al.* 2019; permission pending.

Reproduction

The sexual condition is unknown, but Bakalin *et al.* (2019b) indicated that *Marsupella vietnamica* (Figure 93) is **probably dioicous** because they found no antheridia or sporophytes.

Biochemistry

There seem to be no studies on the biochemistry of *Marsupella vietnamica* (Figure 93), but there appear to be distinct oil bodies in the leaf cells (Figure 95).

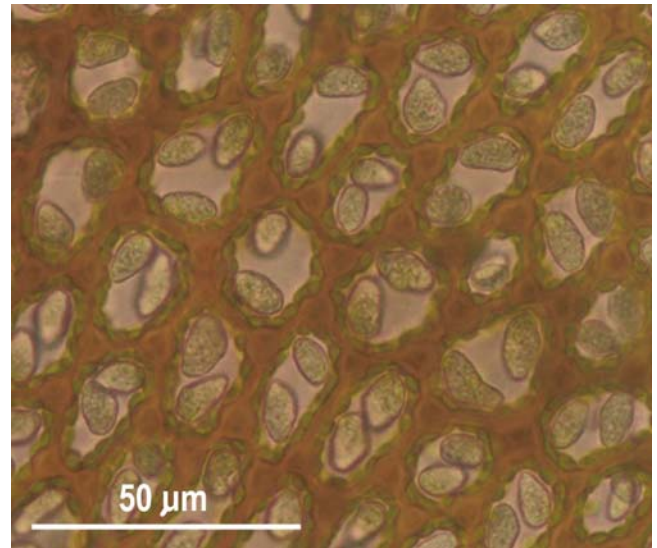


Figure 95. *Marsupella vietnamica* leaf cells and oil bodies? Photo modified from Bakalin *et al.* 2019; permission pending.

Marsupella yakushimensis

Distribution

Marsupella yakushimensis is a south temperate to subtropical Montane East Asian endemic species known in China, the southern part of the Korean peninsula, and the southern half of Japan (Bakalin *et al.* 2021).

Aquatic and Wet Habitats

Marsupella yakushimensis is an acidophilic hydro- to hydrophyte (Bakalin *et al.* 2021). It occurs on wet cliffs at some distance from water courses or on stones washed with sluggishly running water in partly shaded habitats in the middle elevations of mountains with evergreen to deciduous broadleaved forests. Choi *et al.* (2012, 2013) found it on humid soil of a steep mountain slope and on wet cliffs along a stream in Korea.

Adaptations

Commonly, *Marsupella yakushimensis* forms pure patches, but more rarely it is associated with *Scapania undulata* (Bakalin *et al.* 2021). It can have purple to red pigmentation, especially in Japanese populations, perhaps protecting it from UV light in the mountains.

Reproduction

Marsupella yakushimensis is **dioicous** and seems to produce antheridia regularly, but it rarely has archegonia (Bakalin *et al.* 2021). Even where Bakalin *et al.* found the two sexes intermixed there was no evidence of fertilization or a fully developed perianth.

Nardia assamica

Distribution

Nardia assamica is an east Asian species that extends into the Caucasus (Bakalin *et al.* 2009), but also extends into alpine areas in Europe (Geissler 1975) and Australia (ITIS 2020c). Hicks (2003) also includes Alaska.

Aquatic and Wet Habitats

Geissler (1975) reported *Nardia assamica* in European alpine streams. Hicks (2003) listed its habitats as wet exposed soil with water seepage. Bakalin *et al.* (2009) reported on its presence in the South Kuril Islands, East Asia. There, its less aquatic habitats, compared to those in the alpine streams, include oligotrophic peatlands, wet open places, fumaroles and hot sulfur springs at 50°C, areas of bare clayish or sandy ground in places with destroyed vegetation cover (stream banks, travertine cones in hot stream areas), rocks along cool and hot sulfur springs in forested and forestless areas, cliff wall in *Salix-Duscheckia* wet community, among mosses in hummocks in sedge-moss mires, between patches of *Eriophorum* (Figure 96) and *Eleocharis* (Figure 22) in wet depression in wind-stressed community of *Sasa* (bamboo; Figure 97) and small herbs. It frequently occurs with other leafy liverworts.



Figure 96. *Eriophorum scheuchzeri* in the Swiss Alps. *Nardia assamica* lives among plants of this genus in the Alps. Photo by Simon A. Eugster, through Creative Commons.



Figure 97. *Sasa* ground cover in spruce forest at Bihora Pass Japan. *Nardia assamica* lives in association with *Sasa* in wet depressions. Photo by Janice Glime.

Biochemistry

The oil bodies are large (Figure 98). Although there seem to be no biochemical studies, one could conjecture that such large oil bodies might contain some interesting biochemicals.



Figure 98. *Nardia assamica* cells showing large oil bodies. Photo by Yang Jia-dong, Taiwan Encyclopedia of Life, through Creative Commons.

***Nardia compressa* (Figure 99-Figure 102)**

(syn. = *Alicularia compressa*)

Distribution

Nardia compressa (Figure 99-Figure 102) has a worldwide distribution, but avoids the hot tropics, occurring there only at high elevations (DiscoverLife.org 2020).



Figure 99. *Nardia compressa*, a species with worldwide distribution outside the tropics, occurring in lakes and streams. Photo by Hermann Schachner, through Creative Commons.



Figure 100. *Nardia compressa* showing stoloniferous shoots. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Based on early studies, West (1910) reported *Nardia compressa* (Figure 99-Figure 102) to be abundant on wet and submersed rocks (Figure 101) in Scotland, sometimes occurring down to 1 m depth in lakes. Light (1975) reported it from small lakes of the Scottish mountains where it experiences 4-7 months of ice cover and low ion concentrations.



Figure 101. *Nardia compressa* habitat by a stream. Photo by Hugues Tinguy, with permission.

Watson (1919), on the other hand, reported *Nardia compressa* (Figure 99-Figure 102) as a species submerged in slow water with poor mineral salts, as well as rocky and stony beds of fast streams. In the Haute Ardenne rivers of Belgium it seems to be strictly aquatic (Leclercq 1977). In Thuringia, Germany, Marstaller (1987) found it in association with *Platyhypnidium* (Figure 68) and *Fontinalis antipyretica* (Figure 69).

Lepp (2012) reported *Nardia compressa* (Figure 99-Figure 102) from the edges of a small stream running through a steep ravine in Alaska. In swift mountain streams of Yakobi Island, Alaska, USA, Shacklette (1965) found that the intertwined stems can dam the stream, creating a series of terraced pools. The growth of the liverwort closes the pool surface (e.g. Figure 102), permitting tracheophytes to invade the mat.

Vieira *et al.* (2004, 2005) described *Nardia compressa* (Figure 99-Figure 102) in Portugal as the dominant species from granite slabs of the streambed, where it is immersed, often in fast-flowing acidic water. It is most common in high mountain areas, but often in exposed peat bog areas at 700-1400 m asl. It seems to form extensive populations anywhere it can become established. This includes exposed peat bog areas associated with *Fissidens polyphyllus* (Figure 103), *Marsupella aquatica* (Figure 59-Figure 62), *Marsupella sphacelata* (Figure 83-Figure 87), *Platyhypnidium lusitanicum* (Figure 104), and *Scapania undulata* (Figure 60), in these mountain streams of northwest Portugal (Vieira *et al.* 2005).

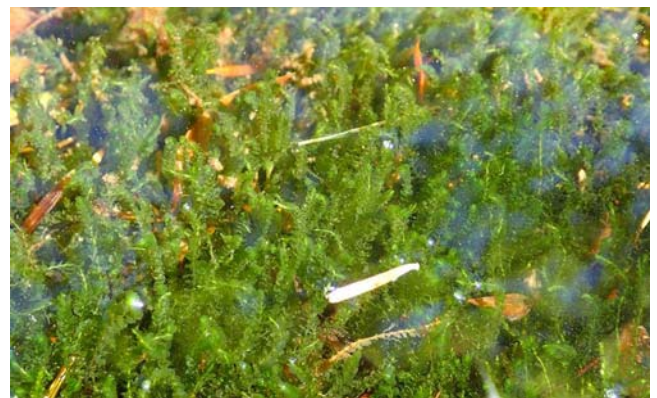


Figure 102. *Nardia compressa* submersed. Photo by Hugues Tinguy, with permission.



Figure 103. *Fissidens polyphyllus*, a species that occurs with *Nardia compressa* in exposed peat bog areas. Photo by David T. Holyoak, with permission.



Figure 104. *Platyhypnidium lusitanicum*, an associate with *Nardia compressa*. Photo by Barry Stewart, with permission.

Geissler (1975) considered *Nardia compressa* (Figure 99-Figure 102) to be a helokrene species associated with alpine streams. Ferreira *et al.* 2008) considered it to be a species of rivers. Scarlett and O'Hare (2006) found it to be among the commonest species in English and Welsh rivers.

Nardia compressa (Figure 99-Figure 102) apparently is unable to tolerate alkaline water well. Wilkinson and Ormerod (1994) studied the effects of catchment liming on bryophytes in upland Welsh streams. *Nardia compressa* had the greatest cover exhibited in any one stream, reaching up to 71% cover. Liming was used to restore acidified streams. Under this treatment, the cover of *N. compressa* declined significantly from 39% to 5%.

Rothero (2020) found it on permanently wet or frequently inundated rocks and stones in acidic turbulent streams and rivers. It can occasionally be embedded in sand and gravel. It typically forms spongy masses, especially in cold, slow-flowing headwaters of upland streams, but it also occurs in **burns** (streams or small rivers) and flushes associated with late-lying snow fields, often forming pure patches of many square meters.

Adaptations

Nardia compressa (Figure 99-Figure 102) varies in color from deep green to reddish-brown or deep purple (Smith 1990). The plants are robust and form large tufts.

Reproduction

Nardia compressa (Figure 99-Figure 102) is **dioicous** and is rarely fertile in the UK (Smith 1990). Gemmae are unknown.

Nardia geoscyphus (Figure 105-Figure 106)

Distribution

Nardia geoscyphus (Figure 105-Figure 106) is a boreal species occurring in Europe, Asia, and North America (Natcheva 2020). Overall, it has a restricted distribution with low population density (Natcheva 2020).



Figure 105. *Nardia geoscyphus*, a boreal Northern Hemisphere species from stream banks and constructed ditches. Photo by Štěpán Koval, with permission.



Figure 106. *Nardia geoscyphus* habitat on a stream bank. Photo by Martine Lapointe, with permission.

Beaucourt *et al.* (1987) reported *Nardia geoscyphus* (Figure 105) from irrigation ditches. It also grows on eroded soil beside roads and on stream banks (Figure 106) (Natcheva 2020).

Adaptations

Nardia geoscyphus (Figure 105-Figure 106) rarely occurs in dense **mats** and the shoots are usually prostrate and closely adhere to the soil (Evans 1912). Rhizoids are numerous (Smith 1990). Its coloration ranges from green to reddish brown or purplish. It often grows among other bryophytes, likely retaining more water due to their presence.

Reproduction

Nardia geoscyphus (Figure 105-Figure 106) is **paroicous** (having archegonia and antheridia on same branch), permitting it to frequently produce capsules (Smith 1990).

Nardia scalaris (Figure 107-Figure 108, Figure 111)

(syn. = *Alicularia scalaris*, *Alicularia scalaris* var. *distans*, *Alicularia scalaris* var. *procerior*, *Alicularia scalaris* var. *rivularis*)

Distribution

Nardia scalaris (Figure 107-Figure 108, Figure 111) is distributed in the North Pacific in Alaska, British Columbia, California, Oregon, Washington in North

America; Chukotka, Kamchatka, Magadan, and Sakhalin in Russia (Bakalin 2012). Elsewhere, it is reported from Tennessee, USA (Sharp 1939), Scotland (West 1910), Serbia (Pantović & Sabovljević 2013), and the Azores (Sjögren 1997). ITIS (2020d) also reports it from southern Asia and Africa.



Figure 107. *Nardia scalaris*, a species from the Northern Hemisphere, southward into the mountains, growing on peaty soils and in springs. Photo by J. C. Schou, with permission.

Aquatic and Wet Habitats

West (1910) reported *Nardia scalaris* (Figure 107-Figure 108, Figure 111) from wet sandy-peaty shores in Scotland, where it is often abundant. Also in Scotland, Harriman and Morrison (1982) found *Nardia scalaris* [and several *Scapania* (e.g. Figure 60) species] to be the most abundant species of bryophytes in the streams. Watson (1919) described it as a species submerged in fast water, on ground or rocks, on banks with frequent submergence and slow water, and in usually drier sites with fast water.

Sharp (1939) reported it on moist, peaty soil in Tennessee, USA, but there it was rare, being more common farther north. Pantović and Sabovljević (2013) found *Nardia scalaris* (Figure 107-Figure 108, Figure 111) on rock by a stream and on soil on Mt. Boranja in western Serbia. Sjögren (1997) found it in a single collection as "accidentally" epiphyllous in the Azores Islands.

In Alaska *Nardia scalaris* (Figure 107-Figure 108) can form continuous carpets (Figure 108) that seem to support the growth of *Saxifraga ferruginea* (Figure 109) (Shacklette 1961). These areas typically are highly disturbed and contaminated with copper, for which these two species seem to have good tolerance. The liverwort provides an organic layer about 1 cm thick. It grows on a variety of substrates and is tolerant of the sulfide found in pyrite. It is often a snowbed species and has a strong requirement for abundant water and light with little or no competition.



Figure 108. *Nardia scalaris* forming continuous carpet. Photo by Hermann Schachner, through Creative Commons.



Figure 109. *Saxifraga ferruginea*, a species that can grow on carpets of *Nardia scalaris* in Alaska. Photo by Paul Slichter, with permission.

The *Scapania* (Figure 60)-*Nardia* (Figure 107-Figure 108, Figure 111) community on Yakobi Island colonizes mountain rivulets, forming carpets that permit *Nephrophyllidium crista-galli* (syn. = *Fauria crista-galli*; Figure 110) to colonize and eventually succeed to a copperbush community (Shacklette 1965).

It is likely that this species has some salt tolerance, as Evans (1912) reported it growing on cliffs at about 3 m above the high tide level in Nova Scotia and New Brunswick, Canada.

Reproduction

Nardia scalaris (Figure 107-Figure 108, Figure 111) is **dioicous** and rarely produces capsules (Figure 111), at least in North America (Evans 1912; Smith 1990). It typically produces prostrate shoots that become suberect when growing in compact mats.



Figure 110. *Nephrophyllidium crista-galli*, a species that colonizes the *Scapania-Nardia* community on Yakobi Island. Photo by Andy Tasler, through public domain.



Figure 111. *Nardia scalaris* with capsules. Photo by J. C. Schou, with permission.

Fungal Interactions

Bidartondo and Duckett (2010) found that *Nardia scalaris* (Figure 107-Figure 108, Figure 111) predominantly and consistently associates with the *Sebacina vermifer* species complex (see Figure 169). An unusual find was that the DNA sequence of the fungus on this liverwort was identical to that on *Lophozia ventricosa* (Figure 112) at Ben Wyvis, Scotland. The only other shared DNA found in their study was for this fungus species on both *Nardia scalaris* and *Schistochilopsis opacifolia* at St. Gotthard, Switzerland. But what are the biological implications of this shared DNA, other than a local population that is able to inhabit more than one host? Does it mean it did so recently?

Biochemistry

This species has been the subject of a number of biochemical studies. Beneš *et al.* (1981) reported on a triterpenoid present in the species, one already known from other liverworts. Then they found a new diterpenoid,

nardiin, from the species (Beneš *et al.* 1982). Langenbahn *et al.* (1993) further described terpenes from the species, revealing 12 diterpene malonates. The aromatic compounds give *Nardia scalaris* (Figure 107-Figure 108, Figure 111) its distinctive carrot-like odor (Beike *et al.* 2010).



Figure 112. *Lophozia ventricosa*, a liverwort that shares the fungus *Sebacina vermifer* with the same DNA as that of the one on *Nardia scalaris*. Photo by Hermann Schachner, through Creative Commons.

Harpanthaceae

Harpanthus flotovianus (Figure 113-Figure 116)

Distribution

Harpanthus flotovianus (Figure 113-Figure 116) occurs in Europe, Asia, and North America (ITIS 2020e), where it is widespread in boreal and montane regions.

Aquatic and Wet Habitats

In early records, *Harpanthus flotovianus* (Figure 113-Figure 116) was found on the sides of fast alpine streams (Watson 1919). Koponen *et al.* (1995) considered it to be aquatic in Finland. In eastern Fennoscandia it occurs in wet habitats – near springs and streams, and in fens and moist forests (Figure 117) (Järvinen 1976). Dulin (2015) reported it from the vicinities of glacial relict lakes, occurring on decaying wood in herbal-*Sphagnum* mixed and birch forests. It occurred there in pure patches and with other liverworts.

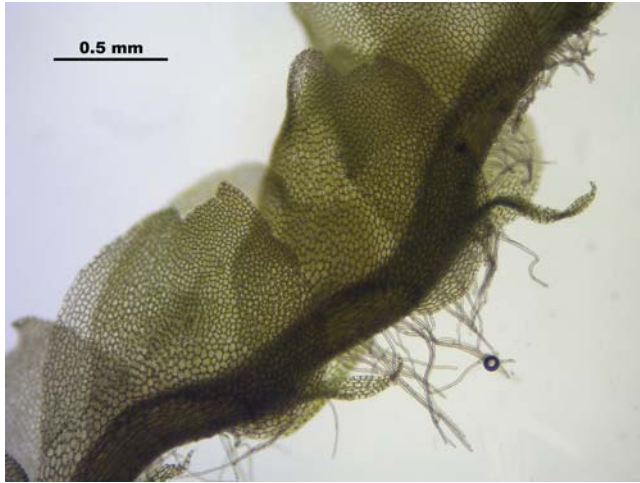


Figure 113. *Harpanthus flotovianus*, a widespread boreal-montane species, occurring in streams, springs, lakes, their banks, and other wet habitats. Photo by Hermann Schachner, through Creative Commons.



Figure 116. *Harpanthus flotovianus* showing its mat growth. Photo by Hermann Schachner, through Creative Commons.

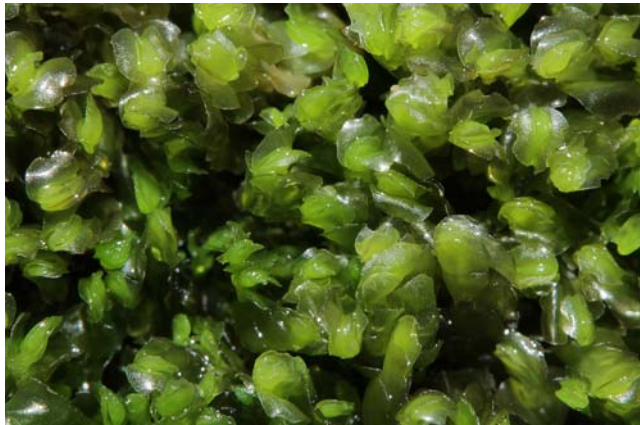


Figure 114. *Harpanthus flotovianus*. Photo by Hermann Schachner, through Creative Commons.



Figure 115. *Harpanthus flotovianus*. Photo by Štěpán Koval, with permission.



Figure 117. *Harpanthus flotovianus* habitat in a wet spruce opening. Photo by Scot Loring, through Creative Commons.

In Estonia, *Harpanthus flotovianus* (Figure 113-Figure 116) occurs in fens, transitional mires, and bogs (Figure 118) (Ingerpuu *et al.* 2014). Emerson and Loring (2010) likewise found it associated with *Sphagnum* in the Rogue River-Siskiyou National Forest. In this forest it formed an association including *Calypogeia sphagnicola* (Figure 44-Figure 46), *Pohlia sphagnicola* (Figure 119), *Cephaloziella spinigera* (Figure 120), and *Kurzia makinoana* (Figure 121).



Figure 118. Peatland habitat suitable for *Harpanthus flotovianus* and associated *Pohlia sphagnicola*. Photo by Michael Lüth, with permission.

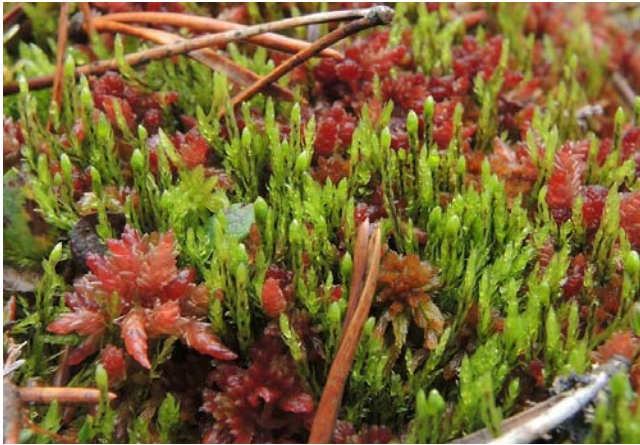


Figure 119. *Pohlia sphagnicola*, often an associate of *Harpanthus flotovianus* in bogs and poor fens. Photo by Michael Lüth, with permission.

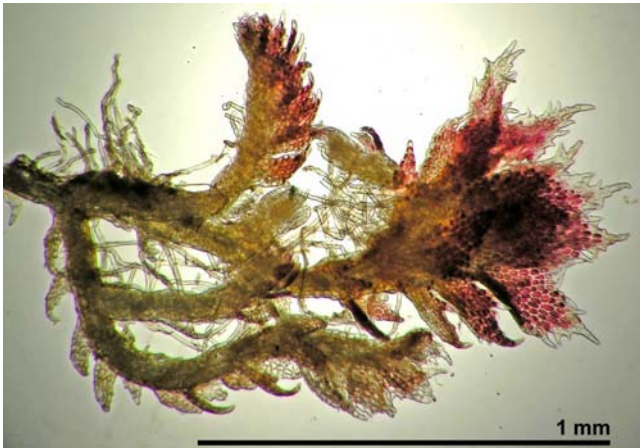


Figure 120. *Cephaloziella spinigera* autoicous shoot, an associate of *Harpanthus flotovianus* in bogs and poor fens. Photo by David Wagner, with permission.



Figure 121. *Kurzia makinoana*, an associate of *Harpanthus flotovianus* in bogs and poor fens. Photo by Blanka Aguero, with permission.

Reproduction

Fertile plants of *Harpanthus flotovianus* (Figure 113-Figure 116) are unknown in the Pacific Northwest (Schofield 2002) and are rare in the British Isles (Paton 1999), where they are **dioicous** (Smith 1990). The paucity of sexual reproduction and lack of gemmae undoubtedly contributes to the rarity in this region. The species is perennial and should be identifiable throughout the year.

Fungal Interactions

Wang and Qiu (2006) found no records of any associated mycorrhizal fungus with this species.

Hygrobiellaceae

Hygrobiella laxifolia (Figure 122)

Distribution

Hygrobiella laxifolia (Figure 122) occurs in Europe, Asia, and North America. However, in 2014, Bakalin and Vilnet explored the genomic makeup of populations from northwestern Europe, Far Eastern Russia, and western USA. They found that the Far Eastern specimens separated from each other and from the North American population. They named the Far Eastern clades as *Hygrobiella intermedia* and *Hygrobiella squamosa*. These two species and *Hygrobiella laxifolia* are **sympatric** (sharing part of their distributional area) in the northern Pacific region. Pigmentation, form of perianth and leaves, stem cross section anatomy, and length of underleaves can be used to separate the species morphologically.

Aquatic and Wet Habitats

Under the name of *Hygrobiella laxifolia* (Figure 122), Nichols (1918) reported the species from a rock ravine streambank on Cape Breton Island, Canada. Watson (1919) considered it to be subalpine, occasionally being submerged. Koponen *et al.* (1995) considered populations under this name to be aquatic in Finland.

Luis *et al.* (2007) reported populations from Madeira Island off the northwest coast of Africa as *Hygrobiella laxifolia* (Figure 122). It grew on rocks in the spray zone

of the stream margins where it was associated with other bryophytes.



Figure 122. *Hygrobiella laxifolia*, a Northern Hemisphere species of stream banks. Photo by Martine Lapointe, with permission.

Adaptations

The plants of *Hygrobiella laxifolia* range in color from green to greenish-brown or reddish-brown (Smith 1990). Its ability to grow mixed with other bryophytes can help it to maintain hydration.

Reproduction

Hygrobiella laxifolia is dioicous (Smith 1990).

Jungermanniaceae

Eremonotus myriocarpus (Figure 123-Figure 126)

Distribution

Eremonotus myriocarpus (Figure 123-Figure 126) is distributed in Europe, Asia, and North America (ITIS 2020f). The species is a rather rare Arctic-alpine species from north and central Europe, China, Japan, the Far East of Russia, and several localities in Greenland and North America (Konstantinova & Savchenko 2008). Although records are widespread, they are not frequent.



Figure 123. *Eremonotus myriocarpus*, a rather rare Arctic-alpine species in the Northern Hemisphere, where it is occasionally submerged. Photo by Kristian Peters, with permission.



Figure 124. *Eremonotus myriocarpus* showing a green mat form. Photo by Kristian Peters, with permission.



Figure 125. *Eremonotus myriocarpus* showing a color variant, perhaps in response to high light intensity. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) considered this to be a subalpine species that is occasionally submerged (Figure 126). Long (1982) reported it from a damp rock face.



Figure 126. *Eremonotus myriocarpus* habitat. Photo by Michael Lüth, with permission.

Adaptations

Eremonotus myriocarpus is minute (Smith 1990). It forms reddish-brown patches, a color uncommon in most submersed species, but beneficial for species in exposed sites. The coloration, however, is also advantageous in cold habitats, even when the plants are submersed.

Reproduction

Eremonotus myriocarpus is **dioicous** (Smith 1990). It lacks gemmae. In the United Kingdom, male plants are frequent while female plants are only occasional.

Fungal Interactions

Fungi seem to find this species to be a suitable habitat. However, Bidartondo and Duckett (2010) found only Ascomycetes in the usually basidiomycete-containing *Eremonotus myriocarpus* (Figure 123-Figure 126) from locations in Europe.

Jungermannia (Figure 127-Figure 128, Figure 130-Figure 133, Figure 135-Figure 137, Figure 140-Figure 143)

Jungermannia (Figure 127-Figure 128, Figure 130-Figure 133, Figure 135-Figure 137, Figure 140-Figure 143) vs. *Solenostoma* (Figure 170-Figure 176, Figure 177-Figure 189, Figure 193-Figure 196) – These two genera have been divided and many species have been moved to *Solenostoma*. They occur in small lakes in southern Finland (Toivonen & Huttunen 1995), small, pristine streams of the Tolvajärvi region, Russian Karelia (Vuori *et al.* 1999), and occur as west African rheophytes (Shevock *et al.* 2017).

Jungermannia atrovirens (Figure 127-Figure 128, Figure 130)

(syn. = *Aplozia riparia*, *Aneura riparia* fo. *potamophila*, *Aneura riparia* var. *rivularis*, *Aplozia riparia* var. *rivularis*, *Haplozia riparia* var. *potamophila*, *Haplozia riparia* var. *rivularis*, *Jungermannia riparia*, *Plectocolea riparia*, *Solenostoma triste*)

Distribution

Jungermannia atrovirens (Figure 127-Figure 128, Figure 130) is listed by ITIS (2020g) for Europe, Asia, Africa, and North America.

Aquatic and Wet Habitats

Jungermannia atrovirens (Figure 127-Figure 128, Figure 130) is often completely submerged and truly aquatic in fast streams, on banks with frequent submergence and slow water, and wet, rocky places associated with fast water (Watson 1919). This description is supported by its occurrence in the Linth River, Switzerland (Koch 1936); in water in Westfalens, northwestern Germany (Koppe 1945); the only bryophyte in four streams of the Black Mountain District of South Wales (Jones 1948); hydrophytic or hydrophilic in the Rhine area, Germany (Philippi 1968); among the most common in upstream and extreme upper reaches and tributaries of the River Tweed, UK (Holmes & Whitton 1975b; Birch *et al.* 1988); above (Figure 128) and below water in the upper reaches of the River Wear, UK (Holmes & Whitton 1977a); in the river and on the river bank of the River Tees, UK (Holmes & Whitton 1977b); in upper to midstream of the River Swale, Yorkshire, UK (Holmes & Whitton 1977c); throughout the River Tyne, UK (Holmes & Whitton 1981); in the *Platyhypnidium* (Figure 68)-

Fontinalis antipyretica (Figure 69) association, Thuringia, Germany (Marstaller 1987); among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006); at spring and river in Tara River canyon and Durmitor area, Montenegro (Papp & Erzberger 2011); and on damp rock face in the Canary Islands (Crundwell *et al.* 1978).



Figure 127. *Jungermannia atrovirens*, a relatively widespread, predominantly Northern Hemisphere species submerged in streams and lakes. Photo by Hermann Schachner, through Creative Commons.



Figure 128. *Jungermannia atrovirens* wet above the water level. Photo by Bernd Haynold, through Creative Commons.

In the UK this species grows in a variety of calcareous situations, including rock, tufa, or soil. On sandstone cliffs, as well as limestone cliffs, it is abundant. But it also occurs on less wet habitats, including forestry tracks with limestone or tufaceous rock. Konstantinova *et al.* (2009) reported it from moist cliffs and rocks on stream banks, primarily in calcium-rich sites. Birk and Willby (2010) considered it to be a species of siliceous mountain brooks, indicating a high quality site, but less frequently than *Scapania undulata* (Figure 60) or *Chiloscyphus polyanthus* (Figure 129).



Figure 129. *Chiloscyphus polyanthos*, a frequent species in siliceous mountain brooks where *Jungermannia atrovirens* is able to grow. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Jungermannia atrovirens is small, forming yellowish-green to dull green patches (Smith 1990). It often grows through patches of other bryophytes where they can help it to retain moisture.

Reproduction

Although the species is **dioicous**, males and females (Figure 130) are typically both abundant (BBS 2020), reducing the disadvantage of separate sexes. Although perianths are frequent, capsules are produced only occasionally in the UK, in spring and summer (Smith 1990).



Figure 130. *Jungermannia atrovirens* with abundant perigynia. Photo by Hugues Tinguy, with permission.

Jungermannia borealis (Figure 131)

Distribution

The distribution of *Jungermannia borealis* (Figure 131) must be viewed with caution because of a number of misidentifications. It seems to be in northern Europe, Asia, and North America, extending southward in the mountains.



Figure 131. *Jungermannia borealis* with perigynium, a species of the Northern Hemisphere, living on stream and river banks and near waterfalls. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Jungermannia borealis (Figure 131) occurs in water near a waterfall of the Upper Bureya River (Russian Far East) (Konstantinova *et al.* 2002). In Yakutia, also in Asian Russia, this species occurs on stream and river banks in the upper course of the Indigirka River (Sofronova 2018). Damsholt and Vána (1977) describe the habitat as typically in basic on shaded rocks and soil.

Reproduction

Like most leafy liverworts, this species is **dioicous** (Figure 131) (Damsholt & Vána 1977).

Fungal Interactions

Wang and Qiu (2006) found no records of fungi associated with this species.

Jungermannia callithrix (Figure 132)

(syn. = *Solenostoma callithrix*)

Distribution

Jungermannia callithrix (Figure 132) is primarily Neotropical (Schumaker & Vána 1999), but is known off the coast of Africa (Luis *et al.* 2015).



Figure 132. *Jungermannia callithrix*, a mostly Neotropical species from narrow mountain streams. Photo by Tomas Hallingbäck, with permission.

Aquatic and Wet Habitats

Luis *et al.* (2015) reported it from a low altitude, narrow stream and low flow in mountain streams on Madeira Island off the northwest coast of Africa.

Jungermannia exsertifolia (Figure 133)

Distribution

Jungermannia exsertifolia (Figure 133) is another Northern Hemisphere species, known from Europe, Asia, and North America (ITIS 2020h). There are a few additional outlying locations on islands. It is a widely distributed Holarctic species with considerable morphological variation throughout its range (Zubel 2008). Vána (1973) considered European populations of this species to differ somewhat from Asian plants and to represent a different subspecies, *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 140), discussed below. This subspecies occurs in the European sub-arctic-boreal-subalpine region. Records of this species should be viewed with caution because it has been confused with *Jungermannia atrovirens* (Figure 127-Figure 128, Figure 130) as well as failure to recognize it as a subspecies in some European records (Zubel 2008).



Figure 133. *Jungermannia exsertifolia* is a widely distributed Holarctic species, primarily in cold-water streams. Photo by Paul Bowyer, through Creative Commons.

Aquatic and Wet Habitats

Koponen *et al.* (1995) considered *Jungermannia exsertifolia* (Figure 133) to be aquatic in Finland. It occurs in regulated portions of the River Rhine (Vanderpoorten & Klein 1999b) and in the Alpine Rhine to the Middle Rhine (Vanderpoorten & Klein 1999c). Yet few aquatic studies seem to have recorded it.

This species seems to have an aversion to warm water. In sub-Arctic streams of Iceland ranging 7.1 to 21.6°C, it occurs in low densities in cold streams, but it is absent in the warmest streams (Gudmundsdottir *et al.* 2011a, b).

Adaptations

Like most of the species in this family, *Jungermannia exsertifolia* ranges in color from dull green to blackish-purple or even black. The dark coloration most likely protects it from photoinhibition in cold streams. It forms

tufts or patches. It has few rhizoids, a character that would seem to be a disadvantage in moving water of streams.

Reproduction

Jungermannia exsertifolia is **dioicous** and lacks gemmae (Smith 1990), suggesting that fragmentation may be an important means of reproduction.

Interactions

Jensen *et al.* (2008) found that *Jungermannia exsertifolia* (Figure 133) was among the first liverworts that showed good dose-dependent activity against the malaria parasite *Plasmodium falciparum* (Figure 134). It is interesting that these liverworts were collected from Iceland where malaria is unknown.

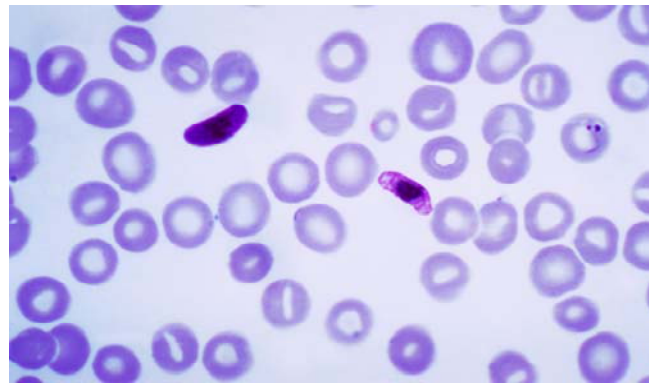


Figure 134. *Plasmodium falciparum* macro and microgametocyte. Photo from CDC - Dr. Mae Melvin Transwiki, through public domain.

Jungermannia exsertifolia subsp. *cordifolia* (Figure 135-Figure 137, Figure 140)

(syn. = *Aplozia cordifolia*; *Jungermannia cordifolia*; *Jungermannia eucordifolia*; *Solenostoma cordifolia*)

Distribution

Jungermannia exsertifolia subsp. *cordifolia* (Figure 135-Figure 137, Figure 140) occurs in Europe, Asia, and North America (ITIS 2020i) where it is sub-Arctic-boreal-subalpine in its distribution (Zubel 2008).



Figure 135. *Jungermannia exsertifolia* subsp. *cordifolia*, a sub-Arctic-boreal-subalpine species of fast water. Photo by Des Callaghan, with permission.



Figure 136. *Jungermannia exsertifolia* subsp. *cordifolia* from a wet habitat. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Nichols (1918) reported this subspecies from ravines on Cape Breton Island, Canada. Watson (1919) considered it to be alpine or subalpine, occurring on submerged rocks in fast water (Figure 137). Geissler (1976) found it in alpine streams in the Swiss Alps. Koponen *et al.* (1995) considered it to be aquatic in Finland; Heino and Virtanen (2006) reported it from streams in northeastern Finland. In Thuringia, Germany, Marsteller (1987) found it in the *Platyhypnidium* (Figure 68)-*Fontinalis antipyretica* (Figure 69) association – a stream association.



Figure 137. *Jungermannia exsertifolia* subsp. *cordifolia* on a partly submerged rock in fast water. Photo by Dick Haaksma, with permission.

When Martínez-Abaigar *et al.* (1993) transplanted several species of bryophytes to polluted water in the River Iregua in northern Spain, *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140) proved to be very sensitive to pollution events; *Fontinalis antipyretica* (Figure 69) was more tolerant. This research team (Martínez-Abaigar *et al.* 2002) also found that this subspecies accumulated phosphorus (P) and potassium (K) dependent on the concentration of KH_2PO_4 in the water in 15 days of exposure. However, K accumulations fluctuated

rather widely, presumably due to the ease with which it can be leaked from the cells. The accumulation of P in the liverwort seems to reach saturation at 20 mg L^{-1} . Increasing the P concentration in the water and tissues failed to increase net photosynthesis. The researchers suggested that the liverwort might be deficient in other mineral nutrients such as N, or that it had an intrinsic inability to use the excess nutrients. When P concentration in the tissues reached 0.45% of the dry mass, net photosynthesis declined with added P, suggesting that it had reached toxic concentrations. Furthermore, P enrichment did not affect chlorophyll concentration, but the *a/b* ratio declined, as did the proportions of chlorophylls to phaeopigments. At the same time, the proportions of carotenoids to chlorophylls increased. These responses likewise suggested P toxicity. In P-enriched aerated and nonaerated conditions, anoxia greatly reduced the P accumulation in just three days. This was likely due to blockage of mitochondrial respiration. This was followed by a distinct net loss of P, suggesting membrane damage. The photosynthetic response to K was lower than that to P.

Adaptations

Jungermannia exsertifolia subsp. *cordifolia* (Figure 135-Figure 137, Figure 140) has been the subject of many studies on the effects of enhanced UV. This interest has resulted in part from the loss of ozone in the stratosphere. Ozone serves as a filter against UV radiation. Hence, when fluorine in the atmosphere destroys ozone, the UV reaching the Earth increases.

One of the leading researchers on the effects of UV-B radiation on bryophytes is Martínez-Abaigar. He and his coworkers have laid the foundation for this research. In particular, they have concentrated on aquatic bryophytes. At higher elevations, the atmosphere is thinner, permitting more UV-B radiation to reach the surface of the Earth. Hence, mountain stream bryophytes are at particular risk because they lack a thick cuticle to help reduce the UV-B light. Martínez-Abaigar *et al.* (2006) specifically named *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140) as a good bio-indicator species for UV-B levels. Fv/Fm ratio, the concentration of UV-absorbing compounds (especially if they are analyzed individually), and DNA damage are good indicator variables for UV damage.

Fabón *et al.* (2011) pursued the effects of UV radiation on DNA in bryophytes, using *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140). DNA damage was significantly greater in PAB (PAR + UV-A + UV-B) treatments than in P (only photosynthetically active radiation, PAR) or PA (PAR + UV-A) treatments, making this species a good biomarker for UV-B damage. Under PAB treatment, DNA damage increased in thymine dimers following a period of high PAR plus UV. But after UV cessation and return of PAR only, there was a rapid and complete repair. The net result showed little damage to this liverwort, indicating it is well adapted to the levels of UV in the lab experiment.

Temperature can make a difference in the amount of UV damage because of the reduced metabolism at low temperatures. Núñez-Olivera *et al.* (2005) cultured

Jungermannia exsertifolia subsp. *cordifolia* (Figure 135-Figure 137, Figure 140) and *Fontinalis antipyretica* (Figure 69) at 2°C for 78 hours with continuous radiation to determine whether acclimation to sun or shade affected the UV-B response. The *F. antipyretica* was more sensitive to UV-B, showing significant decreases in several physiological variables. The sensitivity was present in both sun and shade plants, with shade plants being more sensitive. *Jungermannia exsertifolia* subsp. *cordifolia*, on the other hand, had no difference in effect in shade- vs sun-acclimated plants.

Soriano *et al.* (2019) likewise found that *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140) acclimates to UV radiation intensity. Its response differences between sun and shade plants were moderate compared to those of *Marchantia polymorpha* (Figure 138-Figure 139), but greater than those of *Fontinalis antipyretica* (Figure 69).



Figure 138. *Marchantia polymorpha* gemmae cups on a wet population. Photo by Rudolf Macek, with permission.



Figure 139. *Marchantia polymorpha* with red thallus, often a result of sun exposure. Photo by Paul Slichter, with permission.

Arróniz-Crespo *et al.* (2006) compared the responses of *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140) from mountain streams at a series of altitudes (1140-1816 m asl). They discovered two new caffeic acid derivatives, and the concentrations of

these increased significantly with altitude. There was a significant linear relationship with altitude for additional measured parameters: MEUVAC (methanol-extractable UV-absorbing compounds), the maximal apparent electron transport rate through PSII (ETR_{max}), and the maximal non-photochemical quenching (NPQ_{max}) all increased with altitude. Photoinhibition percentage decreased with altitude, suggesting that those populations from higher altitudes were exhibiting acclimation.

Martínez-Abaigar *et al.* (2009) likewise found evidence of acclimation to high UV radiation in populations of this species from high elevations. In their experiments, UV-B had little negative effect on photosynthetic performance or growth except in *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140). However, some pigments were affected negatively. UV-B protective compounds rarely increased (Figure 140). They attributed these muted responses to acclimation at their field altitudes of 1850-2000 m asl.



Figure 140. *Jungermannia exsertifolia* subsp. *cordifolia* on rock at edge of stream, emergent and underwater. Photo by Dick Haaksma, with permission.

Monforte *et al.* (2015a) similarly found little effect on Fv/Fm or DNA damage levels, hence making them inadequate as UV damage indicators. They supported the hypothesis of a strong acclimation capacity in *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140). On the other hand, coumarins were positively correlated with UV levels.

Martínez-Abaigar *et al.* (2003) found little response by *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140) to UV-A, but it did respond to UV-B. While the moss responded negatively in a number of measured parameters, the liverwort showed only a decreased Fv/Fm ratio, suggesting that this might be the most sensitive physiological variable. In addition, the concentration of UV-absorbing compounds increased with increased UV-B radiation.

Martínez-Abaigar *et al.* (2008) explored the effects of added phosphate on the UV-B response in *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140). They measured photosynthetic pigment composition, chlorophyll fluorescence, photosynthesis and respiration rates, and the accumulation of protecting UV-absorbing compounds – both the commonly used bulk UV-

absorbance of methanol extracts and the concentrations of five hydroxycinnamic acid derivatives in this liverwort. Although most of these variables were affected by the level of UV-B radiation, added phosphate had no significant effect on them except the vitality index (OD430/OD410) in the liverwort. They suggested that the liverwort has low nutrient requirements and that the added phosphate was stored as a luxury nutrient.

Monforte *et al.* (2015b) used 90 herbarium samples from Spain to assess usefulness of *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140) for UV radiation biomonitoring. They assessed both soluble (mostly vacuolar) and insoluble (bound in cell wall) UV-absorbing compounds. These provide a post-event means of assessment. For example, the soluble compound p-coumaroylmalic acid exhibited significantly higher concentrations after ~1975 when stratospheric ozone degradation was initiated. The bulk level of insoluble ultraviolet-absorbing compounds had the best spatial correlation with UV levels based on altitude and latitude. Summer and autumn samples differed significantly in both soluble and insoluble UV-absorbing compounds, reflecting the reduction of UV light in autumn in Spain.

Using a longer period of 82 days, Arróniz-Crespo *et al.* (2008) considered the response of five hydroxycinnamic acid derivatives to UV levels in *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140) from mountain streams. They found that the liverwort was tolerant to UV radiation, with the accumulation of three UV-absorbing hydroxycinnamic acid derivatives: p-coumaroylmalic acid, 5''-(7'',8''-dihydroxycoumaroyl)-2-caffeoylmalic acid, and 5''-(7'',8''-dihydroxy-7-O- β -glucosyl-coumaroyl)-2-caffeoylmalic acid being likely contributors to that tolerance. Thus, these three compounds are potential bioindicators of elevated UV levels.

Fabón *et al.* (2010) examined the effects of UV-B radiation on hydroxycinnamic acid derivatives from different cell compartments in *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140). They found a higher UV absorbance by the soluble fraction when compared to that of the cell-wall-bound fraction. Absorbance for both fractions increased when UV-B radiation was enhanced. The researchers identified five hydroxycinnamic acid derivatives in the soluble fraction and two more in the cell-wall-bound fraction. Of these, only p-coumaroylmalic acid in the soluble fraction and p-coumaric acid in the cell-wall-bound fraction increased under enhanced UV-B. DNA damage exhibited a strong increase under the enhanced UV-B, while the maximum quantum yield of PSII decreased.

Otero *et al.* (2006) assessed the effects of cadmium and enhanced UV radiation on *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140). Both caused degradation of chlorophyll and a decrease in the maximum quantum yield of photosystem II. At the same time, the xanthophyll index increased, permitting an increase in non-photochemical dissipation of energy. Cadmium elicited more stress than did the UV radiation, causing a decrease in net photosynthesis. UV radiation caused the level of trans-p-coumaroylmalic acid to increase, and cadmium caused trans-phenolic and feruloylmalic acids to increase. Elevated UV radiation

alone resulted in DNA damage, and that was exacerbated when cadmium was elevated. This combined effect is probably a function of the ability of cadmium to inhibit DNA repair.

Fabón *et al.* (2012) found that PAB (PAR + UV-A + UV-B) samples increased in the bulk UV absorbance of both soluble and insoluble fractions; this response was most likely due, at least in part, to increases in the concentrations of p-coumaroylmalic acid in the soluble fraction and p-coumaric acid in the cell wall. They found seven hydroxycinnamic acid derivatives in the soluble and insoluble fractions. Most of these showed diel changes, responding within a few hours to radiation changes, but more strongly to UV-B. Significant and rapid changes occurred for Fv/Fm, Φ PSII, NPQ, and the components of the xanthophyll cycle in response to high PAR, UV-A, and UV-B radiation.

Núñez-Olivera *et al.* (2009) considered the seasonal variations in the UV-absorbing compounds and physiological changes with seasons in *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140). Using monthly collections for three years from a mountain stream, they found no DNA damage. The tender young shoots of summer-autumn with high Fv/Fm accumulated higher amounts of several hydroxycinnamic acid derivatives than did shoots collected in winter-spring. The p-coumaroylmalic acid proved to be the compound best associated with radiation changes.

Reproduction

Jungermannia exsertifolia subsp. *cordifolia* is **dioicous** and lacks gemmae (Smith 1990), suggesting that fragmentation may be an important means of reproduction.

Biochemistry

In addition to studies on compounds that protect against high light intensity and elevated UV radiation, there have been studies on other secondary compounds in *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 135-Figure 137, Figure 140). Cullmann *et al.* (1999) found the typical liverwort **lignans** (any of class of polyphenolic compounds and noted for having antioxidant and estrogenic activity) and added three new ones. Nagashima *et al.* (1996) found eight new diterpenoids, added to the seven previously known. These have known biological activity against various cancer cell lines, plant-growth regulating properties, phytotoxic activity on root growth, as well as antiplasmodial, hypoglycemic, hypolipidemic, antimicrobial, antiviral, antifouling, larvicidal, algicidal, and insect antifeedant activities (Banerjee *et al.* 2008; Li *et al.* 2016; Lin-Gen *et al.* 2016; Pal *et al.* 2016; Bao *et al.* 2017; Li *et al.* 2017). They help to explain how a slow-growing liverwort can compete with bigger plants and ward off hungry insects.

To these, Scher *et al.* (2010) added a new diterpene derivative from this liverwort and found three previously known compounds. All of these demonstrated noticeable activity against a virulent tuberculosis pathogen.

***Jungermannia pumila* (Figure 141-Figure 143)**

(syn. = *Aplozia pumila*, *Jamesoniella ruttneri*, *Solenostoma pumila*)

Distribution

Jungermannia pumila (Figure 141-Figure 143) is distributed in Europe, Asia, and North America (ITIS 2020j).



Figure 141. *Jungermannia pumila*, a Northern Hemisphere species that can be found in some fast streams and deep in ponds. Photo by Paul Davison, with permission.

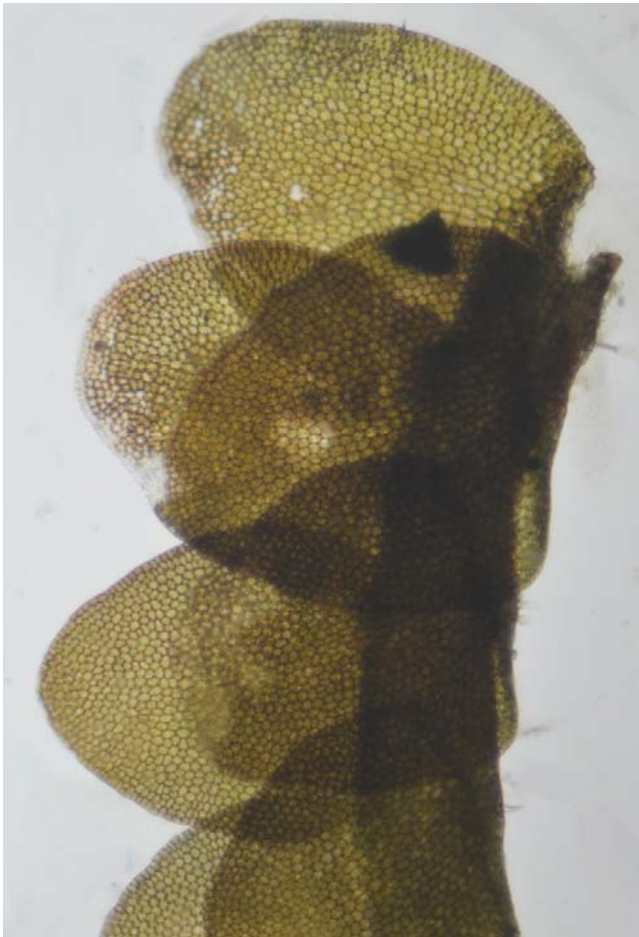


Figure 142. *Jungermannia pumila*. Photo by Rambryo, through Creative Commons.



Figure 143. *Jungermannia pumila* forming a mat. Photo by Rambryo, through Creative Commons.

Aquatic Wet Habitats

Watson (1919) attributed *Jungermannia pumila* (Figure 141-Figure 143) to rocks or gravel associated with fast streams, waterfalls, more aquatic in fast streams. Ruttner (1955) reported it submersed in a pond and <40 cm above water level in the tropics. Philippi (1987) considered it rare in aquatic habitats of eastern Odenwald and southern Spessart, Germany. Marstaller (1987) noted its occurrence in the *Platyhypnidium* (Figure 68)-*Fontinalis antipyretica* (Figure 69) association in Thuringia, Germany. Heino and Virtanen (2006) affirmed its occurrence in streams in northeastern Finland. And Luis *et al.* (2015) found it in mountainous streams on Madeira Island. In the UK, *J. pumila* (Figure 141-Figure 143) usually grows on damp rock on cliffs, low rock outcrops in woodlands, or low down on rock faces by rivers; sometimes it occurs on soil (BBS 2020).

Adaptations

Like many of the species in this genus, *Jungermannia pumila* (Figure 141-Figure 143), this species is small and exhibits a dull green to blackish coloration (Smith 1990). Unlike many of the wet-habitat species in this genus, it produces numerous rhizoids. It often grows with other bryophytes, a behavior that can help it to maintain moisture.

Reproduction

Jungermannia pumila (Figure 141-Figure 143) is **paroicous** and perianths (Figure 144) are common (Smith 1990; Hodgson 2021). Capsules are likewise common, produced in winter and spring. Gemmae are absent.



Figure 144. *Jungermannia pumila* fertile branches with females in center and male bracts below them. Photo by Andrew Hodgson, with permission.

Jungermannia quadridigitata(syn. = *Lepidozia setacea*, *Microlepidozia setacea*)**Distribution**

Jungermannia quadridigitata is listed by Söderström *et al.* (2016) as being of serious doubt. It is possible it is now included in one of the other taxa listed here. For this reason, I am unable to provide distribution information.

Aquatic and Wet Habitats

The species is not a true aquatic, but occurs in moist hollows between *Sphagnum* hummocks (Figure 145) on Cape Breton Island, Canada (Nichols 1918). Weber (1976) also included it among bog bryophytes in Cataracts Provincial Park, Newfoundland, Canada, considering it a typical bog bryophyte.



Figure 145. Raised bog with *Sphagnum fimbriatum* surrounded by *Sphagnum magellanicum*, where *Jungermannia quadridigitata* can occur in the hollows between hummocks like these. Photo through Creative Commons.

***Mesoptychia badensis* (Figure 146-Figure 148, Figure 150)**(syn. = *Lophozia badensis*)**Distribution**

Mesoptychia badensis (Figure 146-Figure 148, Figure 150) is listed by TROPICOS for China and Russia. Crandall-Stotler *et al.* (2013), however, considered it to be widely distributed in the northern hemisphere.

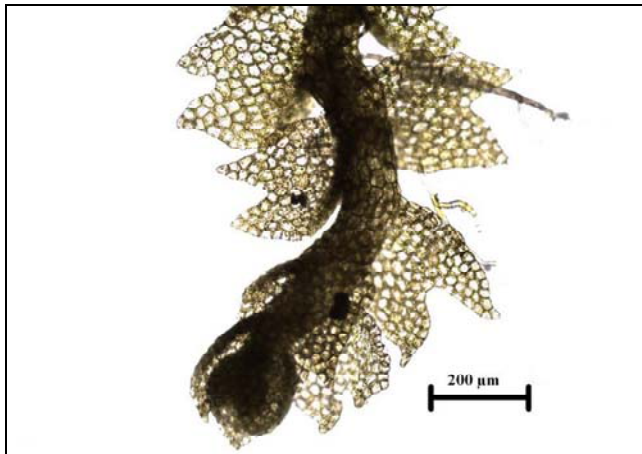


Figure 146. *Mesoptychia badensis*, a species widely distributed in the Northern Hemisphere in calcareous habitats, including streams and rivers. Photo by Hugues Tinguy, with permission.

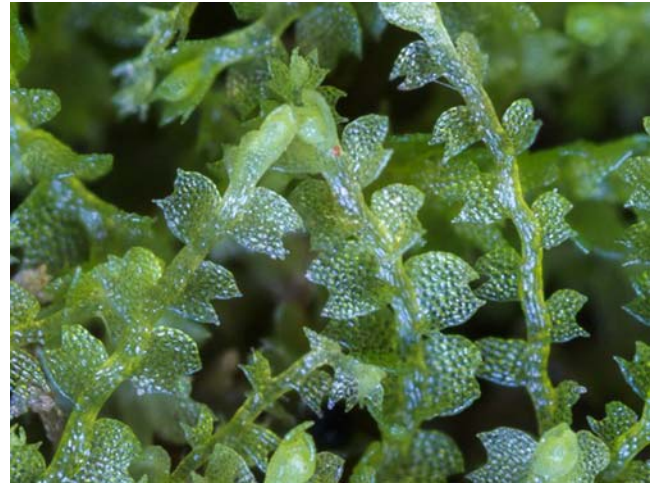


Figure 147. *Mesoptychia badensis*. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Nichols (1916) reported this species from calcareous rivers in Connecticut, USA. Watson (1919) treated it as occasionally submerged. In the Lorraine River, Belgium, it occurred in the travertine *Cratoneuron* (Figure 149) association (de Sloover & Goossens 1984). Bakalin *et al.* (2019a) found the species in the krummholz and tundra-like habitats where it grew in open wet to mesic limestone cliff crevices and on fine limestone deposits near small streams in the Balagan Mountain and Vengeri River Valley (Sakhalin Island, North-West Pacific).



Figure 148. *Mesoptychia badensis*. Photo by Štěpán Koval, with permission.

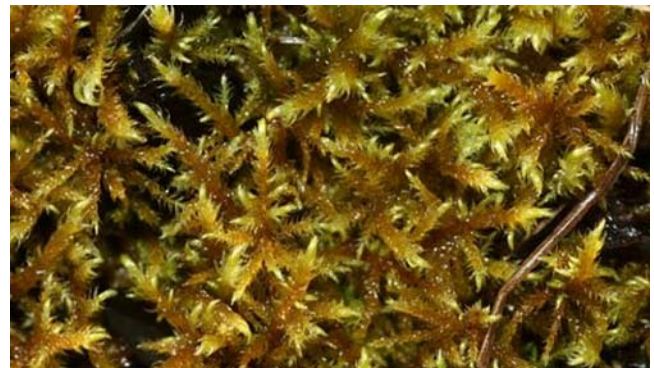


Figure 149. *Cratoneuron filicinum*; *Mesoptychia badensis* occurs in association with *Cratoneuron* in the travertine. Photo by Barry Stewart, with permission.

Reproduction

The species is **dioicous**, but at least sometimes produces capsules (Figure 150). On the other hand, it does not produce gemmae (Potemkin *et al.* 2015). We should look for its ability to reproduce from fragments, especially in the field. This could be especially important in rivers, streams, and areas subject to flooding.



Figure 150. *Mesoptychia badensis* with capsules, despite being dioicous. Photo by Štěpán Koval, with permission.

Mesoptychia bantriensis (Figure 151-Figure 153)

(syn. = *Leiocolea bantriensis*)

Distribution

Mesoptychia bantriensis (Figure 151-Figure 153) occurs in Europe, Asia, and North America (Bakalin 2018). Hodgetts (2015) listed it specifically from Norway, Sweden, United Kingdom, and Italy in Europe.

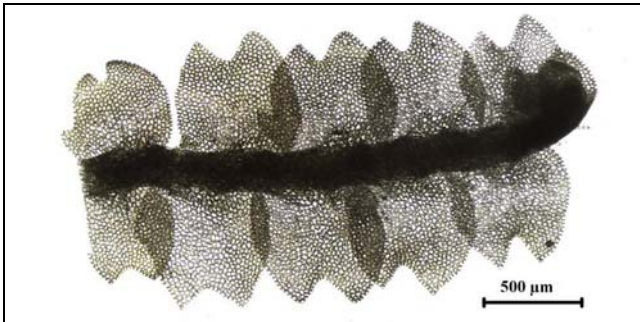


Figure 151. *Mesoptychia bantriensis*, a Northern Hemisphere liverwort of streams, rivers, lakes, and their banks, as well as mires and moist tundra. Photo by Hugues Tinguy, with permission.



Figure 152. *Mesoptychia bantriensis* showing growth habit. Photo by Štěpán Koval, with permission.

Aquatic and Wet Habitats

Watson (1919) listed this species as one of alpine and subalpine rocks and on soil by fast water. Heino and Virtanen (2006) reported it from streams in northeastern Finland. Bakalin *et al.* (2016) reported it from moist soil or on mineral ground of mesic tundras, but also along streams and on lake shores, on cliffs near waterfalls, on peat in mires, on peat in minerotrophic bogs, on silty alluvium along lake shores, and on fine soil and humus along watercourses on the Putorana Plateau in East Siberia. It forms mats on its substrate (Figure 153).

Adaptations

Mesoptychia bantriensis (Figure 151-Figure 153) forms green to reddish-brown tufts and patches (Smith 1990). This coloration can be beneficial in locations where it is exposed to bright light and low temperatures at the same time by protecting it from photoinhibition.



Figure 153. *Mesoptychia bantriensis* showing mat formation. Photo by Barry Stewart, with permission.

Reproduction

Mesoptychia bantriensis is **dioicous** and lacks gemmae (Smith 1990). Perianths can be seen only occasionally and capsules are rare.

Mesoptychia collaris (Figure 154)

(syn. = *Leiocolea collaris*, *Lophozia muelleri*)

Distribution

Mesoptychia collaris (Figure 154) occurs in Europe, Asia, Africa, and North America (ITIS 2019).



Figure 154. *Mesoptychia collaris*, a Northern Hemisphere species that is hemicalciphilous in cold streams and seepage areas. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Mesoptychia collaris (Figure 154) was considered by Watson (1919) to occur on alpine and subalpine rocks by fast water. In western Canada it is submerged in montane streams where it is hemicalciphilous (Vitt *et al.* 1986; Glime & Vitt 1987). In Thuringia, Germany, it occurred in the *Platyhypnidium* (Figure 68)-*Fontinalis antipyretica* (Figure 69) association (Marstaller 1987). In the Tara river canyon and Durmitor area of Montenegro it occurred at a spring and river (Papp & Erzberger 2011). Konstantinova and Lapshina (2014) considered it to be calciphilous in seepage areas on schists on a steep rocky slope to the valley of a rivulet in the eastern subpolar Urals in Russia.

Adaptations

Mesoptychia collaris (Figure 154) forms green to brown patches (Smith 1990), suggesting the possibility of protection from high light intensities. It often grows through patches of other bryophytes, providing a greater opportunity to maintain moisture.

Reproduction

Mesoptychia collaris (Figure 154) is **dioicous** (Smith 1990). Perianths occur only occasionally and capsules are rare. Gemmae are absent.

Mesoptychia gillmanii (Figure 155)

(syn. = *Leiocolea gillmanii*)

Distribution

Mesoptychia gillmanii (Figure 155) is widespread around the northern hemisphere in boreal and montane regions, although it is considered vulnerable in Europe (Hodgetts *et al.*).

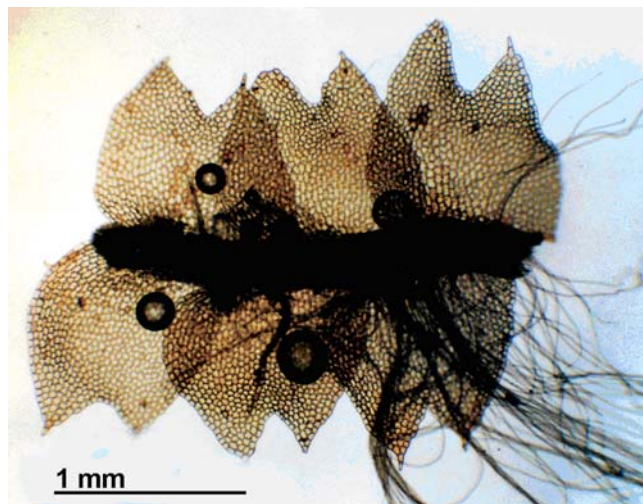


Figure 155. *Mesoptychia gillmanii*, a species from boreal and montane regions of the northern hemisphere. It is a calciphile in streams, on peaty soil, and on cliffs and ledges. Photo by David Wagner, with permission.

Aquatic and Wet Habitats

In Finland, *Mesoptychia gillmanii* (Figure 155) occurs in streams (Heino & Virtanen 2006). In North America, this species is found on peaty soil, typically on cliffs or ledges. Nevertheless, it is an obligate calciphile (Schuster 1969). The species often occurs at elevations where the

snow leaves late in the growing season, giving it a short growing season.

Adaptations

Mesoptychia gillmanii (Figure 155) lacks the coloration seen by many members of this family, instead displaying only green to yellowish-green coloration (Smith 1990). Like many members of the family, it grows among other bryophytes, a behavior that can help it to maintain moisture.

Reproduction

Mesoptychia gillmanii (Figure 155) is a perennial that, like most members of the genus, produces no gemmae. This means its dispersal must be primarily by spores or fragments (Wagner 2018). It is, however, **paroicous** (Smith 1990), increasing the potential for fertilization and spore production.

Mesoptychia turbinata (Figure 156-Figure 157)

(syn. = *Lophozia turbinata*)

Distribution

Mesoptychia turbinata (Figure 156-Figure 157) is apparently restricted to the Mediterranean area of Europe and North Africa (Schuster 1969).

Aquatic and Wet Habitats

Watson (1919) considered *Mesoptychia turbinata* (Figure 156-Figure 157) to be a species on stream banks that experience frequent submergence and to occasionally be submerged. Papp *et al.* (2018) reported it from limestone rock at a rivulet in Albania. This species is a calcicole and does best in a pH range of 4-8 with 3.0 mM Ca^{++} (Jefferies 1969). The K^{+} efflux appears to be unaffected by the Ca^{++} concentration in this species.

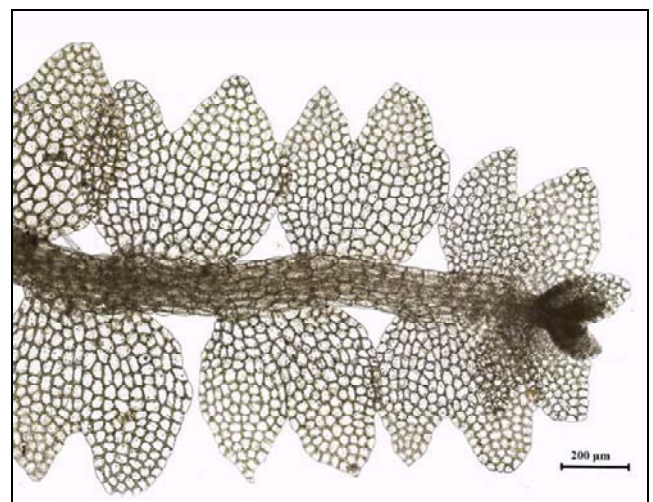


Figure 156. *Mesoptychia turbinata*. Photo by Hugues Tinguy, with permission.

Adaptations

Like the previous species, *Mesoptychia turbinata* (Figure 156-Figure 157) lacks the protective reds and browns that might protect it from exposure to bright light. Instead, its coloration ranges from pale green to yellowish-green (Figure 157). It most likely gains moisture retention

where it grows among other bryophytes, or through its rather dense mats (Figure 157).



Figure 157. *Mesoptychia turbinata* showing the extensive mats that are possible. Photo by Hugues Tinguy, with permission.

Reproduction

Mesoptychia turbinata (Figure 156-Figure 157) is **dioicous**, but nevertheless produces frequent perianths in the UK (Smith 1990). Capsules, however, are only occasional, appearing in winter or spring in the UK.

Notoscyphaceae

Notoscyphus lutescens (Figure 158)

(syn. = *Notoscyphus paroicus*)

Distribution

Notoscyphus lutescens (Figure 158) occurs in the Western Ghats (Udar & Kumar 1981; Singh *et al.* 2016) and in Hong Kong and mainland China, sometimes on wet soil (So & Zhu 1996). It extends into the southern hemisphere to New Zealand (Braggins *et al.* 2014), and is known from South Africa, Madagascar, India, China, Japan, Philippines, Indonesia, Papua New Guinea, north-eastern Australia (Queensland), as well as New Caledonia, Hawaii, Fiji, and Samoa (Schuster 2002). Not surprisingly, it has more recently been found in Australia.



Figure 158. *Notoscyphus lutescens*, an Eastern Hemisphere species, occurring where it is aquatic or wetland, including river banks and seeping cliffs. Photo by David Tng, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported *Notoscyphus lutescens* (Figure 158) as an aquatic or wetland species in the tropics. In Malawi, O'Shea *et al.* (2001) found it on river banks and on both dry and moist granitic and sandstone rocks, among other terrestrial habitats. Pócs and Streimann (2006) reported it from a riverside earth bank in Australia. Omar *et al.* (2016) documented it from a wetland in South Africa. It is also known from a seeping cliff at 900 m in the Nguru Mountains of Tanzania (Pócs & Vána 2015).

Reference to aquatic habitats are rare or non-existent among the reports on its localities. Nevertheless, this species is sold in some areas as an aquarium plant <<https://aquaticarts.com/>, Brownsburg, IN, USA>.

Adaptations

Members of *Notoscyphus* are typically yellowish-green, but can become red with age (Winterton *et al.* 2018).

Reproduction

Notoscyphus lutescens (Figure 158) is dispersed by spores and stem fragments (Winterton *et al.* 2018).

Biochemistry

Wang *et al.* (2014) reported ten new diterpenoids from this species. One of the compounds exhibited activity against human prostate cancer cells. So and Chan (2001) found a new cyclic bis (bibenzyl) derivative with activity against bacteria *Bacillus subtilis* (Figure 159) and two strains of *Staphylococcus aureus* (Figure 160). Zhu *et al.* (2006) found antibacterial activity against all five bacteria they tested, but were unable to find any oil body characters that were linked statistically to antibiotic activity. It is likely that some of these compounds are also inhibitory to environmental pathogens.

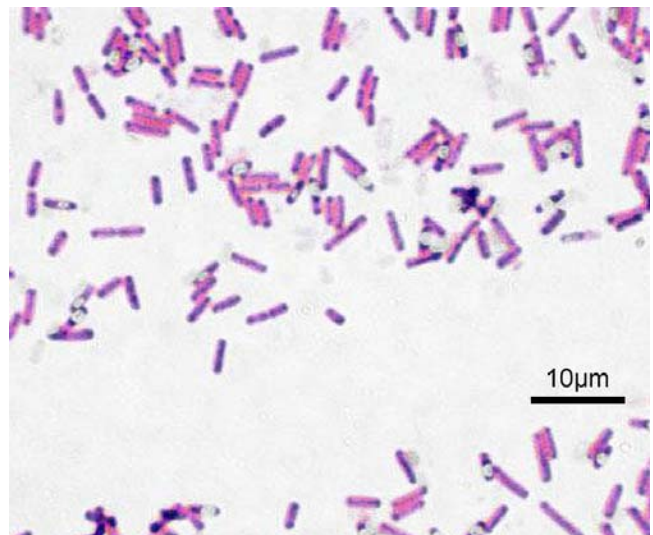


Figure 159. *Bacillus subtilis* with Gram stain, a species that is inhibited by extracts of *Notoscyphus lutescens*. Photo by Y. Tambe, through Creative Commons.

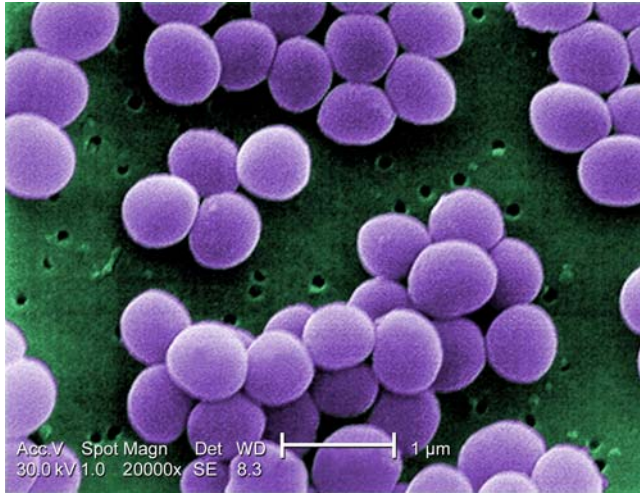


Figure 160. *Staphylococcus aureus*, a species that is inhibited by extracts of *Notoscyphus lutescens*. Photo by Janice Haney Carr, through public domain.



Figure 162. *Saccogyna viticulosa* with branches in a semi-upright position. Photo by Dick Haaksma, with permission.

Saccogynaceae

Saccogyna viticulosa (Figure 161-Figure 163)

Distribution

Saccogyna viticulosa (Figure 161-Figure 163) is listed for Europe, Africa, and Asia by ITIS (2020k). Mateo *et al.* (2013) treat it as a hyper-oceanic species along the Atlantic Ocean. Kürschner (2010) added it to southwest Asia, describing its previous known distribution as western Mediterranean and Atlantic region.



Figure 161. *Saccogyna viticulosa*, a species mostly along the eastern side of the Atlantic Ocean where it is wet for long periods or even submerged. Photo by Dick Haaksma, with permission.



Figure 163. *Saccogyna viticulosa* forming a mat. Photo by Dick Haaksma, with permission.

Aquatic and Wet Habitats

This species is one occurring with high humidity, sometimes being wet for long periods of time or even submerged. In northwestern Portugal, *Saccogyna viticulosa* (Figure 161-Figure 163) occurs in small crevices with humus and high humidity in the stream or waterfall margins that may be subjected to inconstant splashes or inundation. It is never extensive, always mixed with other bryophytes, often associated with *Pellia epiphylla* (Figure 164), *Fissidens polyphyllus* (Figure 103), *Hyocomium armoricum* (Figure 165-Figure 166), *Plagiothecium nemorale* (Figure 167), and *Riccardia multifida* (Figure 168) in wetter situations, with *Radula holtii* in dripping conditions, and in mountain streams (Vieira *et al.* 2004, 2005). In the Laurel forest of the Canary Islands, it occurs on periodically moistened, rather exposed volcanic rocks (Dirkse 1985). On Madeira Island, it occurs in low altitude, narrow streams and low flow in mountainous

streams (Luis *et al.* 2015). In the British Isles, it occurs in many small, rocky streams (Averis & Hodgetts 2013).



Figure 164. *Pellia epiphylla* showing an associated leafy liverwort. Photo by Jan-Peter Frahm, with permission.



Figure 165. *Hyocomium armoricum* habitat such as those where we might find *Saccogyna viticulosa* in association. Photo by Dick Haaksma, with permission.



Figure 166. *Hyocomium armoricum*, sometimes an associate of *Saccogyna viticulosa*. Photo by Michael Lüth, with permission.



Figure 167. *Plagiothecium nemorale*, sometimes an associate of *Saccogyna viticulosa*. Photo by Hermann Schachner, through Creative Commons.



Figure 168. *Riccardia multifida* showing its habitat with a leafy liverwort on the right. Photo by Rick Ballard, through Creative Commons.

In northwestern Portugal, *Saccogyna viticulosa* (Figure 161-Figure 163) was never extensive and always occurred in mixtures with other bryophytes – a behavior suggesting its need for constant moisture (Vieira *et al.* 2004). However, in experiments, *Saccogyna viticulosa* had survival down to 51% relative humidity with only a few cells surviving down to 33% relative humidity (Clausen 1964). It is likely that it would have even greater survival in nature where the drying time would be more extended, permitting the cells to prepare (*e.g.* Stark *et al.* 2013). At -10°C in ice, undeveloped apical cells died within 1-2 days. In other experiments, Proctor (2010) showed that *Saccogyna viticulosa* cells are easily damaged by bright light during initial rewetting. Dilks and Proctor (1974) found that despite the rapid damage and slow recovery of assimilation, this species has the capacity to survive long dry periods. At the beginning of rehydration, dark respiration typically shows a slight stimulation, followed by a longer-term buildup after a moderate or prolonged desiccation. Pressel *et al.* (2009) found that this species can withstand several weeks of natural drying. The estimated recovery time is 0.4 hours. The species typically occurs in shaded sites where they probably are never subject to intense desiccation. Of the species tested in this study, *Saccogyna viticulosa* (Figure 161-Figure 163) lives

in niches with the lowest irradiance and least severe desiccation, especially avoiding direct summer sun.

Reproduction

One reason for the scarcity of *Saccogyna viticulosa* (Figure 161-Figure 163) in some areas is its **dioicous** habit, limiting spore production (Watson & Dallwitz 2019). In northwestern Portugal, Vieira *et al.* (2004) never found the species fertile. This problem is compounded by the absence of gemmae, at least in the UK (Watson & Dallwitz 2019).

Fungal Interactions

Wang and Qiu (2006) reported fungal associations with this species. *Saccogyna viticulosa* (Figure 161-Figure 163) is known to host the fungus *Sebacina* (Figure 169) (Bidartondo & Duckett 2010). It produces numerous hyphae associated with the branched rhizoid apex. Döbbeler (2011) found that the **Ascomycete** fungus *Octospora fortuneata* occurs on terricolous populations of *Saccogyna viticulosa* on the Canary Islands. This fungus produces its spores in sacs that are hidden within the mats of liverworts. Ing (1983) found **Myxomycetes** to be frequently associated with *Saccogyna viticulosa* in wooded ravines in Highland Britain.



Figure 169. *Sebacina incrustans*, in a genus that is known from *Saccogyna viticulosa*, shown here on a moss. Photo through Creative Commons.

Biochemistry

Several biochemical studies have revealed the array of secondary compounds in *Saccogyna viticulosa* (Figure 161-Figure 163). Suleiman *et al.* (1980) demonstrated that even photosynthetic products in this species may differ from that in other families that have been considered closely related. Connolly *et al.* (1994) found two new sesquiterpenoids in *Saccogyna viticulosa*. Hackl *et al.* (2004) identified several new sesquiterpenes from populations on Madeira and unravelled some of the pathways involved in making the volatile essential oils in this species.

Solenostomataceae

Solenostoma (Figure 170-Figure 176, Figure 177-Figure 189, Figure 193-Figure 196)

Solenostoma (Figure 170-Figure 176, Figure 177-Figure 189, Figure 193-Figure 196) has **psychrorithral** (cold upper stream reaches) species in European alpine streams (Geissler 1975).

Solenostoma ariadne

(syn. = *Nardia ariadne*)

Solenostoma ariadne is known from India and China. Ruttner (1955) reported it as a wetland/aquatic species from the tropics.

Solenostoma gracillimum (Figure 170-Figure 172)

(syn. = *Jungermannia gracillima* fo. *crenulata*, *Solenostoma crenulatum*)

Distribution

Solenostoma gracillimum (Figure 170-Figure 172) is known from Europe, Asia, Africa, North America, and South America (ITIS 2020l).



Figure 170. *Solenostoma gracillimum*, a species known from both the Northern and Southern Hemispheres, living in streams, small lakes, and in other wet areas. Photo by Hugues Tinguy, with permission.



Figure 171. *Solenostoma gracillimum* showing its growth habit. Photo by David T. Holyoak, with permission.

Aquatic and Wet Habitats

Most of the wet habitat reports are relatively recent. Bley (1987) reported *Solenostoma gracillimum* (Figure 170-Figure 172) from upstream reaches in the Harz Mountains of Germany. Toivonen and Huttunen (1995) found it in small lakes in southern Finland. It occurs in mountain streams of northwest Portugal (Vieira *et al.* 2005) and in Madeira Island (Luis *et al.* 2015). Ferreira *et al.* (2008) listed it for European rivers. In North America its wet habitats include ditches and ravine walls (Breil 1970).

The plants become reddish (Figure 172) when exposed to the sun (Breil 1970).



Figure 172. *Solenostoma gracillimum* showing red coloration often seen with sun exposure. Photo by Barry Stewart, with permission.

Solenostoma gracillimum (Figure 170-Figure 172) is one of the species that can facultatively live in areas with metalliferous mine waste (Holyoak 2008). In Ireland, it was indicative of copper waste, but it does not require excess copper to colonize. This is a habitat where drying would appear to be frequent.

Solenostoma gracillimum (Figure 170-Figure 172) seems to have an unusual tolerance for zinc. In the Hautes-Pyrénées, this species was one of only three present where Zn had reached such high concentrations that it formed a white precipitate of **anglesite** (Figure 173), along with *Pohlia cruda* (Figure 174) and *Schizothrix* sp. (Figure 175) (Say & Whitton 1982). Similarly, Brown and House (1978) found it growing near a lead mine and on spoil from a copper mine in southwest England.



Figure 173. Anglesite, a rock type that can precipitate onto bryophytes. Photo by Parent G ry, through Creative Commons.



Figure 174. *Pohlia cruda*, a species that occurs with *Solenostoma gracillimum* in areas with high levels of zinc. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

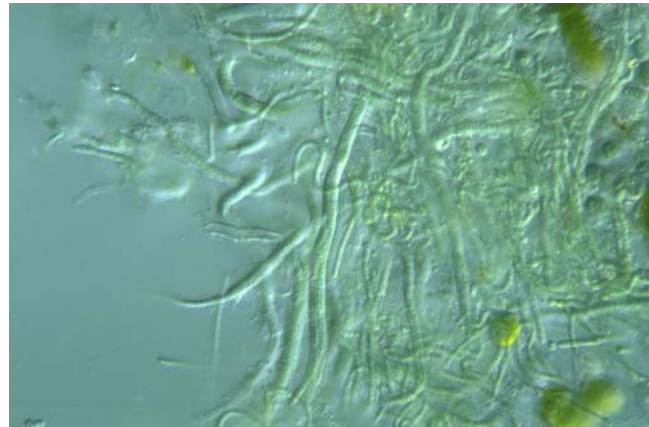


Figure 175. *Schizothrix* sp., member of a genus that occurs with *Solenostoma gracillimum* in areas with high levels of zinc. Photo by Yuuji Tsukii, with permission.

Reproduction

Solenostoma gracillimum (Figure 170-Figure 172) is **dioicous** (Figure 176) (Breil 1970), but has a widespread distribution that suggests that at least some spores have dispersed. It does not produce gemmae (Bakalin 2012).



Figure 176. *Solenostoma gracillimum* with numerous perianths. Photo by David T. Holyoak, with permission.

Fungal Interactions

Solenostoma gracillimum (Figure 170-Figure 172) is one of the hosts of the fungus *Mniaecia jungermanniae* (Figure 24-Figure 26) (Egertová *et al.* 2016). Pressel and Duckett (2006) found that it infected some liverwort species, but not others.

Solenostoma hyalinum (Figure 177-Figure 179)

(syn. = *Eucalyx hyalina*, *Jungermannia hyalina*)

Distributions

Solenostoma hyalinum (Figure 177-Figure 179) is widespread in Europe, south to northern Africa, but up to 1969 only one Asian country had a recorded species (Schuster 1969). It occurs in North America from Quebec, Canada, southward to North Carolina, USA, and westward through the Midwest to Mexico.



Figure 177. *Solenostoma hyalinum*, a Northern Hemisphere species that lives where it is constantly wet or submerged. Photo by Hermann Schachner, through Creative Commons.



Figure 178. *Solenostoma hyalinum*, a Northern Hemisphere species that lives where it is constantly wet or submerged. Photo by Hermann Schachner, through Creative Commons.

Solenostoma hyalinum (Figure 177-Figure 179) in North America occurs primarily at median and low elevations (Schuster 1969). Although it has rare occurrences in the taiga, it does not reach higher elevations in the southeastern states of the USA. It is able to form

extensive mats on river banks. Schuster has never observed it any considerable distance from streams. It seems to require at least some soil, not occurring on bare rocks.

Early in aquatic studies, Watson (1919) reported *Solenostoma hyalinum* (Figure 177-Figure 179) as a species that is occasionally submerged. But others have documented a wider and wetter range of habitats. Vieira *et al.* (2004, 2005), based on their studies in northwest Portugal, reported it from vertical faces of boulders subjected to splashes or constant drippings and in the margins of waterfalls, associated with *Scapania undulata* (Figure 60), *Hyocomium armoricum* (Figure 165-Figure 166), *Fissidens polyphyllus* (Figure 103), and *Platyhypnidium lusitanicum* (Figure 104), as well as in mountain streams. Ferreira *et al.* (2008) reported it from rivers. It occurs in mountain streams on Madeira Island (Luis *et al.* 2015). Duckett and Slack (2013) found it on vertical wet rocks in Tuckerman Ravine on Mt. Washington, New Hampshire, USA. Hong (1972) reports the species from several streams in Montana, USA. Weber (1976) considered it to be a river bank species in the Cataracts Provincial Park, Newfoundland, Canada. Likewise, Kitagawa (1978a) found it on river banks where it can form large, compact mats on rocks.

Reproduction

In northwest Portugal, *Solenostoma hyalinum* (Figure 177-Figure 179) has only been found sterile in pure or mixed well-developed patches (Vieira *et al.* 2004). Nevertheless, it can produce capsules (Figure 179) when both genders are present.



Figure 179. *Solenostoma hyalinum* with a capsule, indicating that some populations can successfully reproduce sexually. Photo by Michael Lüth, with permission.

Fungal Interactions

Solenostoma hyalinum (Figure 177-Figure 179) is one of the known hosts for the Ascomycete fungus *Mniaecia jungermanniae* (Figure 24-Figure 26) (Egertová *et al.* 2016). The exact relationship needs to be explored.

***Solenostoma inundatum* (Figure 180-Figure 181)**

(syn. = *Jungermannia inundata*)

Distribution

Solenostoma inundatum (Figure 180-Figure 181) occurs in Australia and New Zealand (Allison & Child 1975; ITIS 2121).



Figure 180. *Solenostoma inundatum*, a species from Australia and New Zealand. Photo owned by the University of Auckland, with online permission for educational use.



Figure 181. *Solenostoma inundatum*, a species that can be found in some mountain streams. Photo owned by the University of Auckland, with online permission for educational use.

Aquatic to Wet Habitats

Solenostoma inundatum (Figure 180-Figure 181) occurs on soil or rocks in wide-ranging habitats from mountain streams to dry pumice banks (Allison & Child 1975). Its name implies that it lives where it can at least some of the time become submersed. Scott (1985) described it as occurring on wet clay banks in wet sclerophyll forest where it is a common pioneer. It often occurs with other bryophytes, especially *Jackiella* and *Isotachis*.



Figure 182. *Jackiella javanica*, a liverwort that frequently serves as a substrate for *Solenostoma inundatum*. Photo from Taiwan Mosses Color Illustrations, through Creative Commons.



Figure 183. *Isotachis* sp., a liverwort that frequently serves as a substrate for *Solenostoma inundatum*. Photo by Phil Bendle, with permission through John Grehan.

Adaptations

When submersed, the plants of *Solenostoma inundatum* (Figure 180-Figure 181) are bright green, but when on exposed banks they are bright red (Allison & Child 1975). The red coloration is most likely induced by the bright light in exposed sites and can protect for UV damage, especially when dry.

Reproduction

The sexual status of *Solenostoma inundatum* (Figure 180-Figure 181) is unclear, with Scott (1985) listing it as

dioicous and Bakalin (2014) listing it as **dioicous** with a question mark. Smaller plants produce bright pink perianths (Figure 184) that can at times be quite numerous (Allison & Child 1975). The capsules mature (Figure 185) and dehisce with spiral cleavage (Figure 186).



Figure 184. *Solenostoma inundatum* with perianth. Photo owned by the University of Auckland, with online permission for educational use.



Figure 185. *Solenostoma inundatum* capsule. Photo owned by the University of Auckland, with online permission for educational use.



Figure 186. *Solenostoma inundatum* dehiscent capsule. Photo owned by the University of Auckland, with online permission for educational use.

Solenostoma javanicum

(syn. = *Aplozia javanica*)

Solenostoma javanicum occurs in Australia and southern Asia (ITIS 2020m). The only report of a wet habitat I could find was that of Ruttner (1955). He reported it from sulfur springs in the tropics.

Solenostoma obovatum (Figure 187)

(syn. = *Eucalyx obovata*, *Eucalyx obovata* fo. *elegatus*, *Eucalyx obovata* fo. *laxus*, *Eucalyx obovata* var. *rivularis*, *Jungermannia obovata*, *Nardia obovata*, *Plectocolea obovata*)

Distribution

Solenostoma obovatum (Figure 187) occurs sparingly in the Arctic, then southward in the mountains of Europe and North America (Schuster 1969).



Figure 187. *Solenostoma obovatum*, a species from the Arctic southward to the mountains of Europe and North America, occurring in rivers and streams and on their banks. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

An early report by Nichols (1918) attributed *Solenostoma obovatum* (Figure 187) to a rock ravine streambank, Cape Breton Island, Canada (Nichols 1918). Watson (1919) reported it from rocks or soil of fast streams, usually on submerged rocks, and on banks with frequent submergence and slow water. In the mountains of Westfalens, northwestern Germany, it occurs in shallow water (Koppe 1945). But others attribute it to more aquatic habitats. It occurs in alpine streams in the Swiss Alps (Geissler 1976). In Thuringia, Germany, it occurs in the *Platyhypnidium* (Figure 68)-*Fontinalis antipyretica* (Figure 69) association (Marstaller 1987). And it occurs in the Iskur River, Bulgaria, and its main tributaries (Papp *et al.* 2006). Light (1975) reported a species he questionably attributed to *Solenostoma cf. obovatum* from small lakes in Scottish mountains with ice cover 4-7 months per year and low ion concentrations.

Reproduction

Solenostoma obovatum (Figure 187) is **paricous** (Schuster 1969). It apparently lacks gemmae, as is typical for this family.

Solenostoma sphaerocarpum (Figure 188-Figure 189, Figure 193)

(syn. = *Aplozia sphaerocarpa*, *Haplozia sphaerocarpa*, *Jungermannia sphaerocarpa*)

Distribution

Solenostoma sphaerocarpum (Figure 188-Figure 189, Figure 193) occurs across Siberia and is known from Japan (Vána *et al.* 2013). ITIS (2020n) lists Europe, Asia, Africa, Oceania, Australia, North America from Alaska to Mexico, and South America.



Figure 188. *Solenostoma sphaerocarpum*, a worldwide species from streams and rivers and their banks. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Szweykowski (1951) reported *Solenostoma sphaerocarpum* (Figure 188-Figure 189, Figure 193) from moist stones and rocks in stream beds in the Gory Stolowe Mountains of Poland. Konstantinova and Vasiljev (1994) found it on rocks on a stream bank, mixed with *Blepharostoma trichophyllum* (Figure 190), *Mesoptychia heterocolpos* (Figure 191), *Tritomaria scitula*, and *Lophozopsis excisa* (Figure 192) in the Sayan Mountains of southern Siberia. Miller and Shushan (1964) reported it

from stream banks in Oregon, USA. Geissler (1976) found it in alpine streams in the Swiss Alps. It occurs in the upper and middle reaches of streams in the Harz Mountains of Germany (Bley 1987), and in the *Platyhypnidium* (Figure 68)-*Fontinalis antipyretica* (Figure 69) stream association in Thuringia, Germany (Marstaller 1987). Ferreira *et al.* (2008) considered it to be a species of rivers. Tremp and Kohler (1991) consider it to be a species of low-buffered water of streams.



Figure 189. *Solenostoma sphaerocarpum* showing its matted growth habit. Photo by Hugues Tinguy, with permission.



Figure 190. *Blepharostoma trichophyllum*, an associate of *Solenostoma sphaerocarpum* on stream banks. Photo by Jan-Peter Frahm, with permission.

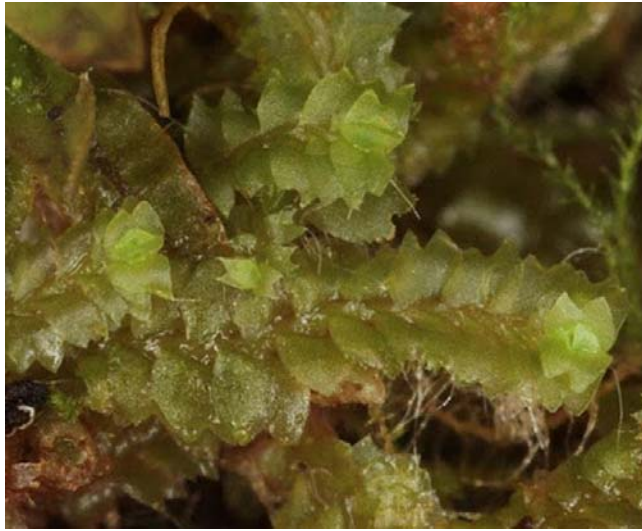


Figure 191. *Mesoptychia heterocolpos*, an associate of *Solenostoma sphaerocarpum* on stream banks. Photo by Jan-Peter Frahm, with permission.



Figure 192. *Lophozipsis excisa*, an associate of *Solenostoma sphaerocarpum* on stream banks. Photo by Štěpán Koval, with permission.

Adaptations

Solenostoma sphaerocarpum (Figure 188-Figure 189, Figure 193) is very **polymorphous** (expressing multiple forms). It becomes red-colored in exposed situations (Vána *et al.* 2013).

Reproduction

Solenostoma sphaerocarpum (Figure 188-Figure 189, Figure 193) is **heteroicous** (male & female organs on same plant; Figure 193), leading to its classification among several species, including *S. rossicum* in Russia and *S. pyriformum* subsp. *purpureum* in west Greenland. Newton

(1983) followed the spore germination and sporophyte development. She found up to six gametophytes could be produced by one protonema. It is interesting that in mature leaves the oil bodies were fewer, but larger, when compared with immature leaves and protonemata. It is one of the few liverworts to possess purple rhizoids.



Figure 193. *Solenostoma sphaerocarpum* with perigynia visible. Photo by Hugues Tinguy, with permission.

Solenostoma stephanii

(syn. = *Aplozia stephanii*)

Distribution

Solenostoma stephanii occurs in Australia, Oceania, and southern Asia (ITIS 2020).

Aquatic and Wet Habitats

Ruttner (1955) reported *Solenostoma stephanii* as submersed in the **littoral** (relating to or situated on shore of sea or lake, usually shallow) zone in the tropics.

Solenostoma tetragonum

(syn. = *Nardia tetragona*)

Distribution

Solenostoma tetragonum is known from Australia, Oceania, and southern Asia (ITIS 2020p). This includes southeast Asia, from Himalayas, India, and Sri Lanka to China, Japan, Micronesia, Samoa, New Guinea, and northern Australia (Li & Vána 2015).

Aquatic and Wet Habitats

The only wetland study that lists *Solenostoma tetragonum* is that of Ruttner (1955) for **tuff** (fine-grained volcanic rock) walls in the tropics. Gupta and Asthana (2016) list this species for soil and dry or wet racks at mid and upper altitudes.

Some people have found this liverwort to be desirable for aquaria (Elo500 2014), indicating its ability to be aquatic.

Solenostoma truncatum (Figure 194)

(syn. = *Nardia truncata*)

Distribution

Solenostoma truncatum (Figure 194) is widespread mostly in southeastern Asia and northern Australia (Li & Vána 2015). It is very variable in leaf shape, cell texture, and perianth characters (Li & Vána 2015), resulting in many synonyms (*e.g.* Vána & Long 2009; Li *et al.* 2017).



Figure 194. *Solenostoma truncatum*, a species mostly from southeastern Asia and northern Australia, occurring on wet rocks, moist soil, and sulfur springs, as well as some drier habitats. Photo from Hong Kong Flora, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported *Solenostoma truncatum* (Figure 194) as a species of sulfur springs in the tropics. Li and Vána (2015) considered it to be the commonest species of *Solenostoma* in southeast Asia. In the Ghats of India it grows on moist soil in shady habitats, either in pure patches or with other bryophytes, expressing the variety *kodaikanalensis* (Alam *et al.* 2012).

The species occurs on soil, wet rocks, and soil-covered rocks at middle and upper altitudes in the Pachmarhi Biosphere Reserve, India (Gupta & Asthana 2016).

Solenostoma vulcanicola (Figure 195-Figure 196)

(syn. = *Jungermannia vulcanicola*, *Nardia vulcanica*)

Distribution

Solenostoma vulcanicola (Figure 195-Figure 196) has a relatively small distribution in Indonesia, Japan, and India (Singh & Singh 2015).



Figure 195. *Solenostoma vulcanicola* removed from clump to show individual plants. This species has a limited distribution in Asia and is restricted to sulfur springs. Photo courtesy of Angela Ares.



Figure 196. *Solenostoma vulcanicola* showing dense clumps from an acid spring in Japan. Photo by Juuyoh Tanaka, through Creative Commons.

Aquatic and Wet Habitats

In 1955, Ruttner listed *Solenostoma vulcanicola* (Figure 195-Figure 196) as one from sulfur springs in the tropics. Satake and coworkers have published multiple papers on its tolerance of the chemistry of Japanese springs and spring-fed streams (Satake 1983). It is able to live and thrive in a pH range of 3.6 to 4.6, disappearing at 5.5 (Satake *et al.* 1989). In fact, it has not been recorded at a pH above 4.6, but it is known from Kusatsu hot spring (Japan) at pH 1.9! At such low pH levels, iron oxide accumulates on the shoots and is difficult to remove. Potassium in the shoots reached as much as 5%.

Bacteria can occur in the cell wall of *Solenostoma vulcanicola* (Figure 195) in acid (pH 4.2-4.6) stream water (Satake & Miyasaka 1984b), suggesting a possible role in decomposition.

Satake (1983) explored the accumulation of various elements in stream waters and in their bryophytes. Satake *et al.* (1989) demonstrated that few species were able to tolerate a variety of heavy metals in their water environment. *Solenostoma vulcanicola* (Figure 195-Figure 196), growing in a pH range of 4.0-4.6, were covered with a precipitate of $\text{Fe}(\text{OH})_2$ that accounted for 5-13% of its dry weight. Its K accumulation was up to 5%.

Shiikawa (1956, 1959, 1960, 1962) found that the liverwort *Solenostoma vulcanicola* (Figure 195-Figure 196) plays an active role in deposition of iron ore. Since Japan has few native sources of usable iron, Ijiri and Minato (1965; Wickens 2001) suggested producing limonite ore artificially by cultivating this liverwort and other bryophytes in fields near iron-rich springs.

Satake and Miyasaka (Satake & Miyasaka 1984a; Satake *et al.* 1990) reported the accumulation of mercury in *Solenostoma vulcanicola* (Figure 195-Figure 196) from a stream (Figure 1) at pH 4.2-4.6. Satake *et al.* (1983; 1984) found the highest mercury content ($12,100 \text{ Hg g}^{-1}$) in basal segments (1.3%, Satake 1985) of *Solenostoma vulcanicola* from an acidic stream in Japan (Figure 1). Satake and coworkers demonstrated that mercury is accumulated from stream water primarily in the cell walls of this species (Satake *et al.* 1983, 1988, 1990; Satake & Miyasaka 1984a; Satake 1985), and not in the **plasmalemma** (cell membrane) or chloroplasts (Satake & Miyasaka 1984a).

The mercury forms electron-dense particles as a mercury-sulfur compound, probably mercuric sulfide, which is not toxic to living organisms.

In addition to mercury, *Solenostoma vulcanicola* (Figure 195) from rivers, streams, lakes, and springs accumulates scandium (Satake & Nishikawa 1990). Among the 18 bryophytes analyzed, only this species and *Scapania undulata* showed a substantial accumulation.

Adaptations

Solenostoma vulcanicola (Figure 195) can become brownish black to black (Figure 197), but not red or purple (Bakalin 2014). Their stems are mostly erect, permitting them to form tight cushions (Figure 196-Figure 197). The rhizoids are sparse.

Reproduction

Solenostoma vulcanicola (Figure 195) is **dioicous** (Bakalin 2014). Despite the difficulty of its sexual reproduction, it can form huge cushiony mats in the right conditions (Figure 1, Figure 197).



Figure 197. *Solenostoma vulcanicola* habitat showing extensive cushions. Photo courtesy of Angela Ares.

Summary

The **Jungermanniaceae** are represented by 11 families in wet and aquatic environments. Some of these, such as *Jungermannia exsertifolia*, *Marsupella aquatica*, *M. sphacelata*, *Nardia compressa*, and *Solenostoma vulcanicola* can be classified as truly aquatic, only occasionally being out of water, although they may occur on emergent rocks where they are constantly saturated. The others in this subchapter occur in wet habitats, but are not restricted to aquatic habitats.

The **Jungermanniaceae** typically grow in mats, but several grow among or on *Sphagnum*. Some are known to host fungi. They often have terpenoids that may serve as antibacterial and antiherbivore agents. Their protective coloration seems to go more to brown than red, but some species do form red pigments.

Acknowledgments

Lars Söderström helped me find the current acceptable names for a number of older taxa. Thank you to Ken Adams, Andi Cairns, David Long, Martha Nungesser, and Chris Preston for helping me to define burn.

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CHAPTER 1-5

AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: LOPHOCOLEINEAE, PART 1

TABLE OF CONTENTS

Suborder Lophocoleineae	1-5-2
Blepharostomaceae	1-5-2
<i>Blepharostoma trichophyllum</i>	1-5-2
Herbertaceae	1-5-8
<i>Herbertus sendtneri</i>	1-5-8
Lepidoziaceae	1-5-9
<i>Bazzania denudata</i>	1-5-9
<i>Bazzania praerupta</i>	1-5-10
<i>Bazzania tricrenata</i>	1-5-10
<i>Bazzania trilobata</i>	1-5-12
<i>Hygrolembidium boschianum</i>	1-5-16
<i>Kurzia makinoana</i>	1-5-16
<i>Kurzia pauciflora</i>	1-5-19
<i>Kurzia trichoclados</i>	1-5-21
<i>Lepidozia reptans</i>	1-5-22
<i>Lepidozia trichodes</i>	1-5-24
<i>Zoopsis argentea</i>	1-5-24
Lophocoleaceae	1-5-25
<i>Chiloscyphus</i>	1-5-25
<i>Chiloscyphus pallescens</i>	1-5-25
<i>Chiloscyphus pallescens</i> var. <i>fragilis</i>	1-5-28
<i>Chiloscyphus polyanthos</i>	1-5-28
<i>Chiloscyphus polyanthos</i> var. <i>rivularis</i>	1-5-30
<i>Hepatostolonophora paucistipula</i>	1-5-31
<i>Heteroscyphus argutus</i>	1-5-32
<i>Heteroscyphus coalitus</i>	1-5-33
<i>Heteroscyphus denticulatus</i>	1-5-36
<i>Heteroscyphus planiusculus</i>	1-5-36
<i>Heteroscyphus zollingri</i>	1-5-37
<i>Lophocolea</i>	1-5-37
<i>Lophocolea bidentata</i>	1-5-37
<i>Lophocolea heterophylla</i>	1-5-39
<i>Lophocolea minor</i>	1-5-42
<i>Lophocolea mollis</i>	1-5-45
<i>Lophocolea semiteres</i>	1-5-45
<i>Pachyglossa</i>	1-5-48
<i>Pachyglossa austrigena</i> subsp. <i>okaritana</i>	1-5-48
<i>Pachyglossa dissitifolia</i>	1-5-48
<i>Pachyglossa tenacifolia</i>	1-5-49
Mastigophoraceae	1-5-50
<i>Mastigophora diclados</i>	1-5-50
Summary	1-5-51
Acknowledgments	1-5-51
Literature Cited	1-5-52

CHAPTER 1-5

AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: LOPHOCOLEINEAE, PART 1



Figure 1. *Chiloscyphus polyanthos* habitat. Photo by Michael Lüth, with permission.

Suborder Lophocoleineae

Blepharostomaceae

Blepharostoma trichophyllum (Figure 2-Figure 3)

Distribution

Blepharostoma trichophyllum (Figure 2-Figure 3) has a widespread Holarctic distribution, but has also been reported from high tropical mountains in both the Eastern and Western Hemispheres (Gradstein *et al.* 1977).



Figure 2. *Blepharostoma trichophyllum* individual plant showing finely divided leaves. Photo by Hermann Schachner, through Creative Commons.



Figure 3. *Blepharostoma trichophyllum* forming mats that are typical of its growth habit. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Blepharostoma trichophyllum (Figure 2-Figure 3) has a broad range of habitats. Watson (1919) reported it from ground, rocks, and stumps associated with fast water. Mamczarz (1970) found it in the ground community associated with streams near Lacko, Western Carpathians. Similarly, Rastorfer *et al.* (1973) found it to be hydro-mesic at Prudhoe Bay, Alaska.

Gradstein *et al.* (1977) reported *Blepharostoma trichophyllum* (Figure 3) from the boggy páramo (Figure 4), associated with species of *Sphagnum* (Figure 5). On Svalbard, it similarly occupied the moss-*Sphagnum* tundra (Figure 5), where it was mixed with *Schistochilopsis opacifolia*, *Fuscocephaloziopsis pleniceps* (Figure 6), *Cephalozia bicuspidata* (Figure 7), and *Cephaloziella varians* on the side of a hillock (Konstantinova & Savchenko 2008). In the Italian Alps, it occurs in peat bogs and on logs (Figure 8) (Privitera *et al.* (2010). In the Pyrenees, Hugonnot (2014) found it colonizing the compacted and decaying *Sphagnum*, along with *Lioclaena lanceolata* (Figure 9).



Figure 4. Marshes at Páramo de Océta, the type of site where one might find *Blepharostoma trichophyllum*. Photo by Álvaro Siabatto and José Próspero Hurtado Caro, through Creative Commons.



Figure 5. *Sphagnum* in tundra, a habitat suitable for *Blepharostoma trichophyllum*. Photo from NPS, through public domain.



Figure 6. *Fuscocephaloziopsis pleniceps*, a species that often grows mixed with *Blepharostoma trichophyllum* in the tundra. Photo from NTNU Museum of Natural History and Archaeology, through Creative Commons.



Figure 7. *Cephalozia bicuspidata*, a species that often grows mixed with *Blepharostoma trichophyllum* in the tundra. Photo by Michael Lüth, with permission.



Figure 8. *Blepharostoma trichophyllum* in a typical habitat on a log. Photo by Hermann Schachner, through Creative Commons.



Figure 9. *Liochlaena lanceolata*, a liverwort that associates with *Blepharostoma trichophyllum* in the Pyrenees. Photo by Hugues Tinguy with permission.

Hong (1977) found *Blepharostoma trichophyllum* (Figure 3) on wet soil, rocks, and decayed wood in Wyoming, USA, but Söderström (1989), working in Sweden, never found it in the earliest decay stages (stages 1-3), occurring in later stages with *Calypogeia suecica* (Figure 10), *Fuscocephaloziopsis leucantha* (Figure 11), and *Neoorthocaulis attenuatus* (Figure 12). Glime (1982) reported it from the humid wall of the Flume at Franconia Notch in New Hampshire, USA.



Figure 10. *Calypogeia suecica*, a liverwort that occurs with *Blepharostoma trichophyllum* on late-decay-stage logs in Sweden. Photo by Michael Lüth, with permission.



Figure 11. *Fuscocephaloziopsis leucantha*, a liverwort that occurs with *Blepharostoma trichophyllum* on late-decay-stage logs in Sweden. Photo by David T. Holyoak, with permission.



Figure 12. *Neoorthocaulis attenuatus*, a liverwort that occurs with *Blepharostoma trichophyllum* on late-decay-stage logs in Sweden. Photo from Earth.com, with permission.

In the Republic of Buryatia, Russia, Konstantinova *et al.* (2018) found *Blepharostoma trichophyllum* (Figure 3) on soil-covered rocks, on soil between rocks, on banks of rivers, on trails under roots sticking out and on mossy logs (Figure 8) in mixed forests, in pure mats or mixed with other bryophytes. In the moist alpine tundra of the Canadian Yukon, Hong and Vitt (1977) found it was frequently associated with *Mesoptychia heterocolpos* (Figure 13), *Schljakovia kunzeana* (Figure 14), and *Scapania irrigua* (Figure 15). In the Sette-Daban Range of eastern Yakutia, Sofronova and Sofronov (2010) found it with mixed with *Radula complanata* (Figure 16) on stream banks. Dulin (2008) found it on stream and river banks, as well as on rotting logs, in the Komi Republic of Russia.



Figure 13. *Mesoptychia heterocolpos*, a species that often accompanies *Blepharostoma trichophyllum* in the moist alpine tundra. Photo by Blanka Aguero, with permission.

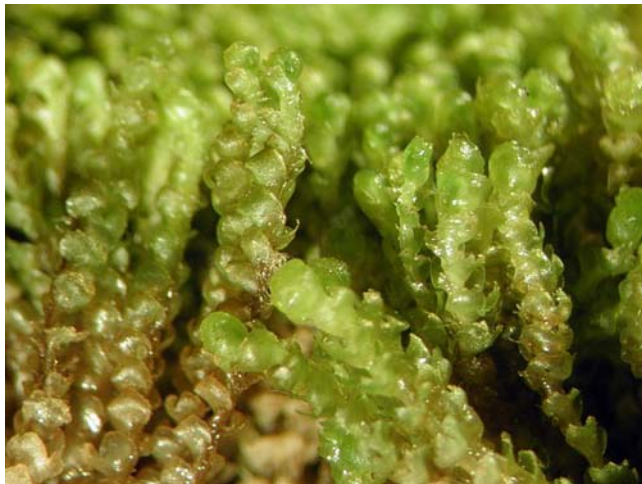


Figure 14. *Schljakovia kunzeana*, a species that often accompanies *Blepharostoma trichophyllum* in the moist alpine tundra. Photo by Michael Lüth, with permission.



Figure 15. *Scapania irrigua*, a species that often accompanies *Blepharostoma trichophyllum* in the moist alpine tundra. Photo by David T. Holyoak, with permission.

But it was also a submerged hemicalciphilous liverwort in montane streams and on streambanks in western Canada (Vitt *et al.* 1986; Glime & Vitt 1987). In the wetter habitats, and when submersed, it often occurs

with other leafy liverworts. Sofronova (2013) likewise found it in water, on the soil of a shallow, temporary brook in southeastern Yakutia, where it occurred with the leafy liverworts *Scapania crassiretis* (Figure 17) and *Plagiochila porelloides* (Figure 18). Lepage (1953) found it on a moist bank of the Roggan River in Québec, Canada, where it was accompanied by *Fossombronina pusilla* (Figure 19), *Scapania mucronata* (Figure 20), and *Fuscocephaloziopsis pleniceps* (Figure 6). In the Sayan Mountains of southern Siberia, Konstantinova and Vasiljev (1994) found it on rocks at the stream bank, typically associated with *Mesoptychia heterocolpos* (Figure 13), *Lophoziopsis excisa* (Figure 21), *Schistochilopsis opacifolia*, *Solenostoma confertissimum* (Figure 22), *Solenostoma sphaerocarpum* (Figure 23), *Tritomaria scitula* (Figure 24), and *Marchantia polymorpha* subsp. *montivagans* (Figure 25); on a brook bank it was mixed with *Fuscocephaloziopsis pleniceps*, *Mesoptychia heterocolpos* (Figure 13), *Lophozia ventricosa* (Figure 26), *Schljakovianthus quadrilobus* (Figure 27), *Scapania cf. irrigua* (Figure 15), and *Solenostoma confertissimum* (Figure 22).



Figure 16. *Radula complanata* with capsules, a species that occurs with *Blepharostoma trichophyllum* on stream banks in the Sette-Daban Range of eastern Yakutia. Photo by Hermann Schachner, through Creative Commons.



Figure 17. *Scapania crassiretis*, a species that occurs with *Blepharostoma trichophyllum* in temporary brooks in southeastern Yakutia. Photo from Earth.com, with permission.



Figure 18. *Plagiochila porelloides*, a species that occurs in temporary brooks in southeastern Yakutia with *Blepharostoma trichophyllum*. Photo by Štěpán Koval, with permission.



Figure 21. *Lophozipsis excisa*, a species that occurs with *Blepharostoma trichophyllum* on stream bank rocks in Siberia. Photo from Earth.com, with permission.



Figure 19. *Fossombronia pusilla*, a species that occurs with *Blepharostoma trichophyllum* on moist river banks. Photo by Clive Shirley, Hidden Forest <hiddenforest.co.nz>, with permission.

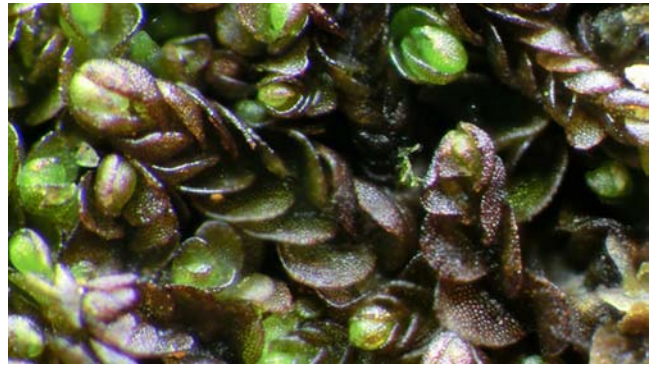


Figure 22. *Solenostoma confertissima*, a species that occurs with *Blepharostoma trichophyllum* on stream bank rocks in Siberia. Photo by Michael Lüth, with permission.



Figure 20. *Scapania mucronata*, a species that occurs with *Blepharostoma trichophyllum* on moist river banks. Photo by Tomas Hallingbäck, with permission.



Figure 23. *Solenostoma sphaerocarpum*, a species that occurs with *Blepharostoma trichophyllum* on stream banks in Siberia. Photo by Hugues Tinguy, with permission.



Figure 24. *Tritomaria scitula* with gemmae, scattered in this mix with *Blepharostoma trichophyllum* and other bryophytes on stream bank rocks in Siberia. Photo from Earth.com, with permission.



Figure 25. *Marchantia polymorpha* subsp. *montivagans*, a species that occurs with *Blepharostoma trichophyllum* and other bryophytes on stream bank rocks in Siberia. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 26. *Lophozia ventricosa*, a species that occurs with *Blepharostoma trichophyllum* on a brook bank in Siberia. Photo by Hermann Schachner, through Creative Commons.



Figure 27. *Schljakovianthus quadrilobus*, a species that occurs with *Blepharostoma trichophyllum* on a brook bank in Siberia. Photo by Štěpán Koval, with permission.

Reproduction

Unlike most aquatic species, where development of early stages is unknown, the sporelings, gemmalings, and regeneration of *Blepharostoma trichophyllum* (Figure 3) were described early by Fulford (1955). Arzeni (1948) described the perianth (Figure 28-Figure 29) and rare gemmae from populations in Reese's, Bog, Michigan, USA.

Biochemistry

Blepharostol, a sesquiterpenoid alcohol, as well as other terpenoids, has been described from this species (Feld *et al.* 2004).



Figure 28. *Blepharostoma trichophyllum* with perianths (brownish) and capsules (nearly black). Photo by Hermann Schachner, through Creative Commons.



Figure 29. *Blepharostoma trichophyllum* showing sporophytes. Photo by Michael Lüth, with permission.

Herbertaceae

Herbertus sendtneri (Figure 30)

(syn. = *Herbertus armitanus*, *Herbertus circinatus*, *Herbertus dicranus*)

Not surprisingly, Feldberg *et al.* (2004) found cryptic species among the *Herbertus sendtneri* (Figure 30) populations. Differences are described as morphological "tendencies," suggesting that the similarity in morphology has developed independently. Furthermore, the differences in leaf shapes between Austrian and Macaronesian populations or Neotropical populations may reflect differences in suboptimal climate in the Austrian Alps where *H. sendtneri* grows in shaded rock crevices of large boulder slopes, compared to other populations such as those in Macaronesia.

Distribution

Herbertus sendtneri (Figure 30) is widespread, especially in the Northern Hemisphere, where it is known from Arctic and alpine areas. *Herbertus dicranus* was originally considered to be unique to the tropics, but later Heinrichs *et al.* (2009) determined it to be conspecific with European and Asian populations of *H. sendtneri*. Like many species, it exhibits **polyphyly** (derived from more than one common evolutionary ancestor or group), but molecular studies allied the tropical populations with the European and Asian populations (Heinrichs *et al.* 2009). Discovery of *H. armitanus* and *H. circinatus* as synonyms has extended the distribution to east Africa (Tanzania) and Malesia (Papua New Guinea and the Solomon Islands).

Aquatic and Wet Habitats

In Alaska on Attu Island, *Herbertus sendtneri* (Figure 30) is uncommon, occurring on damp banks of the tundra, on the wall of a humus hole of a periodic streamlet, on the bank of a gully in the subalpine, on a shaded wall of a gully, and associated with a snow bed (Talbot *et al.* 2018).

One surprising occurrence of *Herbertus sendtneri* (Figure 30) was in a glacial lake (4120 m) in the Andes of Colombia (Gradstein *et al.* 2018). These were previously identified as *H. oblongifolius* due to their dwarf stature and obtuse leaf tips, known as rare from Brazil. This rare taxon was subsequently placed in synonymy with *H. sendtneri*, a widespread taxon. This lake population may

have originated from a rock-inhabiting population that dispersed into the lake through caducous branches or other fragments that washed into the lake. Gradstein and coworkers estimated that such an event occurred in the last 12,000-21,000 years when the lake was ice-free. Such a submersed population is rare for liverworts in the tropics and is unlikely to occur at lower elevations because of the higher temperatures and paucity of dissolved CO₂.



Figure 30. *Herbertus sendtneri*, a widespread Arctic-alpine species known mostly from the Northern Hemisphere. Photo from Earth.com, with permission.

Adaptations

Mägdefrau (1982) described *Herbertus sendtneri* as having a **tall turf** life form (Figure 31).

Reproduction

Herbertus sendtneri (Figure 30) is **dioicous**, and as of 2004, males were still unknown (Feldberg *et al.* 2004). Sporophytes are rare (He & Sun 2017), but He and Sun (2017) found them from a herbarium specimen collected in Austria. The spores are papillose, typical of the Northern Hemisphere, whereas those from the Southern Hemisphere are tuberculate or shortly spinose.

Fungal Interactions

It serves as host for the fungal endophyte *Paenibacillus herberti*, a taxon from Ga Walloon Glacier (Bomi County, Tibet, China) that thus far appears to be unique to this *Herbertus* species (Guo *et al.* 2015). Subsequently, Guo *et al.* (2016) isolated another member of the genus, *Paenibacillus marchantiophytorum*, from this same species of *Herbertus* at Gawalong glacier, Tibet.



Figure 31. *Herbertus sendtneri* showing its **tall turf** life form. Photo by Michael Lüth, with permission.

Biochemistry

Sun *et al.* (2010) used extracts from five bryophyte species, including *Herbertus sendtneri* (Figure 30-Figure 31), to determine effects on seed germination and seedling physiology of the cucumber. They found that all of these extracts promoted growth of the radicle at some concentrations and that *Herbertus sendtneri* extracts could enhance chlorophyll content. It could also enhance the content of soluble sugar.

Lepidoziaceae

Bazzania denudata (Figure 36-Figure 32)

Distribution

Bazzania denudata (Figure 36-Figure 32) is distributed in North America from Alaska, southward to Oregon, Montana, and Kentucky, USA (Clark & Frye 1942). It also occurs in Greenland and Central Europe (Schuster 1969).



Figure 32. *Bazzania denudata*, an epiphyte, but also occurring on moist sandstone canyon walls. Photo from Botany Website, UBC, with permission.

Aquatic and Wet Habitats

Bazzania denudata (Figure 36-Figure 32) is predominantly an epiphyte (*e.g.* Cain 1935; Kitagawa 1978; Hong 1988; Peck *et al.* 1995), especially at tree bases (Schuster 1969). These tend to be in relatively moist forests, and Bakalan (2016) notes that it avoids dry substrata. But it can also occur in wet or very humid places. Fulford (1934) found this species on moist, shaded sandstone in Kentucky, USA. Schuster and Patterson (1957) reported it from a damp recess in a cliff in Virginia, USA, where it occurred with *Metzgeria leptoneura* var. *breviseta* (Figure 33) and *Radula tenax* (Figure 34). McKnight (1985) found it to be occasional on a moist, shaded sandstone wall in Indiana, USA (a westward extension) with *Bryoxiphium norvegicum* (Figure 35). Glime (1982) found it on the wall of the Flume at Franconia Notch, New Hampshire, USA. Bakalin (2016) considers it an acidophilic mesophyte.



Figure 33. *Metzgeria leptoneura*, a species occurring with *Bazzania denudata* in damp recesses of a cliff. Photo by Blanka Agüero, with permission.



Figure 34. *Radula tenax*, a species occurring with *Bazzania denudata* in damp recesses of a cliff. Photo from Earth.com, with permission.



Figure 35. *Bryoxiphium norvegicum* on a sandstone wall, a habitat where it can occur with *Bazzania denudata*. Photo by Bob Klips, with permission.

Adaptations

The leaves of *Bazzania denudata* are deep green to brownish green or yellowish green (Bakalan 2016) – color variations that are most likely environmentally induced. It lacks rhizoids, forming loose patches. This means it would most likely be unable to establish under water, but it can live well in moist habitats.

Reproduction

Bazzania denudata is dioicous, limiting opportunities for sexual reproduction. The leaves in this species are easily deciduous (Figure 36) (Bakalan 2016), presumably serving as propagules, albeit with somewhat limited dispersal.



Figure 36. *Bazzania denudata*, a species mostly distributed in northern parts of the Northern Hemisphere. Photo from Botany Website, UBC, with permission.

Biochemistry

Bazzania denudata has homogenous oil bodies (Bakalan 2016). The secondary compounds contained in these seem to have received little study.

oil bodies homogenous

Bazzania praerupta (Figure 37)

(syn. *Bazzania longa*, *Bazzania lehmanniana*)

Distribution

Bazzania praerupta (Figure 37) is a species of the Palaeotropics (Gradstein 2017). Aryanti and Gradstein (2007) considered its distribution to be Asiatic, but there are reports from some areas of Africa (e.g. Müller 1996). The known distribution has been complicated by the discovery of synonyms. Gradstein (2017) reduced *Bazzania longa* (from Australia only) and *B. lehmanniana* to synonymy with *B. praerupta*, extending the known distribution of *B. praerupta* to Australia.

Aquatic and Wet Habitats

In the Ailao Mountains, SW China, it forms smooth mats on forest trees (Song *et al.* 2011). Like the previous species, this is primarily an epiphyte, as seen on tree branches in Java (Meijer 1960). It seems to prefer bamboo forests in Ethiopia, often occurring on the stems (Hylander 2014). Nevertheless, it can behave like a wet habitat species, as seen by growth in the thermal acidic spray in the tropics (Ruttner 1955).



Figure 37. *Bazzania praerupta*, a Palaeotropical species that can live in acidic thermal spray zones. Photo through Creative Commons.

Reproduction

Bazzania praerupta is dioicous, a characteristic of the genus (Bakalan 2016). Little seems to have been published about its reproduction and dispersal.

Biochemistry

Because of its limited distribution, this species has received little biochemical attention. Kondo *et al.* (1990) confirmed the presence of three previously known sesquiterpenoids. Kudwiczuk and Asakawa (2010) noted that drimenol and albicanol help characterize the species. Drimanones are characteristic, but limonene, anastreptene, trinoranastreptene, ent- α -selinene, and spahulenol are also present.

Bazzania tricrenata (Figure 38)

Distribution

Bazzania tricrenata (Figure 38) is a circumboreal species, extending southward in the mountains (Schuster 1969) to Taiwan, Japan, and the Korean Peninsula (Bakalan 2016). In North America it extends from the Aleutians and Alaska south to California and east to Ellesmere, southward to Tennessee (Bakalan 2016).



Figure 38. *Bazzania tricrenata*, an epiphytic and saxicolous species that can occur on wet cliffs in alpine areas. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

This is not an aquatic species, but it does seem to at least tolerate wet habitats. Nichols (1918) reported it from rock cliffs associated with streams on Cape Breton Island, Canada. Glime (1982) found it on the humid wall of the Flume at Franconia Notch, New Hampshire, USA. Konstantinova *et al.* (2002) found it on a wet cliff on a south-facing slope of the alpine zone of the Bureya River in the Russian Far East, where it was associated with *Anastrophyllum assimile* (Figure 39), *Mylia taylorii* (Figure 40), and *Scapania microdonta* (Figure 41). Bakalan (2016) considered it to be an acido- and basio-tolerant mesophyte, preferring mesic cliff crevices and open (but not full sun) rocks, rarely occurring in shady sites.



Figure 39. *Anastrophyllum assimile*, a species associated with *Bazzania tricrenata* on a wet cliff in the Russian Far East. Photo by Norbert Schnyder, with permission.



Figure 40. *Mylia taylorii*, a species associated with *Bazzania tricrenata* on a wet cliff in the Russian Far East. Photo by Hugues Tinguy, with permission.

Other habitats are not so moist. Ji *et al.* (2001) reported it as epiphyllous in the Matoushan Nature Reserve of Jiangxi Province, China. Schuster (1969) summarized its habitat as occurring almost uniformly on soil-covered

damp to moist rock, especially on shaded, acidic ledges and usually avoiding calcareous areas.



Figure 41. *Scapania microdonta*, a species associated with *Bazzania tricrenata* on a wet cliff in the Russian Far East. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.

Knowing its typical habitats on rocks, desiccation tolerance of *Bazzania tricrenata* is not surprising. In samples from the Faroe Islands, about half the cells remained alive down to 33% relative humidity, but none at 15% (Clausen 1964).

Adaptations

Bazzania tricrenata is yellowish brownish to greenish brown, colors that would seem to enable it to occur in bright light (Bakalan 2016), a trait not consistent with its preference for shaded sites. It forms loose patches and typically lacks rhizoids.

Reproduction

Bazzania tricrenata does not have caducous leaves (Bakalan 2016). The species, like the rest of the genus, is **dioicous**. Its capsules are relative uncommon and are unknown in some regions. Spores are small. This raises the question of its ability to spread. The flagelliform branches that are produced ventrally can help it survive during unfavorable times through protection by the over-arching branches. These flagelliform branches can help it to enlarge its clone, but do they play a role in dispersal and colonization?

Fungal Interactions

Wang and Qiu (2006) found no reports of mycorrhizal fungi associated with this species.

Biochemistry

Bazzania tricrenata has smooth oil bodies (Bakalan 2016). Like other species of liverworts, this one has terpenoids, which could account for its lack of fungi – a relationship that needs to be explored. Sangaiah and Rao (1982) reported the synthesis of a phenolic sesquiterpene from this species. Suleiman *et al.* (1980) determined that the photosynthetic products in this species are volemitol and sedoheptulose in addition to sucrose and fructans.

Bazzania trilobata* (Figure 42)*Distribution**

Bazzania trilobata (Figure 42) is circumboreal, including Western Europe, eastern and western coastal North America, and Japan (Buckowska *et al.* 2010). In Poland, distribution coincides with two parts of the natural distribution range of Norway spruce.



Figure 42. *Bazzania trilobata*, a species common in *Thuja* swamp and poor fen forests. Photo by Allen Norcross, with permission.

Aquatic an Wet Habitats

This is not an aquatic species, but it does like moist or humid places. I know it from *Thuja* swamps and a hemlock forest adjoining a poor fen. It occurs on ledges in the Flume at Franconia Notch, New Hampshire, USA (Glime 1982). In Germany it is reported from upstream reaches of the Harz Mountains (Bley 1987). And in the Great Smoky Mountains, USA, Cain (1935) found it on wet rocks; in Ohio, USA. Hall (1958) found it on moist sandstone and occasionally on adjacent mossy soil. In the Czech Republic it occurs in water-logged spruce stands where it dominates, often along with *Sphagnum girgensohnii* (Figure 43) (Neuhäuslová & Eltsova 2002).



Figure 43. *Sphagnum girgensohnii*, a species occurs in water-logged spruce stands with *Bazzania trilobata*. Photo by Hermann Schachner, through Creative Commons.



Figure 44. *Bazzania trilobata* showing a common growth form. Photo by Michael Lüth, with permission.



Figure 45. *Bazzania trilobata* at Hocking Hills, Ohio, USA, in a moist canyon. Photo by Janice Glime.

Jackson (2015) assessed the potential effects of the hemlock woolly adelgid on the hemlock forest and subsequent effects on *Bazzania trilobata* (Figure 44-Figure 47). She concluded that increases in light intensity and temperatures can cause damage to this species, causing its cover to diminish. On the other hand, we know that *B. trilobata* can survive freezing, perhaps benefitting from insulation by snow (Figure 46).



Figure 46. *Bazzania trilobata* in snow, demonstrating its ability to survive freezing temperatures. Photo by Allen Norcross, with permission.



Figure 47. *Bazzania trilobata* stolons. Photo by Janice Glime.

In the primarily red spruce, yellow birch, or spruce-dominated forests, this liverwort can serve as home for the endemic Cheat Mountain Salamander (*Plethodon nettingi*) (West Virginia, USA) (Figure 48) (Dillard *et al.* 2008; Pauley 2008). *Bazzania trilobata* forms **tall turfs** (Figure 44) or **wefts**, depending on the habitat characteristics (Uniyal *et al.* 2007), providing ample space for the salamanders to move about.



Figure 48. *Bazzania trilobata* with *Plethodon nettingi*. Photo by Michael Graziano, with permission.

Paratley and Fahey (1986) found that one type of swamp in New York, USA, could be termed the *Bazzania trilobata* swamp. It is characterized by a low water table and "favorable" flow. In these swamps, bryophyte richness was high when there was a base-rich inflow and extensive microrelief. Bakalan (2016) considered the species to be an acidophilic to neutro-tolerant mesophyte. It rarely occurs in limestone areas, and when it does, it occurs on thick litter that provides an acidic substrate.

Cleavitt *et al.* (2007) examined the effect of water availability on the seasonal growth of *Bazzania trilobata* (Figure 44-Figure 47) on boulders of an eastern hemlock (*Tsuga canadensis*) stand at Hubbard Brook in New Hampshire, USA. There, it is able to form pure colonies on the boulders. They found that an increase in water availability did not cause a straightforward growth increase. Rather, it appeared to have a short-term initial effect, causing biomass gain with a moderating effect on

elongation. Biomass gain of the stems appeared to be limited by the cost of respiration, but further research is needed to confirm this. Branching was stimulated over stem elongation in less dense stems where light intensity was greater.

Adaptations

Bazzania trilobata (Figure 44-Figure 47) is a large species that can grow prostrate to erect (Bakalan 2016). It forms somewhat loose patches or **tall turfs** (Figure 44) and **wefts** (Uniyal *et al.* 2007). Its color is typically deep green and shiny, but it can become yellowish green or brownish green. It lacks rhizoids.

Reproduction

Like other members of *Bazzania*, *B. trilobata* (Figure 44-Figure 47) is **dioicous**.

Stolons (flagelliform branches) are a common form of asexual reproduction among liverworts in bogs and fens (Duckett *et al.* 1991). These are abundant in *Bazzania trilobata* (Figure 44-Figure 47) and may contribute to their success as a propagule below the surface where moisture remains much longer, and as a way of accomplishing rapid spread once they become established in a new location.



Figure 49. *Bazzania trilobata* stolons, a means of perenniation and asexual reproduction. Photo by Dick Haaksma, with permission.

Fungal Interactions

Fungi are often common on bryophytes, especially in humid habitats. Raudabaugh *et al.* (2011) assessed water stress factors for both the epiphytic and endophytic fungi, including those of *Bazzania trilobata* (Figure 44-Figure 47). Eleven of the twelve endophytic fungi had only limited biomass production at the weakest water matric potential (*ca.* 0 MPa).

Duckett *et al.* (1991) characterized ascomycetous fungi from a number of leafy liverworts. They found that most of the relationships were formed in the **Lepidoziineae** (including *Bazzania trilobata*) and **Cephaloziineae**. Many members of these families have flagelliform axes (stolons) that extend deep into the peat. These frequently bear rhizoids that are infected with fungi. But if these are grown in sand or water, the fungal infection does not develop. Each rhizoid or cluster of rhizoids must be infected

independently – there is no internal connection between them.

Oil Bodies and Biochemistry

Oil bodies have been of taxonomic importance, but bryologists have wondered about their function for the liverworts. Pihakaski (1972) explored these structures in *Bazzania trilobata* (Figure 50). They found that whereas proteins are present in the chloroplast stroma, they are not present in the globules (oil bodies) embedded in the stroma. Instead, the globules are comprised of unsaturated neutral lipids. In *B. trilobata* it appears that the globules are surrounded by a single membrane, differing in that regard from the oil bodies of *Pellia epiphylla* (Figure 51). Huneck *et al.* (1984) examined seasonal dependence on essential oil in *Bazzania trilobata* and described the stereochemistry of (-)-5-hydroxycalamenene.



Figure 50. *Bazzania trilobata* leaf cells showing oil bodies. Photo by Walter Obermayer, with permission.

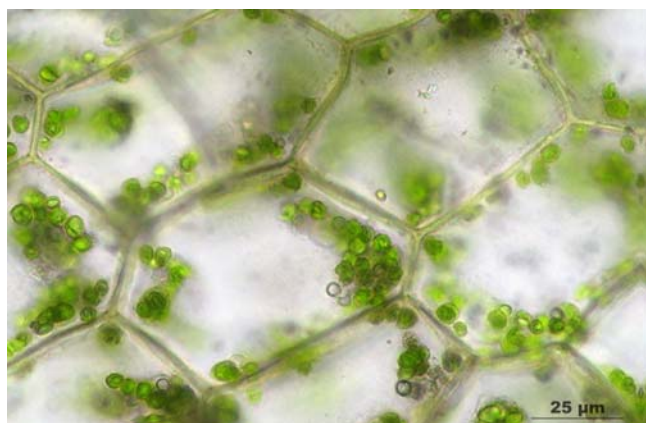


Figure 51. *Pellia epiphylla* thallus cells showing smaller oil bodies. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

There have been a number of biochemical studies on this species. Nagashima *et al.* (1996) identified a new myltaylane-type sesquiterpene alcohol and nine known sesquiterpenoids from *Bazzania trilobata* (Figure 44-Figure 47). Martini *et al.* (1998a) isolated 10 bisbibenzyl derivatives and two biphenyl linkages from *Bazzania*

trilobata. Warmers and König (1999) added two more sesquiterpenes. Scher *et al.* (2004a) isolated antifungal compounds from *Bazzania trilobata* and determined them to be effective against *Botrytis cinerea* (Figure 52), *Cladosporium cucumerinum* (Figure 53-Figure 54), *Phytophthora infestans* (Figure 55-Figure 56), *Pyricularia oryzae* (Figure 57-Figure 58), and *Zymoseptoria tritici* (Figure 59). They were able to isolate six antifungal sesquiterpenes and three bisbibenzyls. Scher *et al.* (2004b) isolated Bazzanin S as a new chlorinated bisbibenzyl from *B. trilobata*. Konečný *et al.* (1985) obtained a series of sesquiterpenoids from Czech populations and determined a number of these were identical to those found in the same species from Japan. They added additional secondary compounds to the known list and presented the seasonal variation in essential oils. They also detailed the wax components in this liverwort.



Figure 52. *Botrytis cinerea*, a fungus inhibited by sesquiterpenoids from *Bazzania trilobata*, on strawberry. Photo by Rasbak, through Creative Commons.



Figure 53. *Cladosporium cucumerinum* on leaf, a fungus that is inhibited by antifungal compounds from *Bazzania trilobata*. Photo by T. A. Zitter, with online permission from <DiscoverLife.org>.

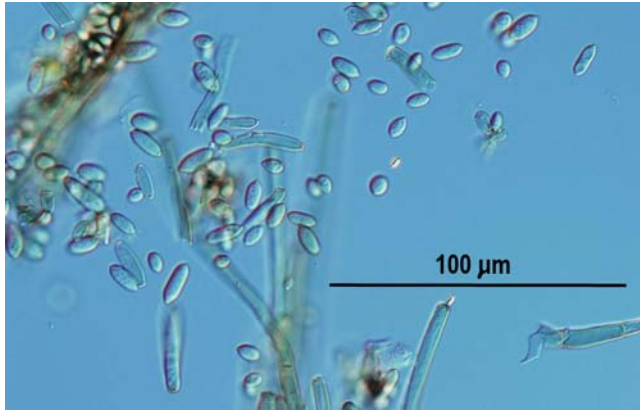


Figure 54. *Cladosporium cucumerinum*, a fungus that is inhibited by extracts from *Bazzania trilobata*. Photo by Bruce Watt, through Creative Commons.



Figure 55. *Phytophthora infestans*, a species of fungus that is inhibited by secondary compounds from *Bazzania trilobata*, on leaf. Photo by Howard F. Schwartz, through Creative Commons.

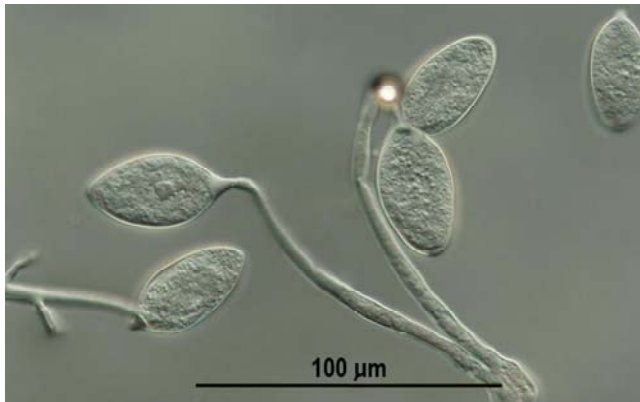


Figure 56. *Phytophthora infestans*, a species of fungus that is inhibited by secondary compounds from *Bazzania trilobata*. Photo by Bruce Watt, through Creative Commons.

Secondary compounds such as these often serve to protect the bryophytes from pathogens and herbivory. Tadesse *et al.* (2003) tested extracts from 17 different bryophyte species against mycelial growth of *Botrytis cinerea* (Figure 52) and *Alternaria solani* (Figure 60-Figure 61), including extracts from *Bazzania trilobata* (Figure 44-Figure 47). Extracts from this liverwort inhibited the mycelial growth of both fungi by more than 50%. Extracts from *B. trilobata* and *Diplophyllum albicans* (Figure 62) were more effective than those of the

other bryophytes tested. Fungal disease control was ineffective after 4 hours, but showed some antifungal activity after 2 days. Nevertheless, the liverwort extracts were less effective than the fungicide dichlofluanide.



Figure 57. *Pyricularia oryzae*, a species of fungus that is inhibited by secondary compounds from *Bazzania trilobata*. Photo by Donald Groth, Louisiana State University AgCenter, Bugwood.org, through Creative Commons.



Figure 58. *Pyricularia oryzae*, a species of fungus that is inhibited by secondary compounds from *Bazzania trilobata*. Photo by Donald Groth, through public domain.



Figure 59. *Zymoseptoria tritici*, a species of fungus that is inhibited by secondary compounds from *Bazzania trilobata*. Photo by Mary Burrows, Montana State University, Bugwood.org, through Creative Commons.



Figure 60. *Alternaria solani* leaf lesions, a species of fungus that is inhibited up to 50% by secondary compounds from *Bazzania trilobata*. Photo from Clemson University – USDA Cooperative Extension Slide Series, through Creative Commons.



Figure 61. *Alternaria solani* conidia; this species is inhibited up to 50% by extracts from *Bazzania trilobata*. Photo by E. McKenzie, Landcare Research, Australia, through Creative Commons.



Figure 62. *Diplophyllum albicans*, a species that is one of the best inhibitors of *Alternaria solani* and *Botrytis cinerea* among the bryophytes tested. Photo by David T. Holyoak, with permission.

Biochemistry

But in addition to the secondary compounds that seem to be useful in protecting the plants from pathogens and herbivory, the liverworts can also possess **lignan** (phytoestrogens; class of polyphenolic compounds including many found in plants and noted for having antioxidant and estrogenic activity) derivatives (Martini *et al.* 1998b; Scher *et al.* 2003).

Hygrolembidium boschianum

(syn. = *Lembidium boschianum*)

Distribution

Hygrolembidium boschianum occurs in the Southern Hemisphere, including southern South America, Australia, and nearby islands (EOL 2021).

Aquatic and Wet Habitats

Hygrolembidium boschianum occurs in sulfur springs in the tropics (Ruttner 1955). Gradstein (2011) verified this habitat with his report of the species submerged in sulfur springs in Indonesia. There seems to be little known about it ecologically.

Kurzia makinoana (Figure 63)

Distribution

Kurzia makinoana (Figure 63) is distributed in Europe, Asia, and western North America (ITIS 2020). Piippo (1990) considered it to be widely distributed in East Asia, with records from Guanxi and Zhejiang in China and from Taiwan, and from Japan (BLM 1996). In North America, the species is widely distributed from Alaska to California (Bakalin 2018).



Figure 63. *Kurzia makinoana*, a widely distributed Northern Hemisphere species, living in a wide range of wet and damp habitats. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Kurzia makinoana (Figure 64) prefers the banks of streams and other watercourses (Bakalin 2018). In North America it occurs in acidic to moderately neutral mesophytic sites as a hygrophyte. It prefers partly to strongly shaded places and can be found on moderately moist peaty banks of streams in more northern sites and on

sandy-loamy banks of ditches in more southern sites and occasionally on acid rock. In its northern locales, it occurs in open swampy areas near the sea coast, whereas in the south it is more frequent in woody evergreen swamps. But it also grows over acidic rocks, *Sphagnum* (Figure 5), and other bryophytes at higher elevations in the Appalachian Mountains. At lower elevations it is confined to peaty and sandy banks of streams. In the Rogue River of the Siskiyou National Forest, Oregon and California, USA, it is associated with *Sphagnum* (Emerson & Loring 2010).



Figure 64. *Kurzia makinoana* forming a loose mat/turf. Photo from Earth.com, with permission.

In Korea, Choi *et al.* (2013) found *Kurzia makinoana* (Figure 63-Figure 64) on cliffs along streams in a broad-leaved forest in the range of 580-1446 m asl. On Bering Island, northwest Russia, it occurs on the peaty banks of ponds formed by freezing and thawing of ground material overlying permafrost (**cryogenic processes**), and in peat moss-shrub mires, occurring with *Diplophyllum taxifolium* (Figure 65), *Fuscocephaloziopsis albescens* (Figure 66), *Gymnocolea inflata* (Figure 67), and *Odontoschisma elongatum* (Figure 68) (Bakalin 2005). On Sakhalin Island in the West Pacific, *Kurzia makinoana* (Figure 63-Figure 64) occurs among mosses on raised oligotrophic dwarf shrub-peat moss mires (Bakalin *et al.* 2005). In Tottori Prefecture, Japan, Bakalin *et al.* (2013) found it on the wet clay of road crust and on tree trunks in the partial shade of broad-leaved or coniferous forests, often on rotten logs. It can be in pure mats or with *Bazzania tridens* (Figure 69), *Blepharostoma minor*, and *Plagiochila ovalifolia* (Figure 70). In Mts. Hakkōda in northern Japan, Kitagawa (1978) found that it was rather common on soil from montane to alpine zones. It occurs in those regions on rotten logs, soil, and rocks, being abundant on the soil along sulfur-rich streams where it is associated with *Diplophyllum albicans* (Figure 62), *Scapania parvixtexta*, *Calypogeia arguta* (Figure 71), and *C. fissa* (Figure 72).



Figure 65. *Diplophyllum taxifolium*, a species that occurs with *Kurzia makinoana* in peat moss-shrub mires of northwest Russia. Photo by Hermann Schachner, through Creative Commons.

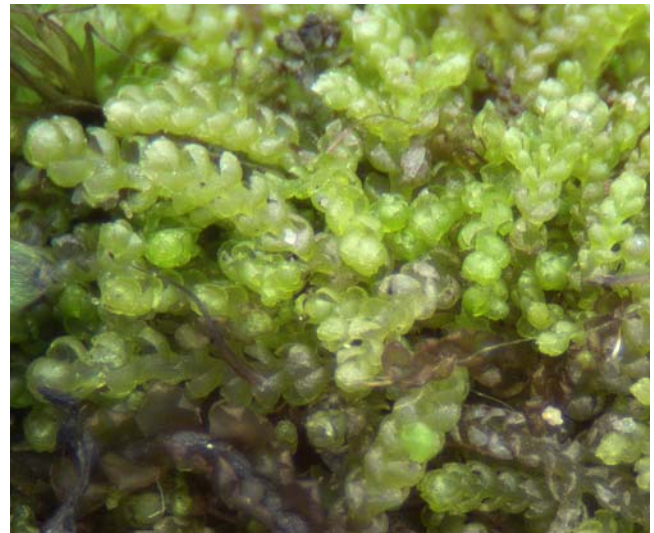


Figure 66. *Fuscocephaloziopsis albescens*, a species that occurs with *Kurzia makinoana* in peat moss-shrub mires of northwest Russia. Photo by Tomas Hallingbäck, with permission.



Figure 67. *Gymnocolea inflata*, a species that occurs with *Kurzia makinoana* in peat moss-shrub mires of northwest Russia. Photo by Michael Lüth, with permission.



Figure 68. *Odontoschisma elongatum*, a species that occurs with *Kurzia makinoana* in peat moss-shrub mires of northwest Russia. Photo by Andrew Hodgson, with permission.



Figure 69. *Bazzania tridens*, a species that occurs with *Kurzia makinoana* in Tottori Prefecture, Japan. Photo from Taiwan Color Illustrations, through Creative Commons.



Figure 70. *Plagiochila ovalifolia*, a species that occurs with *Kurzia makinoana* in Tottori Prefecture, Japan. Photo from Earth.com, with permission.



Figure 71. *Calypogeia arguta*, a species that occurs on the soil along sulfur-rich streams on Mts. Hakkôda, Japan. Photo by George G., through Creative Commons.



Figure 72. *Calypogeia fissa*, a species that occurs on the soil along sulfur-rich streams on Mts. Hakkôda, Japan. Photo by Hermann Schachner, through Creative Commons.

At higher altitudes in Japan, the plants of *Kurzia makinoana* (Figure 63-Figure 64) become atypical, approaching the appearance of the European *K. trichoclados* (Figure 73).



Figure 73. *Kurzia trichoclados*, a species similar to *Kurzia makinoana*. Photo by David T. Holyoak, with permission.

Adaptations

Kurzia makinoana (Figure 63-Figure 64) is a tiny leafy liverwort, dull or deep green to brownish-green (BLM 1996). It occurs in dense tufts or patches with interwoven stems and occasionally creeps among the stems of other bryophytes. Such growth patterns can help it to maintain moisture.

Reproduction

Kurzia makinoana (Figure 63-Figure 64) is **dioicous** (BLM 1996).

Biochemistry

The tiny *Kurzia makinoana* (Figure 63-Figure 64) is aromatic (BLM 1996). It produces the monoterpene limonene as well as a number of sesquiterpenoids (Toyota *et al.* 1997). The chemical constituents differ from those of other *Lepidoziaceae* (Asakawa 1982). Among these compounds in *Kurzia makinoana* several (sesquiterpene lactones) (Asakawa *et al.* 2013) are known for their cytotoxic activity against P-388 lymphocytic leukemia cells (Asakawa 1995).

Kurzia pauciflora (Figure 74)

(syn. = *Jungermannia pauciflora*, *Jungermannia quadridigitata*, *Kurzia setacea*, *Lepidozia setacea*, *Microlepidozia setacea*)

Distribution

Schuster (1958) predicted that *Kurzia pauciflora* (Figure 74) would prove to be transcontinental. Based on a variety of studies, we now know that it occurs in North and South America, Europe, Asia, and Africa (ITIS 2020). It is circumboreal and extends throughout temperate Europe, being common in central Europe (Reinoso & Rodríguez-Oubiña 1988).



Figure 74. *Kurzia pauciflora*, a circumboreal species in the Northern Hemisphere, extending into the European temperate zone. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) included *Kurzia pauciflora* (Figure 74) as an aquatic species that occurs on banks that are frequently submerged and in slow water with poor mineral salts. This latter habitat is consistent with the low-nutrient bog sites where it has been reported frequently.

Bakalin (2018) describes *Kurzia pauciflora* (Figure 74) as a species occurring as single shoots between *Sphagnum* (Figure 5) and *Leucobryum* (Figure 75) in mires. It is sometimes accompanied by *Mylia anomala* (Figure 76), *Odontoschisma fluitans* (Figure 77), *Cephalozia spinigera* (Figure 78), and other liverworts. Hong (1988) contrasts this with his experience in western North America, where it usually grows in pure patches in peat bogs. Less commonly, it occurs on the bare peat of heaths, wetlands, and on wet cliffs and stones in association with *Bazzania denudata* (Figure 36-Figure 32) or *Herbertus aduncus* (Figure 79). Bakalin finds that it is confined to *Sphagnum* carpets in bogs (Figure 5) with pH below 3.8. Schuster (1958) noted its occurrence in a bog near Burt Lake in Michigan, USA. Karofeld and Toom (1999) found it on decaying *Sphagnum* in Mannikjarve bog in central Estonia. Ingerpuu *et al.* (2014) considered the species to be common in bogs in Estonia. Weber (1976) found it in the Cataracts Provincial Park, Newfoundland, Canada, where it occurred in open boggy areas (pH 3-4) in areas where *Sphagnum* spp. predominated. Miller (1960) likewise noted its intimate association with *Sphagnum* in the Laurentian Mountains of Canada. Weber and Brassard (1976) considered to be typical in ombrotrophic bogs in Newfoundland. Van Geel (1978) reported it from peat bog fossils in Germany and the Netherlands – the only liverwort representative that partially fossilized there.



Figure 75. *Leucobryum glaucum*; *Leucobryum* is sometimes a habitat for *Kurzia pauciflora* in mires. Photo by Amadej Trnkoczy, through Creative Commons.



Figure 76. *Mylia anomala*, a species that often grows with *Kurzia pauciflora*. Photo by Blanka Aguero, with permission.



Figure 77. *Odontoschisma fluitans*, a species that often grows with *Kurzia pauciflora*. Photo by David T. Holyoak, with permission.

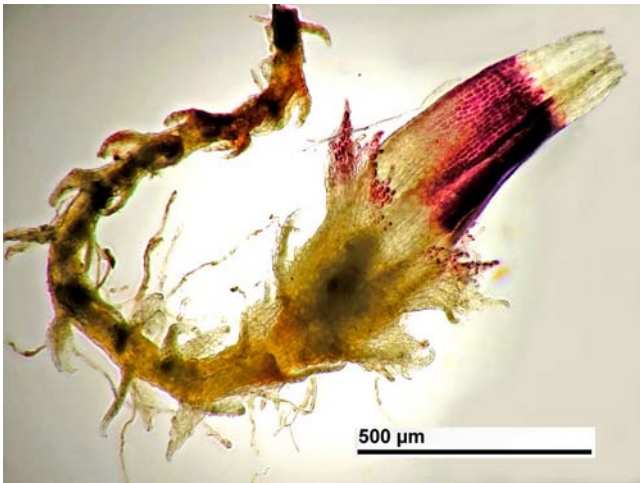


Figure 78. *Cephaloziella spinigera* female shoot, a species that often grows with *Kurzia pauciflora*. Photo by David Wagner, with permission.



Figure 79. *Herbertus aduncus*, a species that often grows with *Kurzia pauciflora* on bare peat of heaths, wetlands, and on wet cliffs and stones. Photo by Botany Website, UBC, with permission.

In the Atlantic blanket bogs in the maritime regions of North-western Europe, water table and *pH* were major determinants of the bryophyte flora, whereas ammonia was important in determining the tracheophyte flora

(Sottocornola *et al.* 2009). *Kurzia pauciflora* (Figure 74), along with *Mylia anomala* (Figure 76) were the most common species in the sampling, with *K. pauciflora* along with species of *Cephalozia* (Figure 80) exhibiting optimal conditions at a lower *pH* than that of other bryophytes.



Figure 80. *Cephalozia bicuspidata*; some species of *Cephalozia* share habitats at optimal conditions of low *pH* with *Kurzia pauciflora*. Photo by Hugues Tinguy, with permission.

On the other hand, van Baaren *et al.* (1988) found it to be characteristic of mesotrophic fens in the Netherlands, typically as a dominant species.

But Redfearn (19622) also found it in association with the moss *Tetraphis pellucida* (Figure 81) on moist, shaded, vertical dolomite of east-facing bluffs in Douglas County, Missouri, USA.



Figure 81. *Tetraphis pellucida*, a moss species associated with *Kurzia pauciflora* on moist, shaded, vertical dolomite bluffs. Photo by Hermann Schachner, through Creative Commons.

Albinsson (1997) determined that *Kurzia pauciflora* (Figure 74) belongs to a group of liverworts with a relatively wide ecological amplitude. One secret to its success in habitats with other bryophytes might be its extensive system of underground axes (Hugonnot *et al.* 2015). These exhibit profuse branching and can reach a maximum depth of 10 cm. They permit the colonization of successive layers of substrate, contributing to the success of the species. They do best on dead rather than live *Sphagnum* (Figure 5) and therefore benefit from disturbance.

Van Diggelen *et al.* (2015) report *Kurzia pauciflora* (Figure 74) as a red-listed species that often achieves as high a cover value as *Sphagnum* (Figure 5) species in restoration sites for acidified and eutrophied fens, most likely due to its regeneration from dead peat layers.

Reproduction

Kurzia pauciflora is **dioicous** (Earth.com 2021), but it seems to have other mechanisms for regeneration and asexual reproduction. Duckett and Clymo (1988) found that *Kurzia pauciflora* (Figure 74) and other species with well-developed underground axes regenerate poorly at the surface, but that their regeneration is much more successful down to 12 cm or so below the surface; they can still be found at 24-30 cm depth. Their presence in these lower layers occurs in both bogs with a live *Sphagnum*-covered surface (Figure 5) and from a much older cut peat surface recently recolonized by liverworts. These results support the contention that regeneration is mainly from the underground axes rather than from spores or gemmae. The underground biomass of these species is typically large.

Interactions

All the axes of *Kurzia pauciflora* (Figure 74) have fungal associates, and it is possible that the fungi are partially saprophytic or parasitic (Duckett & Clymo 1988). Liepiņa (2012) reported that fungal infection causes swollen rhizoids in this species.

Wang and Qiu (2006) noted reports of mycorrhizal relationships with *Kurzia pauciflora* (Figure 74). But earlier, Duckett *et al.* (1991) considered that the rhizoid-Ascomycete associations and flagelliform branches seen in *Kurzia pauciflora* represent secondary parasitic infections rather than a mutualistic relationship. They further argued that the nitrogen fixation observed in these liverworts was due to **Cyanobacteria** (Figure 82) on the surface of the plants.



Figure 82. *Microcoleus* (Cyanobacteria), a nitrogen-fixing periphyton organism such as those you might find on *Kurzia pauciflora*. Photo by Yuuji Tsukii, with permission.

Kowalczyk *et al.* (1997) used *Kurzia pauciflora* (Figure 74), among nine others, to demonstrate sterilization techniques. Using commercial bleach (Ace) diluted with distilled water at 1:1 and 1:3 ratios of bleach to water. The optimal sterilization time was 0.5-2.0 minutes. They determined that the fragments to be sterilized should not be larger than 3x3 mm, taken from the terminal portions of the thallus or leafless shoots of the leafy gametophytes. Greater success is achieved with healthy plants that are turgid.

Pressel *et al.* (2008) found that when *Kurzia pauciflora* (Figure 74) is infected with the Ascomycete fungus *Rhizoscyphus ericae* (Figure 83), the fungus forms a mutualistic association with the rhizoids. This fungus induces branching and septation in the rhizoids in this and a variety of liverworts. This fungus is also associated with members of the **Ericaceae** (heath family), permitting both host groups to provide inoculum for the other (Duckett & Read 1995).

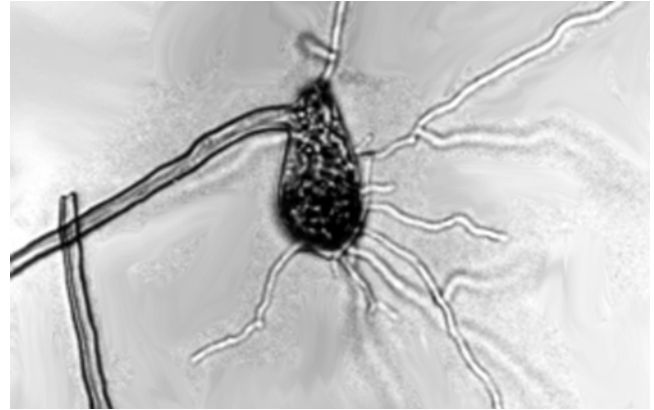


Figure 83. *Kurzia pauciflora* swollen rhizoid tips with fungal hyphae. Photo modified from Duckett & Read 1995.

In a study of 43 bryophyte species, 21 mosses lacked arbuscular mycorrhizal fungi and these were present in only 4 of 21 liverworts, all epigeous species (Liepiņa 2012). Liepiņa considered these fungi to be symbiotic.

Kurzia trichoclados (Figure 85)

(syn. = *Lepidozia trichoclados*)

Distribution

Kurzia trichoclados (Figure 85) is known from Europe, North America, and Southeast Asia, with a recent report from India (Rawat *et al.* 2016). Unfortunately, as is often the case, many collections have been misidentified as *K. pauciflora* (Figure 74) in Belgium (Stieperaere & Schumacker 1986). Despite this rather widespread distribution, the species is red-listed as vulnerable for the Iberian Peninsula (Sergio *et al.* 2007) and as endangered in Poland (Klama & Górski 2018). Nevertheless, Gradstein and Váňa (1987) remind us that this is a very small liverwort that is easily overlooked.



Figure 84. *Kurzia trichoclados* forming mats such as those one might find in heaths and bogs. Photo by David T. Holyoak, with permission.

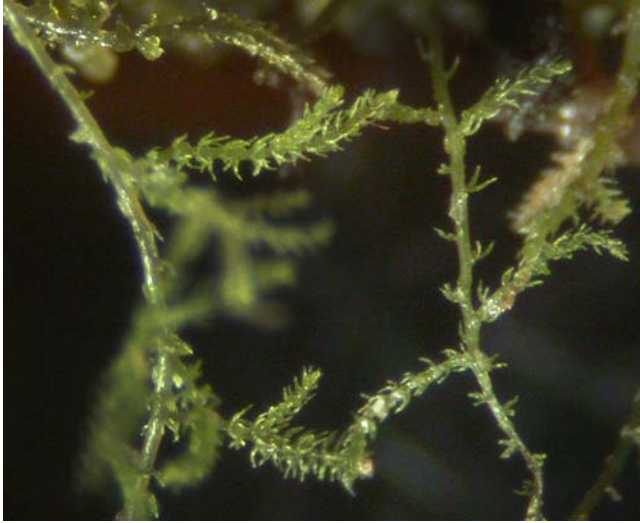


Figure 85. *Kurzia trichoclados*, a tiny Northern Hemisphere liverwort. Photo by Tomas Hallingbäck, with permission.

Aquatic and Wet Habitats

There seems to be little information on this species, in part due to misidentifications. Watson (1919) reported it as occasionally submerged, but I found no more recent record of its aquatic affinities. On the other hand, it is common in peatlands. In the mid-west coast of Britain, within the Oceanic Temperate Region, *Kurzia trichoclados* (Figure 84) is exclusively found on upland heaths and bogs (Callaghan & Ashton 2008).

But it appears that habitats need not even be wet. Porley (2001) reported the species as frequent on the sandstone scarps of the Lough Navar Forest region, Co Fermanagh, in the UK.

Adaptations

Kurzia trichoclados varies in coloration from pale yellow and translucent to brown and slightly opaque (Paton 1986, 1993). These may be responses to differences in light intensity.

Reproduction

Paton (1986, 1993) reported that populations in Great Britain and Ireland are known to have bulbils. These appear on older stems. They are positioned by a short stalk in the axil of an underleaf on leafy stems or of rudimentary leaves on flagella or terminally on long, slender flagella. They readily break away from the stem. They are wider than long and possess three regular vertical rows of diminutive leaves with protuberant basal cells. Although their obvious function would seem to be as propagules, this function has not been observed. These bulbils occur more frequently in deep turfs than in shallow ones, suggesting that they might be developed in response to burial. Like *Kurzia pauciflora* (Figure 74), this species has subterranean axes and swollen rhizoids that most likely contribute to its success in peatlands, particularly since it rarely produces gemmae or capsules (Pocock & Duckett 1985).

Fungal Interactions

With so few studies, it is not surprising that Wang and Qiu (2006) found no records of mycorrhizae on this

species. On the other hand, Duckett and Read (1995) considered it to typically contain rhizoidal Ascomycetes. Furthermore, Pocock and Duckett (1985) reported fungi in association with the subterranean axes. Von Reuß *et al.* (2004; Adio *et al.* 2007) identified a number of sesquiterpene constituents from *Kurzia pauciflora* (Figure 74), perhaps playing a role in limiting the number of fungi that can invade this liverwort.

Lepidozia reptans (Figure 86-Figure 88)

Distribution

Lepidozia reptans (Figure 86-Figure 88) is a relatively cosmopolitan species, occurring in Africa, the Caribbean, Europe, Northern and Southern Asia, North America, Central America, and South America (ITIS 2020).



Figure 86. *Lepidozia reptans*, cosmopolitan species, often occupying river banks. Photo by Hermann Schachner, through Creative Commons.



Figure 87. *Lepidozia reptans* rhizoids showing branched tips. Photo from Botany website, UBC, with permission.

Aquatic and Wet Habitats

Lepidozia reptans (Figure 88) occurs on earthy and gravelly substrates of river banks in Haute Ardenne rivers, Belgium (Leclercq 1977); cracks in the flume at Franconia Notch, New Hampshire, USA (Glime 1982); and middle reaches in the Harz Mountains of Germany (Bley 1987), qualifying it as wetland or aquatic. Cain and Fulford (1948) found it was widely distributed and common on wet rocks, logs, and humus in Ontario, Canada. It was usually mixed with other bryophytes and was especially common in bogs and swamps. Arzeni (1948) found that *Blepharostoma trichophyllum* (Figure 2-Figure 3) was intertwined with *Lepidozia reptans* on rotten logs in Reese's Bog, Michigan, USA.

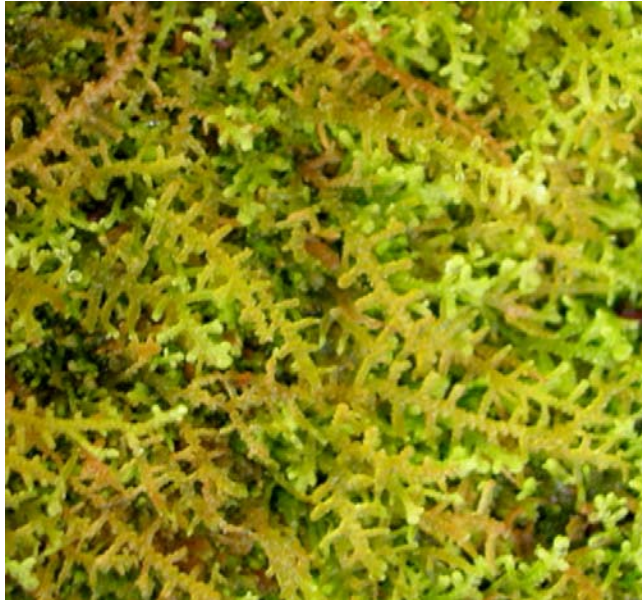


Figure 88. *Lepidozia reptans* forming mats as one might find on logs or stream banks. Photo from Botany Website, UBC, with permission.

Söderström (1989) noted that *Lepidozia reptans* (Figure 86-Figure 88) in Sweden is typically epixylic and does not occur on logs that have much remaining bark. Brūmelis *et al.* (2017) likewise emphasized the importance of **decortication** (loss of bark) for this species to occur on logs in *Picea abies* (Figure 89) forests in Latvia, attributing *Lepidozia reptans* (Figure 88) to mid stages in decay, after the bark was gone but before epigeous species became dominant. It occurs especially near water in shady sites on decaying wood and moist soil, often with *Tetraphis pellucida* (Figure 81) and species of *Calypogeia* (Figure 10, Figure 71, Figure 72) (Botany Website 2020).

Adaptations

Lepidozia reptans occurs in dull, gray-green **mats**, with its branches forming close to right angles (Crum 1991). It sometimes forms flagelliform tips on the branches, but lacks the ventral stolons seen in *Bazzania*.

Bączkiewicz (2013) found a low genotypic diversity within populations of *Lepidozia reptans* (Figure 86-Figure 88, Figure 90) from three regions in Poland, whereas the number of rare alleles in any species in the study was among the greatest in this species.



Figure 89. *Picea abies* forest in Sweden, similar to the ones in Latvia where *Lepidozia reptans* occurs on mid-decay logs. Photo by Enfore, through Creative Commons.



Figure 90. *Lepidozia reptans* demonstrating color variation compared to that in Figure 88; this could be environmentally induced or genetic. Photo from Botany Website, UBC, with permission.

Russell (2010) found an inhibition zone of 1.0 mm from ethanolic extracts of *Lepidozia reptans* (Figure 86-Figure 88), but there was no antibiotic activity against Gram-negative *Escherichia coli* (Figure 91) or *Klebsiella pneumoniae* (Figure 92).



Figure 91. *Escherichia coli*, a species that experiences no antibiotic activity by *Lepidozia reptans*. Photo by Eric Eribe, through public domain.



Figure 92. *Klebsiella pneumoniae*, a species that experiences no antibiotic activity by *Lepidozia reptans*. Photo by IAID, through Creative Commons.

In ravine habitats, it can provide substrate for slime molds (Ing 1983). The nature of this relationship needs to be explored – is it mutualism, competition, or just a preference for the same habitat?

Reproduction

Lepidozia reptans (Figure 86-Figure 88, Figure 90) is **autoicous**, making it easier to achieve sexual reproduction (Crum 1991). On the other hand, its lack of ventral stolons denies it of that reproductive advantage as seen in *Bazzania*.

Biochemistry

Several biochemical studies have included this species. Connolly *et al.* (1986) described the structure of a sesquiterpene diol from *Lepidozia reptans* (Figure 86-Figure 88, Figure 90). Rieck *et al.* (1997) determined the structure of another new sesquiterpene alcohol. Zhang *et al.* (2010) identified lignans and described a new cadinane sesquiterpenoid lactone from this species. Li *et al.* (2018) identified five new terpenoids and nine known ones from Chinese populations of *Lepidozia reptans*, screening them for anti-inflammatory compounds. Suleiman *et al.* (1980) identified volemitol and sedoheptulose as photosynthetic products.

Lepidozia trichodes

Distribution

Lepidozia trichodes has been known for a long time from Java and Bolivia (Stapf 1894-1896). Chuah-Petiot (2011) reported it from Malaysia. Gao and Bai (2002) considered it to be endemic to China and Taiwan, but in fact it is now known from a number of islands north of Australia (DiscoverLife (2020). Even before Gao and Bai considered it to be endemic, it was reported from the Philippines (del Rosario 1967). Pócs and Ninh (2005)

subsequently reported it from Vietnam, Lai *et al.* (2008) from Thailand, and Aryanti and Gradstein (2007; Ariyanti *et al.* 2009) from Sulawesi, Indonesia. Siregar *et al.* (2018) added distributio in Papua New Guinea, Japan, and India.

Aquatic and Wet Habitats

Ruttner (1955) reported *Lepidozia trichodes* from acidic thermal spray in the tropics. Kitayama (1995) likewise reported it from the tropics, occurring in the cloud forest of Mount Kinabalu, Sabah, Malaysia, in dense "moss balls" with other leafy liverworts. Piippo (1984) found it in both the rainforests and cloud forests of the Huon Peninsula, Papua New Guinea. It occurs on moist bark, and although these are not aquatic habitats, they have long moist periods. Pócs and Ninh (2005) found it (rarely) on streambed rocks in Vietnam. Logatec *et al.* (2019) found it along the trail to a mossy forest (almost always humid) in the Philippines.

Adaptations

In *Lepidozia trichodes* of the montane rainforest of Peninsular Malaya, the rhizoids are almost exclusive to the flagella (Pocock *et al.* 1984). Most of them exhibit terminal ramifications, a response to contact with the substratum.

Fungal Interactions

Lepidozia trichodes swollen tips, also on the flagellar axes, contain abundant fungal hyphae (Pocock *et al.* 1984).

Zoopsis argentea (Figure 93)

Distribution

Zoopsis argentea (Figure 93) has a relatively small distribution, occurring in Australia and southern Asia (ITIS 2020).

Aquatic and Wet Habitats

Only Ruttner (1955) seems to attribute it to a somewhat aquatic existence, describing it from acidic thermal spray in the tropics. Rather, it is typically a species of older logs, 33-67 years (Turner & Pharo 2005). In Tasmania, it occurs on the lowest levels of the buttress of *Eucalyptus obliqua* (Figure 94) (Kantvilas & Jarman 2004).



Figure 93. *Zoopsis argentea*, a species of Australia and southern Asia. Photo by Peter de Lange, through Creative Commons.



Figure 94. *Eucalyptus obliqua*, showing bases where one might find *Zoopsis argentea*. Photo by Forest and Kim Starr, with limited online permission.

Adaptations

In *Zoopsis argentea* (Figure 93), the stem has totally taken over the photosynthetic role of the plant (Thiers 1988), forming deep green mats (Allison 1985). The stem is flattened and the leaves reduced (Figure 95), possibly an adaptation to its tropical habitats.

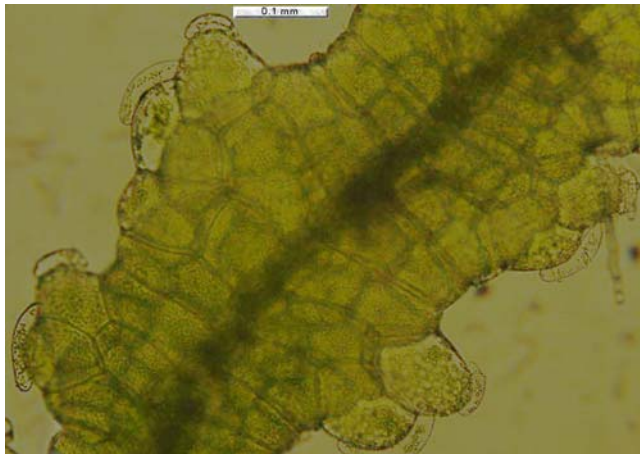


Figure 95. *Zoopsis argentea* showing the photosynthetic stem and reduced, flattened leaves. Photo by Tom Thekathyl, with permission.

Lophocoleaceae

Chiloscyphus (Figure 96-Figure 98, Figure 106-Figure 108)

Chiloscyphus (Figure 96-Figure 98, Figure 106-Figure 108) is a genus that in central France occurs in streams where it is embedded in basaltic rocks with elevated levels of Cu, Zn, Sr, V, Ba, Ni, and Co (Samecka-Cymerman & Kempers 1999). Aquatic varieties are almost black, whereas the typical variety ranges from deep yellow to pale green (Figure 104) to brownish green (Figure 96) (Salachna 2007). Submerged plants often lack rhizoids. It seems that common garden studies in a variety of habitat conditions would be helpful in understanding this genus.



Figure 96. *Chiloscyphus polyanthos* brownish form. Photo by A. Neuman, through Creative Commons.

The species are autoicous or dioicous. Sporophytes (Figure 104) are produced in late winter and spring and can be abundant.

Chiloscyphus pallescens (Figure 97)

Järvinen (1983) considered *Chiloscyphus* to have three taxa in Europe. While she separated variety *fragilis* and variety *rivularis* from typical *Chiloscyphus polyanthos* (Figure 106-Figure 107), she considered *Chiloscyphus pallescens* (Figure 97) to be conspecific with *Chiloscyphus polyanthos*. Nevertheless, in 2016 Söderström *et al.* considered these two to be separate species and placed variety *fragilis* in *C. pallescens*. Factors related to the environment cause leaf variation that could account for the differences in interpretation.



Figure 97. *Chiloscyphus pallescens*, a widespread species that is mostly aquatic, but also occurs above water. Photo by Hermann Schachner, through Creative Commons.

Distribution

Chiloscyphus pallescens (Figure 97) is a species in North America from Alaska to Mexico, Europe, Asia, and Africa (ITIS 2020).

Aquatic and Wet Habitats

In the Tatra National Park of Poland, *Chiloscyphus polyanthos* (Figure 106-Figure 108) grows mainly on rocks and stones in the stream bed and the lowest terrace of stream banks, whereas *C. pallescens* (Figure 97) prefers mires and springs where it most often occurs on the wet soil (Figure 98) and stones (Klama *et al.* 2008). There it prefers temperatures of 3.6-8.5°C (5.12±1.56), pH 7.06. It is more common on north and northeastern slopes, often accompanied by *Scapania undulata* (Figure 99), *Brachythecium rivulare* (Figure 100), and *Rhizomnium magnifolium* (Figure 101).



Figure 98. *Chiloscyphus pallescens*, forming a mat on a stream bank. Photo by Michael Lüth, with permission.



Figure 99. *Scapania undulata*, a frequent associate of *Chiloscyphus pallescens*. Photo by Janice Glime.



Figure 100. *Brachythecium rivulare*, a frequent associate of *Chiloscyphus pallescens*. Photo by David T. Holyoak, with permission.



Figure 101. *Rhizomnium magnifolium*, a frequent associate of *Chiloscyphus pallescens*. Photo by Hermann Schachner, through Creative Commons.

Elsewhere, *Chiloscyphus pallescens* (Figure 97) typically inhabits neutro-alkaline lakes, peat pits, ditches at pH 5.8-8.4, springs at pH ~7.1, calm water with low depth, streaming water at pH 7.2, weakly acid peat pits, lakes, ditches at pH 5.3-8.6 in Denmark (Sørensen 1948). It occurs in intermittent rivers (Dhien 1978), in the *Platyhypnidium-Fontinalis antipyretica* association (Figure 102, Figure 103) in Thuringia, Germany (Marstaller 1987), and in small lakes in southern Finland (Koponen *et al.* 1995; Toivonen & Huttunen 1995). It occurs in the Alsatian Rhine Valley streams (Vanderpoorten & Palm 1998) where it has oligotrophic status (Vanderpoorten & Palm 1998; Vanderpoorten *et al.* 1999), in streams in Polish and Czech Sudety Mountains (Samecka-Cymerman & Kempers 1998b), but is also characteristic in near-water or water environments of oligotrophic waters of the Iskur River, Bulgaria, where it is among the dominant bryophytes, and in its main tributaries (Papp *et al.* 2006a) and other Bulgarian rivers (Gecheva *et*

al. 2010, 2013a, b). In Montenegro, it occurs at the river in the Tara River Canyon and Durmitor area (Papp & Erzberger 2011).



Figure 102. *Platyhypnidium riparioides*, a species common in the same streams as *Chiloscyphus pallescens*. Photo by David T. Holyoak, with permission.



Figure 103. *Fontinalis antipyretica*, a species common in the same stream as *Chiloscyphus pallescens*. Photo by Hermann Schachner, through Creative Commons.

But this species can also occur above water in wet places. Madžule and Brūmelis (2008) found them growing epiphytically in Euro-Siberian alder swamps of Latvia. It also occurs there on mid-decay logs. And it occurs in Estonian transitional mires (Ingerpuu *et al.* 2014) and willow swamps and spring-fed areas of northern Sweden (Sjörs & Een 2000).

However, in the Hungarian beech forests, Ódor and van Hees (2004) found it to be restricted to well-decayed logs. In New York, USA, Burnham (1929) found it on old logs that extended into the water of Three Ponds.

The *Chiloscyphus pallescens* (Figure 97), along with *Platyhypnidium riparioides* (Figure 102) and *Fontinalis antipyretica* (Figure 103) remained unchanged in two years of study in the Ipel' River, a typical submontane river with regular winter/spring floods and with occasional summer floods, while tracheophyte cover fluctuated (Hrivnák *et al.* 2008). These bryophytes were not damaged by the summer flood, whereas the less-well attached tracheophytes were.

In the Alsacian Rhine River, France, *Chiloscyphus pallescens* (Figure 97) exhibited a very broad trophic range but occurred more often in eutrophic streams

(Vanderpoorten *et al.* 1999). This was displayed in its relationship to ammonia vs. nitrate nitrogen and to phosphates. In the Laelatu wooded meadow in Estonia, *Chiloscyphus pallescens* was absent in control plots, but present in some fertilized plots (3.5 g m⁻² N, 2.6 g m⁻² P, and 5 g m⁻² K annually) (Ingerpuu *et al.* 1998). In Polish and Czech Sudety Mountains, *Chiloscyphus pallescens* collects Au (gold) from the stream water (Samecka-Cymerman & Kempers 1998a). It also exhibited significantly more nickel, chromium, and barium, and significantly less zinc and mercury as compared to bryophyte samples from selected areas in the Swiss Alps (Samecka-Cymerman & Kempers 1998b).

Reproduction

Chiloscyphus pallescens (Figure 97) is **monoicous** (Crum 1991). It is among the few species in which the young spermatids are described in detail (Rushing *et al.* 1984). This study suggests that the Jungermannialian spermatids exhibit numerous variations and novel features. In Figure 104, one can see that many sperm are successful at fertilizing the eggs, and sporophytes can be abundant.



Figure 104. *Chiloscyphus pallescens* with capsules. Photo by Wayne Lampa, through Creative Commons.

Role

There are indications that the Great Crested Newt (*Triturus cristatus*, Figure 105) can serve as a dispersal agent for *Chiloscyphus pallescens* (Figure 97). Gustafson *et al.* (2006) found that when ponds with and without the newt were compared, those with the newt exhibited the largest populations of *Chiloscyphus pallescens* (Figure 97). On the other hand, the newt may simply be an indicator of the more suitable conditions that favor the liverwort.



Figure 105. *Triturus cristatus*, a likely dispersal agent of *Chiloscyphus pallescens*. Photo by Rainer Theuer, through public domain.

Biochemistry

With its widespread distribution, it is not surprising that studies have examined its biochemistry. Connolly *et al.* (1982) elucidated the structure of chiloscapholone, a sesquiterpenoid from this species.

Chiloscyphus pallescens var. *fragilis*

(syn. = *Chiloscyphus polyanthus* var. *fragilis*)

Distribution

Although there seem to be clear records for the variety *Chiloscyphus pallescens* var. *fragilis* in North America and Europe, more precise distributional information is difficult because of the taxonomic confusion of the variety. Several records place the variety in North America: in the Ozarks of Arkansas, USA (Redfearn 1979), in the Lake George region, New York, USA (Burnham 1929), and in Wyoming (Hong 1977).

Aquatic and Wet Habitats

Watson (1919), based on European experience, described the habitat as often on rocks just above fast streams, on banks with frequent submergence and slow water, sometimes completely submerged in fast streams. In North America, Redfearn (1979) found *Chiloscyphus pallescens* var. *fragilis* on rocks of a spring branch. Hong (1977) likewise reported it from submerged rocks. Burnham (1929), on the other hand, found it in a dried up streambed on rocks. Bakalin (2005) reported it from stream banks in rhododendron, sedge, and moss tundra and in shady crevices near streams on Bering Island in the northwest Pacific.

Chiloscyphus polyanthus (Figure 106-Figure 107)

Chiloscyphus polyanthus (Figure 106-Figure 107) has been considered by some to be conspecific with *Chiloscyphus pallescens* (Figure 97) (Järvinen 1983). Since researchers have not reached a consensus, I will report the information separately rather than try to judge the decisions of the individual researchers, but this has the caveat that some may not have been interpreted as I am listing them.



Figure 106. *Chiloscyphus polyanthus*, a species widespread in the Northern Hemisphere, exhibiting the darkened color of aquatic forms. Photo by Barry Stewart, with permission.



Figure 107. *Chiloscyphus polyanthus* rhizoids. Photo by Paul Davison, with permission.

Distribution

Chiloscyphus polyanthus (Figure 106-Figure 107) is known from Europe, Asia, Africa, and North America (Damsholt 2002; ITIS 2020).

Aquatic and Wet Habitats

Watson (1919) described this species as one usually found on the margins of fast streams (Figure 1) or on wet ground associated with fast water, but it also occurs in rivers (Ferreira *et al.* 2008). It is typically oligotrophic (Trempe 2003).

The European *Chiloscyphus polyanthus* (Figure 108) is hygrophytic, growing mostly on soil or silt-covered rocks, tree roots, and more rarely on rotting wood along small streams and rivers (Salachna 2007). The variety *polyanthos* is more likely to be terrestrial, with the variety *rivularis* being submerged in running water. The species often is associated with *Pellia epiphylla* (Figure 109), *P. neesiana* (Figure 110), *Marsupella emarginata* (Figure 111), and *Scapania undulata* (Figure 112) (Damsholt 2002).



Figure 108. *Chiloscyphus polyanthus* var. *polyanthos*. Photo by David T. Holyoak, with permission.



Figure 109. *Pellia epiphylla*, a species commonly associated with *Chiloscyphus polyanthus*. Photo by Jan-Peter Frahm, with permission.



Figure 110. *Peltia neesiana*, a species commonly associated with *Chiloscyphus polyanthos*. Photo by Michael Lüth, with permission.

In the Tatra National Park of Poland, Klama *et al.* (2008) reported that *Chiloscyphus polyanthos* (Figure 106-Figure 107) occurs mainly on rocks and stones of the streambed and close to the water on the streambanks (Figure 113). Nevertheless, it prefers mires and springs where it can occupy wet soil and stones (Figure 114). This species is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006). It is occasionally abundant on wet shores and in pools in Scotland (West 1910). It is among the most common bryophytes in the River Tweed, UK (Holmes & Whitton 1975), is known from a river bank of the River Tees, UK (Holmes & Whitton 1977a), occurs upstream in the River Swale, Yorkshire, UK (Holmes & Whitton 1977b), but is mostly in the mid to lower River Tyne, UK, occurring above and below water (Holmes & Whitton 1981), and in northern England it occurs in both streams and rivers (Wehr 1983).



Figure 111. *Marsupella emarginata*, a species commonly associated with *Chiloscyphus polyanthos*. Photo by Barry Stewart, with permission.



Figure 112. *Scapania undulata*, a species commonly associated with *Chiloscyphus polyanthos*. Photo by Hermann Schachner, through Creative Commons.



Figure 113. *Chiloscyphus polyanthos* on rocks above and below the water of a stream. Photo from <www.aphotofauna.com>, with permission.



Figure 114. *Chiloscyphus polyanthos* habitat with brown colonies in the water. Photo by A. Neumann through Creative Commons.

Chiloscyphus polyanthos (Figure 106-Figure 107) occupies alpine streams in the Swiss Alps (Geissler 1976) as well as occurring beside small snowmelt streams in the arctic-alpine zone on granodioritic rocks in southern Europe (Casas & Peñuelas 1985). In Germany it occurs midstream, in unpolluted, upper and middle parts of streams in eastern Odenwald and southern Spessart, Germany (Philippi 1987), in middle and downstream reaches in Harz Mountains of Germany (Bley 1987), in the *Platyhypnidium-Fontinalis antipyretica* association (Figure 102, Figure 103), Thuringia, Germany (Marstaller 1987). It is aquatic in Finland (Koponen *et al.* 1995; Heino

& Virtanen 2006) or facultative aquatic in Finnish streams (Virtanen 1995). It occurs in streams in Greece (Papp 1998) and in mountain streams of northwest Portugal (Vieira *et al.* 2005). It occurs in mountainous streams on Madeira Island (Luis *et al.* 2015). In the Iskur River and its main tributaries in Bulgaria, it is characteristic in the near-water or water environment (Papp *et al.* 2006a) and is typically a hygrophyte in Bulgarian rivers (Gecheva *et al.* 2010, 2013).

North American records are less numerous. In Minnesota, USA, it occurs on boulders in 15-45 cm water of rivers (Moyle 1937). By contrast, it grows on very small rocks on the streambed of Adirondack Mountain streams (Slack & Glime 1985). In West Virginia, USA, mountain streams its preferred pH is 6.6 (Stephenson *et al.* 1995).

Vanderpoorten and Klein (1999) considered *Chiloscyphus polyanthos* (Figure 106-Figure 107) to be acid-sensitive in waterfalls of the Black Forest and the Vosges, Germany. It is able to tolerate low cation concentrations if the concentrations of protons is also low, hence being sensitive to low pH. This creates a fragile physico-chemical balance with low buffering capacity. Thus, only slight changes can cause a rapid reaction by the bryophyte flora, including *C. polyanthos*. Pollution from human activity can increase the input of hydrogen ions, causing the disappearance of the sensitive *C. polyanthos*.

Sossy Alaoui and Rossilon (2013) found that *Chiloscyphus polyanthos* (Figure 106-Figure 107) characterizes acidic and low-impacted streams and rivers in Belgium, an inconsistent behavior when compared to some earlier studies. Gil and Ruiz (1985) reported that it is found in calcareous water. But like other aquatic species, it is likely that local physiological races exist, so differences in pH preferences may indicate such races.

Reproduction

Chiloscyphus polyanthos (Figure 106-Figure 107) is **monoicous** (Crum 1991). It most likely reproduces by fragments.

Biochemistry

Chiloscyphus polyanthos (Figure 106-Figure 107) has a pungent odor (Asakawa *et al.* 1979). This odor, often helping in its identification, is due to a mixture of four sesquiterpene lactones, ent-5 β -hydroxydiplophyllin, ent-3-oxodiplophyllin, diplophyllin, and diplophyllolide. Diplophyllolides cause an intense numbness of the tongue. All the pungent sesquiterpene lactones exhibit inhibitory activity against the germination and root elongation of rice husks. Toyota *et al.* (1999) extracted and described the configuration of an eudesmane-type sesquiterpenoid. Azzollini *et al.* 2016) used *Chiloscyphus polyanthos* to develop an isolation strategy for purifying antifungal compounds. In this study they isolated seven sesquiterpene lactones, five of which were bioactive and one was a new compound.

Another biochemical aspect of importance is the production of UV-absorbing compounds. Arróniz-Crespo *et al.* (2004) reported that in mountain streams these are produced by *Chiloscyphus polyanthos* (Figure 106-Figure 107) and serve to protect them from the stronger UV-B radiation at the high elevations. Sclerophylly had little influence in protecting the ten mosses and four liverworts

in the study. Among these, *Chiloscyphus polyanthos* was the least sclerophyllous species of the 14 species studied.

Chiloscyphus polyanthos var. *rivularis* (Figure 115)

(syn. = *Chiloscyphus rivularis*)

Distribution

Chiloscyphus polyanthos var. *rivularis* (Figure 115) is a variety distributed in North America (ITIS 2020), but it has also been reported from Germany (Koppe 1945), Poland (Szweykowski 1951), and Finland (Heino & Virtanen 2006). Järvinen (1983) likewise considered it to be the aquatic variety of the species in Europe. Schuster (1980) likewise considers it to be abundant in Europe as well as North America.



Figure 115. *Chiloscyphus polyanthos* var. *rivularis* on wet mud. Photo by Jean Faubert, with permission.

Aquatic and Wet Habitats

Whereas *Chiloscyphus polyanthos* var. *polyanthos* (Figure 106-Figure 107) is common at many elevations in Europe and North America, *C. polyanthos* var. *rivularis* (Figure 115) is primarily restricted to the mountainous areas (Järvinen 1983). It differs from the typical variety in always having small leaf cells. It is sometimes completely submerged in fast streams, or submerged in slow water with poor mineral salts (Watson 1919). Fitzgerald and Fitzgerald (1967) describe it from rock in a stream in Ireland. In Westfalens, northwestern Germany, it is a strong hygrophil (Koppe 1945). It is likewise a hydroamphibiont in streams of Gory Stolowe Mountains, Poland, where it prefers neutral and basic (pH 6.4-6.6) water (Szweykowski 1951). It also occurs in streams in northeastern Finland (Heino & Virtanen 2006). In Muddus National Park, North Sweden, it occurs upstream of waterfalls (Sjörs & Een 2000). In the Vologda Region of Russia it occupies a somewhat different habitat on banks and in rapids of a darkwater stream with sandy-rocky ground, where it is rare (Dulin *et al.* 2009).

In North America, *Chiloscyphus polyanthos* var. *rivularis* is hydrophytic in rock ravines in Connecticut, USA (Nichols 1916). Likewise, it occurs on submerged

rocks in Rocky Mountain National Park, Colorado, USA, where it is often accompanied by *Jungermannia exsertifolia* subsp. *cordifolia* (Figure 116) and *Scapania undulata* var. *undulata* (Figure 112) in running water (Hong 1980). It is relatively frequent in Adirondack and Appalachian Mountain streams in northeastern USA, but in their study Slack and Glime (1985) never observed a cover of more than 5%.



Figure 116. *Jungermannia exsertifolia* subsp. *cordifolia*, a frequent associate of *Chiloscyphus polyanthos* var. *rivularis*. Photo by Dick Haaksma, with permission.

Role

Not only do these leafy liverworts contribute to the productivity of the streams they occupy, but in the mountain springfed stream in Adamello-Brenta Regional Park of Northern Italy, they serve as considerable substrate area that is colonized by diatom communities (Cantonati 2001).

Biochemistry

As is often the case, Wu *et al.* (1997) found five new bioactive and other sesquiterpenes in this variety. And Zhang *et al.* (2016) added another seven new entudesmane-type sesquiterpenoids to these, all from Chinese populations. One of these had weak inhibitory activity against a cancer cell line.

Hepatostolonophora paucistipula (Figure 117)

(syn. = *Clasmatocolea paucistipula*)

Distribution

Hepatostolonophora paucistipula (Figure 117) occurs in New Zealand (Suren & Winterbourn 1991), Antipodes, and Tasmania (Engel 1980). It is a species of uncertain taxonomic placement.

Aquatic and Wet Habitats

Suren and Winterbourn (1991) found that *Hepatostolonophora paucistipula* (Figure 117) dominates the bryoflora at shaded sites in an open, headwater tributary of the Otira River and shaded tributary of Bealy River, New Zealand. It was present in some of the 48 streams studied on South Island, New Zealand (Suren & Duncan 1999). It is one of the two most common liverworts on South Island (Suren 1996).



Figure 117. *Hepatostolonophora paucistipula* in its aquatic habitat, a New Zealand species that is one of the most common liverworts on South Island. Photo from Landcare Research, through Creative Commons.

Role

Hepatostolonophora paucistipula is particularly common in chutes, where it provides expanded invertebrate habitat by providing a refuge of reduced flow (Suren 1991). The species is particularly important in providing oviposition sites where young larvae are protected from the harsh flow.

In these New Zealand streams, *Hepatostolonophora paucistipula* (Figure 117) is an important food source for some invertebrates. But its use pales in comparison to that of the mosses, comprising only 2% of the gut contents of larvae of the crane fly *Limonia hudsoni* (Figure 118) compared to 57% mosses (Suren & Winterbourn 1991). They attributed this to the low nutritional quality of *Hepatostolonophora paucistipula*: 2.8% lipids, 3.9% carbohydrates, 23.7 energy (kJ/g), 1.1% starch, 1.1% N, 6.9% protein, 34.7% holocellulose, 27.7% fiber, 7.4% ash. Among the bryophytes, it trapped the lowest total organic matter biomass and lowest LPOM, FPOM, and UFPOM (Suren 1993). One reason for the invertebrate biomass may be the abundant periphyton growing there.



Figure 118. *Limonia* sp.; larvae of *Limonia hudsoni* live among branches of *Hepatostolonophora paucistipula*, but the liverwort contributes little to its diet. Photo by Stephen Moore, Landcare Research, NZ, with online permission.

Biochemistry

Other deterrents to feeding may include the secondary compounds present in the liverwort. Baek *et al.* (2003) reported sesquiterpene lactones. Ludwiczuk and Asakawa (2019) found bioactive volatile terpenoids that are active against leukemia cells. Kim *et al.* (2009a) found a sesquiterpene lactone that is active against the fungus *Trichophyton mentagrophytes* (Figure 119) and a number of other medical conditions. They also isolated another compound with cytotoxic activity (Kim *et al.* 2009b). found that it is a rich source of sesquiterpenes that are very effective against P388 murine leukemia cells (Oh *et al.* 2004). It seems likely that some of these protect the liverwort by discouraging herbivory, but this remains to be tested.

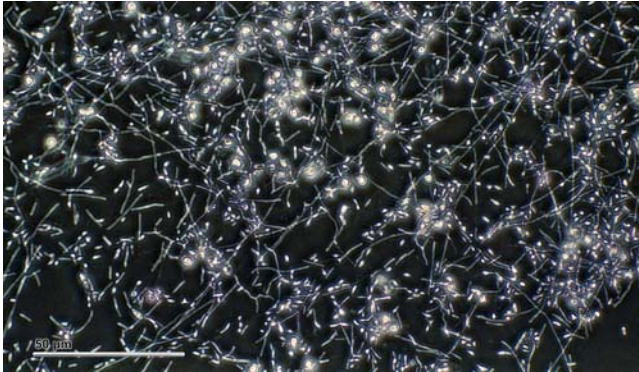


Figure 119. *Trichophyton mentagrophytes* in culture, a fungus that is inhibited by *Hepatostolonophora paucistipula*. Photo by RNDr. Josef Reischig, CSc., through Creative Commons.

Heteroscyphus argutus (Figure 120-Figure 121)

(syn. = *Chiloscyphus argutus*)

Distribution

Heteroscyphus argutus (Figure 120-Figure 121) occurs in southern Asia and Australia (EOL 2020). Ruttner (1955) noted it from a tuff wall in the tropics. Satake (1983) reported it as aquatic from Kyushu, Japan. Srivastava and Srivastava (1989) found it in the western Himalayas, describing it as widespread in tropical Asia and south and central India. In 2011, Glenn *et al.* reported it from the Kermadec Islands (800-1,000 km northeast of New Zealand's North Island).



Figure 120. *Heteroscyphus argutus*, a liverwort of southeastern Asia, Australia, and northern New Zealand. Photo by Lin Shanxiong, through Creative Commons.



Figure 121. *Heteroscyphus argutus* growing in moist, shady conditions, but starting to dry. Photo by Lin Shanxiong, through Creative Commons.

Aquatic and Wet Habitats

This is a species with a wide range of habitats, but mostly in moist, shady conditions on land (Alam *et al.* 2013). So and Zhu (1996) recorded it from Hong Kong, where it is locally common on moist soil and rock, typically associated with *Calypogeia arguta* (Figure 71), *Pallavicinia subciliata* (Figure 122), and *Notoscyphus lutescens* (Figure 123). Grolle and So (1999) also found *Heteroscyphus argutus* (Figure 121) mixed with *Plagiochila* species (Figure 18, Figure 70) on wet rocks in Hong Kong. In Guizhou, southern China, Bakalin *et al.* (2015) found it at 1200-1300 m asl on mesic to wet boulders, often near streams, as well as on decaying wood and tree trunk bases where there was partial shade. It occurred in both pure mats and in mixes with *Syzygiella autumnalis* (Figure 124), *Lophocolea minor* (Figure 161-Figure 162), *Nowellia curvifolia* (Figure 125), and other bryophytes. On Jeju (Cheju) Island, Korea, Song and Yamada (2006) found it on rocks in a stream. But on Luzon and Negros Islands in the Philippines, Hayashi and Yamada (2004) found it on branches, trunk, and roots of trees. In Sri Lanka, Samarakkody *et al.* (2018) found it mixed with *Bazzania* sp. (e.g. Figure 38) on a rock surface near a stream. In India Manjula *et al.* (2013) reported that it grows on bark, soil, and pure populations on soil-covered rocks or associated with other liverworts. It is widely distributed from low to high altitudes, although mostly low to medium altitudes. It furthermore occupies "all microhabitats" as pure populations or in association with bryophytes and ferns. But in their treatment of the genus, Srivastava and Srivastava (1989) treat it as a terrestrial species of soil, rock, or epiphytic in the tropics to warm temperate regions of the Eastern Hemisphere.



Figure 122. *Pallavicinia subciliata*, a species often associated with *Heteroscyphus argutus* on wet soil and rock. Photo by Lin Shanxiong, through Creative Commons.

Reproduction

Heteroscyphus argutus (Figure 120-Figure 121) is dioicous, with short, lateral male branches (Srivastava & Srivastava 1989). Daniels (1998) observed the species in the Western Ghats and noted that its slime papillae helped it to absorb water quickly.



Figure 123. *Notoscyphus lutescens*, a species often associated with *Heteroscyphus argutus* on wet soil and rock. Photo by David Tng, with permission.

Biochemistry

Chemical constituents in *Heteroscyphus argutus* (Figure 120-Figure 121) are effective in controlling wood rot in tea (Nepolean *et al.* 2014), but little work seems to have been done on the biochemistry of this species.



Figure 124. *Syzygiella autumnalis*, a species often associated with *Heteroscyphus argutus* on wet soil and rock. Photo by Hugues Tinguy, with permission.



Figure 125. *Nowellia curvifolia*, a species often associated with *Heteroscyphus argutus* on wet soil and rock. Photo by Botany Website, UBC, with permission.

Heteroscyphus coalitus (Figure 126-Figure 127)

(syn. = *Chiloscyphus coalitus*)

Distribution

Heteroscyphus coalitus (Figure 126-Figure 127) occurs in the Pacific – southwestern Asia, Australia, and Pacific islands (DiscoverLife.com 2020). Nair and Prajitha (2010) elaborated on these areas to include North-east India (Himalayas, Sikkim, Khasi Hills), Andaman Islands, Myanmar, Bhutan, China, Java, Sumatra, Borneo, Japan, New Guinea, Philippines, and Australia.



Figure 126. *Heteroscyphus coalitus*, a species from southwestern Asia, Australia, and Pacific islands. Photo by David Tng, with permission.

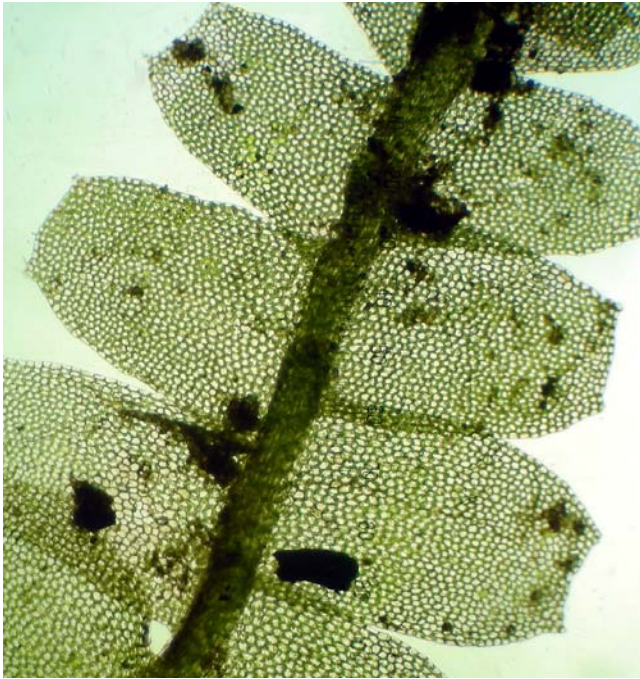


Figure 127. *Heteroscyphus coalitus*, a moist habitat species from southwestern Asia, Australia, and Pacific islands. Photo by Kochibi, through Creative Commons.

Aquatic and Wet Habitats

Ruttner (1955) reported *Heteroscyphus coalitus* (Figure 128) at 10-20 cm above water level where it was kept moist by the acidic thermal spray. It is common in the cool and warm temperate regions of the Australian Rainforest streams (Carrigan 2008). Carrigan and Gibson (2004) described it as forming threadlike mats above waterlevel, downstream, upstream, and sides of rocks in a stream at Cement Creek Turntable, Victoria, Australia. Fleisch and Engel (2006) found it in Victorian rainforest streams that present a cool, strong current. Wilcox (2018) noted that in Craigavon Park, Auckland, New Zealand, where it inhabits the bases of old Monterey pine trees (*Pinus radiata*, Figure 129) and bases of old or dead silver fern trunks (*Cyathea dealbata*, Figure 130), its shaded colonies become especially conspicuous after rain.



Figure 128. *Heteroscyphus coalitus*, a conspicuous species after rain. Photo by Yang Jia-Dong, through Creative Commons.



Figure 129. *Pinus radiata*, a species where *Heteroscyphus coalitus* can grow on the tree bases. Photo by summitcheese, through Creative Commons.



Figure 130. *Cyathea dealbata*, a species that can serve as substrate for *Heteroscyphus coalitus* on bases of old or dead fern trunks. Photo by Leon Perrie, through Creative Commons.

In Guizhou, China, *Heteroscyphus coalitus* (Figure 131) occurs at 1100-1300 m asl on moist to wet cliffs, boulders, and more rarely on decaying wood near streams and in waterfall spray zones, in partly shaded places (Bakalin *et al.* 2015).



Figure 131. *Heteroscyphus coalitus* with the fresh green seen after rain. Photo by Yang Jia-Dong, through Creative Commons.

Adaptations

Heteroscyphus coalitus (Figure 131) is present in pure mats or with *Bazzania bidentula* (Figure 132), *Calypogeia angusta*, *Calypogeia tosana* (Figure 133), *Isotachis indica*/*I. japonica* (Figure 134), *Kurzia gonyotricha*, *Scapania undulata* (Figure 112), and *Schiffneria hyalina* (Figure 135) (Bakalin *et al.* 2015). This growth habit uses the presence of other bryophytes to help maintain moisture.



Figure 132. *Bazzania bidentula*, a species that occurs in mats with *Heteroscyphus coalitus*. Photo by Lin Shanxiong, through Creative Commons.



Figure 133. *Calypogeia tosana*, a species that occurs in mats with *Heteroscyphus coalitus*. Photo from Hiroshima University Museum, with permission.



Figure 134. *Isotachis japonica*, a species that occurs in mats with *Heteroscyphus coalitus*. Photo by Jia-Dong Yang, with online permission.



Figure 135. *Schiffneria hyalina*, a species that occurs in mats with *Heteroscyphus coalitus*. Photo by Jia-Dong Yang, through Creative Commons.

Reproduction

In New Zealand, *Heteroscyphus coalitus* (Figure 128, Figure 131) is usually sterile and sporophytes are rare (Allison & Child 1975).

Biochemistry

Heteroscyphus coalitus (Figure 128, Figure 131) has been the subject of many biochemical studies. Zhu *et al.* (2006) determined that it was active against a number of bacteria. They further determined that there was no correlation between activity and size and number of oil bodies in the 38 liverworts tested. Toyota *et al.* (1996) identified two new diterpenoids and a new sesquiterpenoid from this species. Jong and Wu (2000) identified additional sesquiterpenoids and diterpenoids, with some being new compounds. Lin *et al.* (2012) reported a new dihydroisocoumarin derivative and three previously known terpenoid derivatives, demonstrating that they possessed moderate inhibitory activity against several human tumor cell lines. Wang *et al.* (2020) found 14 new terpenoids. They found that most of these were effective in blocking rhizoidal growth of the yeast *Candida albicans* (Figure 136). Among these, heteroscyphin D could suppress the

ability of *C. albicans* DSY654 to adhere to A549 cells and form biofilms and modulate the transcription of related genes in this yeast.

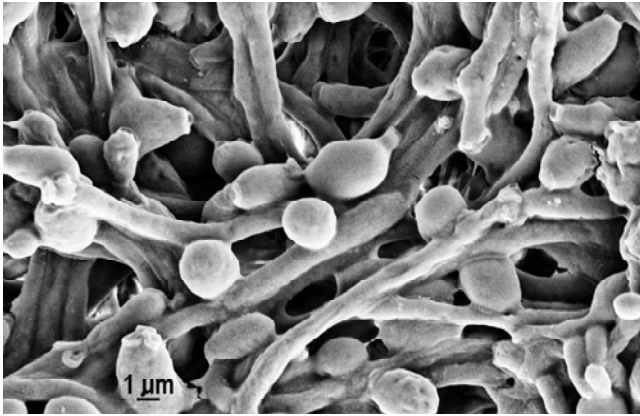


Figure 136. *Candida albicans*; rhizoidal growth is blocked in this species by terpenoids from *Heteroscyphus coalitus*. Photo from Vader 1941, through Wikipedia Creative Commons.

***Heteroscyphus denticulatus* (Figure 137-Figure 138)**

Distribution

Heteroscyphus denticulatus (Figure 137-Figure 138) occurs in Spain and Tenerife (DiscoverLife.com 2020), and the Azores in Portugal (Gabriel & Bates 2005).



Figure 137. *Heteroscyphus denticulatus*, a species known from Spain and nearby regions and South Africa. Photo by Pedro Cardoso, with permission through Azores Biportal.

Aquatic and Wet Habitats

Heteroscyphus denticulatus (Figure 137-Figure 138) seems to be only marginally aquatic. Dirkse (1985) found the species on sheltered wet volcanic rocks in the laurel forest of the Canary Islands and Dirkse *et al.* (2018) found it on humid rocks in dark small ravine in Macaronesia. Luís *et al.* (2010) found it in riparian bryophyte communities on Madeira, a Portuguese island off the northwest coast of Africa. And in Cape Town, South Africa, Mitten (1877) found it on a stream bank. Sjögren (1997) found it to be epiphyllous in the Azores Islands, noting that it was among the few species to preferentially form associations in that habitat.



Figure 138. *Heteroscyphus denticulatus* leaf. Photo by Nidia Homen, with permission through Azores Biportal.

***Heteroscyphus planiusculus* (Figure 139-Figure 140)**

Distribution

Heteroscyphus planiusculus (Figure 139-Figure 140) is an Australian leafy liverwort, being dominant in the Australian Central Highlands (Carrigan 2008).



Figure 139. *Heteroscyphus planiusculus*, an abundant liverwort in the Australian Central Highlands. Photo by Tom Thekathyl, with permission.

Aquatic and Wet Habitats

Little seems to be published about *Heteroscyphus planiusculus* (Figure 139-Figure 140), so I am unable to comment on the breadth of its habitats. In Cement Creek at Turntable, Victoria, Australia, it forms threadlike mats both above and below the water level (Carrigan & Gibson 2004). It had the greatest cover (17%) among the bryophytes. It occurred on all rocks, compared to most other species that occurred on only a few. And it was one of only four species occurring below the water level, but not restricted to it. It was the main species dominating the base of the rocks.

Adaptations

Heteroscyphus planiusculus (Figure 139-Figure 140) forms mats that permit it to live at the bases of rocks in a fast stream (Carrigan & Gibson 2004).

Biochemistry

Heteroscyphus planiusculus (Figure 139-Figure 140) has distinctive large oil bodies (Figure 140). Thus far, it does not seem to have any biochemical studies.

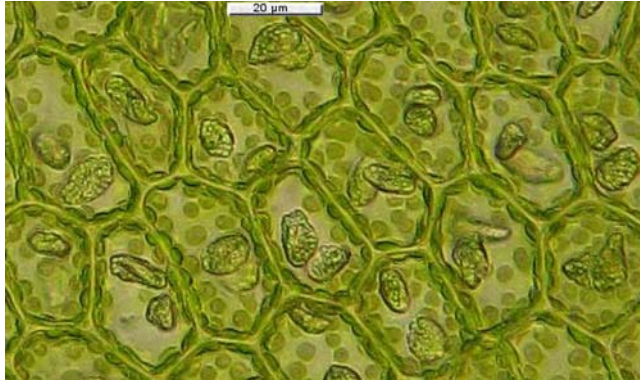


Figure 140. *Heteroscyphus planiusculus* leaf cells showing large oil bodies. Photo by Tom Thekathyl, with permission.

Heteroscyphus zollingeri (Figure 141)

(syn. = *Chiloscyphus zollingeri*)

Distribution

Heteroscyphus zollingeri (Figure 141) occurs mostly in the Pacific tropics.

Aquatic and Wet Habitats

There seems to be little information available on *Heteroscyphus zollingeri* (Figure 141). Ruttner (1955) reported *Heteroscyphus zollingeri* (Figure 141) from thermal acidic spray in the tropics. It is touted as a good aquarium plant, known as Pearl Moss (Aquascaper.org 2017). Although it is not usually an aquatic moss in nature, it is able to grow well as a submerged plant. It has no preference for hard or soft water, high or low light, or low or high CO₂. Its growth is faster than that of other bryophytes in the aquarium industry, sometimes being a desirable trait (and sometimes not!).



Figure 141. *Heteroscyphus zollingeri* from Guizhou, China. Photo courtesy of Li Zhang

Lophocolea (Figure 142-Figure 143, Figure 148-Figure 150, Figure 161-Figure 162, Figure 171-Figure 174)

Lophocolea (Figure 142-Figure 143, Figure 148-Figure 150, Figure 161-Figure 162, Figure 171-Figure 174) occurs in Himalayan streams (Suren & Ormerod 1998) and in central Southern Alps, Australia, in somewhat high rainfall area (Lepp 2012).

Lophocolea bidentata (Figure 142-Figure 143)

(syn. = *Lophocolea bidentata* fo. *latifolia*, *Lophocolea coadunata*, *Lophocolea cuspidata*)

Distribution

Lophocolea bidentata (Figure 142-Figure 143) is a common Northern Hemisphere species from the central parts of Europe and North America, becoming less common toward the north and south (Järvinen 1976). But it is also distributed in Asia, Africa, Australia, and South America, as well as some nearby islands, and in North America from Alaska to Mexico (ITIS 2020).



Figure 142. *Lophocolea bidentata*, a common Northern Hemisphere species of moist locations, occasionally submersed. Photo by Des Callaghan, with permission.

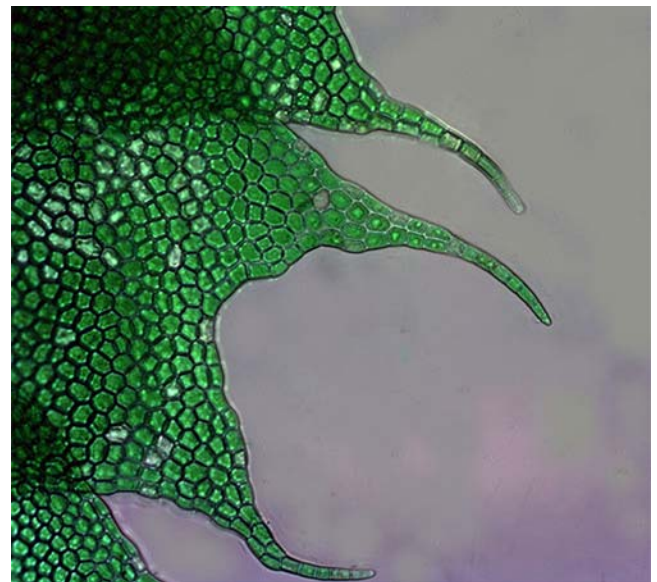


Figure 143. *Lophocolea bidentata* leaves. Photo by Aimon Niklasson, with permission.

Aquatic and Wet Habitats

Watson (1919) treated this species as occasionally submerged. This is consistent with its occurrence on moist rock surfaces or springy banks of ravines in Connecticut, USA (Nichols 1916). Similarly, Redfearn (1979) reported it from moist dolomite rocks in the Ozarks, Arkansas, USA. Glime *et al.* (1987) found it in Adirondack streams in northeastern USA. And Stephenson *et al.* (1995) reported it from mountain streams in West Virginia, USA, preferring a pH of 7.9.

Järvinen (1976) found it in moist places, including lake and river shores or near springs, considering it to be frequent in the central parts of Europe and North America, becoming rarer towards the north and south. It occurs on moist rock surfaces or springy banks of ravines in river bank of the River Tees, UK (Holmes & Whitton 1977a), but Ferreira *et al.* (2008) reported it from rivers. Wiltshire (1995) found it in dry stream beds in Ireland. Clapham (1940) reported it from the tops of high tussocks in calcareous fens of the Oxford District, UK. In Thuringia, Germany, it occurs in locations where one can find the submersed *Platyhypnidium-Fontinalis antipyretica* association (Figure 102, Figure 103), (Marstaller 1987). Also in Europe, it occurs in mountainous streams on Madeira Island (Luis *et al.* 2015).

On the subAntarctic Macquarie Island, Kirkpatrick and Scott (2002) found the species to be almost ubiquitous on the undisturbed coastal slopes.

Dulière *et al.* (2000) found no significant effect of liming on *Lophocolea bidentata* (Figure 142-Figure 143) compared to those on control stumps in a Norway spruce (*Picea abies*; Figure 89) forest in eastern Belgium.

Reproduction

Kent *et al.* (2005) studied the effects of long-term burial on bryophytes in the Outer Hebrides, Scotland. *Lophocolea bidentata* (Figure 142-Figure 143) occurred in the foredune turf and was among the plants experimentally buried to measure subsequent photosynthesis. They did not provide responses of individual species.

Sometimes *Lophocolea bidentata* (Figure 142-Figure 143) comes along for the ride. Fisk (2008) reported it as one of the species that travels with tree ferns [*Dicksonia fibrosa* (Figure 144) and *D. squarrosa* (Figure 145)] in horticultural and botanical garden trade.



Figure 144. *Dicksonia fibrosa*, a vector for spreading *Lophocolea bidentata* when it is planted in botanical gardens and other horticultural sites. Photo by Leon Perrie, through Creative Commons.



Figure 145. *Dicksonia squarrosa*, a vector for spreading *Lophocolea bidentata* when planted in botanical gardens and other horticultural sites. Photo by Jeremy Rolfe, through Creative Commons.

Udar and Srivastava (1977) were able to describe the development of the sporangia. Rincón (1993) examined the growth responses to different light intensities, identifying shoot bending, growth rate, and chlorophyll content. Biomass and growth rates increased as light intensity increased. However, of the six bryophytes in the study, *Lophocolea bidentata* (Figure 142-Figure 143) was the only one that did not exhibit etiolation in decreased light. Chlorophyll concentrations were highest in low light, but the chlorophyll *a:b* ratio did not clearly change with light intensity. Suleiman *et al.* (1980) identified volemitol as a photosynthetic product in *Lophocolea bidentata* in addition to fructose and sucrose.

Role and Fungal Interactions

When *Lophocolea bidentata* (Figure 142-Figure 143) grows on very wet rocks, it often has a significant diatom community forming periphyton on its surface (Round 1957). A species, yet to be identified, of the *Ascomycota* fungus *Octospora* is able to grow on the leaves (Eugenia Ron, Bryonet, 10 April 2021).



Figure 146. *Octosporella* sp. on *Lophocolea bidentata*, a liverwort that also promotes conditions for the growth of diatoms. Photo by Tomás Sobota, with permission.

Rhizoids of *Lophocolea bidentata* (Figure 142-Figure 143), borne in tufts at the bases of the underleaves, penetrate the substratum and their ends becoming profusely branched, like the haustoria of many fungi. Cavers (1903) examined saprophytism and mycorrhizae in liverworts. He determined that in *Lophocolea bidentata*, a species frequently occurring on decaying wood, the leafy gametophyte is entirely free from fungal hyphae. On the other hand, *Lophocolea bidentata* has been found growing on the fruiting body (basidiocarp) of *Phellinus* sp. – a fungus (Figure 147) (Vital *et al.* 2000).



Figure 147. *Phellinus igniarius*; the genus *Phellinus* serves as substrate for several bryophytes, including *Lophocolea bidentata*. Photo by George Chernilevsky, through Creative Commons.

Biochemistry

Mues *et al.* (1973) elucidated the carotenoids, identifying α -carotene, β -carotene, neo- β -carotene U, zeaxanthin, mono-cis-neoxanthin, trans-neoxanthin, poly-

cis-neoxanthin, violaxanthin neo V, violaxanthin, antheraxanthin, lutein, and lutein-5,6-epoxide.

Biochemical studies that might help to explain why fungal relationships in *Lophocolea bidentata* (Figure 142-Figure 143) are rare. Rieck *et al.* (1995) identified an epoxy-trinoreudesmane sesquiterpene but did not include any antibiotic studies. It appears that little is known of the biochemistry of this species.

Lophocolea heterophylla (Figure 148-Figure 150)

(syn. = *Chiloscyphus profundus*)

Distribution

Lophocolea heterophylla (Figure 148-Figure 150) is widely distributed throughout the temperate and subarctic regions of North America, Europe, and Asia (Hatcher 1967; Järvinen 1976). It is even more common when one recognizes *Chiloscyphus profundus* (Figure 151) as conspecific with this species, adding Africa to its distribution.



Figure 148. *Lophocolea heterophylla* showing a form with only shallow leaf lobes. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 149. *Lophocolea heterophylla* showing a form with deep leaf lobes. Photo by Paul Davison, with permission.



Figure 150. *Lophocolea heterophylla* underleaves. Photo by Blanka Agüero, with permission.



Figure 151. *Chiloscyphus profundus*, a former species now considered synonymous with *Lophocolea heterophylla*. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Koponen *et al.* (1995) considered *Lophocolea heterophylla* (Figure 152) to be aquatic in Finland. However, in Michigan, USA, I have found it only on decorticated logs in the forest, not in water. Likewise, Ignatov *et al.* (2005) found it on rotten logs and stumps in Tatarstan in European Russia. Šoltés and Zubařová (2015) considered it to be a species of decaying wood in the forests of the eastern Carpathians, Slovakia. Järvinen (1976) likewise reported it from decaying wood in moist places in eastern Fennoscandia and considered it to be widely distributed in Europe and Asia, as well as in both deciduous and coniferous forests in North America. Hatcher (1967) described its habitat as soil, decaying logs, tree bases, or on the vertical faces of sandstone bluffs.



Figure 152. *Lophocolea heterophylla* in a common log habitat. Photo by Bob Klips, with permission.

Slack and Glime (1985) found it associated with Adirondack Mountain streams in northeastern USA, where it had a broad niche (Glime *et al.* 1987). In western Canada it was restricted to terrestrial locations in montane streams and on stream banks (Vitt *et al.* 1986; Glime & Vitt 1987).

But it can in fact occupy streams. Koponen *et al.* (1995) considered it to be aquatic in Finland, and Toivonen and Huttunen (1995) reported it from small lakes in southern Finland. Marstaller (1987) found it in locations with the *Platyhypnidium-Fontinalis antipyretica* association (Figure 102, Figure 103) in Thuringia, Germany.

Zehr (1977) investigated it in three sandstone canyons in southern Illinois. When he attempted to correlate presence with vapor pressure deficit, plant surface temperature, and radiant energy in the blue, red, and far red wavelengths, as well as substrate pH and exchangeable potassium and phosphorus ions, he found that *Lophocolea heterophylla* (Figure 152) has a wide ecological amplitude. Of these, moisture seemed to be the most important in defining its microhabitat.

Hatcher (1967) also considered *Lophocolea heterophylla* (Figure 152) to be adapted to a wide range of environmental conditions, a fact that contributes to its morphological variability. Under adverse conditions, the plants maintain a prostrate growth, adhering closely to the substrate and attached by tufts of short rhizoids. These rhizoids arise from the lamina of the underleaves. When growing conditions are optimum, the stem tips instead are upright and the stems may attain a length of 3-4 cm. On the other hand, growing conditions seem to have no effect on the relationship of one character to another relating to cell dimensions. The male inflorescence occurs on the same stem as the female inflorescence in this monoicous species.

Some of this wide range of habitats includes decorticated logs. Jansová (2006) found it to be **epixylic** (logs with no bark) in Bohemia in the Czech Republic. She found that the 13 epixylic species in her study grew faster in winter (October-April) than in summer. Winter was also the season of extinction as well as of expansion. *Lophocolea heterophylla* (Figure 148-Figure 152) occurred in small, fragmented colonies.

Reproduction

Sporophyte development studies are lacking for most liverworts (Schertler 1979). A surprising number of studies have examined development of *Lophocolea heterophylla*, particularly looking at the sporophyte (Figure 153-Figure 155). Schertler reported that in this species the hypobasal cell gives rise only to the **haustorium** (sporophyte tissue that penetrates gametophyte for transfer of substances). Thomas and Doyle (1976) learned that during seta elongation, the seta cell walls thin considerably, reaching a 25-fold increase in cell length and a accompanying 2-fold increase in cell wall carbohydrates. Starch diminishes during elongation, with the polyfructosans and sucrose being replaced by fructose and glucose. Is this what nourishes the developing spores (Figure 156)?



Figure 153. *Lophocolea heterophylla* with developing capsules. Photo by Michael Lüth, with permission.



Figure 154. *Lophocolea heterophylla* with a sporophyte near maturity. Photo by Paul Davison, with permission.



Figure 155. *Lophocolea heterophylla* with mature and dehiscing capsules. Photo by David Holyoak, with permission.

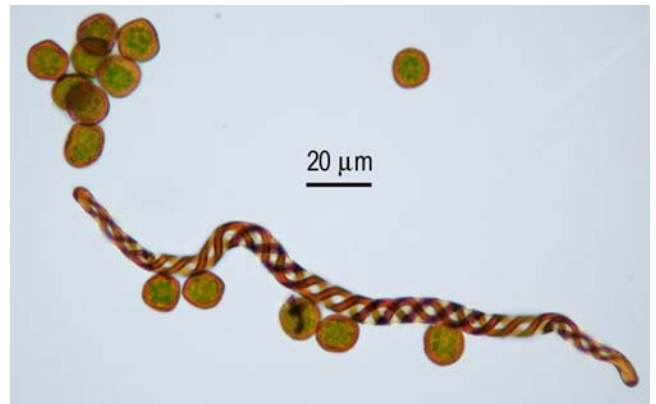


Figure 156. *Lophocolea heterophylla* spores and elater. Photo by Norbert Stapper, with permission.

Role

Lophocolea heterophylla can share its habitat with slime molds (Figure 157). Among these are species of the plasmodial slime mold *Lycogala*. These occur on especially on decorticated log habitats as shown here by Allen Norcross.

Biochemistry

Thomas *et al.* (1970) demonstrated that exogenous IAA could elicit a two-phase growth response in setae, with lower concentrations stimulating growth and higher concentrations inhibiting it. Elongation in the seta cells is facilitated by the increase in osmotic potential to -6 bars, causing a 16-fold increase in both length and water content of the cells (Thomas 1977a). At the same time, there is a correlation between the protein content and cell elongation (Thomas 1976). The seta cells are qualitatively similar to primary cell walls in tracheophytes, with starch content increasing 1.8-fold at they mature (Thomas 1977b). There is no net loss of lipids during elongation, with the primary fatty acid components being arachidonic and eicosapentaenoic acids (Thomas 1975a). This extensive elongation, reaching 50-fold, is accomplished in 3-4 days (Thomas 1977b).

Taylor *et al.* (1972) determined that the young sporophyte exhibits the same basic pigments (chlorophyll *a*, chlorophyll *b*, neoxanthin, violaxanthin, lutein, zeaxanthin, and β -carotene). In fact, the total chlorophyll

concentration is significantly greater in the young sporophyte than it is in the leafy gametophyte. Nevertheless, the photosynthetic activity of the sporophytes is very low when compared to the associated uppermost leaves, perianth, and bracts (Proctor 1982). Rather, most of the carbon is translocated from the gametophyte to the sporophyte. And this is primarily from the leafy shoots, with little from the perianth, bracts, or even the uppermost leaves. It is interesting that the translocation from the gametophyte seems to be greatest when the capsule reaches full size but is still green. Once the capsule reaches its final stages of maturation, the translocation declines. This pattern would provide the greatest translocation of carbon during the spore development phase.



Figure 157. *Lophocolea heterophylla* and the plasmodial slime mold *Lycogala epidendrum* on decorticated log. Photo by Allen Norcross, with permission.

Konečný *et al.* (1982) described a number of sesquiterpenes from *Lophocolea heterophylla* (Figure 148-Figure 152). Herout (1985) considered the fragrance of *Lophocolea heterophylla* to be suitable for perfume, perhaps coming from the oil bodies (Figure 158). Toyota *et al.* (1990) isolated (–)-2-methylisoborneol as the source of its fragrance and described additional sesquiterpenoids. Tazaki *et al.* (1999) demonstrated the formation of lignans. Even the seta exhibits an array of sesquiterpenoids (Thomas 1975b). These vary before and during elongation. In 2002 Tazaki *et al.* isolated a caffeic acid derivative, subulatin, a compound known for its antitoxic effects. (See also Pavletic & Stilinovic 1963; Wolters 1964).

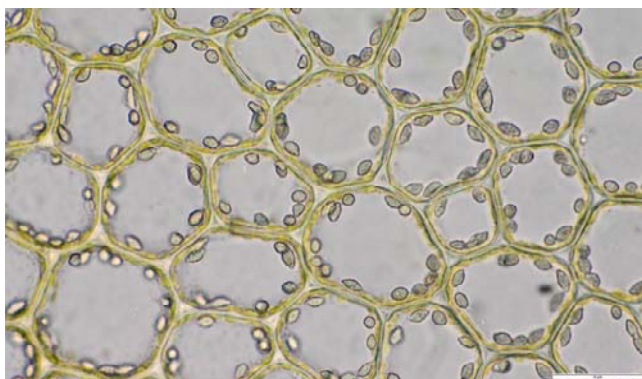


Figure 158. *Lophocolea heterophylla* leaf cells showing oil bodies, the site of at least some of the secondary compounds, especially aromatic ones. Photo by Blanka Aguero, with permission.

Nikolajeva *et al.* (2012) found that an extract of *Lophocolea heterophylla* (Figure 148-Figure 152) inhibited the growth of *Bacillus cereus* (Figure 159), but not the growth of *Escherichia coli* (Figure 160).

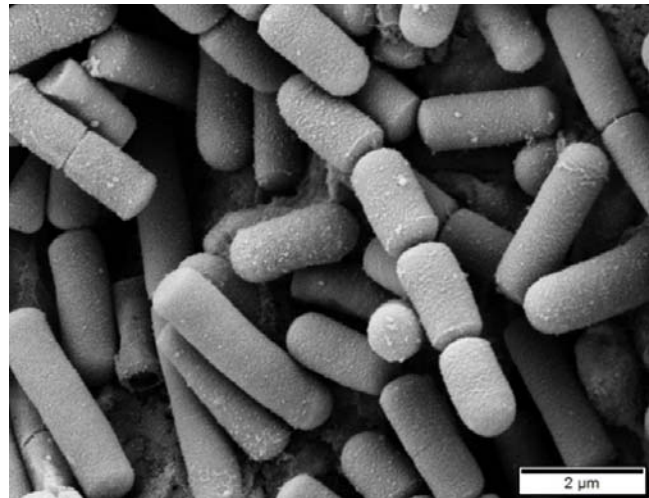


Figure 159. *Bacillus cereus*, a bacterial species inhibited by extracts of *Lophocolea heterophylla*. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.



Figure 160. *Escherichia coli*, a bacterial species not affected by extracts of *Lophocolea heterophylla*. Photo by NIAID, through Creative Commons.

Lophocolea minor (Figure 161-Figure 162)

Distribution

Lophocolea minor (Figure 161-Figure 162) is sometimes included in *Lophocolea heterophylla* (Figure 148-Figure 152), but Söderström *et al.* (2016) maintain it as a separate species. It occurs across the Northern Hemisphere, from Alaska south to the continental USA and in the Eastern Hemisphere south to Spain (EOL.org 2020). Africa and South America also have records (ITIS 2020).



Figure 161. *Lophocolea minor*, a species similar to *Lophocolea heterophylla* that occurs across the Northern Hemisphere. Photo from Earth.com, with permission.

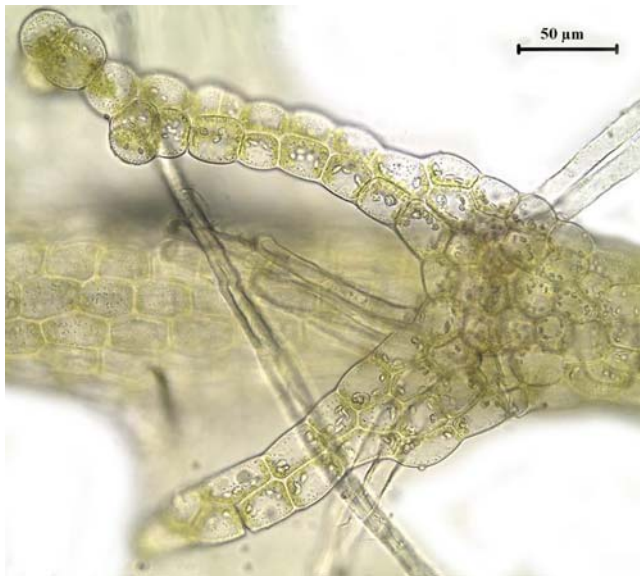


Figure 162. *Lophocolea minor* underleaf. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Among the early records of wet habitats for this species, Nichols (1916) reported it along calcareous rivers in Connecticut, USA. It is a restricted terrestrial along montane streams and stream banks in western Canada (Vitt *et al.* 1986; Glime & Vitt 1987). It also occupies debarked rotting logs in Genesee County, New York, USA (Lyman & Coleman 1966). In Quebec, Canada, it occurs on shaded rocks and banks (Evans 1916), habitats similar to those of the rock ledges and ground at the mouth of the Montreal River in the Upper Peninsula of Michigan, USA (Evans & Nichols 1935). Janssens and Glaser (1986) occasionally found it in the Red Lake peatlands of northern Minnesota, USA. Darlington (1938) found it on an earth bank at the south end of Glen Lake, Michigan, USA. In southern Michigan, USA, Nichols (1933) found this species on high banks of the Henton Creek. In Iowa USA, Conard (1940)

attributed it to mesic woods and Cavanagh (1930) found it on moist, shady banks. However, Statler (1949) found that this species in Henry County, Iowa, preferred drier sites than those of *Lophocolea heterophylla* (Figure 152).

In Thuringia, Germany, it occurs along streams where one can find the *Platyhypnidium-Fontinalis antipyretica* association (Figure 102, Figure 103) (Marstaller 1987). Papp and Erzberger (2007) found it on soil among limestone rocks in Montenegro. In the Djerdap National Park of eastern Serbia, Papp *et al.* (2006b) found it on limestone rock. On the Spanish island of Minorca in the Mediterranean sea, *Lophocolea minor* (Figure 161-Figure 162) was associated with temporary ponds (Pericàs *et al.* 2009).

In the Eastern Caucasus of Russia, Konstantinova (2011) found it on decaying logs on a stream bank or in mats, mixed with other liverworts such as *Conocephalum conicum* (Figure 163), *Pellia endiviifolia* (Figure 164), *Porella platyphylla* (Figure 165), *Plagiochila porelloides* (Figure 18), *Preissia quadrata* (Figure 166), *Reboulia hemisphaerica* (Figure 167), and *Scapania cuspiduligera* (Figure 168). Dulin (2015) added greatly to these records through exploration in the Komi Republic of northwestern Russia. These included decaying wood, on fine grained soil of turned out wood roots, on wet, slightly matted soil, on trails in forests communities with soil surface covered with dead wood leaves, on tree butts in mires and boggy areas. It sometimes occurred in pure patches and other times associated with *Blepharostoma trichophyllum* (Figure 2-Figure 3), *Cephalozia* spp. (Figure 7, Figure 80), *Chiloscyphus polyanthos* (Figure 106-Figure 108), *Geocalyx graveolens* (Figure 169), *Lophocolea heterophylla* (Figure 148-Figure 150), *Lophozia ventricosa* s.l. (Figure 26), *Plagiochila porelloides*, *Scapania* spp. (Figure 168) and other species.



Figure 163. *Conocephalum conicum*, a species that sometimes accompanies *Lophocolea minor* on stream banks or decaying logs. Photo by Janice Glime.



Figure 164. *Pellia endiviifolia*, a species that sometimes accompanies *Lophocolea minor* on stream banks or decaying logs. Photo by Michael Lüth, with permission.



Figure 165. *Porella platyphylla*, a species that sometimes accompanies *Lophocolea minor* on stream banks or decaying logs. Photo by Hugues Tinguy, with permission.



Figure 166. *Preissia quadrata* on wet rock, a species that sometimes accompanies *Lophocolea minor* on stream banks. Photo by Andy Hodgson, with permission.



Figure 167. *Reboulia hemisphaerica*, a species that sometimes accompanies *Lophocolea minor* on stream banks. Photo by Janice Glime.



Figure 168. *Scapania cuspiduligera*, a species that sometimes accompanies *Lophocolea minor* on stream banks and mires or boggy areas. Photo by Hugues Tinguy, with permission.



Figure 169. *Geocalyx graveolens*, a species that sometimes accompanies *Lophocolea minor* in mires and boggy areas. Photo by Hugues Tinguy, with permission.

Reproduction

Statler (1949) described the leaves of *Lophocolea minor* (Figure 161-Figure 162) in Iowa as sometimes being almost entirely composed of gemmae (Figure 170).

Sabovljević *et al.* (2001) considered *Lophocolea minor* to have a distinctive "mossy" smell.

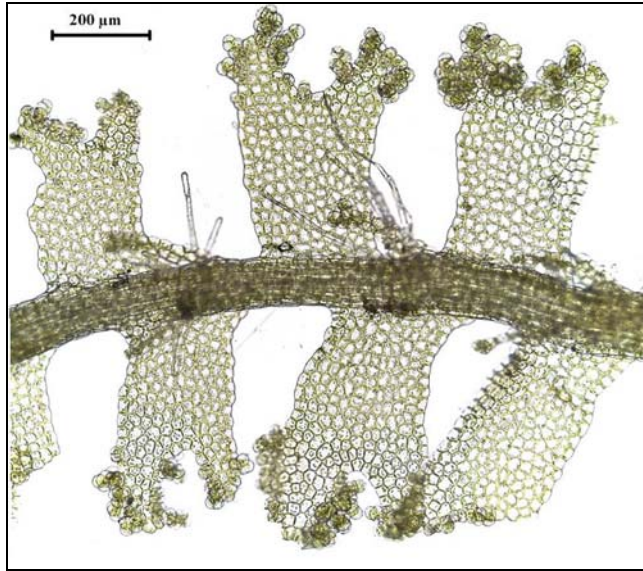


Figure 170. *Lophocolea minor* showing gemmae. Photo by Hugues Tinguy, with permission.

Lophocolea mollis

Ruttner (1955) found *Lophocolea mollis* in acidic thermal sprays in the tropics. Söderström *et al.* (2010) reported it from Java. Otherwise, there seems to be little published about this species.

Lophocolea semiteres (Figure 171-Figure 173)

(syn. = *Chiloscyphus semiteres*, *Jungermannia semiteres*)

Distribution

Lophocolea semiteres (Figure 171-Figure 173) has been recorded from South Africa, where it is relatively common, Australia, New Zealand, Vanuatu, Falkland Islands, Chile, Juan Fernández Islands, Scotland, Belgium, The Netherlands, Northern Ireland, and Marion Island (subAntarctic in Indian Ocean) (Vána & Gremmen 2014). Barry Stewart has photographed its habitat and recorded its presence on Skomer Island, Wales (Figure 174).



Figure 171. *Lophocolea semiteres*, a species of streams in New Zealand, but an invasive species in Europe. Photo by Des Callaghan, with permission.



Figure 172. *Lophocolea semiteres* showing underleaves. Photo from freenatureimages.eu, through Creative Commons.



Figure 173. *Lophocolea semiteres*. Photo by Tom Thekathyl, with permission.



Figure 174. *Lophocolea semiteres* habitat on Skomer Island, Wales. Photo by Barry Stewart, with permission.

Paton (1965) identified this species from a woodland path in Tresco on the Isles of Scilly, a first record for the Northern Hemisphere. By 1982 it was well established in Argyll, Scotland, apparently introduced from New Zealand and occurring in gardens (Long 1982). But now, it is considered an invasive species in Belgium and The Netherlands (Stieperaere 1994). Where it invades a

pinewood forest in Belgium and The Netherlands, it becomes the dominant species of *Lophocolea*, nearly excluding *L. heterophylla* (Figure 148-Figure 150) and diminishing the presence of *L. bidentata* (Figure 142-Figure 143) (Stieperaere *et al.* (1997).

Aquatic and Wet Habitats

Van Zanten (2003) reported its occurrence in The Netherlands on an open ditch wall in oak-birch forest with some spruces and beech and on coarse humus and twigs, sparingly occurring with *Eurhynchium praelongum* (Figure 175) and *Plagiothecium laetum* (Figure 176).



Figure 175. *Eurhynchium praelongum*, a species that accompanies *Lophocolea semiteres* in the oak-birch forest in The Netherlands. Photo by David T. Holyoak, with permission.



Figure 176. *Plagiothecium laetum*, a species that accompanies *Lophocolea semiteres* in the oak-birch forest in The Netherlands. Photo by Hermann Schachner, through Creative Commons.

In New Zealand, *Lophocolea semiteres* (Figure 171-Figure 173) occurs in some of the 48 studied streams on South Island (Suran & Duncan 1999). Fineran (1971) found it in a seepage area above the shore on one of the Auckland Islands off the coast of South Island, New Zealand. But at Pupu Springs (Figure 177), New Zealand, it seems to have its most aquatic habitat, submerged on boulders in water with a strong velocity (Mjchaelis 1977). In Australia it occurs in the Warm Temperate Victorian Rainforest streams (Carrigan 2008).



Figure 177. Pupu Springs, New Zealand, site of submerged populations of *Lophocolea semiteres*. Photo by Kieron Norfield, through Creative Commons.

Elsewhere, *Lophocolea semiteres* (Figure 171-Figure 173) seems to have chosen other types of habitats. On Marion Island, Vána and Gremmen (2014) found it on damp grassland in large mats, often with *Marchantia berteriana* (Figure 178), and growing on black lava rock in a small cave, where it formed large, loose mats.



Figure 178. *Marchantia berteriana* with archegoniophores, a species associated with *Lophocolea semiteres* in damp grassland on Marion Island. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

In northern Japan, on Mt. Hakkōda, this species occurs on the lower portion of various species of tree trunks (Figure 179) (Kitagawa 1978). Floyd and Gibson (2012) described them from urban industrial streetscapes in Victoria, Australia, where they were the most frequently occurring liverwort, forming **weft**-like growths (Figure 180) on gravel, cement, and soil. In addition, they frequently occurred among grass species in very wet, well shaded areas, providing protection from wind erosion.

Its Northern Hemisphere habitats seem drier than those in New Zealand (Figure 181 (Finch *et al.* 2000). Finch and collaborators were the first to find it in a swampy area, in addition to other more terrestrial habitats, in East Anglia, England.



Figure 179. *Lophocolea semiteres* on bark, a substrate where one might find it in northern Japan. Photo by Michael Lüth, with permission.



Figure 180. *Lophocolea semiteres*, approaching a weft-like form. Photo by Brian Eversham, with permission.



Figure 181. *Lophocolea semiteres*, dried. Photo by Barry Stewart, with permission.

Reproduction

Lophocolea semiteres is **dioicous** (Paton 1965). Nevertheless, it can be found with antheridia (Figure 182) capsules (Figure 183-Figure 184). Paton (1999) does not consider the structures on the leaf margins to be true **gemmae**, but rather are asexual reproductive structures

that are regenerants – tiny buds which develop from a cell to form small plantlets. Engel (pers. comm. 20 August 2020) told me it does not produce gemmae.



Figure 182. *Lophocolea semiteres*, showing swollen leaf bases where the antheridia reside. Photo by Dick Haaksma, with permission.



Figure 183. *Lophocolea semiteres* with mature capsules. Photo by David Tng, with permission.



Figure 184. *Lophocolea semiteres* dehiscent capsule. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission.

Biochemistry

Biochemical studies seem to be lacking. The species has large, hyaline oil bodies (Figure 185) that might yield interesting secondary compounds.

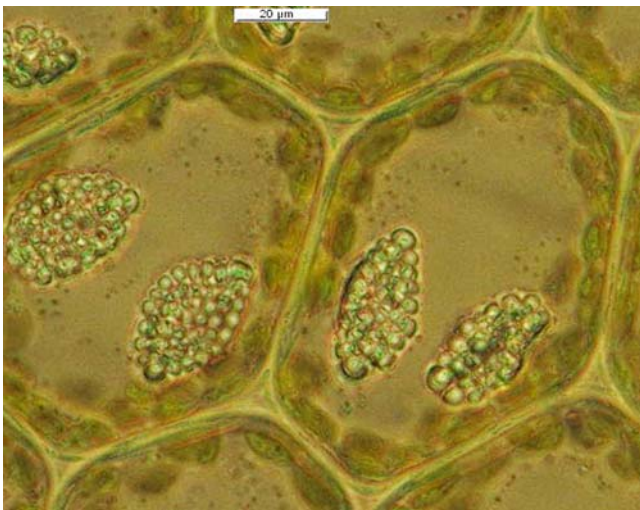


Figure 185. *Lophocolea semiteres* leaf cells with hyaline oil bodies. Photo by Tom Thekathyl, with permission.

Pachyglossa (Figure 186)

Pachyglossa (Figure 186) is a Southern Hemisphere genus with several species. In New Zealand, *Pachyglossa* is known from streams. *Pachyglossa* sp. is positively

correlated with bankfull discharge in the studied 48 streams on South Island, New Zealand (Suran & Duncan 1999).

Pachyglossa austrigena subsp. *okaritana* (Figure 186)

Distribution

Pachyglossa austrigena subsp. *okaritana* (Figure 186) is an Australasian species (Engel 1992).



Figure 186. *Pachyglossa austrigena* subsp. *okaritana*, an Australasian facultative aquatic species. Photo by Peter De Lange, through Creative Commons.

Aquatic and Wet Habitats

Pachyglossa austrigena subsp. *okaritana* (Figure 186) can be obligately or facultatively aquatic in South Island, New Zealand, streams (Suren 1996). It was one of the species that was positively correlated with bankfull discharge in 48 streams in South Island, New Zealand (Suran & Duncan 1999). In the Antipodes Island, New Zealand, it occurred on a wet cliff face (Godley 1989). It appears that its limited distribution has caused it to escape extensive study.

Pachyglossa dissitifolia

Distribution

Pachyglossa dissitifolia is a species of the extreme south. It occurs on Livingston Island in the South Shetland Islands (Bednarek-Ochyra *et al.* 2000). Engelskjøn (1986) noted that *Pachyglossa dissitifolia* occurs on the Antarctic Peninsula, but the distribution in Fuegia - Patagonia is also fairly extensive, reaching eastward to Bouvetøya and northward to Tristan da Cunha. Otero *et al.* (2008) collected *Pachyglossa dissitifolia* on Tierra del Fuego, Argentina.

Aquatic and Wet Habitats

On the South Shetland Islands *Pachyglossa dissitifolia* occurs in Midge Lake at about 1-2 m depth (Bednarek-Ochyra *et al.* 2000). There it is associated with *Drepanocladus longifolius* (Figure 187) and *Warnstorfia sarmentosa* (Figure 188).



Figure 187. *Drepanocladus longifolius*, a species associated with *Pachyglossa tenacifolia* in the epilithic submerged bryoflora of Macquarie Island. Photo by John Game, through Creative Commons.



Figure 188. *Warnstorfia sarmentosa*, a species associated with *Pachyglossa tenacifolia* in the epilithic submerged bryoflora of Macquarie Island. Photo by A. Neumann, Biopix.com, with online permission for educational use.

Otero *et al.* (2008) collected *Pachyglossa dissitifolia* from lakes on Tierra del Fuego, Argentina. They included it among a number of species they tested for range of maximum absorption of light. For this species, the maximum absorption was at 327 nm. It was in the second of two groups of bryophyte species, having lower concentrations of UV-absorbing compounds. This is to be expected for a species collected in the deeper water of lakes where the water serves as a filter of the UV radiation.

Pachyglossa tenacifolia

Distribution

On Macquarie Island in the sub-Antarctic, *Pachyglossa tenacifolia* is an indicator species, occurring in Scoble and Tulloch Lakes (Hughes 1986). Li *et al.* (2009) noted that *Pachyglossa* was the only liverwort reported from an Antarctic lake. They reported *Pachyglossa tenacifolia* was collected from relatively shallow waters at 1-2 m depth in Prion Lake, sub-Antarctic Macquarie Island.

Aquatic and Wet Habitats

Fife (2015) collected *Pachyglossa tenacifolia* among the submerged vegetation at the edge of a small lake at 110 m elevation on Macquarie Island. It was associated there

with *Blindia seppeltii*, *Ditrichum strictum* (Figure 189), and *Riccardia aequicellularis* (Figure 190). In the epilithic submerged bryoflora, it was associated with *Blindia lewinskyae* (Figure 191), *Pachyglossa austrigena* (Figure 192), and *Hepatostolonophora rotata* (see Figure 117).



Figure 189. *Ditrichum strictum* balls, a species that is associated with *Pachyglossa tenacifolia* submerged at the edge of a lake on Macquarie Island. Photo by Franek2, through Creative Commons.



Figure 190. *Riccardia aequicellularis*, a species that is associated with *Pachyglossa tenacifolia* submerged at the edge of a lake on Macquarie Island. Photo by Tom Thekathyil, with permission.



Figure 191. *Blindia lewinskyae*, a species associated with *Pachyglossa tenacifolia* in the epilithic submerged bryoflora of Macquarie Island. Photo by John Braggins, with permission.



Figure 192. *Pachyglossa austrigena*, a species associated with *Pachyglossa tenacifolia* in the epilithic submerged bryoflora of Macquarie Island. Photo by Peter De Lange, through Creative Commons.

Mastigophoraceae

Mastigophora diclados (Figure 193)

Distribution

Mastigophora diclados (Figure 193) is Palaeotropical, distributed in African (including Madagascar), Asian, and Australian tropics, but not the Neotropics (Marline 2018). It is common in the Asiatic tropics (Inoue 1973) and is known from Hong Kong (So & Zhu 1996) and Reunion Island (Molnár *et al.* 2003). Daniels and Kariyappa (2012) reported it from Peninsular India; it was already known from the Eastern Himalaya and Nicobar Islands.



Figure 193. *Mastigophora diclados*, a Palaeotropical species. Photo by Claudine Ah-Peng, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported that *Mastigophora diclados* (Figure 193) occurs in acidic thermal sprays in the tropics. But otherwise, it appears in moist habitats near water, but not in water, and even occurs on trees (Figure 194).



Figure 194. *Mastigophora diclados* on tree on São Tomé Island. Photo by César Garcia, through Creative Commons.

This is a tall species that is abundant at higher elevations (850-2050 m) (Marline 2018). In Taiwan, it occurs in the watershed of the acidic alpine Yuan-Yang Lake (Figure 195) (Wu *et al.* 2001). Similarly, it occurs on the ground in the Upper Montane zone in Tanzania, forming **cushions** (Doggart & Loserian 2007).



Figure 195. Yuan-Yang Lake Reserve in alpine, Taiwan, habitat for *Mastigophora diclados*. Photo from Nature Reserve, through Creative Commons.

Adaptations

In the tropical mountainous rainforest it can be subjected to high light intensity, particularly in the UV-B range. Molnár *et al.* (2003) subjected *Mastigophora*

diclados (Figure 193-Figure 194) from Reunion Island to three hours high light, causing a 50% drop in F_v/F_p (ratio of variable to maximum fluorescence in PS II) in shade plants, compared to a 20% drop in sun plants. This drop in sun plants was due to a pronounced inactivation of functional PS II reaction centers. The sun plants recovered completely in one hour, whereas the shade plants had reached only 70% recovery after three hours.

Biochemistry

Mastigophora diclados (Figure 193-Figure 194) has experienced its share of biochemical studies. Zaki (2014) reported that the oil bodies synthesize and store a variety of lipophilic acetogenins, terpenoids, and aromatic compounds, with *Mastigophora diclados* producing sesquiterpenoid herbertene compounds. Otari (2013) reported that the phenolic sesquiterpenes in this species are known to have cytotoxic, antioxidant, and antimicrobial properties. But in tests to evaluate the effect on glucose levels in rats, there was a 64% reduction by an n-hexane extract of the liverwort; the difference was not significantly different from the control using glibenclamide (medication used to treat diabetes mellitus type 2).

Komala *et al.* (2010) found that *Mastigophora diclados* (Figure 193-Figure 194) contained various volatile sesqui- and diterpenoids and aromatic compounds that presented cytotoxic activity against certain cancer cell lines, radical scavenging activity, and antimicrobial activity against *Staphylococcus aureus* (Figure 196) and *Bacillus subtilis* (Figure 197). Harinantenaina and Asakawa (2007) isolated unique sesquiterpenoids, mastigophorenes, known only from *Mastigophora diclados*. Other studies have named more compounds or elucidated structures (Fukuyama & Asakawa 1991; Leong & Harrison 1997; Hashimoto *et al.* 2000; Harinantenaina & Asakawa 2004; Ludwiczuk *et al.* 2009; Komala *et al.* 2010; Ng *et al.* 2017). Some of these differed between populations and were considered taxonomic markers.

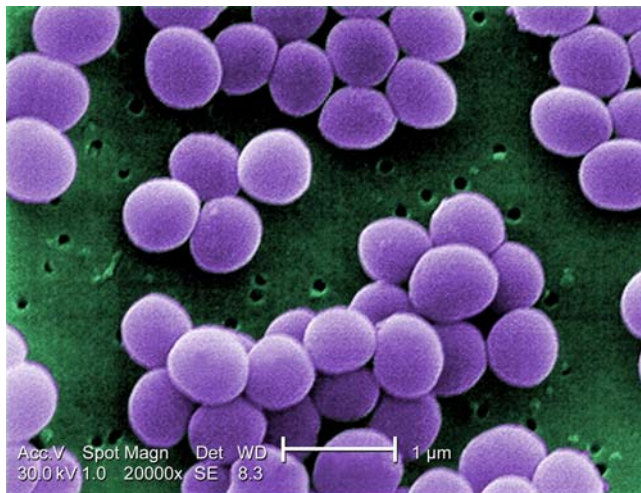


Figure 196. *Staphylococcus aureus*; *Mastigophora diclados* exhibits antibiotic activity against this bacterium. Photo by Janice Haney Carr, CDC, through public domain.

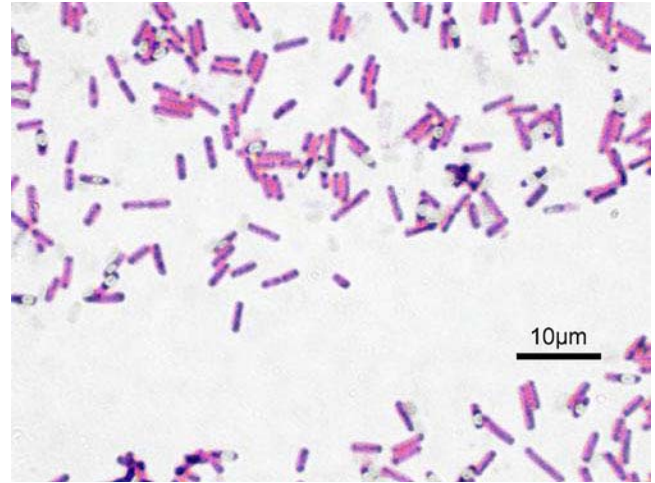


Figure 197. *Bacillus subtilis* with Gram stain; *Mastigophora diclados* exhibits antibiotic activity against this bacterium. Photo by Y. Tambe, through Creative Commons.

Summary

The **Lophocoleineae** occupy a wide range of habitats, many of which are wet, but few are truly aquatic. Among the species that are able to occur and thrive in submersed condition, *Herbertus sendtneri* occurs in a glacial lake in the Andes, but most of its reported habitats are never or rarely submersed. Others, like *Kurzia makinoana*, are common on stream banks and in swamps and mires. *Chiloscyphus polyanthos* is typically submersed, whereas *C. pallescens* prefers mires and springs on wet soil, so both require a habitat that rarely leaves them dry. These two species don't typically develop rhizoids under water and are often dark-colored there. Some species of **Lophocoleineae** are amphibious, being submerged during flooding. Some, like *Lophocolea heterophylla*, are aquatic in some parts of the world, but not in others. *Lophocolea semiteres* is aquatic at Pupu Springs on South Island, New Zealand, but is an invasive terrestrial species in Europe. In bog and other peaty habitats many **Lophocoleineae** survive and reproduce by stolons that penetrate the peat. Many have fungal associates, and probably all have secondary compounds that protect them from infections and herbivory. Even so, many have fungal inhabitants whose roles need further investigation.

Acknowledgments

Lars Söderström provided invaluable help with the current acceptable names for a number of older taxa. Thank you to Eugenia Ron for sharing on Bryonet her find of *Octosporella* on *Lophocolea bidentata* and obtaining permission to use the image.

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CHAPTER 1-6

AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: LOPHOCOLEINEAE, PART 2, MYLINEAE, PERSSONIELLINEAE

TABLE OF CONTENTS

Suborder Lophocoleineae	1-6-2
Plagiochilaceae	1-6-2
<i>Pedinopyllum interruptum</i>	1-6-2
<i>Plagiochila</i>	1-6-5
<i>Plagiochila aspleioides</i>	1-6-5
<i>Plagiochila bifaria</i>	1-6-10
<i>Plagiochila porelloides</i>	1-6-11
<i>Plagiochila punctata</i>	1-6-16
<i>Plagiochila renitens</i>	1-6-17
<i>Plagiochila retrospectans</i>	1-6-17
<i>Plagiochila spinulosa</i>	1-6-18
<i>Plagiochilon oppositum</i>	1-6-20
Trichocoleaceae	1-6-20
<i>Trichocolea tomentella</i>	1-6-20
Suborder Myliineae.....	1-6-24
Myliaceae.....	1-6-24
<i>Mylia anomala</i>	1-6-24
<i>Mylia taylorii</i>	1-6-31
Suborder Perssoniellineae.....	1-6-37
Schistochilaceae.....	1-6-37
<i>Schistochila aligera</i>	1-6-37
Summary.....	1-6-37
Acknowledgments	1-6-37
Literature Cited	1-6-38

CHAPTER 1-6

AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES – LOPHOCOLEINEAE, PART 2, MYLIINEAE, PERSSONIELLINEAE

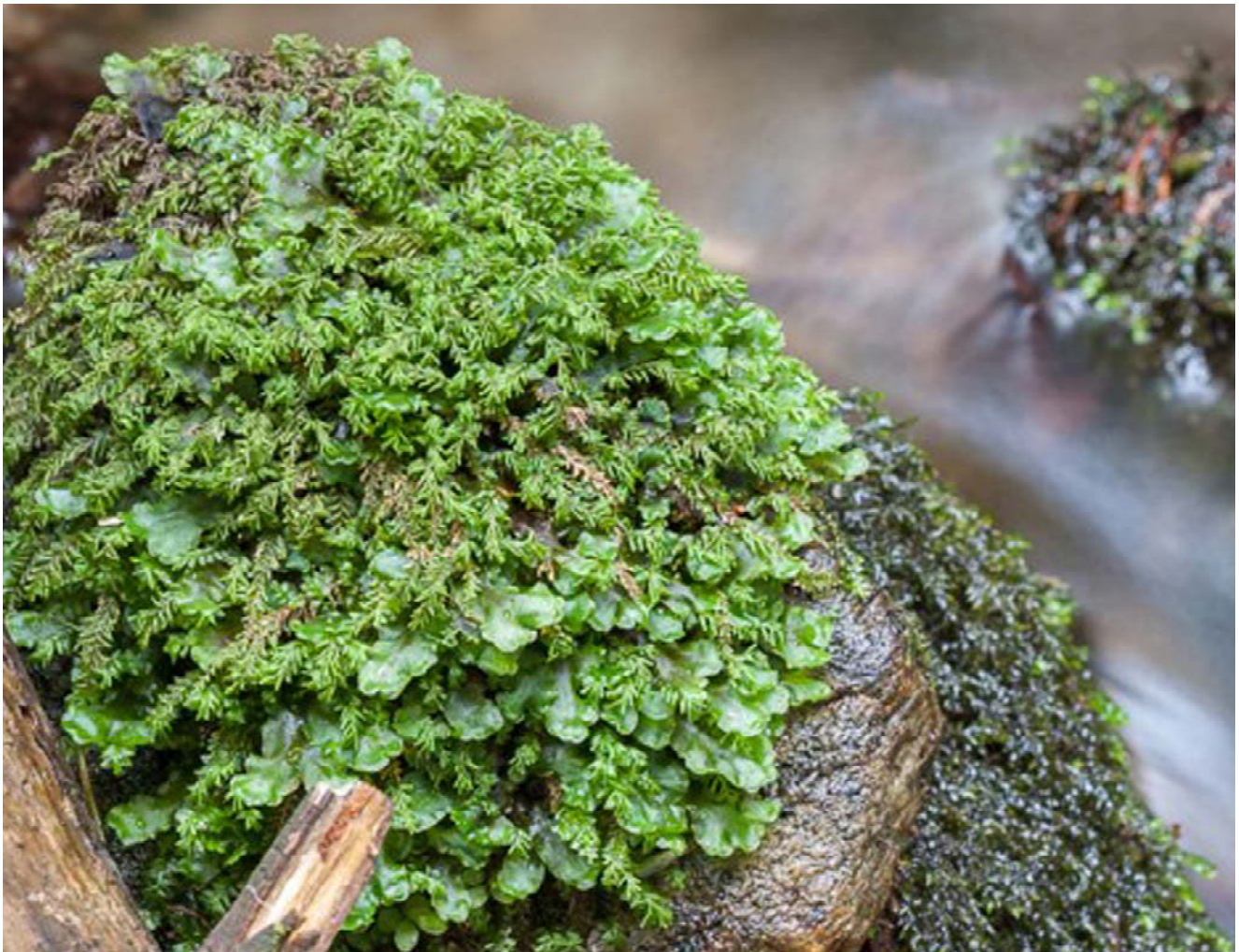


Figure 1. *Plagiochila porelloides* by stream, where it is overgrowing a patch of *Pellia*. Photo by Štěpán Koval, with permission.

Suborder Lophocoleineae, cont.

Plagiochilaceae

Pedinophyllum interruptum (Figure 2-Figure 4)

Distribution

Pedinophyllum interruptum (Figure 2-Figure 4) is a Northern Hemisphere species, best known from Europe,

but also with scattered records in North American and Japan (GBIF 2020). De Miguel and Indurain (1984) considered it to be circumboreal. Martinez-Abaigar and Ederra (1992) reported it from Spain and Sotiaux and Vanderpoorten (2017) from nearby Andorra. There are records from Belgium (Sotiaux *et al.* 2007), Albania, where it was removed from the red list (Marka *et al.* 2012), and Iran (Frey & Kürschner 1983). It is relatively abundant in Croatia (Pandža & Milović 2015).

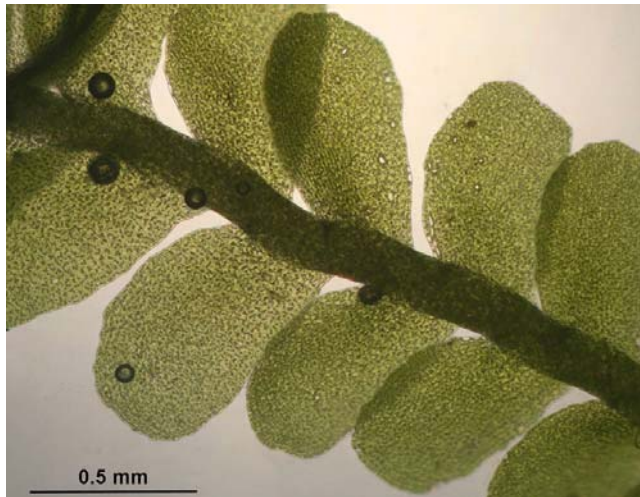


Figure 2. *Pedinophyllum interruptum* branch, a circumboreal species, occurring south into Europe, China, and Iran. Photo by Hermann Schachner, through Creative Commons.



Figure 3. *Pedinophyllum interruptum* underleaf. Photo by Hermann Schachner, through Creative Commons.



Figure 4. *Pedinophyllum interruptum* forming mats. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Watson (1918) recognized the limestone association of *Pedinophyllum interruptum* (Figure 2-Figure 4) in East Somerset, UK. In the Tara River canyon, it occurs on limestone rock and at a spring in the Tara River canyon and the Durmitor area, Montenegro (Papp & Erzberger 2011). In the UK, it typically grows on or near Carboniferous or metamorphic limestone, occupying both rock and soil, or in wooded gorges or other very humid, sheltered upland sites (BBS 2020). It tolerates both open, bare limestone rock and deep shade. It likewise occupies shaded limestone in Croatia (Alegro *et al.* 2014), Macedonia (Papp *et al.* 2016), and Greece (Papp & Tsakiri 2017). Gerdol *et al.* (1991) found it to be frequent in moist carbonatic rocky habitats in the southern Italian Alps. De Miguel and Indurain (1984) considered it a saxicolous calcicole in La Foz de Arbayún, Spain.

Chytrý and Tichý (2003) termed the species **chasmophytic** (referring to plant growing in crevices of rocks) on shaded calcareous cliffs of the Czech Republic. In Bulgaria, Gecheva and Yurukova (2013) found it downstream from a karst spring. Veljić *et al.* (2001) similarly found it at well springs in a karst area of Serbia. Liu *et al.* (2019) found that it was rare outside karst sinkholes in Guizhou Province, Southwestern China, but could be found at the bottom of the sinkholes, a location they considered more suitable because of the greater presence of water and nutrition.

Pedinophyllum interruptum (Figure 2-Figure 4) occurs in Iskur River, Bulgaria, and its main tributaries (Papp *et al.* 2006). Choi *et al.* (2010) found it near streams or at the top of ridges on Mt. Deogyu in Korea. Tacchi *et al.* (2009) on rocks in ravines in the Apennines. In Thuringia, Germany, Marstaller (1987) found that *Pedinophyllum interruptum* occurs in streams with the *Platyhypnidium* (Figure 5) – *Fontinalis antipyretica* (Figure 6) association. But Frahm (1987) also found it in moist, shaded forests in Germany. In the UK, Preston *et al.* (2011) found that it is frequently associated with *Scapania undulata* (Figure 7).



Figure 5. *Platyhypnidium riparioides*, often an indicator of suitable habit for *Pedinophyllum interruptum*. Photo by Hermann Schachner, through Creative Commons.



Figure 6. *Fontinalis antipyretica* in Indian River, often an indicator of suitable habit for *Pedinophyllum interruptum*. Photo by Matt Goff <www.sitkanature.org>, with permission.



Figure 7. *Scapania undulata*, a species often associated with *Pedinophyllum interruptum*. Photo by Hugues Tinguy, with permission.

In North America, *Pedinophyllum interruptum* (Figure 2-Figure 4) was found on dolomite rocks in a ravine in Brookfield, Connecticut, USA (Evans 1910). It is also known from Greenland, Labrador, a few additional locations in Canada, and Ohio, USA.

Reproduction

Pedinophyllum interruptum (Figure 2-Figure 4) is **monoicous** (Rycroft 2021).

Fungal Interactions

Bidartondo and Duckett (2010) examined 30 bryophyte species, represented by a total of 200 collections. Among these, only four species failed to present any fungal DNA sequences. One of these was *Pedinophyllum interruptum* (Figure 2-Figure 4). Perhaps *Pedinophyllum interruptum* is able to inhibit fungal growth through its extensive array of secondary compounds. Wang and Qiu (2006) likewise were unable to find any reference to a mycorrhizal relationship in this species.

But the species is not totally fungus free. Döbbeler (1998) reported *Epibryon pedinophylli* (see Figure 8) as a leaf-perforating ascomycete from *Pedinophyllum interruptum* (Figure 2-Figure 4). However, this fungus might not occur on aquatic populations (Peter Döbbeler, pers. comm. 8 September 2020).



Figure 8. *Epibryon* perithecia (arrows) on *Sphagnum* and surrounded by *Botryococcus*. *Epibryon pedinophylli* is only known from *Pedinophyllum interruptum*. Photo through Creative Commons.

Biochemistry

Pedinophyllum interruptum has oil bodies (Figure 9), where we might expect to find some of its secondary compounds. Feld *et al.* (2004) identified several secondary compounds in *Pedinophyllum interruptum* from Scotland. Liu *et al.* (2013) elucidated the structures of ten diterpenoids in Chinese populations of *Pedinophyllum interruptum*. Seven of the pedinophyllols in this species inhibited seed germination and root growth of *Arabidopsis thaliana* (Figure 10) with a dose-dependent response (Wei *et al.* 2019). Do such compounds provide *Pedinophyllum interruptum* with a means to compete in its limestone habitats?

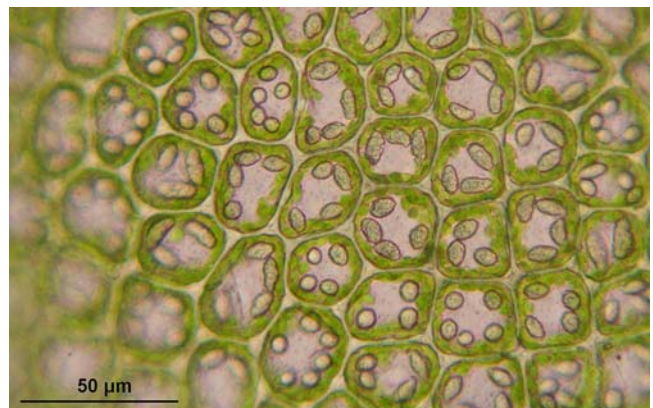


Figure 9. *Pedinophyllum interruptum* leaf cells showing oil bodies, a location of secondary compounds. Photo by Hermann Schachner, through Creative Commons.



Figure 10. *Arabidopsis thaliana*, a species for which root growth is inhibited by extracts from *Pedinophyllum interruptum*. Photo through Creative Commons.

Plagiochila

The genus *Plagiochila* includes rheophytes in the wet tropics of SE Asia (Akiyama 1992) and west Africa (Shevock *et al.* 2017).

Other general characteristics of the genus include the documentation of surface wax in the family, including *Plagiochilon mayebarae* and five species of *Plagiochila* (Heinrichs *et al.* 2000). These waxes were previously unknown in the family and cannot be detected with a light microscope. I am aware of no evidence if these are present in aquatic populations, but it would be interesting to compare them in aquatic and terrestrial populations and through moisture gradients of streambank populations.

***Plagiochila asplenoides* (Figure 11, Figure 14)**

(syn. = *Plagiochila maior*)

Plagiochila asplenoides (Figure 11, Figure 14) has been plagued by disagreements over the taxonomic level of *Plagiochila porelloides* (Figure 12). Schuster (1980) and Damsholt (2002) considered *Plagiochila porelloides* to be a subspecies of *P. asplenoides*. Paton (1999) and Schumacker and Vána (2000), however, consider them to be two separate species with different habitats. The species *Plagiochila asplenoides* s.s. is most common on herb-rich forest floors and moist depressions, whereas the closely related *P. porelloides* occurs at the bases of silicate boulders and in crevices. This taxonomic confusion creates

difficulties in providing accurate descriptions of habitats. Some references attributed here to *P. asplenoides* might actually be for *P. porelloides* in areas where both species occur.



Figure 11. *Plagiochila asplenoides* ventral side. Photo by Ralf Wagner, with permission.



Figure 12. *Plagiochila porelloides* showing the succubous leaf arrangement. Photo by Hugues Tinguy, with permission.

Distribution

Using the two-species concept, in North America, *Plagiochila asplenoides* subsp. *asplenoides* (Figure 13) occurs only in western North America, on logs, rocks, and bases of trees (Hong 1992). It occurs in Europe (Schumacker & Vána 2000). Marsh *et al.* (2010) reported it in Finland, Paton (1999) in the British Isles, Diekmann (1995) in Sweden, Pakalne and Čakare (2001) in Latvia, Grüll and Kvét (1976) in the Czech Republic. But in East and South Asia, So and Grolle (2000) specifically exclude this species from the flora based on their examination of herbarium material.



Figure 13. *Plagiochila asplenioides* subsp. *asplenioides*, an endemic in western North America. Photo from Botany Website, UBC, with permission.

Aquatic and Wet Habitats

Typical of *Plagiochila asplenioides* (Figure 14), but not *P. porelloides* (Figure 12), the former occurs on decaying logs, leaf litter, and humus in Europe (Salachna 2007). Marsh *et al.* (2010) report *Plagiochila asplenioides* from herb-rich forest floors and moist depressions in Finland. It can tolerate slightly higher light levels than those in the forest, occurring among the tall turf (Gimingham & Birse 1957).



Figure 14. *Plagiochila asplenioides*, a species of logs, litter and humus in Europe, but also near streams there. Photo by David T. Holyoak, with permission.

But other reports may represent what I am including as *Plagiochila porelloides* (Figure 12): ground, rock, spring, and water communities in or associated with streams near Lacko, Western Carpathians (Mamczarz 1970); not common in River Tweed, UK (Holmes & Whitton 1975a, b); in intermittent rivers (Dhien 1978); in the *Platyhypnidium* (Figure 5) – *Fontinalis antipyretica* (Figure 6) association, Thuringia, Germany (Marstaller 1987); at a spring in Tara River canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).

Marstaller (2012), in his studies on **epilithic** (rock-dwelling) species, considered *Plagiochila asplenioides* (Figure 13-Figure 18) to be **hygrophytic** (referring to plant living in location with high moisture level, but not

submersed). Similarly, in Latvia, Pakalne and Čakare (2001) found *P. asplenioides* at the foot of river ravine slopes and in forest springs – very wet but not submersed. Baláži *et al.* (2010) termed it a **macrophyte** (easily visible aquatic plant) in the Slovak Republic. Farr *et al.* (2019) report this as a species that occurs on slightly acidic soil of vertical stream banks in the UK at tufa-forming sites. Kelly (1981) found it to be typical of stream banks, but also on limestone rocks in the forest in Killarney, Ireland.



Figure 15. *Plagiochila asplenioides* in a forest habitat. Photo by Hermann Schachner, through Creative Commons.



Figure 16. *Plagiochila asplenioides*, dry, showing a typical growth form on stream banks. Photo from <www.photofauna.com>, with permission.



Figure 17. *Plagiochila asplenioides*, wet, showing a typical growth form on stream banks. Photo from <www.photofauna.com>, with permission.

Sotiaux and Vanderpoorten (2017) again separated the two species by habitat, reporting *Plagiochila asplenioides* (Figure 15-Figure 17) at 1840 m asl in the montane fir woodland. By comparison, they reported *Plagiochila porelloides* (Figure 1, Figure 12, Figure 45) from the sub-Mediterranean to the sub-Alpine belt up to 2250 m asl on montane, base-rich siliceous rocks, shaded, humid montane siliceous rock outcrops, sub-Mediterranean to Alpine siliceous, sometimes base-rich shaded north-facing outcrops, sub-Mediterranean to sub-Alpine limestone outcrops, shaded siliceous boulders in woodlands, base-rich ground along streams, forest floor, and limestone outcrops.

Puczko *et al.* (2018) indicated that *Plagiochila asplenioides* (Figure 15-Figure 17) serves as an indicator of good water quality in lowland spring niches. Papastergiadou (1995) reported this species from Greek wetlands.

Cappers *et al.* (1997) reported that fragments of this species were found as part of the caulking material in shipwrecks excavated in The Netherlands, but it was not used in any abundance.

Adaptations

Proctor (1982) examined the water movement in several bryophytes. He found that bryophytes with central strands had a sustained movement of water upward and outward through transpiration, similar to the transpirational movement in tracheophytes. However, in *Plagiochila asplenioides* (Figure 15-Figure 17), there is no central strand and this transpirational movement does not occur.

Gupta (1977) described the effects of moisture stress on *Plagiochila asplenioides* (Figure 18). He found the highest solute leakage of dried plants to occur in the first two minutes of rewetting, then slowing down. He considered this rapid stoppage to be the result of reassemblage of the membrane structure or to a rapid decrease of the solutes in the injured and dead tissues. The leached solutes are resorbed by the viable cells. This is not different from that found for terrestrial mosses, but may indicate the tools they have to survive in habitats that can dry out for weeks at a time.



Figure 18. *Plagiochila asplenioides* dry, but retaining its green color. Photo by J. C. Schou, through Creative Commons.

Reproduction

Plagiochila asplenioides is **dioicous** (Watson 1965), but sporophytes can be found (Figure 19).



Figure 19. *Plagiochila asplenioides* with capsules. Photo by Hermann Schachner, through Creative Commons.

Fungal Interactions

Stenroos *et al.* (2010) found that four genera of bryophytes (out of 19 checked) exhibited the highest diversity of fungal associates: *Plagiochila*, *Polytrichum*, *Ptilidium*, and *Sphagnum*.

Döbbeler (1997) considered the ascomycete fungus *Epibryon plagiochilae* (Figure 20-Figure 21) to be specific on *Plagiochila asplenioides* (Figure 15-Figure 17) and *P. porelloides* (Figure 12). *Pedinophyllum interruptum* (Figure 2-Figure 4), in the same family **Plagiochilaceae**, does not get infected by this fungus.

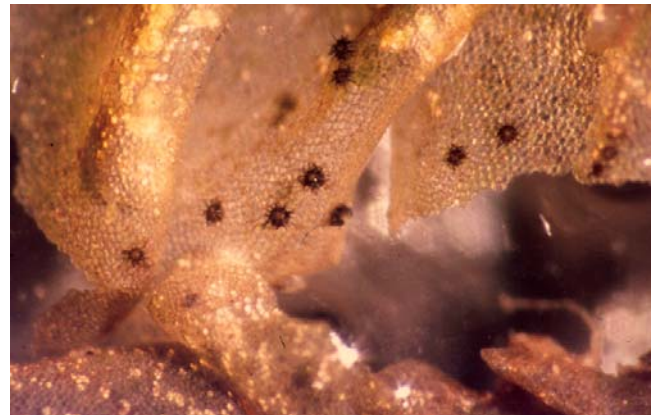


Figure 20. *Epibryon plagiochilae* (dark brown spots) on *Plagiochila asplenioides* leaves. Photo courtesy of Peter Döbbeler.

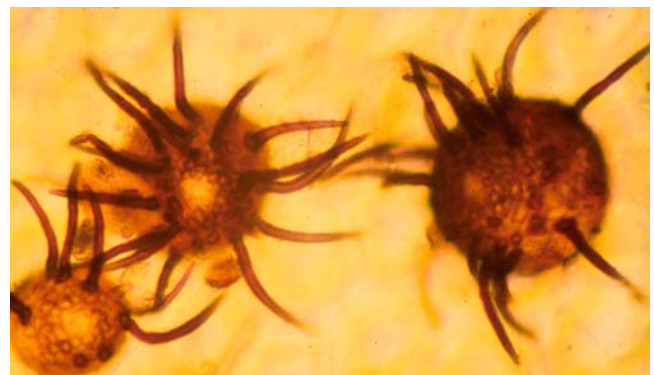


Figure 21. *Epibryon plagiochilae* on *Plagiochila asplenioides* showing the typical spider-like appearance. Photo courtesy of Peter Döbbeler.

Plagiochila asplenioides (Figure 15-Figure 17) serves as substrate for at least 7 genera and 13 species of fungi (Marsh *et al.* 2010). Out of more than 400 Finnish herbarium specimens of this species and *P. porelloides* (Figure 1, Figure 12, Figure 45), about 200 supported bryicolous species of fungi in the ascomycete genera *Bryomyces* (Figure 22-Figure 23), *Dactylospora* (Figure 24-Figure 25), *Epibryon* (Figure 8, Figure 20-Figure 21), *Lichenopeltella* (Figure 26), *Octosporella* (Figure 27-Figure 29), *Pleostigma* (Figure 30), and the **anamorphic** (unnatural grouping of fungi characterized by mitotic rather than meiotic production of spores – conidia) genus *Epicoccum* (Figure 31). *Epibryon plagiochilae* (Figure 20-Figure 21), a species that is apparently specific to *P. asplenioides*, *P. porelloides*, and *P. britannica* (Figure 32), shows a strong preference for the dorsal leaf border of its host liverwort, although ascomata can also occur on the stem or on female bracts and perianths. Bosanquet (2007) was delighted to discover *E. plagiochilae* on *Plagiochila asplenioides* and subsequently on *P. porelloides* and *P. britannica* in Wales. In the next two months, he discovered this distinctive fungus on four of twelve colonies of *P. asplenioides* he examined and on two of three colonies of *P. porelloides*. Many specimens of *P. britannica* had the fungus, but the fungus was absent on all specimens of *Pedinophyllum interruptum* and all other species of *Plagiochila*. Could it be that these species have the chemical ability to prevent the infection, or do the other *Plagiochilaceae* in Wales occur in habitats that are unsuitable for the fungus to become established?



Figure 22. *Bryomyces velenovskyi*, in a genus known from *Plagiochila asplenioides*, on moss leaves. Photo by George Greiff, with permission.



Figure 23. *Bryomyces microcarpus* var. *rhacomitrii* on moss leaf. Photo by George Greiff, with permission.



Figure 24. *Dactylospora stygia* on log; some members of the genus occur on *Plagiochila asplenioides*. Photo by Milan Macalák, with permission.

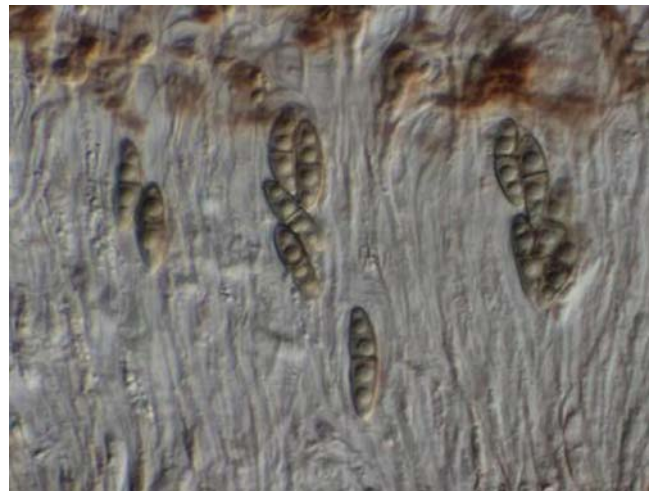


Figure 25. *Dactylospora stygia* asci. Photo through Creative Commons.

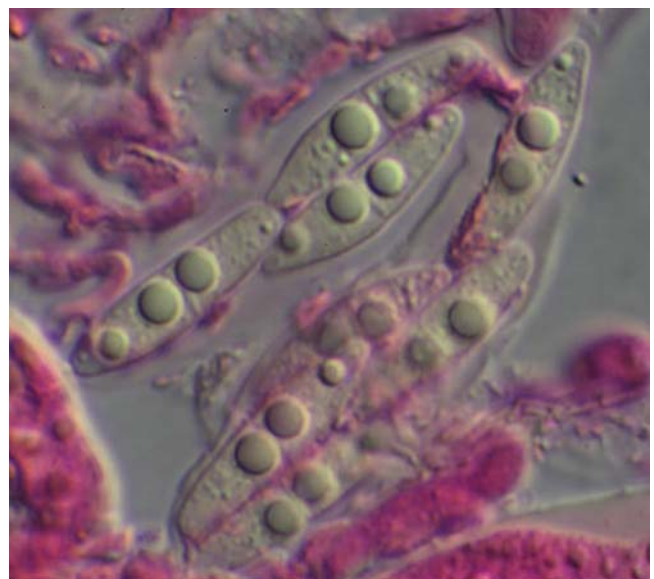


Figure 26. *Lichenopeltella santessonii* ascospores on dead *Peltigera membranacea*; some members of the genus *Lichenopeltella* occur on *Plagiochila asplenioides* leaves. Photo through Creative Commons.



Figure 27. *Octosporella jungermanniarum* probably, a species that occurs on *Plagiochila asplenoides*, as shown here. Photo by Barry Stewart, with permission.



Figure 28. *Octosporella jungermanniarum* on *Plagiochila asplenoides*. Photo courtesy of George Greiff.

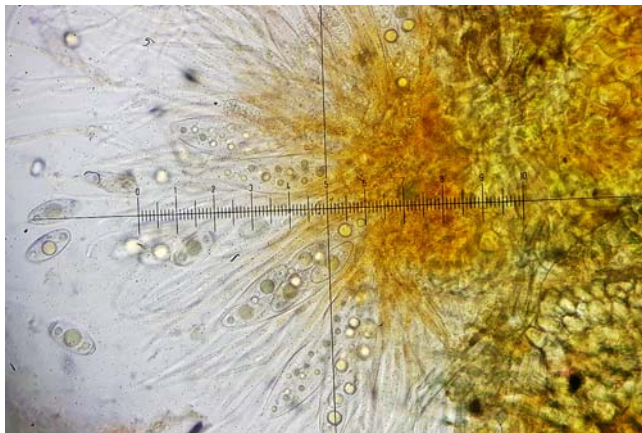


Figure 29. *Octosporella jungermanniarum* probably, showing ascospores. Photo by Barry Stewart, with permission.



Figure 30. *Pleostigma jungermanniarum* on *Plagiochila porelloides*. Photo by courtesy of George Greiff.

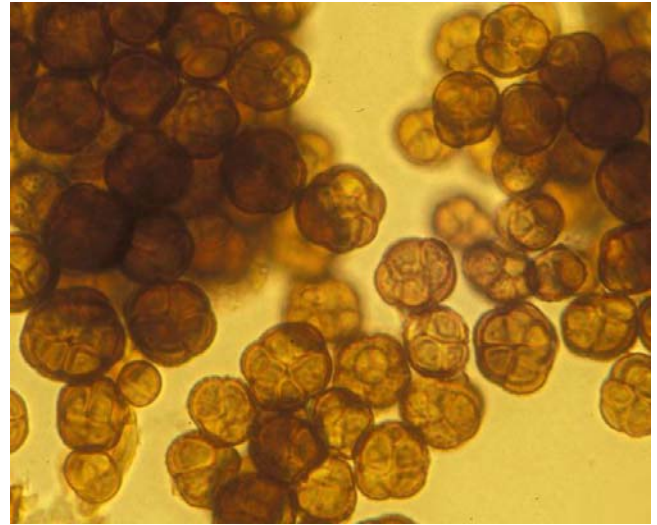


Figure 31. *Epicoccum nigrum*; some members of this genus occur on *Plagiochila asplenoides*. Photo by Gerald Holmes, through Creative Commons.



Figure 32. *Plagiochila britannica*, a species that hosts the fungus *Epibryon plagiochilae*. Photo by David S. Rycroft, with permission.

Epibryon endocarpum (see Figure 8) is another ascomycete that grows, and in this case fruits, within the cells of *Plagiochila asplenoides* (Döbbeler 1980). Among its adaptations is the small size of its ascomata (25-35 μm). In addition to these, George Greiff photographed *Octosporella jungermanniarum* (Figure 28), another ascomycete, on *Plagiochila asplenoides*.

Biochemistry

When Suleiman and Lewis (1980) cultured *Plagiochila asplenoides* (Figure 15-Figure 17) in the dark for four months, the leafy plant rapidly lost starch, but little chlorophyll was lost. When revived, the tissues immediately became viable. The principal photosynthetic products were volemitol, sucrose, and starch, but the more abundant carbohydrates (fructans) were not among those most rapidly formed. Rather, conversion to fructans occurs in the prolonged four months of darkness. The starch turnover is rapid, but the volemitol and sucrose have a very slow turnover, even up to four months in the dark. This survival in the dark undoubtedly contributes to the plant's survival in the long winters in some of its more northerly locations.

Ultraviolet radiation can be a problem for bryophytes in exposed habitats. This can include wooded areas that lose the canopy leaves in winter. Whereas submersion in water reduces the effects of light, this species typically does not benefit from that habitat. Soriano *et al.* (2019) examined the role of phenolic compounds during these UV stress events. They found that the response of phenolic compounds was slow. They identified thirteen flavones in the methanol-soluble (mostly vacuolar) and two hydroxycinnamic acids in the insoluble (cell wall-bound) fractions. Only p-coumaric and ferulic acids, both from the insoluble fraction of *Plagiochila asplenioides* (Figure 15-Figure 17), exhibited a significant and rapid accumulation in response to UV radiation on the first day of exposure to elevated UV. This did not occur in the other leafy liverwort, the two thallose liverworts, or the two moss species. Six additional phenolic compounds accumulated during the 22 days of exposure, especially in the liverworts.

***Plagiochila bifaria* (Figure 33-Figure 35)**

(syn. = *Plagiochila killarniensis*)

Distribution

Plagiochila bifaria (Figure 33-Figure 35) is widespread in the Neotropics, going by a variety of names (Grolle 1998; Gradstein 2015). Heinrichs *et al.* (1998a, b, 2004) argued for a broad species concept based on molecular, morphological, and phytochemical evidence. I have included here only the names I found in the aquatic literature. Heinrichs *et al.* (2004) reported it from the Western Hemisphere from Bolivia, Brazil, Costa Rica, Ecuador, Panama, and Mexico, as well as the British Isles and Tenerife on the eastern side of the Atlantic. Rycroft (2008) documented it from Venezuela and Peru. To these, Gradstein (2015) added Jamaica, Galapagos Islands, and the Barbados.

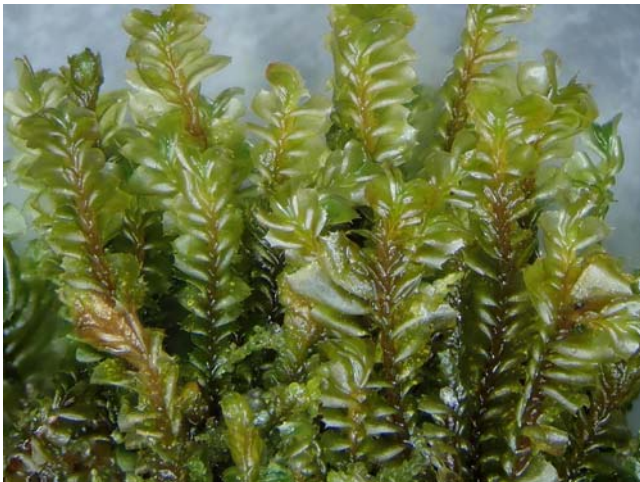


Figure 33. *Plagiochila bifaria*, a Neotropical species, but extending into other hyperoceanic areas. Photo by Paul Bowyer, through Creative Commons.

Its range extends outside the tropics, including the Canary Islands (González M. *et al.* 2007), Madeira (Sim-Sim *et al.* 2005a), France (Hugonnot *et al.* 2013). Hugonnot *et al.* (2013) considered the species to be hyperoceanic.

Aquatic and Wet Habitats

Luis *et al.* (2015) described an aquatic habitat on Madeira Island, where it occurs at low altitudes in narrow streams and in mountainous streams with low flow. But Kürschner *et al.* (2007) found that the Madeira Island bryoflora was dominated by *Plagiochila bifaria*, among others, that formed **tall turfs** (Figure 34-Figure 35).

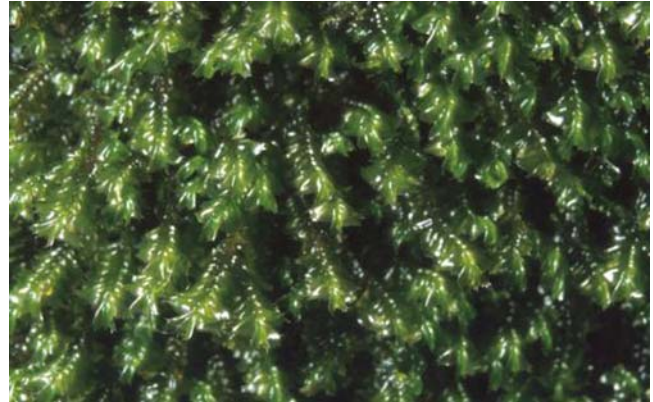


Figure 34. *Plagiochila bifaria* with green color, suggesting it grew in the shade. Photo by David S. Rycroft, with permission.

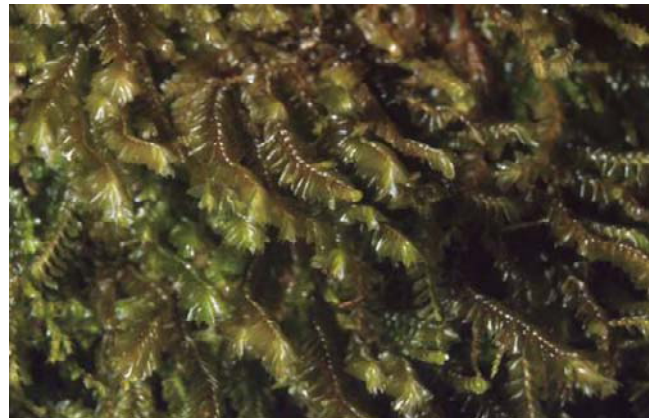


Figure 35. *Plagiochila bifaria* with olive-green color, suggesting sun exposure. Photo by David S. Rycroft, with permission.

In their studies on French populations, Hugonnot *et al.* (2013) reported *Plagiochila bifaria* (Figure 34-Figure 35) as a rock-dwelling forest species. Frahm (2013) reported it as relatively common in Italy, where it benefits from the high precipitation in the mountains. Holz *et al.* (2002) reported it as turfs on twigs and branches in Costa Rico in upper montane *Quercus* forests. On Madeira, it was the most frequent species in the Madeiran laurel forest. In the Azores, it was one of the ten most frequent species (Gabriel & Bates 2005). They found it in 88% of the bark samples and only 12% of the non-bark samples. At mid to high altitudes it is an indicator species of lower water availability and higher bark pH – not exactly what we would expect for an aquatic or wetland bryophyte.

Adaptations

Sim-Sim *et al.* (2005b) described the **rill-like** (upward folded, forming channel; Figure 36) leaf arrangement as an adaptation for condensing water vapor from fog and mist that is frequent at 1000-1299 m asl. This moisture permits

it to maintain a moisture status that is almost as consistent as being submersed.



Figure 36. *Plagiochila bifaria*, from a population originally identified as *Plagiochila killarniensis*, showing rill-like leaf arrangement. Photo by Barry Stewart, with permission.

Reproduction

Heinrichs *et al.* (1998a) noted that the perianths of *P. bifaria* (Figure 34-Figure 35) became rarer toward the northern limits of distribution. Most of the fertilized archegonia appear to be confined to Macaronesia, whereas descriptions of younger perianths with no fertilization led to conflicting descriptions that supported spurious species separations, especially that of *Plagiochila killarniensis* (Figure 36), now considered a synonym (TROPICOS 2020). The Macaronesian perianths match those occurring in the Neotropics. This is consistent with the formation of sporophytes in the Neotropics and Macaronesia, but not in continental Europe (Heinrichs *et al.* 2004).

Biochemistry

Plagiochila bifaria has distinct oil bodies (Figure 37), suggesting the presence of secondary compounds that could be adaptive. Although the ecological information on this species is relatively sparse, it has undergone several biochemical studies. Hackl *et al.* (2006) isolated and identified three eudesmane type sesquiterpenes from *Plagiochila bifaria*. Rycroft (2008) described what appears to be the first example of a monocyclic 4-pyrone that has a polyketide origin. Heinrichs *et al.* (2004) used the biochemical composition of the species to delineate clades within the species, with indications that the basal clade is represented in Costa Rica, Brazil, and Bolivia, concluding that the differences among clades did not support differences at the species level. Rycroft *et al.* (1999) determined that certain minor components were common to both the European *Plagiochila killarniensis* (Figure 36) and the Neotropical populations treated as *Plagiochila bifaria* (Figure 34-Figure 35). Like Heinrichs and coworkers, they considered the biochemical differences between Scottish populations and those of the Azores to be minor.

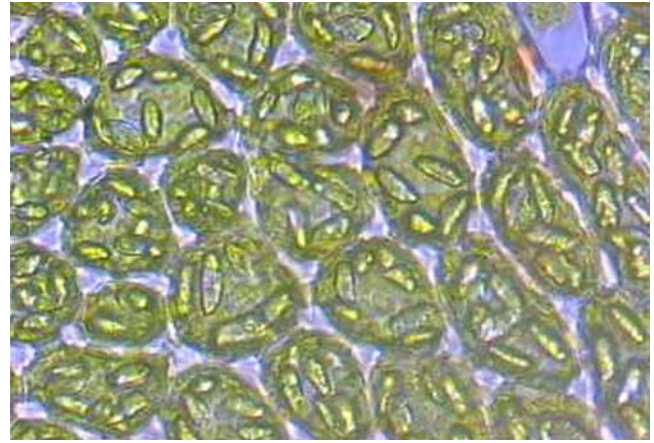


Figure 37. *Plagiochila bifaria* oil bodies (ovals in cells), a site of secondary compounds. Photo by David Rycroft, with permission.

Plagiochila porelloides (Figure 38-Figure 43)

(syn. = *Plagiochila asplenioides* var. *major*)

Distribution

In eastern North America, this species was for a long time interpreted as *Plagiochila asplenioides*. Since it was later determined that these were instead *Plagiochila porelloides*, I have herein included the eastern North American populations reported as *P. asplenioides* as *P. porelloides*.

Plagiochila porelloides (Figure 38-Figure 43) is a circumboreal species (Sim-Sim *et al.* 2005a) distributed throughout Europe, including the Arctic, becoming submontane in the south (Hill *et al.* 1991). Ros *et al.* (2000) added it to Morocco in Africa. In Europe, it occurs in the Nordic countries (Schumacker & Vána 2000; Damsholt 2002), in the British Isles (Paton 1999), in Greece and Poland (Cronberg 2000a, b), and in Germany in the forest (Marstaller 2007). Sim-Sim *et al.* (2005a) reported it as rare in the Madeiran laurel forests, but it occurred there in some sites that had high biodiversity and several rare species. In North America, it occurs from 82°32'N to the southeastern Coastal Plain in the east and California and Arizona in the west (Schuster 1980).



Figure 38. *Plagiochila porelloides*, a species of stream banks in eastern and western North America and Europe. Photo by Hermann Schachner, through Creative Commons.

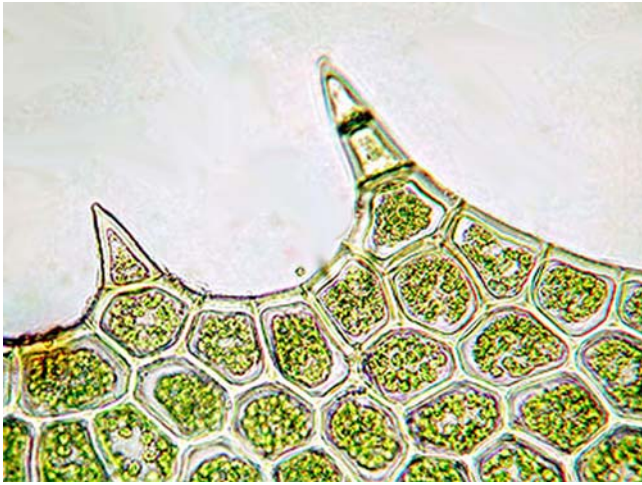


Figure 39. *Plagiochila porelloides* leaf teeth. Photo from Botany Website, UBC, with permission.

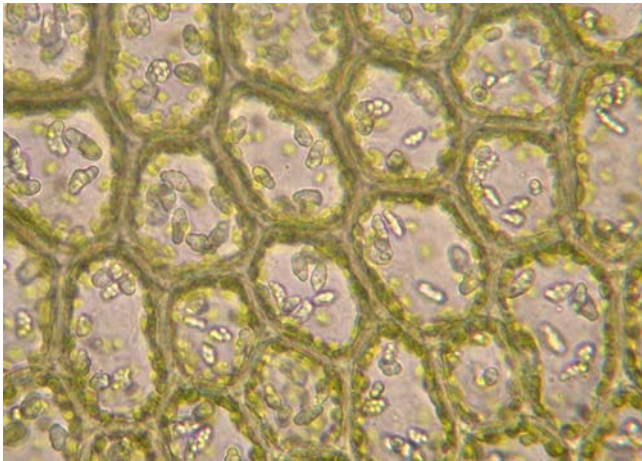


Figure 40. *Plagiochila porelloides* leaf cells showing oil bodies and peripheral chloroplasts. Photo from Botany Web Page, UBC, with permission.



Figure 41. *Plagiochila porelloides* in hydrated state. Photo by Štěpán Koval, with permission.



Figure 42. *Plagiochila porelloides* beginning to dry. Photo by Hermann Schachner, through Creative Commons.



Figure 43. *Plagiochila porelloides* showing leaves rolling as it dries out. Photo by Štěpán Koval, with permission.

Söderström *et al.* (1999) reported *Plagiochila porelloides* (Figure 38-Figure 43) from China in the Changbai Mountain, where it occurred on boulders, in the alpine heathland, and on decaying logs. Konstantinova, among others, (2011) documented it in the Eastern Caucasus of Russia, where it is often abundant.

Aquatic and Wet Habitats

Schuster (1980) comments that its wide variability in form is concurrent with a wide variability in habitat. It can, although rarely, be in xeric extremes at one end of its ecological spectrum to hydric, its most common form, at the other. It is very rarely submerged. Schuster considers it to be most common on moist rocks. And unlike most members of the genus, *P. porelloides* (Figure 38-Figure 43) tolerates high insolation when moisture is adequate. Because of its wide range of habitat conditions, it can be

found with nearly half the species of liverworts found in eastern North America. Its occurrence over such a wide north-south geographic range coincides with its wide temperature tolerance, more than is known for any other member of the genus.

In North America, Nichols (1918) reported *Plagiochila asplenioides* (Figure 15-Figure 17) from streambanks and wet rock cliffs associated with streams, Cape Breton Island, Canada, but in this location it was most probably *Plagiochila porelloides* (Figure 38-Figure 43). Elsewhere in North America, *P. porelloides* occurs on wet or moist cliffs of ravines and on moist rock surfaces or springy banks of ravines in Connecticut, USA (Nichols 1916); in Appalachian Mountain, USA, streams (Glime 1968); just above the water surface most of the year in a headwater stream in New Hampshire, USA (Glime 1970); on the wall in the Flume at Franconia Notch, New Hampshire, USA (Glime 1982); in Adirondack Mountain streams (Slack & Glime 1985; Glime *et al.* 1987); but it is a restricted terrestrial of montane streams and streambanks in western Canada (Vitt *et al.* 1986; Glime & Vitt 1987), perhaps due to the strong flow and spring flooding there. In Minnesota, it occurs in mesophytic calcareous communities, on peat-covered banks, much disintegrated decaying wood, and over wet to saturated humus in *Thuja*-spruce-fir forests (Figure 44).



Figure 44. *Thuja*-spruce-fir swamp in Michigan, USA, a suitable habitat for *Plagiochila porelloides*. Photo from National Park Service, through public domain.

On Cygnes Mountain, Québec, Canada, it occurs on moist granitic rock in mid stream (Kucyniak 1947). In Quaker Run, New York, Matthews (1932) likewise found it on rocks midstream in a stream with a gentle gradient and numerous small waterfalls. It is not uncommon to find *Plagiochila porelloides* (Figure 38-Figure 43) just above the water level (Figure 45) in streams in the Appalachian Mountains of the eastern USA, above but close to the water surface (Figure 45), occasionally becoming submersed (Glime 1970). This keeps it moist most of the time, dry occasionally, and submersed in high water. Similarly, in Cataracts Provincial Park, Newfoundland, Canada, Weber and Brassard (Weber 1976; Weber & Brassard 1976) found it in the inundation zone where it is periodically submerged and exposed as the water level rises and falls along the river. It also occurred in the next higher zone on the river bank.

Plagiochila porelloides subsp. *porelloides* occurs on cliffs, damp soil banks, decayed wood, and bark of trees (Figure 1) in western North America from Alaska

southward to California, USA and in damp, calcareous high Arctic tundra (Hong 1992).



Figure 45. *Plagiochila porelloides* just above water level and *Fontinalis novae-angliae* just below the water level, in a stream in New Hampshire, USA. Photo by Janice Glime.

In Europe, *Plagiochila porelloides* (Figure 1) occurs on rocks or soil of fast streams (Watson 1919); in the arctic-alpine zone of the UK (Watson 1925); in the *Platyhypnidium* (Figure 5) – *Fontinalis antipyretica* (Figure 6) association, in Thuringia, Germany (Marstaller 1987); submersed in low-buffered water of streams (Trempe & Kohler 1991); on stream boulders above mean water level, with low cover and high frequency in Finland (Virtanen 1995); springs in Finland (Heino *et al.* 2005); common in flood valleys of Upper Bureya River (Russian Far East) (Konstantinova *et al.* 2002); emerged and vertical stony streambanks or in waterfall margins, pure patches usually not extensive, associated with *Thamnobryum alopecurum* (Figure 46) and *Lejeunea cavifolia* (Figure 47) in mountain streams of northwest Portugal (Vieira *et al.* 2005); in irrigation ditches in Spain (Beaucourt *et al.* 1987); on montane, base-rich siliceous rocks, shaded, humid montane siliceous rock outcrops, sub-Mediterranean to Alpine siliceous, sometimes base-rich shaded north-facing outcrops, sub-Mediterranean to sub-Mediterranean to Alpine siliceous, sometimes base-rich shaded north-facing outcrops, sub-Mediterranean to sub-Alpine limestone outcrops, shaded siliceous boulders in woodland from the sub-Mediterranean to the sub-Alpine belt at 2550 m asl, on base-rich ground along streams, forest floor, and limestone outcrops from the Mediterranean to the sub-Alpine belt in Andorra (Sotiaux & Vanderpoorten 2017).



Figure 46. *Thamnobryum alopecurum*, an associate of *Plagiochila porelloides* in wet, vertical habitats in Europe. Photo by Hugues Tinguy, with permission.



Figure 47. *Lejeunea cavifolia*, an associate of *Plagiochila porelloides* in wet, vertical habitats in Europe. Photo by Hermann Schachner, through Creative Commons.

Plagiochila porelloides (Figure 38-Figure 43, Figure 53-Figure 55) can be found in the Iskur River, Bulgaria, and its main tributaries (Papp *et al.* 2006) and as a mesophyte in Bulgarian rivers (Gecheva *et al.* 2010, 2013). It occurs on limestone rock and on bark of *Pinus* (Figure 48) at a stream in the Tara river canyon and Durmitor area, Montenegro (Papp & Erzberger 2011); in the upper course in Maritsa River, Bulgaria (Gecheva *et al.* 2011). In the Madeiran laurel forests, *Plagiochila porelloides* grows on moist, shady rocks, forming isolated, small mats near populations of other bryophytes such as *Andoa berthelotiana* (Figure 49), *Fissidens luisieri* (Figure 50), *Thamnobryum maderense* (Figure 51), *Porella canariensis* (Figure 52), and *Plagiochila bifaria* (Figure 33-Figure 35) (Sim-Sim *et al.* 2005a).



Figure 48. *Pinus* bark, a substrate where *Plagiochila porelloides* can occur in Montenegro. Photo by SusquehannahMan, through Creative Commons.

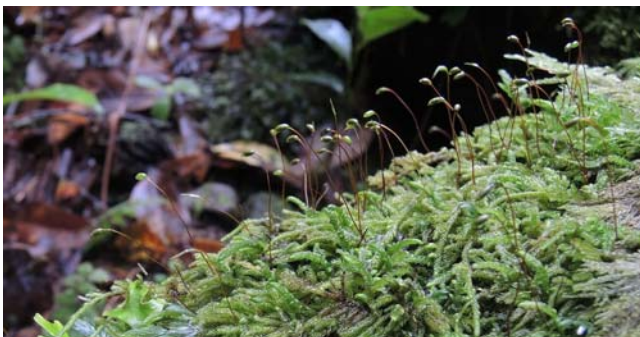


Figure 49. *Andoa berthelotiana* with capsules, a species that often occurs near small mats of *Plagiochila porelloides*. Photo by Michael Lüth, with permission.



Figure 50. *Fissidens luisieri*, a species that often occurs near small mats of *Plagiochila porelloides*. Photo by Jan-Peter Frahm, with permission.



Figure 51. *Thamnobryum maderense*, a species that often occurs near small mats of *Plagiochila porelloides*. Photo by Michael Lüth, with permission.



Figure 52. *Porella canariensis*, a species that often occurs near small mats of *Plagiochila porelloides*. Photo by Paulo A. G. Borges, with permission through Azoresbiportal.

For Portuguese streams, Vieira *et al.* (2004) reported that *Plagiochila porelloides* (Figure 53-Figure 55) was threatened. It occurs there in seasonally emerged locations on vertical stony stream banks (Figure 53) or at waterfall margins, both habitats where it remains wet most of the time and could be occasionally submerged. Its patches were extensive, often pure, but typically not well

developed. It was always found lacking sexual reproductive structures.



Figure 53. *Plagiochila porelloides* on a vertical substrate. Photo from Botany Web Page, UBC, with permission.

In Russia, *Plagiochila porelloides* (Figure 53-Figure 55) was recorded in some areas as *P. asplenioides* (Figure 13-Figure 18), but has since been determined to be *P. porelloides* (Konstantinova 2011). It occurs in a canyon with a rivulet, in deep ravines, on loamy and sandy soil on stream banks, but also on soil, rocks, decaying shaded wood, grasses and rocks in the mountain steppe, and in rock crevices, on ledges, and between boulders.

Adaptations

Color forms occur in response to solar radiation. In exposed sites, the plants are yellowish green (Figure 53-Figure 55); in the shade they can reach a deep green or dull olive green (Figure 41-Figure 43), but not brown (Schuster 1980).



Figure 54. *Plagiochila porelloides*, showing a more yellowish green coloration of a species grown in an exposed site. Photo by Štěpán Koval, with permission.

Reproduction

The species is **dioicous**, with male plants slightly smaller than the females. Nevertheless, sporophytes (Figure 55) are present in at least part of the distribution, so some isozyme variability should be present in some areas.



Figure 55. *Plagiochila porelloides* with capsules. Štěpán Koval, with permission.

Cronberg (2000a,b) found a total absence of genetic variation in Greek and southern Scandinavian populations when comparing 16 isozyme loci. The study included areas that had been severely and mildly affected by the Pleistocene glaciations and supported an earlier study that found no variation among Polish populations. He suggested that the present-day populations may have passed through a severe bottleneck that reduced or eliminated the variability.

When Kowalczyk *et al.* (1997) cultured fragments of ten liverwort species, *Plagiochila porelloides* (Figure 54-Figure 55) was among them. The first problem in such studies is to obtain sterile material, which is difficult with wet and aquatic bryophytes where the surface is often replete with bacteria, algae, protozoa, and detritus, not to mention insects. They successfully sterilized this species with commercial bleach diluted 1:1 and 1:3 with distilled water with optimal time of 0.5-2.0 minutes. (I have found that longer exposures kill the bryophytes or at least destroy most of the chlorophyll.) The fragment should be no more than 3 mm long and should be obtained from a leafless branch or shoot tip.

Fungal Interactions

Marsh *et al.* (2010) compared the fungi on *Plagiochila porelloides* (Figure 54-Figure 55) and those (Figure 22-Figure 31) on *P. asplenioides* (Figure 13-Figure 18) in Finland. The former liverwort occurred on bases and crevices of shady silicate boulders, sometimes by brooks or on dead wood in shady forests, whereas the latter occurred mostly on herb-rich forest floors and in moist depressions. Thirteen species of bryicolous fungi are known to occur on one or both of these two species. Most of those found by Marsh and coworkers positioned their apothecia in leaf axils or perianths. The fungus *Epibryon plagiochilae* (Figure 20-Figure 21), however, strongly prefers the dorsal leaf border, although ascomata can occur on the stem or on female bracts and perianths. Although this fungus species has a strong preference for *P. asplenioides*, it also occurs

on *P. porelloides*, but much less frequently. *Pleostigma jungermannianum* likewise occurs on both *P. porelloides* and *P. asplenioides* (Figure 30).

Biochemistry

One can easily see oil bodies (Figure 56) in fresh cells, indicating the presence of secondary compounds. Toyota *et al.* (1994) verified the presence and established the structure of three sesquiterpene esters in *Plagiochila porelloides* (Figure 54-Figure 55). Asakawa *et al.* (1980) identified sesquiterpenoids from fourteen species of *Plagiochila*, including *P. porelloides*, identifying some that caused the distinctive odors.

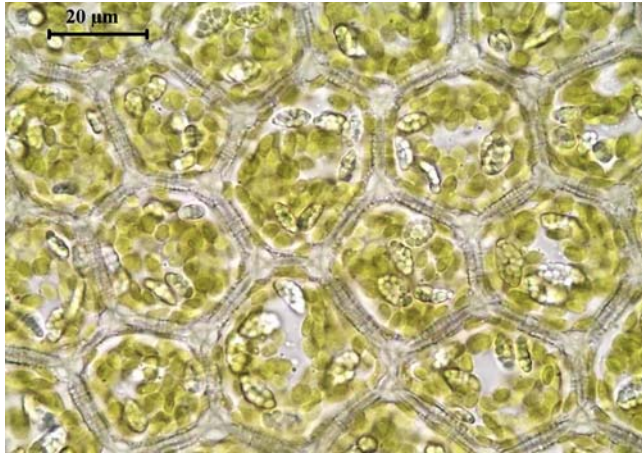


Figure 56. *Plagiochila porelloides* leaf cells showing oil bodies among the chloroplasts. Photo by Hugues Tinguy, with permission.

Plagiochila punctata (Figure 57-Figure 59)

(syn. = *Plagiochila stolonifera*, *Plagiochila choachina*, *Plagiochila patzschkei*, *Plagiochila subalpina*)

Distribution

Plagiochila punctata (Figure 57-Figure 59) is widespread in Neotropical mountains, but has, like so many tropical species, been known by a number of names now considered to be synonyms (Heinrichs *et al.* 2005). As a result of understanding its synonymy, it has been documented for Scotland, Spain, tropical Africa, Tanzania, Madagascar, Zaire, Karthala volcano (in Indian Ocean), Mexico, Venezuela, Ecuador, Colombia, Brazil, Bolivia, Costa Rica, and Dominican Republic. In 2006, Davison *et al.* added a record of *Plagiochila punctata* to the flora of Tennessee, USA.

Aquatic and Wet Habitats

Watson (1919) reported that *Plagiochila punctata* (Figure 58) is occasionally submerged. In the tropics, it is restricted to mountains, but it also occurs in Europe (Figure 58), where it occurs in the lowlands up to 1000 m asl. The feather-like habit is more common in the tropics than in Europe. But it is not always aquatic or in wetlands. It can also grow as an epiphyte (Figure 59).



Figure 57. *Plagiochila punctata* (larger plants with large teeth), a widespread and occasionally submerged species in Neotropical mountains. Photo by Paul Bowyer, through Creative Commons.



Figure 58. *Plagiochila punctata* growing on a vertical substrate. Photo by David Rycroft, with permission.



Figure 59. *Plagiochila punctata* growing as an epiphyte. Photo by Michael Lüth, with permission.

Reproduction

Plagiochila punctata (Figure 57-Figure 59) is dioicous (Gradstein *et al.* (2001).

Fungal Interactions

Plagiochila punctata (Figure 57-Figure 59) has several interesting interactions with other organisms. Döbbeler and Feuerer (2004) reported that *Stenocybe*

nitida, an ascomycete, occurs on this liverwort species. Pilato *et al.* (2002) reported tardigrade specimens and eggs from *Plagiochila punctata* from the Otonga Forest in Ecuador and another two specimens from this liverwort in Alto Tambo, Ecuador.

Plagiochila renitens

Plagiochila renitens occurs in Australia and southern Asia (ITIS 2020). Its habitats are poorly reported. Ruttner (1955) reported it from acidic thermal spray in the tropics, but little else seems to connect it to aquatic or wetland habitats.

Plagiochila retrospectans (Figure 60) and *Plagiochila fuscella* (Figure 61)

Distribution

Engel and Merrill (2009) argued that *Plagiochila retrospectans* (Figure 60) does not occur in New Zealand, and specimens labelled with this name are actually *Plagiochila fuscella* (Figure 61), a New Zealand endemic. Nevertheless, *Plagiochila retrospectans* is known from Victorian rainforest streams in Australia (Carrigan & Gibson 2004; Fleisch & Engel 2006) and from the subAntarctic Macquarie Island (Hughes 1986), but the records of Suren (1988) from high alpine streams in New Zealand may actually be *Plagiochila fuscella*, making that species one of the two dominant liverwort species in those streams.



Figure 60. *Plagiochila retrospectans*, a Southern Hemisphere species that includes the subAntarctic. Photo by David Tng, with permission.



Figure 61. *Plagiochila fuscella*, a segregate from *Plagiochila retrospectans*, that occurs in New Zealand. Photo through Creative Commons.

Aquatic and Wet Habitats

In Cement Creek in Victoria, Australia, *Plagiochila retrospectans* (Figure 60) forms **cushions** on stream rocks (Carrigan and Gibson 2004). In New Zealand, *P. fuscella* (Figure 61) is especially common in chutes. On South Island, NZ, *P. fuscella* is in the group of species that prefer the highest number of days with low flow events, but also with the highest number of floods (Suren 1996). Wells *et al.* (1998) reported it from the 0-5 m sampling depth in a lake in New Zealand, but with low cover values.

Role

Plagiochila fuscella (Figure 61) is important for some aquatic invertebrates, especially insects. In the open headwater tributary of Otira River and shaded tributary of Bealy River, New Zealand, it occurred in 29% and 27% of the invertebrate guts, respectively (Suren & Winterbourn 1991). The liverworts provide habitat for the insects, substrate for periphyton, collector of detritus, and refuge from high flow (Suren 1991). This makes them ideal for oviposition and safe sites for small larvae and naiads while providing an abundant food source. Furthermore, *P. fuscella* contained the most CPOM, perhaps accounting for the greatest abundance of the stonefly *Austroperla cyrene* (Figure 62-Figure 63) and the mites *Oribatida* sp. B and *Paratryssaturus* sp. (Figure 64) occurring there compared to mosses.



Figure 62. *Austroperla cyrene* naiad, a resident on *Plagiochila fuscella* in New Zealand. Photo by James Cooper, through Creative Commons.



Figure 63. *Austroperla cyrene* adult on bryophytes. Photo by Jacob Littlejohn, through Creative Commons.



Figure 64. *Paratryssaturus cantermus*, a mite that inhabits *Plagiochila fuscella* in New Zealand. Photo modified from TePapa website, through Creative Commons.

Biochemistry

Nagashima *et al.* (1994) reported a new sesquiterpenoid from *Plagiochila fuscella* (Figure 61) in New Zealand.

Plagiochila spinulosa (Figure 65-Figure 69)

Distribution

Plagiochila spinulosa (Figure 65-Figure 69) is predominantly an eastern Holarctic species, but it also occurs in Lesotho in southern Africa and both North and South Islands of New Zealand (Renner *et al.* 2017; Renner 2018). González-Mancebo *et al.* (2009) reported that records of this species from the Canary Islands were actually other species, but that it does occur on the more temperate Madeira (Sim-Sim *et al.* 2005a).



Figure 65. *Plagiochila spinulosa*, a species distributed mostly in the eastern Holarctic. Photo by Michael Lüth, with permission.



Figure 66. *Plagiochila spinulosa*, a species distributed mostly in the eastern Holarctic. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Watson (1919) described *Plagiochila spinulosa* (Figure 65-Figure 69) as a species of waterfalls, occasionally becoming submerged. But in Scotland, it occurs in the Atlantic oakwood, forming large cushions or patches (Figure 67) on terrestrial rocks and tree trunks (Figure 68). Proctor (1980) found that this species in similar wooded habitats of the British Isles (Figure 69) received its peak irradiance in the spring before leaf expansion. On the Iberian Peninsula of northern Spain, Qlivan and Fuertes (2000) found it on wet acidic rocks and on quartzite rocks near the River Sobra. Renner (2018) reports that *Plagiochila spinulosa* occurs in a variety of habitats on South Island, New Zealand, including the low windswept broadleaf forest, tall *Nothofagus*-dominated forest (Figure 70), waterfalls, cliff faces (Figure 71), and alpine herbfield. It also grows there as a lithophyte on cliff faces.



Figure 67. *Plagiochila spinulosa* habitat forming large cushion. Photo by Michael Lüth, with permission.



Figure 68. *Plagiochila spinulosa* on a birch log in Scotland. Photo by Michael Lüth, with permission.

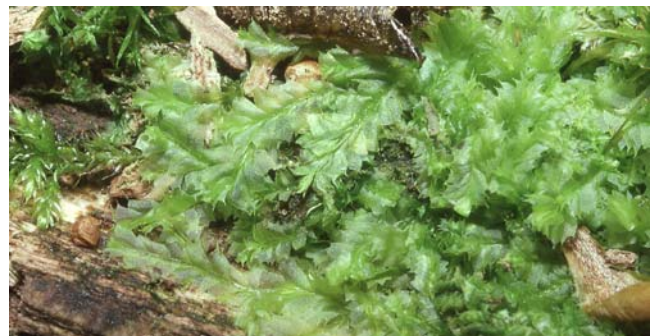


Figure 69. *Plagiochila spinulosa* in a wooded habitat in England. Photo by Janice Glime.



Figure 70. *Nothofagus* forest, Western Ruahine Ranges, NZ. Photo courtesy of Marie-Claude Larivière.



Figure 71. *Plagiochila spinulosa* on a vertical substrate. Photo by Barry Stewart, with permission.

One indication for the preference of *Plagiochila spinulosa* for moist sites is its sensitivity to desiccation. In their comparison of ten species of bryophytes regarding recovery from desiccation, Dilks and Proctor (1974) found that net assimilation and respiration of *Plagiochila spinulosa* and *Hookeria lucens* (Figure 72) showed the greatest sensitivity. Further details were added by Dilks and Proctor (1979), with indications of greater variability of water content in xeric species than in woodland species.



Figure 72. *Hookeria lucens* with capsules, a species that along with *Plagiochila spinulosa* showed the greatest sensitivity to drying. Photo by Michael Lüth, with permission.

Reproduction

Species in the group with *Plagiochila spinulosa* have **caducous** (easily detached; Figure 73-Figure 74) leaves that break at the base (Renner 2018) and permit them to reproduce asexually. These can account for both short- and long-distance dispersal.



Figure 73. *Plagiochila spinulosa* showing the portions of stems with lost leaves (caducous leaves). Photo by Paul Bowyer, through Creative Commons.



Figure 74. *Plagiochila exigua* dispersing caducous leaves. Photo by Des Callaghan, with permission.

Fungal Interactions

Wang and Qiu (2006) found no references to document the presence of mycorrhizae in *Plagiochila spinulosa* (Figure 66-Figure 67, Figure 71-Figure 73).

Biochemistry

Rycroft *et al.* (2002) noted that one can distinguish between *Plagiochila spinulosa* (Figure 66-Figure 67, Figure 71-Figure 73) and *P. stricta* by the odors of the crushed plants. Hiroshi and Asakawa (1988) described oil body types and chemical constituents in *P. spinulosa*, most of which are identical with those of *P. exigua* (Figure 75), a species that also has caducous leaves (Figure 74). Connolly *et al.* (1999) and Rycroft *et al.* (1999) identified some of the aromatic compounds in *P. spinulosa*. Sim-Sim *et al.* (2005c) used the composition of the essential oils to verify the presence of *P. spinulosa* at elevations above the Madeira laurel forest where it is a hyper-humid zone.

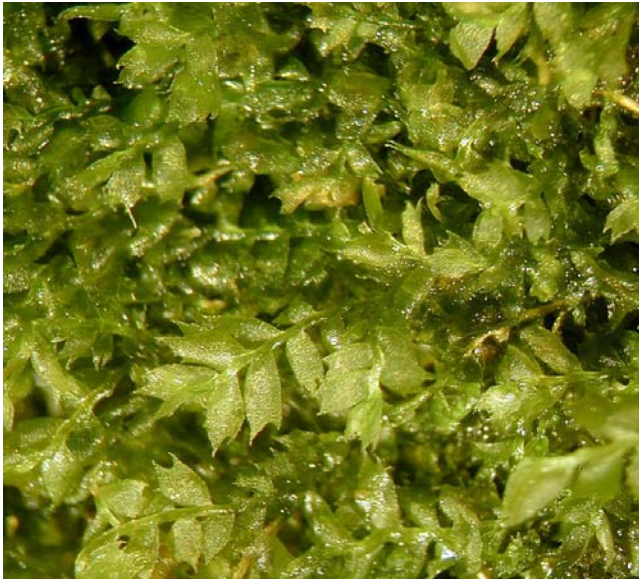


Figure 75. *Plagiochila exigua*, a species with secondary compounds like those of *Plagiochila spinulosa*. Photo by Michael Lüth, with permission.

Plagiochila spinulosa (Figure 66-Figure 69, Figure 71-Figure 73) produces **volemitol** as one of its photosynthetic sugar products (Suleiman *et al.* 1980). It would be interesting to know if this product is in any way connected to its preference for moist habitats. In the intertidal brown alga *Pelvetia canaliculata*, concentrations of both mannitol and volemitol increased with increases in temperatures up to 27°C (Pfetzing *et al.* 2000). Continuous emersion elicited no changes in concentrations of these two sugars at 10°C for 7 days, but when the algae were emersed continuously for 8 or 12 days at 25°C the volemitol concentrations exhibited significant decrease but mannitol concentrations did not change significantly. In its circumpolar distribution *Plagiochila spinulosa* is not likely to encounter such high temperatures in water, but above water it could encounter them for brief periods.

Rycroft (1990) identified two new bibenzyl-fusicoccane conjugates. Anton *et al.* (1997) identified hydroxy-4'-methoxy-bibenzyl in *Plagiochila spinulosa* (Figure 66-Figure 67, Figure 71-Figure 73).

One compound identified is **lunularic acid** (Rycroft *et al.* 1999), a hormone that has similar activity to that of abscisic acid and may help it to live in its wide range of habitats.

***Plagiochilon oppositum* (Figure 76)**

Distribution

Plagiochilon oppositum (Figure 76) has a widespread distribution, including Australia, China, Fiji, India (West Bengal, southern Western Ghats, Eastern Himalaya, and Northeast India), Indonesia, Japan, Malaysia, Myanmar, New Caledonia, New Guinea, Philippines, Samoa, Solomon Islands, Sri Lanka, Taiwan, Thailand, Vanuatu, and Vietnam (Daniels & Kariyappa 2012). Renner *et al.* (2016) noted the variability of the species, but concluded that it "contains significant phylogenetic substructuring that is not necessarily the result of geographic isolation."



Figure 76. *Plagiochilon oppositum*, Yunnan, China. Photo courtesy of Li Zhang.

Aquatic and Wet Habitats

Ruttner (1955) reported *Plagiochilon oppositum* (Figure 76) from waterfalls in the tropics. But it appears that this species is more typical of montane forests (Gradstein *et al.* 2010; Daniels 2020). In West Java, it occurs on bark at higher elevations. It is typical in tropical montane evergreen forests and wet evergreen forests (Daniels 2020). In Sulawesi it occurs in both lowland and montane forests (Nunik & Gradstein 2007).

Trichocoleaceae

***Trichocolea tomentella* (Figure 77-Figure 86)**

Distribution

Trichocolea tomentella (Figure 77-Figure 86) is distributed in the temperate regions in the Northern Hemisphere, where it is mostly oceanic and suboceanic (Korpelainen *et al.* 2004). It occurs in Africa, Oceania, Australia, the Caribbean islands, Europe, Asia, Central America, and North America (ITIS 2020), with the largest number of known locations in Europe and North America. In New Zealand, there are four species of *Trichocolea*, but not *T. tomentella* (Hatcher 1958). These are forest species, on the ground or as epiphytes.



Figure 77. *Trichocolea tomentella* leaf, a highly dissected structure. Photo by Hermann Schachner, through Creative Commons.

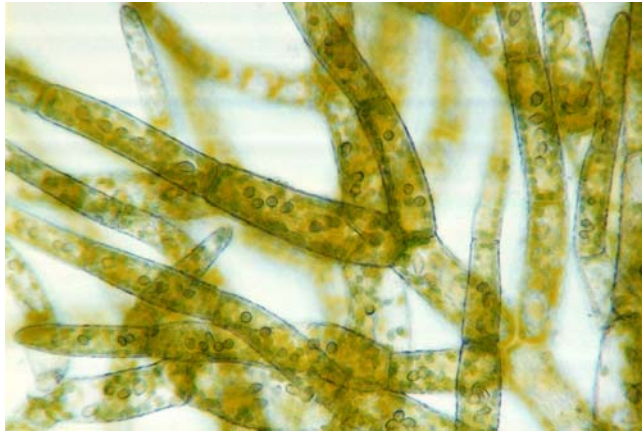


Figure 78. *Trichocolea tomentella* microscopic view showing chloroplasts and the very different arrangement of cells when compared to most leafy liverworts. Photo through Creative Commons.



Figure 79. *Trichocolea tomentella* forming clumps like one can find in a wetland. Photo by Hugues Tinguy, with permission.



Figure 80. *Trichocolea tomentella* with red pigmentation, suggesting it has been exposed to bright sunlight. Photo by Rick Ballard, through Creative Commons.

Aquatic and Wet Habitats

Because of its moisture requirements, *Trichocolea tomentella* (Figure 81-Figure 84) is habitat limited, occurring in springs and mesic habitats in woodlands.



Figure 81. *Trichocolea tomentella* showing its branching pattern. Note the whitish color of the dry form. Photo by Almantas Kulbis, through Creative Commons.



Figure 82. *Trichocolea tomentella* wet. Note the change in color to green in the wet form. This results from water filling in the spaces and probably activates the chloroplasts. The reflection of light waves by dry cells might account for the color change when water fills in the spaces. Photo by Li Zhang, with permission.



Figure 83. *Trichocolea tomentella* dry, showing the tight spacing of the leaf dissections. Photo by Erika Mitchell, through Creative Commons.



Figure 84. *Trichocolea tomentella*, showing water clinging in the many capillary spaces, permitting it to remain hydrated longer. Photo by Hermann Schachner, through Creative Commons.



Figure 86. *Trichocolea tomentella* on a stream bank. Photo Erika Mitchell, through Creative Commons.

Trichocolea tomentella (Figure 77-Figure 86) grows in shaded and humid habitats in seminatural or natural forests (Korpelainen *et al.* 2004). It is a vulnerable species in Finland and rare in Lithuania, while declining in southern England due to habitat loss (Korpelainen *et al.* 2004). Likewise, in southern Norway it is becoming extinct in many localities due to logging and draining near streams, springs, and gullies (Rydgren *et al.* 2012).

In Norway and Sweden, *Trichocolea tomentella* (Figure 77-Figure 86) occurs mostly in moist, well-shaded places, especially in deciduous forests (Figure 85) (Rydgren *et al.* 2012). It is common near springs, streams (Figure 86), and gullies. In earlier studies, Watson (1919) reported it from ground associated with fast water. Mamczarz (1970) reported it from a spring community in streams near Lacko, Western Carpathians. Marstaller (1987) reported it as occurring with the *Platyhypnidium* (Figure 5) – *Fontinalis antipyretica* (Figure 6) association in Thuringia, Germany. In northwest Portugal, Vieira *et al.* (2005) reported it in dripping and steep granite slabs in fresh environments, associated with *Sphagnum subsecundum* var. *auriculatum* (Figure 87), *Fissidens polyphyllus* (Figure 88), and *Radula holtii*, in mountain streams, and similarly, Vieira *et al.* (2004) found it on dripping and steep granite slabs in Portugal. In Latvia, it not only occurs in the swampy spruce and mixed forests, but also on brook banks and springs (Bambe 2004).



Figure 85. *Trichocolea tomentella* on a tree base, with melting snow. Photo by Ekaterina Rozantseva, through Creative Commons.



Figure 87. *Sphagnum subsecundum* var. *auriculatum*, a species that associates with *Trichocolea tomentella* on dripping, steep granite slabs in Portugal. Photo by Hugues Tinguy, with permission.



Figure 88. *Fissidens polyphyllus*, a species that associates with *Trichocolea tomentella* on dripping, steep granite slabs in Portugal. Photo by Michael Lüth, with permission.

These records adequately describe most of its habitat in North America and other locations as well (Schuster 1953). Slack and Glime (1985) found it associated with Adirondack Mountain, USA, forest streams. In their study

of 138 localities in the Polish Carpathians, Klama *et al.* (2019) concluded that *Trichocolea tomentella* (Figure 77-Figure 86) prefers wetland habitats, primarily in forests (Figure 89). These included areas in the vicinity of springs (34% stands), stream banks (32%; Figure 86), wet parts of the forest floor (20%), and mountain bogs (16%). The species is diminishing in frequency due to the loss of these habitats.



Figure 89. *Trichocolea tomentella* growing on a vertical bank. Photo by Bernd Haynold, through Creative Commons.

Vieira *et al.* (2004) reported that some populations of *Trichocolea tomentella* (Figure 77-Figure 86, Figure 89) in Portugal streams are threatened by human trampling in areas with easy access. They never found it fertile in the three years (2001-2004) that they studied it. It is a vulnerable species in Finland and rare in Lithuania, while declining in southern England due to habitat loss (Korpelainen *et al.* 2004). In Norway, this species has been lost from 23% of the localities where it occurred in 1950 (Rydgren *et al.* 2012). In southeastern Norway, losses are greater due to urbanization and logging and draining near streams, springs, and gullies.

Trichocolea tomentella (Figure 77-Figure 86, Figure 89) is a long-day plant, at least in southern Illinois (Zehr 1979). In southern Illinois it grows in restricted habitats, especially sandstone canyons with high moisture levels (Zehr 1977). It grows any time of the year that temperatures are above freezing (Zehr 1979). The finely divided leaves and paraphyllia seem to enable it to retain water. While it may cease growth during a drought, it resumes within 1-2 weeks upon rehydration. Zehr suggests that its lack of antheridia or sexual reproduction in southern Illinois may be due to the low irradiation in its habitats there. In more northern locations, more daylight reaches the plants in their habitats and sexual reproduction occurs at least occasionally. It is common for red light to be a stimulus for the production of gametangia.

Reproduction

Pohjamo *et al.* (2008) examined the genetic diversity, gene flow, and population structure in 18 populations of this species in Finland, Lithuania, UK, and Canada. This species is dioicous, so it is not surprising that gene flow between populations is limited. Spore production needed for longer dispersal distances requires sexual reproduction, a process that is difficult or impossible when only one sex is present in a population or the clones are disconnected. Rather, short-range dispersal of fragments is suggested by colonization within populations. Fortunately, this is promoted by the long life span of the species and its ramet productions that permit it to compete well in a suitable location with no disturbance. Nevertheless, the populations are small and becoming more and more fragmented, increasing the vulnerability of this dioicous species.

Although sporophytes (Figure 90) are rare in this dioicous species, most likely contributing to its increasing rarity, gametangia have been reported more frequently (Korpelainen *et al.* 2004). Nevertheless, the species exhibits a relatively high level of genetic diversity (Pohjamo *et al.* 2008), but gene flow between the disconnected populations is infrequent and suggests the occasional movement of fragments into new populations. The shoots have a long life span once they reach a suitable habitat. It expands its populations by efficient ramet production.



Figure 90. *Trichocolea tomentella* with capsule. Photo by Hermann Schachner, through Creative Commons.

Fungal Interactions

The fungus *Penicillium chrysogenum* (Figure 92) occurs on *Trichocolea tomentella* (Figure 77-Figure 86, Figure 89-Figure 90) (Rakotondraibe *et al.* 2015). Extracts from this fungus are known to be bioactive against the HT-29 colon cancer cell line. Ali (2017) and coworkers (Ali *et al.* 2017) found that *Penicillium concentricum* (see Figure 91-Figure 92) occurs as an endophyte in *T. tomentella*. The interaction between the liverwort and its fungus induces the production of bioactive secondary metabolites by the fungus. Many of these are of medicinal value, including treatment for some types of cancer. Anaya-Eugenio *et al.* (2019) further elaborated on the medicinal compounds produced by endophytic *P. concentricum*. Preziuso *et al.* (2018) explored the medicinal implications for the genus *Trichocolea*.



Figure 91. *Penicillium* sp. on the moss *Hylocomium splendens*. The genus *Penicillium* occurs on *Trichocolea tomentella*. Photo courtesy of George Greiff.



Figure 92. *Penicillium chrysogenum*, a species that is bioactive against the HT-29 colon cancer cell line, occurs on *Trichocolea tomentella*. Photo by Crulina 98, through Creative Commons.

Biochemistry

Perry *et al.* (1996) identified structures of isoprenyl phenyl ethers and noted that these compounds were active as cytotoxic and antifungal agents. Nevertheless, fungi in the genus *Penicillium* (Figure 91-Figure 92) occur on and within *Trichocolea tomentella* (Figure 77-Figure 86, Figure 89). Barlow *et al.* (2001) described pathways of some of the isoprenyl phenyl ethers.

Asakawa *et al.* (1981) determined that isoprenyl benzoates serve as important chemical markers for *Trichocolea tomentella* (Figure 77-Figure 86, Figure 89) when compared to two other species in the Jungermanniales, supporting systematic classifications.

Suborder Myliineae

Myliaceae

Mylia anomala (Figure 93-Figure 102)

(syn. = *Leiomylia anomala*)

Distribution

Mylia anomala (Figure 93-Figure 102) occurs in the Northern Hemisphere, in Europe, Northern Asia, and North America. It has been recorded from Cape Breton Island, Canada (Nichols 1918), northern Alberta, Canada (Belland & Vitt 1995), Newfoundland, Canada (Weber 1976), New Hampshire, USA (Glime 1982), the Alps (Geissler & Selldorf 1986), Russia (Konstantinova *et al.* 2002; Shishkonakova *et al.* 2016), Finland (Pakarinen & Tolonen 1977; Pakarinen 1978; Välianta *et al.* 2007), Sweden (Albinsson 1997), Spain (Reinoso & Rodríguez-Oubiña 1988), and UK (Duckett *et al.* 1991).



Figure 93. *Mylia anomala*, a species that is widespread in the Northern Hemisphere. Photo by Hugues Tinguy, with permission.

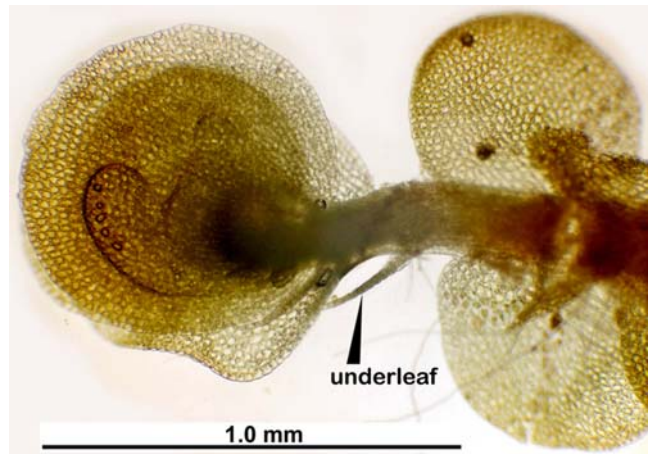


Figure 94. *Mylia anomala* branch. Photo modified from David H. Wagner, with permission.



Figure 95. *Mylia anomala* stem and leaf cross section. Photo by Kristian Peters, with permission.



Figure 98. *Mylia anomala* developing pigments in response to exposure. Photo by Michael Lüth, with permission.

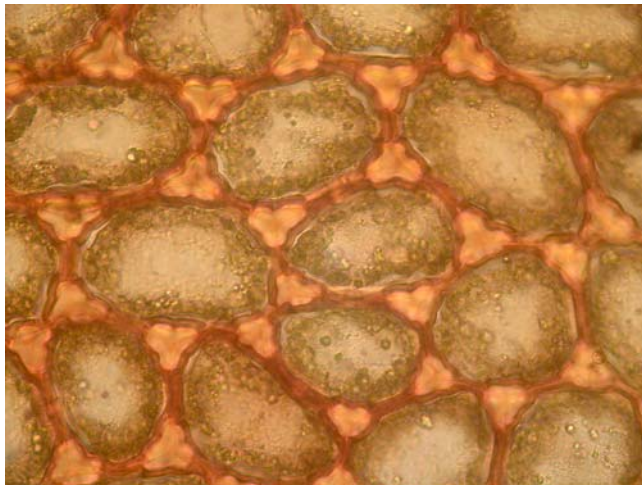


Figure 96. *Mylia anomala* cells showing trigones and wall pigmentation. Photo by Michael Lüth, with permission.



Figure 99. *Mylia anomala* forming a pigmented mat, indicative of exposure. Photo by Blanka Aguero, with permission.



Figure 97. *Mylia anomala* forming a tight mat on *Sphagnum*. Photo by Michael Lüth, with permission.



Figure 100. *Mylia anomala* forming a green mat, indicative of shade. Photo by Jan-Peter Frahm, with permission.



Figure 101. *Mylia anomala* growing in an upright position. Photo by Des Callaghan, with permission.



Figure 102. *Mylia anomala* showing compact growth form. Photo by David Holyoak, with permission.

Aquatic and Wet Habitats

The habitats of this species typically are associated with *Sphagnum* (Figure 103). *Mylia anomala* (Figure 93-Figure 102) occurs in moist hollows between *Sphagnum* hummocks, Cape Breton Island, Canada (Nichols 1918). It occurs with *Sphagnum* at the edges of lakes (Figure 107) in New Hampshire (Lorenz 1908). Using macrofossil analysis, Välimäki *et al.* (2007) identified a wet lawn habitat in a southern Finnish boreal bog, based on the presence of *Sphagnum rubellum* (Figure 103) and *Mylia anomala*.



Figure 103. *Sphagnum rubellum*, species, along with *Mylia anomala*, used to identify macrofossil wet lawn habitat in southern Finland. Photo by B. Gliwa, through Creative Commons.

Working in Finland, Pakarinen and Tolonen 1977) found that dead *Sphagnum fuscum* (Figure 104) could be covered by a thin layer of *Mylia anomala* (Figure 105). Pakarinen (1978) found that as the growth rate of *Sphagnum fuscum* decreases, liverworts, especially *Mylia anomala* (Figure 93-Figure 102), colonize the hummocks, increasing the volumetric density.



Figure 104. *Sphagnum fuscum*; when this species dies, *Mylia anomala* can overgrow it. Photo by Hermann Schachner, through Creative Commons.



Figure 105. *Mylia anomala* overgrowing a hummock of *Sphagnum fuscum*. Photo by Tuomo Kuitunen <luopioistenkasvisto.fi>, with permission.

In a study of peatland restoration Poulin *et al.* (2013) found that peatlands treatments differed in the responses they incurred after 8 years. Forest and ruderal species were more prominent in unrestored sites than in a reference site. Diversity and richness differed among sites. The peatland, forest, and wetland species were dominant in the restored sites. *Mylia anomala* (Figure 93-Figure 102), along with *Sphagnum rubellum* (Figure 103) and *Pohlia nutans* (Figure 106), were the main drivers of the revegetation.



Figure 106. *Pohlia nutans* with capsules, a species that, along with *Mylia anomala* and *Sphagnum rubellum* is a primary driver of revegetation in peatland restoration. Photo by Michael Lüth, with permission.

Shishkonakova *et al.* (2016) considered *Mylia anomala* (Figure 93-Figure 102), along with a number of lichen species, to be an indicator species for the soil subtype of destructive oligotrophic peat soils in the Russian classification of palso bogs. These are found in regressive bogs in the north taiga subzone of West Siberia. In Cataracts Provincial Park, Newfoundland, Canada, Weber (1976) considered *Mylia anomala* to be among the typical bog bryophytes. I should note here that at that time, North American botanists defined bogs as wetlands dominated by *Sphagnum* (Figure 103, Figure 104), thus not distinguishing them from poor fens.

In eastern Canadian bogs, the identification of early indicator species is a useful tool to indicate the need for intervention soon after restoration (González *et al.* 2013). Certain species are indicative when a site is not on a desired successional path. Important indicator species that signal a successful restoration are the bryophytes *Sphagnum rubellum* (Figure 103) and *Mylia anomala* (Figure 93-Figure 102), along with the black spruce tree *Picea mariana* (Figure 107-Figure 108).



Figure 107. *Picea mariana* "bog" forest in taiga (fen as described by Europeans), Quebec, Canada. Photo by Peupleloup, through Creative Commons.



Figure 108. *Mylia anomala* in a spruce fen. Photo by Michael Lüth, with permission.

In their study of boreal bog plants, Nordbakken *et al.* (2003) found that the lowest N percentages (0.8%) occurred in *Mylia anomala* (Figure 93-Figure 102). The N content increased in this species with experimental addition of N throughout the three years of the experiment. They suggested that the increases in the labelled N values in this species may represent an increasing importance of ammonium as the N source, or it could be due to its slow growth rate. Since this species grows between and over the top of the *Sphagnum* (Figure 103, Figure 104) shoots in the hummocks, the positive change in the N obtained may be due to its higher dependence on N in precipitation rather than that supplied by mycorrhizal relationships common in many tracheophytes of bogs. Prokaryotic endosymbionts are absent in these liverworts, so Duckett *et al.* (1991) considered the reports of nitrogen fixation by this and other liverworts to be due to associated *Cyanobacteria* (Figure 109).



Figure 109. *Chroococcus* sp. (Cyanobacteria) such as that one might find on *Mylia anomala* leaves. Photo by Jason Oyadomari, with permission.

Albinsson (1997) considered *Mylia anomala* (Figure 93-Figure 102) to have a narrow ecological amplitude in the mire habitat, particularly when compared to smaller species (Figure 110) like *Cephalozia* (Figure 111) or *Kurzia* (Figure 112) species. Gerdol (1995) determined that it likewise had a narrow nutrient niche. In the Swedish mires, it was among the most frequent of the 43 liverworts described by Albinsson (1997) and preferred poor mire

conditions, occupying hummocks (Figure 113-Figure 116). The adaptations of *Mylia anomala* to this elevated habitat include increased desiccation resistance, ability to overgrow *Sphagnum* (Figure 103, Figure 104, Figure 113-Figure 116), penetration of leaves by liverwort rhizoids, and a high reproductive output (Økland 1990), including gemmae (Figure 117-Figure 119). Albinsson considered this to be a compromise strategy.



Figure 110. *Mylia anomala* in association with smaller liverworts. Photo by Michael Lüth, with permission.



Figure 111. *Cephalozia bicuspidata*, in a genus that has a wider ecological amplitude than *Mylia anomala*. Photo by Hugues Tinguy, with permission.



Figure 112. *Kurzia trichoclados*, in a genus that has a wider ecological amplitude than *Mylia anomala*. Photo by David T. Holyoak, with permission.



Figure 113. *Mylia anomala* overgrowing *Sphagnum* on a hummock in Perrault Fen, Upper Peninsula of Michigan, USA. Photo by Janice Glime.



Figure 114. *Mylia anomala* growing with cranberries on a hummock in a poor fen. Photo by Michael Lüth, with permission.



Figure 115. *Mylia anomala* growing with *Sphagnum* and *Polytrichum*. Photo by Michael Lüth, with permission.



Figure 116. *Mylia anomala* with apical gemmae (yellow), growing with *Sphagnum*. Photo by Michael Lüth, with permission.

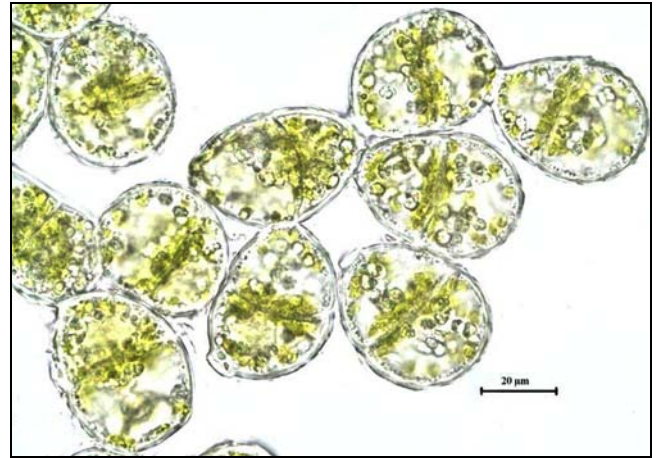


Figure 119. *Mylia anomala* gemmae. Photo by Hugues Tinguy, with permission.



Figure 117. *Mylia anomala* with gemmae on leaf tips. Photo by David Holyoak, with permission.



Figure 118. *Mylia anomala* with marginal and leaf-tip gemmae. Photo by Jan-Peter Frahm, with permission.

But it is able to occupy other aquatic and wetland habitats as well; it appears on the walls in the flume (Figure 120) at Franconia Notch, New Hampshire, USA (Glime 1982). Some occur in moist moors (Figure 121). In the Alps, it is uncommon with *Eleocharis quinqueflora* (Figure 122) (Geissler & Selldorf 1986). In the Russian far east, it occurs on streambanks (Figure 123) at treeline of the Upper Bureya River (Konstantinova *et al.* 2002).



Figure 120. Flume at Franconia Notch, New Hampshire, USA, where one can find *Mylia anomala* on the walls. Photo by Janice Glime.



Figure 121. *Mylia anomala* with heather. Photo by Michael Lüth, with permission.



Figure 122. *Eleocharis quinqueflora*, a wet habitat species in the Alps, but where *Mylia anomala* occurs uncommonly. Photo by Max Licher, through Creative Commons.



Figure 123. *Mylia anomala* habitat on streambank. Photo by Hermann Schachner, through Creative Commons.

Fungal Interactions

Duckett *et al.* (1991) found rhizoid-ascomycete fungi in *Mylia anomala* (Figure 93-Figure 102). In that liverwort, the fungi are restricted to the rhizoids (Figure 124) because this is one of the species that lacks flagelliform branches. They determined that the rhizoids swell in response to infection, with swelling being absent in

sterile culture of the liverwort. It is in these swollen tips that most of the fungal hyphae reside.

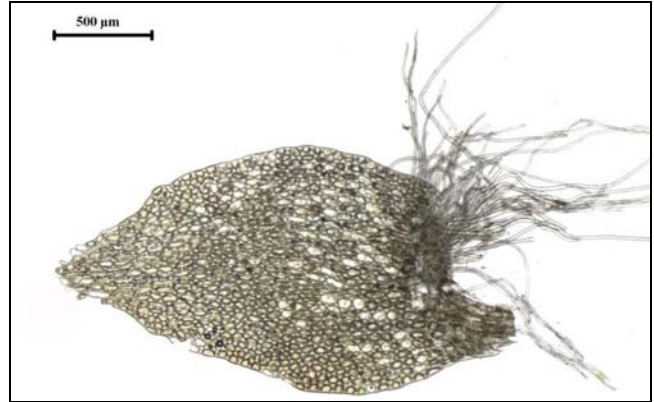


Figure 124. *Mylia anomala* underleaf with rhizoids, the site of ascomycete fungi. Photo by Hugues Tinguy, with permission.

Paul Davison has provided interesting images of the leaf cuticle of *Mylia anomala* (Figure 125). This cuticle may explain its ability to occupy habitats above water where it can become periodically dry. We know that the cuticle has a role in protecting tracheophytes from fungal invasions (Kolattukudy 1985). Could it serve any role in protection of these bryophytes against fungi?

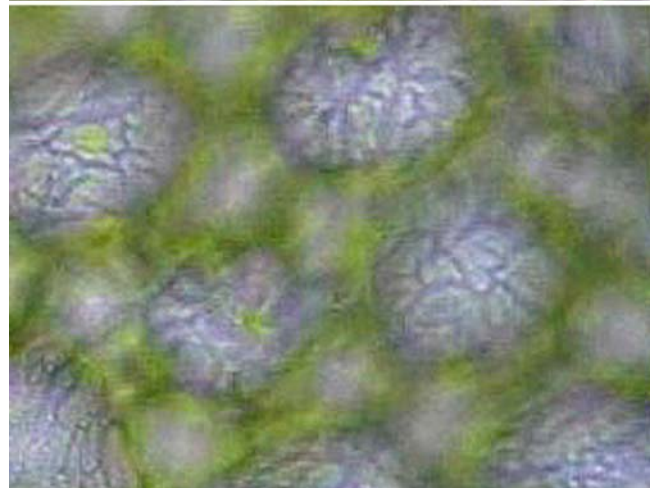


Figure 125. *Mylia anomala* showing cuticle. Photo by Paul G. Davison, with permission.

Biochemistry

Other potential protections against fungal presence are secondary compounds. Aromatic and other secondary compounds occur in oil bodies (Figure 126) of leaf cells. Ludwiczuk and Asakawa (2015) determined that *Mylia anomala* (Figure 93-Figure 102) produces mainly cyathane-type diterpenoids.

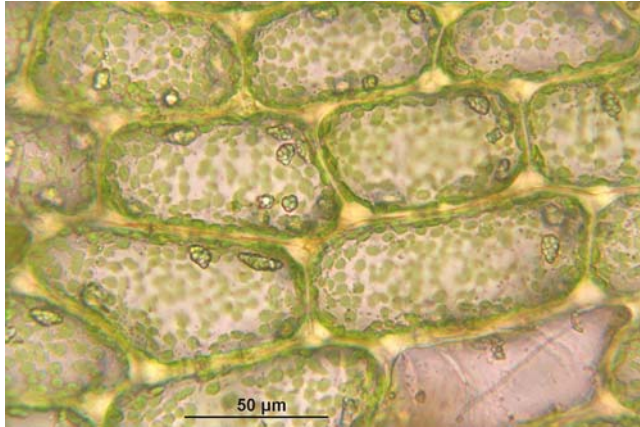


Figure 126. *Mylia anomala* cells with oil bodies, showing here mostly around the cell margins as oblong structures. Photo by Hermann Schachner, through Creative Commons.

Mylia taylorii (Figure 127-Figure 142)

Distribution

Mylia taylorii (Figure 127-Figure 142) is a circumboreal, mostly montane species with a suboceanic distribution (Engel & Braggins 2005). It occurs in mountainous districts of northern Europe, mountains of Continental Europe, Greenland, and eastern North America from Newfoundland to Tennessee (Wikipedia 2020). It is uncommon in western North America and eastern Asia, where it is known from Guizhou Province, China (Zhang & Chen 2006). It is best known from Great Britain and Scandinavia.



Figure 127. *Mylia taylorii*, a circumboreal species. Photo by Tuomo Kuitunen <luopioistenkasvisto.fi>, with permission.



Figure 128. *Mylia taylorii* with succubous leaves that help to conserve water. Photo by Martin Hutten, with permission.



Figure 129. *Mylia taylorii* showing the ability of the leaves to fold, reducing surface area for water loss. Photo by Kristian Peters, with permission.

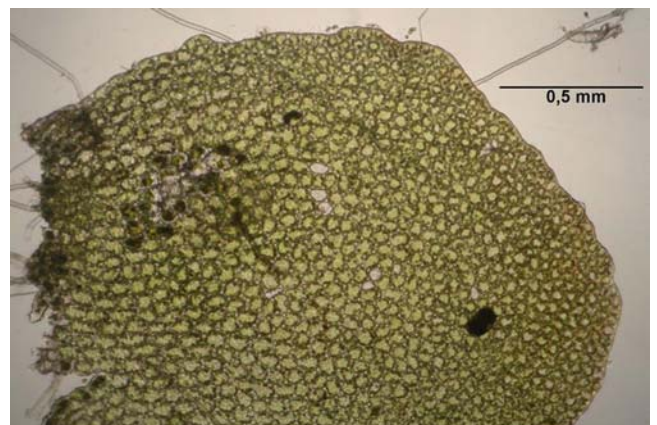


Figure 130. *Mylia taylorii* leaf. Photo by Snappy Goat, through public domain.

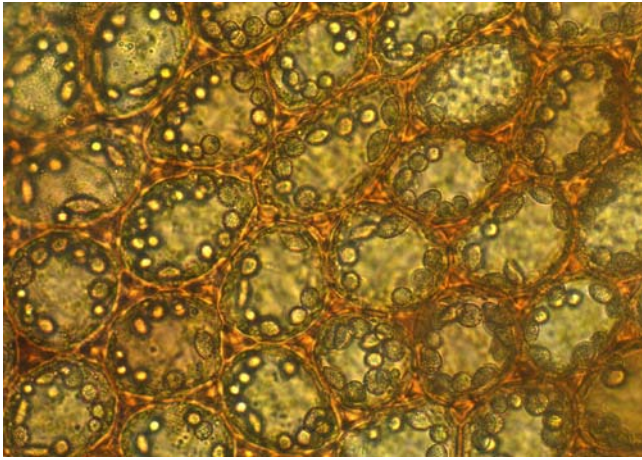


Figure 131. *Mylia taylorii* leaf cells showing trigones; the bright spots are oil bodies. Photo by Blanka Aguero, with permission.



Figure 134. *Mylia taylorii* red form that is typical of exposed sites. Photo by Hermann Schachner, through Creative Commons.



Figure 132. *Mylia taylorii* forming a mat. Photo by Snappy Goat, through public domain.



Figure 135. *Mylia taylorii* deep red form. Photo by Barry Stewart, with permission.



Figure 133. *Mylia taylorii* green form that is typical of shade. Photo by Hermann Schachner, through Creative Commons.

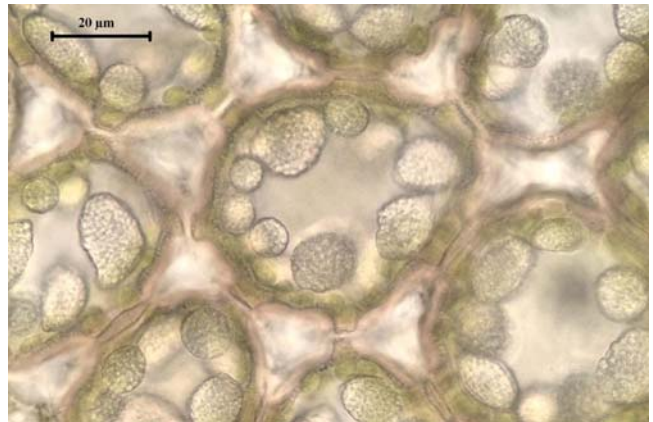


Figure 136. *Mylia taylorii* leaf cells showing oil bodies. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Mylia taylorii (Figure 127-Figure 142) occurs on wet shore rocks and wet sandy shores in Scotland (West 1910), on wet rock cliffs associated with streams, Cape Breton Island, Canada (Nichols 1918), and in upstream reaches in the Harz Mountains of Germany (Bley 1987).

On the very wet Queen Charlotte Islands, British Columbia, Canada, Hong (2007) found it on shaded, decayed wood and moist soil. In the Bavarian Alps, Lotto

(1987) also found it on logs, humus, and the acidic forest floor.

In Germany, *Mylia taylorii* (Figure 127-Figure 142) forms large tufts that are easy to recognize on moist non-calcareous rocks, including sandstone, granite, and gneiss (Schnittler *et al.* 2010). It occupies sheltered conditions with high humidity and a cool climate, but it is rarely found on decaying wood, humus, or *Sphagnum* peat (Figure 137) there.



Figure 137. *Mylia taylorii* habitat in a seep with *Sphagnum*. Photo by Michael Lüth, with permission.

Engel and Braggins (2005) consider *Mylia taylorii* (Figure 127-Figure 142) to be mostly restricted to acidic rocks never occurring on calcareous rocks. This makes moist siliceous rocks suitable, as well as vertical rock walls (Figure 138- Figure 141), but as just seen above, the species also finds suitable habitat on calcareous rocks and decaying logs.



Figure 138. *Mylia taylorii* habitat on rock. Photo by Richtid, with permission.

On the other hand, in Sakhalin, Russia, Bakalin *et al.* (2009) found *Mylia taylorii* (Figure 127-Figure 142) in wet moss mats on the seeping water in limestone cliff crevices. In these locations it can occur in pure mats (Figure 142) or with *Sphenolobus minutus* (Figure 143). It occurs on shady limestone cliffs and on decaying wood in *Abies* forests (Figure 144). In the tundra, it grows over moss mats on the seeping permafrost water and also in

crevices of limestone cliffs. In addition to pure mats, it occurs with *Bazzania denudata* (Figure 145), *Calypogeia integristipula* (Figure 146), *Eocalypogeia schusterana*, *Douinia plicata* (see Figure 147), *Odontoschisma macounii* (Figure 148), and *Tritomaria exsecta* (Figure 149).



Figure 139. *Mylia taylorii* habitat on rock. Photo by Richtid, with permission.



Figure 140. *Mylia taylorii* (red) habitat on rocks of an embankment. Photo by Michael Lüth, with permission.



Figure 141. *Mylia taylorii* showing growth form on a vertical substrate. Photo by Hugues Tinguy, with permission.

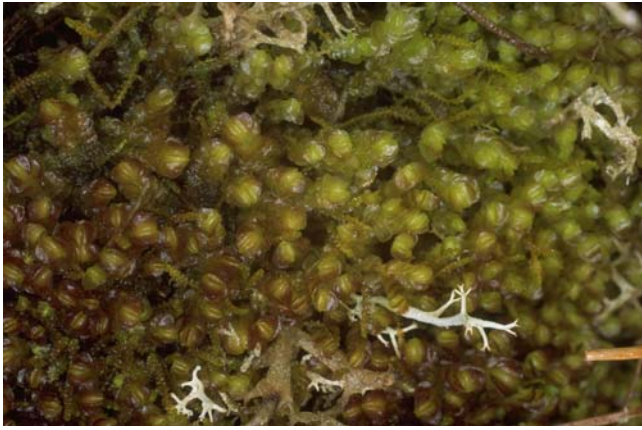


Figure 142. *Mylia taylorii* forming a pure wet mat (with occasional lichens), as one might find in seepage water of rock cliffs. Photo by Jan-Peter Frahm, with permission.



Figure 145. *Bazzania denudata*, a species that occurs with *Mylia taylorii* on limestone cliffs in the tundra. Photo from Botany Website, UBC, with permission.



Figure 143. *Splenolobus minutus*, a species that occurs with *Mylia taylorii* in seeping water in limestone cliff crevices. Photo by Jan-Peter Frahm, with permission.



Figure 146. *Calypogeia integristipula*, a species that occurs with *Mylia taylorii* on limestone cliffs in the tundra. Photo by Hermann Schachner, through Creative Commons.



Figure 144. *Abies sibirica* forest, where *Mylia taylorii* can occur on shady limestone cliffs and decaying wood. Photo by Krasnoyarsk Territory, through Creative Commons.



Figure 147. *Douinia ovata*; *Douinia plicata* is a species that occurs with *Mylia taylorii* on limestone cliffs in the tundra. Photo by Des Callaghan, with permission.



Figure 148. *Odontoschisma macounii*, a species that occurs with *Mylia taylorii* on limestone cliffs in the tundra. Photo from Earth.com, with permission.



Figure 149. *Tritomaria exsecta*, a species that occurs with *Mylia taylorii* on limestone cliffs in the tundra. Photo by Hermann Schachner, through Creative Commons.

Mylia taylorii (Figure 127-Figure 142) requires at least 120-140 wet days per year, a condition found in sessile oak (*Quercus petraea*; Figure 150) and downy birch (*Betula pubescens*; Figure 151) forests of the western UK (Ratcliffe 1968). It also occupies deep, wet bogs, but prefers sites where the *Sphagnum* (Figure 137) is unhealthy or has limited growth. It is interesting that Bakalin *et al.* (2009) found it in limestone habitats in Russia, whereas Ratcliffe and many other authors describe it as a calcifuge. Gaddy (2002) likewise reported *Mylia taylorii* from a montane acidic cliff, as well as on a spray cliff.



Figure 150. *Quercus petraea* forest, a habitat that typically provides the 120-140 wet days required by *Mylia taylorii*. Photo by Gruban, through Creative Commons.



Figure 151. *Betula pubescens* forest, a habitat that typically provides the 120-140 wet days required by *Mylia taylorii*. Photo by Dan Aamlid, through Creative Commons.

Juutinen *et al.* (2016) reported *Mylia taylorii* (Figure 127-Figure 142) from scree and stones at Kuusamo, Finland. Härtel *et al.* (2007) also considers this to be a liverwort of "rock cities."

Mylia taylorii (Figure 127-Figure 142) is a calcifuge, but it is able to live on rotten logs in calcareous areas (Olleck *et al.* 2020), finding there both acidic conditions and moisture. Perhaps there were mediating factors that provided acidic microhabitats with acidic conditions that could explain the report by Bakalin *et al.* (2009). Another possibility is that there are ecological races.

Its intolerance for desiccation explains the distribution of *Mylia taylorii* (Figure 127-Figure 142) in wet environments. At 85% relative humidity, about 75% of the cells remain alive (Clausen 1964). At 75% relative humidity, few cells remain alive. After 4-5 days at -10°C in ice, only about 1/4 of the cells remain alive.

Adaptations

Many populations exhibit red coloration (Figure 152). Such coloration is usually an indication of stress, typically bright light or low temperatures or a combination of these. Nutrient stress could also be a factor. Research is needed to determine the stimulus for the coloration in this species.



Figure 152. *Mylia taylorii* exhibiting red coloration that typically is an indication of stress, including bright sunlight. Photo by Štěpán Koval, with permission.

Reproduction

In Finland where it grows on rock scree, *Mylia taylorii* (Figure 127-Figure 142) produces gemmae (Figure 153) on the margins of the upper leaves.

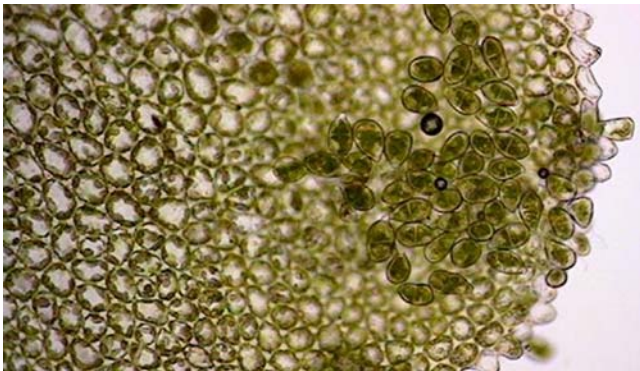


Figure 153. *Mylia taylorii* gemmae on leaf. Photo by Paul G. Davison, with permission.

Fungal Interactions

Mylia taylorii (Figure 127-Figure 142) is an indicator species for ravine myxomycetes, at least in parts of Germany (Schnittler *et al.* 2010). This liverwort was present in 64% of the myxomycete habitats in Saxonian Switzerland (Germany). And 96% of the records for the myxomycete *Colloderma robustum* (Figure 154) were associated with *Mylia taylorii*. The liverwort turfs in this region are restricted to the deepest parts of the ravines where the climate is most uniform (Schnittler *et al.* 2010). The myxomycete plasmodium of *Colloderma robustum* lives in these turfs that are typically 2-5 cm thick. *Colloderma robustum* often has 500-1000 plasmodiocarps on a single *Mylia taylorii* turf of 10-20 cm diameter. The

plasmodia are initially creamy-white, hiding within the turfs along with green algae. In about 2-3 weeks before fructification, these plasmodia emerge, later turning to a sulfur-yellow color. They then start to form their plasmodiocarps at the tips of the *M. taylorii* shoots and secrete a solid translucent slime sheath.



Figure 154. *Colloderma robustum*, a common slime mold on *Mylia taylorii* in ravines. Photo by Sarah Lloyd, with permission.

Unlike *Mylia anomala* (Figure 93-Figure 102), *Mylia taylorii* (Figure 127-Figure 142) has normal rhizoids (Figure 155-Figure 156), indicating the absence of the ascomycete fungi that invade *Mylia taylorii* (Duckett *et al.* 1991).

Schnittler *et al.* (2010) observed that *Mylia taylorii* turfs (Figure 156) grow thicker each year. Eventually their weight causes them to drop from the rock and the growth cycle starts over. The result is that if a rock exceeds 60° inclination, it will not achieve more than 50% cover by this species due to this periodic loss.

Biochemistry

Matsuo *et al.* (1977) identified a new tetracyclic sesquiterpene ketone from *Mylia taylorii* (Figure 127-Figure 142). Later, the structure of another sesquiterpene ketone was described (Matsuo *et al.* 1979). Reuß *et al.* (2004) identified essential oils in this species.



Figure 155. *Mylia taylorii* rhizoids on ventral side of stem (left) and with underleaf (right). Photo by Paul G. Davison, with permission.



Figure 156. *Mylia taylorii* forming a turf, showing rhizoids along stem. Photo by Michael Lüth, with permission.

Suborder Perssoniellineae

Schistochilaceae

Schistochila aligera (Figure 157)

Distribution

Schistochila aligera (Figure 157) is distributed in Asia and Melanesia (So 2003a). It occurs in Indonesia, Java, Philippines, Fiji Islands, Samoa Islands, New Guinea, Tahiti, Cook Islands, New Caledonia, and Vanuatu (So 2003b). Daniels and Daniels (2008) have rediscovered it in India. More recently it has been reported from Thailand, where it is the most common species in the genus (Juengprayoon *et al.* 2015). Gao and Wu (2004) reported it from Taiwan and Hainan. But like so many tropical species, it is extremely variable and thus has been known by a number of names now considered synonyms.



Figure 157. *Schistochila appendiculata*; *Schistochila aligera* occurs mostly in Asia and Ruttner (1955) listed it as aquatic in the tropics. Photo by Larry Jensen, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported this species as an aquatic species in the tropics. In Thailand it is epiphytic or lithophilic (Juengprayoon *et al.* 2015). Similarly, Gao and Wu (2004) described it from old trunks and decayed wood

in Taiwan and Hainan. In Sulawesi, Indonesia, *Schistochila aligera* (Figure 157) forms one of three distinctive associations on bark (Gradstein & Culmsee 2010). We need to gather more information on its habitats and to determine just what sort of "aquatic" habitat it can occupy.

Reproduction

Schistochila aligera (Figure 157) can be **dioicous** or **autoicous** (Daniels & Daniels 2008), suggesting that it needs more biochemical and genetic studies to look for races and subspecies. Nagashima *et al.* (1991) identified diterpenoids in this species from Japan. Similarly Ludwiczuk and Asakawa (2008) reported pimarane-type diterpenoids from *Schistochila aligera* in Malaysia. Secondary compounds from *Schistochila aligera* from China and Mongolia have evidenced antibacterial activity against several species of bacteria (Zhu *et al.* 2006).

Fungal Interactions

An *Octosporella*-like ascomycete (Figure 27-Figure 29) forms appressoria and haustoria on the leaves of *Schistochila aligera* (Figure 157) (Döbbeler 1978, 1997). However, there are no records of rhizoid infections on this liverwort (Pressel *et al.* 2008).

Summary

Members of the **Plagiochilaceae** and other families included here are mostly terrestrial, but some are restricted to or common in wet habitats, occupying stream banks, spray areas, and wetlands. The family is large, especially in the tropics, so the few presented here are only a small segment of the family.

Trichocolea tomentella occurs in fens, on streambanks, and in wet spots in forests.

Mylia anomala is predominantly a bog/poor fen species and other acidic habitats. *Mylia taylorii* seems to be restricted to non calcareous habitats in most of its range, but occupies limestone in Russia – a contrast that needs further study.

A number of the aquatic liverworts in these jungermannialian families have fungi on the surface or in the cells. The interactions of these fungi are not well known, but there is evidence that for some the bryophyte stimulates the fungus to produce antibiotic compounds that are active against some kinds of cancer cells.

Acknowledgments

Lars Söderström provided me with the current acceptable names for a number of older taxa. Peter Döbbeler and George Greiff provided me with needed images and references. Many images came from the internet, and I thank all who have put their images in Creative Commons or given me permission to use their images.

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CHAPTER 1-7

AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: JUBULINEAE, PART 1

TABLE OF CONTENTS

Porellales – Suborder Jubulineae	1-7-2
Frullaniaceae	1-7-2
<i>Frullania asagrayana</i>	1-7-2
<i>Frullania riparia</i>	1-7-4
<i>Frullania tamarisci</i>	1-7-5
<i>Frullania teneriffae</i>	1-7-7
Jubulaceae	1-7-9
<i>Jubula hutchinsiae</i>	1-7-9
<i>Jubula hutchinsiae</i> subsp. <i>pennsylvanica</i>	1-7-12
<i>Jubula hutchinsiae</i> var. <i>integrifolia</i>	1-7-13
Lejeuneaceae	1-7-13
<i>Acanthocoleus aberrans</i>	1-7-13
<i>Bromeliophila</i>	1-7-13
<i>Bromeliophila helenae</i>	1-7-14
<i>Bromeliophila natans</i>	1-7-14
<i>Cephalantholejeunea temnanthoides</i>	1-7-15
<i>Ceratolejeunea temnantha</i>	1-7-15
<i>Cheilolejeunea clypeata</i>	1-7-16
<i>Cololejeunea biddlecomiae</i>	1-7-18
<i>Cololejeunea calcarea</i>	1-7-22
<i>Cololejeunea hodgsoniae</i>	1-7-23
<i>Cololejeunea madothecoides</i>	1-7-23
<i>Cololejeunea microscopica</i>	1-7-23
<i>Cololejeunea rossettiana</i>	1-7-24
<i>Cololejeunea stotleriana</i>	1-7-25
<i>Colura</i>	1-7-26
<i>Colura calyptrifolia</i>	1-7-27
<i>Colura irrorata</i>	1-7-28
<i>Diplasiolejeunea cavifolia</i>	1-7-30
Summary	1-7-32
Acknowledgments	1-7-33
Literature Cited	1-7-33

CHAPTER 1-7

AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: JUBULINEAE, PART 1



Figure 1. *Jubula hutchinsiae* habitat. Photo by Michael Lüth, with permission.

Nomenclature for this chapter is based primarily on Söderström *et al.* (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species.

To develop this list, I used my own bibliography, collected over the past 56 years, and Google Scholar. These papers soon led me to others. I do not pretend that this is complete. It includes streams, lakes, and a wide range of other wetlands. It deliberately ignores bogs (especially *Sphagnum*) and mostly ignores fens, but nevertheless includes some species from these habitats because they were found in a wetland study. Bogs and poor fens have been treated in whole books and provide an extensive literature; fens seem somewhat less studied. They would require considerably more review and time. Thus I felt that less-reviewed topics, particularly the

aquatic habitats with which I am most familiar, should be given priority.

Many of the species in this subchapter are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study. Their relative frequency can be inferred based on the number of references cited.

Porellales – Suborder Jubulineae

Frullaniaceae

This family occurs predominantly on boulders and tree trunks and branches. However, a few taxa seem at least tolerant of more moist habitats and have been included here.

Frullania asagrayana (Figure 2)

(syn. = *Frullania tamarisci* subsp. *asagrayana*)

Although *Frullania asagrayana* (Figure 2) has been treated as a subspecies of *Frullania tamarisci* (Figure 3), Crandall-Stotler *et al.* (1987) found that both morphological and biochemical differences among these subspecies indicated a greater genetic distance than that expected for subspecies. This includes unique flavonoid profiles and a considerable level of terpenoid and phosphoglucoisomerase dissimilarity. Heinrichs *et al.* (2010) likewise supported its recognition as a separate species based on DNA markers, but found these were not as strongly supported by morphological differences. They considered this species complex to be "the most explicit example of a complex of semi-cryptic and cryptic liverwort species." Their findings "support frequent short-distance migration, rare successful long-distance dispersal events, extinction, and recolonization as an explanation for the range formation in these *Frullania* species."



Figure 2. *Frullania asagrayana* (reddish) with *Drepanolejeunea appalachiana* (green) growing on it. Photo by Ken McFarland and Paul Davison, with permission.



Figure 3. *Frullania tamarisci* (Tamarisk Scalewort); *Frullania asagrayana* was originally included as a subspecies of this species. Photo by Barry Stewart, with permission.

Distribution

Frullania asagrayana (Figure 2) is distributed broadly throughout eastern North America from Canada to the Gulf Coast (Ramaiya *et al.* 2010) and westward to the Ozarks (Schuster 1992). The leaves have **ocelli** (Figure 4-Figure 5), a character absent in many *Frullania* species.

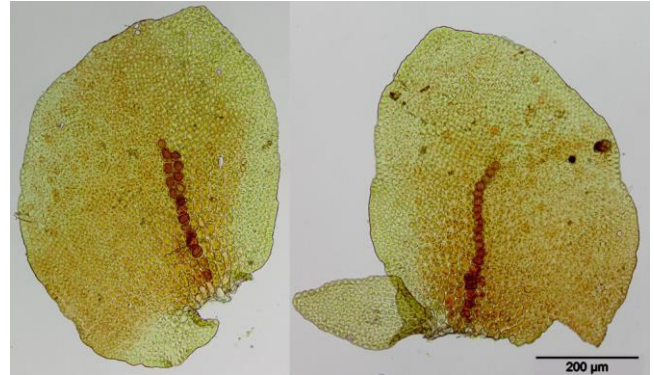


Figure 4. *Frullania asagrayana* leaf cells and ocelli (line of brown cells). Photo by Blanka Aguero, with permission.

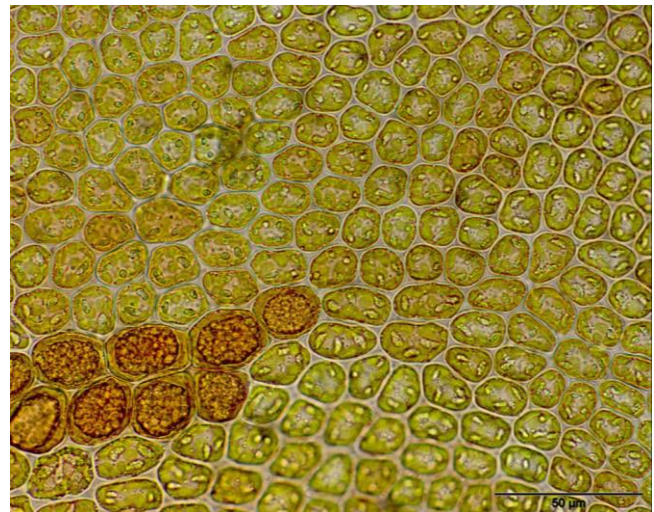


Figure 5. *Frullania asagrayana* ocelli and leaf cells showing oil bodies where secondary compounds are stored. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Frullania asagrayana (Figure 2) occurs in crevices or the surface of drier cliffs in a ravine in Connecticut, USA, but Nichols (1916) lists it in his study along rivers and streams from these habitats. Otherwise, it does not seem to be truly aquatic or wetland. More frequently, *Frullania asagrayana* (Figure 2) is epiphytic (Davison 1997).

Reproduction

Frullania asagrayana is **dioicous** (Figure 6), so one is not likely to see sporophytes often. It does, however, reproduce through regeneration. This permits leaves and leaf fragments to produce new plants.



Figure 6. *Frullania asagrayana* showing perianths on female plant. Photo by Blanka Shaw, with permission.

Fulford (1956) described regeneration from a leaf cell of *Frullania asagrayana* (Figure 2, Figure 6). First a cell dedifferentiates. Then it becomes swollen. The protonema pushes through the swollen area, creating a flap or lid that remains at the side of this new protonema and ultimately can appear at the base of the rhizoid of the developing plant. Fulford suggests that some cells that have been interpreted as gemmae are in fact these swollen regeneration cells.

Interactions

Cornejo and Scheidegger (2016) considered that cyanobacterial interactions with liverworts were important in the composition and dynamics in bryophyte and lichen-dominated epiphytic communities. They concluded that the liverwort *Frullania asagrayana* (Figure 2, Figure 6) serves as a reservoir for **Cyanobacteria** (Figure 7) that are partners for the lichens. The authors confirmed by DNA bar coding that strains of the cyanobacterial lichen partner *Rhizonema* were able to live on the surface of *Frullania asagrayana*. Some of the strains of *Rhizonema* were very specific about the lichens that served as their partners, whereas others appeared to be generalists, a phenomenon also noted by Rikkinen (2013).



Figure 7. *Nostoc*, a cyanobacterial genus that often occurs as a symbiont with leafy liverworts such as *Frullania asagrayana* and also as a symbiont in some lichens. Photo by Ralf Wagner, with permission.

Biochemistry

Asakawa *et al.* (1991) reported that the Type-T chemotype of *Frullania moniliata* (formerly *F. tamarisci* subsp. *ovata*; Figure 8) was similar to that of *F. asagrayana* (Figure 2). *Frullania moniliata* produces an intense mossy odor, but *Frullania asagrayana* lacks the two sesquiterpenoids that apparently are responsible for that odor.



Figure 8. *Frullania moniliata*, a species with chemistry similar to that of *F. asagrayana*, but with a mossy odor. Photo by Jia-dong Yang, through Creative Commons.

Frullania riparia (Figure 9-Figure 10)

Frullania riparia (Figure 9-Figure 10) is a rare species that occurs on both sides of the Atlantic in mostly middle latitudes (Schuster 1992). It is not part of the *Frullania tamarisci* (Figure 11, Figure 13-Figure 16) complex, but it has had its share of synonyms. Here, as elsewhere, I have only included those synonyms that occurred in the aquatic literature reported here.

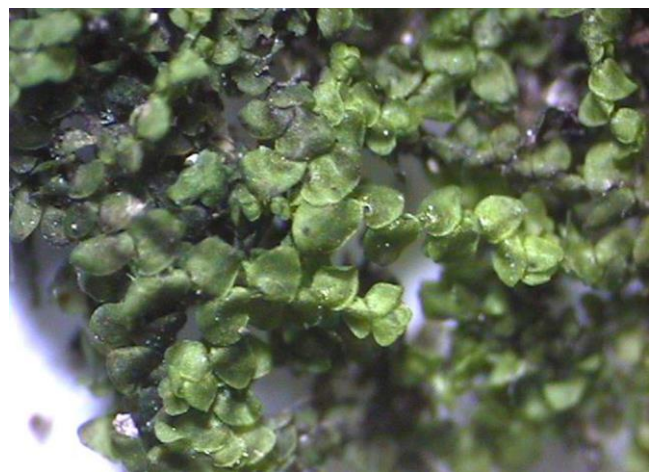


Figure 9. *Frullania riparia* exhibiting a hydrated shade form. Photo by Paul Davison, with permission.

Distribution and Habitats

Frullania riparia (Figure 9-Figure 10) occurs along calcareous rivers in Connecticut, USA (Nichols 1916). By

contrast, Schuster (1992) declares it "a pronounced xerophyte," colonizing vertical faces of shaded, dry rocks. He likewise considers it to be a calciphile, but not absolutely restricted to calcareous surfaces. On rare occasions it can be found on bark. Nevertheless, "riparian" means relating to or situated on the banks of a river, suggesting that early collections came from streamside habitats.



Figure 10. *Frullania riparia* on rock, exhibiting its xerophytic tendencies and the brown color expresses in sun exposure. Photo by Jan-Peter Frahm, with permission.

***Frullania tamarisci* (Figure 11-Figure 16)**

Frullania tamarisci (Figure 11-Figure 16) now has a narrower concept than an earlier one. Heinrichs *et al.* (2010) reviewed the subspecies that had been described. It was once considered a polymorphic species with four allopatric subspecies [subsp. *asagrayana* (Figure 2), *moniliata* (Figure 6), *nisquallensis* (Figure 12), and *tamarisci* (Figure 11)]. Heinrichs *et al.* used sequences of the nuclear internal transcribed spacer region and the plastid trnL-trnF and atpB-rbcL regions to reveal at least eight main lineages within the *Frullania tamarisci* complex that can be considered as cryptic and semicryptic species, lacking morphological distinctions.



Figure 11. *Frullania tamarisci*. Photo from Proyecto Musgo, through Creative Commons.



Figure 12. *Frullania nisquallensis*, a member of the *Frullania tamarisci* complex. Photo by Dale Vitt, with permission.

Distribution

Schuster (1992) considered *Frullania tamarisci* (Figure 11-Figure 13) to be circumboreal and mostly suboceanic to oceanic, but its more recent separation into multiple species warrants a re-evaluation of its distribution.

Aquatic and Wet Habitats

West (1910) reported *Frullania tamarisci* (Figure 11-Figure 16) from damp rocks by lake shores in Scotland. Watson (1919) reported it as occasionally submerged (Watson 1919). Schuster (1992) considered it to be a species of tree bark, rock walls (Figure 14-Figure 16), and ledges. In Macaronesia, it is **epiphyllous** (growing on leaves) (von Konrat & Braggins 1999). My own experience suggests that it occurs in humid sites, such as stream canyons (Figure 17), but not in the water. It is able to grow in exposed sites and can form margins along grasses on rock where it is exposed to direct sunlight (Figure 18).



Figure 13. *Frullania tamarisci* forming a **smooth mat**. Photo by Hermann Schachner, through Creative Commons.



Figure 14. *Frullania tamarisci* on a canyon wall at Cwm Idwal National Nature Reserve, Wales. Photo by Janice Glime.



Figure 15. *Frullania tamarisci* on cliff at Cwm Idwal National Nature Reserve, Wales. Photo by Janice Glime.

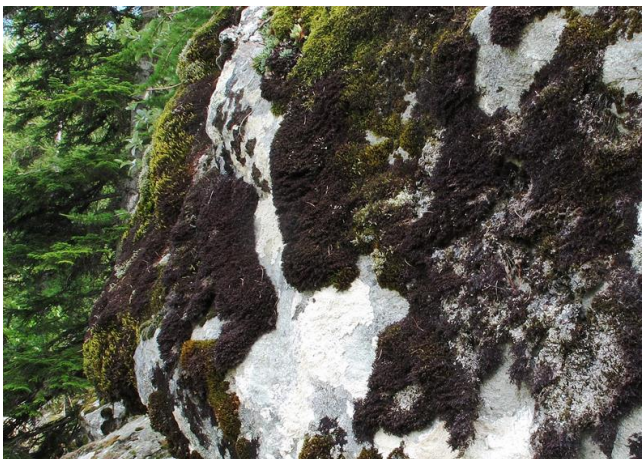


Figure 16. *Frullania tamarisci* on a cliff. Photo by Michael Lüth, with permission.



Figure 17. Path between canyon walls with *Frullania tamarisci* in black patches on rock wall at left, Cwm Idwal National Nature Reserve, Wales. Photo by Janice Glime.



Figure 18. *Frullania tamarisci* showing zonation where it has the advantage of sun while benefitting from the moisture held by the adjoining grasses. Photo by Michael Lüth, with permission.

Adaptations

Like *F. asagrayana* (Figure 2), *F. tamarisci* (Figure 11) has lobules (Figure 19-Figure 20) that can retain water, permitting it to live in places that get dry. Nevertheless, it also lives in moist habitats near streams and in canyons, exhibiting a wide range of habitats. Its dark color protects it from the bright sunlight in exposed habitats.



Figure 19. *Frullania tamarisci* ventral side showing lobules. Photo by Snappy Goat, through public domain.

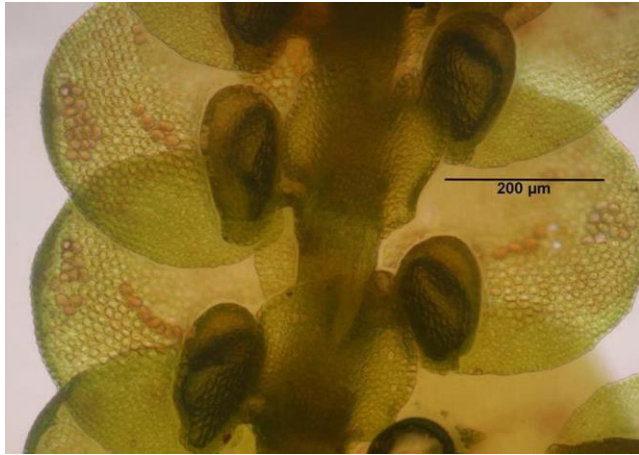


Figure 20. *Frullania tamarisci* showing lobules (that can hold water), ocelli, and underleaves. Photo from Snappy Goat, through public domain.

Reproduction

Frullania tamarisci is **dioicous** (Figure 21). Blackstock (2015) found that corticolous populations of *Frullania tamarisci* exhibited a very high sporophyte frequency when the colonies had both sexes. These colonies were highly fertile with male and female shoots (Figure 21), but fertilization nevertheless reduced the number of **gynoecia**. Exposed coastal populations, on the other hand, were sub-fertile with rare presentations of sporophytes. Furthermore, the coastal populations had a distinct female bias, with male scarcity limiting the production of sporophytes. Bisang (1987) defined the subspecies *Frullania tamarisci* ssp. *tamarisci*. She described a globose, many-celled protonema that forms within the stretched spore.



Figure 21. *Frullania tamarisci* with perianths. Photo by Hermann Schachner, through Creative Commons.

Biochemistry

Connolly *et al.* (1984) reported **tamariscol** from *Frullania tamarisci* (Figure 21), a new sesquiterpenoid alcohol isolated from this population in Scotland. Asakawa *et al.* (1991) found evidence that *Frullania tamarisci* s.l. (Figure 21) has a Type T chemotype similar to that of *F. asagrayana* (Figure 2). Paul *et al.* (2001) identified tamariscene with a new sesquiterpene skeleton, in

Frullania fragilifolia (s.l.?; Figure 22). Other research has been on subspecies that are now considered separate species, such as the finding of a new sesquiterpenoid in *Frullania moniliata* (formerly *F. tamarisci* subsp. *ovata*; Figure 8) (Toyota & Asakawa 1990).



Figure 22. *Frullania fragilifolia*, a species that also has tamariscene. Photo by David T. Holyoak, with permission.

Frullania teneriffae (Figure 23, Figure 27-Figure 30)

Distribution

Frullania teneriffae (Figure 23, Figure 27-Figure 30) is distributed in Africa, Europe, and Asia (ITIS 2020). Its common name in the UK of sea scalewort suggests, along with the records I could find, that it is a coastal species, including islands.



Figure 23. *Frullania teneriffae* growing on rock. Photo by Stan Phillips, through public domain.

Aquatic and Wet Habitats

Frullania teneriffae (Figure 23, Figure 27-Figure 30) is recorded from mountainous streams on Madeira Island (Figure 24-Figure 25) (Luis *et al.* 2015). In Macaronesia it is also facultatively epiphyllous (von Konrat & Braggins 1999), a habitat it might invade from one of its epiphytic

locations (Figure 28). But on the islands of Canna and Sanday off the coast of Scotland, it occurs frequently on rocks near the sea (Figure 26) and on dry, rather exposed rock faces and boulders (Figure 27) (Birks *et al.* 1991).



Figure 24. Madeira Island at Ponta de São Lourenço (north side). Photo through Creative Commons.

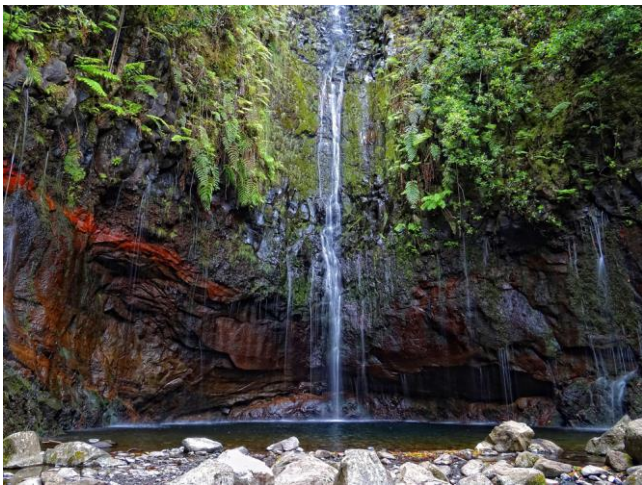


Figure 25. Madeira Island 25 Fontes-waterfall during dry period. Photo by Bjørn Christian Tørrissen, through Creative Commons.



Figure 26. Shoreline where one can find *Frullania teneriffae*. Photo by Michael Lüth, with permission.



Figure 27. *Frullania teneriffae* growing on exposed rock. Photo by Hugues Tinguy, with permission.



Figure 28. *Frullania teneriffae* dry on a branch. Photo by Jan-Peter Frahm, with permission.

Frullania teneriffae has small lobules (Figure 29-Figure 30) and is typically dark in color. The dark coloration gives it a shield from the bright sunlight in its exposed habitats.

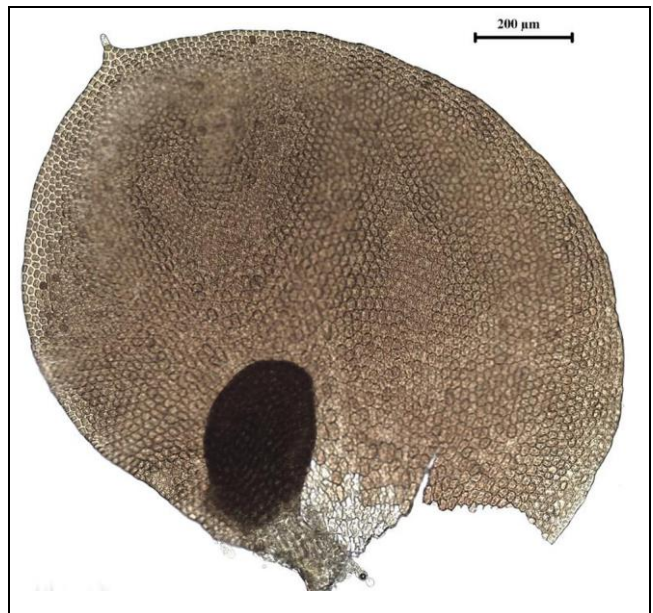


Figure 29. *Frullania teneriffae* leaf with lobule. Photo by Hugues Tinguy, with permission.

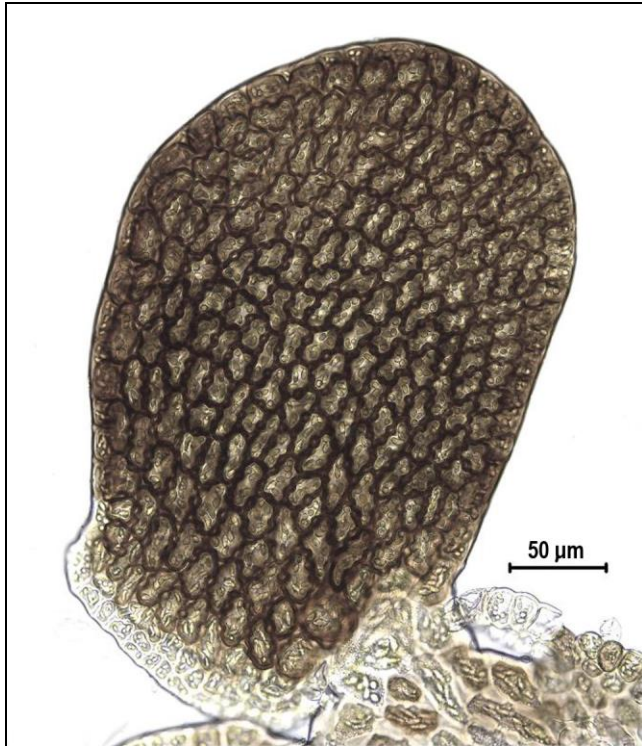


Figure 30. *Frullania teneriffae* leaf lobule. Photo by Hugues Tinguy, with permission.

Role

The ability of the lobules to hold water when the rest of the plant is drying is demonstrated by the presence of the aquatic invertebrates that can live there. Among these are the rotifers (Figure 31). The rotifers are able to go dormant when the leaves do dry out, surviving as resting eggs (Figure 32).



Figure 31. *Frullania* with rotifer "galls" in the lobules, showing the dormant egg stage of the rotifers. Photo courtesy of Puterbaugh, Skinner, and Miller.



Figure 32. *Frullania* with rotifer. Photo courtesy of Andi Cairns.

Biochemistry

Biochemical studies on *Frullania teneriffae* (Figure 23, Figure 27-Figure 30) are lacking. Wang and Qiu (2006) found no references reporting mycorrhizal fungi on *Frullania teneriffae*.

Jubulaceae

Schuster (1992) considered all members of *Jubula* (Figure 33-Figure 37, Figure 38, Figure 43, Figure 45-Figure 47) to be restricted to humid or damp sites, frequently occurring near flowing water. In North America it is almost entirely **saxicolous** (growing on rock), although it can be epiphyllous on ferns in the tropics or corticolous in humid rainforests.

Jubula hutchinsiae (Figure 1, Figure 33-Figure 38, Figure 43, Figure 45-Figure 47)

Like so many of the species of moist and wet habitats, *Jubula hutchinsiae* (Figure 33) is highly polymorphic (Sim-Sim *et al.* 2002). Päscht *et al.* (2001) used nuclear and chloroplast DNA sequences to distinguish five subspecies: *J. hutchinsiae* subsp. *bogotensis*, subsp. *hutchinsiae* (Figure 33), subsp. *japonica* (Figure 34-Figure 35), subsp. *javanica*, and subsp. *pennsylvanica* (Figure 47).



Figure 33. *Jubula hutchinsiae*. Photo by David T. Holyoak, with permission.



Figure 34. *Jubula hutchinsiae* ssp. *japonica*. Photo by Jia-dong Yang, though Creative Commons.

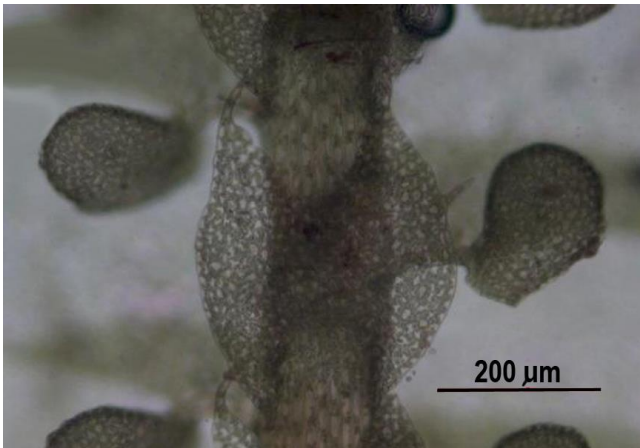


Figure 35. *Jubula hutchinsiae* ssp. *japonica* leaves and lobules. Photo by Jia-dong Yang, though Creative Commons.

Distribution

Jubula hutchinsiae (s.l. Figure 33-Figure 35) is known from Japan, Taiwan, and India in Asia, the Pacific Islands, Europe, and Macaronesia (Guerke 1978; Majumdar & Singh 2016). It is likely that all reports from Japan and Taiwan are the subspecies *japonica* (Figure 34-Figure 35). Pócs and Cairns (2008) added Australia to its distribution, but identified it as subspecies *australiae*. Kürschner (2013) added subspecies *caucasica* to the flora of Turkey and Iran. Sukkharak (2017) added the subspecies *javanica* to the known flora of Thailand.

Aquatic and Wet Habitats

Jubula hutchinsiae (Figure 33) occurs on rocks in fast water (Figure 1), on rocks or in caves associated with fast water (Figure 36, Figure 37), and waterfalls (Watson 1919). Sim-Sim *et al.* (2002) likewise report it from waterfalls in the Canary Islands (Figure 38). In Thuringia, Germany, *Jubula hutchinsiae* is associated with streams that have the *Platyhypnidium* (Figure 39)-*Fontinalis antipyretica* (Figure 40) association (Marstaller 1987). It is known in the UK from a ravine (Wallace 1952).



Figure 36. *Jubula hutchinsiae* forming mats on boulders in a common stream habitat. Photo by Michael Lüth, with permission.

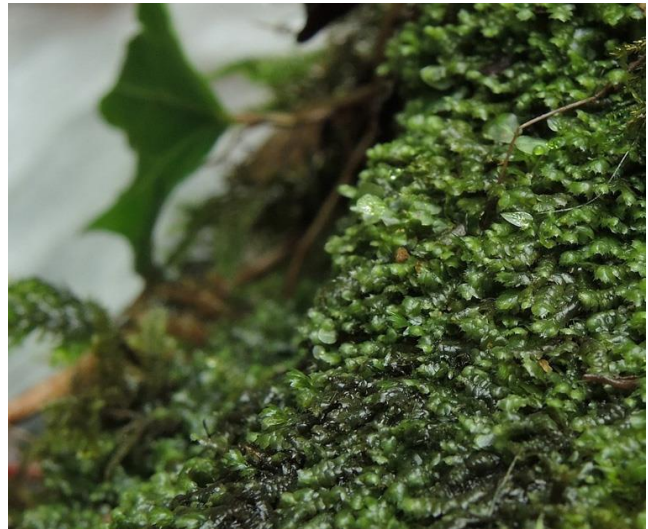


Figure 37. *Jubula hutchinsiae* showing wet habitat at margin of fast stream. Photo by Michael Lüth, with permission.



Figure 38. *Jubula hutchinsiae* on Tenerife, Canary Islands, in the Macaronesian Islands. Photo by Jonathan Sleath, with permission.



Figure 39. *Platyhypnidium riparioides* in Europe, a species that occurs in the same streams as *Jubula hutchinsiae*. Photo by Michael Lüth, with permission.



Figure 40. *Fontinalis antipyretica*, a species that occurs in the same streams as *Jubula hutchinsiae*. Photo by Tab Tannery, through Creative Commons.

The Australian subspecies *australiae* occurs in the tropical rainforest and the Wet Tropics (Pócs & Cairns 2008). In Macaronesia, Sim-Sim *et al.* (2002) found *Jubula hutchinsiae* (Figure 33) frequently in the native forests (Figure 38), as well as Atlantic Europe. In Thailand, it (subspecies *javanica*?) occurred on the filmy fern *Vandenboschia maxima* (= *Crepidomanes maximum*; Figure 41-Figure 42) at the edge of a stream (Sukkharak 2017). On Achill Island off the west coast of Ireland, *Jubula hutchinsiae* occurs on wet rocks under an overhang by a stream (Warburg 1963). Proctor (1999) found it in Devon, UK, on dripping rocks in a shady stream gully. Averis *et al.* (2012) found it in Scotland on wet rocks beside a fast-water stream.



Figure 41. *Vandenboschia maxima*, a fern where one can sometimes find *Jubula hutchinsiae* as an epiphyll in Thailand. CalPhotos, through Creative Commons.



Figure 42. *Vandenboschia maxima* leaf segments close-up – substrate where one can sometimes find *Jubula hutchinsiae* in Thailand. Photo from CalPhotos, through Creative Commons.

This species can also survive in humid habitats that are not subject to inundation (Figure 43). Gabriel *et al.* (2008) found that it occurs in cave (lava tube and volcanic pit) entrances (Figure 44) in the Azores, occupying particularly humid sites, where it is a frequent species.

In a main ravine in the UK, Callaghan *et al.* (2019) found large clumps of *Jubula hutchinsiae* (Figure 33); it often grew through, and upon, larger competitive species. It was among the three most frequent species in the study, but was also the most unevenly distributed. Following the development of hydroelectric power, it was one of two liverworts showing an increase, whereas the other three species declined. It appears to be a very stable species, occupying a position low down on the river bank where it experiences relatively frequent hydrological disturbance.



Figure 43. *Jubula hutchinsiae* forming shelves on vertical rock. Photo by Stan Phillips, through public domain.



Figure 44. Volcanic cave, Algar do Carvão, on Terceira Island, Portugal, the type of location where one might find *Jubula hutchinsiae*. Photo by Vitor Oliveira, through Creative Commons.

Richards (1947) noted his surprise at finding no damage to *Jubula hutchinsiae* (Figure 33) after several days of being frozen solid, even though it seemed to be restricted to sheltered habitats.

Reproduction

Jubula hutchinsiae (Figure 33) is **autoicous**. It forms discoid gemmae from the lobe surfaces (Schuster 1992), a character also found in some species of **Lejeuneaceae** (Pócs 2012).

Biochemistry

Suire (2000) compared development of oil bodies (Figure 45-Figure 46) among liverworts. He found that *Jubula hutchinsiae* oil bodies (Figure 45) originate from the dilation of ER cisternae. Their membrane is thickened by an osmophilic material. Each leaf cell contains several oil-bodies.

Biochemical studies seem to be lacking on this species. Wang and Qiu (2006) found no publications of mycorrhizal fungi on *Jubula hutchinsiae*.

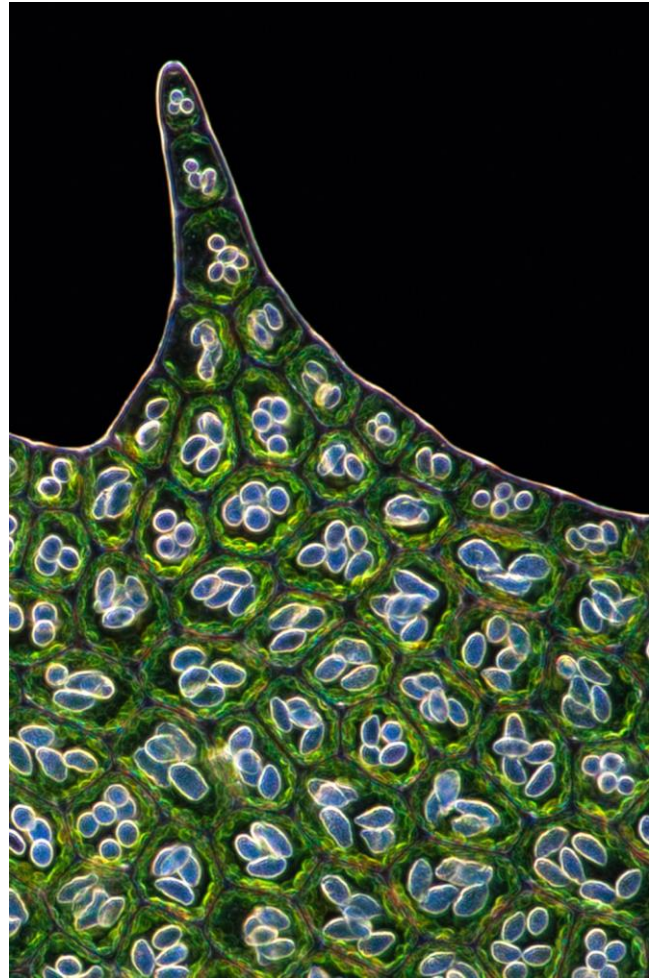


Figure 45. *Jubula hutchinsiae* leaf tip showing oil bodies. Photo by Des Callaghan, with permission.

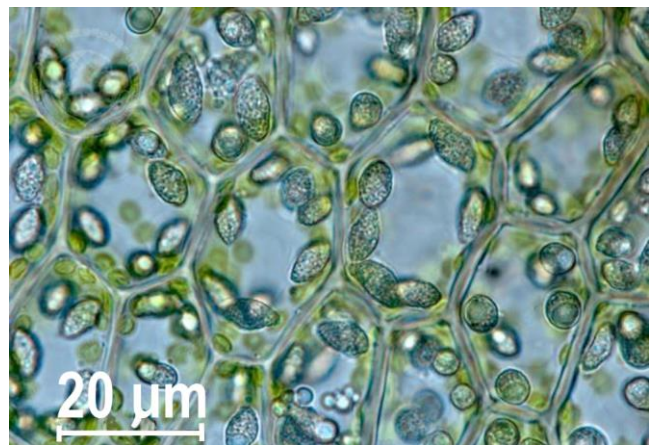


Figure 46. *Jubula hutchinsiae* ssp. *japonica* leaf cells and oil bodies. Photo by Jia-dong Yang, through Creative Commons.

Jubula hutchinsiae subsp. *pennsylvanica* (Figure 47)

(syn. = *Jubula pennsylvanica*)

Distribution

Clark and Frye (1945) reported the distribution of *Jubula hutchinsiae* subsp. *pennsylvanica* (Figure 47) from Nova Scotia to Ohio, south to Oklahoma, Alabama,

and Georgia in North America, Bermuda, Azores, and Madeira (the latter two probably a different subspecies). Later, Schuster (1992) considered it to be an Appalachian (eastern North America) endemic (Schuster 1992). It ranges from Nova Scotia, south to Georgia, but also occurs in isolated locations in Ohio, west of the Appalachians.



Figure 47. *Jubula hutchinsiae* subsp. *pennsylvanica*, a subspecies probably restricted to eastern North America, south to Bermuda. Photo by Wayne Lampa, through Creative Commons.

Aquatic and Wet Habitats

Jubula hutchinsiae subsp. *pennsylvanica* (Figure 47) has been found on moist rock surfaces or springy banks of ravines in Connecticut, USA (Nichols 1916); in streams in the Great Smoky Mountains National Park, Kentucky, USA (Knapp & Lowe 2009). It can be a rare species along rocky streams in the southern part of its range. In central New York, USA, *Jubula hutchinsiae* subsp. *pennsylvanica* lives in both large and small ravines on shady, permanently wet rock faces (Trigoboff 2013). Clark and Frye (1945) summarize the habitat for the eastern USA as occurring on rocks or soil in damp or wet situations or in deep shade.

Stephenson *et al.* (1995) found that *Jubula hutchinsiae* subsp. *pennsylvanica* (Figure 47) preferred a pH range of 5.95-6.6 in West Virginia, USA, mountain streams.

Reproduction

Jubula hutchinsiae subsp. *pennsylvanica* (Figure 47) is **monoicous** (having both sexes on the same plant) (Clark & Frye 1945) and often fertile, typically from April to early July (Schuster 1992). The capsule appears on a long stalk.

Jubula hutchinsiae var. *integrifolia*

Jubula hutchinsiae var. *integrifolia*, the most frequent liverwort in the Madeira Archipelago, has questionable taxonomic status (Lars Söderström, pers. comm. 9 October 2020). Söderström suggests that it is probably a synonym of var. *javanica* or subsp. *japonica* (Figure 34-Figure 35), but some plants definitely do not belong to either. Accordingly, the record from Madeira is best referred to subsp. *hutchinsiae*.

Distribution

Jubula hutchinsiae var. *integrifolia* occurs in mountainous streams in Madeira Island (Luis *et al.* 2015) and has been reported from the Canary Islands (Sim-Sim *et al.* 2002).

Aquatic and Wet Habitats

Sim-Sim *et al.* (2002) distinguished var. *integrifolia* as occurring completely submerged in waterfalls, whereas the typical variety occurs on humid slopes covered with soil along rivulets, not in waterfalls. These habitat differences may account for the morphological differences that led to the separation of the varieties. Perhaps they should be considered forms, but we need common garden experiments to be certain.

Lejeuneaceae

The **Lejeuneaceae** is represented by several species in Himalayan streams (Suren & Ormerod 1998).

Acanthocoleus aberrans

Distribution

Faria *et al.* (2012) report the distribution of *Acanthocoleus aberrans* as Neotropical and African. Schäfer-Verwimp (1999) considered it to be "rather rare" in the Neotropical region, noting only a few collections from Mexico, Costa Rica, Guatemala, Jamaica, French Guiana, and only once from Dominica. It occurs on the Guadalupe archipelago in the French West Indies (Bernarda & Schäfer-Verwimp 2011).

Aquatic and Wet Habitats

Acanthocoleus aberrans occurs in mountainous streams on Madeira Island (Luis *et al.* 2015). But other than this report, it appears that this species is terrestrial and seldom occurs in wet areas.

Reproduction

There seems to be little information on reproduction of *Acanthocoleus aberrans*. We know it is **dioicous** (dos Santos *et al.* 2017), perhaps accounting for its relative rarity.

Bromeliophila (Figure 52)

This is a unique genus with only two species [*Bromeliophila natans* (Figure 52) and *B. helenae*], both of which are restricted to the tanks made by leaves of **Bromeliaceae**, but may occur on many different bromeliad host species (Gradstein 1997). Heinrichs *et al.* (2014) used a three-marker dataset – chloroplast genome *rbcL* gene and *trnL-F* region, and nuclear ribosomal ITS1-5.8S-ITS2 region – to determine relationships of this genus to *Prionolejeunea* (Figure 48) and *Cyclolejeunea* (Figure 49).

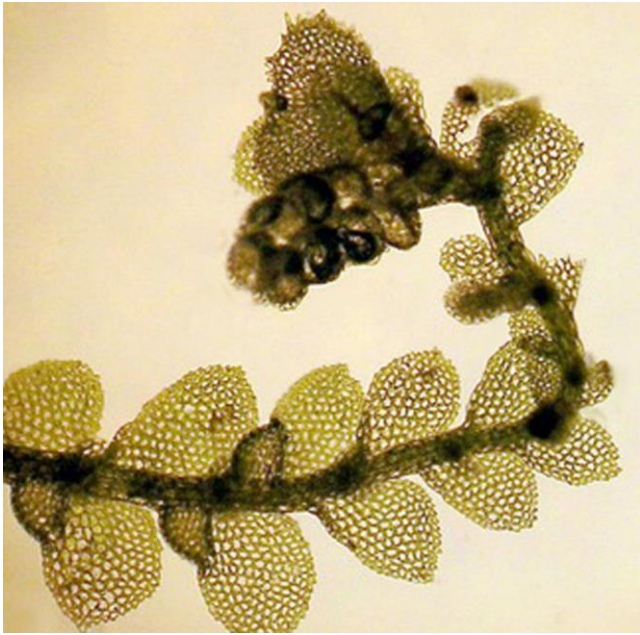


Figure 48. *Prionolejeunea saccatiloba* with perianth and male branch, in a genus that may be related to *Bromeliophila*. Photo by Michaela Sonnleitner.

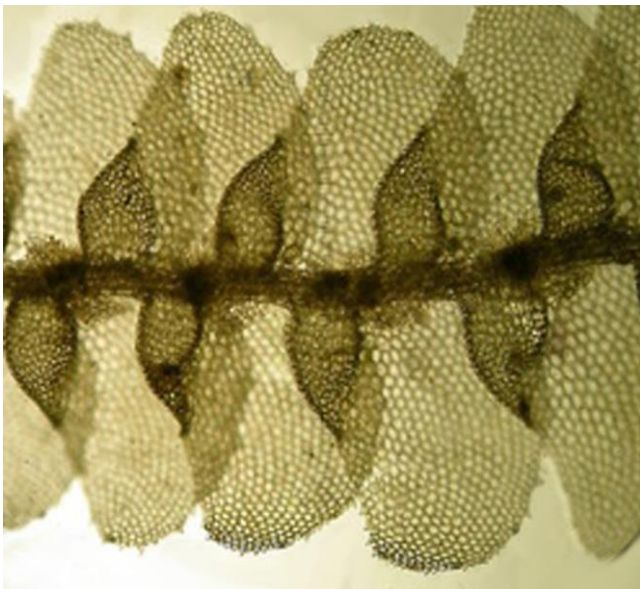


Figure 49. *Cyclolejeunea peruviana*, in a genus that may be related to *Bromeliophila*. Photo by Michaela Sonnleitner, with permission.

Because the **Bromeliaceae** hosts are restricted to the tropics and subtropics, *Bromeliophila* (Figure 52) is likewise (Gradstein *et al.* 2001). Its habitat is one in which the lower parts of the leafy gametophyte shoots are "often" submerged; only the upper parts extend above the water (Heinrichs *et al.* 2014).

Bromeliophila helenae

Distribution

Bromeliophila helenae is reported from Colombia (Gradstein 1997; Benavides & Callejas 2004; Campos & Uribe-M. 2006). *Bromeliophila helenae* also occurs in the

Guayana Highland (Gradstein *et al.* 2001) and on Martinique in the Lesser Antilles (Bernard 2018).

Aquatic and Wet Habitats

The habitat for this species is in the water at the base of bromeliad leaves, including those of *Brocchinia tatei* (Figure 50-Figure 51) (Gradstein *et al.* 2001).



Figure 50. *Brocchinia tatei*, home for *Bromeliophila helenae* in South America. Photo by Adalberto Jose Perez Lopez, through Creative Commons.



Figure 51. *Brocchinia tatei* showing the basin of water where *Bromeliophila helenae* lives. Photo by Imerú Alfonzo-Hernandez, through Creative Commons.

Bromeliophila natans (Figure 52)

Distribution

Bromeliophila natans (Figure 52), like *Bromeliophila helenae*, occurs in bromeliad basins in South America (Gradstein 1997), particularly Neotropical countries (Heinrichs *et al.* 2014). Because it occurs only in these water-filled basins, Imbassahy *et al.* (2009) consider it to be "exclusively" aquatic.

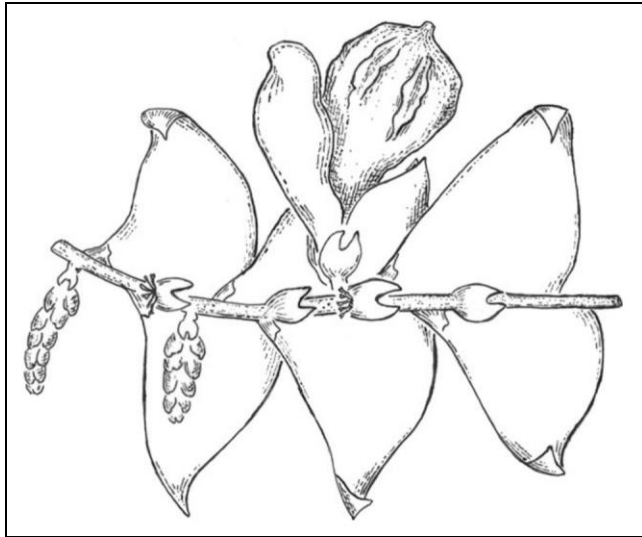


Figure 52. *Bromeliophila natans* with perianth, a species that lives in the water of bromeliad basins. Drawing from Heinrichs *et al.* 2014 through Rob Gradstein.

Visnadi (2010) considered *Bromeliophila helenae* to be restricted to the **restingas** of Brazil. This points to its dependence on water of the bromeliad basin. **Restingas** are a distinct type of coastal tropical and subtropical moist broadleaf forest in eastern Brazil. **Restingas** form on spits of sandy, acidic, nutrient-poor soil with trees and shrubs that are adapted to drier conditions with low nutrients.

Cephalantholejeunea temnanthoides

Distribution

Cephalantholejeunea temnanthoides is the only species in its genus (Shi *et al.* 2015), and it is a rare Amazonian **rheophyte** (aquatic plant that lives in fast-moving water currents in environment where few other organisms can survive) (da Costa 2003; Shi *et al.* 2015).

Aquatic and Wet Habitats

Cephalantholejeunea temnanthoides occurs on stems that are flooded by the Rio Negro (Reiner-Drehwald 2011). S. Robbert Gradstein (pers. comm. 3 November 2011) told me that he has found it in Andean streambeds. Daly *et al.* (2006) noted that it is characteristic of **salões** (lowland moist tropical environments in which virtually all plant diversity is accounted for by herbs). This unique habitat occurs along canalized portions of the Purus and Juruá river basins. As such, the available substrate is exposed parent materials with only a thin (<1 m) layer of soil. These **salões** are wetlands that remain constantly moist due to seepage. *Cephalantholejeunea temnanthoides* associates with *Plagiochila martiana* and *Dumortiera hirsuta* (Figure 53) in these habitats.

Reproduction

Cephalantholejeunea temnanthoides is **monoicous** (Schuster 1990; Reiner-Drehwald & Weis 2001). Thus its sexual condition does not explain its rarity. Reiner-Drehwald and Weis (2001) described sporophytes for the first time.



Figure 53. *Dumortiera hirsuta*, an associate of *Cephalantholejeunea temnanthoides* in wetland areas. Photo by Michael Lüth, with permission.

Ceratolejeunea temnantha (Figure 56-Figure 55)

(syn. = *Lejeunea temnantha*)

Distribution

Ceratolejeunea temnantha (Figure 56-Figure 55) is another Amazonian endemic rheophyte (Sierra *et al.* 2018). Sierra and coworkers suggested that the evolution of rheophytes, including this species, in northern South America correlates with the expansion into novel ecological niches and dramatic landscape changes in the Miocene.

Aquatic and Wet Habitats

Ceratolejeunea temnantha (Figure 56-Figure 55) is a rheophyte of seasonally inundated black-water forests (Sierra *et al.* 2018). It was reported from a tree root (Figure 54) that is inundated at high water and likewise tree trunks that become inundated (Figure 55).



Figure 54. *Ceratolejeunea temnantha* on woody roots in an inundated area. Photo by Juan Carlos Villarreal, with permission.



Figure 55. *Ceratolejeunea temnantha* on inundated tree trunk. Photo by Juan Carlos Villarreal, with permission.

Reproduction

Ceratolejeunea temnantha is **monoicous** (Figure 56). It seems to lack any specialized asexual reproductive structures.



Figure 56. *Ceratolejeunea temnantha* with antheridial branches (hanging down) and perianth (upper left). Photo by Juan Carlos Villarreal, with permission.

Biochemistry

The oil bodies of this species are relatively large, with multiple bodies per cell (Figure 57). Descriptions of their chemical constituents remain unknown, partly due to the rarity of the species.

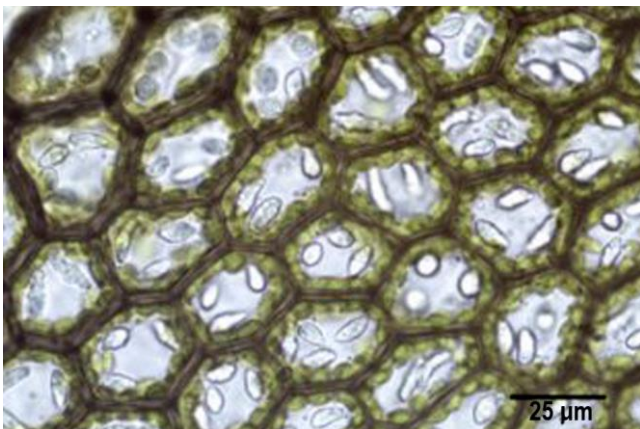


Figure 57. *Ceratolejeunea temnantha* leaf cells with oil bodies. Photo by Juan Carlos Villarreal, with permission.

Cheilolejeunea clypeata (Figure 58-Figure 60, Figure 69)

(syn.= *Leucolejeunea clypeata*)

Distribution

Ye and Zhu (2010) investigated synonyms in the genus *Leucolejeunea*, contributing to the recognition of *Leucolejeunea clypeata* as a species of *Cheilolejeunea*, *Cheilolejeunea clypeata* (Figure 58-Figure 60, Figure 69). *Cheilolejeunea clypeata* is endemic to eastern North America (New York to Florida), from sea level to 2000 m asl (Schuster 1980).



Figure 58. *Cheilolejeunea clypeata*, an eastern North American endemic. Photo by Blanka Aguero, with permission.



Figure 59. *Cheilolejeunea clypeata* showing relatively small lobules. Photo by Blanka Aguero, with permission.

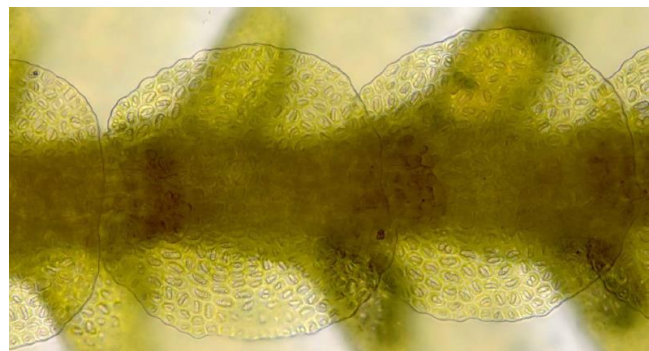


Figure 60. *Cheilolejeunea clypeata* showing underleaves. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Nichols (1916) reported this from crevices or surfaces of drier cliffs in a ravine in Connecticut, USA. Schuster (1980) describes *Cheilolejeunea clypeata* (Figure 58-Figure 60, Figure 69) as having a highly diversified ecology. Its substrata are bark, rock walls, and boulders. It is on both calcareous and noncalcareous rocks, typically shaded, often moist, but sometimes dry. Its best habitats seem to be rich mesophytic forests and swamp forests, where it lives on bark of a variety of tree species. Its status as a wetland species is somewhat marginal.

Lendemer *et al.* (2016) discovered the lichen *Catinaria brodoana* (Figure 61) to occur most frequently on *Cheilolejeunea clypeata* (Figure 58-Figure 60, Figure 69) in swamp forests with *Chamaecyparis* (Figure 62), *Taxodium* (Figure 63), and mixed hardwoods [*Acer* (Figure 64), *Magnolia virginiana* (Figure 65), *Persea* (Figure 66)] with an understory of *Lyonia* (Figure 67)-*Ilex glabra* (Figure 68). The lichen has a much narrower distribution than its liverwort substrate.

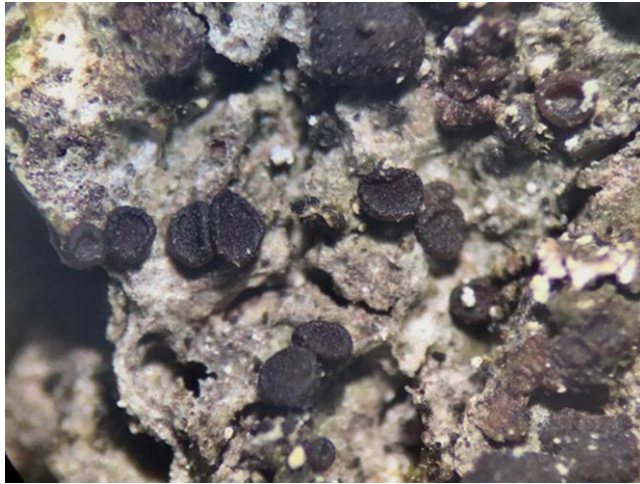


Figure 61. *Catinaria atropurpurea*; the lichen *Catinaria brodoana* occurs most frequently on the liverwort *Cheilolejeunea clypeata*. Photo by Tomás Curtis, through Creative Commons.



Figure 62. *Chamaecyparis thyoides* near edge of bog in Brendan T. Byrne State Forest, New Jersey, USA. Photo by Famarton, through Creative Commons.



Figure 63. *Taxodium distichum* (bald cypress) swamp, habitat for *Cheilolejeunea clypeata*. Photo courtesy of Kim Barton.



Figure 64. *Acer rubrum* in forest, a common species in swamps where *Cheilolejeunea clypeata* lives. Photo by Digby Dalton, through Creative Commons.



Figure 65. *Magnolia virginiana*, a common species in swamps where one can find *Cheilolejeunea clypeata*. Photo courtesy Great Plant Picks, with online permission.



Figure 66. *Persea americana* with fruit, a common species in swamps where one can find *Cheilolejeunea clypeata*. Photo by M. Clara Salviano, through Creative Commons.



Figure 67. *Lyonia lucida* with fruit; *Lyonia* is a common understory genus in swamps where *Cheilolejeunea clypeata* lives. Photo by Homer Edward Price, through Creative Commons.



Figure 68. *Ilex glabra* with flowers, a common understory species in swamps where *Cheilolejeunea clypeata* lives. Photo by Siddarth Machado, through Creative Commons.

Reproduction

The species is **autoicous** (Schuster 1980). This suggests that its narrow distribution is limited either by dispersal or narrow habitat requirements that do not occur frequently enough to provide stepping stones to any distant locations.

Biochemistry

Zhu and Gradstein (2003) described a single oil body per cell (Figure 69). There seem to be no biochemical studies to indicate what antibiotic/antiherbivore compounds might be sequestered there.

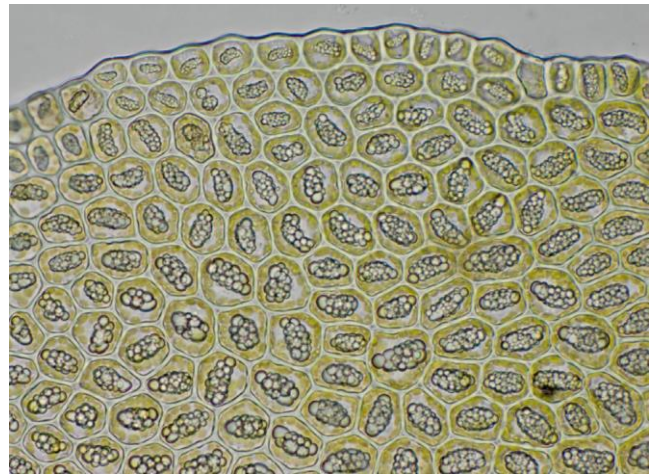


Figure 69. *Cheilolejeunea clypeata* leaf cells showing oil bodies. Photo by Blanka Aguero, with permission.

Cololejeunea biddlecomiae (Figure 70, Figure 74, Figure 78, Figure 81-Figure 85)

Distribution

Evans (1938) considered *Cololejeunea biddlecomiae* (Figure 70, Figure 74, Figure 78, Figure 81-Figure 85) to be the most widely distributed species of *Cololejeunea*. It occurs from Nova Scotia, New Brunswick, and Ontario in Canada, south to Georgia and Oklahoma in the USA. Schuster (1956) described this as a species of temperate and sub-boreal North America, occurring in the southern half of the spruce-fir forest, throughout deciduous forests, and into the broad-leaved evergreen forests of the southeastern coastal plain.

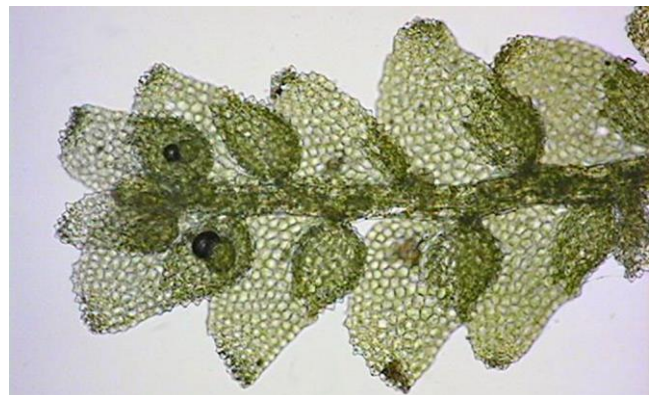


Figure 70. *Cololejeunea biddlecomiae* with lobules. Photo by Ken McFarland and Paul Davison, with permission.

Aquatic and Wet Habitats

Nichols (1916) reported *Cololejeunea biddlecomiae* (Figure 70, Figure 74, Figure 78, Figure 81-Figure 85) growing along calcareous rivers in Connecticut, USA. Wittlake (1950) reported that it occurs under and around springs along with *Riccardia multifida* (Figure 71), *Aneura pinguis* (Figure 72), *Calypogeia sullivantii* (Figure 73) in Spy Rock Hollow, Arkansas, USA. It occurs in Adirondack Mountain streams (Slack & Glime 1985). In central New York, it occurs in fine, yellow-green mats in ravines (Schuster 1956). In southern Illinois, Skorepa (1968) found it on sandstone in a creek bed.



Figure 71. *Riccardia multifida*, a species associated with *Cololejeunea biddlecomiae* at springs. Photo by Paul G. Davison, with permission.



Figure 72. *Aneura pinguis*, a species associated with *Cololejeunea biddlecomiae* at springs. Photo by Hermann Schachner, through Creative Commons.



Figure 73. *Calypogeia sullivantii*, a species associated with *Cololejeunea biddlecomiae* at springs. Photo by Paul Davison, with permission.

This species is not restricted to stream and riverine habitats. Schuster (1956) described a wide variation in its habitats. In his words, it is "almost indiscriminately corticolous (Figure 74) and saxicolous, occurring in shaded, relatively damp sites, especially moderately dry calcareous sandstone rocks." In New Jersey, USA, Barringer (2011) treated it as a tree bark species that rarely occurs on rocks in shaded ravines. Ammons (1933) found it in McKinney's Cave, West Virginia (Figure 75).



Figure 74. *Cololejeunea biddlecomiae* in its habitat on bark and wood. Photo by Ken McFarland and Paul Davison, with permission.

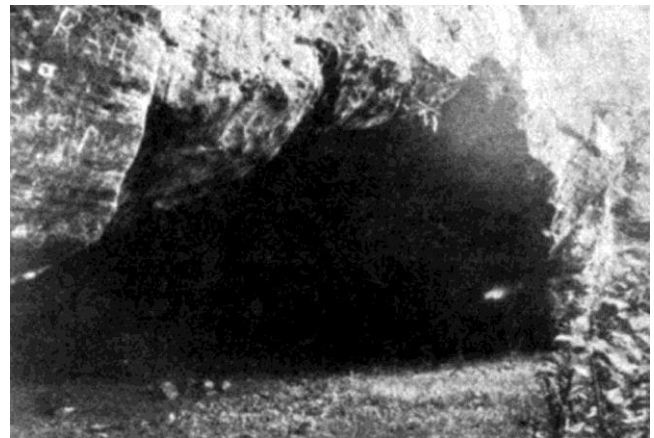


Figure 75. McKinney's cave, West Virginia, USA, entrance, where Ammons (1933) found *Cololejeunea biddlecomiae*. Photo from Ammons 1933.

Interestingly, *Cololejeunea biddlecomiae* (Figure 70, Figure 74, Figure 78, Figure 81-Figure 85) is less calciphilic in the southernmost part of its range (Schuster 1956). Trigoboff (2013), reporting from central New York, considered *Cololejeunea biddlecomiae* (Figure 70, Figure 74, Figure 78, Figure 81-Figure 85) in his report of aquatic bryophytes, but mostly described it from shade and high humidity with a high frequency on trees. Brown (1948), also in New York, reported the species as occurring among other liverworts on the lower trunk and stumps in gorges and *Thuja* swamps (Figure 76) on both hardwoods and *Thuja occidentalis* (Figure 77), but not in the mountains.

Darlington (1938) found it in a slightly more humid environment on a rotten log (Figure 78) along the Crystal River in Leelanau County, Michigan, USA. Schuster and Patterson (1957) found it growing in Dismal Swamp, Virginia, USA, on tree trunks, along with *Radula obconica* (Figure 79) and *R. australis* (Figure 80).



Figure 76. *Thuja occidentalis* along stream – home for many bryophytes, including *Cololejeunea biddlecomiae*. Photo by Peter M. Dziuk, with online permission.



Figure 77. *Thuja occidentalis* saplings, a species that can provide a substrate for *Cololejeunea biddlecomiae*. Photo from Superior National Forest, through Creative Commons.



Figure 78. *Cololejeunea biddlecomiae* on log. Photo by Paul Davison, with permission.



Figure 79. *Radula obconica* with perianths, a species that accompanies *Cololejeunea biddlecomiae* on tree trunks in Dismal Swamp, Virginia, USA. Photo by Paul G. Davison, with permission.



Figure 80. *Radula australis*, a species that accompanies *Cololejeunea biddlecomiae* on tree trunks in Dismal Swamp, Virginia, USA. Photo by Paul G. Davison, with permission.

Adaptations

Cololejeunea biddlecomiae (Figure 70) produces **styli** (Figure 81-Figure 82) that might help in moving water along the stem by providing capillary spaces.

Reproduction

Cololejeunea biddlecomiae (Figure 70, Figure 74, Figure 78, Figure 81-Figure 83) produces gemmae (Figure 84-Figure 85), mostly on the lower surface of the leaf lobes, but never on the lobules (Stevens 1910). But these are not numerous, typically with only a few and not more than five or six on an individual leaf. Even the numbers of gemmae-bearing branches in a population is only a relatively small proportion. Plants with large numbers of gemmae are typically closely associated with plants having none. As we might expect, plants with sexual organs have fewer gemmae, but gemma production is not completely inhibited in these plants. The gemmae sometimes occur on the bracts associated with the sexual organs, but they never seem to occur on perianths. These gemmae continue to increase in size after cell division ceases, resulting from cell growth (Figure 85). This increase continues until the time the gemmae are shed. The gemmae are shed by splitting of the cell wall between the stalk cell and gemma.



Figure 81. *Cololejeunea biddlecomiae* with **styli**. Photo by Paul Davison, with permission.

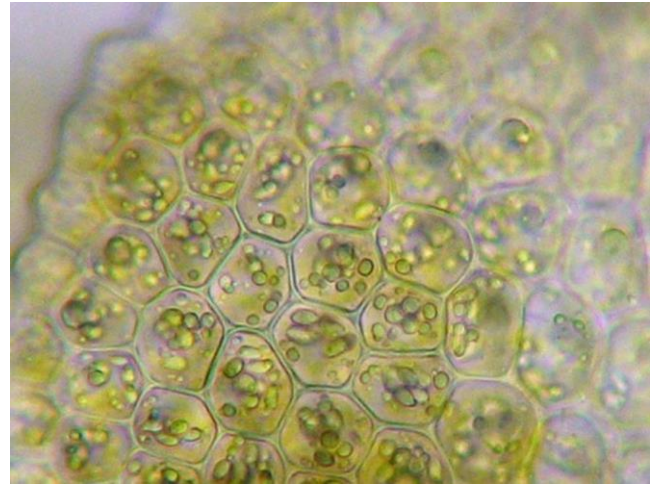


Figure 83. *Cololejeunea biddlecomiae* leaf cells showing oil bodies. Photo by Ken McFarland and Paul Davison, with permission.



Figure 84. *Cololejeunea biddlecomiae* with gemmae on the leaf surface. Photo by Ken McFarland and Paul Davison, with permission.



Figure 82. *Cololejeunea biddlecomiae* with **stylus**. Notice the **tuberculate** (having protuberances) cells on the surface of the lobule. Photo by Paul Davison, with permission.



Figure 85. *Cololejeunea biddlecomiae* leaf gemmae showing various sizes and number of cells. Photo by Ken McFarland and Paul Davison, with permission.

Risk *et al.* (2011) found that leaves had been lost in a colony of epiphyllous *Cololejeunea biddlecomiae*. This suggests a potential means of reproduction, whether it is by caducous leaves or transport by herbivores that have nibbled on the leaves. The species produces green, multicellular spores that can give a dispersed spore a good start when it arrives in a new location.

Hatcher (1965) reported difficulties in trying to establish a pure culture of *Cololejeunea biddlecomiae* (Figure 70, Figure 74, Figure 78, Figure 81-Figure 85), noting that it failed to differentiate stems and leaves, instead developing as an amorphous mass of cells. This suggests that it may need very specific environmental conditions for its early development.

***Cololejeunea calcarea* (Figure 86-Figure 90)**

Distribution

Cololejeunea calcarea (Figure 86-Figure 90) occurs in Europe and northern Asia. Schuster (1955) considers it to be frequent in western Europe. Konstantinova (2011) reported it from the Eastern Caucasus, Russia.

Aquatic and Wet Habitats

Cololejeunea calcarea (Figure 86-Figure 90) is occasionally submerged (Watson 1919). It occurs on limestone rock in the Tara River canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).



Figure 86. *Cololejeunea calcarea*, showing imbricate leaves. Photo by Štěpán Koval, with permission.

Evans (1911) states that *Cololejeunea calcarea* (Figure 86-Figure 90) seems to be confined to rock (Figure 87). Watson (1918) attributed it to shaded limestone cliffs and skrees. Alegro *et al.* (2014), reporting from Croatia, likewise concluded that it occurs on shaded limestone rock. Blockeel (1991) provided more details on finding it on shaded limestone in a ravine at 200 m asl in the gorge of the River Akheron in Greece.



Figure 87. *Cololejeunea calcarea* habitat on rock wall in South Wales. Photo by Barry Stewart, with permission.



Figure 88. *Cololejeunea calcarea* showing large leaf lobules. Photo by Hermann Schachner, through Creative Commons.



Figure 89. *Cololejeunea calcarea* with perianths. Photo by Hermann Schachner, through Creative Commons.

Reproduction

This species has gemmae that it uses for asexual reproduction (Cavers 1903). These are produced on the leaf surfaces, mostly on the lower surface of the lobes but occasionally on the upper surface (Stevens 1910). These are small in numbers, not more than 5-6 on an individual leaf. Although the gemmae are relatively common in New England, USA, they only occur on a comparatively small proportion of the plants in any mat. One plant may have a "considerable number" while an adjacent plant has none. As in *C. biddlecomiae*, fertile plants often have gemmae, but they are more abundant on sterile plants. They may even occur on the bracts, but never on the perianths. After cell division ceases, the gemmae continue to grow by cell expansion, not even stopping until sometime after the gemmae are shed. The gemma forms a flat disc that is one cell thick with no dorsi-ventral differentiation. The gemma is shed by splitting of the cell wall between the stalk cell and the gemma. *Cololejeunea calcarea* (Figure 86-Figure 90) is one of the species in southern Turkey that has frequent asexual reproduction (Kürschner 2014).



Figure 90. *Cololejeunea calcarea* showing perianths. Photo by Stan Phillips, through public domain.

Fungal Interactions

Wang and Qiu (2006) found no records of mycorrhizae associated with *Cololejeunea calcarea* (Figure 86-Figure 90).

Cololejeunea hodgsoniae

Distribution

Cololejeunea hodgsoniae is distributed in Australia (ITIS 2020) and New Zealand (de Lange *et al.* 2015), finding both warm temperate and cool temperate climates suitable.

Aquatic and Wet Habitats

One of the interesting habitats of *Cololejeunea hodgsoniae* in Australia is to grow on the leaves of the leafy liverwort *Radula marginata* (Figure 91) on rocks in streams (Renner 2003). In fact, Renner suggested that it might be muscicolous (bryicolous?).



Figure 91. *Radula marginata*; *Cololejeunea hodgsoniae* grows on the leaves of *R. marginata* on rocks in Australian streams. Photo by Peter de Lange, through Creative Commons.

Reproduction

Cololejeunea hodgsoniae is **autoicous**, making spore production likely (de Lange *et al.* 2015).

Cololejeunea madothecoides

(syn. = *Hemilejeunea ruttneri*)

Distribution

Cololejeunea madothecoides ranges from India and Indochina to Japan and Borneo (Asthana & Srivastava 2003; Manju *et al.* 2012). Shu *et al.* (2016) later reported it from Vietnam.

Aquatic and Wet Habitats

Ruttner (1955) reported *Cololejeunea madothecoides* as a species that occurs in a zone less than 15 cm above water level in the tropics. Pócs and Ninh (2005) found it to be very abundant on streambed stones in parts of Vietnam and considered its subgenus to be especially adapted to riverine conditions. In the Western Ghats of India, the species is epiphyllous (Nair & Prajitha 2016; Manju *et al.* 2012). In northeastern India, Singh and Kumar (2106) reported it as epiphytic.

Adaptations

These adaptations include thick stems, rigid leaves, and adherence of large masses to temporarily inundated streambed rocks. Smets (2003) found it on very humid calcareous rocks in the western Carpathians in Romania.

Reproduction

Gradstein *et al.* (2011) reported that *Cololejeunea madothecoides* lacked gemmae in Ecuador.

Cololejeunea microscopica (Figure 92)

(syn. = *Aphanolejeunea microscopica*)

Distribution

Cololejeunea microscopica (Figure 92) occurs in India (Tripura), Africa, and Europe (Pócs 1984; Singh & Kumar 2017).

Aquatic and Wet Habitats

Cololejeunea microscopica (Figure 92) grows in shaded, humid places on damp or dry rocks, especially by streams and waterfalls (Hodgetts 2020). In India, it is epiphytic, growing on bark of trees in moist and shady places (Singh & Kumar 2017). It can even be epiphyllous on other bryophytes, as on *Pyrrhobryum spiniforme* in Brazil (Sierra *et al.* 2019).



Figure 92. *Cololejeunea microscopica*, a sometimes epiphyllous species (as shown here) that grows near streams. Photo by Jan-Peter Frahm, with permission.



Figure 93. *Pyrrhobryum spiniforme*, a moss on which *Cololejeunea microscopica* can be an epiphyll. Photo by John Brinda, through Creative Commons.

Cololejeunea rossettiana (Figure 94-Figure 97)

Distribution

Cololejeunea rossettiana (Figure 94-Figure 97) occurs in Africa, Europe, and Northern Asia (ITIS 2020). Kürschner and Erdağ (2005) reported it from Turkey.



Figure 94. *Cololejeunea rossettiana*, a species found in Africa, Europe, and Northern Asia. Photo by Des Callaghan, with permission.

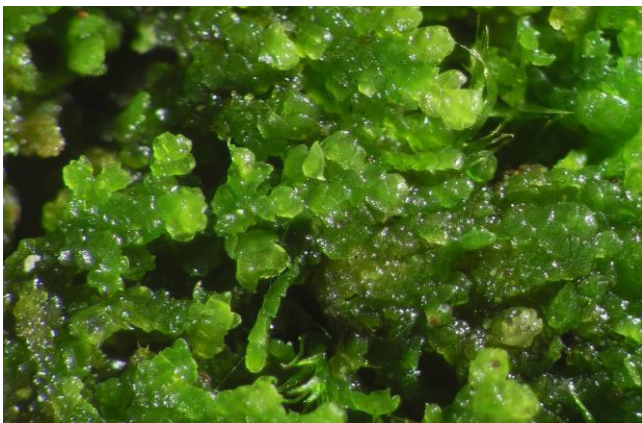


Figure 95. *Cololejeunea rossettiana*, typically an epiphytic or saxicolous liverwort. Photo by Michael Lüth, with permission.



Figure 96. *Cololejeunea rossettiana* showing the bulging (trabeculate) cells. Photo by Michael Lüth, with permission.



Figure 97. *Cololejeunea rossettiana* showing trabeculate projections from cells. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

Watson (1919) noted that *Cololejeunea rossettiana* (Figure 94-Figure 97) is occasionally submerged, but no other reports seem to consider it to be aquatic.

Although it occurs in most of the southeastern European countries, *Cololejeunea rossettiana* is nevertheless rare and occurs on many European Red Lists of bryophytes (Hodgetts 2015).

Reproduction

Cololejeunea rossettiana is **monoicous** (Figure 98-Figure 99) (Arnell 1953). That should make its sexual reproduction relatively easy. Part of its apparent rarity may be due to its very small size and inconspicuous appearance (Lawley 2010), causing it to be undercollected.



Figure 98. *Cololejeunea rossettiana* with perianths. Photo by Michael Lüth, with permission.

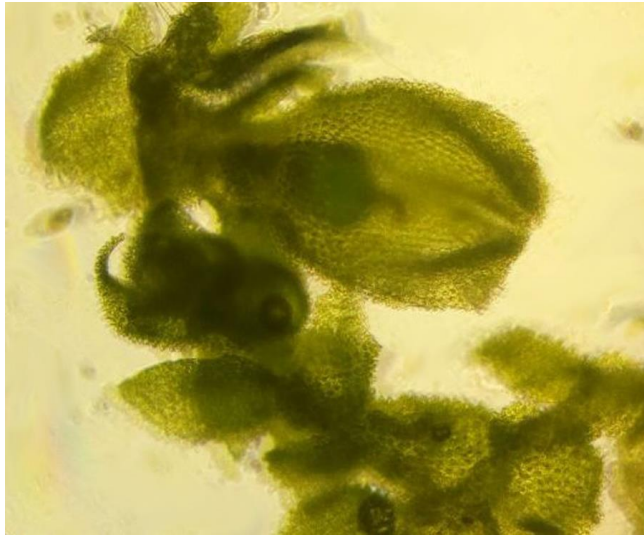


Figure 99. *Cololejeunea rosettiana* with perianth and swollen archegonium inside. Photo by Andy Hodgson, with permission.



Figure 101. *Cololejeunea stotleriana* growing as an epiphyll on a fern leaf in Ecuador. Photo by M. Richter, courtesy of Robbert Gradstein.

Cololejeunea stotleriana (Figure 100-Figure 101)

Distribution

The rare *Cololejeunea stotleriana* (Figure 100-Figure 101) is known from South America (ITIS 2020) and was originally described from Ecuador (Gradstein *et al.* 2011).

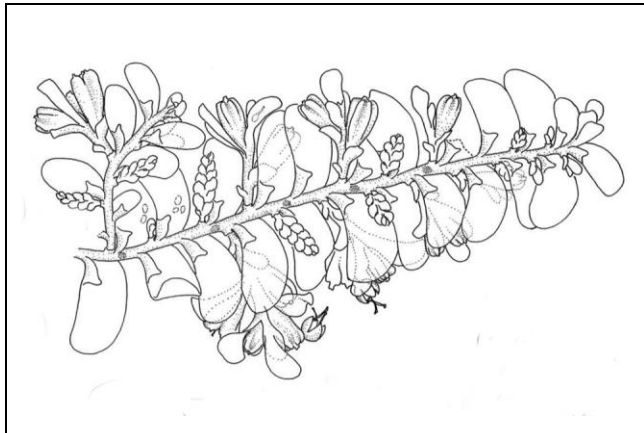


Figure 100. *Cololejeunea stotleriana* showing both perianths and antheridial branches (monoicous). Image from Gradstein *et al.* 2010, with permission.

Aquatic and Wet Habitats

Cololejeunea stotleriana (Figure 100) is rare, epiphyllous (Figure 101) or periodically submerged in streams at 950 m asl in Ecuador (Gradstein *et al.* 2011). It is the only common epiphyllous liverwort found in the flood zone of the river (Figure 102). But also in Ecuador, Gradstein *et al.* found this species on bark and rock.

In Ecuador, Gradstein *et al.* (2011) found that *Cololejeunea stotleriana* (Figure 100) grew in association with other rare bryophytes – the mosses *Fissidens hydropogon* (Figure 103) and *Lepidopilum caviusculum* (Figure 104).

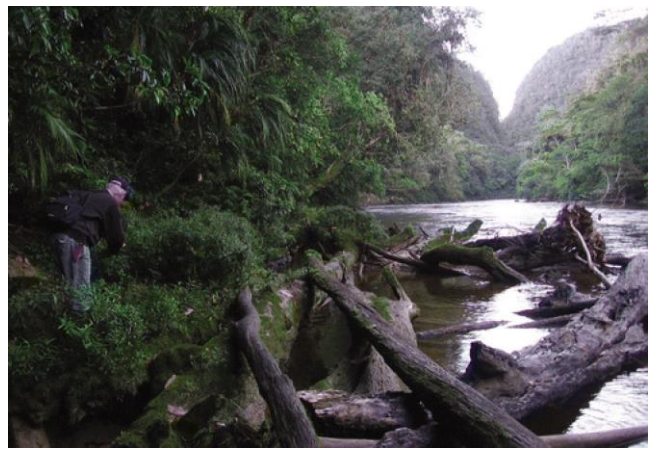


Figure 102. *Cololejeunea stotleriana* habitat in the Río Nangaritza, southern Ecuador. Photo by F. Werner, courtesy of S. Robbert Gradstein.



Figure 103. *Fissidens hydropogon*, a rare moss that grows in association with *Cololejeunea stotleriana* in Ecuador. Photo from Earth.com, with permission.



Figure 104. *Lepidopilum* sp.; *Lepidopilum caviusculum* is a rare moss that grows in association with *Cololejeunea stotleriana* in Ecuador. Photo by Janice Glime.

Adaptations

Gradstein *et al.* (2011) found the new species *Cololejeunea stotleriana* (Figure 100-Figure 101) as rheophilous and epiphyllous (Figure 101) in Ecuador. It seemed well adapted to these habitats with its robust stem, flattened habit, triangular lobules, large rhizoid fields not produced near each leaf base, super fertility, and clustered gynoecea (Figure 100). Yu *et al.* (2014) likewise considered that the adaptations of this species (to extreme ephemeral substrate, smooth surfaces, limited access to water and nutrients, and light exposure) permit it to extend beyond the typical epiphyllous or epiphytic habitats of the genus.

Reproduction

In Ecuador, *Cololejeunea stotleriana* produces abundant gemmae (Figure 105).

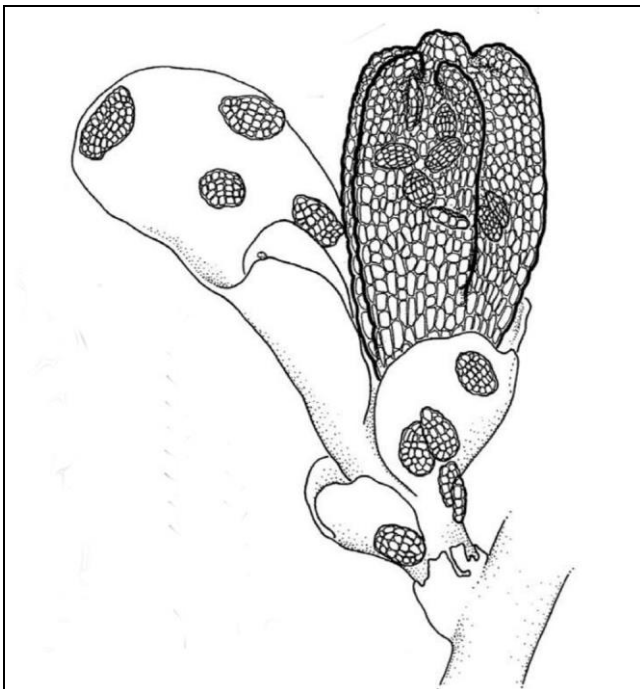


Figure 105. *Cololejeunea stotleriana* with perigynium and gemmae. From Gradstein *et al* 2010, with permission.

Biochemistry

Ludwiczuk and Asakawa (2014) used fingerprinting of secondary compounds in chemosystematics of *Cololejeunea stotleriana* (Figure 100-Figure 101) and were able to report only pinguicines in this species.

Colura (Figure 109-Figure 110, Figure 121-Figure 122, Figure 124-Figure 125)

(syn. = *Myriocolea*)

The genus *Colura* (Figure 109-Figure 110, Figure 121-Figure 122, Figure 124-Figure 125) is represented by several species in Andean streambeds (S. Robbert Gradstein pers. comm. 3 November 2011).

One of the interesting discoveries about the genus *Colura* (Figure 109-Figure 110, Figure 121-Figure 122, Figure 124-Figure 125) is its ability to hold water in its leaf lobules (Figure 106) (Barthlott *et al.* 2000). The lobule has a complex opening with a movable lid that closes. Ciliate **Protozoa** (Figure 107-Figure 108) live in these lobules and feed on bacteria on the liverwort surface.



Figure 106. *Colura* showing water-holding lobule where protozoa live. Photo courtesy of Jan-Peter Frahm.

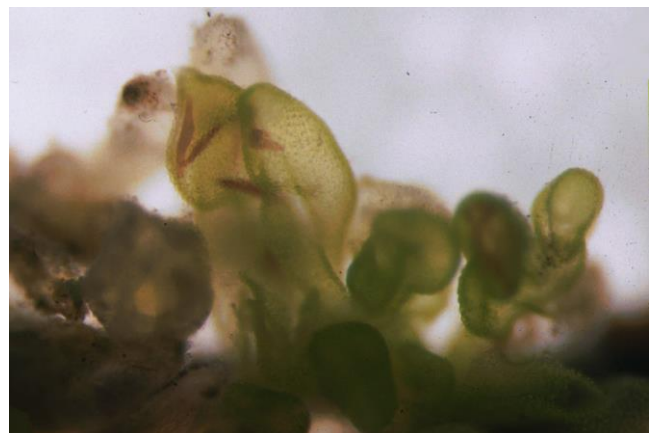


Figure 107. *Colura* with protozoa (stained pink). Photo courtesy of Jan-Peter Frahm.

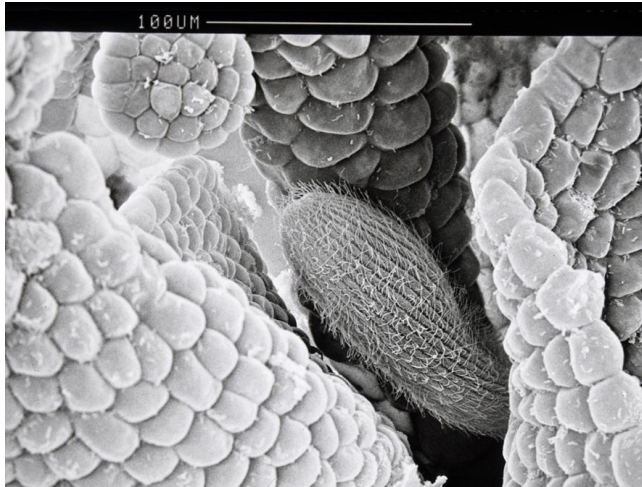


Figure 108. SEM of *Colura* with a ciliate (center). Photo by Wilhelm Barthlott, with permission.

***Colura calyptrifolia* (Figure 109-Figure 110)**

(syn. = *Colurolejeunea calyptrifolia*)

Distribution

Colura calyptrifolia (Figure 109-Figure 110) is the only species of **Lejeuneaceae** that extends into the sub-Antarctic (Grolle 2002). Its distribution is oceanic-temperate Afro-American and European (Gradstein *et al.* 1983). Frahm (2005) reported it from the Azores. Zhu and Long (2003) reported its range as Africa, Europe, Central America, Sri Lanka, and Nepal, adding their own new collections from the Himalayas. It occurs in the Western Ghats of India as a tiny and rare species (Mufeed *et al.* 2018). An additional Asian record is from Taiwan (Yang *et al.* 2013). It has been reported several times from Brazil (Schäfer-Verwimp & Giancotti 1996; Bôas-Bastos & Bastos 2016). Gradstein *et al.* (2018) found it in the high Andes of Colombia, where it is rare. It is widely distributed in South America, from the Caribbean to southern Chile (Hassel *et al.* 2014). Newton (2004) considered it one of the most infrequent oceanic species in Britain, where it occurs mostly in the extreme west of Scotland and Ireland as well as Wales, requiring sustained high humidity. Bates and Preston (2011) contend that the range of this species is increasing in response to climate change.



Figure 109. *Colura calyptrifolia*, an occasionally submersed species that grows in damp places. Photo by Michael Lüth, with permission.



Figure 110. *Colura calyptrifolia* showing the saccate leaves. Photo by Barry Stewart, with permission.

Aquatic and Wet Habitats

Colura calyptrifolia (Figure 109-Figure 110) is occasionally submerged (Watson 1919). Zhu and Long (2003) found it in a ravine in a dense forest in the Himalayas with *Rhododendron* (Figure 111), *Betula* (Figure 112), and *Abies* (Figure 113), where it occurred on a wet cliff face. Hassel *et al.* (2014) found it in Norway on a nearly vertical cliff wall about 5 m high, facing east to northeast with a small brook at the base of the cliff. There it grew at the base of the cliff in a zone 0.5-2 m above the brook.



Figure 111. *Rhododendron* in the Himalayas, a genus that can provide habitat for *Colura calyptrifolia*. Photo by Nidhi Jamwal, through Creative Commons.



Figure 112. *Betula utilis*, Himalayan birch in the Himalayas, a genus that can provide habitat for *Colura calyptrifolia*. Photo by J. M. Garg, through Creative Commons.

Colura calyptrifolia (Figure 109-Figure 110) seems to have a rather wide habitat tolerance, and at most it is apparently facultatively aquatic. It tolerates some submersion, but does not grow continually submersed. *Colura calyptrifolia* occurs on heather stems in the dwarf shrub heaths of the western Scottish Highlands (Figure 114) (Averis 2007). In some heaths, it occurs as an epiphyll on the fronds of the fern *Blechnum spicant* (Figure 115). The long, very humid microclimate provides a long growing season on these fronds with only a 2-year life span.



Figure 113. *Abies pindrow* at Mt. Mukeshpuri, Pakistan. The genus *Abies*, along with *Betula* and *Rhododendron*, can provide habitat for *Colura calyptrifolia*. Photo by Khalid Mahmood, through Creative Commons.



Figure 114. *Calluna vulgaris* (Scottish Heather), where *Colura calyptrifolia* grows on the stems of these shrubs. Photo by John McLeish, through Creative Commons.



Figure 115. *Blechnum spicant*, a substrate for epiphyllous *Colura calyptrifolia*. Photo by Robert Flogaus-Faust, through Creative Commons.

Reproduction

Colura calyptrifolia (Figure 109-Figure 110) is **autoicous** (Gradstein *et al.* 1983; Hassel *et al.* 2014). This permits it to have sexual reproduction and produce spores more easily than dioicous species. It produces large spores that give it a good start on new plants, but it also has fragmentation and produces abundant discoid gemmae that occur on the leaf tips (Figure 116).



Figure 116. *Colura calyptrifolia* with gemmae on tips of leaves at the upper left. Photo by David T. Holyoak, with permission.

With its ability to live on a wide range of inorganic substrates, along with its wide range of habitats, it is not surprising that Hill and Preston (2014) found significant increases in *Colura calyptrifolia* (Figure 109-Figure 110, Figure 116) between the 1960-1989 period and the 1990-2013 period.

Fungal Interactions

Thus far, there seem to be no records of mycorrhizae associated with *Colura calyptrifolia* (Figure 109-Figure 110, Figure 116) (Wang & Qiu 2006). Perhaps these have been missed because of the small size of the liverwort, but then, perhaps they just don't occur.

Biochemistry

The species is also lacking in biochemical studies, preventing us from developing good hypotheses regarding antifungal behavior.

Colura cataractarum (Figure 117-Figure 118)

Distribution

Colura cataractarum (Figure 117-Figure 118) is a new species, described in 2020 from Madagascar (Pócs 2020). Thus far, it has not been found elsewhere and is thus endemic to a small area at the Andringitra Massif.

Aquatic and Wet Habitats

Colura cataractarum (Figure 117-Figure 118) occurs on granite rocks in cataracts where it is steadily irrigated (Figure 119) (Pócs 2020). These cataracts are surrounded by mossy montane forest at 1,230 m asl.

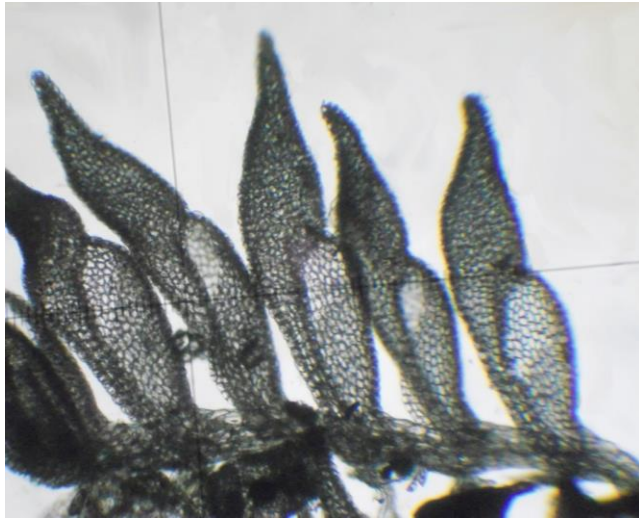


Figure 117. *Colura cataractarum* leaves. Photo courtesy of Tamás Pócs.

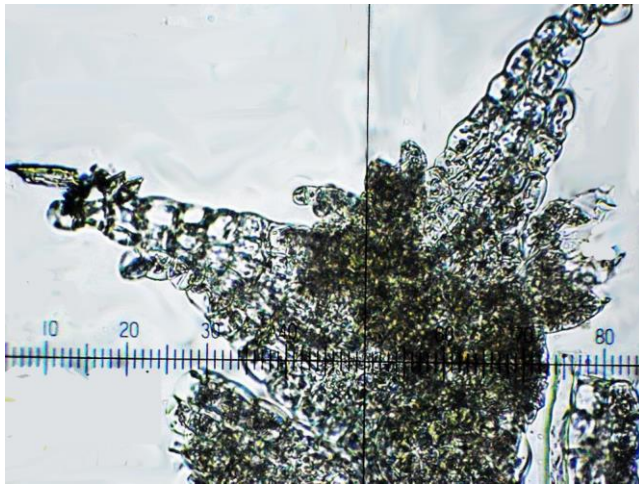


Figure 118. *Colura cataractarum* underleaf. Photo courtesy of Tamás Pócs.



Figure 119. *Colura cataractarum* being collected by András Szabó at its type locality in Madagascar, on irrigated granite rocks. Photo courtesy of Tamás Pócs.

Reproduction

Only female reproductive structures have been seen, so the species is presumably **dioicous** (Pócs 2020). Gemmae are produced at the perianth mouth.

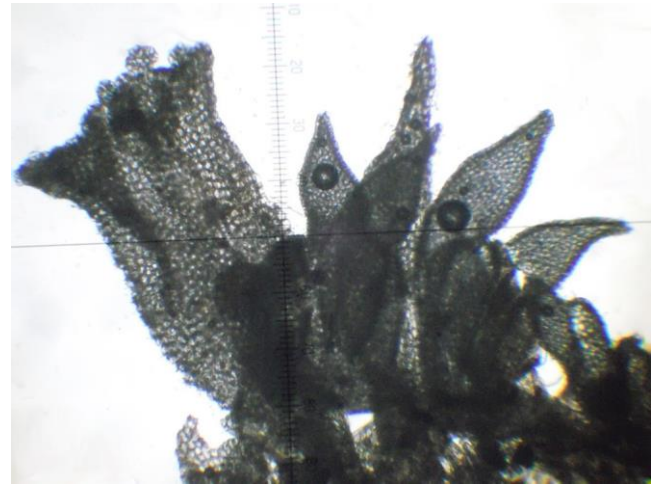


Figure 120. *Colura cataractarum* with perianths. Photo courtesy of Tamás Pócs.

Colura irrorata (Figure 121, Figure 124-Figure 125)

(syn. = *Myriocolea irrorata*)

Distribution

Colura irrorata (Figure 121, Figure 124-Figure 125) is known from the Andean Topo River in Ecuador (Gradstein & Jost 2004). It is rare and red-listed, being known from only a few localities (Figure 122) (Gradstein *et al.* 2004; Heinrichs *et al.* 2012).



Figure 121. *Colura irrorata* on stems of *Cuphaea bombonassae* along the Numpatakaima River in Ecuador at 1540 m asl. Photo by Lou Jost, EcoMinga, with permission.



Figure 122. *Colura irrorata* conservation site. Photo courtesy of S. Robbert Gradstein.

Aquatic and Wet Habitats

This tropical montane species occurs on small shrubs of *Cuphea bombonasae* (Figure 123) that are periodically submerged (Gradstein *et al.* 2004). Its submersion seems to be short-lived, but frequent, with floods causing water levels to rise and fall "dramatically" over just a few hours (Gradstein *et al.* 2004; Gradstein & Benitez 2014). It is threatened by the construction of a hydroelectric dam on the Rio Topo.



Figure 123. *Cuphea bombonasae*, substrate for *Colura irrorata* in Ecuador. Photo from <swbiodiversity.org>, through Creative Commons.



Figure 124. *Colura irrorata* growing on *Cuphea bombonasae* in a location that becomes inundated. Photo courtesy of S. Robbert Gradstein.

Adaptations

Colura irrorata (Figure 121, Figure 124-Figure 125) exhibits long, robust stems, pinnate branching, and numerous small gametoeical branches, characteristics typical of other rheophytic members of **Lejeuneaceae** (Gradstein *et al.* 2004).

Reproduction

Colura irrorata (Figure 121, Figure 124-Figure 125) is **paroicous** and develops innovations between the gynoecia and male bracts. It produces numerous, but very tiny, sporophytes (Figure 125), but no vegetative reproduction has been found and its leaves decay while still on the shoots, suggesting they may not serve as propagules.



Figure 125. *Colura irrorata* with sporophytes (tiny grey structures seen at plant margins) on stems of *Cuphea bombonasae* along the Numpatakaima River, Ecuador, at 1540 m asl. Photo by Lou Jost, EcoMinga, with permission.

Biochemistry

Despite its rarity and tiny size, *Colura irrorata* (Figure 121, Figure 124-Figure 125) has been subjected to several biochemical studies. Ludwiczuk *et al.* (2013) found only β -pinguisene in the species, contributing to the understanding of phylogenetic relationships. Coulerie *et al.* (2015) found only pinguinanes when testing for epidozanes, pinguinanes, fusicocanes, monocyclofarnesanes. In further studies, Ludwiczuk and Asakawa (2014) tested for lepidozanes, pinguinanes, fusicocanes, and monocyclofarnesanes; once again they found only pinguinanes.

Diplasiolejeunea cavifolia (Figure 126, Figure 128-Figure 129)

(syn. = *Lejeunea cavifolia*)

Schäfer-Verwimp and Reiner-Drehwald (2009) considered *Diplasiolejeunea cavifolia* Figure 126, Figure 128-Figure 129) a "somewhat variable" species. Dong *et al.* (2012) considered this pantropical species, along with *D. rudolphiana*, to have a broader ecological amplitude than other members of the genus. This variety of habitats may help to explain its perceived variability.

Distribution

The distribution of *Diplasiolejeunea cavifolia* (Figure 126, Figure 128-Figure 129) is pantropical. In the Neotropics it occurs in Mexico (in the Chiapas; Bourell 1992), Colombia (Benavides & Gutierrez 2011), Panama (common; Schäfer-Verwimp 2014), and the Guianas (Eggers *et al.* 2006; Gradstein 2006). Fuentes and Churchill (2005) also found it in Bolivia. Morales (2010) reported it from Venezuela.



Figure 126. *Diplasiolejeunea cavifolia*, a sometimes submersed species that is usually in moist habitats. Photo by Hermann Schachner, through Creative Commons.

Tixier (1995) reported *Diplasiolejeunea cavifolia* (Figure 126, Figure 128-Figure 129) from San Thomé, Mt. Caffé, at 700 m asl, in the country of São Tomé and Príncipe, 4.5 km west of Trinidad off the northeastern coast of Brazil. Giancotti and Vital (1989) recorded it from Brazil, while noting that many *Lejeuneaceae* species seem to be disappearing; da Costa and Peralta (2015) reported it from the Atlantic Rainforest in Rio de Janeiro, Brazil. Dong *et al.* (2012) reported it from 3 m asl in Brazil, 1000 m asl in Dominica, 1540 m in Ecuador, 800 m in the Fiji Islands, 743-900 m in Graham *et al.* (2016) described its habitat in Peru. Guadeloupe, 970 m in Panama, and 370 m in Venezuela. Bernarda and Schäfer-Verwimp (2011) reported it from Guadeloupe archipelago and Martinique in the French West Indies. Mervin *et al.* (2001) found it in primary forests of Monteverde, Costa Rica.

In the old tropics, Ah-Peng *et al.* (2007) have reported *Diplasiolejeunea cavifolia* (Figure 126, Figure 128-Figure 129) on Réunion Island. Pócs *et al.* (2011) reported it from the Fiji Islands in the South Pacific. Wang *et al.* (2011) found it in Taiwan. Vanden Berghen (1960) reported it from Tanganyika (now Tanzania). Sánchez and Pérez (1998) reported it from the Republic of Equatorial Guinea (West Central Africa). Stam *et al.* (2020) reported it from a fog net in the lower montane forest in the Taita Hills in Kenya. But Tixier (1995) considered the genus *Diplasiolejeunea* to be "relatively depauperate" in Africa. Ariyati *et al.* (2009) reported it from Sulawesi, Indonesia. In 2016, Abay *et al.* included it in the flora of Rize, Northeast Turkey. It is telling that so many records for this species have occurred since 2000.

Dong *et al.* (2012) reported *Diplasiolejeunea cavifolia* (Figure 126, Figure 128-Figure 129) from 1580 m asl in Indonesia, 865-1015 m in Madagascar, 1280-1340 m in Malaysia, and 1030 m on Réunion Island. Long and Rubasinghe (2014) reported it from Sri Lanka. Yodphaka *et al.* (2018) found it in Thailand. Bakalin and van Sinh (2016) reported it from Vietnam.

Aquatic and Wet Habitats

Nichols (1916) found *Diplasiolejeunea cavifolia* (Figure 126, Figure 128-Figure 129) on wet or moist cliffs of ravines in Connecticut, USA, causing me to include it in this chapter. On Cape Breton Island, Canada, Nichols (1918) found it on rock cliffs associated with streams. Watson (1919) treated it as occasionally submerged. In the aquatic habitats of eastern Odenwald and southern Spessart, Philipp (1987) found it in association with *Thamnobryum alopecurum* (Figure 127). Vieira *et al.* (2005) found *Diplasiolejeunea cavifolia* in mountain streams of northwest Portugal.



Figure 127. *Thamnobryum alopecurum*, a species that accompanies *Diplasiolejeunea cavifolia* in aquatic habitats in Germany. Photo by David T. Holyoak, with permission.

Benavides and Gutierrez (2011) reported *Diplasiolejeunea cavifolia* (Figure 126, Figure 128-Figure 129) from a cloud forest in the northern Andes of Colombia. In Bolivia, Fuentes and Churchill (2005) found it as an epiphyte. Schäfer-Verwimp (1992) found *Diplasiolejeunea cavifolia* (Figure 126, Figure 128-Figure 129) was not rare in Brazil, growing as an epiphyte in the restinga, on a rotting log, as an epiphyte in humid secondary shrub at the edge of banana plantations, in the rain forest, and as an epiphyll.

Siregar and Pasaribu (2020) found *Diplasiolejeunea cavifolia* (Figure 126, Figure 128-Figure 129) on bark in Indonesia. In Sabah of Malaysian Borneo, Pócs *et al.* (2020) found it in the epiphyllous communities on Mt. Silam, where it occurred in a lower montane rainforest at 600-740 m asl. In the Republic of Equatorial Guinea, Sánchez and Pérez (1998) found it in the most exposed places, occurring as epiphyllous and corticolous along river banks, in tree crowns, or rocky cliffs, between 75 and 1140 m asl. In fact, Alvarenga and Pôrto (2010) considered it to be a sun epiphyte in the Brazilian Atlantic forest.

On the other hand, one can find **mats** of *Diplasiolejeunea cavifolia* (Figure 126, Figure 128) growing as a corticolous species in the submontane rainforest and fallows in Bolivia (Acebey *et al.* 2003). *Diplasiolejeunea cavifolia* occurs not only in moist forests, but also in more mesic woods, plantations, and orchards. In Monteverde, Costa Rica, it is epiphytic in primary forests (Mervin *et al.* 2001) and occupies the wide range of 1-3000 m asl (Eggers 2001). Holz and Gradstein (2005) reported it from oak forests in the páramo of the Cordillera in Costa Rica; Holz *et al.* (2002) found it in **mats** on shrubs and trees in Costa Rican oak forests.

In Panama it can be epiphytic on shrubs, dead trees and branches in the canopy of a fallen tree, or epiphyllous, sometimes at riverside (Schäfer-Verwimp 2014). In the superhumid lowland tropical forest of Chocó, Colombia, Benavides and Sastre-De Jesús (2011) found it as an epiphyll on natural palms (frequency = 20, natural with no palms (14), secondary palm (10), and no palm (10) out of 240 leaf samples. In the eastern Andes of Peru, Graham *et al.* (2016) found it in a gallery forest on a sand substrate. In fact, Visnadi (2004) found it on sandy seashores in Brazil, where it was subjected to saline conditions due to waves and winds.

Adaptations

Zhu and So (2001) considered the small stem, imbricate leaves (Figure 126), absence of papillose cells, inflated lobules (hold water), neotenous habit, and asexual propagules (Figure 129) to adapt *Diplasiolejeunea cavifolia* (Figure 126, Figure 128-Figure 129) to the epiphyllous condition (see also Gradstein 2006; Kraichak 2012). These same characters could also be an advantage to a species that cliffs that are not always moist.

Reproduction

Zhu and So (2001) considered the **monoicous** condition of *Diplasiolejeunea cavifolia* (Figure 126, Figure 128-Figure 129) among its adaptations to its epiphyllous habitat. The same can be said for its epiphytic habitat (Figure 128), and for rock cliffs that are not always moist.

Kraichak (2012) considered asexual propagules such as gemmae (Figure 129) to be an adaptive trait for epiphyll among the tropical **Lejeuneaceae** and found that it was the only trait that was more likely to evolve among epiphyllic species. In *Diplasiolejeunea cavifolia* (Figure 126, Figure 128-Figure 129), the diaspores (gemmae) seem to be tolerant of both drought and frost, perhaps explaining the pantropical success (Dong *et al.* 2012).

Biochemistry

Kis and Pócs (1997) studied the oil bodies of this species from African populations. The species has smaller oil bodies (204 µm) than the average for members of the genus *Diplasiolejeunea*. There seem to be no studies thus far on the biochemistry of this tiny species.



Figure 128. *Diplasiolejeunea cavifolia* with perianths and capsules. Photo by Hermann Schachner, through Creative Commons.

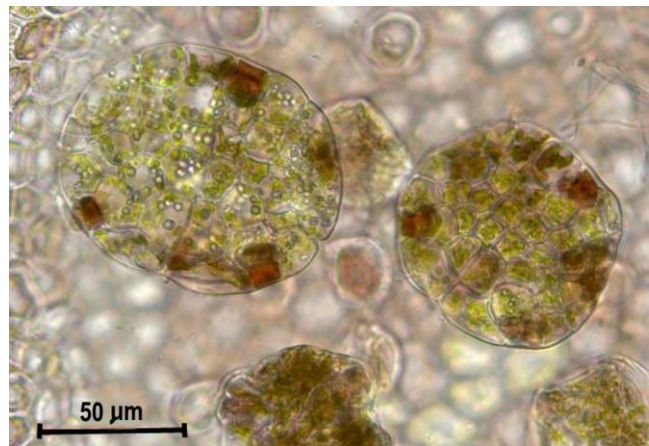


Figure 129. *Diplasiolejeunea cavifolia* showing gemmae developed on the leaf surface. Photo by Jia-ping Dong, through Creative Commons.

Summary

The **Jubulineae** are primarily terrestrial, but some also occur where they get wet or stay wet, sometimes getting submerged. The **Frullaniaceae** species here are **dioicous**; They are particularly adapted to xeric habitats with dark colors, mats, and water-holding leaf lobules. Most live on rocks or are epiphytes, but a few species of *Frullania* live in constantly moist habitats. Some serve as a reservoir for lichen-forming **Cyanobacteria**.

In the **Jubulaceae**, *Jubula* mostly occurs on rocks in humid or damp sites near or in flowing water and in waterfalls. However, thus far I have found only *Jubula hutchinsiae* and its subordinates in the aquatic literature. These are **monoicous**.

The family **Lejeuneaceae** is a family of very small leafy liverworts, mostly **monoicous**. They can mix with other bryophytes or grow alone. Many, such as *Acanthocoleus aberrans*, are facultative aquatic bryophytes, occurring sometimes in streams or becoming inundated during flooding, but usually

terrestrial. *Bromeliophila* is aquatic, restricted to bromeliad basins. *Cephalantholejeunea temnanthoides* is a rare species and is a rheophyte in Andean streambeds. *Ceratolejeunea temnantha* is likewise an endemic rheophyte, occurring in the Amazon region and being seasonally inundated. *Cheilejeunea clypeata* occurs in mesic and swamp forests on a variety of substrates, but is not a true aquatic. *Cololejeunea biddlecomiae* often occurs along calcareous rivers and springs, but also occurs along the acidic Adirondack Mountain streams and becomes less of a calciphile in the southern part of its range. *Cololejeunea calcarea* is most frequent on limestone rock and may become submersed. *Cololejeunea hodgsoniae* can be found on the leaves of the leafy liverwort *Radula marginata* on rocks and streams of Australia and New Zealand. *Cololejeunea madothecoides* is adapted to riverine conditions with thick stems, rigid leaves, and adherence to its substrate. *Cololejeunea microscopica* is most frequent on rocks near streams and waterfalls, but can also be epiphytic or epiphyllous; it is also known to grow on the moss *Pyrrhobryum spiniforme*. *Cololejeunea rossettiana* often grows on other bryophytes, but also occurs on shaded limestone and on trees; it is only occasionally submerged. *Cololejeunea stotleriana*, like many of these species, is rare, but is a common epiphyll in the river flood zone. *Colura calyptrifolia* has been found in a ravine in the Himalayas and on a wet cliff face; it tolerates some submersion, but not continuous submersion. It accepts a wide range of substrates, including *Polytrichastrum* leaves, and can occur on rubbish! *Colura irrorata* is a rare epiphyte, growing on shrubs of *Cuphea bombonae* in areas where it becomes inundated. *Diplasiolejeunea cavifolia* can occur on wet or moist cliffs or even be submerged, but it is more commonly epiphytic or epiphyllous.

Acknowledgments

Lars Söderström provided me with the current acceptable names for a number of older taxa and helped me sort out some of the species, varieties, and subspecies. S. Robbert Gradstein provided me with a number of papers and images. As always, I thank all who have contributed their images to Creative Commons or public domain or have given me permission to use their images.

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CHAPTER 1-8

AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: JUBULINEAE, PART 2

TABLE OF CONTENTS

Porellales – Suborder Jubulineae	1-8-2
Lejeuneaceae, cont.	1-8-2
<i>Drepanolejeunea hamatfolia</i>	1-8-2
<i>Harpalejeunea molleri</i>	1-8-7
<i>Lejeunea</i>	1-8-12
<i>Lejeunea aloba</i>	1-8-12
<i>Lejeunea eckloniana</i>	1-8-12
<i>Lejeunea jurana</i>	1-8-13
<i>Lejeunea lamacerina</i>	1-8-13
<i>Lejeunea patens</i>	1-8-18
<i>Lejeunea polyantha</i>	1-8-21
<i>Lejeunea subaquatica</i>	1-8-21
<i>Lejeunea topoensis</i>	1-8-21
<i>Lopholejeunea nigricans</i>	1-8-21
<i>Myriocoleopsis</i>	1-8-23
<i>Myriocoleopsis fluviatilis</i>	1-8-24
<i>Myriocoleopsis gymnocoleopsis</i>	1-8-25
<i>Myriocoleopsis minutissima</i>	1-8-26
<i>Myriocoleopsis minutissima</i> subsp. <i>myriocarpa</i>	1-8-28
<i>Myriocoleopsis vuquangensis</i>	1-8-28
<i>Ptychanthus striatus</i> var. <i>intermedius</i>	1-8-29
<i>Schusterolejeunea inundata</i>	1-8-31
Summary	1-8-32
Acknowledgments	1-8-32
Literature Cited	1-8-32

CHAPTER 1-8

AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: JUBULINEAE, PART 2



Figure 1. *Drepanolejeunea hamatifolia* habitat on rocks by a rapid stream. Photo by Michael Lüth, with permission.

Many of the species in this chapter are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study. Their relative frequency can be inferred based on the number of references cited.

Porellales – Suborder Jubulineae

Lejeuneaceae, cont.

Drepanolejeunea hamatifolia (Figure 1-Figure 8)

Distribution

Drepanolejeunea hamatifolia (Figure 1-Figure 8) is an Atlantic species (Rhind 2010). It is, so far, restricted to the Atlantic coasts of Portugal (in laurel forests; Gutierrez 2007), Spain (species of least concern; Sérgio *et al.* 2007), France (in Pyrénées; Dismier 1914), Ireland, England, Scotland (oceanic; Rothero 2003), and Macaronesia (Aleffi 2005). It is not known from Italy (Aleffi 2005), and it is known from only one site in continental Portugal (Cacciatori *et al.* 2015). To these records, Söderström and Pócs (2011) added South Africa. Sim-Sim *et al.* (2011) found it on Madeira Island.



Figure 2. *Drepanolejeunea hamatifolia*, a species of eastern Atlantic coastal regions. Photo by Hugues Tinguy, with permission.



Figure 3. *Drepanolejeunea hamatifolia* showing overlapping leaves. Photo by Michaela Sonnleitner, with permission.

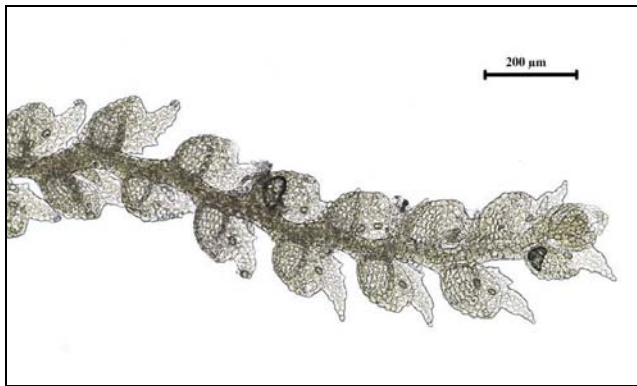


Figure 4. *Drepanolejeunea hamatifolia*. Photo by Hugues Tinguy, with permission.



Figure 5. *Drepanolejeunea hamatifolia* showing underleaves. Photo by Hugues Tinguy, with permission.

Rothero (2003) considered *Drepanolejeunea hamatifolia* (Figure 2-Figure 8) to be rare in Europe, with the exception of Macaronesia and the Azores. In fact, Borges and Gabriel (2009) found it to be among the most common epiphyllous species in the Azores (see also Gabriel & Bates 2005).

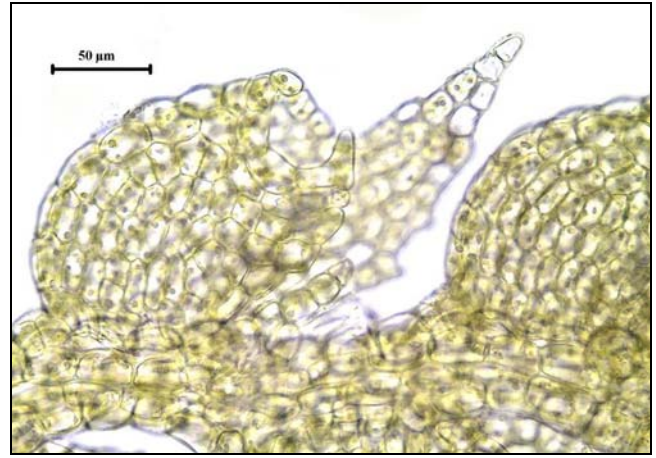


Figure 6. *Drepanolejeunea hamatifolia* leaf lobule. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Watson (1919) considered *Drepanolejeunea hamatifolia* (Figure 2-Figure 8) to be occasionally submerged (Figure 1), thus justifying its inclusion here. Hodgetts *et al.* (1999) reported it from streamside rocks in a ravine woodland at 1750 m asl in Lesotho, the Natal Drakensberg and the Orange Free State in southern Africa. In the UK, Rothero (2010) reported that it occurs on steep granitic rock of a ravine at 300 m asl. In Ireland, Jones (1954) found that it was "not uncommon" on basalt in deep, shady stream ravines. In Scotland, Long (2016) located it along a ravine. Damsholt *et al.* (1980) reported it from a wooded ravine in NW Scotland, where it occurred on moist, shaded rock faces. Brown (1954) found it in northeast Ireland on basalt in deep, shady stream ravines, where it was "not uncommon."

Rothero (2005) found it on large rocks in ravines of the Atlantic oakwoods. These rocks were regularly inundated, but did not suffer scouring. *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) formed a zone above the leafy liverwort *Lejeunea patens* (Figure 68-Figure 69) on these dark rocks (Figure 7-Figure 8).

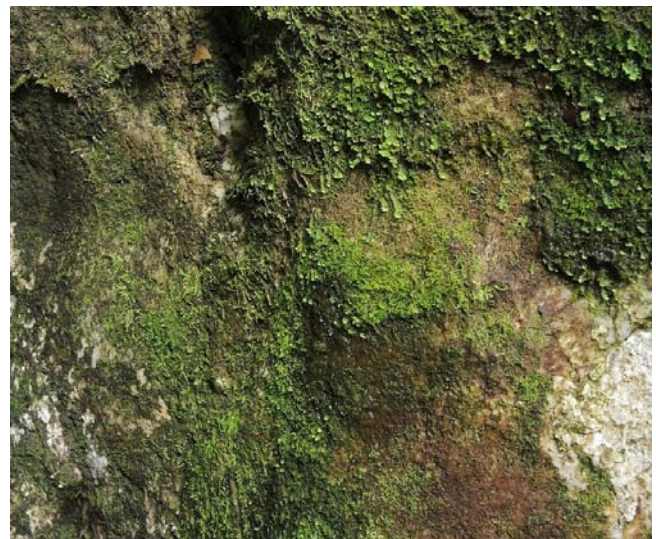


Figure 7. *Drepanolejeunea hamatifolia* showing zonation patterns on boulder near a stream. Photo by Michael Lüth, with permission.

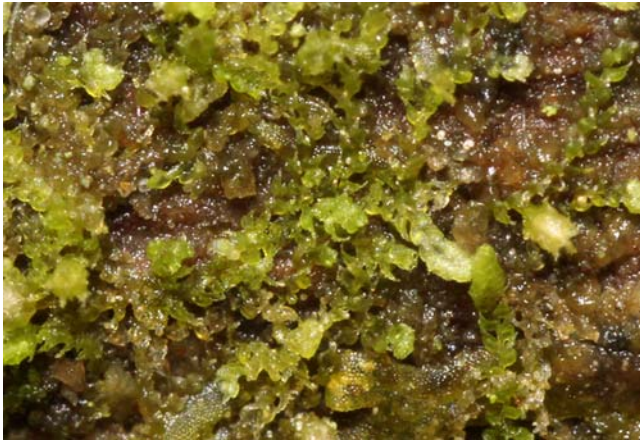


Figure 8. *Drepanolejeunea hamatifolia* on a wet rock. Photo by Barry Stewart, with permission.

Bosanquet (2015) discussed the effects of topography and rainfall on the distribution of Atlantic bryophytes in Wales. He recognized that rainfall in Wales ravines was not the sole driver of bryophyte diversity there. He considered that water courses and waterfalls were able to provide the mists that permitted the success of **hygrophilous** (humidity-demanding) bryophytes, in particular *Drepanolejeunea hamatifolia* (Figure 1-Figure 8). This species has a very patchy distribution due to its habitat restrictions. It is a desiccation-sensitive hyperoceanic species and is thus restricted to rocky cascades and other habitats that create a mist and moist environment.

Averis *et al.* (2012) found that those water courses that have the potential for electric power provide good habitats for *Drepanolejeunea hamatifolia* (Figure 1-Figure 8). Hence, if the construction of a power plant changes the mist and humidity of the area, the species is likely to become endangered there. Callaghan *et al.* (2019) found about 23% of colony losses following hydroelectric power development, including those changes to *Drepanolejeunea hamatifolia*, were due to larger bryophytes multiplying or invading and excluding them. The most aggressive of these was the moss *Ctenidium molluscum* (Figure 9).



Figure 9. *Ctenidium molluscum* in rock canyon in Europe, a larger species that can overtake *Drepanolejeunea hamatifolia*. Photo by Michael Lüth, with permission.

But it appears that the requirement of mist or high humidity is not always the case. Schwarz and Schumm (2019) reported *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) from the Canary Islands on dry, shaded to half-shaded bark (Figure 10), stone, or leaves. Likewise, on Tenerife in the Canary Islands, Gónzalez-Mancebo *et al.* (2004a) reported it as a pioneer epiphyte on *Laurus azorica* (Figure 11), occurring only in the Pijaral area, and with a low frequency. But laurel forests are typically humid and shady (Kürschner *et al.* 2007a). They are dominated by bryophytes that form **mats** (Figure 8) or **fans** and are **perennial stayers** or **perennial shuttle** species. *Drepanolejeunea hamatifolia* occurs in the laurel forests of Madeira Island with a **thread** life form. In the Azores, it occurs on stem bases in dense stands of *Persea* (Figure 12), *Pittosporum* (Figure 13), and *Acacia* (Figure 14) (Sjögren 2003). It also occurs as an epiphyte in laurel forests on the Madeira archipelago (Gutierrez 2007). Bates (2012) found it on *Cryptomeria* (Figure 15) on the higher hills of the Azores, where it joins acidophilic bryophytic epiphylls. Patiño and González-Mancebo (2011) reported it from subtropical cloud forests in the Canary Islands, growing on ericaceous shrubs. All of these habitats are moist.



Figure 10. *Drepanolejeunea hamatifolia* on bark in Bretagne. Photo by Michael Lüth, with permission.

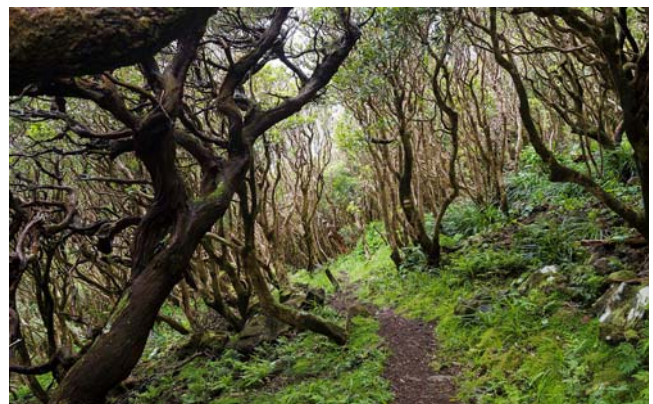


Figure 11. Laurel forest (*Laurus azorica*), Macaronesia, on Flores Island. Photo by B. T. Varusko, through Creative Commons.



Figure 12. *Persea americana* with fruit; *Persea* can have *Drepanolejeunea hamatifolia* on bark at its base. Photo by M. Clara Salviano, through Creative Commons.



Figure 13. *Pittosporum coriaceum*; species in this genus can have *Drepanolejeunea hamatifolia* on bark at the base. Photo by Krzysztof Ziarnik, through Creative Commons.

The epiphyllous habitat of *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) is not restricted to leaves of tracheophytes. It also occurs on other bryophytes, such as *Thamnobryum alopecurum* (Figure 16), another wet habitat species, in Killarney, Ireland (Kelly 1981). In the same woods, it grew on branches and upper parts of the trunk of yew trees, and Rose (1974) found it on oaks in Killarney. Similarly, Durfort (2015) found that this liverwort occurs as an epiphyte on mosses on tree trunks in Brittany, France. But it also occurs on rocks, old gorse, willows, birches, and larger trees in Brittany. Despite this variety of substrata, it is very rare in France.



Figure 14. *Acacia saligna* on Cyprus; *Acacia* can have *Drepanolejeunea hamatifolia* on bark at its base. Photo by Anna Anichkova, through Creative Commons.



Figure 15. *Cryptomeria japonica* in Azores, substrate for *Drepanolejeunea hamatifolia*. Photo by Mary Anne Melo, through Creative Commons.



Figure 16. *Thamnobryum alopecurum*, a substrate for *Drepanolejeunea hamatifolia*. Photo by Michael Lüth, with permission.

Proctor (1980) measured the radiation for *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) in several locations in the British Isles (North Wales and Yorkshire). In the wooded lowland habitats, peak irradiance occurred immediately before leaf expansion. Direct radiation was negligible in the ravine sites where *Drepanolejeunea hamatifolia* occurred.

Corley (1983) found *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) in the Inner Hebrides, where it occurred on boulders in the stream and rocks at the edge, accompanied by *Hycomium armoricum* (Figure 17), *Thamnobryum alopecurum* (Figure 16), *Cololejeunea microscopica* (Figure 18), *Douinia ovata* (Figure 19), and *Colura calyptrifolia* (Figure 20).



Figure 17. *Hycomium armoricum* in its common habitat where it might be accompanied by *Drepanolejeunea hamatifolia*. Photo by Dick Haaksma, with permission.

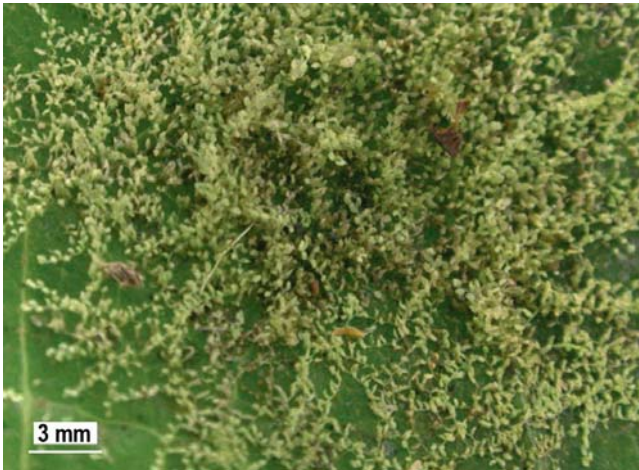


Figure 18. *Cololejeunea microscopica*, a species that might be accompanied by *Drepanolejeunea hamatifolia*. Photo by Jan-Peter Frahm, with permission.

But the reported habitats suggest that submersion is an unusual condition for the species. Instead, it occupies more terrestrial sites. Sim-Sim *et al.* (2011) report *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) as an epiphyte on Madeira Island, where it is an indicator species for the high-altitude *Erica* habitat (Figure 21). Roden *et al.* (2007) found it in the oak woods in the valley of the Owendalullegh River in Ireland.



Figure 19. *Douinia ovata*, a species that might be accompanied by *Drepanolejeunea hamatifolia*. Photo by Des Callaghan, with permission.



Figure 20. *Colura calyptrifolia*, a species that might be accompanied by *Drepanolejeunea hamatifolia*. Photo by Barry Stewart, with permission.



Figure 21. *Erica maderensis*; *Drepanolejeunea hamatifolia* is an indicator species for the high altitude *Erica* habitat on Madeira Island. Photo by Thomas Dellinger, through Creative Commons.

Sjögren (1993) considered *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) to be a species with no substrate preference on the island of Corvo in the Azores. He also considered it to be a pioneer on bark. The species was able to colonize with thin carpets that were frequently split up by areas almost nude of bark. To add further to

this lack of substrate preference, Schwarz and Schumm (2019) reported it from wet, shaded plastic pipe.

The invasive *Rhododendron ponticum* (Figure 22) in Atlantic oak woodlands impacted the oak woodland community (Maclean *et al.* 2017). However, *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) seemed to have an affinity for these dense *Rhododendron* areas.



Figure 22. *Rhododendron ponticum*, a species whose invasion seemed to have a favorable impact on *Drepanolejeunea hamatifolia*. Photo by Rasbak, through Creative Commons.

Adaptations

Although it appears that *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) seems to be most common in moist microclimates, it is nevertheless also adapted to drier conditions. **Lobules** (water sacs) in this species help it to survive in the sometimes dry epiphytic habitat (Sim-Sim *et al.* 2005a).

Unlike the report by Kürschner *et al.* (2007a) that considered *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) to be a **perennial stayer** or **perennial shuttle species**, other researchers considered it to be a **short-lived shuttle species** in the Canary Islands (González-Mancebo *et al.* 2004b; Lloret & González-Mancebo 2011; Patiño & González-Mancebo 2011), with 2% cover and 2.98% frequency (González-Mancebo *et al.* 2004b).

Reproduction

Drepanolejeunea hamatifolia can be **autoicous** or **dioicous** (Paton 1999), probably accounting for some of its morphological variability. The perianth has various projections from the folds, suggesting they might attach to an animal or trap air bubbles that help them to float. This requires experimentation and would necessitate the disarticulation of the perianth.

In running water, fragmentation is a frequent form of asexual reproduction. I would assume that this is facilitated by the caducous branches (Paton 1999) in *Drepanolejeunea hamatifolia* (Figure 1-Figure 8). Paton reported frequent sporophytes, but did not report gemmae.

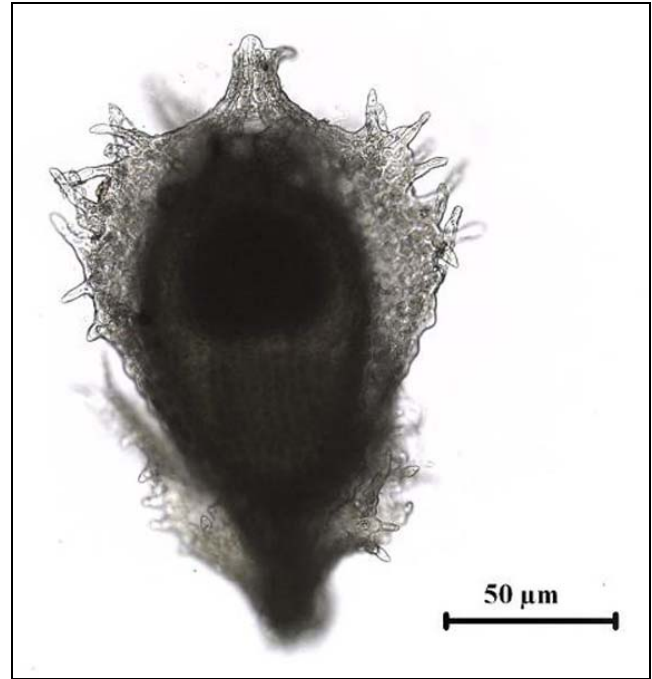


Figure 23. *Drepanolejeunea hamatifolia* perianth; note the spiny projections on the folds. Photo by Hugues Tinguy, with permission.

Fungal Interactions

Despite its association with ericaceous shrubs, known for the presence of mycorrhizae, there seem to be no records of mycorrhizal associations (Wang & Qiu 2006). Although the Ericaceae typically have mycorrhizae (Read & Stribley 1975; Specht 1979; Selosse *et al.* 2007), epiphytes such as this tiny liverwort usually do not.

Drepanolejeunea vandenberghenii

Distribution

Rwanda (Pócs 2021)

Aquatic and Wet Habitats

In Rwanda, *Drepanolejeunea vandenberghenii* occurs on dripping rocks, growing among *Sphagnum* and *Breutelia*; not known in submerged condition (Pócs 2021).

Adaptations

Plants of *Drepanolejeunea vandenberghenii* are yellowish to light brownish-green (Pócs 2021). This is in contrast to the blackish appearance of *D. vanderpoortenii* and suggests a difference in light intensity or quality.

Drepanolejeunea vanderpoortenii

Distribution

Drepanolejeunea vanderpoortenii is known only in Madagascar (Pócs 2021).

Aquatic and Wet Habitats

Drepanolejeunea vanderpoortenii occurs on streambed stones, often under water (Pócs 2021). Such locations include on wet boulders in streams in submontane rainforest and on streambed stones of Mahavoho River, at 220 m asl.

Adaptations

Drepanolejeunea vanderpoorteni has blackish pigmentation, julaceous habit, thick-walled stems (Pócs 2021). The blackish color and thick-walled stems could be adaptations to its rheophytic habitat (Gradstein & Vital 1975, Pócs 2010). I would suggest that the julaceous habit is also an adaptation against the abrasion caused by flowing water. I would predict that it causes less turbulence than other forms, and certainly less subject to abrasion than are keeled leaves.

Reproduction

The sexual and vegetative reproduction are both unknown at this time (Pócs 2021). It is likely that it experiences vegetative reproduction with dispersal by water flow.

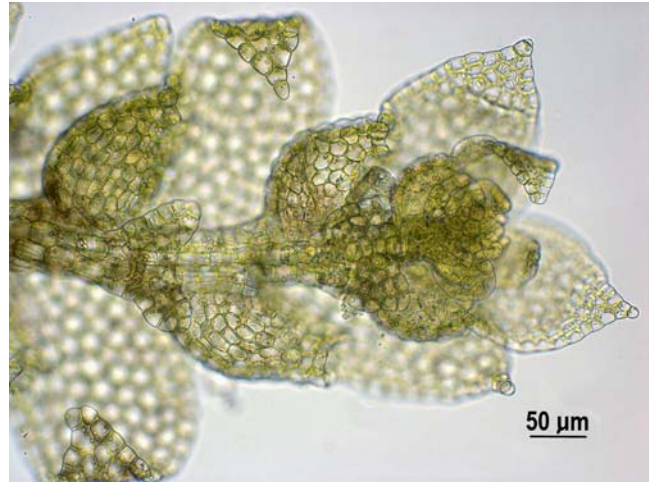


Figure 25. *Harpalejeunea molleri* underside. Photo by Blanka Aguero, with permission.

Harpalejeunea molleri (Figure 24-Figure 28, Figure 33-Figure 38)

(syn. = *Harpalejeunea ovata*; *Lejeunea molleri*)

Distribution

Harpalejeunea molleri (Figure 24-Figure 28, Figure 33-Figure 38) has had several synonyms (Grolle 1989) and there has been confusion about the use of some names (Schuster 1999). It is a widespread oceanic and suboceanic species from southern Norway south to Spain, Portugal, southern France, Tuscany, and Corsica (Sotiaux *et al.* 2007), the Canaries (Mancebo *et al.* 2007), and the Azores (Schuster 1980). In North America it extends from the Southern Appalachians from Virginia southward and outer Coastal Plain (Schuster 1980).

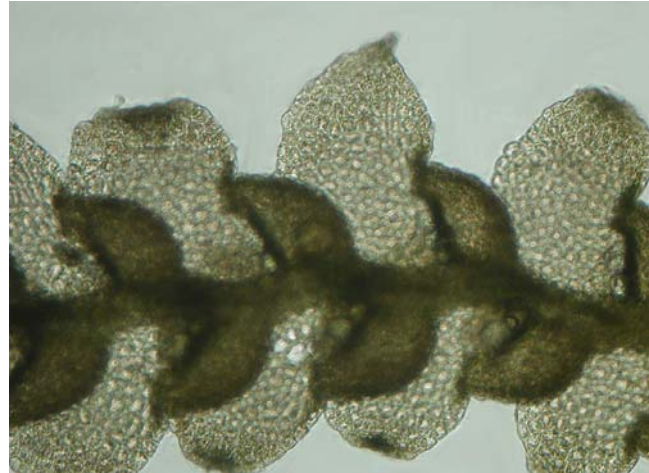


Figure 26. *Harpalejeunea molleri* showing leaf lobes that appear darker in this photo. Photo by Jan-Peter Frahm, with permission.



Figure 24. *Harpalejeunea molleri*, a species from both sides of the Atlantic in oceanic and suboceanic regions. Photo by Stan Phillips, through public domain.



Figure 27. *Harpalejeunea molleri* subsp. *integra*. Photo by Blanka Aguero, with permission.



Figure 28. *Harpalejeunea molleri* subsp. *integra* giving a view of leaf insertion and leaf cells. Photo by Blanka Aguero, with permission.

Aquatic and Wet Habitats

Schuster (1980) describes the wetter habitats of *Harpalejeunea molleri* as shaded humid rocks, in swamps, along black-water streams, or on damp rocks. Dirkse (1985) reported it from sheltered wet volcanic rocks in the laurel forests (Figure 11) of the Canary Islands. González-Mancebo *et al.* (2004b) found it growing in areas with high mist in the laurel forests of the Canary Islands. Sim-Sim *et al.* (2005a) found *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38) growing with *Plagiochila exigua* (Figure 29) on moist rock surfaces and slopes near water courses on Madeira, but it also occurred epiphytically, often with *Frullania tamarisci* (Figure 30) and other bryophytes.



Figure 29. *Plagiochila exigua* growing with smaller liverworts such as *Harpalejeunea molleri*. Photo by Jan-Peter Frahm, with permission.



Figure 30. *Frullania tamarisci*, a species that occurs epiphytically with *Harpalejeunea molleri* on Madeira. Photo by Proyecto Musgo, through Creative Commons.

Rothero (2005) reported *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38) as a very small liverwort making a delicate green pattern (Figure 24) against the dark stone of large rocks in ravines. These rocks were regularly inundated, but escaped scouring. Bosanquet (2015) described seven hotspots in Wales, noting that these are located away from high-rainfall areas. These typically are in woodland ravines in locations with mist zones and periodic inundation, usually governed by areas of high upstream rainfall. These habitats include waterfalls and rocky cascades. Such areas are suitable habitats for *Harpalejeunea molleri*. Bosanquet considers this species to be desiccation intolerant. Pescott and Preston (2014) found that *Harpalejeunea molleri* in Britain and Ireland occurred with a group of species that experienced the most wet days. In hyperoceanic places in Scotland, Hodgetts *et al.* (2013) found it associated with *Lejeunea mandonii* (Figure 31) and other bryophytes on ash trees next to burns in ravines in a base-rich area. Denyer (2012) found it associated with crags that had calcareous seepage in the UK.

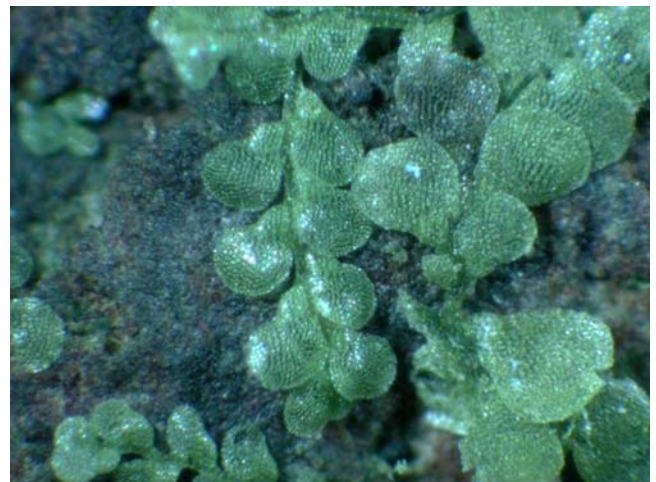


Figure 31. *Lejeunea mandonii*, a species that can occur with *Harpalejeunea molleri* on ash bark. Photo by Jan-Peter Frahm, with permission.

In Nova Scotia, *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38) occurs on the bases of the eastern white cedar *Thuja occidentalis* (Figure 32) in a swamp (Haughian & Neily 2020).



Figure 32. *Thuja occidentalis* in snow; *Harpalejeunea molleri* grows on the bases of this species in Nova Scotia. Photo by Peter M. Dziuk, with online permission.

Averis *et al.* (2011, 2012) considered that watercourses with hydroelectric potential are an important habitat for *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38). Since their declaration of concern for this species, Callaghan *et al.* (2019) found that following disturbance in the flow regime caused by a new hydroelectric power development, *Harpalejeunea molleri* was one of the first species to be diminished. *Harpalejeunea molleri* can be overtaken by larger bryophytes, especially *Ctenidium molluscum* (Figure 9).

Like so many of the wet habitat *Lejeuneaceae*, *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38) can occur on dry bark or stone in half-shaded to shaded habitats of Madeira Island (Schwarz & Schumm (2019). In these habitats, other very small liverworts often grow on it.

Harpalejeunea molleri (Figure 24-Figure 28, Figure 33-Figure 38) occurs in small, yellowish-green patches (Schuster 1980). It can be found on bark and shaded humid rocks. In the North American Coastal Plain it is known only on bark, usually in swamps or deep, mesic, evergreen wood, often near or along black-water streams. But elsewhere it occurs on damp rocks, usually on shaded vertical sides of ledges or cliffs, less often on large boulders. It also occurs in relatively open xerophytic oak-hickory-chestnut forests.

Adaptations

González-Mancebo *et al.* (2004b) considered *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38) to be a **short-lived shuttle** species on the forest floor of the laurel forest (Figure 11) in the Canary Islands. Kürschner *et al.* (2007a) considered it to be a **thread** (Figure 38) on the Canary Islands. At its small size, the threads can form a **mat**.

Biodiversity, ecology, and morphology of bryophytes are related (Fontinha *et al.* 2010). In Madeira, Fontinha and coworkers measured the variables related to the

distribution of bryophytes and found that temperature, precipitation, altitude, species cover, presence of snow, substrate pH, microaspect, and topography could be related to the morphological characters of underleaf (Figure 33) and lobule surfaces, lobule width, lobe length (Figure 34), lobe surface, and length of median cells of the lobe (Figure 35) in several liverwort species, including *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38). **Trigones** (cell wall thickenings, especially where three cells join; Figure 36-Figure 37) don't seem to be one of these characters. In these habitats, *H. molleri* was associated with other liverwort species (Figure 38), including *Porella canariensis* (Figure 39), *P. inaequalis*, and *P. obtusata* (Figure 40).



Figure 33. *Harpalejeunea molleri* underleaf. Photo by Jan-Peter Frahm, with permission.



Figure 34. *Harpalejeunea molleri* subsp. *integra* showing lobes on ventral side. Photo by Blanka Aguero, with permission.

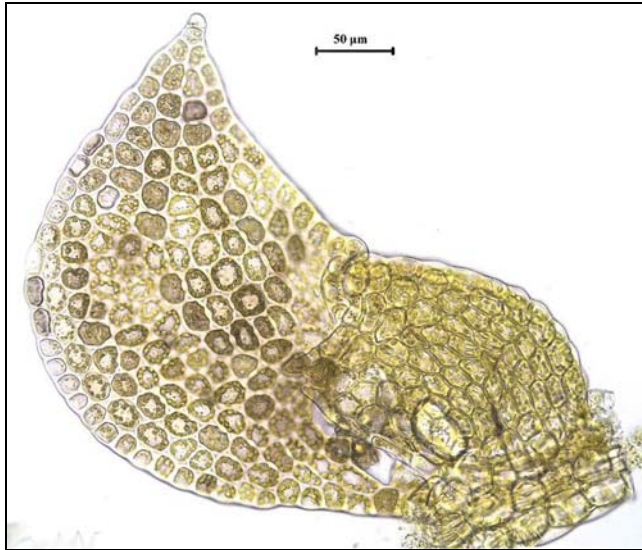


Figure 35. *Harpalejeunea molleri* leaf showing lobe. Photo by Hugues Tinguy, with permission.

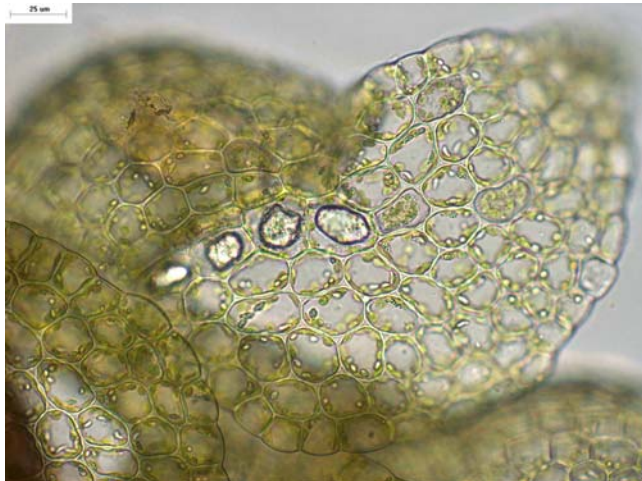


Figure 36. *Harpalejeunea molleri* subsp. *integra* leaf and leaf lobe cells. Photo by Blanka Aguero, with permission.

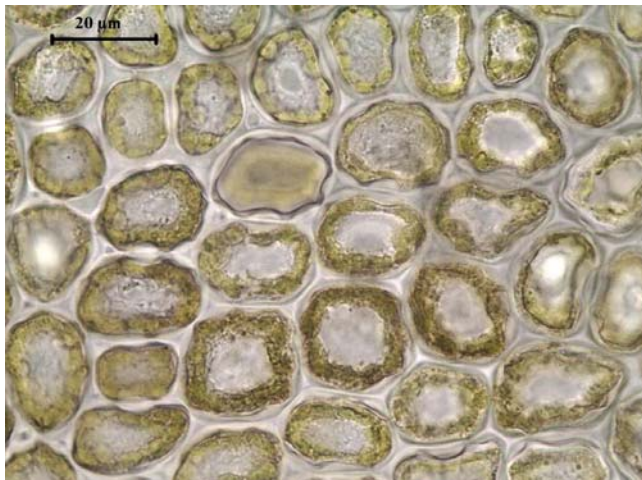


Figure 37. *Harpalejeunea molleri* leaf cells with trigones. Photo by Hugues Tinguy, with permission.



Figure 38. *Harpalejeunea molleri* growing as a thread on larger liverworts. Photo by Jan-Peter Frahm, with permission.



Figure 39. *Porella canariensis*, a species that associates with *Harpalejeunea molleri*. Photo by Jan-Peter Frahm, with permission.



Figure 40. *Porella obtusata*, a species that associates with *Harpalejeunea molleri*. Photo by Stan Phillips, through public domain.

Reproduction

Harpalejeunea molleri (Figure 24-Figure 28, Figure 33-Figure 38) is **dioicous**, usually sterile, usually without asexual reproduction.

Fungal Interactions

There seems to be little information about the interactions of *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38), although it seems to occur at least some of the time with other bryophytes (Figure 41). However, Vital *et al.* (2000) found that it can grow on the fungus *Hyphodontia* sp. (Figure 42), a capability of other liverworts as well.



Figure 41. *Harpalejeunea molleri* mixed with other bryophytes. Photo by Michael Lüth, with permission.



Figure 42. *Hyphodontia sambuci* overgrown by leafy liverworts, one of which can be *Harpalejeunea molleri*. Photo by Roger Griffith, through public domain.

Lejeunea (Figure 43-Figure 44, Figure 47-Figure 51, Figure 61-Figure 71)

(syn. = *Neopotamolejeunea*)

S. Robbert Gradstein (November 2011) related to me that multiple species in the genus *Lejeunea* (Figure 43-Figure 44, Figure 47-Figure 51, Figure 61-Figure 71) are common in Andean streambeds. The genus has lobes that approach the structure of lobules. Both terms are used in the literature.

Lejeunea aloba

(syn. = *Eulejeunea aloba*, *Rectolejeunea aloba*, *Rectolejeunea submersa*)

Distribution

Lejeunea aloba occurs in the tropics. Records include Nilgiri Hills (Verma & Rawat 2013), Jog Falls (Schwarz

2013) and other locations in India (Shah & Gujar 2016; Singh & Singh 2016). It occurs in the African countries of Kenya (Chuah-Petiot & Pócs 2003; Enroth *et al.* 2019) and Rwanda (Biedinger & Fischer 1996). Söderström *et al.* (2014) included in the flora of Java.

Aquatic and Wet Habitats

Ruttner (1955) included *Lejeunea aloba* in his treatment of aquatic taxa of the tropics. But little seems to be known of its ecology. Biedinger and Fischer (1996) reported it in their epiphytic study in Rwanda. Malombe *et al.* (2016) found it growing as an epiphyll in the edges of Afromontane fragmented forests. Rashid *et al.* (2012) noted its altitudinal range in the Kashmir state of India to be 800-1100 m.

Lejeunea eckloniana (Figure 43-Figure 44)

Distribution

Lejeunea eckloniana (syn. = *Lejeunea holtii*; Figure 43-Figure 44) has been reported in South Africa (Jones 1974), Cape Verde Islands, Teneriffe, Sierra Leone and Angola to Kenya, Tanzania, Cape, and to the Mascarenes (widespread; Pócs 1993), Ethiopia (Hylander *et al.* 2010), Ghana (Hodgetts *et al.* 2016), Taita Hills region, Kenya (Enroth *et al.* 2019), Bioko Island in Equatorial Guinea (Müller & Pócs 2007), Réunion Island (Ah-Peng & Bardat 2005), India (Schwarz 2013; Singh & Pócs 2016; Kasiani *et al.* 2019), Portugal (Sérgio *et al.* 2012; Cacciatori *et al.* 2015), Azores (Gabriel & Bates 2005; Frahm 2006), Macaronesia (Sérgio 1978), Canary Islands (González-Mancebo & Hernández-García 1996), Pico Branco-Porto Santo Island, Madeira (rare; Lobo 2008; Ruas *et al.* 2015), Malaysia and Indonesia (Kasiani *et al.* 2019), UK (rare; Pescott 2016; Bosanquet *et al.* 2018), Ireland (endangered; Kingston 2012).



Figure 43. *Lejeunea eckloniana*, a mostly tropical species in the Eastern Hemisphere and that can occur at waterfalls. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

Lejeunea eckloniana (Figure 43-Figure 44) seldom occurs as a true aquatic, but it usually prefers damp habitats. Watson (1919) reported it from waterfalls in Europe. Dirkse (1985) found it on sheltered wet volcanic

rocks in the laurel forest (Figure 11) of the Canary Islands, Luís *et al.* (2015) found it in mountainous streams on Madeira Island. And Sim-Sim *et al.* (2005b) found it was a frequent part of the flora in the vicinity of temporary lagoons and swamps in the Madeira Archipelago. But Schwarz and Schumm (2019) reported it from wet to dry shaded stone or bark in the Madeira Island. In the Canary Islands, González-Mancebo and Hernández-García (1996) found it to be frequent in the laurel forest, but only occasional in the *Erica-Myrica* (Figure 45) woodland. On the other hand, in the Azores Gabriel and Bates (2005) found it to be a characteristic epiphyte, but it occurred where there was lower water availability and higher bark pH.



Figure 44. *Lejeunea eckloniana*. Photo by Jan-Peter Frahm, with permission.



Figure 45. *Myrica* on Canary Islands. Photo through Creative Commons.

Bosanquet *et al.* (2018) considered *Lejeunea eckloniana* (Figure 43-Figure 44) to be a rare hyperoceanic species in British Atlantic woodlands. Crundwell *et al.* (1994) reported that it occurs on a *Pittosporum* (Figure 13) trunk near a stream, but also in small quantities among the moss *Andoa berthelotiana* (Figure 46) on rocks at a roadside in the UK. In the Iberian Peninsula, it is likewise quite rare except in the oceanic flora in semi-natural woodlands (Franco *et al.* 2003).



Figure 46. *Andoa berthelotiana*, a moss that may have small quantities of *Lejeunea eckloniana* growing with it. Photo by Pedro Cardoso, with permission through Azoresbiportal.

Adaptations

Lejeunea eckloniana (Figure 43-Figure 44) seems to be best adapted to epiphytly, with small stems, imbricate leaves, and lobules, but no papillae (Kraichak 2012), perhaps reflecting its occurrence in both wet and dry habitats. Sim-Sim *et al.* (2005a) noted the use of water sacs to adapt the species to the variable water conditions. Its oil bodies are minute, with only 2-4 per cell (Kis & Pócs 1997). But the species is variable in other ways, with innovations in particular varying (Jones 1979).

Reproduction

Lejeunea eckloniana (Figure 43-Figure 44) is **monoicous** (Jones 1974).

Lejeunea juruana

(syn. = *Neopotamolejeunea uleana*, *Potamolejeunea ulena*)

Lejeunea juruana is endemic to Andean Brazil (Gradstein & Reiner-Drehwald 2007). It is a specialized rheophyte, occurring as rare in the rainforest on leaves of trees or shrubs in rivers (Bastos & Gradstein 2020). In this habitat it is periodically submerged. In the lowland rainforest, it is likewise periodically submerged, but can occur on rock and pendent on branches of shrubs in the rivers.

Lejeunea lamacerina (Figure 47-Figure 51)

Distribution

Lejeunea lamacerina (Figure 47-Figure 51) is a Holarctic species with a North American and a European/Macaronesian clade (Heinrichs *et al.* 2013; Lee *et al.* 2016; Bastos & Gradstein 2020), where it represents a euoceanic element (Vieira *et al.* 2005). Bastos and Gradstein (2020) reviewed the genus in Brazil and concluded that this species probably does not occur there. Although Schumacker and Váña (2000) originally considered it to be a European/Macaronesian endemic, Cogoni *et al.* (2002) included North America, as well as Japan, Siberia, and Iceland in its distribution. They found it to be of limited occurrence in Italy. Blockeel (2004) expanded its known localities in Italy. Heinrichs *et al.* (2012) reported it from the Canary Islands. Vieira *et al.*

(2004) considered it to be a relic on Macaronesia due to its worldwide distribution. Özenoğlu and Gökler (2002) reported it from Turkey in the Dilek Peninsula National Park. In the Azores, it occurs on all nine islands (Frahm 2005).



Figure 47. *Lejeunea lamacerina*, a Holarctic species often found in mountain streams. Photo by Andy Hodgson, with permission.



Figure 48. *Lejeunea lamacerina*, a species often living in spray from rapids and waterfalls. Photo by David T. Holyoak, with permission.



Figure 49. *Lejeunea lamacerina*, showing lobes. Photo by Michael Lüth, with permission.

In North America, as subsp. *gemminata* (Figure 64), it is known from Newfoundland and Nova Scotia in Canada, south to Georgia, USA (Schuster 1980). Miller (1964) reported this subspecies from Hocking Co., Ohio. Schuette and Kratesky (2014) reported the subspecies from Wayne Co., Pennsylvania. Briscoe *et al.* (2009) reported it from Maine.



Figure 50. *Lejeunea lamacerina* showing underleaves. Photo by Michael Lüth, with permission.

Aquatic and Wet Habitats

In Tuscany and Piedmont, Italy, *Lejeunea lamacerina* (Figure 47-Figure 51) grows on damp rocks along the Riu Rica Bianca (Cogoni *et al.* 2002) and is "not rare" on rocks in streams of the Apuanian Alps (Frahm 2013). Vieira *et al.* (2005) reported it as rare in the Portuguese mountain stream habitats, where it is either seasonally immersed or receives splash or spray (Figure 50-Figure 51). It also occurs in Portugal on dripping schistose wall (Vieira *et al.* 2004) and deeply shaded steep dripping granitic surfaces (Vieira *et al.* n.d.). On Madeira Island it occurs in mountain streams (Luís *et al.* 2015). Sim-Sim *et al.* (2005b) found it on Madeira Island on shaded rocks and rocky slopes near streams and ravines; it typically was associated with *Plagiochila punctata* (Figure 52). In the laurel forest (Figure 11) slope communities, it occurs along shaded rivulets, often with other liverworts. It had a 1.4% frequency in the stream, but a 27.1% frequency on the stream bank (Luís *et al.* 2010). Haury (1995) found it at a Breton (France) brook, a stream that also had *Platyhypnidium riparioides* (Figure 53) and *Leptodictyum riparium* (Figure 54). On Islay, the southernmost of the Inner Hebrides islands of Scotland, it occurs on wet, shaded rocks in a gully on the north coast (Birks & Adam 1978). In Turkey it occurs on tree roots and straight rocks, as well as damp shaded rocks, especially base-rich substrata, and not so often on the sheltered stream banks and tree trunks (Özenoğlu & Gökler 2002).



Figure 50. *Lejeunea lamacerina*, showing a common stream habitat. Photo by Michael Lüth, with permission.



Figure 51. *Lejeunea lamacerina* on boulders in a stream – a common habitat for this species. Photo by Michael Lüth, with permission.



Figure 52. *Plagiochila punctata*, a species often associated with *Lejeunea lamacerina* on shaded rocks and rocky slopes near streams and ravines on Madeira Island. Photo by Stan Phillips, through public domain.

Vieira *et al.* (2012) considered *Lejeunea lamacerina* (Figure 47-Figure 51) to be especially important in the northwestern streams of Portugal. These streams are their best habitat in the country, but these researchers considered them to be among the "most threatened" by a warming climate, thermal pollution, and changed hydrological regimes. Heras *et al.* (2002) reported it from humid, acidic conditions in the Botanical Garden of Madrid, Spain.



Figure 53. *Platyhypnidium riparioides*, a species that often occurs in the same streams as *Lejeunea lamacerina* in Breton, France. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 54. *Leptodictyum riparium*, a species that often occurs in the same streams as *Lejeunea lamacerina* in Breton, France. Photo by Štěpán Koval, with permission.

But like so many of the *Lejeuneaceae*, *Lejeunea lamacerina* (Figure 47-Figure 51) also occurs as an epiphyte. Kelly (1981) reported it to be frequent on epiphytic mosses in Killarney, southwest Ireland. Sim-Sim *et al.* (2011) found it on all the tree species on Madeira Island.

One of the habitats of *Lejeunea lamacerina* (Figure 47-Figure 51), at least in the Azores, is in lava tubes (Figure 55) and volcanic pits, where it is a frequent species (Gabriel *et al.* 2008). In central Spain, Luceño *et al.* (2017) occurs on the wet granites in the alder grove forest. Ravines with *Prunus lusitanica* (Figure 56) there serve as refugia for oceanic species such as this.



Figure 55. Volcanic cave (lava tube) at Algar do Carvão, on Terceira Island, Portugal. Photo by Vitor Oliveira, through Creative Commons.



Figure 56. *Prunus lusitanica* epiphytes, which can include *Lejeunea lamacerina*, using these trees as refugia in ravines in the Azores. Photo by Krzysztof Ziarnek, through Creative Commons.

Pescott (2019) found it on drystone wall in the UK. Gökler (1998) found it on stones at 1200 m asl in the Altindere Valley National Park of Turkey. In Maine, USA, the subsp. *gemminata* (Figure 64) occurs on serpentine rock (Briscoe *et al.* 2009).

Like so many members of this family, *Lejeunea lamacerina* (Figure 47-Figure 51) occurs on a wide range of habitats. These include thin patches on rock and bark in damp to almost dry locations (Schuster 1980). Kürschner *et al.* (2007a, b) found that on Madeira Island it was among the dominant epiphytes in the laurel (Figure 11) and ericaceous forests (Figure 57). In the Canary Island subtropical cloud forests, it is the only species that is "distinctive" of the laurel forests (Patiño & González-Mancebo 2011). On Corvo in the Azores, Sjögren (1993) found that *Lejeunea lamacerina* is among the most frequent in the epiphyllous associations and also occurs in the epiphytic associations (Figure 56). It occurs as a primary invader in areas of almost nude bark on *Erica* (Figure 57) and *Juniperus* (Figure 58).

Kürschner *et al.* (2007b) found that *Lejeunea lamacerina* (Figure 47-Figure 51) is able to survive under minimal light in the Madeira laurel (Figure 11) and ericaceous forests (Figure 57). These forests exhibit deep shade and constantly humid conditions.



Figure 57. *Erica azorica*, in a genus where *Lejeunea lamacerina* can be a primary invader in the Azores. Photo by Felix Gertz, through Creative Commons.



Figure 58. *Juniperus cedrus*, in a genus where *Lejeunea lamacerina* can be a primary invader in the Azores. Photo by H. Zell, through Creative Commons.

In the Leyre valley of southwestern France, *Lejeunea lamacerina* (Figure 47-Figure 51) arrived after a mud wash with only a slight salt and nutrient enrichment (Hugonnot 2010). Mosses, particularly *Dichelyma capillaceum*

(Figure 59), trapped and retained the mud, creating a suitable habitat for the *L. lamacerina*.



Figure 59. *Dichelyma capillaceum*, a species that traps mud during flooding, providing a suitable habitat for *Lejeunea lamacerina* in southwestern France. Photo by Michael Lüth, with permission.

In The Netherlands, van der Pluijm *et al.* (2015) reported that *Lejeunea lamacerina* (Figure 47-Figure 51) is usually found on rocks in or near streams that are sheltered by forests in lowland valleys. They suggested that this area is humid and provides protection from frost and drought. But their new find was epiphytic in a relatively open landscape, occurring at 1.5 m height on an oak (*Quercus robur*; Figure 60) stem.



Figure 60. *Quercus robur* in Dartmoor, UK; *Lejeunea lamacerina* grows on its trunks in The Netherlands. Photo by Alex Jane, through Creative Commons.

Adaptations

The life form of *Lejeunea lamacerina* is typically that of a **small mat** (Figure 61-Figure 62) (Sim-Sim *et al.* 2003, 2005b; Kürschner *et al.* 2007a; Patiño *et al.* 2009). Its life strategy in the Madeiran laurel (Figure 11) and ericaceous forests (Figure 57) is that of a **long-lived shuttle**, surviving in minimal light (Kürschner *et al.* 2007b). Schuster (1980) described these mats as thin, whitish to pale yellowish green, occurring in patches or scattered on rock or bark.



Figure 61. *Lejeunea lamacerina* (yellowish patches) forming mats on a rock. Photo by Michael Lüth, with permission.



Figure 62. *Lejeunea lamacerina* forming a mat. Photo by Michael Lüth, with permission.

Lejeunea lamacerina can exhibit modified form in some environments (Figure 63). This can be expressed as very slender stems with small leaves, and when shaded the leaves can be longer than usual (BAP 2001).



Figure 63. *Lejeunea lamacerina* exhibiting a shelf-like growth form. Photo by George G., through Creative Commons.

Kraichak (2012) describes its epiphyllous characteristics as being **monoicous** (facilitating sexual reproduction) and having imbricate leaves (Figure 65) and

lobules (Figure 66) to retain water, but at the same time it lacks the advantage of neoteny and asexual reproductive structures.

Reproduction

Lejeunea lamacerina (Figure 47-Figure 51) is **autoicous** and has no specialized asexual reproduction (Schuster 1980); the female perianth of subsp. *gemminata* is shown in Figure 64. Nevertheless, van der Pluijm *et al.* (2015) found buds of young plants on the margin or lamina of old weathered leaves. They suggested that these probably act as a means of vegetative propagation.



Figure 64. *Lejeunea lamacerina* subsp. *gemminata*, with perianth. Photo by Ken McFarland and Paul Davison, with permission.



Figure 65. *Lejeunea lamacerina* showing imbricate leaves, lobules, and underleaves. Photo by Michael Lüth, with permission.



Figure 66. *Lejeunea lamacerina* showing underleaves and leaf lobes. Photo by David T. Holyoak, with permission.

Fungal Interactions

No studies have found any mycorrhizal relationships (Wang & Qiu 2006), but once more the small size may account for a lack of studies.

Biochemistry

Lejeunea lamacerina has a few small oil bodies per cell (Figure 67), indicating the presence of secondary compounds. Due to its small size, it is not surprising that biochemical studies are few. Asakawa *et al.* (2018) used chemical relationships of sesquiterpenoids to argue for its relationship among several Japanese species.



Figure 67. *Lejeunea lamacerina* leaf cells showing oil bodies. Photo by David T. Holyoak, with permission.

Lejeunea patens (Figure 68-Figure 69)

(syn. = *Crossotolejeunea polyantha*, *Neopotamolejeunea polyantha*, *Potamolejeunea polyantha*)

Lejeunea patens (Figure 68-Figure 69) has experienced misidentification in various geographic areas. Confusion between *Lejeunea patens* and other similar liverwort species and confusion in its synonymy in its various locations makes records of its occurrence

incomplete and sometimes misleading (see Söderström *et al.* 2007). For example, Miller (1964) considered *Lejeunea patens* Lindb. (Frye and Clark, 1947) to be the same as *Lejeunea lamacerina* Gott. ex. Steph. ssp. *gemminata* Schuster (Figure 64), but Söderström *et al.* 2016) consider both to be valid species.



Figure 68. *Lejeunea patens* on a boulder beside the river near Swallow Falls, Wales. Photo by Janice Glime.

Distribution

Lejeunea patens (Figure 68-Figure 69) has an Atlantic-Mediterranean distribution (Damsholt 2017). The species has been reported from Spain (Sérgio *et al.* 2007), Portugal (Sérgio *et al.* 2007; Cacciatori *et al.* 2015). Yamaguchi *et al.* (2005) found it in Indonesia in two unburned plots. Bakalin (2019) reported it from the Caucasus of western Russia. Bosanquet *et al.* (2018) reported it from the British Atlantic woodland. It is known in Britain and Norway (Barbour (1903; Frahm 2012), Ireland, Bretagne in France, the Iberian Peninsula, and the Faroe Islands (Frahm 2012). Hugonnot *et al.* (2013) reported it from the Massif Central in France.

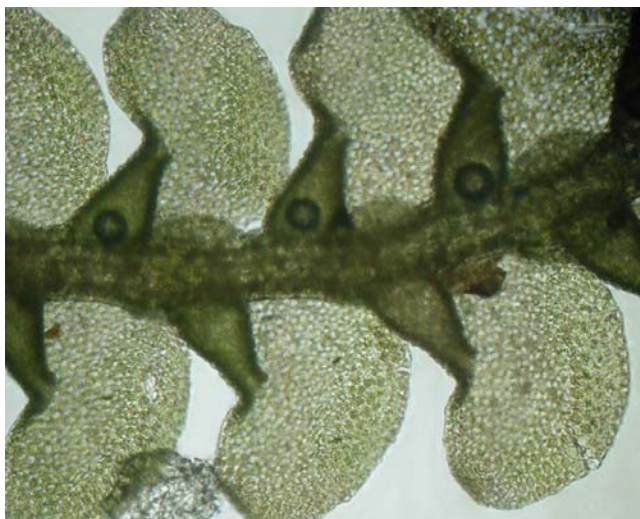


Figure 69. *Lejeunea patens* showing leaf lobes and underleaves. Photo by Jan-Peter Frahm, with permission.

Frahm (2005) reported it from eight of the nine Azorean islands, occurring in the Madeira laurel forests (Figure 11) (Sim-Sim *et al.* 2005a,b; Ruas *et al.* 2015). Gil and Guerra (1981) found it at Sierras de Algeciras in the Iberian Peninsula. Casas *et al.* (1983) found it at l'Alt Empordà in Spain. Poponessi and Aleffi (2016) listed it for the Sardinian region of Italy, Macaronesia, Spain, France, Madeira, Portugal, and Turkey. They termed it a Mediterranean-mountain hemiboreal species.

In North America, Barbour (1903) found that *Lejeunea patens* (Figure 68-Figure 69) occurs in Newfoundland and Nova Scotia and northern borders of the USA. Andrews (1921) reported it from several locations in North Carolina. Evans (1923) added Maine, New Hampshire, Vermont, Massachusetts, and Connecticut, USA.

Aquatic and Wet Habitats

Lejeunea patens (Figure 68-Figure 69) can be occasionally submerged (Watson 1919) and occurs in rivers (Ferreira *et al.* 2008). Cros (1982) found it on rocks in the Escalonada torrent of the Balearan Islands in the Mediterranean.

More likely one can find it on damp, shaded rocks in such locations as gorges (Poponessi & Aleffi 2016). Sim-Sim *et al.* (2003) reported it from rocks, boulders, and stone walls that were in either sheltered or exposed habitats (Figure 70) along water courses. These formed loose to dense patches, often with other bryophytes, on moist rock surfaces and slopes near the water (Figure 71). In the Faroe Islands, *Lejeunea patens* (Figure 68-Figure 69) occurs in rocky ravines or clefts where species richness is greater than in any other habitat in the Faroes (Damsholt 2017). In Turkey, Ezer *et al.* (2009) found it in humid locations.

In gorges in France, Hugonnot *et al.* (2016) report it from shaded and dry walls that have an accumulation of organic matter. They describe its habitat as having moderate shade with a "certain quantity" of light. In Bretagne, northern France, Durfort (2015) found it in ravines, wooded ridges, and mountainous areas with high atmospheric humidity.



Figure 70. *Lejeunea patens* habitat on vertical boulder surfaces. Photo by Michael Lüth, with permission.



Figure 71. *Lejeunea patens* on boulder near Swallow Falls, Wales, growing with *Thamnobryum alopecurum* in a humid environment. Photo by Janice Glime.

The habitat for *Lejeunea patens* (Figure 68-Figure 69) is clearly broadly defined, but usually in places with nearly constant humidity. It has even been found, but rarely, in a salt marsh in Britain (Adam 1976). In the Madeira Archipelago, Sim-Sim *et al.* (2005b) found it growing as an epiphyte where it was humid and shady in the laurel forest (Figure 11). It also often occurred with *Plagiochila exigua* (Figure 29) in loose turfs on moist rocks and slopes near water courses.

Long and Williams (2007) found that the intense shading of *Rhododendron ponticum* (Figure 22) causes the complete loss of a number riparian bryophytes. Only occasional patches of *Lejeunea patens* (Figure 68-Figure 69) on sheltered boulder faces are present. They assumed that this species could be washed in from stands living higher up on the rock face. Several reports mention that it tends to occur in brighter areas.

Lorenz (1924) found *Lejeunea patens* (Figure 68-Figure 69) on Mt. Desert Island, Maine, USA, on trees, rocks and the northern white cedar, *Thuja occidentalis* (Figure 32) – a swamp forest species.

Adaptations

The wide range of habitats is supported by the humidity and temperature tolerance of this species from the Faroes. In his experiments, Clausen (1964) found that at 43% and 51% relative humidity, half the cells of *Lejeunea patens* (Figure 68-Figure 69) were dead, but at 63% humidity, all cells remained alive. It did best between 70% and 100% rh with a temperature of ~35°C and 60% relative humidity at 20°C. All died at ~45°C at all humidities and at 20°C with 10% rh. These parameters placed it close to the middle among the liverwort species from various northern locations in the experiments. When maintained in ice at -10°C for 2-5 days, about 3/4 of the cells remained alive, but the dead cells were mostly at the shoot apices. After 11-12 days, all cells were dead. However, if it was partly desiccated over sugar, all cells remained alive for 5 days. At -40°C, all cells were dead in 1 day.

Lejeunea patens (Figure 68-Figure 69) can modify its form in different environments, sometimes having very slender stems with small leaves (BAP 2001). When so attenuated, shaded stems can produce leaves that are longer than usual.

Reproduction

Lejeunea patens (Figure 68-Figure 69) is **autoicous** (Evans 1902; Hugonnot *et al.* 2016). In the Faroe Islands, Damsholt (2017) found that perianths were frequent, but despite its autoicous sexuality, it only occasionally produces sporophytes there. Perhaps the climate is unsuitable for the antheridia or for sperm transfer for this species that extends southward to the Mediterranean. It is possible that the signals for antheridial and archegonial maturation are out of sync. On the other hand, even in Galicia in northwestern Spain, the species is frequent, but sporophytes are encountered only occasionally (Reinoso 1985). And in the gorges of the Rhue in France it does not produce sporophytes at the studied site, nor does it have any specialized vegetative propagation (Hugonnot *et al.* 2016).

Role

Des Callaghan (pers. comm.) has found rotifers (Figure 72) living among the mats of *Lejeunea patens* (Figure 68-Figure 69) in Wales (Figure 73).



Figure 72. *Frullania*, showing how a rotifer can live in a lobule such as those found in *Lejeunea patens*. Photo courtesy of Andi Cairns.



Figure 73. *Lejeunea patens* – home of rotifers near Swallow Falls, Wales, mixed with the moss *Thamnobryum alopecurum*. Photo by Janice Glime.

Biochemistry

The species has larger oil bodies, usually 4-6 per cell, up to 10. Biochemical studies seem to be lacking. Wang and Qiu (2006) were unable to find any records of mycorrhizae associated with *Lejeunea patens* (Figure 68-Figure 69), but is this the result of biochemical inhibition, or just lack of study?

Lejeunea polyantha

Confusion quickly arises in finding information on this species because there are two taxa that have had this name (**homonyms**): *Lejeunea polyantha* Mont. and *Lejeunea polyantha* Mitt. – the homonym (TROPICOS 2020). At times like this I regret not including authors in the text of this book.

Distribution

(syn. = *Crossotolejeunea polyantha*, *Neopotamolejeunea polyantha*, *Potamolejeunea polyantha*)

Lejeunea polyantha occurs in South America (Reiner-Drehwald 1999), including Brazil and Venezuela (Gradstein & Reiner-Drehwald 2007; Bastos & Gradstein 2020).

Aquatic and Wet Habitat

I must admit that this species did not appear in my search for aquatic species. But, as I found information on other species, this one showed up as being a rheophyte, occurring in lowland rainforests and being periodically submerged on rock and pendent on branches of shrubs in rivers (Reiner-Drehwald 2000a, b; Bastos & Gradstein 2020).

Lejeunea subaquatica

Lejeunea subaquatica seems to be a barely known species, but it is still recognized by Söderström *et al.* (2016).

The only wet/aquatic record I have found thus far is for its occurrence in the tropics at 10-20 cm above water level (Ruttner 1955).

Lejeunea topoensis

Distribution

Lejeunea topoensis is a rare Andean species, occurring in Brazil and Ecuador (Gradstein & Reiner-Drehwald 2007; Bastos & Gradstein 2020). It has an interesting disjunction between the Andes and the Atlantic coastal region in Brazil (Gradstein & Reiner-Drehwald 2007).

Aquatic and Wet Habitats

Lejeunea topoensis is a rheophyte, occurring in fast water and often submerged (Gradstein & Reiner-Drehwald 2007). In Ecuador it grows on the dwarf shrub *Cuphea bombonasae* (Figure 74) where it forms large mats (Gradstein & Benitez 2014). In Brazil they found it in a spring bog, growing submerged in running water. Gradstein *et al.* (2011) found it in great abundance in torrential water currents of the Topo River in the Ecuadorian Andes.



Figure 74. *Cuphea bombonasae*, substrate for *Lejeunea topoensis*. Photo from <swbiodiversity.org>, through Creative Commons.

Adaptations

Lejeunea topoensis is green when fresh, forming large mats (Gradstein & Reiner-Drehwald 2007).

Reproduction

Lejeunea topoensis is very fertile, a benefit of its **autoicous** condition. The seta is **articulate** (having joint between two separable parts), probably contributing to its dispersal in running water. Its oil bodies are numerous (20-30 per cell) and thus small. The spores are green and germination is **precocious** (occurring early – germinating within capsule). The spores are irregular in shape with a surface covered with small granules and rosettes, perhaps giving the spores better flotation. Long-distance spore dispersal is quite possible, based on experiments by van Zanten and Gradstein (1988). This premise is supported by molecular phylogenetic studies in other species (Heinrichs *et al.* 2005, 2006).

Biochemistry

Ludwiczuk and Asakawa (2014) used fingerprinting of secondary metabolites to show that *Lejeunea topoensis* lacks isolepidozene, pinguisanes, fusicocanes, and monocyclofarnesanes that are found in many of the genera of the **Lejeuneaceae**. No vegetative propagules were observed, but fragmentation remains a possibility.

Lopholejeunea nigricans (Figure 75-Figure 78)

(syn. = *Heterolejeunea javanica*)

Lopholejeunea nigricans (Figure 75-Figure 78) has lots of synonyms (Staples & Imada 2006), an expected outcome for this species with lots of variation.



Figure 75. *Lopholejeunea nigricans* showing variation in leaf color. Photo by Jia-dong Yang, through Creative Commons.



Figure 76. *Lopholejeunea nigricans* habit showing leaf lobes. Photo by Michaela Sonnleitner, with permission.

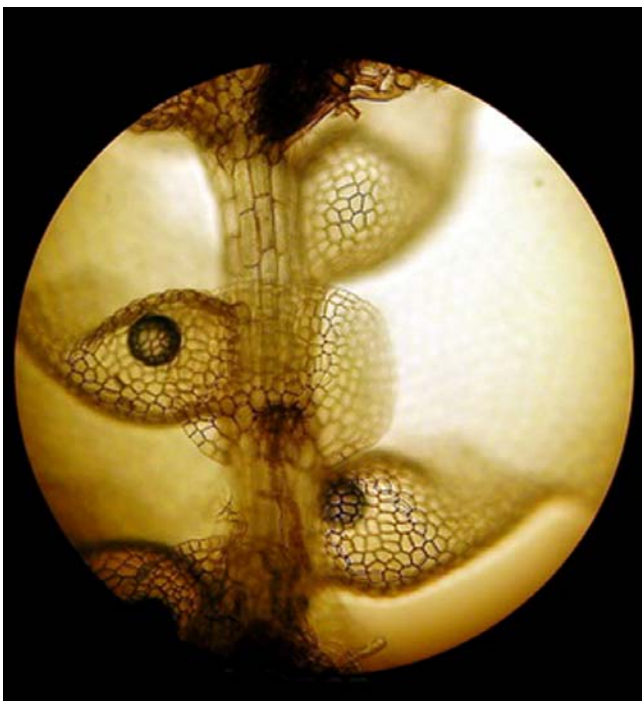


Figure 77. *Lopholejeunea nigricans* underleaves and lobes. Photo by Michaela Sonnleitner, with permission.

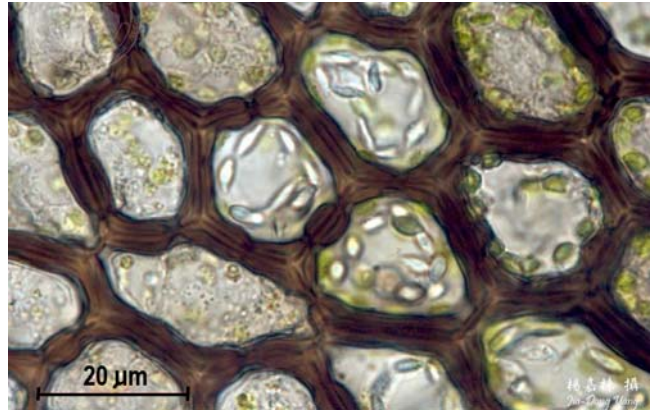


Figure 78. *Lopholejeunea nigricans* leaf cells showing oil bodies. Photo by Jia-dong Yang, through Creative Commons.

Distribution

Lopholejeunea nigricans (Figure 75-Figure 78) is a widespread pantropical species (Müller *et al.* 2011; Kornochalart *et al.* 2012; do Carmo & Peralta 2016). In Asia it is known from Bangladesh, Bhutan, Borneo, Cambodia, China, Hong Kong, India, Indonesia, Japan, Malaysia, Myanmar, Nepal, Papua New Guinea, Philippines, Taiwan, Thailand, Vietnam, and Yemen (Zhu & Gradstein 2005; Schwarz 2013). Kürschner and Ochrya (2003) found it in the Arabian Peninsula. Kornochalart *et al.* (2012) added much more information on the species in Thailand. Pócs and Chantanaorrapint (2016) reported it among non-epiphyllous species from several lowland areas in Thailand. Rajesh and Manju (2014) reported it from both lowlands and midlands in Kerala, India. In Sulawesi, an Indonesian island, Ariyanti and Gradstein (2007) found it in both lowland and montane regions. Zhu *et al.* (1998) added Zhejiang Province in China.

Haerida *et al.* (2010) found that *Lopholejeunea nigricans* (Figure 75-Figure 78) has a moderately wide distribution in West Java, occurring in both lowland and montane habitats (200-1700 m asl). Hodgetts *et al.* (2016) found it in the Eastern Region of Ghana. Hedderson *et al.* (2015) reported it from 1274 m asl in Mozambique and Wigginton (2001) from Malawi (up to 1635 m asl). It has been reported from Réunion Island off the eastern coast of Africa in the Indian Ocean (Ah-Peng & Bardat 2005) and the Central African island country of São Tomé and Príncipe. Carreon *et al.* (2016) added it to the Philippines. It also occurs in the Hawaiian Islands (Staples & Imada 2006).

In the Neotropics, *Lopholejeunea nigricans* (Figure 75-Figure 78) is known from Brazil (da Costa 2003; Peralta & Yano 2008; Visnadi 2009), Cocos Island in Costa Rica (Dauphin 1999), a tropical lowland cloud forest in central French Guiana (Gradstein 2006), Bolivia (Fuentes & Churchill 2005), and Peru (Drehwald 2003).

Aquatic and Wet Habitats

Lopholejeunea nigricans (Figure 75-Figure 78) occurred in a water spout of a tuff wall in the tropics (Ruttner 1955). Zhu and Gradstein (2005) reported that it occurs up to 1200 m asl in Asia, occasionally occurring on stones in running water. Hodgetts *et al.* (2016) reported it

from damp, shaded rocks by streams in Ghana, where it is locally abundant at 350-630 m asl. In India, Das and Sharma (2013) reported it from the bank of the River Boleswar at 70 m asl, as well as on loose moist soil of rock crevices. In Malawi, Wigginton (2001) found it on rocks beside rivers and streams. Müller *et al.* (2011) found it in the central African island country of São Tomé and Príncipe on exposed hardwood roots along a river. In Equatorial Guinea, Sánchez and Pérez (1998) found it both on rocks and bark near streams at 5-75 m asl.

The habitats of *Lopholejeunea nigricans* (Figure 75-Figure 78) are rather variable, including tree bases, roots, trunks, branches, shrubs, lianas, stumps, decaying logs, rocks, soil, occasionally on stones in running water, or on living leaves, from sea level to 2900 m asl (Zhu & Gradstein 2005). Hodgetts *et al.* (2016) found it forming small colonies in earthy rock crevices in the eastern region of Ghana.

Records for *Lopholejeunea nigricans* (Figure 75-Figure 78) on rock seem less frequent than epiphytic records except in or near water. Hedderson *et al.* (2015) found it on a small boulder in the *Streptocarpus* (Figure 80) forest on Mabu Mountain in Mozambique (Figure 81). Wigginton (2001) reported it from rocks, including granite, close to rivers. Müller *et al.* (2011) found it on soil and litter over volcanic rock where it received filtered light.

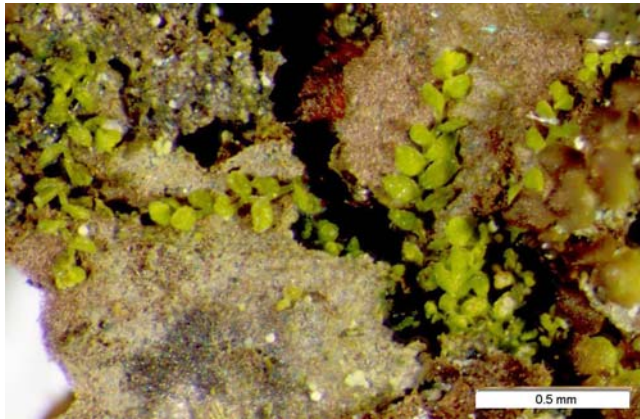


Figure 79. *Myriocoleopsis minutissima*, a species that grows on *Lopholejeunea nigricans*. Photo by Blanka Aguero, with permission.



Figure 80. *Streptocarpus* sp.; *Lopholejeunea nigricans* has been found in the *Streptocarpus* forest on Mabu Mountain in Mozambique. Photo by Mokkie, through Creative Commons.



Figure 81. Mount Mabu, Mozambique, where one can find *Lopholejeunea nigricans* on small boulders in the *Streptocarpus* forest. Photo by Conradie *et al.* 2016, through Creative Commons.

Adaptations

Sass-Gyarmati (2015) considered *Lopholejeunea nigricans* (Figure 75-Figure 78) to be the most variable species in the genus *Lopholejeunea*. For example, in some cases the lobules may be reduced (Zhu & Gradstein 2005). In a moist environment these modifications include reduced female bract lobules, weakly lacinate perianths, and very small leaf lobules. These modifications have resulted in the description of several species that are now considered synonyms.

Lopholejeunea nigricans (Figure 75-Figure 78) forms mats (Figure 75) (Batista & Santos 2016) and has a dark pigmentation (de Oliveira 2018). De Oliveira found that the dark pigmentation was significantly more frequent among liverworts in the canopy and significantly less at the tree bases. This dark coloration (Figure 75) presumably protects the canopy liverworts from the bright light there.

Reproduction

Lopholejeunea nigricans (Figure 75-Figure 78) has both monoicous and dioicous sexuality, giving it the advantages of both ease of fertilization and diversity of cross fertilization. He and Zhu (2011) found that the spore output from *Lopholejeunea nigricans* was 936-1254 from a tree trunk population. But it lacks asexual reproduction. De Oliveira (2018) suggested that the absence of overrepresentation of asexual propagules in canopy liverworts challenges the current views of bryophyte strategy, especially in the canopy. But Zhu and Gradstein (2005) found that *Lopholejeunea nigricans* accomplishes asexual reproduction with *caducous* (falling off easily) or fragmenting leaves.

Myriocoleopsis (Figure 79, Figure 87-Figure 91)

Myriocoleopsis (Figure 79, Figure 87-Figure 91) can be found in Andean streambeds (S. Robbert Gradstein pers. comm. 3 November 2011). Discovery of the molecular relationship of *Cololejeunea vuquangensis* with *Myriocoleopsis* has also placed the genus in Asia from Vietnam as *Myriocoleopsis vuquangensis* (Pócs 2010). For a discussion of species and their affinities in this genus, see Pócs (2010).

In this genus, the development of robust stems seems to be an adaptation to the periodic submergence it

experiences (Reiner-Drehwald & Gradstein 1995). Gradstein *et al.* (2018) noted that it exhibits **neoteny** with perpendicular leaf segmentation, absence of underleaves, and stem with only one row of medullary cells.

But *Myriocoleopsis* (Figure 79, Figure 87-Figure 91) also is epiphyllous (Yu *et al.* 2013), a habitat much more subject to drying conditions. Yu and coworkers described the rheophytic relatives of these epiphyllous species, including *Myriocoleopsis*. They found that the rheophytic taxa differed from epiphyllous species by having creeping stolons, robust stems, and long androecial spikes, and they considered these characters adaptive for running water. In addition to its epiphyllous substrata, the genus also occurs on rock (Gradstein *et al.* 2014), where these adaptations also could be beneficial, but especially on rocks in running water. Wilson *et al.* (2007) noted that rheophytes from unrelated taxonomic groups are driven to parallel development, resulting in similar adaptations to habitats of swiftly flowing water and regular flooding. These included long, robust stems with pinnate branching and numerous, small gametoeical branches on both sides of the stem.

Myriocoleopsis fluviatilis

(syn. = *Myriocoleopsis puiggarii*)

Distribution

Myriocoleopsis fluviatilis is endemic in Brazil (Gradstein & da Costa 2003; da Costa and dos Santos 2009), where it is classified as endangered (da Costa and dos Santos 2009; de Gasper *et al.* 2012), and thus threatened in the world (Hallingbäck and Hodgetts (2000).

Aquatic and Wet Habitats

Myriocoleopsis fluviatilis grows on rocks and shrubs that are periodically submerged in rivers (Gradstein & da Costa 2003). It is "very rare" and occurs at 150-1300 m asl in Brazil. It grows primarily on bare rocks or small rocky cliffs in the middle and along the edges of the River Pardo (Gradstein & Vital 1975). But it also grows on the bases of low shrubs, always in exposed places in or near running water, in or near a river with small waterfalls and rapids and a rocky bottom. The species is only found in exposed places in or near running water.

Myriocoleopsis fluviatilis colonizes bare rocks and small rocky cliffs in the middle and edges of the River Pardo (Gradstein & Vital 1975). The life form is a **mat**, which forms a dense, pale greenish growth. It has short, creeping, stoloniform primary stems and secondary stems that are ascending to erect, up to 3 cm long.

Continuous submergence is not suitable for the health of the plants. After a period of 5-15 days of submergence, leafy shoots die and only the stoloniferous stems survive (Gradstein & Vital 1975).

Adaptations

Gradstein *et al.* (2003a) ascribed the thicker stems with more numerous rows of cells to adaptations for the rheophytic habitat of *Myriocoleopsis fluviatilis*. This species is also neotenous, but I know of no experimental study that shows any rheophytic advantage to this

developmental strategy. It is common among epiphylls and among some aquatic **Lejeuneaceae**, as seen above.

Reproduction

Despite its autoicous sexuality, sporophytes develop only on plants that occur on emerged substrates, a phenomenon that has been noted for a number of other flowing-water bryophytes (Gradstein & Vital 1975). It has multicellular disciform gemmae that arise from the leaf surfaces, but these are rare.

Role

In the continuously wet habitat of this species, many diatoms find a suitable home on the liverworts: *Melosira* (in great number; Figure 82), *Gomphonema* (Figure 83), *Synedra* (Figure 84), *Cymbella* (Figure 85), and some *Naviculaceae* (Figure 86) (Gradstein & Vital 1975).

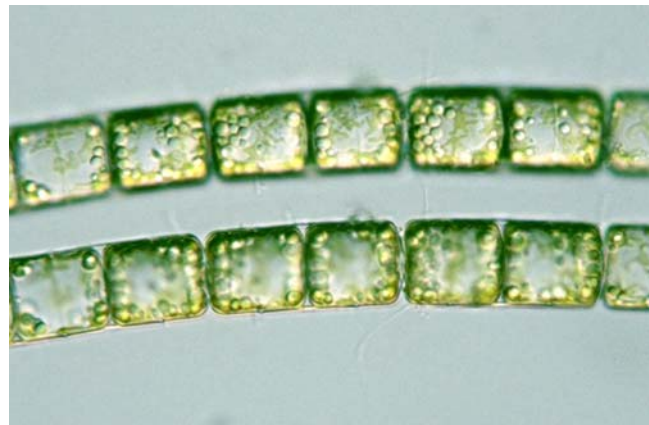


Figure 82. *Melosira* sp., a genus that can occur on *Lopholejeunea nigricans* in wet habitats. Photo by Yuuji Tsukii, with permission.



Figure 83. *Gomphonema* sp., a genus that can occur on *Lopholejeunea nigricans* in wet habitats. Photo by Yuuji Tsukii, with permission.

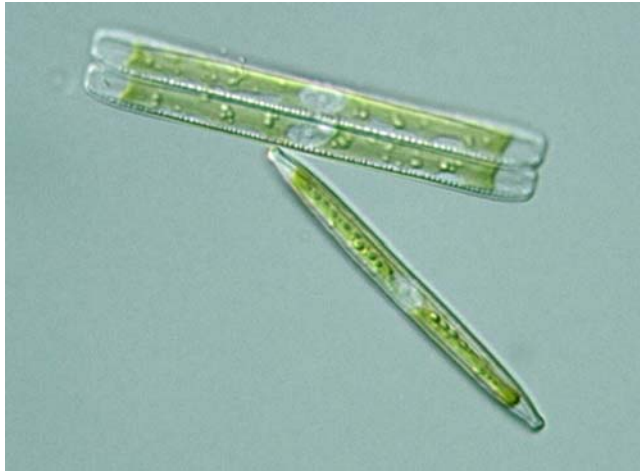


Figure 84. *Synedra cf. ulna*, in a genus that can occur on *Lopholejeunea nigricans* in wet habitats. Photo by Yuuji Tsukii, with permission.



Figure 85. *Cymbella cf. lanceolata*, in a genus that can occur on *Lopholejeunea nigricans* in wet habitats. Photo by Yuuji Tsukii, with permission.



Figure 86. *Navicula* (Naviculaceae), in a genus that can occur on *Lopholejeunea nigricans* in wet habitats. Photo by Phyto'pedia – The Phytoplankton Encyclopaedia Project, through Creative Commons.

Myriocoleopsis gymnocolea

(syn. = *Myriocoleopsis riparia*)

Distribution

Myriocoleopsis gymnocolea is known from Argentina (Reiner-Drehwald & Gradstein 1995; Gradstein & da Costa 2003), Bolivia (Gradstein *et al.* 2003b), Brazil (Reiner-Drehwald & Gradstein 1995; Gradstein *et al.* 2003a; dos Santos & da Costa 2010; do Carmo *et al.* 2018), and Ecuador (Gradstein & da Costa 2003; Gradstein *et al.* 2004; Pócs 2010; Benitez & Gradstein 2011; Gradstein 2020).

In Ecuador *Myriocoleopsis gymnocolea* occurs at 500–1300 m asl (León-Yanez *et al.* 2006; Gradstein 2020), 100–1300 m asl in Brazil (Gradstein & da Costa 2003), 100–1300 m asl in Argentina (Reiner-Drehwald 1995).

Aquatic and Wet Habitats

Like *Myriocoleopsis fluviatilis*, this species occupies periodically submerged rocks in rivers (Gradstein & da Costa 2003). Reiner-Drehwald (1995) found *Myriocoleopsis gymnocolea* above a waterfall, where it is sometimes submerged, but primarily on rocks that are periodically submerged. The species occurs in the center and on the banks of rivers, typically in rapid currents. The rapid currents provide splash that keep it moist in its emergent positions.

The species can occur as an epiphyte at the base of small shrubs and on river banks, occupying a niche similar to that of *M. fluviatilis* (Reiner-Drehwald 1995).

Adaptations

Myriocoleopsis gymnocolea exhibits traits that we have seen in previous rheophytic members of the **Lejeuneaceae**. It is **monoicous** and neotenous (Kraichak 2012), the latter a character that needs further investigation to determine its advantages in the aquatic environment. In fast water, this may permit it to remain small, thus creating little or no drag, while also permitting sexual structures to develop. The guarantee of a wet film over the plants at the right time would facilitate its ability to transfer sperm from antheridia to archegonia in this monoicous species.

Myriocoleopsis gymnocolea has thin stems with only 5 rows of cortical cells (Reiner-Drehwald & Gradstein 1995). Yu *et al.* (2014) considered certain remarkable characters to include its dimorphic stems with creeping stolons and erect leafy axes arising from them, reduced lobules, and long male spikes. The reduced lobules are often expressed in rheophytic species. In addition, they noted the absence of underleaves, another character that could be part of the neotenous development of many aquatic **Lejeuneaceae**. It might be interesting to examine the differences in **hydroxyproline** (component of plant hormones essential for growth, cell differentiation, and defense) concentrations surrounding the leaves in the aquatic environment (see Basile 1967). Could it be that the condition of immersion changes the concentrations of this component, thus affecting development? This could be accomplished by reduced diffusion in water.

Reproduction

Myriocoleopsis gymnocolea is **monoicous** (Kraichak 2012).

Role

Myriocoleopsis gymnocolea serves as a suitable substrate for diatoms (Figure 82-Figure 86) and other algae (Reiner-Drehwald 1995).

Biochemistry

Despite its small size, Ludwiczuk *et al.* (2013) examined chemical relationships in the **Lejeuneaceae**, including this species. *Myriocoleopsis gymnocolea*, like a number of members of this family, has only pinguianes and not isolepidozenes, fusicocanes, or monocyclofarnesanes. The researchers considered this chemistry to be a marker of the subtribe **Cololejeuneinae**.

Like other members of the genus, *Myriocoleopsis gymnocolea* lacks lepidozenes, fusicocanes, monocyclofarnesanes, having only pinguianes (Coulerie *et al.* 2015), strengthening its relationship to those species of **Lejeuneaceae** not placed in *Myriocoleopsis*.

Myriocoleopsis minutissima (Figure 79, Figure 87-Figure 91)

(syn. = *Cololejeunea minutissima*)

Distribution

Myriocoleopsis minutissima (Figure 79, Figure 87-Figure 91) was originally described as a species of *Cololejeunea* (see Chapt. 1-7 in this volume), but has been moved to *Myriocoleopsis* (Yu *et al.* 2014). It is a widespread pantropical species (Cañiza *et al.* 2016; Hodgetts *et al.* 2020) that is distributed in North America from Virginia and Tennessee to Florida and Texas (Stotler & Crandall-Stotler 2017). It is also known from Central America, South America, western and central Europe, central and eastern Asia, and Australia (Stotler & Crandall-Stotler 2017; Hugonnot (2019), southern Africa and South Indian Ocean islands (Bischler 2004; Hugonnot 2019).



Figure 87. *Myriocoleopsis minutissima* in a large patch on rock. Photo by Hugues Tinguy, with permission.

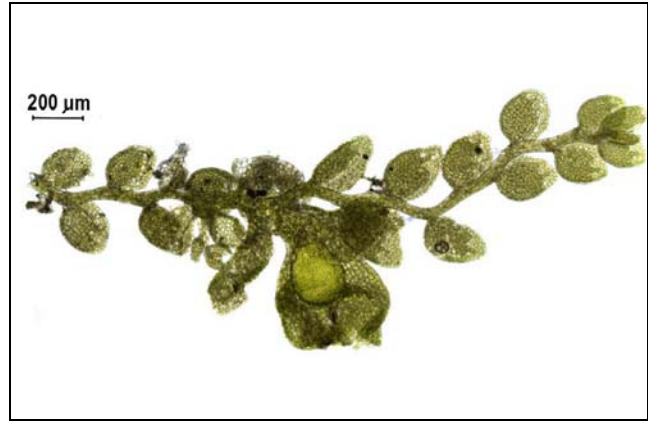


Figure 88. *Myriocoleopsis minutissima* with perianth. Photo by Hugues Tinguy, through Creative Commons.

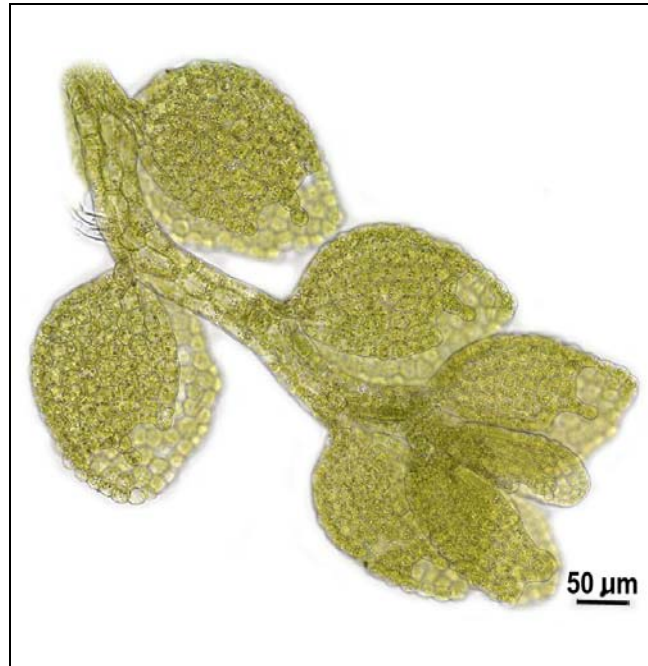


Figure 89. *Myriocoleopsis minutissima*, showing large leaf lobes. Photo by Hugues Tinguy, through Creative Commons.

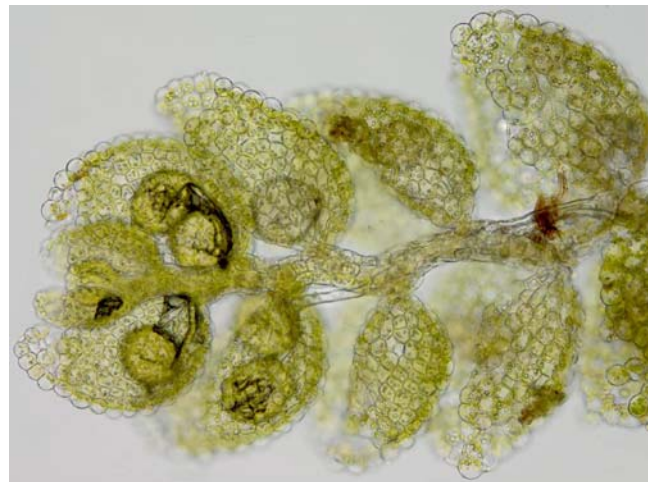


Figure 90. *Myriocoleopsis minutissima* showing large lobes. Photo by Blanka Agüero, with permission.



Figure 91. *Myriocoleopsis minutissima* leaf cells with oil bodies. Photo by Blanka Agüero, with permission.

In Europe *Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) exhibits a Mediterranean-oceanic character (Düll 1983). European records include Madeira Island (Schwarz & Schumm 2019), Montseny massif in the Iberian Peninsula (very rare; Sáez *et al.* 2018), Corsica (Hugonnot 2019), Sicily (Dia *et al.* 2017), and France (Hugonnot *et al.* 2017; Hugonnot & Simont 2018). It is rare in the Mediterranean region, occurring in the Azores, Canary Islands, Cape Verde Islands, Madeira, Croatia, Greece, Italy, Montenegro, Portugal, Serbia, and Spain (Hugonnot 2019).

In Asia *Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) is known from Vietnam (Shu *et al.* 2016), Singapore (Zhu *et al.* 2018), southern Thailand (Pócs and Chantanaorrapint 2016), Lebanon in southwestern Asia (Hugonnot 2019), and Sabah in Malaysian Borneo (Pócs *et al.* 2020).

Wigginton (2018) found *Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) in the flora of Africa and the African islands. Enroth *et al.* (2019) included it in the checklist of the Taita Hills region of Kenya, noting that it is widely distributed in sub-Saharan Africa. Hugonnot (2019) included it in the flora of Algeria and Tunisia in northern Africa.

In Central and South America, Ristow *et al.* (2015) reported *Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) from Brazil. It occurs in Ecuador (Gradstein 2020) and Paraguay (Cañiza *et al.* 2016). Schäfer-Verwimp and van Melick (2016) reported it from Jamaica and Stotler and Crandall-Stotler (2017) from Bermuda.

Myriocoleopsis minutissima (Figure 79, Figure 87-Figure 91) has a varied altitudinal range. It has a known altitudinal range of 1500-2800 m asl in Ecuador (Gradstein 2020). In Malaysian Borneo, it occurs in the mossy cloud forest at 1900-1940 m asl (Pócs *et al.* 2020). On the Iberian Peninsula it occurs at 750 m. It is known from lowlands in Thailand, where it has expanded into the warm temperate, oceanic areas (Pócs & Chantanaorrapint 2016).

Aquatic and Wet Habitats

Myriocoleopsis minutissima (Figure 79, Figure 87-Figure 91) has little claim to the aquatic environment, but

it is at least tolerant of a humid environment, living in "well preserved" humid riparian forests of Paraguay, where it is an epiphyte on the corky bark of *Chloroleucon tenuiflorum* (Figure 92) (Cañiza *et al.* 2016). Most records for *Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) present it as an epiphyte.



Figure 92. *Chloroleucon tenuiflorum*, a species of humid riparian forests of Paraguay and substrate for *Myriocoleopsis minutissima*. Photo by CECOAL, through Creative Commons.

Reproduction

Myriocoleopsis minutissima is **autoicous**. Images of perianths are in Figure 93-Figure 95. It produces large gemmae (Figure 96) with 16-48 cells, mostly on the lobes, but sometimes on the leaf periphery.

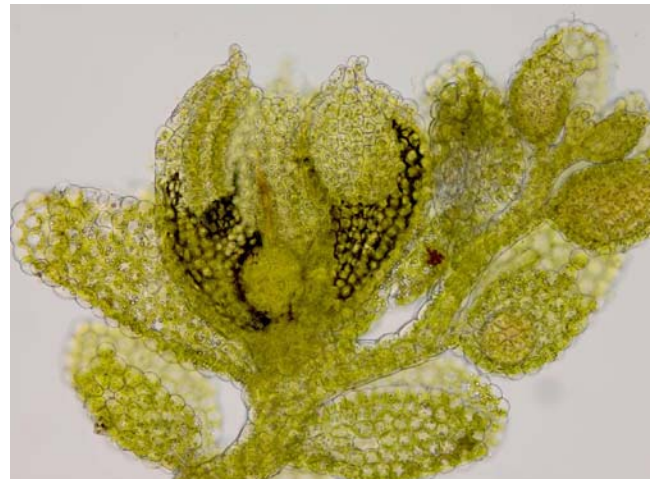


Figure 93. *Myriocoleopsis minutissima* with perianths and archegonia. Photo by Blanka Agüero, with permission.

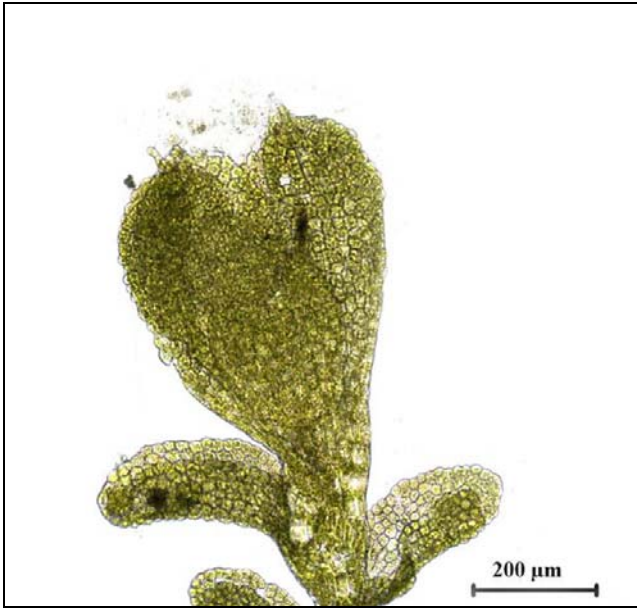


Figure 94. *Myriocoleopsis minutissima* perianth. Photo by Hugues Tinguy, through Creative Commons.

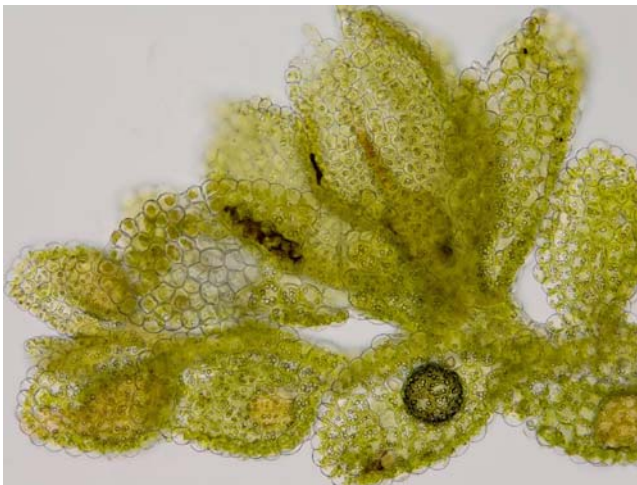


Figure 95. *Myriocoleopsis minutissima* with archegonium showing reddish neck. Photo by Blanka Aguero, with permission.

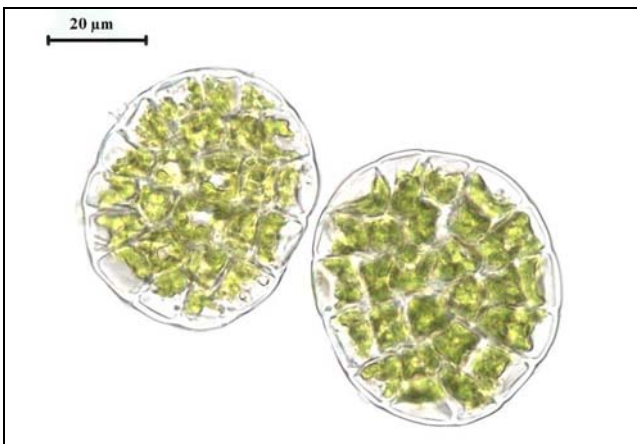


Figure 96. *Myriocoleopsis minutissima* gemmae. Photo by Hugues Tinguy, through Creative Commons.

Myriocoleopsis minutissima subsp. *myriocarpa*

Distribution

Like the subspecies *minutissima* (Figure 79, Figure 87-Figure 91), *Myriocoleopsis minutissima* subsp. *myriocarpa* is widespread in the tropics (Hodgetts *et al.* 2020). It is thus pantropical, with records in Europe, North America, and South America. Gradstein (2020) found it in Ecuador at 100-3000 m asl.

Aquatic and Wet Habitats

In Florida, USA, *Myriocoleopsis minutissima* subsp. *myriocarpa* occurs in mahogany (*Swietenia mahogani*) hammocks (Figure 97), in Everglades National Park (Schuster 1971; Zona & Sadle 2017). These are islands of trees in wetlands or on slopes between wetlands and uplands. Those serving as home for this species are low hammocks, surrounded by marshland (Schuster 1971).



Figure 97. *Swietenia mahogani* hammock, Everglades. Photo by Miguel Vieira, through Creative Commons.

Myriocoleopsis vuquangensis

Distribution

Myriocoleopsis was considered a Neotropical genus until Pócs (2010) reported it from Vietnam in southeast Asia. Wilson *et al.* (2007) used molecular evidence to identify similarities of *Cololejeunea vuquangensis* to the Neotropical *Myriocoleopsis* (Figure 79, Figure 87-Figure 91), causing its transfer to *Myriocoleopsis vuquangensis*. In the Neotropics it is known from the Nangaritza River in Ecuador (Pócs 2010).

Aquatic and Wet Habitats

This species has more qualifications as a wetland species, living as a rheophyte on twigs of the euphorbiaceous shrub *Homonoia riparia* (Figure 98) (Pócs 2010). In its known Asian home, this species of *Myriocoleopsis* (Figure 79, Figure 87-Figure 91) exists on the bush vegetation on riverbed shoals where it gets inundated twice a year during the monsoons. These shrubs occur in groups on river banks, rocky (fast-running) stream beds, and along the coast. Soil in these locations is usually

(temporarily) inundated, in some areas for months, creating a humid or wet environment.



Figure 98. *Homonoia riparia*, a rheophyte that can support *Myriocoleopsis vuquangensis* on its twigs, where they are occasionally inundated. Flora of Peninsular India, through Creative Commons.

Adaptations

Like other *Myriocoleopsis* (Figure 79, Figure 87-Figure 91) species, *Myriocoleopsis vuquangensis* has both creeping stolons and erect leafy stems (Pócs 2010).

Reproduction

Myriocoleopsis vuquangensis is monoicous, with male branches and "very abundant" perianths (Pócs 2010).

Ptychanthus striatus var. *intermedius* (see Figure 99-Figure 101)

(syn. = *Ptychanthus intermedius*)

Although *Ptychanthus striatus* var. *intermedius* was described in 1934 by Verdoorn as *Ptychanthus intermedius*, I have not been able to find much ecological information on it under either name, so the information contained here is for the species *Ptychanthus striatus* (Figure 99-Figure 101).



Figure 99. *Ptychanthus striatus*. Photo by Jia-dong Yang, through Creative Commons.



Figure 100. *Ptychanthus striatus*, dry, growing on a vertical surface in Bhutan. Photo by David Long, with permission.



Figure 101. *Ptychanthus striatus* ventral side showing underleaves and perianths. Photo by Boon Chuan Ho, courtesy of Rob Gradstein.

Distribution

Ptychanthus striatus (Figure 99-Figure 101) is a variable species (Gradstein 1985). Singh and Singh (2016) noted that the species *Ptychanthus striatus* has many synonyms. He (1997) considered it to have worldwide distribution, especially in the Palaeotropics (Gradstein 1985), but it appears to be absent in the Western Hemisphere. It was considered to occur in warm temperate regions including South Africa, the Himalayas, Japan, and Australasia (Gradstein & Inoue 1980). Pócs *et al.* (2007) summed its distribution up as widespread in the whole Indopacific region.

Gradstein and Inoue (1980) also included Central Africa to the western Pacific, with several records indicating that *Ptychanthus striatus* (Figure 99-Figure 101) occurs in Africa (Bizot & Pócs 1974; Frahm 1994; Braun *et al.* 2004; Müller 2006). Müller (2006) even considered it to be widely distributed in tropical Africa. However, using both morphology and molecular characteristics, Ahonen *et al.* (2005) and Pócs and Luke (2007) considered all African records of *Ptychanthus striatus* to be the separate species *Ptychanthus africanus*.

Thiers (1990) and Haerida *et al.* (2010) reported *Ptychanthus striatus* (Figure 99-Figure 101) from

Australia. It also has been found in Java and Sumatra (Verdoorn 1933), Peninsular Malaysia, Borneo, Sulawesi, Moluccas, Philippines, West Irian, New Zealand, Pacific Islands, India, Sri Lanka, Taiwan, Indochina, and China (Haerida *et al.* 2010). Kornochalert *et al.* (2012) reported its presence in Thailand. Additional Asian records include China (He 1997), including Sichuan (Piippo *et al.* 1997) and Yunnan (Han *et al.* 2010), Western Ghats in India (Pócs *et al.* 2007), and southern India (as *Spruceanthus wiggintonii*; Wang *et al.* 2014). The finding that *Ptychanthus africanus* replaces it in Africa and the Himalayas suggests that the remaining populations should be re-examined to determine whether they indeed all belong to *Ptychanthus striatus* (Figure 99-Figure 101).

Haerida *et al.* (2010) reported *Ptychanthus striatus* (Figure 99-Figure 101) in both lowlands and montane habitats at elevations ranging 1000-2400 m asl. Kornochalert *et al.* (2012) reported its range from 50-2480 m asl in Thailand. Frahm (1994) reported it at less than 1500 m on Mt. Kahuzi, Zaire. Pócs *et al.* (2007) found it at 2350 m asl in the Western Ghats in India. It even is considered common in the Himalayas at altitudes below 4000 m asl (Zhu & Long 2003), but those records might actually represent *Ptychanthus africanus* (see Singh & Singh 2008). Hence, the altitudinal ranges described here need to be verified following a more thorough assessment of the species.

Aquatic and Wet Habitats

It doesn't appear that *Ptychanthus striatus* (Figure 99-Figure 101) is particularly aquatic. Ruttner (1955) listed *Ptychanthus striatus* var. *intermedius* as aquatic in the tropics. Thiers (1990) reported *Ptychanthus striatus* (Figure 99-Figure 101) as growing especially near waterfalls (Figure 102) and steep escarpments in Australia, where the species forms large, "festooning" bodies in the mist that keeps these areas humid. In India, Singh and Singh (2008) reported the species *Ptychanthus africanus* as rare from moist places where it grew on rocks on a thin layer of soil.

Ptychanthus striatus also occurs in a variety of terrestrial habitats, including grassland (Gradstein & Inoue 1980), forest epiphytes (Müller 2006; Pócs *et al.* 2007), and on rocks (Kornochalert *et al.* 2012).

Several studies have examined the impact of heavy metals on *Ptychanthus striatus* (Figure 99-Figure 101). Shakya *et al.* (2008a, b) found that the metal accumulation in *P. striatus* increased with metal concentration in the water. Copper had a significant inhibition of both chlorophyll *a* and *b*. Similarly, zinc and lead accumulation caused a significant decrease in chlorophyll. They suggested that the greater loss of chlorophyll from *P. striatus* than from moss species in the experiments may have been caused by relatively more K⁺ efflux in the leafy liverwort than in the mosses. However, there was no significant decrease in chlorophyll when the liverworts were exposed to copper, zinc, and lead together. The metals zinc and copper exhibited leaching in *P. striatus*, indicating that they occur on exchange sites under hydrated conditions. Competition for these exchange sites might explain the lowered toxicity when the three metals were provided together. These results are consistent with the presence of the species only in clean sites, not those

contaminated with heavy metals. This study has led to the use of *P. striatus* and other bryophytes in determining heavy metal loading near roads (Shakya *et al.* 2012).

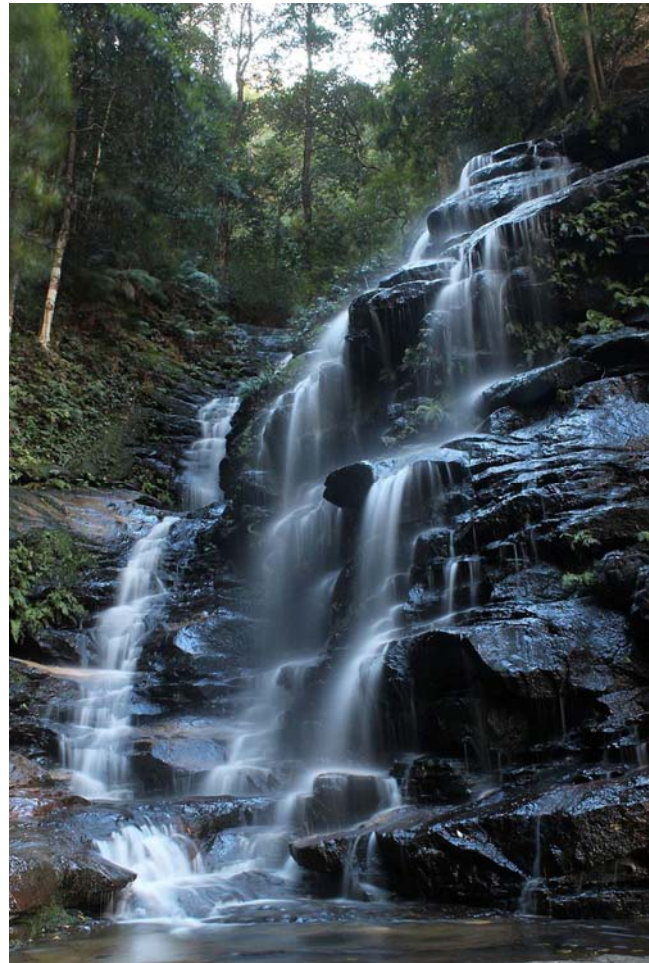


Figure 102. Waterfalls at Wentworth, Australia, a habitat where one might find *Ptychanthus striatus*. Photo by Jack Brogan, through Creative Commons.

Adaptations

Ptychanthus striatus (Figure 99-Figure 101) is a robust species, up to 10 cm long, contrasting with the many tiny members of the *Lejeuneaceae*. These plants are either pendent or stand up away from their substrate.

Reproduction

Ptychanthus striatus is autoicous (see perianths in Figure 103) (Haerida *et al.* 2010), contrasting with its sister species, *Ptychanthus africanus*, in which dioicous specimens "are not rare" (Bizot & Pócs 1974). The spore output of *Ptychanthus striatus* is high (up to 5750) among the Chinese *Lejeuneaceae* (He & Zhu 2011).

Biochemistry

Ptychanthus striatus (Figure 99-Figure 101) has 6-10 grayish-yellow oil bodies per cell (Figure 104) (Singh *et al.* 2008). These presumably are sites of concentrations of a number of secondary compounds. This species has one of the longest lists of biochemical studies. Such studies include the isolation and description of structures of a number of sesquiterpenoids (Takeda *et al.* 1982, 1983;

Nabeta *et al.* 1998, 2000; Wu *et al.* 2015), isolation and structure of diterpenoids such as ptychantins with elaboration of their synthetic pathway (Hashimoto *et al.* 1995, 1999; Hagiwara & Nozawa 2009; Wu *et al.* 2015). Like many of the **Lejeuneaceae**, it produces several pinguicane-type sesquiterpenes and striatene, but is poor in diterpenes (Gradstein *et al.* 1985).



Figure 103. *Ptychanthus striatus* with perianths. Photo by Jan-Peter Frahm, with permission.

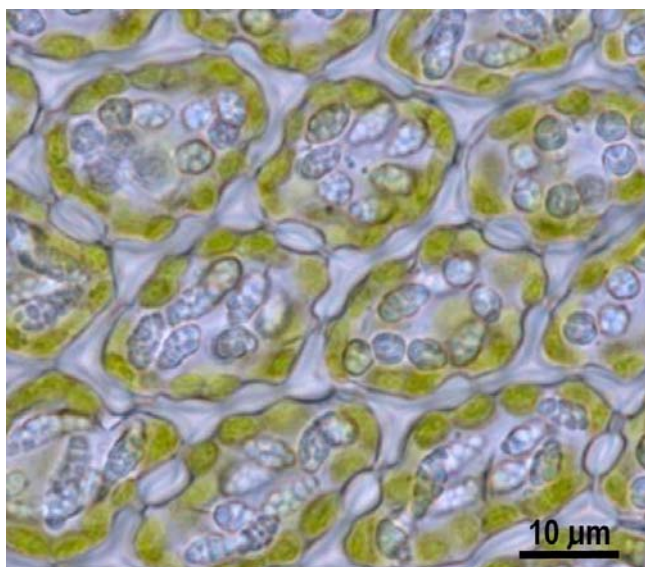


Figure 104. *Ptychanthus striatus* leaf cells with oil bodies. Photo by Jia-dong Yang, through Creative Commons.

In addition to the exploration of secondary compounds, other biological pathways were explored. Karunagoda *et al.* (Karunagoda *et al.* 2001, Karunagoda & Nabeta 2004) elucidated the biosynthesis of the phytol side-chain of chlorophyll *a* using this species.

Ptychanthus striatus (Figure 99-Figure 101) is among the liverworts that have shown antidiabetic activity and antioxidant activity (Mukhia *et al.* 2015), as well as antifungal activity against human pathogens (Dikshit *et al.* 1982). Other fungal interaction studies seem to be lacking.

Schusterolejeunea inundata

(syn. = *Cladocolea inundata*, *Lejeunea inundata*, *Potamojeunea sprucei*)

Schusterolejeunea inundata is the only known species in *Schusterolejeunea* (Grolle 1980; Söderström *et al.* 2016).

Distribution

Schusterolejeunea inundata is a rare Amazonian endemic (Gradstein & Costa 2003; Gradstein & Costa 2003; Dauphin *et al.* 2008; Désambré *et al.* 2014; Costa *et al.* 2017; Sierra *et al.* 2018). It was known only along the Rio Negro of Brazil (da Silva 2019) and Venezuela (Sierra *et al.* 2018). The latest records show it from Venezuela (Moreno 1992; Söderström *et al.* 2020), Brazil (Gradstein & da Costa 2003; da Silva 2019), the Guianas (Gradstein & Hekking 1985; Gradstein *et al.* 1990; Gradstein & da Costa 2003; Söderström *et al.* 2020), Surinam (Söderström *et al.* 2020), Guyana (Söderström *et al.* 2020), Ecuador (Gradstein *et al.* 2018), and Peru (Gradstein & da Costa 2003; Söderström *et al.* 2020).

Aquatic and Wet Habitats

Schusterolejeunea inundata occurs in Andean streambeds as a rheophyte on branches of trees, roots, and rocks that occur in these beds in undisturbed lowlands up to 100 m asl (Gradstein *et al.* 1990; Gradstein & da Costa 2003). Hallingbäck and Hodgetts (2000) considered it an indicator of undisturbed lowland rainforest.



Figure 105. *Schusterolejeunea inundata* with sediments imbedded in it from inundation. Photo from BioPortal, through Creative Commons.

Schusterolejeunea inundata occurs with *Ceratolejeunea temnantha* (Figure 106) in large mats in seasonal habits on rocks, lower portions of tree trunks, twigs, and roots in running water of seasonally inundated black-water forest habitats. It can also occur on river banks (Gradstein *et al.* 2011). Gradstein *et al.* (2001) described it as a liverwort of lakes and rivers in Amazonia.

Adaptations

Schuster (1990) considered the genus *Schusterolejeunea* to be among the most **apomorphic** (having novel evolutionary trait) of the liverwort genera (see also Vanderpoorten *et al.* 2010, 2012; Gradstein *et al.*

2011). This is among the **stenotypic** genera (those with 1-3 species) (Schuster 1990; Désambré *et al.* 2014). Gradstein *et al.* (2011) contend that habitat specialization drives the evolution of unusual characters in such species as *Schusterolejeunea inundata*. Such characters in this species are highly specialized for living in and out of water as the water level changes, permitting them to live on emergent vegetation and river banks.



Figure 106. *Ceratolejeunea temnantha* on tree roots, a habitat also occupied by *Schusterolejeunea inundata*. Photo by Juan Carlos Villarreal, with permission.

Gradstein *et al.* (2001) describe the rheophytic adaptations of *Schusterolejeunea inundata*. These include creeping rhizomes, thick stems, and "superfertility" (Thiers 1988). The species lacks **neoteny**, a common character of epiphylls, but one that seems to be mostly absent among species that become submersed.

Summary

Most of the **Lejeuneaceae** are not true aquatics, but many do occur in wetlands and very humid habitats. Splash from waterfalls and rapids in streams are often the source of such water. Many have wide substrate tolerances, particularly for both rocks and bark, and many also occur as epiphylls. And many, like *Lejeunea lamacerina* and *L. patens*, have a wide moisture tolerance, from drying out to being submersed for short periods. This variety of habitat conditions leads to environmental forms that confound understanding of the taxonomy. Most **Lejeuneaceae** form mats, but some species are larger and have other growth forms. Many are dioicous, thus seldom producing sporophytes, but fragmentation and gemmae often provide an adaptive alternative. Their moisture retention allows many of them to provide suitable habitats for diatoms.

There seem to be almost no reports of these from polar regions, but they do often occur on mountains, some to relatively high elevations.

Drepanolejeunea hamatifolia is a desiccation-sensitive hyperoceanic species that is restricted to rocky cascades and similarly wet habitats. Humidity maintenance is sometimes achieved by growing on other bryophytes.

Harpalejeunea molleri is one of the species from moist habitats such as swamps, but not typically submerged. Many species, like *Lejeunea lamacerina* in mountain streams, are seasonally submersed.

Some *Myriocoleopsis* species can occupy rocks in streams that become inundated, but they occur more commonly as epiphytes in moist forests, mahogany hammocks, and other damp locations.

Ptychanthus striatus can form substrata suitable for nitrogen-fixing **Cyanobacteria**, as can a number of other moist-habitat bryophytes. Lobules/lobes in some, perhaps many, of the **Lejeuneaceae** can serve as watery habitats for rotifers.

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Lars Söderström provided me with the current acceptable names for a number of older taxa and helped me sort out some of the species, varieties, and subspecies.

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CHAPTER 1-9

AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: PORELLACEAE

TABLE OF CONTENTS

Porellales – Suborder Porellineae	1-9-2
Porellaceae	1-9-2
<i>Porella cordaeana</i>	1-9-2
<i>Porella pinnata</i>	1-9-9
<i>Porella platyphylla</i>	1-9-15
<i>Porella platyphylloidea</i>	1-9-24
Summary	1-9-27
Acknowledgments	1-9-27
Literature Cited	1-9-27

CHAPTER 1-9

AQUATIC MARCHANTIOPHYTA,

CLASS JUNGERMANNIOPSIDA,

ORDER PORELLALES: PORELLACEAE



Figure 1. *Porella pinnata* on *Nyssa ogeche*, indicating the high water line. Many of the species of **Porellales** included here occur in this floodwater zone. Photo by Christine Davis, with permission.

Porellales – Suborder Porellineae

Porellaceae

Porella cordaeana (Figure 2-Figure 6)

(syn. = *Madotheca cordaeana*, *Madotheca rivularis*; Figure 2-Figure 6)

Porella cordaeana is a species with many more synonyms that I won't list here.

Distribution

It is a circumboreal species (Dia & Not 1991; Schofield *et al.* 2002), with a highly disjunctive

distribution in the Northern Hemisphere. It occurs in Europe, northern Africa, Asia, and western North America from Alaska south to California and northern Mexico (Clark 1953; Piippo & Norris 1996). It has been reported from Finland (Sallantausta & Syrjänen 2005), Serbia (Sabovljević & Cvetić 2003; Cvetić & Sabovljević 2005; Papp *et al.* 2012), Yugoslavia (Sabovljević 2000; Cvetić & Sabovljević 2005), the Carpathians and Sudety Mountains of Poland (Górski *et al.* 2017), Estonia (protected; Vellak & Ingerpuu 2012), Bulgaria (Ganeva & Natcheva 2003), South Bohemia (Kučera *et al.* 2013), Montenegro (Dragičević *et al.* 2007), Switzerland (Meier *et al.* 2013), Croatia (Papp *et al.* 2013), France (Casas & Barrón 2003), Italy (Aleffi 2005; Düll 2006; Campisi *et al.* 2008; Aleffi *et*

al. 2009), Spain (Brugués *et al.* 2002; Casas & Barrón 2003; Elías *et al.* 2006); Portugal (Vieira *et al.* 2012), Greece (Blockeel 1991); Turkey (Gökler 1998; Kürschner 1999; Ursavaş & Abay 2009), Faeroe Isles (Damsholt 2017), and Madeira and Canary Islands (Ekstein 2010). In North America, it has been reported from British Columbia, Canada (Hong 1981; Schofield 1988), and Nevada, USA (Hong 1983).



Figure 2. *Porella cordaeana*, a circumboreal leafy liverwort. Photo by Hugues Tinguy, with permission.



Figure 3. *Porella cordaeana*, showing its bright green color. Photo by Jiří Kameníček, with permission.



Figure 4. *Porella cordaeana* in a moist condition. Photo by Hugues Tinguy, with permission.



Figure 5. *Porella cordaeana* ventral side. Photo by Hugues Tinguy, with permission.

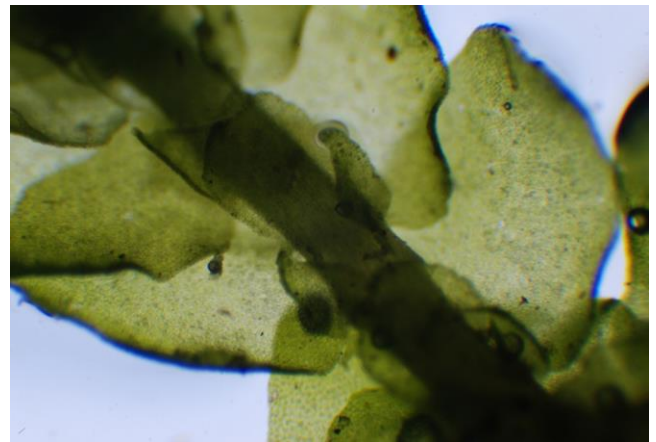


Figure 6. *Porella cordaeana* showing underleaves and lobes. Photo by J. C. Schou, with permission.

Aquatic and Wet Habitats

Porella cordaeana (Figure 2-Figure 6) is occasionally submerged, on rocks in fast water (Figure 7) (Watson 1919, as *Scapania madothca porella*). It occurs in the Danube around Ulm, Germany (Muhle *et al.* 1974-1979), and in the *Platyhypnidium* (Figure 8)-*Fontinalis antipyretica* (Figure 9) association, Thuringia, Germany (Marstaller 1987). Similarly, Koponen *et al.* (1995) consider it to be aquatic in Finland. It occurs in the Iskur River, Bulgaria, and its main tributaries in Bulgaria (Papp *et al.* 2006b). In Montenegro, it is reported at a stream, on bark of *Fagus* (Figure 18) in the Tara River canyon and Durmitor area (Papp & Erzberger 2011).

Porella cordaeana (Figure 2-Figure 6) is among the bryophytes in Portuguese watercourses (Vieira *et al.* 2012). Sallantausta and Syrjänen (2005) similarly found it on stones in brooks in Finland, where one could also find *Scapania undulata* (Figure 10), *Lejeunea cavifolia* (Figure 11), and *Dichelyma* (Figure 12) species. In Central Europe, Jusik *et al.* (2015) found it in calcareous mountain and upland streams, accompanied by *Chiloscyphus polyanthos* (Figure 13) and *Pellia endiviifolia* (Figure 14).



Figure 7. *Porella cordaeana* on emergent rock in stream. Photo by Hugues Tinguy, with permission.



Figure 10. *Scapania undulata*, a species that accompanies *Porella cordaeana* in streams in Finland. Photo by Hermann Schachner, through Creative Commons.

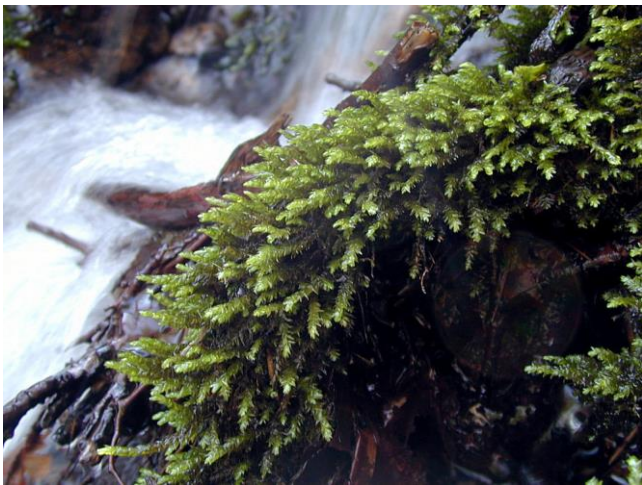


Figure 8. *Platyhypnidium riparioides*, a species characteristic of some streams where one can find *Porella cordaeana* in Europe. Photo by Michael Lüth, with permission.



Figure 11. *Lejeunea cavifolia*, a species that accompanies *Porella cordaeana* in streams in Finland. Photo by Dick Haaksma, with permission.



Figure 9. *Fontinalis antipyretica*, a species characteristic of some streams where one can find *Porella cordaeana* in Europe. Photo by Chris Wagner, through Creative Commons.



Figure 12. *Dichelyma pallescens*; *Dichelyma* sp. accompanies *Porella cordaeana* in streams in Finland. Photo by Blanka Aguero, with permission.



Figure 13. *Chiloscyphus polyanthos*, a species that accompanies *Porella cordaeana* in calcareous mountain and upland streams of Central Europe. Photo by Hermann Schachner, through Creative Commons.



Figure 14. *Pellia endiviifolia*, a species that accompanies *Porella cordaeana* in calcareous mountain and upland streams of Central Europe. Photo by David T. Holyoak, with permission.

In España, Brugués *et al.* (2002) reported *Porella cordaeana* (Figure 2-Figure 6) from stones in water courses, where it was among the most common bryophytes and one of the two most common liverworts. These were mostly, however, on the edge of the ravines on slopes with a mix of soil and rock. Aleffi *et al.* (2009) reported it from moist rocks in southeastern Italy. Papp and coworkers (Papp & Erzberger 2005; Papp *et al.* 2012) found it on siliceous stones in a stream in southwest Serbia, as well as on the streambank.

In somewhat less aquatic conditions in the UK, Rothero (2010) found *Porella cordaeana* (Figure 2-Figure 6) on the wall of old river "workings" in a flood plain. Papp *et al.* (2006b) reported it from the zone of water level fluctuations along the Iskur (Iskar) River.

In North America, Nichols (1938) reported it from submerged rocks in Cedar Creek in the Huron Mountain region of Michigan, USA.

Although *Porella cordaeana* (Figure 2-Figure 6) can be fully aquatic, it seems to be more a species of high moisture, tolerating occasional submersion. Kürschner (1999) even considered it to be an indicator of better moisture conditions when it occurred as an epiphyte in Mediterranean *Pinus* forests (Figure 15) and *Platanus*

orientalis (Figure 16) alluvial forests of Turkey. Dia and Not (1991) considered it mesophytic. Papp *et al.* (2012, 2013) reported it "at" the stream, but also found it on bark of the beech (*Fagus*; Figure 18), on exposed as well as shaded siliceous rock, in limestone grassland, and on decaying wood. Papp and Erzberger (2007) similarly found it on bark of *Salix*, as well as *Fagus* bark (Figure 17) in eastern Serbia. Dragičević *et al.* (2007) found *P. cordaeana* on the bark of a decaying tree in the *Abies-Fagus* forest (Figure 19) of Montenegro.



Figure 15. *Pinus pinea* in Spain, the type of forest where *Porella cordaeana* can occur as an epiphyte in Mediterranean areas. Photo by Ori Fragman-Sapir, Board of Trustees, RBG Kew, through Creative Commons.

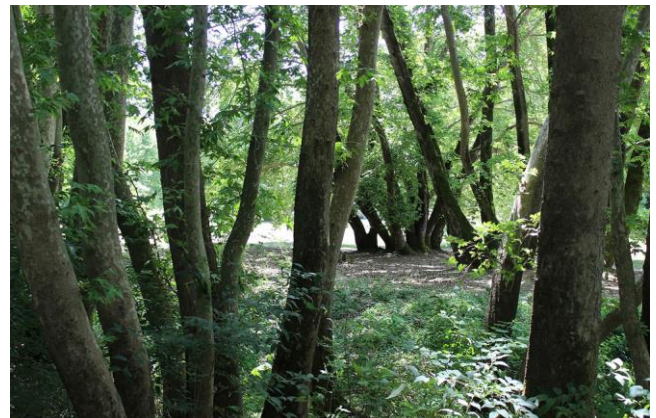


Figure 16. *Platanus orientalis* forest, the type of forest where *Porella cordaeana* can occur as an epiphyte in Turkey. Photo by Grecomara, through Creative Commons.



Figure 17. *Salix pentandra*, where one can find *Porella cordaeana* on the bark in Serbia. Photo by MPF, through Creative Commons.



Figure 18. *Fagus* forest in Serbia, where one can find *Porella cordaeana* on the bark. Photo by Vladimir Pecikoza, through Creative Commons.



Figure 19. *Abies bornmuelleriana*, *Fagus orientalis*, and *Populus tremula* forest in Montenegro where one can find *Porella cordaeana*. Photo by Marijn van den Brink, with permission.

Porella cordaeana (Figure 2-Figure 6) can also occur on soil, as observed by Campisi *et al.* (2008) in southern Italy. These occurred on slopes at 1400-1500 m asl. Similarly, in the Central Pyrenees of Spain and France, Casas and Barrón (2003) found this among the species on the humid soils of the forest, often associated with

decomposed substrates. They considered the moisture and acidic conditions of the decomposing substrate to be suitable for these **saprolignous** (inhabiting dead wood) species. Piippo and Norris (1996) found it to be rare on logs and soil in California, USA.

In Louisiana, USA, *Porella cordaeana* (Figure 2-Figure 6) occupies cypress knees (indicative of a wet habitat), exposed roots, and small bushes and tree bases in swampy forests (Correll & Correll 1941). Vitt *et al.* (1973) found *Porella cordaeana* growing as epiphylls in the *Thuja plicata* forests (Figure 20) of western British Columbia, Canada.



Figure 20. *Thuja plicata* forest where one might find *Porella cordaeana* growing as an epiphyll. Photo by Crusier, through Creative Commons.

In Serbia and Yugoslavia, Sabovljević and Cvetić (2003) found that *Porella cordaeana* (Figure 2-Figure 6) occurs not only on roots and soil, but at tree bases by streams. Bijlsma *et al.* (2010) found it on the base of two poplars (*Populus*; Figure 18) along the river in The Netherlands.

In British Columbia, Canada, Schofield (1988) concluded that *Porella cordaeana* (Figure 2-Figure 6) is primarily restricted to areas with high precipitation, thus seemingly continuing its aquatic tolerances into its terrestrial habitats. As already noted, Kürschner (1999) considered it to be an indicator of better moisture conditions in the *Pinus* (Figure 15) and *Platanus orientalis* (Figure 16) forests in Turkey.

In northern Europe, Nordén *et al.* (2007) considered *Porella cordaeana* to be a **Signal species**. These are predominantly cryptogamic species that indicate Woodland Key Habitats. They signal the potential of finding **red-listed** (may be becoming extinct) species. Nordén and coworkers found that Signal species may be more useful for finding relatively valuable sites in a matrix of production forest. They furthermore concluded that Signal species can be useful surrogates for total cryptogam species richness.

Despite the commonness of the genus *Porella* on Madeira Island, the populations of *Porella cordaeana* (Figure 2-Figure 6) are small and fragile (Fontinha *et al.* 2010). *Porella cordaeana* is the rarest species in the genus there, being restricted to the central higher peaks of Madeira Island (mostly 1750-1800 m asl), where it occurs on rocks and stone walls in sheltered habitats. On Madeira in the Canary Islands, it occurs on wet volcanic rocks

(Ekstein 2010). In central Spain, it occurs on slopes and rocks that are near water (Elías *et al.* 2006). Gökler (1998) found it on stones by water in Turkey. In Greece, it occurs, but rarely, on moist rocks (Blockeel 2017). In the Lapland Nature Reserve in Murmansk Province, Russia, Borovichev and Koroleva (2015) found that it occurred mostly on stones and fine-grained soils.

Blockeel (1991) found *Porella cordaeana* (Figure 2-Figure 6) on limestone in the *Abies cephalonica* (Figure 21) forest. In Serbia and Montenegro, Papp *et al.* (2004) found it on limestone rock. But where more acidic rocks are available, it can inhabit them as well. Papp and Erzberger (2005) found it on soil and limestone rock, but also on siliceous stones in southwest Serbia. Papp *et al.* (2006a) found *Porella cordaeana* on both limestone rock and sandstone rock. These included rock crevices and wet sandstone (Papp & Erzberger 2007). Blockeel (2003) likewise found it in rock crevices as well as shaded boulders on a steep bank. In addition to limestone rock, it occurs in limestone grassland in Croatia (Papp *et al.* 2013).

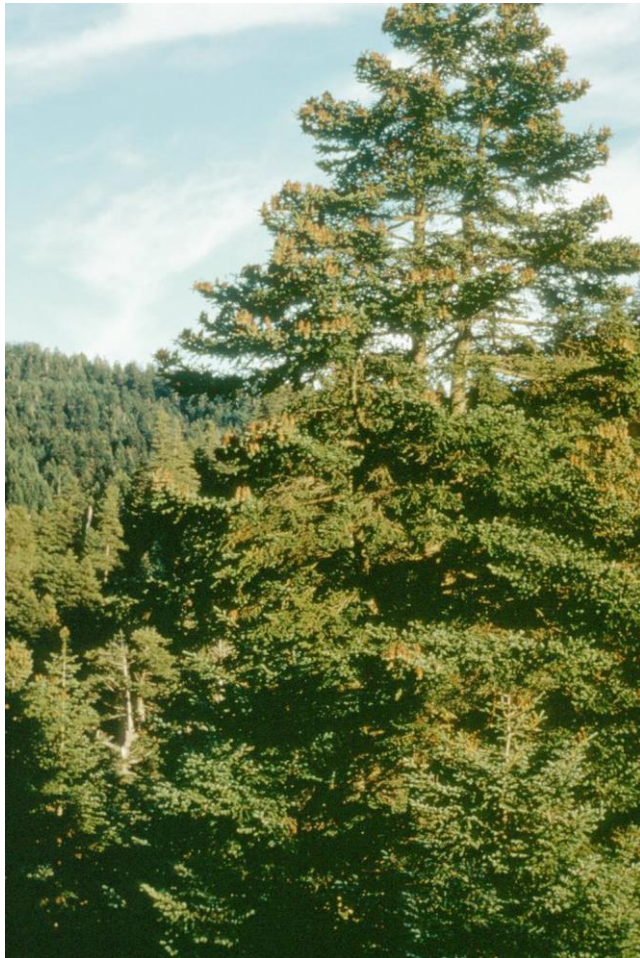


Figure 21. *Abies cephalonica*, a forest type where *Porella cordaeana* can be found on limestone. Photo by W. H. Hodge, through Creative Commons.

As in several other studies, in Alaska Schofield *et al.* (2002) found *Porella cordaeana* (Figure 2-Figure 6) on shaded rock faces at lower elevations. Light does not seem to be an issue, as the species occurs on both exposed and shaded siliceous rock in Serbia (Papp *et al.* 2012). Furthermore, it seems to have a wide moisture tolerance as

well (Figure 22-Figure 23) (Piippo & Norris 1996). It occurs on boulders and outcrops in both dry areas and along rivers. Sager and Wilson (2009) likewise found it in a semi-arid habitat in the Santa Monica Mountains, California, USA. In these locations, it required a suitable habitat that occupied at least 1 m².



Figure 22. *Porella cordaeana* in a drying condition. Photo by Jiří Kameníček, with permission.



Figure 23. *Porella cordaeana*, showing underleaves and lobes in dry state. Photo by Jiří Kameníček, with permission.

Adaptations

Porella cordaeana (Figure 2-Figure 6) forms loose **mats** or **wefts** (Figure 24) (Piippo & Norris 1996). Its size and color vary, depending on the habitat. In wet conditions it is usually dark green, but the color varies from green to light brown (Figure 24) (Clark 1953; Piippo & Norris 1996).

Reproduction

Porella cordaeana (Figure 2-Figure 6) is a **dioicous** species (Clark 1953; Piippo & Norris 1996). This presents a problem for sexual reproduction because sperm might have a long distance to travel to a female. Not only that, but in their examination of specimens from Alaska, Schofield *et al.* (2002) found all specimens to be **sterile** (having no sexual structures). Fontinha *et al.* (2010) found no sexual reproduction or vegetative propagation for this

species on Madeira Island, most likely contributing to its rarity there, despite the genus being the most frequent liverwort genus on the island. This lack of both specialized vegetative reproduction and sexual reproduction also most likely is the cause for the lack of morphological variation. Most, and perhaps all, of the populations on this island could be the result of fragmentation from a single clone. Nevertheless, Uedo was able to photograph it with dehiscing sporophytes (Figure 24-Figure 25) in Japan.



Figure 24. *Porella cordaeana* with capsules, showing both green and brown color forms and a weft life form. Photo by Ken-Ichi Ueda, through Creative Commons.



Figure 25. *Porella cordaeana* with open capsules. Photo by Ken-Ichi Ueda, through Creative Commons.

Role

We know that many of the leafy liverworts have a close association with nitrogen-fixing **Cyanobacteria**, especially with *Nostoc* (Figure 26) (Dalton & Chatfield 1985). In the western United States, such associations occur with *Porella cordaeana*, but these are not as common or abundant as on other *Porella* species.

Fungal Interactions

Wang and Qiu (2006) found no references to mycorrhizal associations in *Porella cordaeana* (Figure 2-Figure 6).



Figure 26. *Nostoc*, a potential nitrogen fixer on liverworts like *Porella cordaeana*. Photo by Ralf Wagner, with permission.

Biochemistry

Porella cordaeana (Figure 2-Figure 6) has numerous oil bodies (Figure 27) in each leaf cell. These can contribute compounds that are antifungal or that discourage herbivory. In 1998 Asakawa described the species as having an odor that is "dried seaweed-mossy like." Noting that this species is tasteless, Asakawa *et al.* (2012) found that it has drimane sesquiterpenoids. Toyota *et al.* (1989) identified three new pinguicane-type sesquiterpenoids in *P. cordaeana* in American populations.

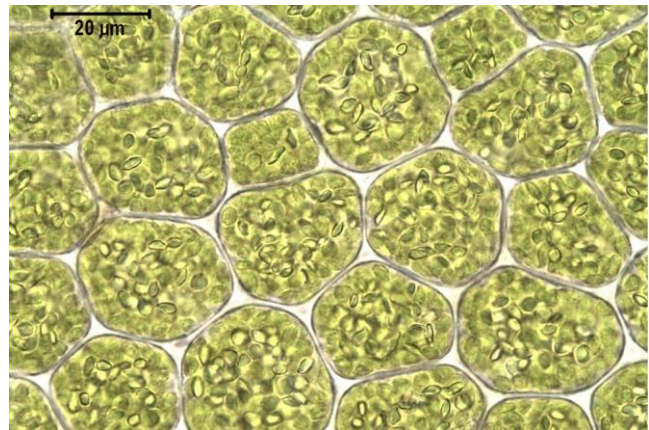


Figure 27. *Porella cordaeana* leaf cells with chloroplasts and oil bodies. Photo by Hugues Tinguy, with permission.

Bukvicki *et al.* (2012) identified a rich array of terpenoids in *Porella cordaeana* (Figure 2-Figure 6): sesquiterpene hydrocarbons (53.12%, 51.68%, 23.16%) and monoterpene hydrocarbons (22.83%, 18.90%, 23.36%), in methanol, ethanol, and ethyl acetate extracts, respectively. The dominant compounds in the extracts were β -phellandrene (15.54%, 13.66%, 12.10%) and β -caryophyllene (10.72%, 8.29%, 7.79%, respectively). All three extracts were highly active against tested yeast species; the activity against bacteria was somewhat less. The Gram-negative bacteria exhibited somewhat greater resistance than did the Gram-positive bacterium. The researchers expressed hope that these extracts may prove to be as potent and safer compared to the strong antibiotic cycloheximide. Furthermore, the *P. cordaeana* extracts exhibit significant antimicrobial potential against food

microorganisms. The researchers suggested that the high percentages of monoterpene and sesquiterpene hydrocarbons in *P. cordaeana* could be the agents responsible for its very effective antimicrobial activity.

Tan *et al.* (2017) demonstrated that *Porella cordaeana* (Figure 2-Figure 6) exhibits a weak anticancer activity against human breast cancer and human colorectal cancer. Tosun *et al.* (2013) found an inhibitory effect on carrageenan-induced paw edema (highly sensitive and reproducible test for nonsteroidal anti-inflammatory drugs), but the effect was rather small, ranging 25.4-29.4% inhibition. Its activity against p-benzoquinone-induced abdominal constriction animal models was more effective, ranging 27.6-41.1%. Nevertheless, *P. cordaeana* did not show any wound-healing effects (Tosun *et al.* 2016).

***Porella pinnata* (Figure 1, Figure 28-Figure 31)**

Distribution

Porella pinnata (Figure 1, Figure 28-Figure 31) has a worldwide distribution (Garcia *et al.* 2010). In North America, it is abundant, and extends from Quebec (Evans 1916a), Nova Scotia, and Ontario in Canada (Evans 1916b), southward to Minnesota, Florida, Louisiana (Evans 1916b), and Arkansas (Redfearn 1964, 1979) in the USA, and Cuba in Central America (Evans 1916b). In Europe it is more restricted and rare, occurring in the British Isles and the western coast of France, with a possible occurrence in Portugal. Its presence in Portugal was confirmed in 2005 by Vieira *et al.* and again in 2010 by Garcia *et al.* In 2003, Ganeva and Natcheva added Bulgaria. Ekstein (2010) reported it from Madeira in the Canary Islands.



Figure 28. *Porella pinnata*, a species mostly distributed in the Appalachian Deciduous Forest in eastern North America, but also occurs in Europe. Photo by Bob Klips, with permission.

Porella pinnata was also reported from China and South India, but when Bai *et al.* reviewed the Chinese *Porella* records, they found instead that these represented *Porella chinensis*, *P. densifolia*, *P. gracillima*, *P. japonica* (Figure 32), *P. oblongifolia*, and *P. platyphylla* (Figure 52-Figure 58), but not *P. pinnata* (Figure 28-Figure 31). Records from India may represent similar misidentifications and need to be confirmed.



Figure 29. *Porella pinnata* that is drying. Photo by David Holyoak, with permission.



Figure 30. *Porella pinnata* in a well-hydrated condition. Photo by Des Callaghan, with permission.



Figure 31. *Porella pinnata* showing a pale color. Photo by Hugues Tinguy, with permission.



Figure 32. *Porella japonica* ssp. *appalachiana*; *Porella japonica* was once considered to be part of *Porella pinnata*. Photo by Ken McFarland and Paul Davison, with permission.

Aquatic and Wet Habitats

Evans (1916a) reported *Porella pinnata* (Figure 1, Figure 28-Figure 31) from running water in Quebec. Brown (1929) found it on rocks in a streamlet in Nova Scotia. In Ontario, Cain and Fulford (1948) did not find it to be common, occurring on rocks or wood in small streams. It similarly occurs in rocky ravines in Connecticut, USA (Nichols 1916). Nichols (1918) considered *Porella pinnata* to be hydrophytic. Nichols (1935) found it attached to submerged rocks in Cliff Creek in the Huron Mountains of the Upper Peninsula of Michigan. Gilbert (1958) found *Porella pinnata* attached to submerged rocks in a stream in Iosco County, Michigan, USA, the first record for the Lower Peninsula of Michigan. Hall (1958) found it on moist sandstone adjacent to waterfalls in Ohio, where he considered it to be apparently rare. In Missouri, USA, Redfearn (1979) found it on shaded rocks in creeks and springs in the Ozark National Forest of Arkansas, USA. Solberg and Miller (1979) reported that it not only was frequent on rocks in a stream in North Carolina, but also occurred on trees along the stream. Conard (1946) reported it in a walled-in spring tributary, where it was plentiful along with *Hygroamblystegium tenax* (Figure 33).



Figure 33. *Hygroamblystegium tenax*, a species that occurs with *Porella pinnata* in a walled-in spring tributary. Photo by Hermann Schachner, through Creative Commons.

Lanfear (1933) similarly found *Porella pinnata* (Figure 28-Figure 31) on emergent rocks in spring streams, where it was associated with *Chiloscyphus polyanthos* var. *rivularis* (Figure 34, *C. pallescens* var. *fragilis* (Figure 12, Figure 35), *Riccardia multifida* (Figure 36), *Jubula hutchinsiae* subsp. *pennsylvanica* (Figure 37), and *Scapania* (Figure 10), both above and below water. On the Appalachian Plateau in northern Georgia, USA, Carroll (1945) found it in abundance on submerged rocks and tree roots. In the Chapel Hill area of North Carolina, USA, Coker (1904) found it either immersed or on rocks close to the spray zone where humidity was high. In August in the Ozark springs of Missouri, USA, Drouet (1933) found dense growths of *P. pinnata* on rocks receiving spray from a spring.



Figure 34. *Chiloscyphus polyanthos* var. *rivularis*, a species that associates with *Porella pinnata* in spring streams. Photo by Jean Faubert, with permission.



Figure 35. *Chiloscyphus pallescens*, a species that associates with *Porella pinnata* in spring streams. Photo by Michael Lüth, with permission.



Figure 36. *Riccardia multifida*, a species that associates with *Porella pinnata* in spring streams. Photo by Manju Nair, through Creative Commons.



Figure 37. *Jubula hutchinsiae* subsp. *pennsylvanica*, a species that associates with *Porella pinnata* in spring streams. Photo by Wayne Lampa, through Creative Commons

In Walker Branch, Tennessee, USA, *Porella pinnata* (Figure 28-Figure 31) is the most abundant contributor to the biomass (Steinman & Boston 1993). It occurs in streams in the Great Smoky Mountains National Park, Kentucky, USA (Knapp & Lowe 2009). It is a common bryophyte on rocks and wood in seasonally inundated habitats in eastern North America, extending above and below the water line (Wood *et al.* 2016), and likewise occupies periodically inundated sites on river banks in Portugal (Garcia *et al.* 2010). Plitt (1908) found that in the Piedmont region of Maryland, USA, it was common on rocks that are frequently submerged. In the mid-order Middle Oconee River, Georgia, USA, it typically has a significantly higher density, organic matter, and invertebrate biomass than do the adjacent bare rock faces (Wood *et al.* 2016). Noble (2003) reported it as one of the dominant taxa on rocks in the east bank, center stream, and west bank of the riparian zone at Falls Branch Falls in Tennessee, USA.

Vieira *et al.* (2004, 2005) found that in northwest Portugal *Porella pinnata* (Figure 28-Figure 31) is seasonally emergent on stony streambanks and riparian tree

roots along lowland rivers, including those that flow where agriculture and natural forest formations still co-exist. In the mountain stream locations it can be associated with *Fontinalis squamosa* (Figure 38). In some rivers it was frequently associated with *Cinclidotus fontinaloides* (Figure 39). Its distribution in Portugal was usually in medium to large rivers with moderate pollution, including river margins that were seasonally inundated. Ferreira *et al.* (2008) stated its habitat as simply rivers.



Figure 38. *Fontinalis squamosa*, a species that is sometimes associated with *Porella pinnata* in Portugal. Photo by Janice Glime.



Figure 39. *Cinclidotus fontinaloides*, a species that is sometimes associated with *Porella pinnata* in Portugal. Photo by Hermann Schachner, through Creative Commons.

Garcia *et al.* (2010) found that *Porella pinnata* (Figure 28-Figure 31) occurred along rivers with moderate water velocity and turbulence, where it experienced periodic inundation (Figure 40). These were typically well oxygenated waters in the middle and terminal portions of the river, but where the substrate was still rocky. In these reaches, the water typically has accumulated minerals from the soil, rocks, and leaf litter as it swelled onto the river banks. Garcia and coworkers have found it mostly in shaded conditions, created by overhanging vegetation or in granitic rock crevices, as well as on soil under the riparian

trees. Submerged populations of *Porella pinnata* (Figure 28-Figure 31) seem to prefer low conductivity with low concentrations of nitrogen and phosphorus.



Figure 40. *Porella pinnata* at high water line, *Taxodium* swamp near Tallahassee, Florida, USA. Photo by Janice Glime.

In North America, Howe (1897) likewise reported *Porella pinnata* (Figure 28-Figure 31) on the banks of shaded streams where it was subject to flooding (Figure 41). Barbour (1902) described its North American habitat as occurring at the base and on exposed roots of trees subject to flooding. Bakalin (2018) described its North American habitat as shaded stones and decaying wood along streams, where it occurred as a hygrophyte or hydrophyte, subject to submersion during high water. Evans (1916b) also considered it to occur most commonly on stones and logs both in the streams and on streambanks where it became submerged during part of the year. Although Sharp (1930) found it to be uncommon in southeastern Oklahoma, he also found it along stream margins on rocks and roots.



Figure 41. *Porella pinnata* habitat on roots in a flooding zone. Photo by Li Zhang, with permission.

Bosanquet (2010) described zonation along streambanks in the UK, reporting that *Porella pinnata* (Figure 28-Figure 31) dominates in a band along rivers and streams, with only occasional occurrences in the zone with *Cinclidotus fontinaloides* (Figure 39) and *Schistidium rivulare* (Figure 42) above it. In Bulgaria, Ganeva and Natcheva (2004) reported it from water sprayed rocks.



Figure 42. *Schistidium rivulare*, a species that occurs in the streambank zone above the *Porella pinnata* zone in the UK. Photo by Janice Glime.

Vergouw and Siebel (1991) found it to be a "good acidophile" where it occurred in the water of the Chartreux source in Cahors, France.

Porella pinnata (Figure 28-Figure 31) appears to require nearness to water, thriving in places where it occasionally becomes submersed, but in most cases does not remain that way for long. Even in its terrestrial habitats, such as those growing on trees along Lake Superior in Michigan (Evans & Nichols 1935), are subject to high humidity and splash resulting from the activity of the lake. Similarly, Haynes (1927) reports it from river banks in Virginia, USA, but I have not found records of many truly terrestrial dry habitats. On trees, it can often exhibit a feather life form (Figure 43).



Figure 43. *Porella pinnata*, showing its growth habit. Photo by Alan Cressler, with permission.

Adaptations

Hill *et al.* (2007) described *Porella pinnata* (Figure 28-Figure 31) as being attached to an aquatic substrate and trailing in the water, a description that suggests the **streamer** life form of Glime (1968). In terrestrial habitats, it can form shelves, a **feather** life form.

Howe (1897) described a southern USA form that dries out. When doing so, the leaves become closely wrapped around the stem or decurved; the branches are often sub-circinate (Figure 44-Figure 45). This could help to protect the liverwort from water loss, thus permitting it to live in somewhat drier habitats. This evidence suggests that it might be interesting to look for chemical evidence of cryptic species in *Porella pinnata* (Figure 28-Figure 31), separating the northern and southern populations.



Figure 44. *Porella pinnata* dry showing leaves rolling around the stem and sub-circinate branches. Photo by Li Zhang, with permission.



Figure 45. The same *Porella pinnata* wet. Photo by Li Zhang, with permission.

Reproduction

Porella pinnata (Figure 28-Figure 31) is **dioicous** (Howe 1897; So 2005; Garcia *et al.* 2010), with identifying male structures (Figure 46) unseen in Europe (Garcia *et al.* 2010). Garcia *et al.* (2010) reported that sporophytes (Figure 47-Figure 48) are unknown in Europe. Vieira *et al.* (n.d.) likewise reported that it was never found fertile in streams of northwest Portugal. Barbour (1902) reported that it is usually sterile in eastern North America. Howe (1897), however, reported that the "form" in the southeastern states (USA) produces sporophytes more commonly than the type, and that it grows in somewhat drier situations – more evidence there may be cryptic

species. Evans (1916b), in his treatment of New England liverworts, may have shed some light on its sporophyte rarity; he reported that they only mature when the plants are exposed to air.



Figure 46. *Porella pinnata* with antheridial branch. Photo by Paul Davison, with permission.



Figure 47. *Porella pinnata* with capsules, near Tallahassee, FL. Photo by Janice Glime.



Figure 48. *Porella pinnata* with capsules. Photo by Janice Glime.

Guisen *et al.* (1996) examined the chromosomes of Chinese *Porella pinnata* (Figure 28-Figure 31) and determined $n=8$. This is the most common number for liverworts (see Volume 1, Chapter 2-7) and does not suggest any hybrid origin.

Fulford (1944) described vegetative reproduction in *Porella pinnata* (Figure 28-Figure 31). Plants of this species that had been kept in a moist chamber for a month became badly contaminated with a cottony fungus and filamentous green algae. The plants remained healthy and green, but showed no signs of regeneration. New cultures were set up in Petri dishes and supplied regularly with nutrient solution. After another month these plants showed numerous vegetative developments of bulging leaf cells and leafy shoots. These developing bulges were abundant, especially on older leaves, and were more common on the dorsal surface than on the ventral surface. These never formed on the leaf margins. When these brood bodies reached their approximate size, they formed rhizoids that branched at the tips and anchored the brood body to the leaf surface. A new leafy shoot developed from the tip of this globose brood body. Fulford provided a detailed description of the development of the new plant and noted that it was similar to development from spores in the genus.

Role

Roberts *et al.* (2007) monitored a forested headwater stream in eastern Tennessee, USA, to determine temporal differences in the stream metabolism. *Porella pinnata* (Figure 28-Figure 31) was the most abundant cover. Its cover increased during the study from 4.2% in May 2004 to 18.0% in January 2006.

In Walker Branch, Tennessee, *Porella pinnata* (Figure 28-Figure 31) is the most abundant bryophyte (Steinman & Boston 1993). The abundance peaked in late summer, then was reduced by a severe winter storm in the 13-month study. Stable substrate and water velocity were important in determining abundance, making bedrock steps and riffles good habitats. In this stream, the *P. pinnata* had significantly greater area-specific rates of photosynthesis and phosphorus uptake than did periphyton (freshwater organisms attached to plants) in all seasons. In the autumn, biomass-specific photosynthetic rates were also greater for *P. pinnata*. But in winter and spring the periphyton on the cobble exceeded that of the liverwort. This was not the case on introduced cylinders. When translated to a year-round productivity and phosphorus uptake for the entire sampling area, the patchy distribution of the liverwort reduced its contribution, with rates similar to that of periphyton in late summer and autumn, but being exceeded by 3-5X greater rates by the periphyton in spring and early summer.

Steinman (1994) enriched Walker Branch with phosphorus to determine the effects on the dominant bryophyte, *Porella pinnata* (Figure 28-Figure 31). In a second-order reach of the stream, there was an N:P ratio of 3.5-1. The P:C ratio in *P. pinnata* was not significantly affected by the enrichment, but there was a significant increase in the P:N ratio. On the other hand, in Sludge Creek, which initially had an N:P ratio of 21.6:1 in the stream water, enrichment caused a significant increase in both the P:C and P:N ratios. To further complicate the results, the *P. pinnata* in Walker Branch actually had a significant decrease in phosphorus concentrations in its tissues after enrichment, whereas the same species in

Sludge Creek had a significant increase in phosphorus in the enriched populations, but not in the controls. Steinman suggested that the increased P:N and P:C ratios could have resulted from either assimilation or adsorption.

Productivity in these streams increased by 15% following enrichment, but the increase was not significant (Steinman 1994). The periphyton did not increase significantly in either stream, but Steinman suggested that grazing by snails may have mitigated those results.

Bain and Proctor (1980) explored the requirement of aquatic bryophytes for free CO₂ for its carbon source. Results for *Porella pinnata* (Figure 28-Figure 31) were puzzling. Most of the species reached their photosynthetic compensation points at around pH 8.0-9.0. *Anthoceros punctatus* (Figure 49), now known to use the pyrenoid as a CO₂-concentrating mechanism, reached 9.5. *Porella pinnata* showed a similar, but less pronounced, anomaly. The researchers considered the ability to use bicarbonate, present in water instead of CO₂ at higher pH levels like this, was an unlikely source of CO₂ for the *P. pinnata*. I am waiting for a micro pH probe that can measure the pH at the leaf cell surface. My hypothesis is that the bryophytes, possibly through cation exchange, lower the pH at the cell surface. This could permit the bicarbonate to convert to CO₂ for cellular uptake.



Figure 49. *Anthoceros punctatus*, a species with pyrenoids and a high CO₂ compensation point. Photo by Jonathan Sleath, with permission.

Mulholland *et al.* (2000a) found the highest rates of ammonium uptake per unit area in a forest stream were accomplished by *Porella pinnata* (Figure 28-Figure 31), decomposing leaves, and fine benthic organic matter. The epilithon had the highest N uptake per unit biomass N. The *Porella pinnata* covered 19.1% of the stream, making it a major contributor to the nitrogen dynamics.

Wood *et al.* (2016) have demonstrated higher biomass and density of macroinvertebrates and greater organic matter content in patches of *Porella pinnata* (Figure 28-Figure 31) than that found on adjacent bare rocks in the Middle Oconee River, Georgia, USA. Average insect density was five times as great within the *P. pinnata* mats compared to the controls. Previously, these periodically submerged bryophytes were mostly ignored in aquatic food chains. In this case, they were submerged only when there was a substantial increase above the base flow level.

In cypress swamps, bryophytes can extend the oxygenated periods by growing on the cypress knees (*Taxodium distichum*; Figure 50) (Mehring *et al.* n.d.). *Porella pinnata* (Figure 28-Figure 31) is a common liverwort on these knees (Figure 1, Figure 50), and they generate enough oxygen to counteract significant portions of the oxygen used by the decomposing organic matter in the Little River in southern Georgia, USA. The highest levels of daily oxygen released by the liverworts occurred when the river was high enough to submerge them, while maximizing their light exposure. This provides a function for the cypress knees that adds to the theories that have been presented.



Figure 50. *Porella pinnata* on cypress (*Taxodium distichum*) knees. Photo by Paul Davison, with permission.

The role of bryophytes as a food source has been ignored until relatively recently. In the aquatic habitat, they not only are eaten themselves, but bryophytes can trap large quantities of detrital particles and provide homes for bacteria, fungi, protozoa, and numerous small invertebrates. Mulholland *et al.* (2000b) found that *Porella pinnata* (Figure 28-Figure 31) had similar values of labelled N to those of the epilithon. They suggested that the *P. pinnata* could be a possible food source for both *Elimia* (freshwater snail; Figure 51) and mayflies.



Figure 51. *Elimia*, a snail that lives with *Porella pinnata* and could find food there. Photo through Creative Commons.

Fungal Interactions

Wang and Qiu (2006) were unable to find any records of mycorrhizal associations with *Porella pinnata* (Figure 28-Figure 31).

Biochemistry

The oil bodies in this species are small, but numerous (So 2005). With its widespread distribution and abundance in some locations, and its size extending up to 30 cm long (So 2005), it is surprising that it lacks biochemical studies to elaborate on what secondary compounds might be found in these oil bodies.

Porella platyphylla (Figure 52-Figure 58)

(syn. = *Madotheca platyphylla*; Figure 52-Figure 58)

Porella platyphylla is widespread in the temperate regions, especially in the deciduous forests, and reaching southward into the subtropics (Schuster 1980).



Figure 52. *Porella platyphylla*, a widespread temperate leafy liverwort. Photo by Evan Raskin, through Creative Commons.



Figure 53. *Porella platyphylla*, hydrated. Photo by Hugues Tinguy, with permission.



Figure 54. *Porella platyphylla*. Photo by Malcolm Storey, DiscoverLife, with online permission.



Figure 55. *Porella platyphylla* showing hydrated form. Photo courtesy of Betsy St. Pierre.



Figure 56. *Porella platyphylla* dorsal surface. Photo by Paul Davison, with permission.



Figure 57. *Porella platyphylla* underleaves and lobes. Photo by Paul Davison, with permission.



Figure 58. *Porella platyphylla* wet. Photo by Tim Waters, through Creative Commons.

The status of *Porella platyphylla* (Figure 52-Figure 58) and that of *P. platyphylloidea* (Figure 91-Figure 93) has been debated for a long time. Evans (1916c) considered the double spirals of the elaters to separate them, with *P. platyphylloidea* apparently lacking elaters with two spirals throughout its entire length, whereas at least some are present in *P. platyphylla*. With this understanding, he reported *P. platyphylloidea* to be the commonest species of *Porella* in eastern North America.

Barbour (1902) considered the American plants to be the "form" *Porella thuja*, but acknowledged that the European *P. platyphylla* (Figure 52-Figure 58) also occurs. *Porella thuja* is no longer recognized as a legitimate taxon (Söderström *et al.* 2016).

But Boisselier-Dubayle *et al.* (1998) argued that *Porella platyphylloidea* (Figure 91-Figure 93), while being reported Europe, had never been confirmed there. Instead, they considered it to be restricted to North America. Furthermore, they considered the often cited *P. platyphylla* (Figure 52-Figure 58) to be absent in North America.

Therrien *et al.* (1998) used isozyme and morphometric analysis to attempt to clarify these two taxa. Based on 11 loci, they identified three discrete genotypes. They found no variation within populations, but each of the genotypes exhibited variation among populations. Each genotype possessed several unique alleles. Unfortunately, the

morphological characters for these two species had a continuous pattern rather than defining distinct entities. Furthermore, the two species type specimens fell into the same cluster. Unlike the report of Evans (1916c), they found that both single and double spiralled elaters occurred within identical genotypes. Therrien and coworkers concluded that instead of two species, *P. platyphylla* (Figure 52-Figure 58) and *P. platyphylloidea* (Figure 91-Figure 93) represented cryptic species of *Porella platyphylla*.

Like Therrien *et al.* (1998), Hentschel *et al.* (2007) found that *P. platyphylla* (Figure 52-Figure 58) split into a European and a North American clade, with one tested North American population belonging with the European clade. Heinrichs *et al.* (2011) suggest that the North American *P. platyphylloidea* (Figure 91-Figure 93) might be an ancient hybrid between *P. cordaeana* (Figure 3-Figure 6) and *P. platyphylla s.str.* Based on their cladistic analysis, they likewise concluded that *P. platyphylla s.l.* has three main clades, with the nuclear and chloroplast loci providing incongruent phylogenetic signals. They considered *P. platyphylla s.l.* to consist of a North American main clade and a European clade, with the latter clade also present in North America and Asia. Blisard and Kleinman (2012) supported the conclusion that these two were cryptic species that cannot be separated based on morphological characters, requiring molecular studies for identification.

To illustrate the difficulty in defining this species, Wyatt *et al.* (2005) reported that *Porella platyphylla* (Figure 52-Figure 58) has high levels of genetic variation, contrasting with earlier studies suggesting that liverworts have little genetic variation. They found 26 multilocus genotypes and more than 80% of the enzyme loci to be polymorphic within a single population from southwestern North Carolina.

If I have not convinced you that *P. platyphylloidea* (Figure 91-Figure 93) is merely a cryptic species within *P. platyphylla* (Figure 52-Figure 58), you are not alone. In their 2016 list of accepted names of liverworts, Söderström *et al.* have listed both species as accepted.

Distribution

Shaw (2001) considered *Porella platyphylla* (Figure 52-Figure 58) to be widespread in North America and Europe. Bakalin (2018) listed *Porella platyphylla* from Alaska and British Columbia in the west, south to Texas, and in the east from Nova Scotia south to Florida in North America, and in Eurasia. Önder and Özenoğlu (2019) considered it to be the most common liverwort species in the Turkish flora, occupying a wide range of habitats (Özenoğlu & Gökler 2002; Ezer *et al.* 2009). Shaheen and Srivastava (1986) reported it from the western Himalayas in India.

Aquatic and Wet Habitats

Porella polyphylla (Figure 52-Figure 58) is not an aquatic bryophyte, but it is often associated with wet habitats. Dhien (1978) found it in intermittent rivers. But streambanks are more common than instream habitats for it. Önder and Özenoğlu (2019) found it on streambanks in Turkey; Özenoğlu and Gökler (2002) reported it from rocks and bark near a stream in Turkey.

Ezer *et al.* (2009) called *Porella platyphylla* (Figure 52-Figure 58) a **cortico-saxicolous** species in Turkey, a testimony to its broad niche. Özenoğlu and Gökler (2002) listed sheltered tree boles, walls, rocks, soil, stones on banks, rocks, and tree bark (Figure 59-Figure 60) as the habitats for *Porella platyphylla* in Turkey. Some of these were near streams, but the species was not restricted to nearness to streams.



Figure 59. *Porella platyphylla* with lichen on bark. Photo by Tim Waters through Creative Commons.



Figure 60. *Porella platyphylla* from the mid region of a tree trunk in the Hiawatha National Forest, Michigan, USA. Photo by Janice Glime.

A number of researchers (Barbour 1902; Plitt 1908; Özenoğlu & Gökler 2002; Heinrichs *et al.* 2011) have reported populations of *Porella platyphylla* (Figure 52-Figure 58) as sometimes occurring on rocks (Figure 61-Figure 63). Haynes (1927) considered damp rocks to be among its substrates in Virginia, USA. Redfearn (1964, 1979), in the Interior Highlands of North America in Arkansas, USA, found *Porella platyphylla* on shaded vertical limestone. Bakalin (2018) attributed its North American habitat to both dry and wet shaded rocks. Gustafsson *et al.* (1992) found it on shaded cliffs in Sweden. Özenoğlu and Gökler (2002) reported it from rocks, walls, stones on stream and river banks, and canyon rocks in Turkey.



Figure 61. *Porella platyphylla* on boulder. Photo by Owen C. Larkin, through Creative Commons.

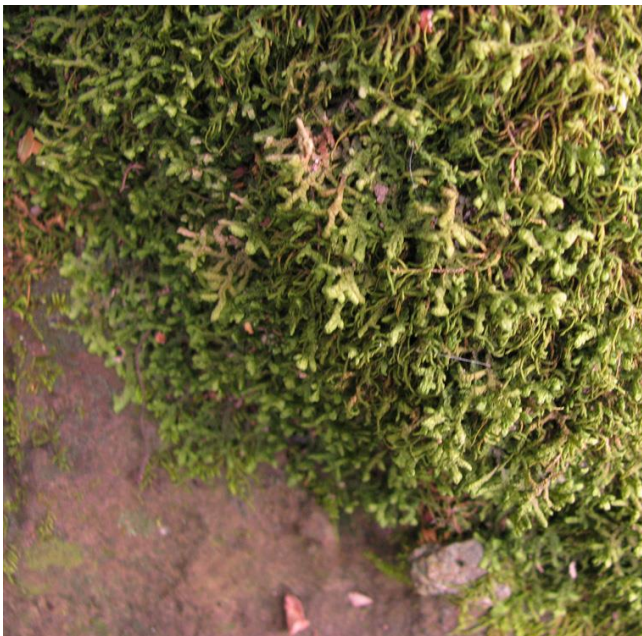


Figure 62. *Porella platyphylla* on rock trail at Lost River Caverns, Poconos, Pennsylvania, USA. Photo by Janice Glime.

Callaghan and Ashton (2008) considered *Porella platyphylla* (Figure 52-Figure 58) to be a calciphile. Osadowski (2010) found it on calcareous tufas in Western Pomerania, noting that it prefers high concentrations of calcium. Proctor (2010) likewise found it on limestone rock.



Figure 63. *Porella platyphylla* on rock, Czech Republic. Photo by Vita Plasek, with permission.

Adaptations

Evans (1899) found *Porella platyphylla* forming pure mats (Figure 64) in the northeastern USA. The young plants grew prostrate and adhered to the substrate. As they aged, they would form considerable mat size and hide the decayed portions under them (Figure 64). These often take on a **feather** life form on vertical substrata (Figure 65-Figure 66).



Figure 64. *Porella platyphylla* forming a **pure** mat on bark. Photo by Janice Glime.



Figure 65. *Porella platyphylla* forming shelves on tree in the Upper Peninsula of Michigan, USA, a **feather** life form. Photo by Janice Glime.



Figure 66. *Porella platyphylla* forming shelves, a **feather** life form. Photo by Suzanne Cadwell, through Creative Commons.

Proctor (2000a) defined desiccation-tolerant bryophytes as photosynthesizing and growing as long as water is readily available, but suspending metabolism when it is not. These, including *Porella platyphylla* (Figure 52- Figure 58), are typically ectohydric (moving water in external capillary spaces). The physical structure (Figure 67) of the bryophyte contributes to the rate at which a bryophyte loses water in drying conditions. *Porella platyphylla*, along with the aquatic *Palustriella commutata* (Figure 68), required only five hours to reach an air-dried state (Deltoro *et al.* 1998). The other bryophytes in the experiments typically took 5-16.7 hours.



Figure 67. *Porella platyphylla* ventral side showing underleaves; the curling edges suggest it is drying. Photo by Hermann Schachner, through Creative Commons.



Figure 68. *Palustriella commutata*, a species that, like *Porella platyphylla*, dries in air in only 5 hours. Photo by Hermann Schachner, through Creative Commons.

Gupta (1977a) used *Porella platyphylla* (Figure 52- Figure 58) among the species in a study of photosynthesis and leakage in bryophytes. Decrease in photosynthesis is an indicator of desiccation injury. In this study, all the species reached the highest level of cell leakage in the first 2 minutes of rewetting, then slowed down. This reduction seems to be due to the reassemblage of the cell membranes or to a rapid decrease of solutes in damaged cells. Viable cells are able to reabsorb much of this lost leachate upon rehydration. Gupta (1977b) considered *Porella platyphylla* to be drought resistant, compared to the non-resistant *Scapania undulata* (Figure 10). In both species the relative water content dropped steadily for up to 50 hours at 96.5% relative humidity, then remained unchanged. Photosynthesis actually peaked after two hours of desiccation in *P. platyphylla* and six hours in *Scapania undulata*. Proctor (2010) found wide variation in the half-recovery time, ranging from a few tens of seconds in *Syntrichia ruralis* (a xerophyte; Figure 69) and *Porella platyphylla* to an hour or more in **pteridophytes** (mostly club mosses and ferns).



Figure 69. *Syntrichia ruralis*, a xerophytic species that has a half-recovery time from desiccation of several minutes, similar to that of *Porella platyphylla*. Photo by Hermann Schachner, through Creative Commons.

Hinshiri and Proctor (1971) found that recovery from desiccation up to 60 days is normally completed within 3-4 hours upon rehydration. Longer periods of desiccation

cause an initial negative net assimilation, but it becomes positive as it increases progressively for several days. They attributed this to initial enhanced respiration and delayed recovery. *Porella platyphylla* (Figure 52-Figure 58) is desiccation tolerant (Figure 70) (Marschall & Proctor 1999; Marschall 2017). As such, it does not suffer photooxidative damage due to the coexistence of zeaxanthin-dependent NPQ (nonphotochemical chlorophyll fluorescence quenching) mechanisms and a desiccation-induced thermal energy dissipation.



Figure 70. *Porella platyphylla* dry. Photo courtesy of Betsy St. Pierre.

Proctor (2000b) found that *Porella platyphylla* (Figure 52-Figure 58) did not recover as rapidly as the xerophytic *Syntrichia ruralis* (Figure 69) or *Grimmia pulvinata* (Figure 71). In fact, although *Porella platyphylla* is among the more tolerant bryophytes, it had the worst performance at the lowest water potentials (Proctor 2001). But Proctor (2003) modified that description to call it moderately desiccation tolerant and found that it survived best in the highest humidity (74% r.h.) used. These experiments suggest that this species is adapted to the intermittent water conditions of streambanks and inundation areas as well as mesic forests, but not in conditions that remain dry for long periods of time.



Figure 71. *Grimmia pulvinata*, a xerophyte that recovers more quickly from desiccation than does *Porella platyphylla*. Photo by Darkone, through Creative Commons.

It is important to examine the effect of temperature on desiccation survival as our planet continues to warm. Hearnshaw and Proctor (1982) experimented with seven bryophytes kept dry in a range of 20-100°C. The differences in chlorophyll content were largely in the time required for recovery. Survival times ranged from a few minutes or less for 50% loss of chlorophyll at 100°C to weeks or even months at 20° and 37° for the more resistant species. *Porella platyphylla* (Figure 52-Figure 58) lost 50% of its chlorophyll content at 37°C after 42.5 days, but at 60°C, the same damage occurred in only 19.7 hours. This is consistent with the finding that the thylakoid membranes of the chloroplasts and the processes of PSII are sensitive to water stress (Marschall *et al.* 1998a). The species also survives freezing temperatures in winter (Figure 72-Figure 73). Because of its vertical position, snow cannot cover it completely to protect it, thus causing it to experience even sub-freezing temperatures.



Figure 72. *Porella platyphylla* with snow. Photo by Gergely Pápay, through Creative Commons.



Figure 73. *Porella platyphylla* with snow on bark in Europe. Photo by Michael Lüth, with permission.

Marschall *et al.* (1998a) demonstrated that drought in *Porella platyphylla* (Figure 52-Figure 58) leads to an accumulation of high-molecular-weight fructan. Marschall *et al.* (1998b) reported that the major soluble carbohydrates in *Porella platyphylla* (Figure 52-Figure 58) are sucrose and a homologous series of fructans (see also Marschall 2010). Adding glucose and fructose to the medium did not

affect the composition of the soluble carbohydrate pool, but sucrose caused the fructan pool to increase and inhibited photosynthetic oxygen evolution and respiration. In the dark, the fructan pool was amplified, and desiccation increased the proportion of the high-molecular-weight fructan. Marschall (2010) found that adding glucose, fructose, and sucrose to the medium, in light or dark, cause the down regulation of photosynthetic activity. Dark "starvation" of these sugars for one week does not cause a significant decrease in photosynthetic capacity.

Marschall (1998) found that in *Porella platyphylla* (Figure 52-Figure 58) the nitrogen reductase activity remained relatively constant, but at a low level, in the light, but increased in the dark. On the other hand, nitrogen reductase activity during the first hour of rehydration in the xerophyte *Syntrichia ruralis* (Figure 69) decreased considerably in both dark and light, although to a greater degree in the light. The nitrogen reductase activity of *Porella platyphylla* decreased to a low level after 4 days in the dark, but increased when sucrose was added to the medium. Thus, the behavior of *Porella platyphylla* is somewhat different from that of the xerophyte *Syntrichia ruralis*.

Marschall and Proctor (1999) suggest that desiccation tolerance in *Porella platyphylla* (Figure 52-Figure 58) is essentially constitutive, *i.e.* always there and not requiring induction. Recovery of photoprotection in light is mostly complete within 24 hours. This strategy should work well for this species that grows epiphytically and thus experiences frequent wetting and drying cycles.

Sütő and Marschall (2016) looked for cell morphology changes in *Porella platyphylla* (Figure 52-Figure 58) following various abiotic stresses. They identified suitable stains for the best viewing of these changes, finding neutral red at pH 7.6 to be the best. Strong osmotic treatment (1 M KSCN) caused the central vacuole to fragment into small pieces, then rupture in 10 minutes. This osmotic shock caused irreversible damage to the chloroplasts. Oil bodies were the most resistant structures against the stresses tested (freezing, natural drying, heat, and osmotic stress). When plants were cold-hardened for 5 months, they were able to regenerate both cell structure and metabolism within 24 hours after a 24-hour natural drying regime.

Ezer *et al.* (2010) found that the highest chlorophyll *a/b* ratio occurred in the non-aquatic species, including *Porella platyphylla* (Figure 52-Figure 58), compared to such aquatic species as *Cinclidotus aquaticus* (Figure 74) and *Platyhypnidium riparioides* (Figure 8).

Aydin (2020) looked at free radical scavenging activities in *Porella platyphylla* (Figure 52-Figure 58). He found that the moss *Dicranum scoparium* (Figure 75) has significantly more scavenging activity than does *P. platyphylla*. He noted that there is a strong relationship between phenolic content in methanol extracts and the DPPH (1, 1-diphenyl-2-picrylhydrazyl) radical scavenging efficiency. Fatty acid content was higher in *P. platyphylla* than in *D. scoparium* except for α -linolenic acid.

Reproduction

Porella platyphylla (Figure 52-Figure 58) is **dioicous** (Evans 1899; Heinrichs *et al.* 2011), with male plants that are more slender than the female plants (Evans 1899). Andrews (1908) described an abnormal archegonium in the

species and observed branched elaters in the species. Manning (1914) observed similar abnormal archegonia and described a sporophyte surrounded by a cluster of broad leaves. Shaheen and Srivastava (1986) described the spores of the species using SEM.



Figure 74. *Cinclidotus aquaticus*, a species with a lower chlorophyll *a:b* ratio than that of *Porella platyphylla*. Photo by Hermann Schachner, through Creative Commons.



Figure 75. *Dicranum scoparium*, a moss species with less fatty acid content than that of *Porella platyphylla*, but significantly more free radical scavenging activity. Photo by Richard Orr, with permission.

Interactions

Dudka and Romanenko (2006) enumerated **Myxomycetes** and other organisms associated with *Porella platyphylla* (Figure 52-Figure 58) in Crimea. These included *Arcyria cinerea* (Figure 76), *Echinostelium arboreum* (Figure 77), *E. minutum* (Figure 78), *Macbrideola cornea* (Figure 79), *Perichaena vermicularis* (Figure 80), *Physarum cinereum* (Figure 81), and *Symphytocarpus impexus* (Figure 82-Figure 83). On the other hand, Wang and Qiu (2006) found no publications on mycorrhizal associations with *Porella polyphylla*.



Figure 76. *Arcyria cinerea*, a known associate of *Porella platyphylla*. Photo by George Barron, with permission.



Figure 77. *Echinostelium arboreum*, a species known to associate with *Porella platyphylla*, with two sporocarps showing the persistent shiny peridium. Photo through Creative Commons.



Figure 78. *Echinostelium minutum*, a species known to associate with *Porella platyphylla*. Photo by Carlos de Mier and Carlos Lado, through Creative Commons.



Figure 79. *Macbrideola cornea*, a species known to associate with *Porella platyphylla*. Photo by Shirokikh125.



Figure 80. *Perichaena vermicularis*, a species known to associate with *Porella platyphylla*. Photo by Carlos de Mier and Carlos Lado, through Creative Commons.



Figure 81. *Physarum cinereum*, a species known to associate with *Porella platyphylla*. Photo by Bjorn S., through Creative Commons.



Figure 82. *Symphytocarpus impexus*, a species known to associate with *Porella platyphylla*. Photo from Eumycetozoon Project, www.discoverlife.org, with online permission.



Figure 83. *Symphytocarpus impexus*, a species known to associate with *Porella platyphylla*, showing capillitium and spores. Photo from Eumycetozoon Project, www.discoverlife.org, with online permission.

Smith (2000) contended that most plants in natural ecosystems form mycorrhizal relationships that facilitate acquisition of nutrients. Döbbeler (2004) reported that Ascomata were unknown on epiphytic *Porella platyphylla* (Figure 52-Figure 58) and several other epiphytes. However, he found *Bryocentria metzgeriae* (Figure 84) on this liverwort. This species regularly perforates the leaves of *P. platyphylla*. The Ascomata develop on the protected lower side of the leaf and grow through the single layer of cells so that the ostiolar region is on the side away from the substrate. Occasionally single perithecia may develop in the perianths. Some leaves of *Porella platyphylla* may have several fruiting bodies of *B. metzgeriae* that do not perforate the leaves.

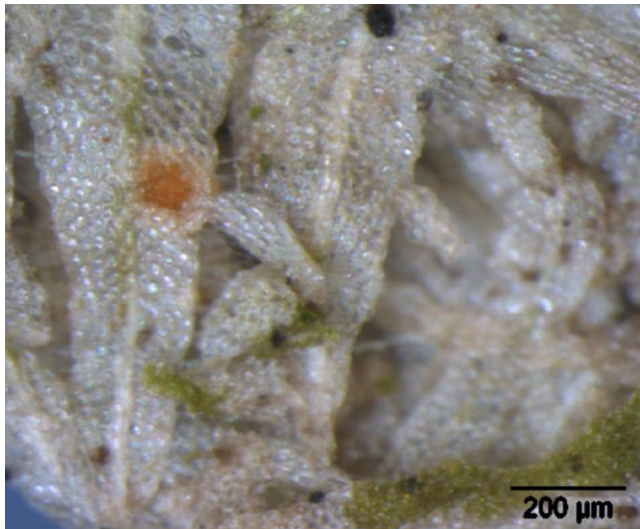


Figure 84. *Bryocentria metzgeriae*, a species of Ascomycetes that penetrates leaves of *Porella platyphylla*. Photo from Bold Systems, through Creative Commons.

Biochemistry

Schuster (1980) reported the oil bodies (Figure 85-Figure 86), a storage site for secondary compounds, to be minute to small. This can cause them to be difficult to notice (Figure 85-Figure 86).

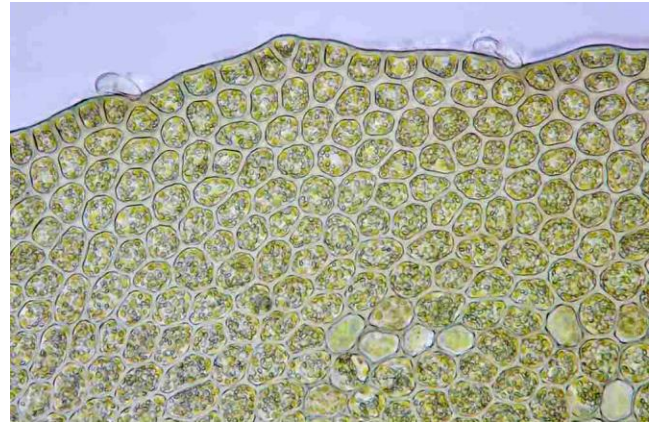


Figure 85. *Porella platyphylla* leaf cells showing numerous small oil bodies. Photo by Kristian Peters, with permission.

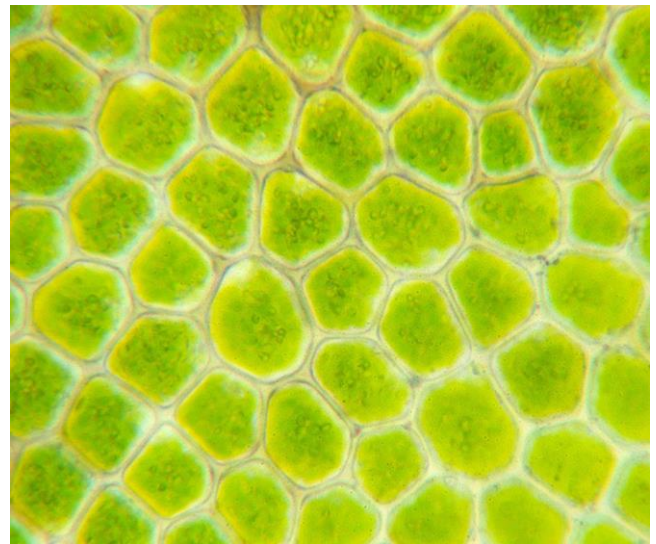


Figure 86. *Porella platyphylla* leaf cells with oil bodies not apparent. Photo by Malcolm Storey, with online permission.

Porella platyphylla (Figure 52-Figure 58) has a variety of color forms (e.g. Figure 87), but the cause of these color changes or forms does not seem to be documented. Nilsson (1969) described pigments in *Porella platyphylla*, identifying the metabolite isovitexin-7-glucoside, a C-glycosyl compound. Nilsson (1973) later identified apigenin-6,8-di-C-glycoside from the same species.



Figure 87. *Porella platyphylla* golden brown form. Photo by Bob Klips, with permission.

Although there seem to be few discussions of the morphological adaptations of *Porella platyphylla* (Figure 52-Figure 58), there have been a number of studies that have used it to study physiology and biochemistry in bryophytes. Suleiman *et al.* (1980) found that polyols are not the primary assimilatory products in *Porella platyphylla*, and they suggested that differences in these products among bryophytes could serve in classifying them.

Perhaps the secondary compounds in *Porella platyphylla* (Figure 52-Figure 58) can account for the scarcity of reports of fungal relationships. Suire and Borgeois (1977) reported monoterpenes in this species. Ludwiczuk *et al.* (2011) identified monoterpenoids, sesquiterpenoids, diterpenoids, flavonoids, and steroids in this species. Asakawa *et al.* (1979) identified three new pinguisane-type sesquiterpenes. Extracts of this species inhibited fungal growth, but only at higher concentrations (15 μ L) compared to effective doses of *Anomodon viticulosus* (Figure 88) and *Cinclidotus fontinaloides* (Figure 39) (5 μ L) (Latinovic *et al.* 2019). Mycelial growth of several fungal species was affected.



Figure 88. *Anomodon viticulosus*, a species that is more effective at inhibiting fungal growth than is *Porella platyphylla*. Photo by Hermann Schachner, through Public Domain.

In their study, Haas *et al.* (1978) found that the external alkane content of *Porella platyphylla* (Figure 52-Figure 58) was only 22.5%, whereas in the moss *Polytrichum commune* (Figure 89) it was up to 44.8%. More work needs to be done to see if this explains the more waxy leaves of *Polytrichum*.

In addition to the antifungal activity, extracts of *Porella platyphylla* (Figure 52-Figure 58) exhibited antimicrobial activity against some gram-positive bacteria (Beike *et al.* 2010). And they inhibited the germination of cress seeds by 30% and lettuce seeds by 40% (Frahm *et al.* 2012).

Many bryophytes have demonstrated medicinal properties. The wound healing ability of *Sphagnum* (Figure 90) is well known. However, Tosun *et al.* (2016) were unable to demonstrate any wound-healing potential in Turkish populations of *Porella platyphylla* (Figure 52-Figure 58), although other liverworts in the study did improve healing.



Figure 89. *Polytrichum commune*, a species with twice the external alkane content of *Porella platyphylla*. Photo by Kristian Peters, through Creative Commons.



Figure 90. *Sphagnum* sp., a genus known for its wound-healing properties. Photo by Janice Glime.

Porella platyphylloidea (Figure 91-Figure 93)

The genus *Porella* is known for its high phenotypic plasticity (Bischler *et al.* 2006). This is further compounded by the presence of more than one clone within a single colony. Whereas the genetic component can differ between cryptic species, the morphological characters often do not. Evans (1916c) separated them by double-spiraled elaters, but others demonstrated that these could occur in both. And even chemical testing with IKI does not separate *Porella platyphylla* (Figure 52-Figure 58) and *P. platyphylloidea* (Figure 91-Figure 93), with both turning purple (Piippo & Norris 1996). The confusing complex that includes *P. platyphylla* and *P. platyphylloidea* is discussed above under *P. platyphylla*. For this chapter, it is probably best to think of the information as referring to *Porella platyphylla/platyphylloidea*. I have kept them separate based on the authors' and photographers' perspectives, but at different points in time, the concepts of these two species have changed.



Figure 91. *Porella platyphylloidea*, part of the complex of cryptic species. Photo by C. Chapman, through Creative Commons.

Distribution

Based on more recent understanding of the species, *Porella platyphylloidea* (Figure 91-Figure 93) occurs from Ontario and Quebec in eastern Canada, south to Florida, and in western North America from British Columbia south to New Mexico and Arizona, USA (Bakalin 2018). It also occurs in Europe.



Figure 92. *Porella platyphylloidea*, a common species in North America and Europe. Photo by KHA, through Creative Commons.

Aquatic and Wet Habitats

Porella platyphylloidea (Figure 91-Figure 93) is usually not a true aquatic, but it is often associated with damp or wet habitats. It occurs in crevices or on the surface of drier cliffs in a ravine in Connecticut, USA (Nichols 1916). Nichols (1918) also found it on rock cliffs associated with streams on Cape Breton Island, Canada.

Iltis (1950) reported it from a moist side of a rock in a stream in Virginia, USA.



Figure 93. *Porella platyphylloidea* dry. Photo by Wayne Lampa, through Creative Commons.

Tree bark is probably the most common habitat for *Porella platyphylloidea* (Figure 94) (e.g. Burnham 1919; Nichols 1922; Fulford 1934; Little 1936a, b; Conard 1940, 1946; Schuster & Patterson 1957; Ehrle & Coleman 1963, 1968; Vitt 1967; Gunderson 1971). But even this habitat is frequently in wet forests. Schuster (1980) considered *Porella platyphylloidea* (Figure 91-Figure 93) to be widely distributed on bark of deciduous trees (Figure 94), frequently as a pioneer. It occurs mostly in open woods. Bakalin (2018) described mostly terrestrial habitats for *Porella platyphylloidea* in North America, noting that these ranged from wet to dry even on bark. Among its terrestrial habitats, Alteri and Coleman (1965) found it on a dead yellow birch (*Betula alleghaniensis*; Figure 95) log in a swamp forest in New York, USA. Darlington (1938) reported it as most common at the bases of trees in damp woods in the Glen Lake area of Michigan, USA.



Figure 94. *Porella platyphylloidea* on bark, the most common substrate for this species. Photo by Jan-Peter Frahm, with permission.



Figure 95. *Betula alleghaniensis*, a substrate for *Porella platyphylloidea* on a dead tree in a swamp in New York, USA. Photo by Joseph OBrien, through Creative Commons.

Adaptations

Porella platyphylloidea (Figure 91-Figure 93) can dry (Figure 96) and rehydrate, then begin photosynthesis and growth again. When it dries, its leaves roll under (Figure 97), making small chambers on the ventral side (Figure 98-Figure 99). We need experiments to see how this structure affects water conservation and water absorption. I would hypothesize that the small spaces take advantage of the adhesion and cohesion of water to hold water droplets. At the same time, the underleaves, lobes, and dorsal leaves combine to reduce surface area and thus reduce the rate of evaporation.



Figure 96. *Porella platyphylloidea* dry on a vertical substrate, showing the wiry appearance of dry plants. Photo by BKChallenge, through Creative Commons.

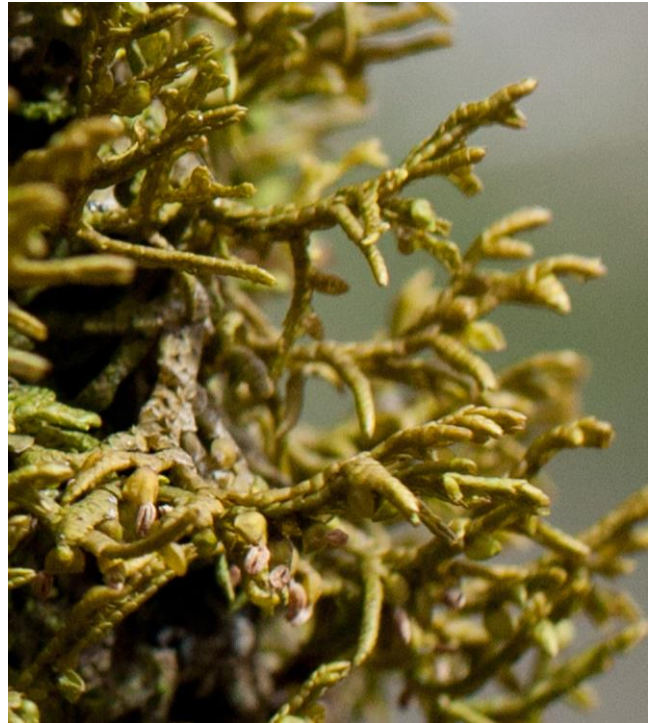


Figure 97. *Porella platyphylloidea* showing the reduction in surface area caused by the curling of the leaves around the stem. Photo by BKChallenge, through Creative Commons.



Figure 98. *Porella platyphylloidea* dry, showing leaves rolling to the under side of the stem. Photo by Bob Klips, with permission.



Figure 99. *Porella platyphylloidea* dry, showing overlapping leaves, lobes, and underleaves on the under side. Photo by Alex Graeff, through Creative Commons.

Reproduction

Schuster (1980) describes *Porella platyphylloidea* (Figure 91-Figure 93) as **dioicous** and usually fertile. The spores are large. It lacks any specialized asexual reproductive structures. Thus we must assume that its sexual reproduction is relatively successful because the species is widespread and relatively common (whether it is *P. platyphylla* or *P. platyphylloidea*). Nevertheless, we cannot rule out dispersal of fragments, a feat that might be accomplished by birds gathering nesting materials or insects that carry very small fragments.

Biochemistry

Unlike those of *Porella platyphylla* (Figure 52-Figure 58), few studies have described the biochemistry of *Porella platyphylloidea* (Figure 91-Figure 93), at least by this name. Ludwiczuk *et al.* (2011) noted that it possessed flavonoids that might be useful as a taxonomic tool.

Summary

I found only four species in the **Porellaceae** that were associated with wet habitats. The most distinctive aquatic representative of these is *Porella pinnata* growing on cypress knees in swamps and marking a broad high water line. *Porella cordaeana* is occasionally submerged on rocks in fast water. *Porella polyphylla* is sometimes associated with intermittent streams and streambanks. *Porella platyphylloidea* is often growing epiphytically on trees in moist or wet habitats.

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CHAPTER 1-10

AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA: RADULACEAE AND PTILIDIACEAE

TABLE OF CONTENTS

Porellales – Suborder Porellineae.....	1-10-2
Radulaceae.....	1-10-2
<i>Radula aquilegia</i>	1-10-2
<i>Radula carringtonii</i>	1-10-5
<i>Radula complanata</i>	1-10-6
<i>Radula holtii</i>	1-10-12
<i>Radula lindenbergiana</i>	1-10-13
<i>Radula obconica</i>	1-10-16
<i>Radula prolifera</i>	1-10-18
<i>Radula voluta</i>	1-10-19
<i>Radula wichurae</i>	1-10-21
Ptilidiales.....	1-10-21
Ptilidiaceae.....	1-10-21
<i>Ptilidium ciliare</i>	1-10-21
<i>Ptilidium pulcherrimum</i>	1-10-28
Summary.....	1-10-31
Acknowledgments.....	1-10-31
Literature Cited.....	1-10-31

CHAPTER 1-10

AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA: RADULACEAE AND PTILIDIACEAE

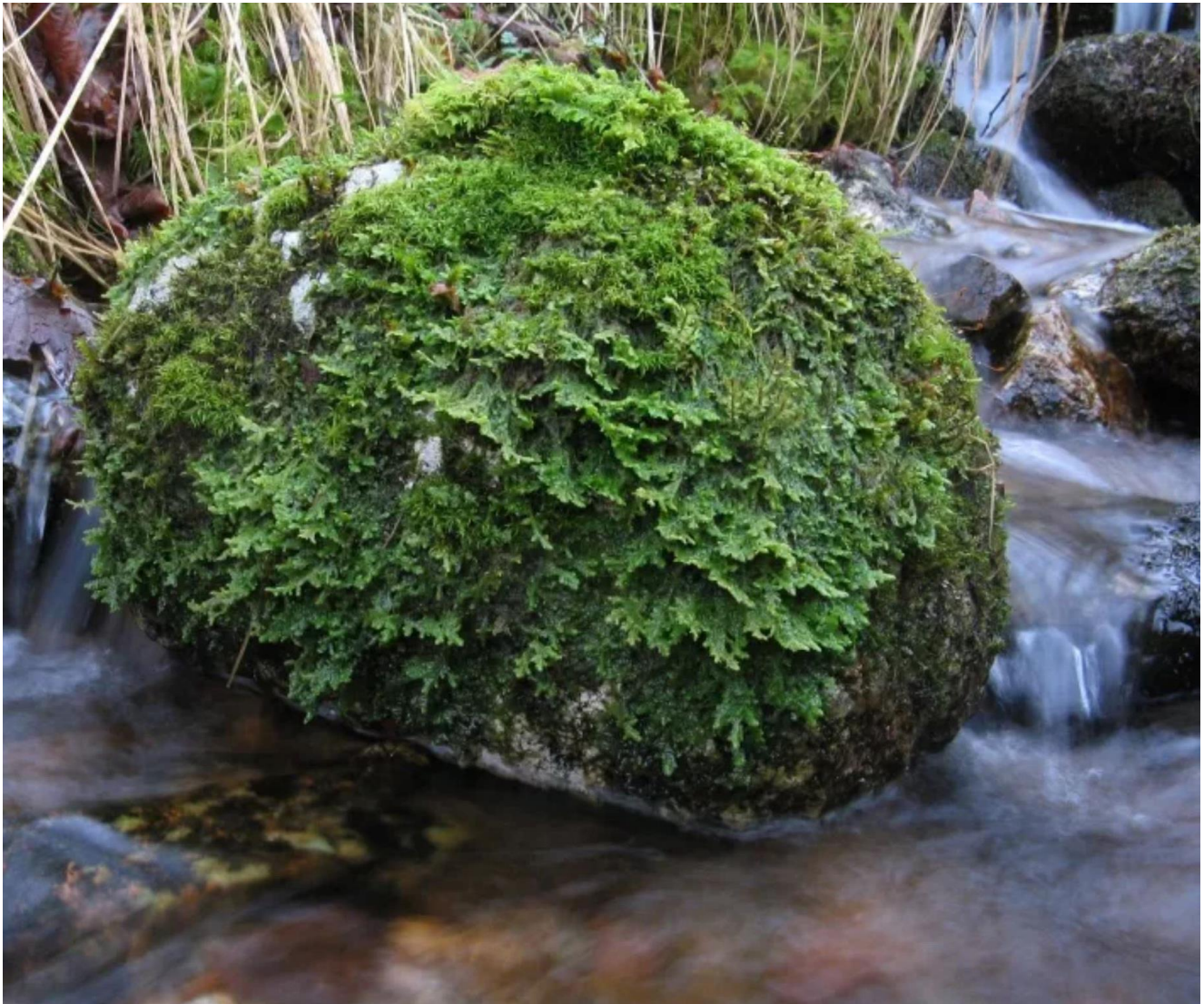


Figure 1. *Radula voluta* on a rock, typical of its more aquatic habitat. This colony is likely to be submerged during times of increased flow. Photo by Stan Phillips, through public domain.

Porellales – Suborder Radulineae Radulaceae

Radula aquilegia (Figure 2-Figure 3)

Distribution

Radula aquilegia (Figure 2-Figure 3) is distributed in Africa (Jones 1977), Australia, Europe, and Asia (ITIS

2020), including China and the Himalayas (Damsholt 2017). In Europe *R. aquilegia* occurs in Norway, the Faroes, British Isles, Iberian Peninsula, and Macaronesia (Söderström *et al.* 2002). In mainland Portugal it was considered extinct (Luís *et al.* 2005), but Cecília Sergio later rediscovered it there (Söderström *et al.* 2002; Luís *et al.* 2005). However, that appears to be a misidentification, once again making it absent in mainland Portugal (Luís *et al.* 2005).



Figure 2. *Radula aquilegia*, a leafy liverwort distributed in Africa, Australia, Europe, and Asia. Photo by Michael Lüth, with permission.

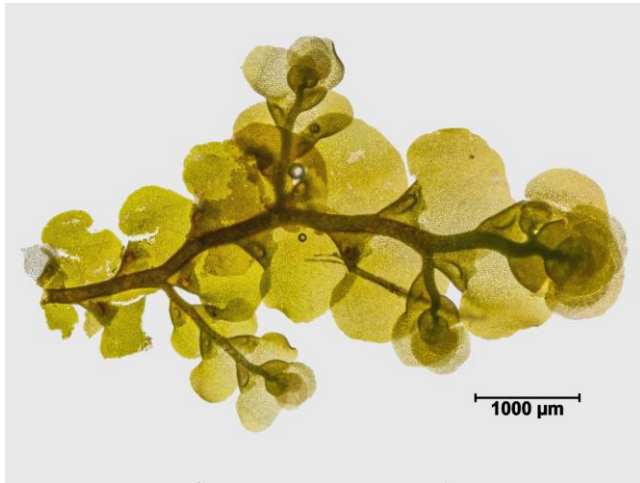


Figure 3. *Radula aquilegia* showing leaf lobes. Photo by Kristian Peters, with permission.

Aquatic and Wet Habitats

Watson (1919) reported that *Radula aquilegia* (Figure 2-Figure 3) is occasionally submerged, but that is not its primary habitat. Rothero (2005) reported that this species can occur in ravines in Scotland. Damsholt *et al.* (1980) similarly reported it from moist rock faces in a wooded ravine in Scotland, and Bosanquet (2015) found it in Wales in a humid area near a waterfall, but not in the direct splash.

For bryophytes that occur in the water, rocks are the typical substrate. Even the facultatively aquatic species *Radula aquilegia* (Figure 2-Figure 3) occurs frequently on rocks. In Scotland, it lives on shaded rocks (Rothero 2005). Heegaard (1997) reported it from small crevices in the Bergen area, Hordaland, Norway. Hassel *et al.* (2014) found it on a cliff wall in Norway where a stream at the base of the cliff maintained moisture. Ratcliffe (1968) likewise found indications of a preference for moist habitats, finding the species on rocks that were in damp, shady locations, especially in areas with the heaviest rainfall.

Radula aquilegia also occurs both as an epiphyte and an epiphyll. Frahm (2005) reported *Radula aquilegia* (Figure 2) from bark in the Azores. Luís *et al.* (2005) reported it from stems, trunks, and roots of *Laurus azorica* (Figure 4), *Erica arborea* (Figure 5-Figure 7), and *E.*

cinerea (Figure 8) on Madeira. It sometimes even occurs on other bryophytes such as the wet-habitat moss *Thamnobryum* (Figure 9). It can even be epiphyllous on this moss (Sjögren 1975).



Figure 4. *Laurus azorica*, a woody species where *Radula aquilegia* can grow on stems, trunks, and roots on Madeira. Photo by Ixitixel, through Creative Commons.



Figure 5. *Erica arborea*, a woody species where *Radula aquilegia* can grow on stems, trunks, and roots on Madeira. Photo by Ehoarn Bidault, through Creative Commons.



Figure 6. *Erica arborea* showing flowers, leaves, and twigs; *Radula aquilegia* can grow on its stems, trunks, and roots. Photo by Ehoarn Bidault, through Creative Commons.



Figure 8. *Erica cinerea*, a woody species where *Radula aquilegia* can grow on stems, trunks, and roots on Madeira. Photo by Dirk Hilbers, through Creative Commons.



Figure 7. *Erica arborea* showing upright stems where *Radula aquilegia* can grow on Madeira. Photo by Ehoarn Bidault, through Creative Commons.



Figure 9. *Thamnobryum alopecurum*, a moss where one might find *Radula aquilegia* as an epiphyll. Photo by David T. Holyoak, with permission.

Adaptations

Clausen (1964) experimented with *Radula aquilegia* (Figure 2-Figure 3) from the Faroe Islands. At 15% relative humidity, only about 25% of the cells remained alive for 12 hours at 20°C (Figure 10). At 35% humidity, all cells survived for 12 hours (Figure 10).

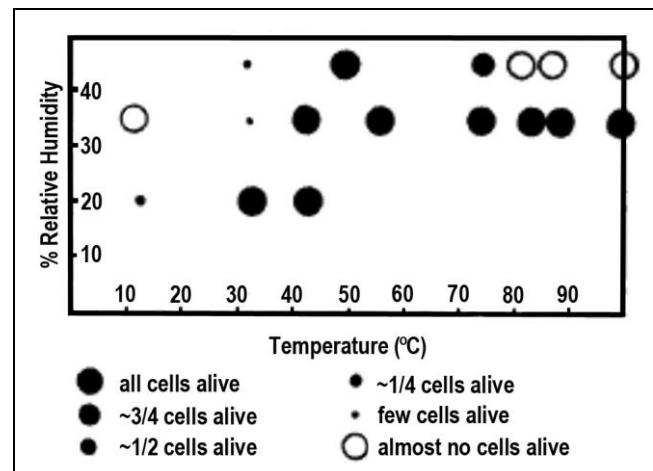


Figure 10. Relationship of temperature and relative humidity on the cell viability of *Radula aquilegia* after 12 hours of exposure. Redrawn from Clausen 1964.

Lloret and González-Mancebo (2011) considered *Radula aquilegia* (Figure 2-Figure 3) to be a **long-lived shuttle** species on the Canary Islands. Kürschner *et al.* (2007) noted that species on Madeira island benefitted from the humidity and shade of the undisturbed laurel forests, favoring **mat** (Figure 11) and **fan** (Figure 12) **perennial stayers** and **perennial shuttle** species. These species typically have moderately low sexual and asexual reproduction. In the ericaceous woodland, on the other hand, the habitat is more xeric and sunny, favoring **tall** and **short turf** but also **perennial stayers** and **perennial shuttle** species. These, however, have high levels of sexual reproduction. *Radula aquilegia* occurs in both woodland types. As an epiphyte it is typically **mat-forming** (Figure 11). Its sexual reproduction is limited.

Reproduction

Radula aquilegia is **dioicous** (Bouman & Dirkse 1990; Damsholt 2017). Damsholt found a male plant in the Faeroes, but no sporophytes have been found in the Faeroes. Sporophytes are rare in Great Britain. Lloret and González-Mancebo (2011) likewise noted limited sexual reproduction in the Canary Islands. Leaves never have gemmae (Bouman & Dirkse 1990).



Figure 11. *Radula aquilegia* forming a mat on bark. Photo by Gordon Rothero, with permission.

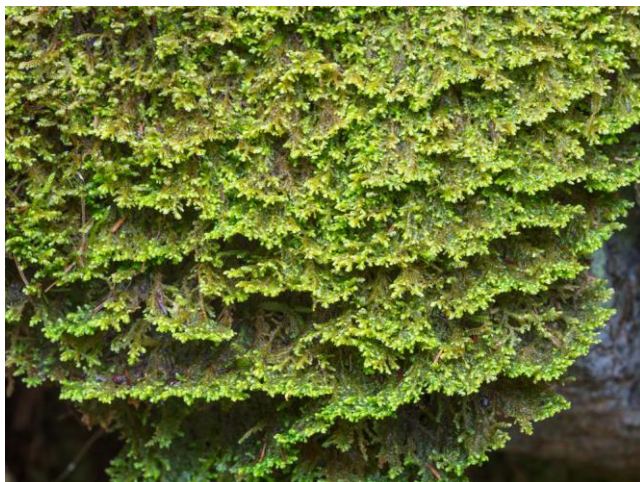


Figure 12. *Radula aquilegia* exhibiting the **fan** life form typical in high humidity habitats. Photo by Kristian Peters, with permission.

Fungal Interactions

Wang and Qiu (2006) were unable to find any records of mycorrhizae in *Radula aquilegia* (Figure 2-Figure 3). Apparently none of the oils from this species has been tested for antifungal or other activity.

Biochemistry

Figueiredo *et al.* (2009) extracted volatiles from seven species of *Radula* from the Azores and Madeira as well as mainland Portugal and Switzerland. One cluster of species, including *R. aquilegia* (Figure 2-Figure 3) from the Azores, exhibited large amounts of several sesquiterpenes from the oil bodies (Figure 13-Figure 14). Most of the species could be distinguished by their oil components, but in these tests, *R. aquilegia* could not be separated from *R. complanata* (Figure 18-Figure 20) or *R. lindenbergiana* (Figure 50-Figure 53).

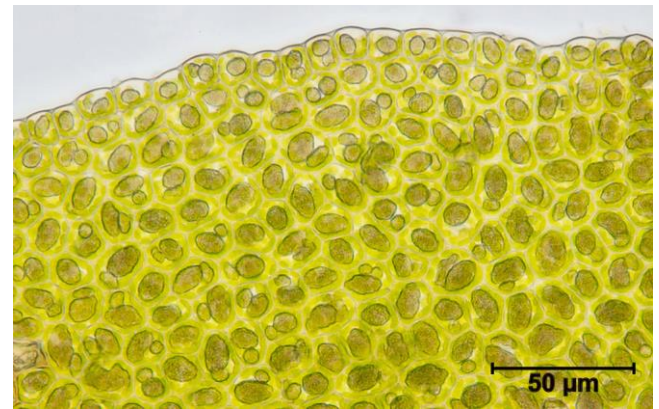


Figure 13. *Radula aquilegia* leaf cells with oil bodies. Photo by Kristian Peters, with permission.

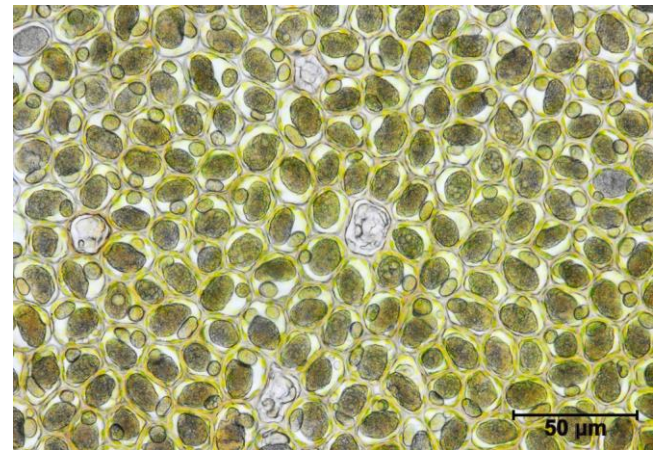


Figure 14. *Radula aquilegia* leaf cells with oil bodies. Photo by Kristian Peters, with permission.

Radula carringtonii (Figure 15-Figure 16)

Distribution

Radula carringtonii (Figure 15-Figure 16) has a narrow distribution in Scotland, Ireland, and Macaronesia (Bouman & Dirkse 1990). Later Yamada (1995) added Costa Rica, Central America, British Isles, and Spain. Yamada later (2000) reported it from Bolivia. Longton and Hedderson (2000) considered the species to be rare.



Figure 15. *Radula carringtonii* forming a **mat**, a species with known volatiles that are the same as those in *Radula lindenbergiana*. Photo by David T. Holyoak, with permission.

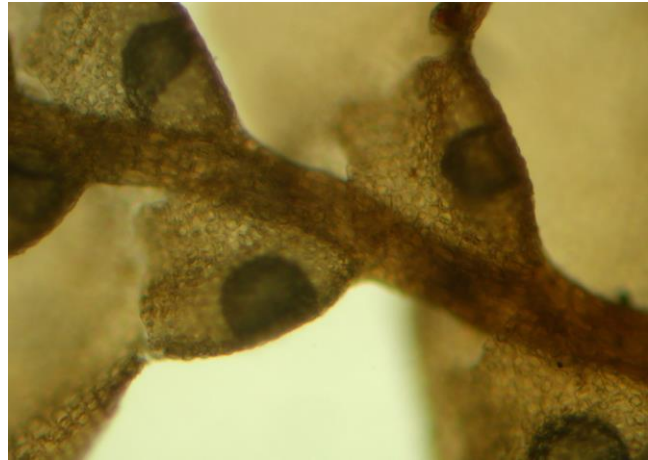


Figure 17. *Radula nudicaulis*, a species that can be separated from *Radula carringtonii* by its chemistry. Photo by Nidia Homem, with permission from Rosalina Gabriel.

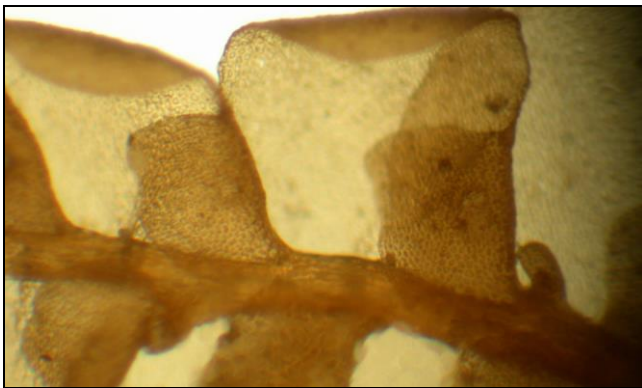


Figure 16. *Radula carringtonii* showing leaf lobes. Photo by Nidia Homem, with permission from Rosalina Gabriel.

Aquatic and Wet Habitats

Radula carringtonii (Figure 15-Figure 16) occurs on periodically wet rocks in the dense forests of Macaronesia (Bouman & Dirkse 1990).

Adaptations

The cell walls of *Radula carringtonii* (Figure 15-Figure 16) are thickened with trigones (Bouman & Dirkse 1990), a character that could add strength, but I don't know its value in this habitat, if any.

Reproduction

Radula carringtonii (Figure 15-Figure 16) is **dioicous** (Bouman & Dirkse 1990). The leaves never have gemmae. Therefore, we must assume it reproduces mostly by fragments. This limited reproduction can account for its narrow distribution.

Biochemistry

Mues (1984; Figueiredo 2009) reported flavone glycosides from *Radula carringtonii* (Figure 15-Figure 16). Stech *et al.* (2010) found that *R. aquilegia* (Figure 2-Figure 3), *R. carringtonii*, *R. complanata* (Figure 18-Figure 20), *R. holtii* (Figure 43), *R. jonesii*, *R. lindenbergiana* (Figure 50-Figure 53), *R. nudicaulis* (Figure 17), and *R. wichurae* (Figure 54) could be separated based on their chemistry.

Radula complanata (Figure 18-Figure 20)

Distribution

Radula complanata (Figure 18-Figure 20) is widely distributed in North America, Europe, Asia, and northern Africa (Stevens 1910), Greenland, and South America (Krayesky *et al.* 2018). It seems to be nearly absent from the tundra and lowland tropics (Krayesky *et al.* 2018). On Mount Musa in Turkey, *Radula complanata* is one of the three most common species of liverworts (Ezer *et al.* 2009). In the coastal area of the Ukrina River, Bosnia and Herzegovina, *Radula complanata* is the only bryophyte present (Šarčević-Todosijević & Šarčević 2018).



Figure 18. *Radula complanata*, a leafy liverwort widely distributed in North America, Europe, Asia, and northern Africa, Greenland, and South America. Photo by Allen Norcross, with permission.



Figure 19. *Radula complanata* showing leaf lobes. Photo by Sture Hermansson, with online permission.



Figure 20. *Radula complanata* showing leaf lobes and collected detrital material. Photo courtesy of Norbert Ethan.

Aquatic and Wet Habitats

Krayesky *et al.* (2018) reported that *Radula complanata* (Figure 18-Figure 20) is **epicortic** (growing on bark), **epilithic** (growing on rock), and **terricolous** (living on ground), occurring in various habitats, including oceanside cliffs, peatlands, woodlands, waste places, riparian habitats, and subalpine crags. But it does indeed occupy wetter habitats such as wet or moist cliffs of ravines in Connecticut, USA (Nichols 1916); rock cliffs associated with streams, Cape Breton Island, Canada (Nichols 1918); streams characterized by the *Platyhypnidium-Fontinalis antipyretica* association, Thuringia, Germany (Marstaller 1987); aquatic and on vertical surfaces and moist habitats in Finland (Koponen *et al.* 1995; Virtanen 1995); on bark of *Fagus* and *Fraxinus*, at a stream in Tara River canyon and Durmitor area, Montenegro (Papp & Erzberger 2011); in Ibar gorge, along the River Ibar (Papp *et al.* 2016). Alataş *et al.* (2017) considered it a hygrophyte in Turkey.

Coker (1993) reported *Radula complanata* (Figure 18-Figure 20) from branches that emerged above the winter water level. It occurred in **turloughs** (in Ireland, low-lying areas on limestone that become flooded in wet weather through welling up of groundwater) with their highest water level in winter.

There are few reports of *Radula complanata* (Figure 18-Figure 20) on rocks. Papp *et al.* (2016) reported it from shaded serpentine rock in the Ibar gorge of southwest

Serbia. Hallingbäck and Holmåsén (1982) found it on rocks in Sweden. It occupies both acidic and basic substrates (Krayesky *et al.* 2018).

Adaptations

Šarčević-Todosijević and Šarčević (2018) considered *Radula complanata* (Figure 18-Figure 20) to be a **hemicryptophyte** (perennial plant having overwintering buds located at soil surface), a term usually reserved for tracheophytes. It nevertheless does describe the habit of this species to occur on the ground in the Ukrina River area of Bosnia and Herzegovina. Krayesky *et al.* (2018) described it as growing in **mats** (Figure 21) or among other bryophytes. On the other hand, Alataş *et al.* (2017) considered the species of epiphytes in Turkey to be mostly **weft** and **cushions** that are **perennial stayers**. That is consistent with the observations of Hazell *et al.* (1998) in Sweden, where *Radula complanata* forms **wefts** that adhere tightly to the bark surface.



Figure 21. *Radula complanata* forming a mat. Photo by Allen Norcross, with permission.

Reproduction

Radula complanata (Figure 18-Figure 20) has no **caducous** (falling off easily) leaves, but has asexual reproduction through discoid gemmae that are usually not only present, but numerous (Stevens 1910; Krayesky *et al.* 2018). Furthermore, gemma production is not suppressed by development of sexual structures (Stevens 1910), as is common in many bryophytes. At maturity, the gemmae are 2 cells thick throughout most of the gemma, presumably improving survivability during and after dispersal. The species is **paroicous** [having male (Figure 22) and female reproductive organs (Figure 23-Figure 25) beside or near each other] and often fertile (Krayesky *et al.* 2018), all of which suggest that it has a high reproductive potential (Figure 26-Figure 30) and may explain its wide distribution. Alataş *et al.* (2017) considered high sexual reproductive activity to be the dominant life strategy among the epiphytes at the Boraboy and Destek Forests in Turkey, an ideal location for the spread of windborne spores. This species produces copious spores (Arnell 1956; Nyholm 1954-1969; During 1992). On the other hand, Castle (1925) considered sexual structures to be rare in North America, especially when gemmae (Figure 31-Figure 36) were abundant.



Figure 22. *Radula complanata* antheridium in leaf axil. Photo courtesy of Norbert Ethan.



Figure 23. *Radula complanata* with numerous perianths. Photo by Andrew Hodgson, with permission.



Figure 24. *Radula complanata* with perianths. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

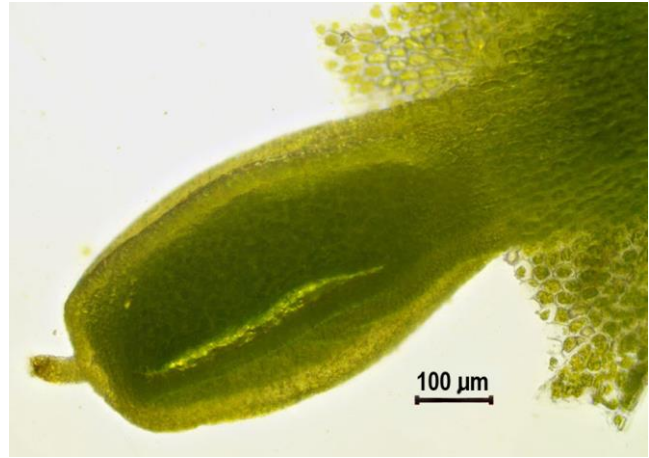


Figure 25. *Radula complanata* perianth. Photo courtesy of Norbert Ethan.



Figure 26. *Radula complanata* with capsules before seta elongation. Photo by Hermann Schachner, through Creative Commons.



Figure 27. *Radula complanata* with capsules and elongated seta. Photo by Andrew Hodgson, with permission.



Figure 28. *Radula complanata* with dehiscent capsules. Photo by Hermann Schachner, through Creative Commons.



Figure 31. *Radula complanata* with gemmae. Photo by J C. Schou, Biopix, through Creative Commons.



Figure 29. *Radula complanata* capsule dehiscing. Photo courtesy of Norbert Ethan.



Figure 32. *Radula complanata* with perianths, dorsal view. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

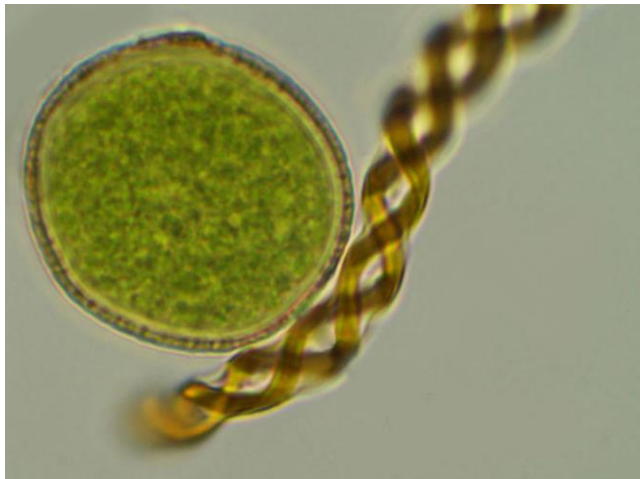


Figure 30. *Radula complanata* spore and elater. Photo courtesy of Norbert Ethan.

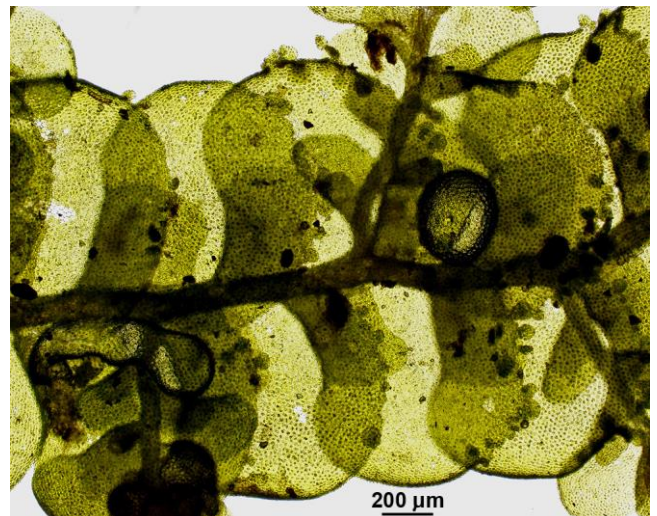


Figure 33. *Radula complanata* with gemmae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

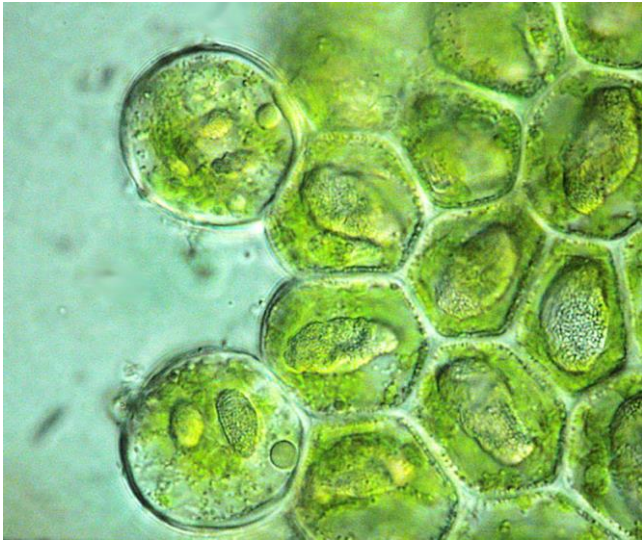


Figure 34. *Radula complanata* gemmae. Photo by Walter Obermayer, with permission.

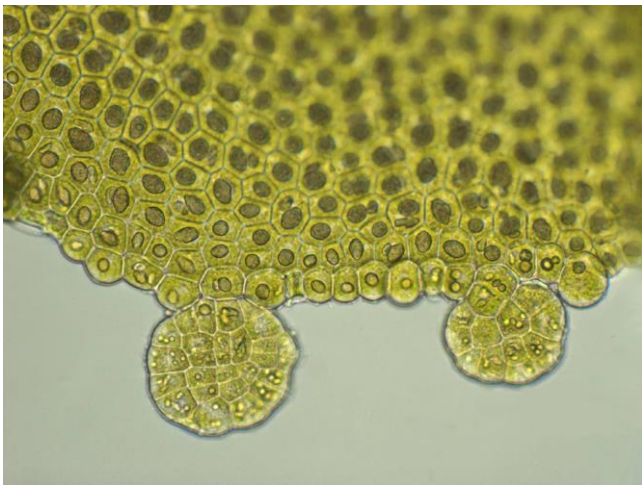


Figure 35. *Radula complanata* multicellular gemmae on leaf margin. Photo by Blanka Agüero, with permission.



Figure 36. *Radula complanata* gemmae. Photo by Walter Obermayer, with permission.

Heylen and Hermy (2008) implied that *Radula complanata* (Figure 18-Figure 20) might not be a good competitor. This species appears to be a good disperser,

and thus is typically a pioneer on trees, reaching a maximum at 2-3 years, but then declining. They considered that its inability to colonize new patches at that stage was due to the presence of other bryophytes, particularly larger ones. Thus, good dispersal is definitely an advantage and a common adaptation for a pioneer.

Mehra and Pathania (1959) reported a chromosome number of $n=6$ for western Himalayan populations, noting that the diploid is present in the Himalayas. But Kapila (2016) reported the chromosome number as $n=9$ for some Indian populations.

Role

A number of bryophytes serve as habitat for testate amoebae (Davidova *et al.* 2016). *Radula complanata* (Figure 18-Figure 20) is among a group of bryophytes with protozoan species numbering 11-14, but it had the lowest number of dominants (three), compared to *Brachythecium velutinum* (Figure 37) with eight. *Radula complanata* did, however, have the most specific and different fauna of these testate amoebae. *Euglypha ciliata glabra* (Figure 38) was the dominant amoeba species on this liverwort.



Figure 37. *Brachythecium velutinum* with capsules, a species with more dominant protozoan species than found on *Radula complanata*. Photo by Michael Lüth, with permission.

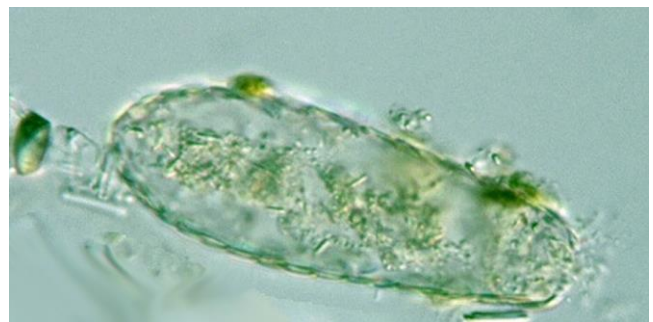


Figure 38. *Euglypha ciliata*, a testate protozoan that inhabits *Radula complanata*. Photo by Yuuki Tsujii, with permission.

In addition to protozoa, *Radula complanata* (Figure 18-Figure 20) is inhabited by *Mesostigmata* mites, at least in forests of Latvia (Salmane 2007). *Holoparasitus excipuliger*, *Pergamasus crassipes* (Figure 39), *Pergamasus parinteger*, and *Pergamasus wasmanni* inhabited *R. complanata* in the deciduous forest.



Figure 39. *Pergamasus crassipes* ventral side. Photo by Matthew Shepherd, through Creative Commons.

Fungal Interactions

Döbbeler (2004) reported the new *Ascomycetes* genus *Bryocentria* (Figure 40) from *Radula complanata* (Figure 18-Figure 20) as well as other bryophytes. It produces small, orange-colored perithecia and is parasitic on bryophytes. The presence of *Bryocentria metzgeriae* (Figure 40) on *Radula complanata*, but not on *Radula lindenbergiana* (Figure 50-Figure 53) suggested to Döbbeler that corticolous hosts are preferred; *R. complanata* appeared to be an excellent host, but not the only host. Could it be a difference in secondary compounds?

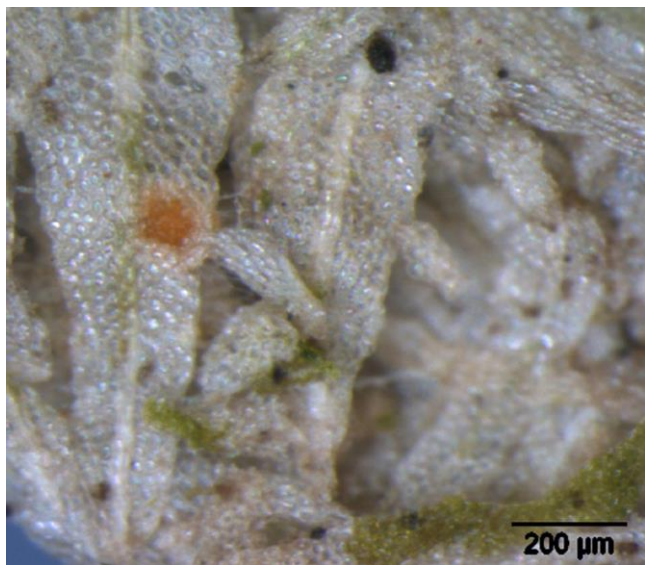


Figure 40. *Bryocentria metzgeriae* on *Metzgeria*. Photo from Bold Systems, through Creative Commons.

Biochemistry

Rattray (1886) noted that *Radula complanata* (Figure 18-Figure 20) has oil bodies (Figure 41) that are embedded in a medium with a different refractive index. The oil bodies of *Radula complanata* are usually limited to one per cell and are conspicuous (Krayesky *et al.* (2018). Flegel and Becker (2000) characterized the contents of these oil bodies in *Radula complanata* and determined that 3-methoxybibenzyl is the main constituent.

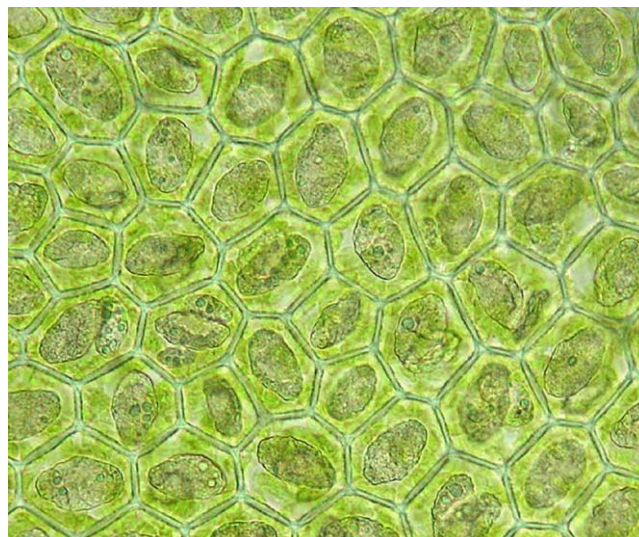


Figure 41. *Radula complanata* cells showing massive oil bodies. Photo by Walter Obermayer, with permission.

Figueiredo *et al.* (2009) reviewed the known volatile composition of *Radula* species from Portugal. Suire (1970) identified α -pinene, β -pinene, camphene, six sesquiterpenes (including b-caryophyllene), and 3-methoxybibenzyl in *Radula complanata* (Figure 18-Figure 20). In Japanese populations, Asakawa *et al.* (1978) identified methanol bibenzyls in *Radula complanata*. Asakawa *et al.* (1982) reported ether + methanol extractions of bibenzyls and one sesquiterpene from French populations (see also Takikawa *et al.* 1989). Asakawa *et al.* (1991) reported prenyl bibenzyls from this species and identified Radulanin. Mues (1984) used an array of populations from Canada, Austria, France, Germany, Italy, Poland, Spain, and Switzerland, reporting on aqueous methanol flavone glycosides. Markham and Mues (1984) made aqueous extracts of flavone glycoside from Swiss populations.

Asakawa *et al.* (1991) provided an idea of the activity of some of these compounds. For example, some prenyl-containing bibenzyls exhibited 5-lipoxygenase and calmodulin inhibitory activity and vasopressin antagonist activity. Nikolajeva *et al.* (2012) were unable to demonstrate any antibacterial activity against the bacterium *Staphylococcus aureus* (Figure 42).

One of the roles of some secondary compounds is to inhibit the growth of fungi. But in many cases, fungi are common on bryophytes. The *Ascomycete* *Belonioscyphella hypnorum* uses *Radula complanata* (Figure 18-Figure 20) as one of its bryophyte hosts in calcareous areas of the Czech Republic (Egertová *et al.* 2016).

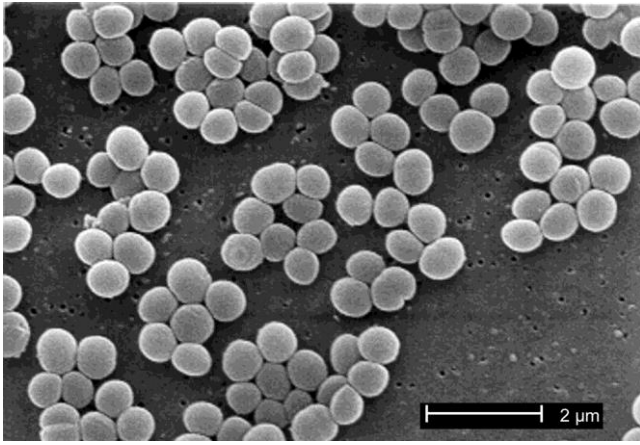


Figure 42. *Staphylococcus aureus* SEM. Photo from CDC - Matthew J. Arduino and Janice Carr, through public domain.

***Radula holtii* (Figure 43)**

Figueiredo *et al.* (2009) used volatile compounds as chemotaxonomic characters to separate species of *Radula* from Portugal. They were able to differentiate geographic populations based on their chemistry, separating *R. holtii* (Figure 43) on the mainland from that of Madeira.

Distribution

Luís *et al.* (2005) reported that *Radula holtii* (Figure 43) was confined to Ireland, the Iberian Peninsula, and Macaronesia. Pescott (2016) reported it as new for Britain. Geissler *et al.* (1997) found that this species is rare wherever it occurs.

Aquatic and Wet Habitats

Radula holtii (Figure 43) occurs in water splash or steep, dripping granite surfaces deeply shaded by surrounding vegetation (Vieira *et al.* 2005). It is typically associated with *Thamnobryum alopecurum* (Figure 9), *Dumortiera hirsuta* (Figure 44-Figure 45), *Pellia epiphylla* (Figure 46), *Plagiothecium nemorale* (Figure 47), and *Fissidens polyphyllus* (Figure 48), in mountain streams of northwest Portugal. Ferreira *et al.* (2008) reported it from rivers. Geissler *et al.* (1997) reported it from wet rocks in southwest Ireland, Spain, Portugal, and Macaronesia.

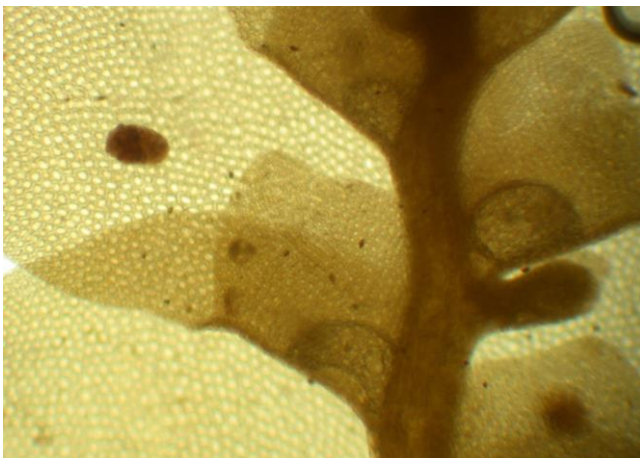


Figure 43. *Radula holtii* leaves and lobes. Photo by Nidia Homem, with permission from Rosalina Gabriel.



Figure 44. *Dumortiera hirsuta* showing a typical habitat; it is often associated with *Radula holtii*. Photo by Michael Lüth, with permission.

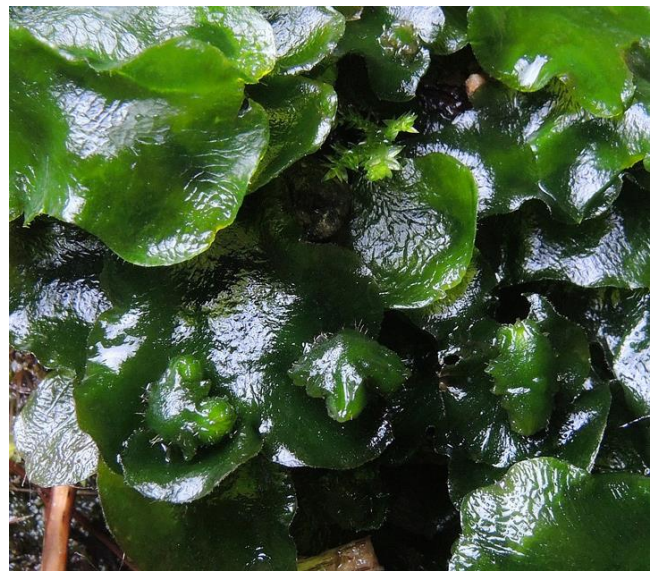


Figure 45. *Dumortiera hirsuta*, a species often associated with *Radula holtii*. Photo by Michael Lüth, with permission.



Figure 46. *Pellia endiviifolia*, a species often associated with *Radula holtii*. Photo by David T. Holyoak, with permission.



Figure 47. *Plagiothecium nemorale*, a species often associated with *Radula holtii*. Photo by Hermann Schachner, through Creative Commons.



Figure 48. *Fissidens polyphyllus*, a species often associated with *Radula holtii*. Photo by David T. Holyoak, with permission.

Vieira *et al.* (2016) considered *Radula holtii* (Figure 43), a species already rare, to be vulnerable to hydrologic change such as that created by hydroelectric plants. This species prefers 1st to 3rd order mountain streams with permanent flow. In its localities in Ireland, Scotland, Iberian Peninsula, and Macaronesia these streams run through vertical granite surfaces where they create dripping rocks and spray zones in deeply shaded niches. It also occurs in drainage ditches of a thermal park. In these habitats they were often associated with a similar group of species as found in mountain streams: *Thamnobryum alopecurum* (Figure 9), *Dumortiera hirsuta* (Figure 44-Figure 45), *Pellia epiphylla* (Figure 46), *Plagiothecium nemorale* (Figure 47), *Fissidens polyphyllus* (Figure 48) (Vieira *et al.* 2005). It forms medium-sized pure patches near these and other hygrophilic and hydrophilic species. It also occurs on granite walls on river margins in northwestern Portugal (Vieira *et al.* 2007). Monteiro and Vieira (2017) likewise reported this vulnerable species from headwater streams in northwest and central west Portugal, being of "great interest" in waterfalls and on dripping walls. Vieira *et al.* (n.d.) found them in a pH range of 6.8 to 7.2 and clean to moderately polluted waters.

They occupied slopes of 30-100%. O'Reilly (2020) summarized the habitat in Britain as growing where it is easily overlooked in deep shade on dripping rocks, in caves, by waterfalls, or in ravines.

Among the terrestrial habitats that suffice or encourage the development of bryophyte populations are cave entrances – habitats that can remain cooler and moister than the surrounding habitats. Among these cave-dwelling bryophytes is *Radula holtii* (Figure 43) (Gabriel *et al.* 2018). This species occurs at cave entrances in the Azores, but these habitats are threatened by climate change, severe weather, habitat change and degradation, and invasive plant species.

Adaptations

Radula holtii is green to olive-green, becoming more olive-green with age. The leaf cell walls are thin and lack trigones.

Reproduction

Radula holtii (Figure 43) is **paroicous** (Bouman & Dirkse 1990; O'Reilly 2020), but its sexual reproduction is apparently rare. O'Reilly (2020) stated that its perianths (Figure 49) are rarely produced, but when present they are of taxonomic importance. Furthermore, it "almost never has gemmae." Vieira *et al.* (n.d.) noted that it does sometimes produce perianths and sporophytes in the northwest Portugal populations. Leaf gemmae unknown (Bouman & Dirkse 1990).



Figure 49. *Radula holtii* with rarely occurring perianths. Photo by Rory Hodd, with permission.

Radula lindenberghiana (Figure 50-Figure 53)

(syn. = *Radula lindberghiana*)

Radula lindenberghiana (Figure 50-Figure 53) and *R. complanata* (Figure 18-Figure 20) are difficult to separate in the field when they lack reproductive structures (Kürschner *et al.* 2012). It has at times been considered a subspecies of *Radula lindenberghiana* (Stech *et al.* 2010).



Figure 50. *Radula lindenberghiana*. Photo by Jan-Peter Frahm, with permission.



Figure 51. *Radula lindenberghiana*, a species known from Macaronesia, Europe, Africa, and North America. Photo by Hermann Schachner, through Creative Commons.

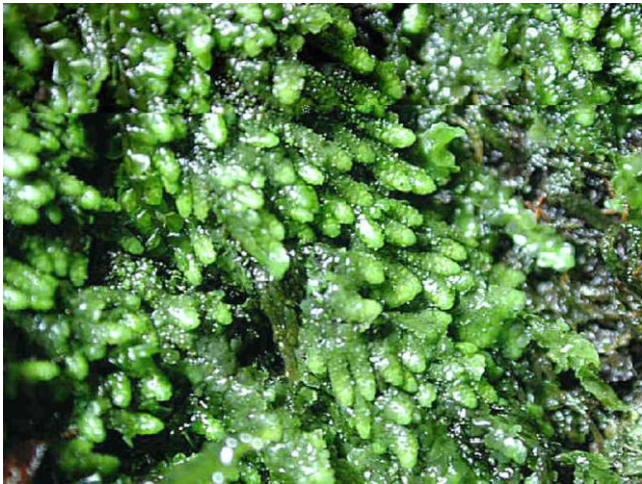


Figure 52. *Radula lindenberghiana* in a wet condition. Photo by Michael Lüth, with permission.

Figueiredo *et al.* (2009) used volatiles to separate species in *Radula* from Portugal. However, they found no geographic separation for *R. carringtonii* (Figure 15-Figure 16), *R. wichurae* (Figure 54), and *R. lindenberghiana* (Figure 50-Figure 53). Laenen *et al.* (2011) considered Macaronesian populations to be a source of genetic diversity in the post-glacial recolonization of western Europe by *R. lindenberghiana*. DNA results suggest that

the mutation rate exceeds the dispersal rate in this species. Laenen and coworkers concluded that Macaronesia most likely served as a refugium during Quaternary glaciations.



Figure 53. *Radula lindenberghiana*, Madeira. Michael Lüth, with permission.



Figure 54. *Radula wichurae*, a species with known volatiles that are the same as those in *Radula lindenberghiana*. Photo by Nídia Homem, with permission from Rosalina Gabriel.

Distribution

Laenen *et al.* (2011) sampled *Radula lindenberghiana* (Figure 50-Figure 53) in Macaronesia, Europe, and Africa. Gökler (1998) listed its known distribution from Turkey (Özenoğlu & Gökler 2002), Europe, Russia, Caucasus, Iran, Korea, Japan, Taiwan, Himalayas, Tunisia, Morocco, Algeria, Greenland, and S. Africa. To these, Figueiredo *et al.* (2009) added Austria, Azores, Portugal, Canary Islands, Spain, Crete, Germany, and Yugoslavia. Sotiaux and Sotiaux (2000) added Belgium, referring to the species as circumboreal. Kravesky *et al.* (2018) added Alaska and Tennessee (not a boreal state) in North America, and Atlantic Islands.

Aquatic and Wet Habitats

Gökler (1998) reported the habitat of *Radula lindenberghiana* (Figure 50-Figure 53) as wet rocks. Blockeel (2017) likewise treated it as a species of moist rocks in the Cyclades of Greece. Koponen *et al.* (1995)

described it as aquatic in Finland. In Flora North America, Kravesky *et al.* (2018) cited flooded rocks in streams among its habitats. Özenoğlu and Gökler (2002) considered it to be a species mainly of wet rocks in Turkey at the Dilek Peninsula National Park. Gabriel *et al.* (2019) reported it from coastal wetlands in the Azores.

Mogensen and Damsholt (1981) reported *Radula lindenbergiana* (Figure 50-Figure 53) from boulders in a river in Sweden. There it was accompanied by *Hygroamblystegium tenax* (Figure 55), *Jungermannia pumila* (Figure 56), and *Platyhypnidium riparioides* (Figure 57).

Rocks serve as suitable substrates for *Radula lindenbergiana* (Figure 50-Figure 53) on land as well as in the water. Papp (2004) found it on shaded volcanic rocks and on a rock wall. Kravesky *et al.* (2018) include dry to moist rocks among its habitats, but state that epilithic populations are found in forested localities and on sheltered rock faces. It occurs in low to high elevations.

It seems that most of the streambank and inundated species of liverworts also occur as epiphytes. This is likewise true for *Radula lindenbergiana* (Figure 50-Figure 53) – "very" occasionally on bark of trees (Kravesky *et al.* 2018).



Figure 55. *Hygroamblystegium tenax*, a species that accompanies *Radula lindenbergiana* on boulders in Swedish rivers. Photo by Hermann Schachner, through Creative Commons.



Figure 56. *Jungermannia pumila*, a species that accompanies *Radula lindenbergiana* on boulders in Swedish rivers. Photo from Earth.com, with permission.



Figure 57. *Platyhypnidium riparioides*, a species that accompanies *Radula lindenbergiana* on boulders in Swedish rivers. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Adaptations

Radula lindenbergiana (Figure 50-Figure 53) usually grows in mats or singly among other bryophytes (Patiño *et al.* 2009; Kravesky *et al.* 2018).

Reproduction

Radula lindenbergiana (Figure 50-Figure 53) is dioicous and rarely fertile (Kravesky *et al.* 2018). Désamoré (2013) suggested that island populations lose their dispersal power, certainly a consequence of being dioicous, but noted that the Macaronesian Islands seem to have back-colonized the European mainland at least twice. Furthermore, the species exhibits its highest genetic diversity on Macaronesia. Like most of the liverworts the chromosome number for *Radula lindenbergiana* (Figure 50-Figure 53) is $n=8$ (Zheng & Zhu 2009).

Özenoğlu and Gökler (2002) reported that they frequently found abundant gemmae on the leaf margins of *Radula lindenbergiana* (Figure 50-Figure 53) in the Dilek Peninsula National Park, Turkey. Kravesky *et al.* (2018; see also Losada-Lima *et al.* 2001) likewise noted that the gemmae were usually "copious," but that caducous leaves were absent. The predominance of gemmae and limited sexual reproduction may explain the lack of diversity in populations of mainland Europe.

Fungal Interactions

Although many liverworts serve as host for Ascomycetes fungi, *Radula lindenbergiana* (Figure 50-Figure 53) seems not to be one of them. Döbbeler (2004) found that whereas *Radula complanata* (Figure 18-Figure 20) seemed to be an excellent host for the fungus *Bryocentria* (Figure 40), not a single record existed for *R. lindenbergiana*. He suggested that this may be due to the substrate of siliceous rocks for *R. lindenbergiana* in his study.

Biochemistry

Oil bodies, usually only one per cell, are conspicuous (Kravesky *et al.* 2018) and may hold the secret to the apparent absence of fungi. Biochemical studies seem to be

lacking. These may explain further the absence of parasitic or epiphytic fungi on *R. lindenberghiana*.

***Radula obconica* (Figure 58)**

Distribution

Radula obconica (Figure 58) is a North American endemic (Risk *et al.* 2011). It occurs in eastern North America, from southern Quebec, south to Florida, west to Minnesota and Arkansas (Schuster 1980). Even in the southern Appalachians, it doesn't reach into the spruce-fir zone.

Aquatic and Wet Habitats

Nichols (1916) reported *Radula obconica* (Figure 58) as calciphobic along rivers in Connecticut, USA. Lorenz (1918) found it in moister situations, occurring on rocks in brooks, damp places near waterfalls, and on dripping rocks. Haynes (1927) reported it from wet river banks in Virginia, USA. Wittlake (1950) found it on open dripping ledges with *Jubula hutchinsiae* subsp. *pennsylvanica* (Figure 59), *Amblystegium serpens* (Figure 60), *Rhizomnium punctatum* (Figure 61), and *Philonotis fontana* (Figure 62). In a humid, but not constantly wet location in Missouri, USA, Redfearn (1964b) found it along a gulley on a north-facing wooded slope.



Figure 58. *Radula obconica*, a leafy liverwort species endemic to eastern North America. Photo by Blanka Aguero, with permission.



Figure 59. *Jubula hutchinsiae* subsp. *pennsylvanica*, a subspecies in eastern North America that accompanies *Radula obconica* on dripping ledges. Photo by Wayne Lampa, through Creative Commons.



Figure 60. *Amblystegium serpens*, a species in eastern North America that accompanies *Radula obconica* on dripping ledges. Photo by Michael Lüth, with permission.



Figure 61. *Rhizomnium punctatum* with capsules, a species in eastern North America that accompanies *Radula obconica* on dripping ledges. Photo by Michael Lüth, with permission.



Figure 62. *Philonotis fontana*, a species that accompanies *Radula obconica* on dripping ledges in eastern North America. Photo by Michael Lüth, with permission.

Typical water substrata for bryophytes are rocks. Redfearn (1964a) reported *Radula obconica* (Figure 58) from shaded sandstone in Arkansas, USA, and later (Redfearn 1979) on vertical sandstone. Lorenz (1918) reported it generally as occurring on both granitic and **trap rock** [any dark-colored, fine-grained, non-granitic intrusive or extrusive igneous rock, including basalt, peridotite,

diabase, and gabbro; also referring to flood (plateau) basalts]. Standley (1914) reported *Radula obconica* from moist, shaded rocks in North Carolina, USA. Solberg and Miller (1979) found it on rocks near streams in North Carolina. Gunderson (1971) found it on igneous rock in Wisconsin. In Minnesota it occurs on shaded, relatively humid, sheltered cliffs (Schuster 1957). Ammons (1933) found it in McKinney's Cave (Figure 63), a sandstone cave in West Virginia, on the rock wall.

Nichols (1916) considered *Radula obconica* (Figure 58) to be **calciphobous** (lime avoiding). But he went even farther in concluding that it was mostly restricted to **potassic rocks** (comprising $K_2O > Na_2O$ in percent weight and include compositional ranges from leucite-bearing basanites to K-enriched rock like leucitites, lamprophyres, orangeites, shoshonites, and lamproites).

Schuster and Patterson (1957) reported *Radula obconica* (Figure 58) from tree trunks in Dismal Swamp in Virginia, USA. McAvoy *et al.* (2011) reported it from the bark of trees in swamps in the Delmarva Peninsula (parts of Delaware, Maryland, and Virginia), and considered it rare. Lorenz (1918) noted that it occurs in moister habitats than does *R. complanata* (Figure 18-Figure 20), and reported it from bark, where it exhibited a dark olive-green color. Fulford (1934) reported it from trees in moist woods in Kentucky. In the Appalachian Plateau of Kentucky, USA, Risk *et al.* (2011) found it growing on *Rhododendron maximum* (Figure 64) as an epiphyll (Figure 65). *Radula obconica* did not appear on 1-year-old leaves, but increased in cover in the second and third years.



Figure 63. McKinney's cave, WV, entrance, showing the rock wall. Photo from Ammons 1933.



Figure 64. *Rhododendron maximum* leaves with small patches of epiphylls; in southern areas of the United States one can find *Radula obconica* on these leaves, but not commonly. Photo by Janice Glime.

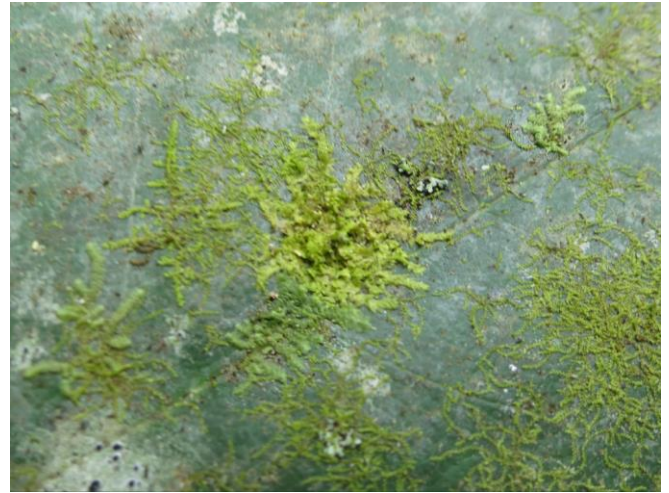


Figure 65. Epiphylls on *Rhododendron* in North Carolina, USA; the larger liverwort in the middle could be *Radula obconica*. Photo courtesy of Jessica Nelson.

In the area of Athens, Ohio, Hall (1958) found *Radula obconica* (Figure 58) on moist sandstone, but also on rootlets and on other bryophytes. Hall reported it as "sometimes" occurring on tree trunks. In the Athens area the species is fairly common.

Carroll (1945) found it on moist soil in northern Georgia. Solberg and Miller (1979) likewise found it on soil in North Carolina.

Adaptations

Zhu and So (2001) suggested the leaf lobules of liverworts like *Radula obconica* (Figure 58) served as water reservoirs, an adaptation useful for their epiphytic and epiphyllous habitats and terrestrial rock substrates. This is probably not helpful in constantly moist or wet habitats, but for this species in swamp habitats, it is likely to have multiple drying events per year.

Reproduction

Radula obconica (Figure 58) is **monoicous** (Lorenz 1918), suggesting that it should produce frequent sporophytes. It appears to produce lots of perianths (Figure 66). However, Standley (1914) found only sterile plants in North Carolina.



Figure 66. *Radula obconica* with numerous perianths. Photo by Paul G. Davison, with permission.

Biochemistry

Crandall-Stotler (1971) described the development of oil bodies in *Radula obconica* (Figure 58). These develop in the youngest cells by fusing small, osmiophilic droplets that originate from chloroplasts. She suggested that these oil bodies function in storage of reserve photosynthate. Other researchers argue that the function is primarily ecological, performing such adaptive functions as frost protection, desiccation protection, or inhibiting insect attack (Crandall-Stotler 1971; Gradstein 1978). We now know that oil bodies serve as a reservoir of secondary compounds, and these have a wide range of ecological functions (Millar *et al.* 2007).

In experiments, Chen *et al.* (2018) found that *Radula obconica* plants grown in continuous darkness for 31 days lacked osmiophilic spherules in the matrix. Chen and coworkers concluded that this suggests a degradation of lipophilic contents in the dark.

Millar *et al.* (2007) examined the antimicrobial properties of this and a number of other North American species. *Radula obconica* (Figure 58) exhibited the greatest antibacterial activity, especially against the bacterium *Bacillus subtilis* (Figure 68). They concluded that antimicrobial activity is greater in taxa having oil bodies, such as this one. The most activity from the extracts was that of bibenzyls – widespread compounds in liverworts.

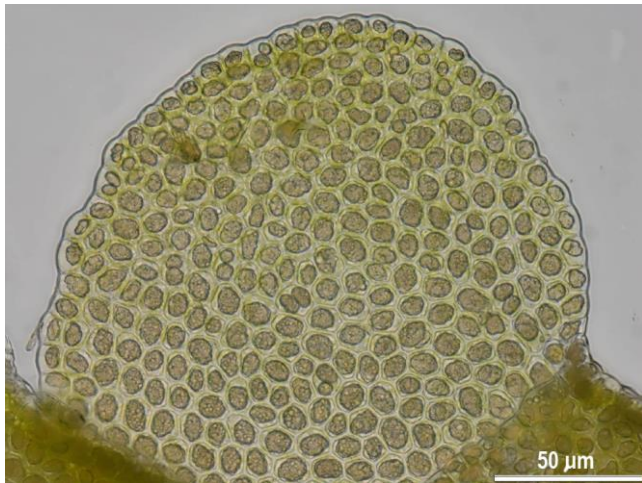


Figure 67. *Radula obconica* leaf cells with a single large, segmented oil body. Photo by Blanka Aguero, with permission.

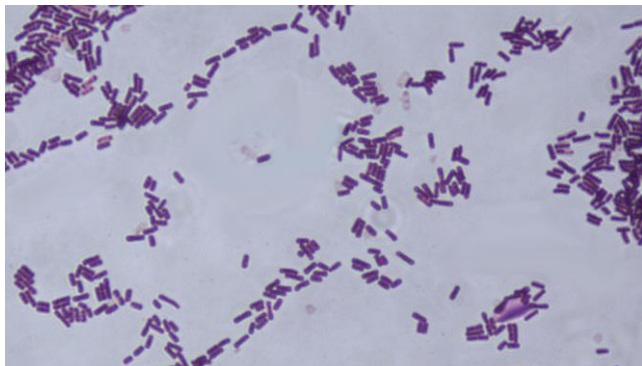


Figure 68. *Bacillus subtilis* with Gram stain, a species that is inhibited by *Radula obconica* extracts. Photo by Rirqa25, with permission.

Radula prolifera (Figure 69)

Distribution

Radula prolifera (Figure 69) is a boreal species from Siberia, Alaska (Renner *et al.* 2010), Yukon, Northwest Territories, and British Columbia (Hong 1987; Godfrey & Schofield 1979).

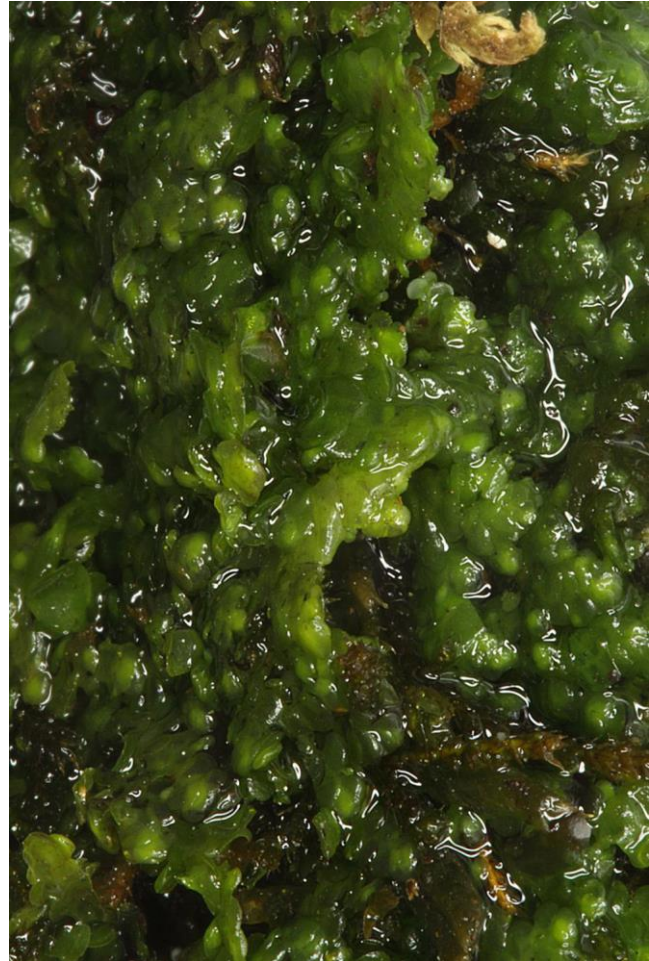


Figure 69. *Radula prolifera*, a mostly boreal species. Photo by Earth.com, with permission.

Aquatic and Wet Habitats

Records of *Radula prolifera* (Figure 69) are somewhat scanty. Its claim to aquatic and wetland habitats is its appearance on a south-facing wet cliff in the Upper Bureya River of the Russian Far East (Konstantinova *et al.* 2002). Fedosov *et al.* (2018) found it on dry clayish ground on a gentle slope in the Russian Arctic – not an aquatic habitat. Similarly, Köckinger (2016) found it in cold, wind-exposed habitats of the Siberian Arctic and Alaska, another terrestrial habitat. But Sofronova (2015) found it on soil, stones covered with soil, and on rock outcrops in wet and lichen tundra of northeastern Yakutia.

Adaptations

Radula prolifera (Figure 69) forms both large and small continuous **mats** in northeastern Yakutia (Sofronova 2015). It has extensive branching that enables it to spread through mosses and other plants that provide it with shelter

(Schuster & Steere 1958) and most likely help it to maintain hydration.

Reproduction

Castle, in 1950, described the species with little information on its reproduction. Perianths were unknown, as were any specialized means of asexual reproduction. Zheng and Zhu (2009) reported that the chromosome number of *Radula prolifera* (Figure 69) was $n=6$.

Radula voluta (Figure 70-Figure 72)

Distribution

Radula voluta (Figure 70-Figure 72) is widespread in the tropics. It occurs in Uganda (Sass-Gyarmati & Pócs 2014), Kenya (Enroth *et al.* 2019), Rwanda, and Zaire, (as *R. allamanoi*) (Yamada 1993). To these, Hylander *et al.* (2010, 2013) have added Ethiopia and noted that the species is widespread in Africa. Kürschner (2003) likewise considered it to be widespread in Africa and added Bioco, Madagascar, Malawi, Mauritius, Réunion, South Africa, and Tanzania to this list (Jones 1977; Wigginton 2002; Wigginton & Grolle 1996). Chuah-Petiot (2001) reported it from Kenya. In Europe it has been reported only from the British Isles (Yamada 1993). It is also known from North America (Mescal *et al.* 1980) – North Carolina and Tennessee (Schuster 1980), South America – Brazil and Peru (Schuster 1980), Costa Rica (Holz & Gradstein 2005), and the Galapagos Islands (Yamada & Gradstein 1991). In Bolivia it was known as both *Radula appendiculata* and *Radula grandiloba* (Yamada 2000; Kürschner 2003).



Figure 70. *Radula voluta*, a widespread tropical species. Photo by Paul G. Davison, with permission.

Bosanquet (2015) noted that the British Isles, and in particular Wales, were disjunct locations for *Radula voluta* (Figure 70-Figure 72). He noted the importance of humidity from a waterfall in creating a suitable habitat there for this tropical species.

Aquatic and Wet Habitats

Watson (1919) reported *Radula voluta* (Figure 70-Figure 72) as occasionally submerged. M'Ardle *et al.* (1898) found it at the Torc Waterfall in Killarney, Ireland. It occurred on rocks in the stream (Figure 1) and covered one boulder that they considered would be frequently submerged.

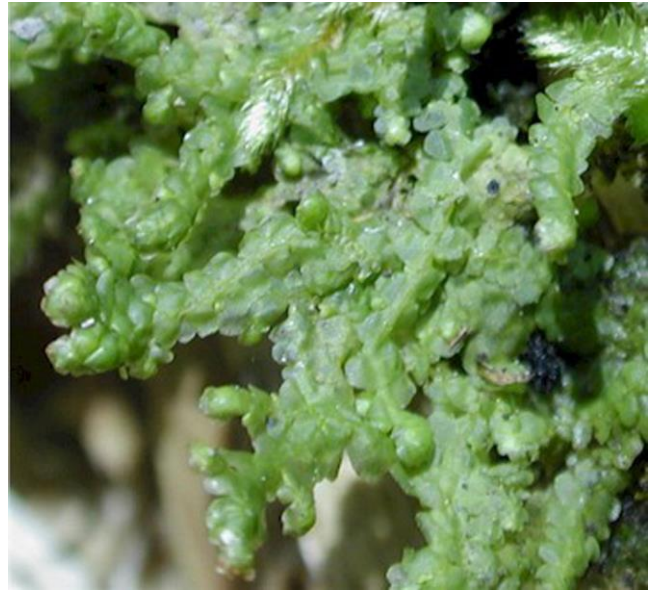


Figure 71. *Radula voluta*. Photo by Paul G. Davison, with permission.



Figure 72. *Radula voluta* showing ventral lobes and underleaves. Photo by Paul G. Davison, with permission.

Callaghan *et al.* (2019) described *Radula voluta* (Figure 70-Figure 72) as a hyperoceanic liverwort having conservation interest. Since ravines are preferred sites for many bryophytes, the researchers were concerned with the potential loss of species due to hydroelectric power development. They were fortunate to mark population areas (Figure 74) and assess before and after populations with an interval of 4 years. They found that larger bryophytes, especially *Ctenidium molluscum* (Figure 73-Figure 75), increased in area, crowding out smaller species. *Radula voluta*, however, was able to grow over and through these larger species. On the other hand, this species declined by the greatest cover (by 40%), due to loss of a small population on a single large rock.

In Kenya, Chuah-Petiot (2001) considered *Radula voluta* (Figure 70-Figure 72) to be **rupicolous** (living among, inhabiting, or growing on rocks; Figure 73). Pescott (2019) reported it among the rare bryophytes from calcareous rocks in the Galtee Mountains of Ireland. This most likely applies to both aquatic and terrestrial habitats.



Figure 73. *Ctenidium molluscum* in rock canyon in Europe, a species that crowds out other bryophytes following modification of the habitat for hydroelectric power; *Radula voluta* is able to grow over and among it. Photo by Michael Lüth, with permission.

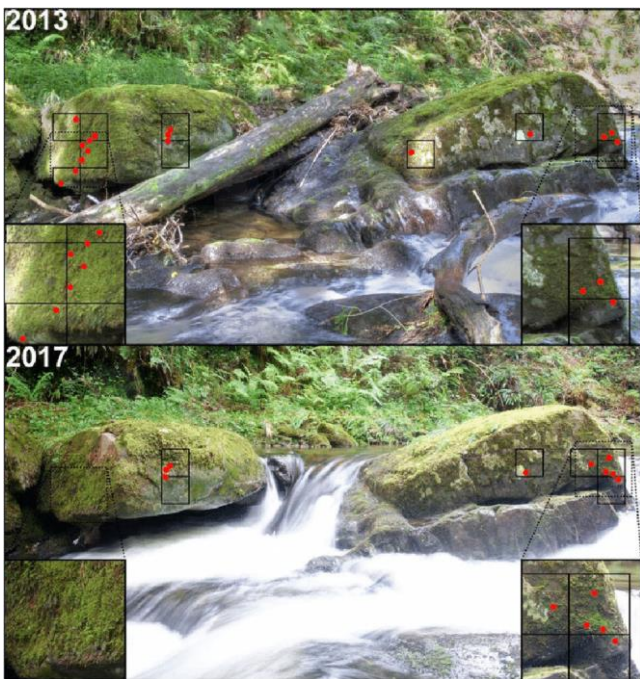


Figure 74. *Radula voluta* marked locations and occupied 25 cm grid cells of *Radula voluta* in Plot 4 at Period 1. From Callaghan *et al.* 2019, with permission.



Figure 75. *Ctenidium molluscum*, a competitor of many bryophytes when the habitat is modified. Photo by Michael Lüth, with permission.

Adaptations

Gradstein and León-Yáñez (2020) described *Radula voluta* (Figure 70-Figure 72) as a **smooth mat** (Figure 76) on *Polylepis pauta* (Figure 77-Figure 78) in Ecuador. They found that life forms of bryophytes differed based on moisture, with **smooth mats** predominating in the drier Mojanda and **rough mats** in the more moist páramo Papallacta. Holz *et al.* (2002) described their growth on shrubs in Costa Rica as **feathers** (Figure 79). In sharp contrast to the **smooth mats** in the *Polylepis pauta* forest, Homeier *et al.* (2008) reported *Radula voluta* as **pendent** in the Andean forests of southern Ecuador.



Figure 76. *Radula voluta* growing in a **smooth mat** life form. Photo by Paul G. Davison, with permission.



Figure 77. *Polylepis pauta* forest with numerous bryophyte cushions on the branches and trunks. Photo from Gradstein & León-Yáñez 2020, with permission.



Figure 78. *Polylepis pauta* forest. Photo from Gradstein & León-Yáñez 2020, with permission.



Figure 79. *Radula voluta* growing with a **feather** life form. Photo by Stan Phillips, through public domain.

Discussions of adaptations in *Radula voluta* (Figure 70-Figure 72) seem to be absent. The photo of the stem (Figure 80) by Paul Davison seem to indicate no adaptation there for drying out, with all cells thin-walled.



Figure 80. *Radula voluta* stem cross section showing no special adaptations for drying out. Photo by Paul G. Davison, with permission.

Reproduction

This species is **dioicous** and usually sterile (Figure 81) (Krayesky *et al.* 2018). Furthermore, sporophytes are unknown. It also lacks caducous leaves as a reproductive mechanism. It does, however, produce gemmae on the margins and median cells of the leaves, but these are produced rarely and often absent. Thus it is not surprising that this species is a poor disperser, at least in the British Isles where asexual propagules are unknown (Bosanquet & Dines 2011). However, in Rio de Janeiro, da Costa (2009) did find it with male branches and described it as a widespread species in southern Brazil.

Biochemistry

Kraut *et al.* (1997) verified the presence of two prenylated bibenzyl derivatives from *Radula voluta* (Figure 70-Figure 72). Nagashima and Asakawa (2011) isolated two known bibenzyls and elucidated their structure. Potential uses of bis-bibenzyls in liverworts include antimicrobial, antifungal, antiviral, cytotoxic, anti-

oxidant, muscle relaxing, and antiobesity activity (Asakawa 2017).



Figure 81. *Radula voluta* with perianths but no indication of sporophytes. Photo by Jan-Peter Frahm, with permission.

Radula wichurae

Distribution

Radula wichurae occurs in the Azores, Madeira, and Canary Islands (Bouman & Dirkse 1990).

Aquatic and Wet Habitats

Radula wichurae is known from deep ravines and wet rocks in the Canary Islands (Bouman & Dirkse 1990).

Adaptations

Radula wichurae is olive-green, becoming brown with age (Bouman & Dirkse 1990). The cell walls are typically thin, but can be thick and have trigones. This suggests variability, either genetic or induced by habitat conditions.

Reproduction

Radula wichurae is **dioicous** and leaf gemmae are unknown (Bouman & Dirkse 1990).

Ptilidiales: Ptilidiaceae

Ptilidium ciliare (Figure 82-Figure 85)

Ptilidium ciliare (Figure 82-Figure 85) is a bipolar species and was considered to be the progenitor of *P. pulcherrimum* (Figure 112-Figure 114) and *P. californicum* (Figure 86-Figure 88). However, using chloroplast DNA, Kreier *et al.* (2010) show that while this seemed to be a sound conclusion for *P. pulcherrimum*, it was not for *P. californicum*. They found indications that *P. ciliare* shared DNA with populations in Europe and the Southern Hemisphere; *P. pulcherrimum* shared DNA similarities with that in Europe. In New Zealand, it is sometimes recognized as a separate species, *Ptilidium hodgsoniae*, a species not recognized by Söderström *et al.* (2016). Kreier and coauthors proposed that long-distance dispersal resulted in its bipolar distribution, including southern South America.

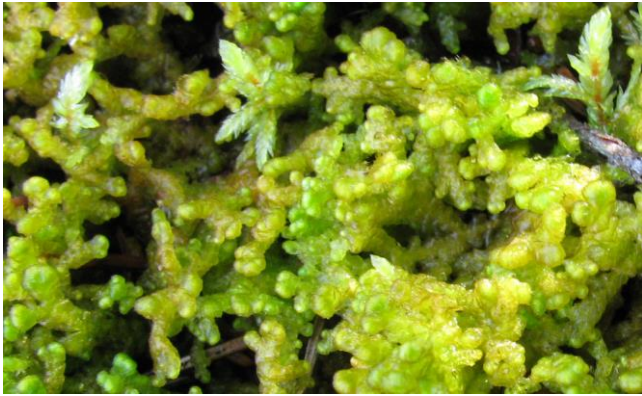


Figure 82. *Ptilidium ciliare*, a bipolar species of leafy liverwort. Photo by Janice Glime.



Figure 85. *Ptilidium ciliare* showing its finely divided leaves. Photo by Michael Lüth, with permission.

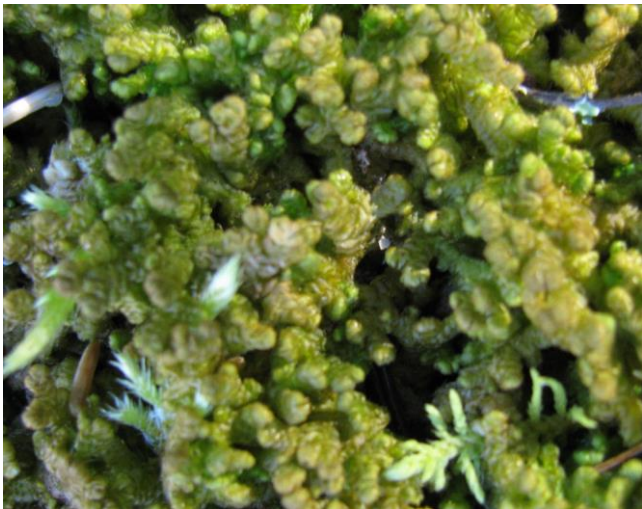


Figure 83. *Ptilidium ciliare* growing at Horseshoe Harbor, Copper Harbor, Michigan, USA. Photo by Janice Glime.



Figure 86. *Ptilidium californicum*, a species once thought to be a derivative of *Ptilidium ciliare*. Photo by Chris Wagner, through Creative Commons.



Figure 84. *Ptilidium ciliare*, a mostly terrestrial species but that also occurs in poor fens and bogs. Photo by Hermann Schachner, through Creative Commons.

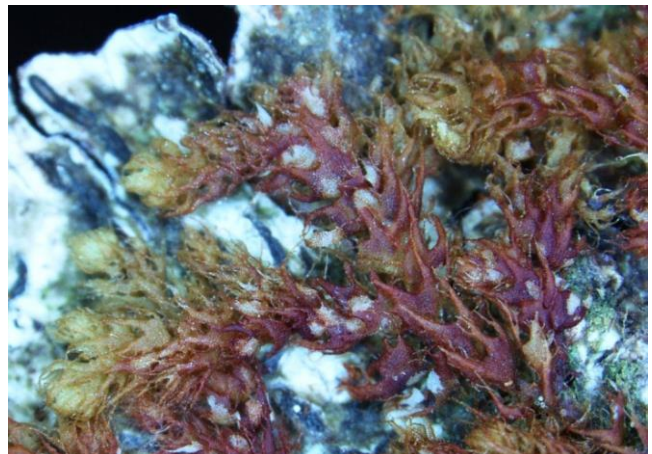


Figure 87. *Ptilidium californicum* showing divided leaves and red coloration except at growing tips. Photo from Botany Website, UBC, with permission.

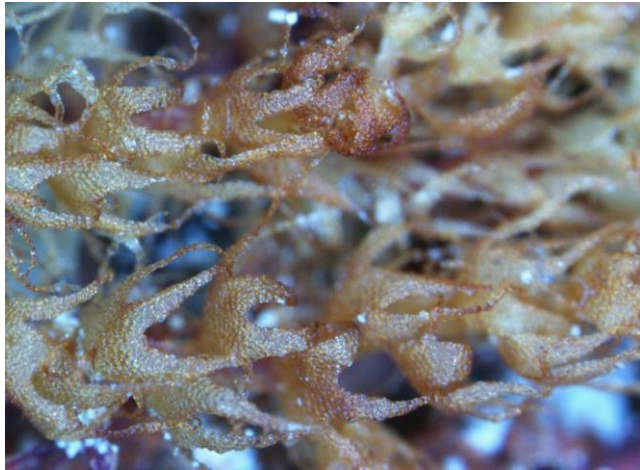


Figure 88. *Ptilidium californicum* close view of divided leaves. Photo from Botany Website, UBC, with permission.

Distribution

Ptilidium ciliare (Figure 82-Figure 85) occurs in the northeastern USA, south to Pennsylvania, where it is rare (Schuster 1966). More recently, Sass-Gyarmati *et al.* (2005) found it in the Metaliferi Mountains in Romania. It is distributed in Greenland, Scandinavia, south to Spain and Italy, and very rare in Japan. It is well adapted to cold climates, making it widespread in the boreal region (Schuster 1966).

Aquatic and Wet Habitats

I know this liverwort mostly from the overhanging cliffs along the Lake Superior shore. Nichols (1918) reported it from the moist hollows between *Sphagnum* hummocks (Figure 89) on Cape Breton Island, Canada. Schuster (1966) considered it to be rare in bog holes such as those in Minnesota. But in most cases, this is a terrestrial species (Elumeeva *et al.* 2011).



Figure 89. *Sphagnum fuscum* hummock; *Ptilidium ciliare* can be found in moist hollows between *Sphagnum* hummocks. Photo by Michael Lüth, with permission.

Boudreault *et al.* (2002) considered *Ptilidium ciliare* (Figure 82-Figure 85) to be a robust species in eastern boreal forests of Canada. They found that its importance value, along with that of *Sphagnum fuscum* (Figure 90), increased over time since fire, becoming maximal in forests more than 200 years old. Turetsky *et al.* (2012) found that

late successional bryophyte species such as *Ptilidium ciliare* and the feather mosses diminish soon after fires in boreal forests and peatlands, being replaced by *Polytrichum piliferum* (Figure 91) and *Polytrichum juniperinum* (Figure 92). On the other hand, Nguyen-Xuan *et al.* (2000) found that *Ptilidium ciliare* tended to be more frequent after logging in black spruce (*Picea mariana* - Figure 93) forests.



Figure 90. *Sphagnum fuscum* hummock, a species that increases following fire. Photo by Jutta Kapfer, with permission.



Figure 91. *Ptilidium ciliare* and *Polytrichum piliferum* on sand; *Polytrichum piliferum* can replace *Ptilidium ciliare* after a fire. Photo by Janice Glime.



Figure 92. *Polytrichum juniperinum* with capsules, a species that can replace *Ptilidium ciliare* after a fire. Photo by Paul Wilson, with permission.



Figure 93. *Picea mariana* forest, a habitat where the presence of *Ptilidium pulcherrimum* indicates a low pH. Photo from Western Arctic National Parklands, through Creative Commons.

In his North American treatment, Schuster (1966) described the habitat of *Ptilidium ciliare* (Figure 94) as mostly on thin soil over rock.



Figure 94. *Ptilidium ciliare* on rock, showing lack of a thick soil layer. Photo by Andy Hodgson, with permission.

Bryophytes are able to collect heavy-metal pollution and can thus be used in bioassays. Salemaa *et al.* (2001) assessed heavy-metal pollution along a gradient in southwest Finland and found the lichen *Cladina* spp. (Figure 95) could not be found within 2 km of the source, with some *Cladina* spp. not found within 3 km. *Ptilidium ciliare* (Figure 82-Figure 85), on the other hand, was found for the first time in the area, but only beyond 2 km. Al-Asheh and Duvnjak (1999) included *Ptilidium ciliare* in their assessment of sorption of heavy metals from synthetic metal solutions and industrial wastewater, but they did not separate the results by species.



Figure 95. *Cladina* spp., a genus less sensitive to heavy metal pollution than *Radula ciliare* in Tyresta. Photo by Peder Curman, through Creative Commons.

Jägerbrand *et al.* (2003) determined responses of various bryophytes to simulated environmental change in northern Sweden. The greatest response was by *Rhytidium rugosum* (Figure 96), which exhibited a significant decrease in abundance following treatment of increased temperature and fertilizer. *Ptilidium ciliare* (Figure 82-Figure 85) showed a similar but not significant trend.



Figure 96. *Rhytidium rugosum*, a moss species that exhibits a significant decrease in abundance in response to increased temperature. Photo by Hermann Schachner, through Creative Commons.

Adaptations

In its tundra and boreal forest habitats, *Ptilidium ciliare* (Figure 82-Figure 85) typically forms **cushions** (Figure 97) (Elumeeva *et al.* 2011; Soudzilovskaia *et al.* 2011), but Elumeeva and coworkers also referred to it as a **mat** (Figure 97). Similarly, Schuster (1966) described these growths as "deep, loose, often flocculent **mats** or **tufts**" (Figure 98). Soudzilovskaia *et al.* (2011) found that in these northern habitats, cushion thickness (Figure 99) was a good predictor of temperature and was species-specific.



Figure 97. *Ptilidium ciliare* forming a cushion or thick mat. Photo by Janice Glime.



Figure 98. *Ptilidium ciliare* showing thick mat or "tuft." Photo by Li Zhang, with permission.



Figure 99. *Ptilidium ciliare* exhibiting a life form that approaches a **cushion** or **weft**. Photo by David Holyoak, with permission.

A common adaptation in aquatic plants is dissected leaves. This often is manifest in divided underwater leaves and ovate or otherwise undivided leaves that develop above water. This adaptation does not seem to occur among aquatic bryophytes. We have assumed that the fine divisions facilitate CO₂ absorption and thus increase photosynthetic efficiency. With leaves only one cell thick,

this is much less of a problem for liverworts. So we might ask why *Ptilidium* species have finely divided leaves (Figure 100). It is not a species that is commonly submersed. But it does permit parts of leaves to be exposed to the sun, including the ability of the sun to penetrate into the mat which can at times become quite thick. I am inclined to think that the fimbriate leaves of species like *Ptilidium ciliare* and *Trichocolea tomentella* might be an adaptation for rapid uptake and later retention of water by creating numerous capillary spaces – an advantage in their sometimes quite wet and other times quite dry habitats.



Figure 100. *Ptilidium ciliare* showing the finely divided leaves. Photo by Jan-Peter Frahm, with permission.

Water economy is important in the rocky habitats where *Ptilidium ciliare* (Figure 82-Figure 85) lives, due to the drying events (Figure 101). Elumeeva *et al.* (2011) described water economy traits of shoots and colonies for 22 subarctic species. They found that individual shoot properties (leaf cell wall properties, water retention capacity, and desiccation rate) did not correspond with colony water retention capacity. Rather, the colony desiccation rate depended on the density of the water-saturated colonies (Figure 102). It appears that *Ptilidium ciliare* acts much like a sponge, with its dissected leaves providing small capillary spaces that trap water and hold it by adhesion and cohesion.



Figure 101. *Ptilidium ciliare* in a dry state at Horseshoe Harbor, Copper Harbor, Michigan, USA. Photo by Janice Glime.

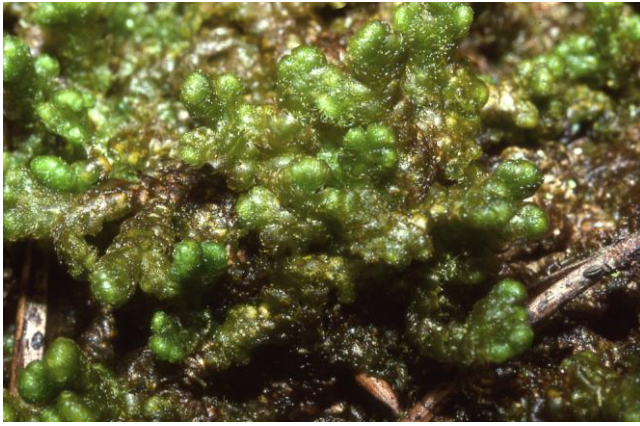


Figure 102. *Ptilidium ciliare* wet. Photo by Janice Glime.

Lang *et al.* (2012) conducted a 5-year experiment on the warming effect on tundra bryophytes on two continents. These showed no significant effect on *Ptilidium ciliare* (Figure 82-Figure 85), but I must caution that in this ecosystem with a short growing season and slow-growing organisms, it may take longer before any significant effect is rendered. In a longer experiment (9-16 years), bryophytes were less sensitive to warming than were lichens.

Street *et al.* (2018) tested the responses of the moss layer to increased nitrogen and phosphorus in a tundra environment. They found that individual bryophyte species responded differently. This included the increase of *Ptilidium ciliare* (Figure 82-Figure 85) in P-treated plots.

I have thus far not found studies on the effects of bright light, especially UV light, on *Ptilidium ciliare*, but my own experience (Figure 103) and the pictures I have found (Figure 104-Figure 105) suggest that development of reddish to brown coloration may protect it from light damage. It could also be beneficial in absorbing sunlight and warming the liverwort on sub-freezing days with no snow cover.



Figure 103. *Ptilidium ciliare* showing the red coloration that can protect it from bright light, especially in cold weather that can occur before snow protects it or before leaves form a canopy (late April 1983) in Michigan, USA. Photo by Janice Glime.

Reproduction

Ptilidium ciliare (Figure 82-Figure 85) is **dioicous**, making sexual reproduction difficult, but it does sometimes occur (106). However, it is possible that fragments may

play a role in its asexual reproduction and dispersal. Kowalczyk *et al.* (1997) cultured sterilized gametophyte fragments. Typically, for the ten species tested, including *Ptilidium ciliare*, terminal portions and leafless shoots proved to be most suitable for culture of new shoots. They found that 50% commercial bleach (ACE) solution for 0.5-1 minute was the most effective way to sterilize this species.



Figure 104. *Ptilidium ciliare* exhibiting a dark coloration, presumably protecting it from high light intensity. Photo by Michael Lüth, with permission.



Figure 105. *Ptilidium ciliare* exhibiting reddish coloration among grasses and mosses that are typical sun species. Photo by Andrew Hodgson, with permission.



106. *Ptilidium ciliare* with capsules, Dollar Bay, Michigan, USA. Photo by Janice Glime.

Role

Bryophytes often serve as seed beds because they can alter the soil environment in ways that are often favorable for germination. Soudzilovskaia *et al.* (2011) assessed the role of six bryophyte species, including *Ptilidium ciliare* (Figure 82-Figure 85), in the germination of tracheophyte seeds. Temperature was modified by the thickness of the cushions of bryophytes and the specific temperatures created by each species was an important parameter in determining germination in these locations (Figure 107). The highest level of germination under bryophyte cover occurred under *P. ciliare* (Figure 107). Soil temperatures under *Ptilidium ciliare* had one of the top two highest amplitudes in monthly and growing season temperatures. The sums of temperatures in May were higher, but those in September were lower under *P. ciliare* than under most other species in the study.

In the tundra, bryophytes can be an important food source, especially during seasons with low productivity of tracheophytes. *Ptilidium ciliare* (Figure 82-Figure 85) is one of the common species there, so Olofsson *et al.* (2004) included it in their study of herbivore impacts. They found that large and small herbivores did indeed use *P. ciliare* as a food source. But at the same time, it was the only species in the study for which the enclosure led to a decrease in species abundance. Liverworts are considered to be weak competitors, succeeding only where herbivores or disturbance eliminate some of the competitive pressures. Size-dependent enclosures revealed that voles and lemmings have larger effects on the plant community structure than do reindeer at all four locations in the study.

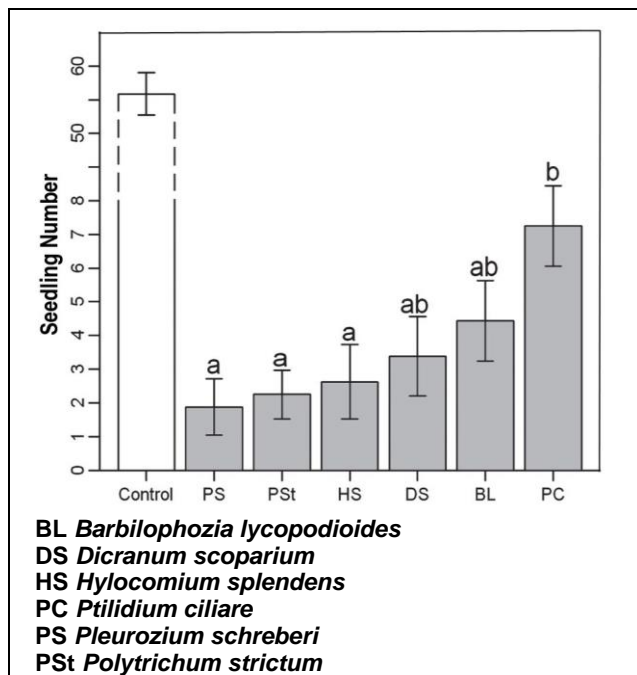


Figure 107. Number of tracheophyte plant seedlings (pooled) germinated in the field experiment by Soudzilovskaia *et al.* (2011) as affected by bryophyte species. Values are mean \pm standard error; $n=8$. Different letters indicate significant differences in mean (Tukey *post hoc* test). Controls were not included in the statistical analysis in order to show the more subtle differences among bryophyte species. Modified from Soudzilovskaia *et al.* 2011.

Nitrogen fixation by Cyanobacteria in association with *Ptilidium ciliare* (Figure 82-Figure 85) appears to be absent in the Abisko region of Sweden (Gavazov *et al.* 2010). Testing locations included a nutrient-poor birch forest with ericaceous undergrowth, an oligotrophic bog dominated by *Sphagnum fuscum* hummock (Figure 90) communities, and a minerotrophic mire (fen).

Salemaa *et al.* (2019) found that low levels of nitrogen pollution suppressed N_2 fixation in the boreal forest, including that of *P. ciliare*, but this species did show positive activity in a growth chamber. For it to register a positive nitrogen fixation, the colony had to acclimate to the high temperature of the growth chamber. These restrictions might account for the absence of N fixation for this species in the Gavazov *et al.* study. Rousk *et al.* (2017) found contrasting results in the High Arctic, where *P. ciliare* was also among the dominant bryophytes. They reported that all vegetation types exhibited a rapid transfer of fixed N_2 to other ecosystem components. On the other hand, hardly any ^{15}N was recovered in soil microbes in the bryophyte plots. Uptake was greater in the cottongrass-bryophyte plots, and the researchers suggested that the wetness of this bryophyte-dominant ecosystem could be responsible for the greater rate, or a difference in bryophyte species. Their data suggested that nitrogen fixation by bryophyte-Cyanobacteria associations provide a high contribution of N to the habitat where they occur.

Fungal Interactions

Döbbeler (1997) reported the *Ascomycetes* fungus *Octospora ptilidii* (Figure 108) growing on *Ptilidium ciliare* (Figure 82-Figure 85). Later, Döbbeler *et al.* (2015) reported that 12 *Ascomycetes* have been recorded on both *Ptilidium pulcherrimum* (Figure 111-Figure 114) and *P. ciliare*.



Figure 108. *Octospora fusispora*; *Octospora ptilidii* is known from *Ptilidium ciliare*. Photo by A. Gardiennet, through Creative Commons.

Biochemistry

The biochemistry is a little better known for this large liverwort species than for the tiny ones. Deoxopinguinone was isolated from *Ptilidium ciliare* (Figure 82-Figure 85) (Krutov *et al.* 1973). *Ptilidium ciliare* is known to have barbatane-, daucane- and pinguinane-type sesquiterpenoids

and dolabellane- and fusicoccane-type diterpenoids (Nagashima *et al.* 1999).

Adamczak *et al.* (2005) used genetic markers to distinguish between *Ptilidium ciliare* (Figure 82-Figure 85) and *P. pulcherrimum* (Figure 111-Figure 114). Both species were polymorphic; *P. ciliare* exhibited alternative alleles at three loci; *P. pulcherrimum* exhibited alternative alleles at four. They furthermore found that asexually reproducing *P. ciliare* had lower total gene diversity than did the sexual plants of *P. pulcherrimum*. *Ptilidium ciliare* further exhibited allele numbers and frequency differences between geographic regions.

***Ptilidium pulcherrimum* (Figure 109, Figure 111-Figure 114)**

Ptilidium pulcherrimum (Figure 109) has the reputation of occurring in Eocene Baltic amber (Figure 110), but Heinrichs *et al.* (2015) challenge this identification. On re-investigation, they found that it was a better fit for the liverwort genus *Tetralophozia*, renaming it *Tetralophozia groehnii* as a new species. A second specimen could not be located, but based on the description, they considered it to be morphologically similar to the North Pacific endemic *Ptilidium californicum* (Figure 86-Figure 88). DNA evidence from *Ptilidium pulcherrimum* supported the conclusion that the fossil did not represent *P. pulcherrimum*.

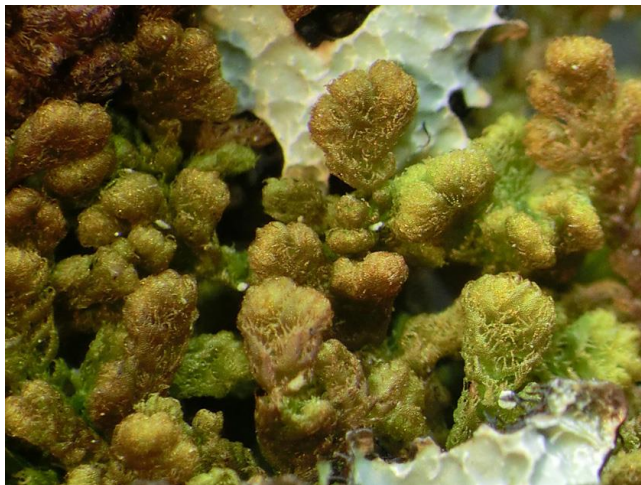


Figure 109. *Ptilidium pulcherrimum* a species once considered to be the same as one found in amber. Photo by Michael Lüth, with permission.

Distribution

Ptilidium pulcherrimum (Figure 111-Figure 114) has a Holarctic distribution, south to the deciduous forest. In Europe, it extends from Scandinavia to Italy and Bulgaria, England and Scotland, eastward to Siberia, China, and Japan (Schuster 1966). In North America, it occurs from Alaska southward to British Columbia, Alberta, Montana, Idaho, and Washington. In 2005, Keçeli and Çetin reported *P. pulcherrimum* as new from Turkey. In 2011, Singh and Singh reported it as new from India. But in Japan, it was already considered to be "not uncommon" in 1952 (Hattori 1952).

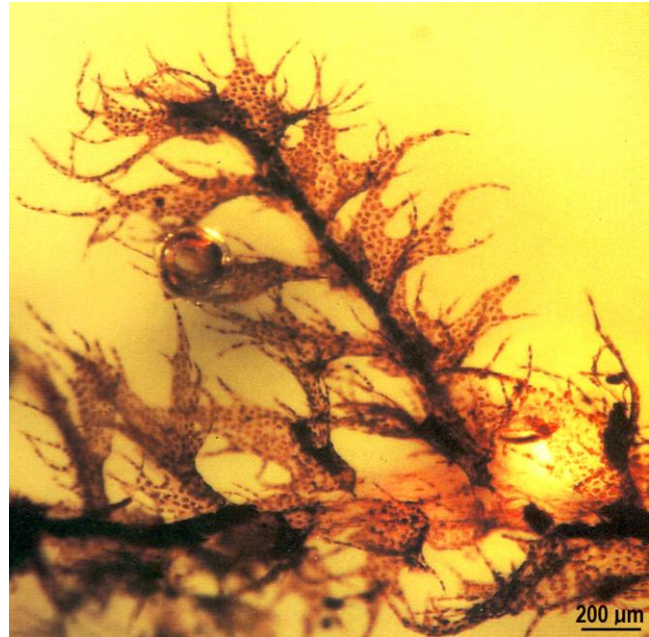


Figure 110. *Tetralophozia groehnii* (previously identified as *Ptilidium pulcherrimum*) in amber. Photo from Heinrichs *et al.* 2015, through PLOS One Creative Commons.



Figure 111. *Ptilidium pulcherrimum*, a Holarctic species with deeply divided leaves. Photo by Michael Lüth, with permission.



Figure 112. *Ptilidium pulcherrimum* branches. Photo by J. C. Schou, with permission.



Figure 113. *Ptilidium pulcherrimum* showing the deeply divided leaf. Photo by Michael Lüth, with permission.

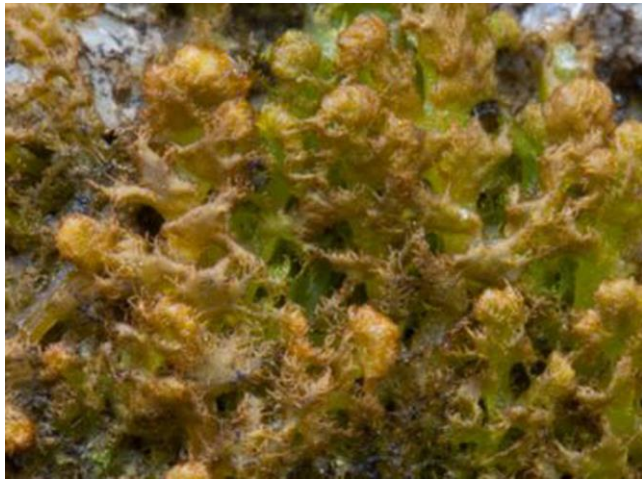


Figure 114. *Ptilidium pulcherrimum* showing leaves curling as they begin to dry. Photo by Martin Hutten, with permission.

Aquatic and Wet Habitats

Like *Ptilidium ciliare* (Figure 82-Figure 85), *P. pulcherrimum* (Figure 111-Figure 114) has little claim to the aquatic environment. For the eastern United States, Schuster (1966) reported as mostly restricted to trees in bogs (& poor fens) among its habitats, although I know it mostly from decorticated logs in that region. It was one of the bryophytes I found on the wall of the Flume, a damp habitat at Franconia Notch, New Hampshire, USA (Glime 1982).

Adaptations

In India, Singh and Singh (2011) found that *Ptilidium pulcherrimum* (Figure 111-Figure 114) grows prostrately or ascending in thin, straggling, or dense **mats**. It is yellowish-brown (Figure 115) to purplish-brown, becoming reddish-brown (Figure 116) when dry in the herbarium.

Clausen (1964) found evidence that *Ptilidium pulcherrimum* (Figure 111-Figure 114) is very desiccation tolerant. Using Danish populations, he showed that it retains 100% cell viability after 12 hours at 15% relative humidity at 20°C. It also survived 11-12 days at -10°C and in ice at -40°C for 24-26 hours.



Figure 115. *Ptilidium pulcherrimum* exhibiting the brownish golden color that can be seen in locations with more light. Photo by Michael Lüth, with permission.



Figure 116. *Ptilidium pulcherrimum* in a dry state and showing its reddish-brown coloration in an exposed situation. Photo by Michael Lüth, with permission.

Reproduction

Söderström (1989) found sexually reproducing individuals at nearly all locations, despite the **dioicous** condition of this species (Schuster 1966). Its frequent fertility (Figure 117) has been reported multiple times (Schuster 1966; Söderström 1989; Singh & Singh 2011).

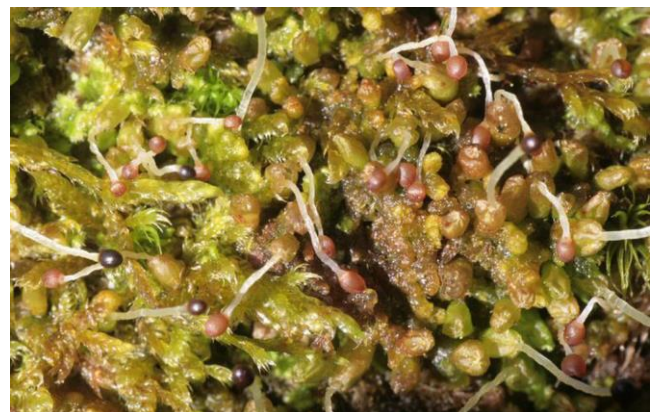


Figure 117. *Ptilidium pulcherrimum* with capsules, a relatively common appearance despite its dioicous condition. Photo from Snappy Goat, through public domain.

Söderström (1994) suggested that the size of spores may be important in limiting spore dispersal distance. In *Ptilidium pulcherrimum* (Figure 111-Figure 114) these are typically 25-27 μm , with most (52%) deposited within only a few meters. By comparison those of *Bryum argenteum* (Figure 118) has spores 8-14 μm , with only 2-5% landing within the same distance (Söderström & Johnson 1989). For *Ptilidium pulcherrimum* in a Swedish coastal spruce forest, the main substrate was rotting wood, accounting for 75% of its occurrences. Its annual spore production was 68,500 spores m^{-2} forest, 640,000 spores m^{-2} substrate, and 44,000,000 spores m^{-2} colony.



Figure 118. *Bryum argenteum* with capsules, a species with small spores that travel much farther than the larger ones of *Ptilidium pulcherrimum*. Photo by Hermann Schachner, through Creative Commons.

Ptilidium pulcherrimum (Figure 111-Figure 114) has no known asexual reproductive structures (Söderström 1989).

Jonsson and Söderström (1988) studied the growth and reproduction of *Ptilidium pulcherrimum* (Figure 111-Figure 114) in northern Sweden. They found that the growth rate varied between years (4-year study), but that it was independent of colony size. The mean growth rate was 5.2 mm year^{-1} , range 3.5-6.3 mm year^{-1} . It has a strikingly long period to first reproduction – 9 years – at a size of about 68 cm^2 . The capsules produce an average of 27,000 spores each, with a range of 18,000-44,000.

Jonsson and Söderström (1988) studied reproductive rate in 50 colonies of *Ptilidium pulcherrimum* (Figure 111-Figure 114) in northern Sweden. They found that antheridia were not produced until the third year. As the colony size increased, so did capsule density and spore production.

Fungal Interactions

Stenroos *et al.* (2009) described a new genus of lichen, *Puttea* (Figure 119), based on the previous lichen species known as *Fellhanera margaritella*. This new monospecific genus occurs almost exclusively on the liverwort *Ptilidium pulcherrimum* (Figure 111-Figure 114), but compared to its widespread host, it is relatively rare and has almost entirely a European distribution. It was thus far known from Austria, the Czech Republic, Finland, Norway, Russia, Slovakia, Sweden, and Switzerland. Since 2009, it has been reported from Quebec, Canada, in eastern North America (Buck & Lendemer 2012). *Puttea margaritella*

(Figure 119) clearly harms the host, causing clearly visible infected areas. The ascomata, on the other hand, develop only on the decaying shoots of the host. Buck and Lendemer (2012) found the same restriction to dead and decaying plant parts. It appears that this lichen also occurs in western North America, but there it occurs on *Ptilidium californicum* (Figure 86-Figure 88).

Döbbeler *et al.* (2015) reported two new bryophilous *Ascomycetes*. One of these fungi, *Trichosphaerella goniospora*, occurs on *Ptilidium pulcherrimum* (Figure 111-Figure 114) and was found in New Brunswick Canada. At that time, twelve species of *Ascomycetes* were known from *P. pulcherrimum*.



Figure 119. *Puttea margaritella* (white spots), a species that occurs almost exclusively, but relatively rarely, on *Ptilidium pulcherrimum*. Photo by Einar Timdal, Natural History Museum, University of Oslo, Norway, through Creative Commons.

Biochemistry

Ptilidium pulcherrimum (Figure 111-Figure 114) is one of the few bryophytes with complete sequencing of the chloroplast genome using NGS technology (Shanker 2012, 2014). Its plastid genome is 119,007 base pairs long, comprising 122 genes. Of these, 88 code for proteins, 4 for rRNAs, and 30 for tRNAs. Forrest *et al.* (2011) suggested that this sequencing could indicate an evolutionary stasis in the plastid genome structure of this liverwort.

Asakawa *et al.* (1981) reported pinguicane-type sesquiterpenes in *Ptilidium pulcherrimum* (Figure 111-Figure 114). Guo *et al.* (2009) reported a new trinortriterpenoid and a new diphenylmethane derivative, along with ten previously described pentacyclic triterpenoids and four aromatic compounds. They also evaluated toxicity and found moderate toxicity against PC3 cells. Asakawa *et al.* (2014) noted that liverworts rarely have triterpenoids. But *Ptilidium pulcherrimum* possesses several ursane triterpenoids that were active against the growth of PC3 human prostate cancer cells.

The presence of secondary compounds always raises the question of their antibiotic activity, whether it is to discourage herbivores or to be antimicrobial. Veljić *et al.* (2010) found that extracts of *Ptilidium pulcherrimum* (Figure 111-Figure 114) showed a stronger effect against tested Gram (+) than Gram (-) bacteria. A methanol extract exhibited a strong antifungal activity. When compared to the synthetic fungicide bifonazol, its best antifungal activity was against *Trichoderma viride* (Ascomycota; Figure 120) – a fungus that itself has antifungal activity. This fungus causes green mold rot of onions, dieback of *Pinus nigra* seedlings (Figure 121), and green mold disease of mushrooms. But it also has antifungal activity against pathogens on plants.

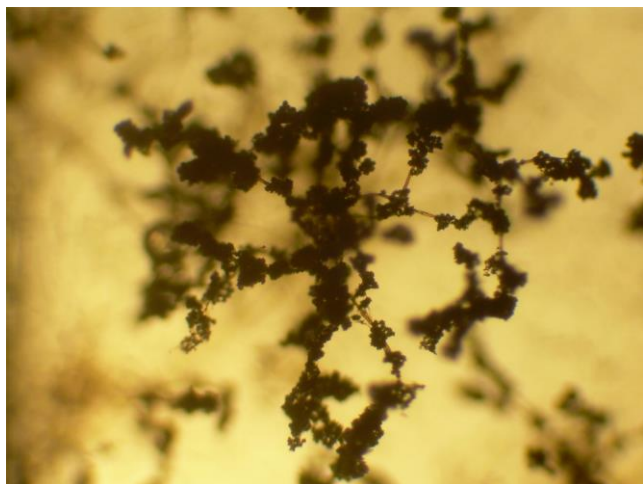


Figure 120. *Trichoderma viride*, a species that occurs on *Ptilidium pulcherrimum*, showing its conidiophores from an onion. Photo by Ninjatacoshell, through Creative Commons.

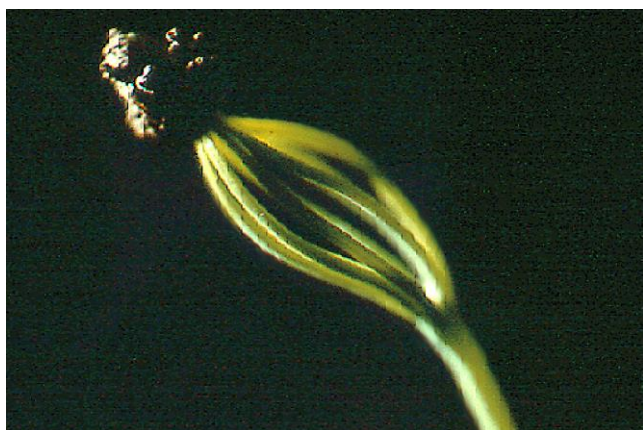


Figure 121. *Pinus nigra* seedling, a seedling that can suffer from infection by *Trichoderma viride* (Ascomycota). Photo by Janice Glime.

Summary

Both **Radulaceae** and **Ptilidiaceae** occur primarily in terrestrial habitats, especially logs and bark. *Radula aquilegia* is occasionally submersed or on wet rocks. *Radula carringtonii* occurs on rocks that occasionally

are wet. *Radula complanata* seems to have a broader niche that includes wet cliffs and uncommonly submerged. *Radula holtii* occurs in splash zones, on wet rocks, and mountain streams. *Radula lindenbergiana* and *Radula obconica* likewise occur on wet rocks. *Radula prolifera* seems to only rarely be on wet rocks. *Radula voluta* is more tolerant of wet habitats, occurring on stream banks, in spray of waterfalls, and sometimes submerged. *Radula wichurae* occurs in deep ravines and on wet rocks. *Ptilidium ciliare* and *Ptilidium pulcherrimum* are predominantly terrestrial, sometimes occurring on cliffs that remain moist because of nearby water, but never submersed.

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Lars Söderström provided me with the current acceptable names for a number of older taxa.

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CHAPTER 1-11: AQUATIC AND WET MARCHANTIOPHYTA, ORDER METZGERIALES: ANEURACEAE

TABLE OF CONTENTS

SUBCLASS METZGERIIDAE.....	1-11-2
Order Metzgeriales.....	1-11-2
Aneuraceae.....	1-11-2
<i>Aneura</i>	1-11-2
<i>Aneura maxima</i>	1-11-2
<i>Aneura mirabilis</i>	1-11-7
<i>Aneura pinguis</i>	1-11-14
<i>Lobatiriccardia</i>	1-11-24
<i>Lobatiriccardia alterniloba</i>	1-11-24
<i>Lobatiriccardia athertonensis</i>	1-11-25
<i>Lobatiriccardia coronopus</i>	1-11-25
<i>Lobatiriccardia oberwinkleri</i>	1-11-25
<i>Lobatiriccardia verdoornoides</i>	1-11-25
<i>Lobatiriccardia yakusimensis</i>	1-11-26
<i>Lobatiriccardia yunanensis</i>	1-11-26
<i>Riccardia</i>	1-11-26
<i>Riccardia aequicellularis</i>	1-11-26
<i>Riccardia chamedryfolia</i>	1-11-27
<i>Riccardia crassiretis</i>	1-11-33
<i>Riccardia crenulata</i>	1-11-33
<i>Riccardia diminuta</i>	1-11-33
<i>Riccardia elata</i>	1-11-33
<i>Riccardia graeffei</i>	1-11-34
<i>Riccardia jackii</i>	1-11-34
<i>Riccardia marginata</i>	1-11-36
<i>Riccardia multifida</i>	1-11-37
<i>Riccardia multifidoides</i>	1-11-42
<i>Riccardia parvula</i>	1-11-43
<i>Riccardia singaporensis</i>	1-11-43
<i>Riccardia subexalata</i>	1-11-43
<i>Riccardia tenuis</i>	1-11-43
<i>Riccardia tjibodensis</i>	1-11-43
<i>Riccardia wettsteinii</i>	1-11-43
Summary.....	1-11-43
Acknowledgments.....	1-11-44
Literature Cited.....	1-11-44

CHAPTER 1-11: AQUATIC AND WET MARCHANTIOPHYTA, ORDER METZGERIALES: ANEURACEAE



Figure 1. *Aneura pinguis* growing in a zone that is just above and below the water surface, keeping it constantly wet. Photo by Michael Lüth, with permission.

As in the other chapters on liverworts in aquatic and wet habitats, nomenclature for this chapter is based primarily on Söderström *et al.* (2016). In addition, Lars Söderström has provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. Information on habitats of these unverifiable taxa has been included with the species.

Many of the species on this list are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study.

SUBCLASS METZGERIIDAE

Order Metzgeriales

Aneuraceae (Figure 1)

***Aneura* (Figure 2, Figure 3, Figure 7-Figure 10, Figure 18-Figure 26, Figure 29-Figure 32, Figure 52-Figure 57)**

In a study of 48 streams on South Island, New Zealand, Suren and Duncan (1999) found that *Aneura* sp. was positively correlated with bankfull discharge. This genus has several species that are typically associated with water.

Bidartondo and Duckett (2010) found sebacinoid fungi in several species of *Aneura*.

***Aneura maxima* (Figure 2, Figure 3, Figure 7-Figure 10; Figure 18-Figure 26)**

The species *Aneura maxima* (Figure 2, Figure 3, Figure 7-Figure 10), *A. pellioides* (Figure 4), and *A. pinguis* (Figure 5-Figure 6) have created confusion in their identification (Frahm 2012). Frahm (2012) used water culture to determine if characters are modified by the culture conditions. This was done to understand the

distinctions among several *Aneura* species. The unilayered thallus margin was retained in *Aneura maxima* (Figure 3) and the multilayered thallus margin was retained in *Aneura pinguis* in common garden culture of aquatic and terrestrial conditions.



Figure 2. *Aneura maxima*, one of three species that have been confused with each other. Photo by Jan-Peter Frahm, with permission.

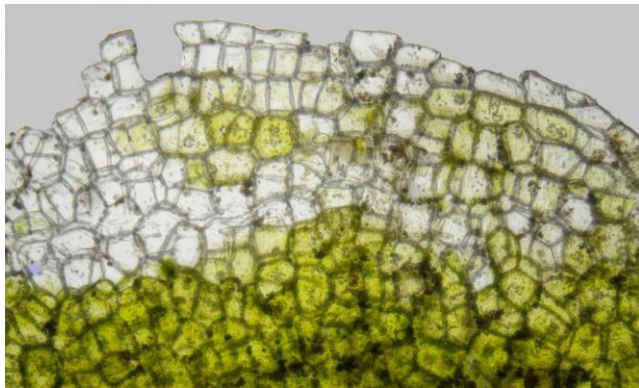


Figure 3 *Aneura maxima* showing 1-cell-thick thallus margin. Photo by Dick Haaksma, with permission.



Figure 4. *Aneura cf. pellioides*, one of three species that have been confused with each other. Photo by David Long, with permission.



Figure 5. *Aneura pinguis*, one of three species that have been confused with each other. Photo by Hermann Schachner, through Creative Commons.

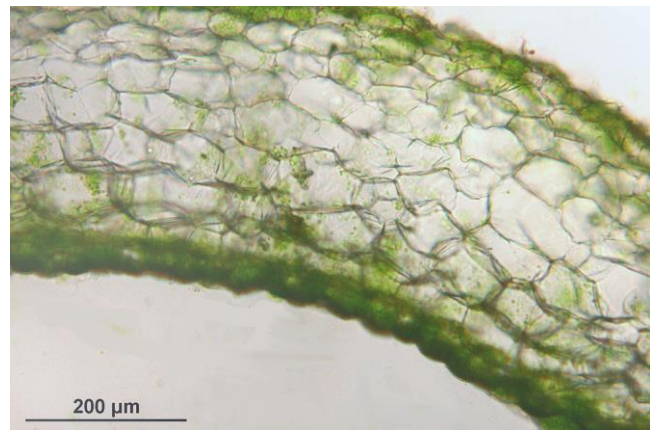


Figure 6. *Aneura pinguis* thallus cross section. Photo by Hermann Schachner, through Creative Commons.

Bączkiewicz *et al.* (2017) used DNA evidence to argue that *Aneura pinguis* (Figure 5-Figure 6) was comprised of many cryptic species, including *Aneura maxima* (Figure 2-Figure 3, Figure 7-Figure 10). I have treated the ones included here as separate species for two reasons. It is easy for the reader to combine the information to describe *Aneura pinguis*, but once combined under one name it cannot be separated out without further research. Second, I have followed the nomenclature used by Söderström *et al.* (2016) throughout these wet habitat chapters, and they have listed it as a valid species. Furthermore, Buczkowska *et al.* (2016) demonstrated, using ISSR primers, that the *Aneura maxima* populations were genetically distinct from those of *A. pinguis* and these researchers maintained recognition of the species *Aneura maxima*.

Distribution

Andriessen (1995) reported *Aneura maxima* (Figure 7-Figure 10) from Belgium in Europe, Asia (Indonesia, Japan, India), New Caledonia, and eastern North America. Miller (2002) noted its presence in Maine, and a number of other states in eastern USA. In 2006, Loskotová reported it from the Czech Republic and Slovakia. Later, Sérgio and Garcia (2009) reported it from the Iberian Peninsula, Frahm (2011) from Norway, Ștefănuț (2012) from Romania, and Buczkowska and Bączkiewicz (2006) from Poland (see also Mierzeńska & Vončina 2010; Wawrzyniak *et al.*

2014). Frahm *et al.* (2009) reported it from Thailand. It is likely to have been collected elsewhere in Europe, hiding under a misidentified name.



Figure 7. *Aneura maxima* showing the wavy edge of the thallus. Photo by Hugues Tinguy, with permission.



Figure 8. *Aneura maxima* thallus. Photo by Dick Haaksma, with permission.



Figure 9. *Aneura maxima* showing new lobes. Photo by Jiří Kameníček, with permission.



Figure 10. *Aneura maxima* with upward-growing branching lobes. Photo by Jiří Kameníček, with permission.

Currently, neither TROPICOS nor Söderström *et al.* (2016) consider *Aneura pellioides* (Figure 4) a valid species, with the former listing it as a synonym of *Aneura maxima* (Figure 7-Figure 10).

Aquatic and Wet Habitats

Loskotová (2006) reported *Aneura maxima* (Figure 7-Figure 10) as most frequently occurring on wet mineral soil in spring habitats in Slovakia and the Czech Republic. The individual plants grow vertically upward (Figure 9-Figure 10) from the water, forming compact growths that resemble lettuce. It is a more robust species than common *Aneura pinguis* (Figure 5-Figure 6). It frequently occurs with *Brachythecium rivulare* (Figure 11), *Chiloscyphus pallescens* (Figure 12), *Conocephalum conicum* (Figure 13), *Thuidium tamariscinum* (Figure 14), and *Trichocolea tomentella* (Figure 15).



Figure 11. *Brachythecium rivulare* habitat, a species that sometimes accompanies *Aneura maxima*. Photo by Michael Lüth, with permission.



Figure 12. *Chiloscyphus pallescens*, a liverwort species that sometimes accompanies *Aneura maxima*. Photo by Michael Lüth, with permission.



Figure 13. *Conocephalum conicum* by a stream from Poland where it can be associated with *Aneura maxima*. Photo by Panek, through Creative Commons.



Figure 14. *Thuidium tamariscinum*, a species that sometimes accompanies *Aneura maxima*. Photo by David T. Holyoak, with permission.

In Poland, Buczkowska and Byczkiewicz (2006) found that *Aneura maxima* (Figure 7-Figure 10) was similarly associated with *Conocephalum conicum* (Figure 13) and *Trichocolea tomentella* (Figure 15). At other locations it occurred with *Pellia epiphylla* (Figure 16) or *Pellia*

epiphylla subsp. *borealis*. In all its locations, it was accompanied by cryptic species of *A. pinguis* (Figure 5-Figure 6). However, the substrata differed. *Aneura maxima* occurred on wet humus, peaty soil, a mire on river banks, and wet peaty soil of alder swamps. Jan-Peter Frahm photographed its habitat in a ravine near a lake (Figure 17)



Figure 15. *Trichocolea tomentella*, a species that can be associated with *Aneura maxima* in Poland. Photo by Li Zhang, with permission.



Figure 16. *Pellia epiphylla* with developing sporophytes, a species that sometimes associates with *Aneura maxima* in Poland. Photo by Hermann Schachner, through public domain.



Figure 17. *Aneura maxima* habitat where a ravine enters a lake. Photo by Jan-Peter Frahm, with permission.

Schuster (1992) added habitats under waterfalls for some *Aneura maxima* (Figure 7-Figure 10) populations in North Carolina, USA. Furuki (2006) reported it from decaying logs in the mossy forest of the Philippines.

Vanderpoorten *et al.* (2006) developed a model to assess the rareness of *Aneura maxima* (Figure 7-Figure 10). They found that its localities in deep ravines on damp loamy soils (Figure 18-Figure 20) with light tree cover on the border between France and Belgium differed from conditions in other European localities. They considered this as evidence that it is not limited by a narrow ecological range. Rather, they considered it to be limited by poor dispersal ability. It is thus threatened by drainage of its preferred wet habitats.



Figure 18. *Aneura maxima* on a soil habitat. Photo by Dick Haaksma, with permission.



Figure 19. *Aneura maxima* in a habitat on soil. Photo by Dick Haaksma, with permission.



Figure 20. *Aneura maxima* in its habitat on soil. Photo by Dick Haaksma, with permission.

Adaptations

Aneura maxima has large, fleshy thalli that are deep green when fresh (Figure 21-Figure 22), pale brown when dry (Furuki 2006). These thalli sometimes grow upright (Figure 21), and they have pale margins that are one cell thick (Figure 23). The uppermost cells are lens-shaped and translucent (Figure 24-Figure 25), possibly focussing the light on the chloroplasts beneath.



Figure 21. *Aneura maxima* growing in upright clumps of fleshy thalli. Photo by Jiří Kameníček, with permission.

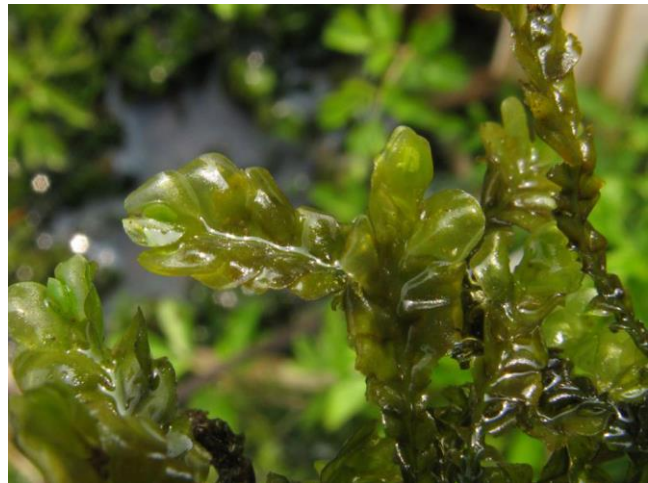


Figure 22. *Aneura maxima* showing its wavy margin and upright growth form. Photo by Jiří Kameníček, with permission.



Figure 23. *Aneura maxima* with translucent thallus wings. Photo by Jan-Peter Frahm, with permission.



Figure 24. *Aneura maxima* thallus showing lens-like upper cells. Photo by Dick Haaksma, with permission.



Figure 25. *Aneura maxima* showing lens-like upper cells that could focus light on the cells below. Photo by Dick Haaksma, with permission.

Reproduction

Aneura maxima (Figure 7-Figure 10) is **dioicous** and rarely fertile (Vanderpoorten *et al.* 2006). Gemmae are unknown (Preußing *et al.* 2010b). This combination seems to be responsible for its rarity. It is possible that the lobes (Figure 26) break off to form new plants and could even be dispersed short distances.



Figure 26. *Aneura maxima* with potentially reproductive branches. Photo by Jiří Kameníček, with permission.

Fungal Interactions

Duckett and Ligrone (2008) noted that whereas most species of *Aneura* have fungi, *Aneura maxima* (Figure 7-Figure 10) had never been investigated. Likewise, Bidartondo and Duckett (2010) were unable to find any

associated with *Aneura pellioides* (Figure 4)/*maxima* (Figure 7-Figure 10).

Biochemistry

Wawrzyniak *et al.* (2014) reported that volatile sesquiterpenoids, oxygenated sesquiterpenoids, and aliphatic hydrocarbons differed among the cryptic species within the *Aneura pinguis* (Figure 5-Figure 6) complex and *Aneura maxima* (Figure 7-Figure 10). They found that such compounds in all of the cryptic species within *A. pinguis* differed from those of *A. maxima*.

Aneura mirabilis (Figure 29-Figure 32)

(syn. = *Cryptothallus mirabilis*)

This is perhaps the most unusual of all bryophytes because it is parasitic and totally lacking in chlorophyll.

Davis (2004) asserted that *Cryptothallus mirabilis* (Figure 27) was related to *Aneura* (Figure 7-Figure 10), a genus in the same family. Soon after that, Wickett *et al.* (2008a; Wickett & Goffinet 2008) used plastid genome sequencing to demonstrate the close relationships of the species to members of *Aneura*. This **achlorophyllous** (lacking chlorophyll) species revealed loss of five chlororespiration (*ndh*) genes (Wickett *et al.* 2008a) compared to those of *Marchantia polymorpha* (Figure 28) (Wickett *et al.* 2008b), the only other liverwort with a completely sequenced chloroplast genome. Furthermore, six *ndh* genes that are subunits of PS I, PS II, and the cytochrome *b6f* complex were inferred to be **pseudogenes** (sections of chromosome that are imperfect copies of functional gene) (Wickett *et al.* 2008a). Bączkiewicz *et al.* (2017) used DNA barcoding to demonstrate the strong relationship between what was named *Cryptothallus mirabilis* and members of the genus *Aneura*. Based on these studies, the species has been placed in *Aneura* as *Aneura mirabilis* (Figure 27, Figure 29-Figure 32).



Figure 27. *Aneura mirabilis* showing the many small branches typical of *Aneura*, but totally lacking chlorophyll. Photo by Jan-Peter Frahm, with permission.



Figure 28. *Marchantia polymorpha*, a thallose liverwort that has had its entire genome, including the chloroplast genome, sequenced. Photo by Holger Casselmann, through Creative Commons.

Distribution

Aneura mirabilis (Figure 29-Figure 32) is primarily a north oceanic species, but it is known as far south as Portugal (Sérgio *et al.* 2005). Its European distribution includes England, Germany, France, Portugal, Russia, Sweden, Norway, Scandinavia, and Greenland (Bates & Hodgetts 1995; Merckx 2013; Merckx *et al.* 2013). Temperature, precipitation, and degree of continentality can define its distribution pattern (Sérgio *et al.* 2005).



Figure 29. *Aneura mirabilis* that has been exposed from among mosses in a peatland. Photo by Jan-Peter Frahm, with permission.



Figure 30. *Aneura mirabilis* exposed amid peat. Photo by Jeff Duckett and Silvia Pressel, with permission.



Figure 31. *Aneura mirabilis* thalli that have been exposed. Photo courtesy of Martin Bidartondo.



Figure 32. *Aneura mirabilis* revealed in a peat mire. Photo by Jeff Duckett and Silvia Pressel with permission.

Aquatic and Wet Habitats

Aneura mirabilis (Figure 29-Figure 32) is not a submersed species, but it does seem to prefer moist habitats (Figure 33-Figure 34). In Welsh Marches, it grows underground under birch trees, hiding under *Hyocomium armoricum* (Figure 35) and *Sphagnum quinquefarium* (Figure 36) near a stream (Lawley 2012). Hill (1988) characterizes its habitat in North Wales as acid boggy woodland (see also Hill 1969). Boudier *et al.* (1999) found it on "the fringes of Tardais pond" in France. It also occurs in a Lakeland (UK) habitat where it was found in a steep, wooded gully on the north bank of a stream, 70-100 cm above the stream, growing in several places in a patch of *Pellia* (Figure 37) (Hopkins 1953). Sérgio *et al.* (2005) found that it was not rare in Portugal, where it occurred mainly in wet forests with an oceanic influence. Richards (1959) noted that it often lives in surface litter (Figure 38) beneath *Molinia* (grass; Figure 39) or large mosses such as *Hylocomium splendens* (Figure 40). Its association with birch trees can be explained by its need for a fungal association with species that are also attached to birch roots (Read *et al.* 2000). Its subterranean habitat means that it is likely to be easily overlooked.



Figure 33. *Aneura mirabilis* habitat in Bretagne. Photo by Michael Lüth, with permission.



Figure 36. *Sphagnum quinquefarium*, a species that contributes to the habitat of *Aneura mirabilis*. Photo by Michael Lüth, with permission.



Figure 34. *Aneura mirabilis* revealed in a *Sphagnum* mire. Photo by Michael Lüth, with permission.



Figure 37. *Pellia epiphylla*, a species that was associated with *Aneura mirabilis* in a wooded gully in the UK. Photo by Hermann Schachner, through public domain.



Figure 35. *Hyocomium armoricum*, a species that contributes to the habitat of *Aneura mirabilis*. Photo by David T. Holyoak, with permission.



Figure 38. *Aneura mirabilis* in a wet litter habitat. Photo by Michael Lüth, with permission.



Figure 39. *Molinia caerulea*, a species that can occur in the same habitats as *Aneura mirabilis*, where the liverwort hides beneath the surface. Photo by James K. Lindsey, with permission.



Figure 40. *Hylocomium splendens*, a species that may have *Aneura mirabilis* growing beneath it in peatland habitats. Photo by Hermann Schachner, through Creative Commons.

Aneura mirabilis (Figure 29-Figure 32) is acidophilic and occurs in locations with high bryophyte cover (Sérgio *et al.* 2005). Williams (1950) found it near an ant's nest. Could it be that the ants helped in its dispersal?

Adaptations

Aneura mirabilis (Figure 29-Figure 32) typically lives in dark habitats – deep forest, ravines, or otherwise well-shaded areas. This makes it difficult for a plant to supply enough carbohydrate through photosynthesis (Merckx 2013). But *A. mirabilis* has evolved a novel means of gaining its carbohydrate, unique among liverworts – it gets it from birch trees by way of a fungus (Hawksworth 2003), as discussed below under fungal interactions. It succeeds

in this relationship, completely lacking chlorophyll in either generation (Hill 1969; Mårtensson & Nilsson 1974). Even the spores lack green color (Hill 1969; Mårtensson & Nilsson 1974), and Hill (1969) found no development of chlorophyll in spores that were cultured in light. The young thallus shows some evidence of plastid structure, but this never develops chlorophyll (Sigeo 1969). In fact, Sigeo found that proplastids, similar to those of normal green plants, developed in the apical cell and the surrounding cells. However, in more mature cells there was no evidence of development of a chloroplast. The early development of protoplasts and their subsequent changes occurred before any evidence of fungal invasion, but rather is similar to early stages in other mutant plant albinos wherein a genetic change causes the albino development.

Mårtensson and Nilsson (1974) noted that we do not know the extent to which precursors of chlorophyll are present, and I am not aware of any more recent studies on the topic, although the genes of the chloroplasts have been sequenced (Wickett *et al.* 2008b). On the other hand, Wickett *et al.* (2008b) found little reduction in the genome size. In this case, all the losses of genes and pseudogenes are also seen in the parasitic flowering plant *Epifagus virginiana*, a forest plant connected through a fungus to beech (*Fagus*) roots. These gene losses are typical of early "decay" stages of the genes in consort with the relaxation of selection pressures. This would seem to imply that evolutionarily, the genes were lost after the mycorrhizal relationship developed.

Although *Aneura mirabilis* (Figure 29-Figure 32) lives below the surface in wet peatlands, these plants can dry out. Duckett *et al.* (1990) discovered that when *Aneura mirabilis* dries out over a period of 420 days, it develops a covering of multicellular hairs on the dorsal (upper) surface. These could serve to deflect excessive light as the peat shrinks upon drying, reduce water loss, and provide capillary spaces for water uptake. But we have no data to determine if any of these properties actually help it in the field.

Reproduction

Aneura mirabilis is **dioicous** (Figure 41), and in Portugal Sérgio *et al.* (2005) found that it is usually fertile with both male and female plants present (Figure 41). Female plants have a greater longevity than do male plants in this species (Benson-Evans 1960). Lewis and Benson-Evans (1960) suggested that this longevity difference might account for the **female-biased** (more females than males) sex ratio.

Induction of antheridia in *Aneura mirabilis* (Figure 29-Figure 32) responds to temperature, but not to photoperiod or light intensity (Benson-Evans 1961). When collected from the field in winter, the plants formed sex organs after 5 weeks at 21°C. If kept continuously at 18°C, they remained vegetative through winter and the following year. Benson-Evans interpreted this to mean that they must need a period of low temperatures before developing gametangia.

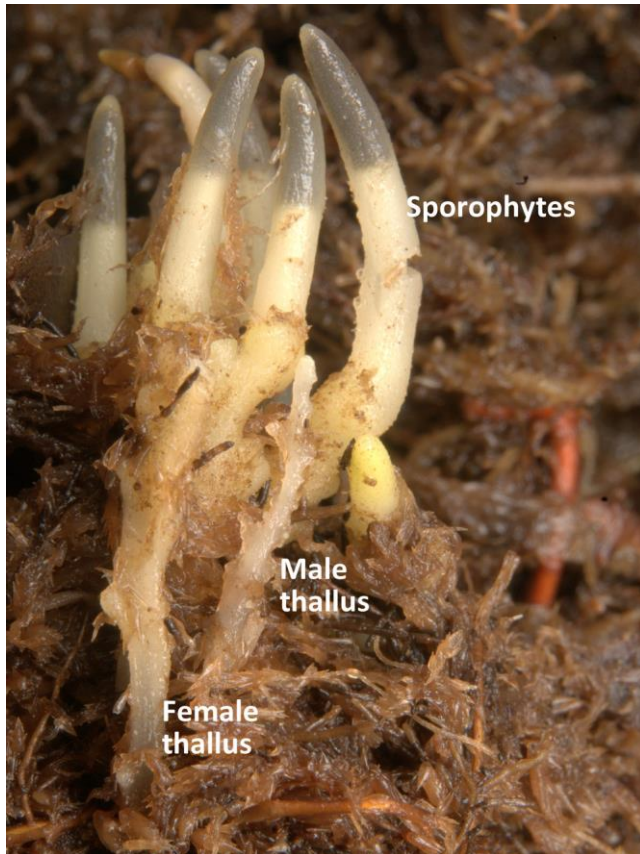


Figure 41. *Aneura mirabilis*, showing male and female thalli and developing sporophytes *in situ* beneath *Sphagnum* among silver birch (*Betula pendula*). Photo by Brian Eversham, with permission.

Capsules of *Aneura mirabilis* (Figure 29-Figure 32) reach the surface of the moss layer through elongation of the seta (Figure 42-Figure 47) (Williams 1950), thus can be exposed to light at maturity (Benson-Evans 1960). Both Sjörs (1949) and Malmberg (1933) found that at least some capsules reach the surface and dehisce there in the light. The large spores fall nearby and thus receive diffused light prior to germination.



Figure 42. *Aneura mirabilis* with developing sporophytes and exposed gametophyte thallus. Photo by David T. Holyoak, with permission.



Figure 43. *Aneura mirabilis* with peat and litter cleared away to expose the thallus and sporophytes protruding above the buried thallus. Photo by Hugues Tinguy, with permission.



Figure 44. *Aneura mirabilis* with sporophytes protruding. Photo by Hugues Tinguy, with permission.



Figure 45. *Aneura mirabilis* with sporophytes; exposed thallus is at the right, and evidence of the buried thallus is below the sporophytes in the image. Photo by David G. Long, through Creative Commons.



Figure 46. *Aneura mirabilis* under *Hypnum cupressiforme*, showing mature capsules. Photo modified from Sérgio *et al.* 2005, with permission.



Figure 47. *Aneura mirabilis* dehiscing capsule. Photo modified from Sérgio *et al.* 2005, with permission.

In Portugal, the mature spores of *Aneura mirabilis* (Figure 29-Figure 32) are present in January to March, in France they are present in March, but farther north they appear in summer (Sérgio *et al.* 2005). The spores are large (30 μm) (Benson-Evans 1960). The spores remain in tetrads, even after dispersal. Upon germination, the tetrads separate and germination in culture occurs within a week. Keeping the tetrad intact until time for germination could explain the frequent presence of sporophytes – the male and female spores travel together and thus would germinate in proximity to each other.

Spores germinated on peat and peat extract agar, but not on Knop's agar or Voth's solutions (Benson-Evans 1960). Those cultured at -18°C germinated within a few days. Germination was promoted by diffused daylight, but inhibited by strong light. In laboratory experiments, spores fail to germinate after 11-12 months, but they do remain viable throughout one season.

Young sporelings of *Aneura mirabilis* (Figure 29-Figure 32) may be washed to greater depths in the peat by rainwater (Benson-Evans 1960). Spores in culture never developed beyond the 20-30-cell stage, an indication that the developing gametophyte might be dependent on the fungus by that stage. The spores themselves seem to be free of fungal hyphae, so the fungal connection must be made at the site of germination for the *Aneura mirabilis* to succeed. It is therefore probably of little advantage for the species to have much long-distance dispersal as it has little chance of landing where it can find its partners. In the peatlands of the liverwort parents, the fungus is readily available nearby.

Hill (1969) notes that the achlorophyllous spores of *Aneura mirabilis* (Figure 29-Figure 32) nevertheless require light for germination, an accepted requirement for bryophyte spore germination (de Forest Heald 1898). But Benson-Evans (1960) found that reduced light was necessary even for germination of *Aneura mirabilis* spores.

Fungal Interactions

We are learning that most plant species are colonized by multiple species of mycorrhizal fungi, and in turn, the fungi are able to colonize many species of plants (Merckx 2013). Such is not the case for *Aneura mirabilis* (Figure 29-Figure 32) and associated fungi. In fact it seems that the *Metzgeriidae* often have specificity (Bidartondo & Duckett 2010). Thus far, only members of the *Aneuraceae* [*Cryptothallus* (now in *Aneura*), *Aneura* (Figure 7-Figure 10, Figure 18-Figure 26, Figure 29-Figure 32, Figure 52-Figure 57), and *Riccardia* (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133)] are known to host *Basidiomycete* endophytes (Pocock & Duckett 1984). These form extensive hyphal coils in the cells of the liverworts, similar to those in orchid *endomycorrhizae* (close relationship between plant and root fungi in which hyphae of fungus actually penetrate cells of root, rather than just colonizing on its surface). Pocock and Duckett suggested that these fungi in *Aneura mirabilis* might be the same as those living as an ectotroph (fungus living on root surface) of *Betula* roots.

The interaction between *Aneura mirabilis* (Figure 48) and the fungus *Tulasnella* (Figure 49) is unique among the liverworts (Bidartondo *et al.* 2003; Hawksworth 2003;

Wickett & Goffinet 2008; Wickett *et al.* 2008b; Oberwinkler *et al.* 2017). *Aneura mirabilis* is the only **mycoheterotrophic** (having symbiotic relationship between plant and fungus, in which plant gets all or part of its carbohydrate from parasitism upon fungi rather than from photosynthesis) liverwort (Merckx 2013). This relationship has been referred to as "cheating" (Bidartondo *et al.* 2003). The plant, in this case *Aneura mirabilis*, is able to exploit the existing mycorrhizal relationship that already exists between the **Basidiomycete** fungus *Tulasnella* and a tree (Read *et al.* 2000; Wickett *et al.* 2008b). Bidartondo *et al.* (2003) demonstrated, using ^{14}C in CO_2 , that the carbon was transferred from *Betula pendula* seedlings (Figure 50) through a species of *Tulasnella* to this achlorophyllous liverwort. It appears that *Aneura mirabilis* is able to share *Tulasnella* with both *Betula* and *Pinus* (Figure 51) (Bidartondo *et al.* 2003; Davis & Shaw 2008), depending on an otherwise suitable habitat.



Figure 48. *Aneura mirabilis* with the fungal partner *Tulasnella*. Photo by Martin Bidartondo, with permission.

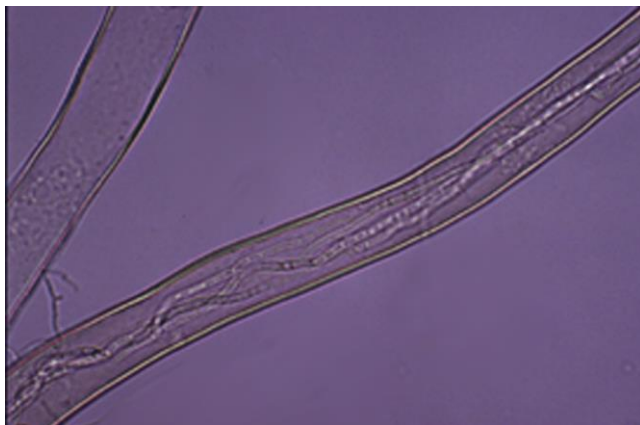


Figure 49. *Aneura mirabilis* rhizoid with *Tulasnella* inside. Photo by Martin Bidartondo, with permission.

When *Aneura mirabilis* (Figure 29-Figure 32) and *A. pinguis* (Figure 52-Figure 57) were collected from a variety of sites, the fungi were confined to specific regions of the gametophyte thallus in both liverwort species, and hyphal contact with the substratum occurred through the liverwort rhizoids (Ligrone *et al.* 1993). The colonization

cycle presents a growth phase when the fungus forms large intracellular coils, host cytoplasm proliferates, and the starch content of the plastids decreases. This phase is followed by senescence in which the hyphae die back and aggregate into large masses. The fungus exhibits repeated colonization cycles. In *Aneura mirabilis* the young hyphae contain abundant glycogen and sometimes amyloid deposits. Despite these behavioral similarities, Ligrone *et al.* found that these two liverwort hosts did not share the same species of fungal partner. It seems that there is thus far no species name of the *Tulasnella* (Figure 48-Figure 49) species associated with *Aneura mirabilis*.



Figure 50. *Betula pendula* seedling, a species that is able to share the fungus *Tulasnella* with *Aneura mirabilis*. Photo by Krzysztof Ziarnek, through Creative Commons.



Figure 51. *Pinus* in peatlands, a habitat where the pines can share the fungus *Tulasnella* with *Aneura mirabilis*. Photo by Runa S. Lindebjerg <Grida.no> with online permission.

Biochemistry

Although there have been a large number studies on the fungal partnership of *Aneura mirabilis* (Figure 29-Figure 32), the biochemical studies are relatively few. Rycroft (1998) reported that the new sesquiterpenoid 15-acetoxypinguisone was clearly the predominant compound in an extract of this species. But Rycroft and Cole (1998) noted that its relative abundance was much less in a second specimen. It would be interesting to determine to what degree the fungus alters the biochemical spectrum, and if the tree host plays any role in determining what secondary compounds are produced.

***Aneura pinguis* (Figure 52-Figure 57)**

(syn. = *Riccardia pinguis*)

Wachowiak *et al.* (2007) used chloroplast DNA sequence variation and polymerase chain reaction-restriction fragment length polymorphism to demonstrate cryptic species in the *Aneura pinguis* (Figure 52-Figure 57) complex. (See also Myszczyński *et al.* 2017). Interestingly, they found that lowland and mountain populations exhibited different tRNA^{Leu} types, with two types in the mountains and a third in the lowlands. Later, Wawrzyniak *et al.* (2018) demonstrated a number of cryptic species within *Aneura pinguis*, using mostly differences in sesquiterpene hydrocarbons. What is even more interesting in our ecological context, Bączkiewicz *et al.* (2017) found that the cryptic species, based on DNA differences, clearly differed in habitat preferences.



Figure 52. *Aneura pinguis* habit. Photo by Bernd Haynold, through Creative Commons.



Figure 53. *Aneura pinguis* in a slightly dry condition. Photo by Chris Wagner, with permission.



Figure 54. *Aneura pinguis* habit. Photo by Hermann Schachner, through Creative Commons.



Figure 55. *Aneura pinguis* habit. Photo by Hermann Schachner, through Creative Commons.



Figure 56. *Aneura pinguis* growing over mosses. Photo by Hermann Schachner, through Creative Commons.



Figure 57. *Aneura pinguis* terrestrial form among mosses. Photo by Jan-Peter Frahm, with permission.

But perhaps the cryptic species are not so cryptic. Buczkowska *et al.* (2006a) found that 13 quantitative traits differed significantly among the cryptic species of *Aneura pinguis* (Figure 52-Figure 57). These were mostly in the area of dorsal epidermal cells, thickness and number of cells in the thallus cross section, size of inner cells in the thallus cross section, and thallus width. Furthermore, there were differences in sizes of various aspects of males vs. females as well as male:female ratios.

Different forms have been identified in nature (Figure 58), so we must ask if these are due to genetic differences or to habitat modification. Frahm (2012) reported *Aneura pinguis* (Figure 52-Figure 57) fo. *rivularis* growing under water in a mill pond in the Vosges Mountains. However, when the form *rivularis* is grown in the same conditions as the typical form, the form *rivularis* retains the unistratose borders (Figure 59), whereas *Aneura pinguis* (Figure 52-Figure 57) retains the multistratose margins (Figure 60). Frahm implies that *Aneura pinguis* fo. *rivularis* is actually *Aneura maxima* (Figure 2-Figure 3, Figure 7-Figure 10, Figure 17-Figure 25). But Schuster (1992) seems certain that *Aneura maxima* from North America is really the same as *Aneura pellioides* (Figure 4) from Japan, but *A. pellioides* in Europe may not be synonymous with *A. maxima*.

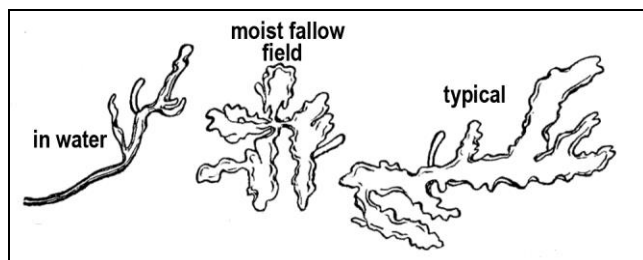


Figure 58. *Aneura pinguis* growing in water, in a moist fallow field, and in its typical growth form. Image modified from Watson 1915.

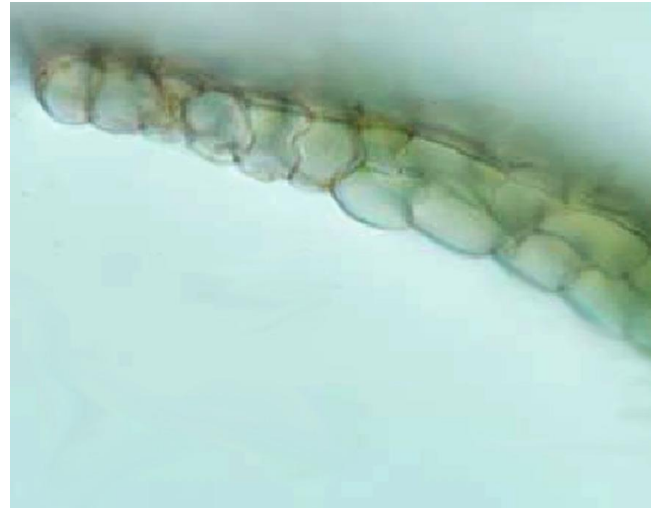


Figure 59. *Aneura pinguis* form *rivularis* thallus margin section after growing in water culture. Photo by Jan-Peter Frahm, with permission.



Figure 60. Typical form of *Aneura pinguis* thallus cultured in water for 4 months, showing its failure to develop thin margins. Photo by Jan-Peter Frahm, with permission.

Distribution

Aneura pinguis (Figure 52-Figure 57) is very cosmopolitan (Schuster 1992; Preußing *et al.* 2010a), extending from the High Arctic to the tropics (Schuster 1992). It occurs throughout most of Europe and North America, southward to the West Indies, South America, Africa, Asia, New Guinea, Australia, and New Zealand, south to Campbell Island (Schuster 1992), and in the Caribbean (Preußing *et al.* 2010b) and the Philippines (Furuki 2006).

Aquatic and Wet Habitats

Schuster (1992) refers to "enormous" habitat range for this species. Nevertheless, it seems to prefer basic conditions in moist habitats (Figure 61). Ceschin *et al.* (2012) considered the habitats of *Aneura pinguis* (Figure 52-Figure 57) to be so variable that it was an "invalid" indicator species.



Figure 61. *Aneura pinguis* on mud. Photo by Bas Kers, through Creative Commons.

Aneura pinguis (Figure 52-Figure 57) occurs on stream and river banks (Figure 62) with frequent submergence and slow water, often among wet rocks or soil, on rocks or soil in fast water, or submerged in slow water with poor mineral salts (Watson 1919). In Wales I found it near a stream and large waterfall (Figure 63). At Prudhoe Bay, Alaska, it is hydro-mesic or hydric (Rastorfer *et al.* 1973). It occurs in alpine streams (Figure 64) in the Swiss Alps (Geissler 1976). De Sloover and Goosens (1984) reported it from the travertine *Cratoneuron* (Figure 65) association of Lorraine River, Belgium. Geissler and Selldorf (1986) found that in their European studies it occurred with other wet habitat species (Figure 66), the moss *Paludella squarrosa* (Figure 67) and tracheophytes *Eleocharis quinqueflora* (Figure 68) and *Trichophorum cespitosum* (Figure 69), but was not common there. It occurs in streams in Belgium (Vanderpoorten & Tignon 2000), in mountain streams of northwest Portugal (Vieira *et al.* 2005), on European travertines (Pentecost & Zhang 2006), in rivers (Ferreira *et al.* 2008), and in poorly mineralized and basic waters in the Tiber River basin, Italy (Ceschin *et al.* 2012). On travertines, seepages and aspect are important and the liverworts are kept moist by capillarity (Pentecost & Zhang 2006).



Figure 62. *Aneura pinguis* in a streambank habitat at Cwm Idwal National Nature Reserve, Wales. Photo by Janice Glimme.



Figure 63. *Aneura pinguis* at Cwm Idwal National Nature Reserve where it is kept moist by the nearby river and large waterfall. Photo by Janice Glimme.



Figure 64. *Aneura pinguis* in water, where one can find it in alpine streams. Photo from Proyecto Musgo, through Creative Commons.



Figure 65. *Cratoneuron filicinum*; *Cratoneuron* appears with *Aneura pinguis* on travertine rock in Belgium. Photo by Hugues Tinguay, with permission.



Figure 66. *Aneura pinguis* in wet habitat with other bryophytes. Photo by Kristian Peters, through Creative Commons.



Figure 67. *Paludella squarrosa*, a species that occurs with *Aneura pinguis* in wet habitats. Photo by Hermann Schachner, through Creative Commons.



Figure 68. *Eleocharis quinqueflora*, a species that occurs with *Aneura pinguis* in wet habitats. Photo by Ed Stikvoort, Saxifraga, through Creative Commons.

In western Canadian montane streams, *Aneura pinguis* (Figure 52-Figure 57) is submerged and hemicalciphilous (Vitt *et al.* 1986) in some, but can also occur on streambanks (Glime & Vitt 1987). Vitt and Horton (1990) reported it from fens in Missouri, USA. At Mountain Lake,

Virginia, USA, Sharp (1944) reported *Aneura pinguis* from wet soil at the edge of a stream.



Figure 69. *Trichophorum cespitosum*, a species that occurs with *Aneura pinguis* in wet habitats. Photo by Elke Freese, through Creative Commons.

In a Somerset, UK, heath, zonation depends on the supply of fresh water (Watson 1915). The streams have *Potamogeton polygonifolius* (Figure 70), and immediately above that constantly submersed zone of deeper water one can find *Aneura pinguis* (Figure 52-Figure 57) along with *Pellia epiphylla* (Figure 71). If the water is present continuously, these two species are present, including also living in furrows that may be too shallow for *Potamogeton polygonifolius*. In these submersed locations, *Aneura pinguis* usually becomes long and narrow (Figure 72). Above that liverwort zone, where the water supply is intermittent and the zone remains above water for some time, *Riccardia multifida* (Figure 71) occurs instead. In shallow boggy pools, *Aneura pinguis* is usually absent and the pools are occupied instead by *Scorpidium scorpioides* (Figure 73), whether by competition or by a habitat that is otherwise unsuitable for *Aneura pinguis*.



Figure 70. *Potamogeton polygonifolius*, a species found in deeper water of heathland streams and wet areas, just below the *Aneura pinguis* zone. Photo by Bert Lanjouw, through Creative Commons.

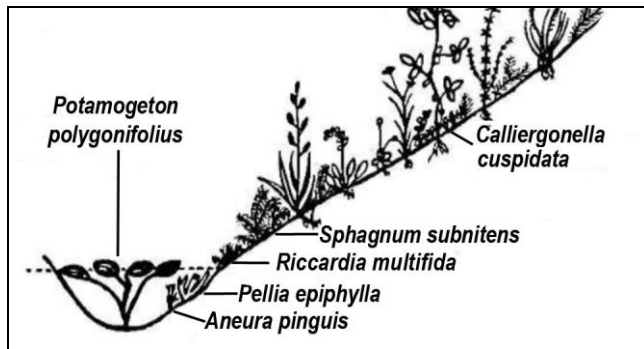


Figure 71. *Aneura* zonation in streams of wet heathland. Drawing modified from Watson 1915.

The habitats of the various cryptic species of *Aneura pinguis* (Figure 52-Figure 57) differ. Gonera and Buczkowska (2016) reported that cryptic species A typically grows on humus over limestone rocks in the Western Carpathians, B is mainly on clay soil in Bieszczady Mts. and in clayish areas of lowlands, C grows both in lowlands and mountains and it occupies mostly wet sandy soils on the shores of oligotrophic lakes and river and mountain stream banks, E is associated with calcareous rocks in flowing water in mountains. Cryptic species A, B, and C differ somewhat in morphology, but the differences are subtle and relate mainly to thickness of the thallus and differences in thallus cells (Figure 74-Figure 76) (Buczkowska & Adamczak 2006).



Figure 72. *Aneura pinguis* form *rivularis* thallus grown in water in a mill pond for 20 years. Photo by Jan-Peter Frahm, with permission.



Figure 73. *Scorpidium scorpioides*, a species that occurs in shallow pools that lack *Aneura pinguis*. Photo by Gróa Valgerður Ingimunda, through Creative Commons.

Pentecost and Zhang (2006) examined effects of exposure and water availability on European travertine bryophytes, including *Aneura pinguis* (Figure 52-Figure 57). Only *A. pinguis* was significantly affected by aspect. It was also confined to seepages where moisture was ensured through capillarity.

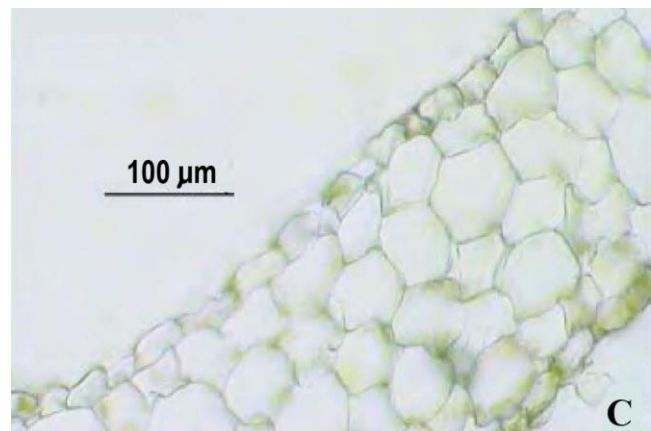
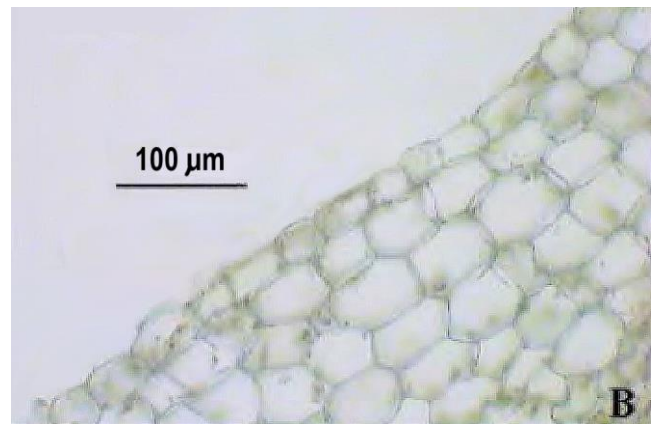
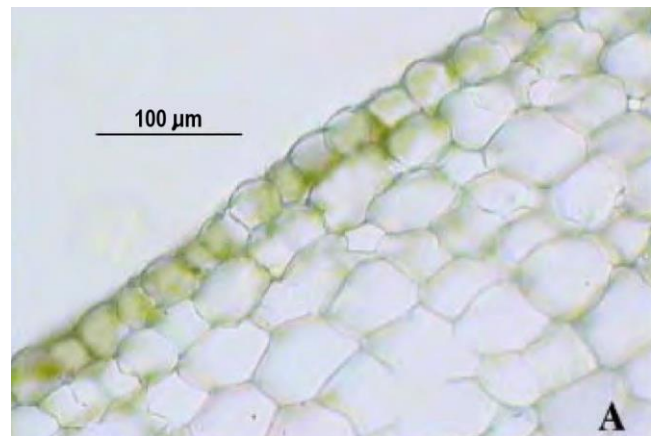


Figure 74. Cross sections of *Aneura pinguis* showing epidermis and median cells of cryptic species A, B, and C. Photo by Katarzyna Buczkowska, with permission.

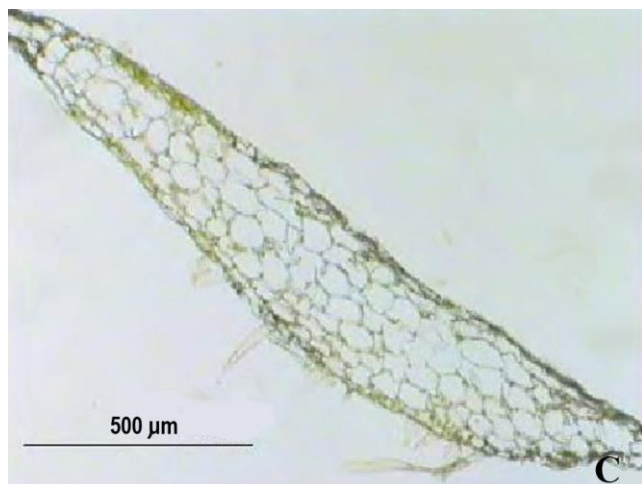
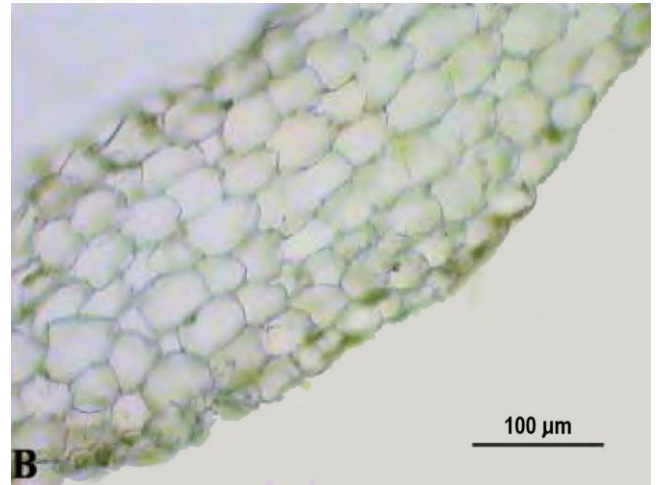
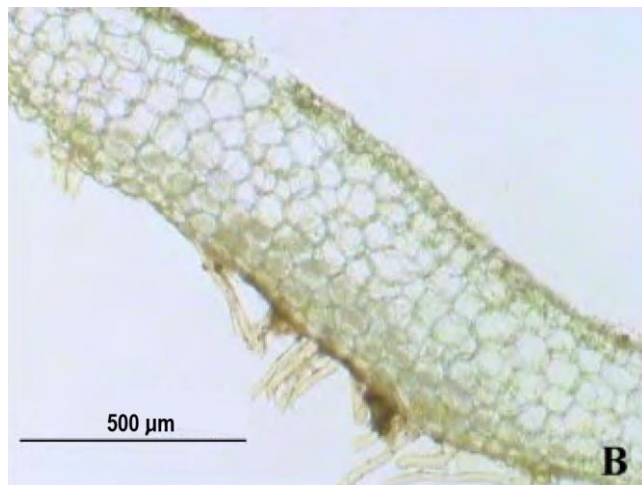
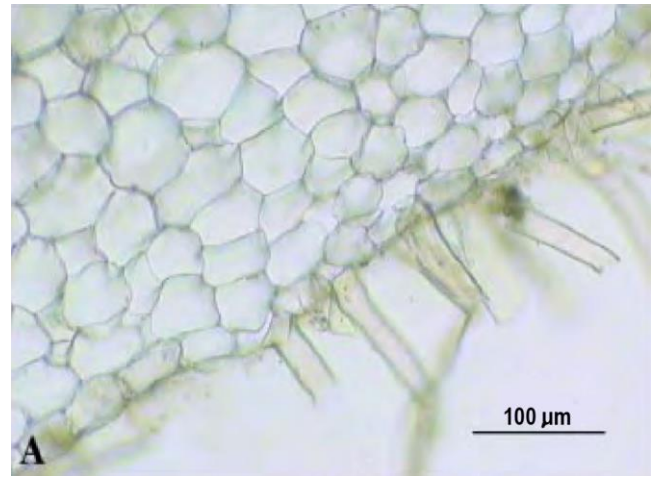
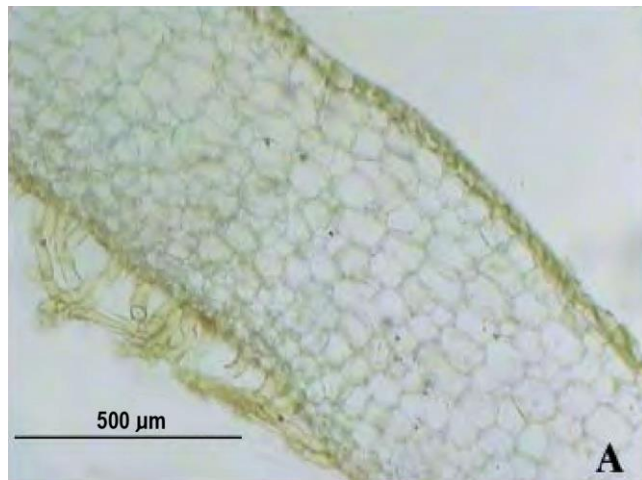


Figure 75. *Aneura pinguis* thallus cross section showing differences between cryptic species A, B, and C. Photo by Katarzyna Buczkowska, with permission.

Figure 76. Cross section of *Aneura pinguis* showing ventral side of thallus in cryptic species A, B, and C. Photo by Katarzyna Buczkowska, with permission.

Váňa and Ignatov (1995) reported that they found *Aneura pinguis* (Figure 52-Figure 57) in two types of habitats: wet sandy banks and bars of creeks and rivers; on rotten logs in conifer woods (Figure 77). While both of these are moist habitats, the substrata are quite different, as well as the former having the possibility of submersion. Could these be cryptic species differences?

Fojt and Harding (1995) explored the effects of changes in Suffolk fens on the species composition of plants. Changes in the mires included lack of traditional management, changes in water regime, and increased fertility. In unmanaged areas, all of the fen associates and bryophytes were lost and replaced by non-fen species and ruderal tall herbs. When traditional management was maintained, small characteristic species of wet fens and semi-aquatic conditions still disappeared, but recruitment was not as evident. Those species that remained tended to

be species that are either quite common in fens or non-fen recruits. When the fens remained wet, but were derelict, some species remained, with *Aneura pinguis* (Figure 52-Figure 57) and *Riccardia multifida* (Figure 140-Figure 149) among them. The researchers concluded that stable hydrology is more important than extensive management in conserving these sites.



Figure 77. *Aneura pinguis* on bark; it can be found on decaying logs. Photo by Li Zhang, with permission.

Despite the ability of *Aneura pinguis* (Figure 52-Figure 57) to occupy a wide range of habitats, and to survive changes to its fen habitats, Albinsson (1997) determined that liverworts, including *Aneura pinguis*, have a narrow ecological amplitude in mires, whereas smaller liverworts tend to have wider amplitudes. Albinsson used the term **compromise strategy** to describe those species that rely on habitats created by other living bryophytes. These include species that are frequently sterile.

In Japan, *Aneura pinguis* (Figure 52-Figure 57) also occurs on decaying logs (Figure 77) in the mossy forest (Furuki 2006), but once again in a constantly moist environment. Logs that are in advanced stages of decay, especially missing bark, hold more water.

Adaptations

Aneura pinguis (Figure 52-Figure 57) has light green thalli when fresh, turning brown as they dry (Furuki 2006). Could this color change protect the species against bright light in the dry condition, helping to prevent photo damage?

Proctor *et al.* (1992) measured stable carbon isotope discrimination of $\delta^{13}\text{C}$ in relation to different sites and heights above water level in a North Carolina, USA, lake, and from two Marchantialean and two Metzgerialean liverworts from various habitats. Among these bryophytes, *Aneura pinguis* (Figure 52-Figure 57) had a slightly more negative reading. The researchers suggested that *A. pinguis* might have some uptake of recycled CO_2 . But where is it stored? Buczkowska *et al.* (2006a) compared the thallus morphology among various cryptic species of *Aneura pinguis*. This liverwort does not have internal air chambers (Figure 60, Figure 74-Figure 76) (Clapp 1912), but the thickness differs (Figure 75) among the cryptic species (Buczkowska *et al.* 2006a). Could the distance required for CO_2 to travel to exit the plant cause retention that would permit nearby cells to benefit from its attempt to

escape? This raises interesting questions that require more exploration. Could greater thickness of the thallus facilitate recycling of CO_2 ? Could larger cell size cause a longer retention of respired CO_2 ? Does cell wall thickness play any role in recycling respired CO_2 in photosynthesis?

One growth form of *Aneura pinguis* is upright (Figure 78). This form is an advantage in wet habitats where there is little danger of drying out because it exposes more surface to gas exchange and sunlight.



Figure 78. *Aneura pinguis* growing upright, a form that is possible in continuously wet habitats. Photo by Jiří Kameníček, with permission.

Reproduction

Aneura pinguis (Figure 52-Figure 57) is a thallose, **dioicous** species with sexual dimorphism (Buczkowska *et al.* 2006a). Male thalli are smaller and less branched than female thalli (Müller 1951-1958; Furuki 1991; Schuster 1992). d'Artenay and Renzaglia (2011) described the architecture of the spermatid in *Aneura pinguis* and provided high resolution images.

In cryptic species A of *Aneura pinguis* (Figure 52-Figure 57) only 55% of the gametophytes were fertile, compared to 80% (Figure 79) in B and almost 70% in C (Buczkowska *et al.* 2006a). Most colonies consisted of only one sex. Sex ratios differed among the three cryptospecies. Furthermore, the cryptic species are partly intersterile, differing in time of gametangial maturity (Showalter 1926, 1928; Buczkowska *et al.* 2006a).

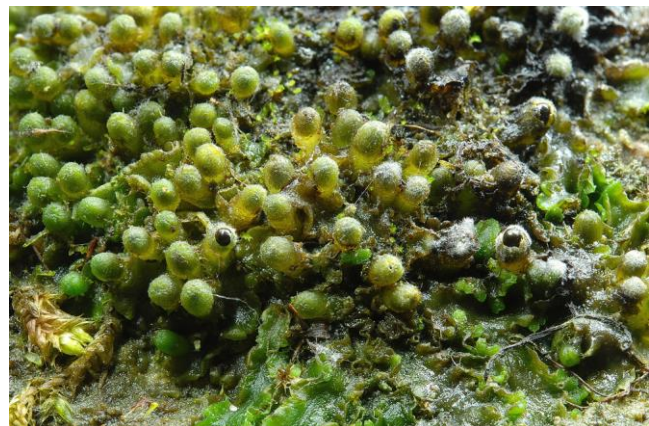


Figure 79. *Aneura pinguis* perianths and young sporophytes. Photo by Dick Haaksma, with permission.

Clapp (1912) described the development of the capsules of *Aneura pinguis* (Figure 80-Figure 85) from first embryo cell to splitting of the capsule into four valves. The capsules are "highly specialized" (Clapp 1912). Horner *et al.* (1966) described the development of the spores (Figure 86). Showalter (1925) described the early stages of spore germination.



Figure 80. *Aneura pinguis* with sporophytes emerging from the perianth. Photo by Bernd Haynold, through Creative Commons.



Figure 81. *Aneura pinguis* perianths with embryonic capsules inside. Photo by Dick Haaksma, with permission.



Figure 82. *Aneura pinguis* perianth with embryonic sporophyte inside. Photo by Dick Haaksma, with permission.



Figure 83. *Aneura pinguis* with maturing sporophytes. Photo by Štěpán Koval, with permission.



Figure 84. *Aneura pinguis* with maturing capsules and elongating setae. Photo by Jan-Peter Frahm, with permission.



Figure 85. *Aneura pinguis* with dehiscent sporophyte and perianths. Photo by Li Zhang, with permission.

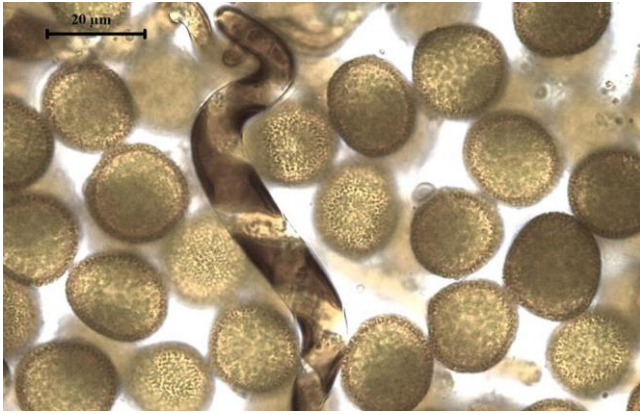


Figure 86. *Aneura pinguis* spores. Photo by Hugues Tinguy, with permission.

Gemmae are unknown in *Aneura pinguis* (Figure 52-Figure 57) (Clapp 1912; Preußing *et al.* 2010b). Vegetative reproduction occurs as older parts of the thallus die and apical portions become separated (Figure 87). This is facilitated by the production of lobes (Figure 88) that can break away. We do not know the degree to which these portions are dispersed, but we can assume that they are at least sometimes dispersed by flowing water. Waterfowl and insects might also contribute to dispersal.



Figure 87. *Aneura pinguis* showing older portions that are dying while tips are growing. Photo by Jouko Rikkinen, through Creative Commons.



Figure 88. *Aneura pinguis* showing vegetative lobes that can break off to form new plants. Photo by Hugues Tinguy, with permission.

Fungal Interactions

Aneura pinguis (Figure 52-Figure 57) is well known for its fungal interactions. In a study of symbiotic associations with liverworts, *Aneura pinguis* was associated with *Tulasnella* sp. (Figure 89; see also Figure 49), one of very few **Basidiomycetes** known to have a symbiotic relationship with liverworts (Kottke *et al.* 2003). These fungal interactions are typically highly species specific. Kottke *et al.* (2003) and Leake (2005) noted that the fungus in *Aneura pinguis* are closely related to those in *Aneura mirabilis*. Liepiņa (2012) also demonstrated specificity between *Fossombronia foveolata* (Figure 90) and *A. pinguis* where thalli of the two species growing side-by-side housed different species of fungi.



Figure 89. *Tulasnella violea* on tree trunk, in a genus that is often associated with liverworts, including *Aneura pinguis*. Photo by Esa Borén, through Creative Commons.



Figure 90. *Fossombronia foveolata*, a species that can grow beside *Aneura pinguis*, but that has different fungal associations. Photo by Hugues Tinguy, with permission.

Duckett *et al.* (2004) found different fungal endophytes in upland and lowland populations of *Aneura pinguis* (Figure 52-Figure 57) and likewise noted that the fungi had high host specificity. Bidartondo and Duckett (2010) considered the few overlaps of fungal species between *Aneura pinguis* and *Aneura mirabilis* (Figure 29-Figure 32) and the scattered occurrence of the fungus *Sebacina* (Figure 91-Figure 92) in *Aneura pinguis* may relate to the broad molecular diversity (cryptospecies) of this liverwort. Preußing *et al.* (2010a) determined that the composition of the communities of tulasnelloid fungi in *A. pinguis* differs between Ecuador and Europe, with a much higher diversity of tulasnelloid fungal partners at the Ecuadorian site, further supporting the hypothesis that the partnerships were related to cryptic species differences.



Figure 91. *Sebacina sparassoides* with moss. Photo by Lloyd P. Roberts, through Creative Commons.

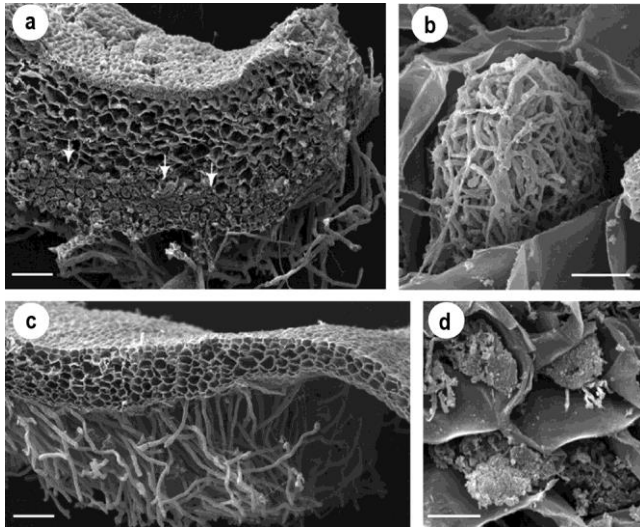


Figure 92. *Sebacina* infecting *Aneura* (a,b,d); *Aneura pellioidea* hypha-free (c). Modified from Bidartondo and Duckett 2010, with permission.

Preußing *et al.* (2010b) consider the appearance of the mycothallus in the *Aneura* clade to be remarkably homogenous. Hyphae penetrate through living rhizoids; they colonize the parenchymal cells from the base of the rhizoid intracellularly by penetrating the cell walls, then forming dense coils of hyphae. Colonization of epidermal

cells is rare (Brown & Braggins 1989) and intercellular infections are unknown (Preußing *et al.* 2010b).

Ligrone *et al.* (1993) learned through ultrastructural study that the interactions of endophytic Basidiomycetes were very similar in *Aneura mirabilis* (Figure 29-Figure 32) and *Aneura pinguis* (Figure 52-Figure 57). In both liverwort species, the fungus is confined to specific thallus regions. The fungus makes hyphal contact with its substrate through the rhizoids. Following the colonization phase, the fungus forms large intracellular coils. The liverwort cytoplasm then proliferates and starch content in the plastids diminishes. The fungal hyphae then senesce and die back, aggregating into large masses. A number of developmental characteristics of the *A. mirabilis* are identical to those of *A. pinguis* from alpine sites, but differ from those of *A. pinguis* from sand dunes and a chalk pit. These habitat differences further support the degree of differences among the cryptospecies. On the other hand, could the differences found among the cryptospecies be a result of different fungal epiphytes (see Damsholt 2002)?

Krause *et al.* (2011) followed the fungal colonization in *Aneura pinguis* (Figure 52-Figure 57) and a number of species of *Riccardia* (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133). They found that the mode of colonization of tulasnelloid mycobionts differs in the species of these genera, despite having identical fungal sequences. Thus they suggested that the mode of colonization may be host-dependent.

Culturing

For many, **axenic** (sterile; culture with no living organisms but intended one) culturing bryophytes has been a challenge. Buczkowska *et al.* (2006b) developed a protocol for axenic culturing of *Aneura pinguis* (Figure 52-Figure 57) that permitted them to regenerate. The two most successful media were hormone-free: the special liverwort medium of Lukavsky *et al.* (1991) and the MS medium of Murashige and Skoog (1992).

Biochemistry

Duckett and Renzaglia (1987) noted the difficulty of preserving the oil bodies for TEM studies, but confirmed their presence in *Aneura*. As you can see in the image of *Aneura pinguis* below (Figure 93), they can be difficult to discern even in fresh material.

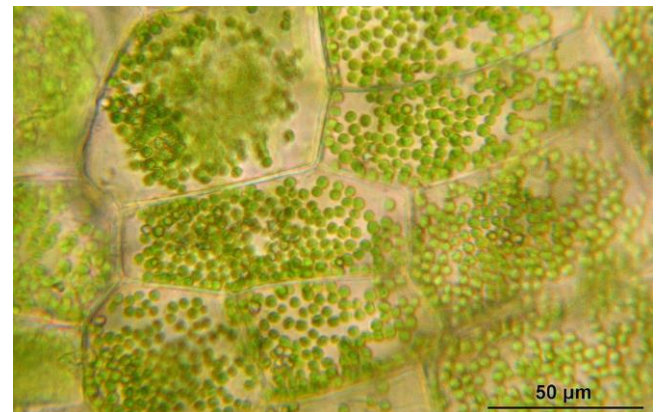


Figure 93. *Aneura pinguis* cells in which one cannot distinguish the oil bodies easily. Photo by Hermann Schachner, through Creative Commons.

In their study of cryptic species of *Aneura pinguis* (Figure 52-Figure 57), Wawrzyniak *et al.* (2018) found that the dominant compound among their samples was pinguisone, with deoxopinguisone being the second dominant. The differences among the samples were primarily due to genotype and little to habitat. Tazaki *et al.* (1995) reported that the concentrations of pinguisone were significantly high in the species. They were able to describe the structures of three new pinguisane-type sesquiterpenes (Tazaki *et al.* 1996).

Asakawa *et al.* (1981) demonstrated that the sesquiterpenes in *Aneura pinguis* (Figure 52-Figure 57) are chemically very different from those of two relatives that have been retained in *Riccardia* [*R. multifida* (Figure 140-Figure 159), *R. jackii*]. The pinguisones are not the dominant sesquiterpenes in the *Riccardia* (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133) species.

***Lobatiriccardia* (Figure 94-Figure 95)**

Lobatiriccardia is a Southern Hemisphere genus, mostly in Australia and New Zealand, but more recently reported from Ecuador in South America (Preußing *et al.* 2010b). Preußing *et al.* (2010b) suggested that the positioning of female gametangia on the lobe margins of *Lobatiriccardia*, rather than in a central position, permits the development of more sporophytes, thus increasing reproduction.

Symbiotic fungi occur in parenchymal cells in this genus, inhabiting 3-10 layers on the ventral side, never occurring in epidermal cells or intercellular locations (Duckett & Ligrone 2008).

***Lobatiriccardia alterniloba* (Figure 94-Figure 95)**

(syn. = *Aneura alterniloba*; *Riccardia alterniloba*)

Several varieties have been described for *Lobatiriccardia alterniloba* (Figure 94) (Nebel *et al.* 2013).

Distribution

Lobatiriccardia alterniloba (Figure 94) is known from New Zealand, Australia, Tasmania, and Vanuatu (Hewson 1970; Furuki 2002; Preußing *et al.* 2010b).



Figure 94. *Lobatiriccardia alterniloba* on a soil bank. Photo by Marley Ford, through Creative Commons.

Aquatic and Wet Habitats

Lobatiriccardia alterniloba (Figure 94) occurs in Cool Temperate Victorian Rainforest streams (Carrigan & Gibson 2004; Carrigan 2008). In Cement Creek, Victoria, Australia, it occurs below the water line, but can also occur above (Carrigan & Gibson 2004). It does not occur on upstream sides of rocks that receive the full force of the current, but can occupy downstream, top, and base locations that do not receive the full force of the current. It was one of the two dominant species at the bases of rocks and achieved 8% cover in the study area.

Preußing *et al.* (2010b) described its habitat as occurring on rock, or soil in damp to wet conditions, often in the spray of waterfalls, or in running water. Nebel *et al.* (2013) similarly reported *Lobatiriccardia alterniloba* (Figure 94) var. *robusta* from Russell Falls, in Tasmania.

Not all of the habitats of *Lobatiriccardia alterniloba* (Figure 94) are so wet. Wilcox (2018) reported it from exposed roots of a pine tree in a shaded forest, near a small stream in Craigavon Park, Auckland, New Zealand.

Adaptations

Lobatiriccardia alterniloba (Figure 94) forms tight, thin mats that reduce the force of the current at the base of the mat (Carrigan & Gibson 2004; Carrigan 2008).

Preußing *et al.* (2010b) suggested that the reduction of lateral thallus branches to short, gametangia-bearing branches may save resources. The ventral position of gametangia under thallus lobes could result in better protection of the young sporophyte from injury and stronger anchoring and direct nutrient uptake by the dense rhizoid coverage at the capsule foot.

Reproduction

Lobatiriccardia alterniloba is dioicous but does at least sometimes reach successful fertilization (Figure 95); gemmae are unknown (Preußing *et al.* 2010b).



Figure 95. *Lobatiriccardia alterniloba* with young capsule. Photo by Marley Ford, through Creative Commons.

Fungal Interactions

Duckett and Ligrone (2008) described the Basidiomycota endophyte in *Lobatiriccardia alterniloba* (Figure 94) as limited to five cell layers, contrasting with colonization of the entire thallus in *Aneura mirabilis*.

Biochemistry

Oil bodies of *Lobatiriccardia alterniloba* (Figure 94) are typically 2-5 per cell (Preußing *et al.* 2010b). I found no studies on the biochemistry of the species.

Lobatiriccardia athertonensis

Distribution

Thus far, *Lobatiriccardia athertonensis* is only known from Australia (Preußing *et al.* 2010b) and New Guinea (Hewson 1970).

Aquatic and Wet Habitats

In disturbed rainforests, *Lobatiriccardia athertonensis* occurs with other bryophytes on basalt rocks on creek banks (Preußing *et al.* 2010b).

Reproduction

Lobatiriccardia athertonensis is **dioicous**; gemmae are unknown (Preußing *et al.* 2010b).

Biochemistry

Oil bodies are few, 1-3(4) per cell (Preußing *et al.* 2010b). No biochemical studies seem to be available for this species.

Lobatiriccardia coronopus

Distribution

Lobatiriccardia coronopus occurs in the Philippines, Malay Peninsula, Borneo, Sumatra, Java, Seram, and New Guinea (Furuki 1996, 2006)

Aquatic and Wet Habitats

Lobatiriccardia coronopus occurs on rocks and fallen logs at the waterside (Furuki 1996, 2006)

Lobatiriccardia oberwinkleri

Distribution

Lobatiriccardia oberwinkleri has a known distribution limited to South America, in Ecuador, at two locations in the same ravine (Preußing *et al.* 2010b). More recently, Schäfer-Verwimp and Nebel (2011) have added it to the flora of Brazil.

Aquatic and Wet Habitats

Lobatiriccardia oberwinkleri was found in a ravine in the upper mountain rainforest belt, where it occurs on steep, dripping rock faces beside two small cascades (Preußing *et al.* 2010b). It occurs there with *Asterella macropoda*, *Dumortiera hirsuta* (Figure 96), and *Riccardia* (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133) species. In southern Ecuador it occurs on shady, humid soil and on dripping cliffs of the lower to upper montane rainforest from 1760 to 2880 m asl (Gradstein & Reeb 2018).



Figure 96. *Dumortiera hirsuta*, a species that occurs with *Lobatiriccardia oberwinkleri*. Photo by Luis Funez, through Creative Commons.

Reproduction

Lobatiriccardia oberwinkleri is **dioicous**, with male plants unknown (Preußing *et al.* 2010b). Gemmae are unknown.

Lobatiriccardia verdoornioides

Distribution

Lobatiriccardia verdoornioides is thus far known only from Cuenca, El Cajas, and Quito, Pichincha, in Ecuador (Preußing *et al.* 2010b).

Aquatic and Wet Habitats

Lobatiriccardia verdoornioides was described as a new species from wet páramo-vegetation, where it was found in a bog on the bank of a small lake, embedded in cushions of flowering plants, together with other bryophytes [*Riccardia* (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133) and *Campylopus* (Figure 97) species], and in rivulets (Preußing *et al.* 2010b).



Figure 97. *Campylopus atrovirens*; in the Páramo; *Campylopus* can occur with *Lobatiriccardia verdoornioides*. Photo by Andrew Hodgson, with permission.

Schäfer-Verwimp *et al.* (2013) reported *Lobatiriccardia verdoornioides* from remnants of *Polylepis*

(Figure 98) stands, where it occurred on very wet ground at 3995 m asl in Ecuador.



Figure 98. *Polylepis rugulosa* in Andes highland; *Lobatiriccardia verdoornioides* occurs in remnants of the *Polylepis* forest. Photo by Alexander Yates, through Creative Commons.

Adaptations

Thalli of *Lobatiriccardia verdoornioides* are very succulent and deeply embedded in the surrounding vegetation, which most likely protects them from the strong wind and sunlight (Preußing *et al.* 2010b).

Reproduction

Lobatiriccardia verdoornioides is **dioicous**; gemmae are unknown (Preußing *et al.* 2010b).

Lobatiriccardia yakusimensis

(syn. = *Riccardia lobata* var. *yakusimensis*)

Distribution

Lobatiriccardia yakusimensis is known only from the Ryukyu archipelago in southern Japan (Furuki 1991; Preußing *et al.* 2010b).

Aquatic and Wet Habitats

Lobatiriccardia yakusimensis occurs on wet rocks along streams, often submerged in running water (Preußing *et al.* 2010b).

Adaptations

The thallus of *Lobatiriccardia yakusimensis* is large and bluish-green when fresh (Preußing *et al.* 2010b). I don't know what this color indicates or if it is in any way adaptive.

Reproduction

Lobatiriccardia yakusimensis is **dioicous**; gemmae are unknown (Preußing *et al.* 2010b).

Biochemistry

Oil bodies occur in all epidermal and inner cells of *Lobatiriccardia yakusimensis* with 1-10 in each cell (Preußing *et al.* 2010b). Their biochemistry remains unknown.

Lobatiriccardia yunnanensis

Distribution

Lobatiriccardia yunnanensis is known only from Yunnan, China (Furuki & Long 2007; Preußing *et al.* 2010b). Unfortunately, a new road has been constructed, coming within a few meters of its only known location, accompanied with light deforestation, causing Furuki and Long (2007) to consider the species severely threatened.

Aquatic and Wet Habitats

Lobatiriccardia yunnanensis occurs on shady dripping cliffs of a river gorge in dense broadleaf evergreen forest in a humid subtropical valley at 1425 m asl (Furuki & Long 2007; Preußing *et al.* 2010b). In its single known location, it was associated with a number of other bryophytes (Furuki & Long 2007).

Adaptations

Plants of *Lobatiriccardia yunnanensis* form dense colonies with numerous rhizoids (Furuki & Long 2007), presumably facilitating their ability to persist on dripping cliffs. Is it possible that the translucent thallus permits light to penetrate to or focus on deeper layers in this low-light habitat?

Reproduction

Lobatiriccardia yunnanensis is **dioicous**, with its archegonia and sporophytes on the margins (Preußing *et al.* 2010b). As already suggested, this positioning permits more than one sporophyte to develop in a season on the same lobe, increasing the potential for reproduction. No gemmae are known.

Riccardia

Members of the genus *Riccardia* (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133) are positively correlated with bankfull discharge in 48 streams in South Island, New Zealand (Suren & Duncan 1999). They are also among west African rheophytes (Shevock *et al.* 2017). Preußing *et al.* (2010b) suggested that the positioning of female gametangia on the lobe margins instead of the central position permits the development of more sporophytes, thus increasing reproduction. Furthermore, **endogenous** (formed within vegetative cells) gemmae are found regularly in *Riccardia* (Renzaglia, 1982), but are unknown in *Aneura* (Figure 7-Figure 10, Figure 18-Figure 26, Figure 29-Figure 32, Figure 52-Figure 57) or *Lobatiriccardia* (Figure 94-Figure 95).

Riccardia aequicellularis (Figure 99)

Distribution

Riccardia aequicellularis (Figure 99) occurs in Australia (English & Blyth 2000; Carrigan & Gibson 2004), Tasmania (Ratkowsky 1987; Jarman & Kantvilas 2001), and New Zealand (de Lange *et al.* 2020). Selkirk (2012) reported the species from the sub-Antarctic Macquarie Island.



Figure 99. *Riccardia aequicellularis*, a species of the Eastern Southern Hemisphere. Photo by Tom Thekathyl, with permission.

Aquatic and Wet Habitats

Riccardia aequicellularis (Figure 99) occurs in Cool Temperate Victorian Rainforest streams (Carrigan & Gibson 2004; Carrigan 2008). In Cement Creek (Figure 100), Victoria, Australia, it occurs below the water line, but can also occur above. It is able to occupy upstream, downstream, and sides of rocks, but does not occupy the tops of rocks in the study stream. This is the only species in the studied area of Cement Creek that is able to withstand the force of the current on the upstream side of rocks. With these restrictions, it occupies less than 1% cover in the stream and occurs in only 2 of the 5 study locations.

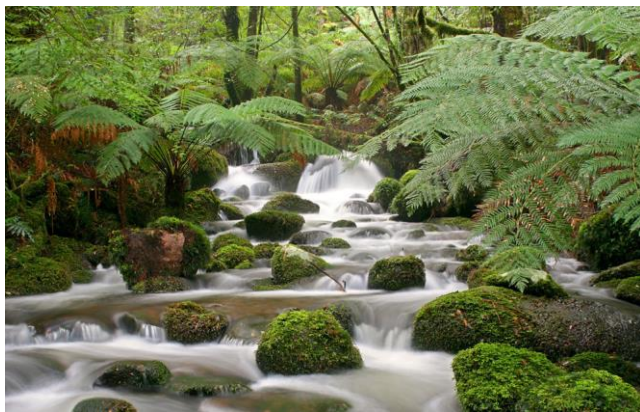


Figure 100. Cement Creek, Yarra Ranges National Park, Victoria, Australia 1 98Octane, through Creative Commons.

Downes *et al.* (2003) listed *Riccardia aequicellularis* (Figure 99) as semi-aquatic. In two of the studied creeks in Australia it had a higher percentage cover on emergent than submerged rocks, but in another there was no difference; in a fourth the cover was greater on the submerged rocks. This is one of the species that seems to benefit from the additional habitats provided by splash zones above water.

Riccardia aequicellularis (Figure 99) occurs on peat mounds of tumulus springs (mound springs) in the Swan Coastal Plain of western Australia (English & Blyth 2000).

Downing *et al.* (2007) found it in their study of a deep gully (Figure 101) in a closed canopy forest in the Blue Mountains of New South Wales, Australia.



Figure 101. Deep gully in Blue Mountains, Victoria, Australia, such as the ones where one might find *Riccardia aequicellularis*. Photo by David Noble, with permission.

Adaptations

Riccardia aequicellularis (Figure 99) forms **threadlike mats** that permit it to reduce the rate of flow within the mat (Carrigan & Gibson 2004). At Deep Stream in New Zealand, it is a colonist (Michel *et al.* 2013).

Riccardia chamedryfolia (Figure 102-Figure 108)

(syn. = *Aneura sinuata*, *Aneura sinuata* fo. *submersa*, *Riccardia sinuata*)

Distribution

Riccardia chamedryfolia (Figure 102-Figure 108) is Holarctic, but is rare in the Arctic (Schuster 1992). It extends from Europe and the islands off the coast of Portugal, southward to northern Africa and eastward to China, Japan, Bonin, and Micronesia. In North America it extends along the western coastal states from Alaska to California and in some locations in the eastern USA states. Bakalin (2005) reported on its locations on the Kamchatka Peninsula, Russia.



Figure 102. *Riccardia chamedryfolia* (Jagged Germanderwort), a Holarctic species. Photo by Barry Stewart, with permission.



Figure 103. *Riccardia chamedryfolia*. Photo by Des Callaghan, with permission.



Figure 106. *Riccardia chamedryfolia*. Photo by Martin Hutten, with permission.

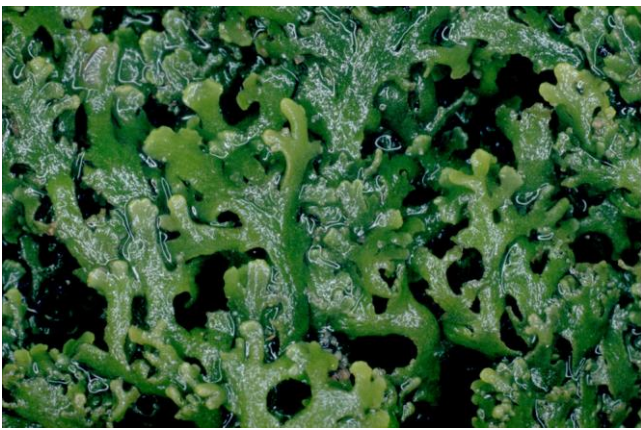


Figure 104. *Riccardia chamedryfolia*. Photo by Jan-Peter Frahm, with permission.



Figure 107. *Riccardia chamedryfolia* showing lush growth. Photo by Michael Lüth, with permission.

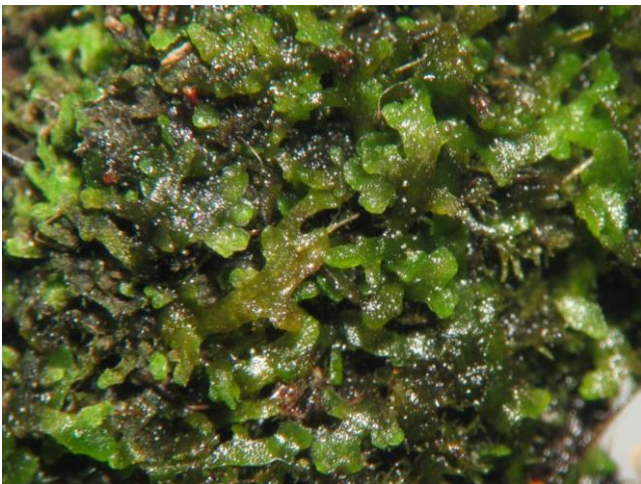


Figure 105. *Riccardia chamedryfolia*. Photo by Kristian Peters, with permission.

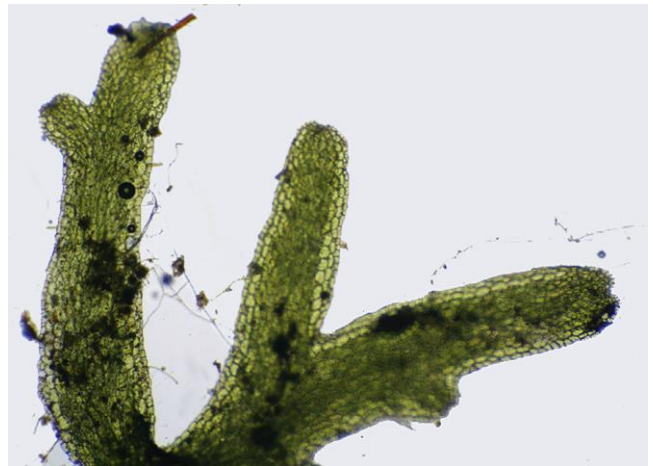


Figure 108. *Riccardia chamedryfolia*. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Aquatic and Wet Habitats

Schuster (1992) described *Riccardia chamedryfolia* (Figure 102-Figure 108) as being typically associated with running water, but not always submersed. It is often kept wet by splash, or on damp to dripping rocks of ravines or gravelly bottoms of shallow springs.

Watson (1919) considered *Riccardia chamedryfolia* (Figure 102-Figure 108) to be the most hydrophilous of the "*Aneura*" species. It occurs on stony beds in fast water. It also occurs in rivers (Ferreira *et al.* 2008). In Westfalens, northwestern Germany, it occurs in water (Figure 109) and, less commonly, as a marsh plant (Koppe 1945). In Odenwald and southern Spessare, Philippi (1987) found it in spring areas in aquatic habitats; van Zanten and Colpa (2008) found it in seepage in North Gronigen, The

Netherlands. In southern Finland it occurs in small lakes (Toivonen & Huttunen 1995). It occurs in Portugal water courses (Vieira *et al.* 2012) and in northwest Portugal it can be found in mountain streams (Vieira *et al.* 2005). On Madeira Island, it occurs in upstream areas in mountainous streams (Luís *et al.* 2015). In the eastern USA, *Riccardia chamedryfolia* (Figure 102-Figure 108) occurs in Appalachian Mountain streams (Figure 110) (Glime 1968). Tremp (2003) considered the species to be oligo- to mesotrophic.



Figure 109. *Riccardia chamedryfolia* in water. Photo by Michael Lüth, with permission.



Figure 110. Appalachian Mountain stream, where some are inhabited by *Riccardia chamedryfolia*. Photo by Janice Glime.

Barringer (2011) found *Riccardia chamedryfolia* (Figure 102-Figure 108) on dripping rocks near streams in New Jersey, USA. Vieira *et al.* (n.d.) found it at a mean of 8 cm above water that had velocities of 0-1.5 m s⁻¹ in northwest Portugal. Daniel *et al.* (2006) found a negative correlation of depth with rheophilous bryophytes, including *Riccardia chamedryfolia*, in the Scorff River and its tributaries, a salmon river system in southern Brittany of France. These studies support its description as living in habitats that stay wet (Figure 111), but not necessarily submerged.



Figure 111. *Riccardia chamedryfolia* above water, but wet on a wet rock. Photo by Bernd Haynold, through Creative Commons.

Bakalin (2007) found *Riccardia chamedryfolia* (Figure 102-Figure 108) in wet hollows in the southern Kuril Islands. Callaghan and Ashton (2007) found it locally in younger dune slacks in England. In Japan, Bakalin *et al.* (2013) found it on moist and wet boulders and cliffs along streams, in spray zones of waterfalls, but also on clayish road cuts in mesic conditions and partial shade of secondary forests.

Hugonnot (2011) reported *Riccardia chamedryfolia* (Figure 102-Figure 108) from fens in Aubrac, France. Vellak *et al.* (2015) listed *Riccardia chamedryfolia* as sporadic in Estonia. Ingerpuu *et al.* (2014) found it to be rare in fens, transitional mires, and bogs in Estonia. It is likewise rare in the southeastern Carpathians of Romania (Jakab 1999). Similarly, Albinsson (1997) reported it from only one location out of 67 mire sites in southern Sweden, despite its being considered a characteristic mire species.

Philippi (1987) described the aquatic vegetation of streams in the eastern Odenwald and southern Spessart, Germany. He described the *Riccardia chamedryfolia* (Figure 102-Figure 108) community and the *Fontinalis antipyretica* (Figure 112) community as the characteristic communities of the spring area. Both are sensitive to high water velocity. *Riccardia chamedryfolia* is one of the few species that characterize the source. In these locations, it forms fresh, olive-green to yellow-green lawns that are under water most of the year.

Schuster (1992) found that *Riccardia chamedryfolia* (Figure 102-Figure 108) was mostly in acidic sites, but was not confined to them. Gabriel and Bates (2005) found that in the Azores, the mean pH for this species was 5.0 and water availability was not the highest among the groups of bryophytes. On Madeira, *Riccardia chamedryfolia* occurs where there are low nutrient concentrations, preferring reaches with low temperatures and little turbulence (Luís *et al.* 2012). It is acidophilic, indicating low pH in summer.

It is related to low dissolved oxygen, low magnesium, and low calcium ions in summer, and low concentrations of phosphates and high ammonium in winter. These latter relationships may explain its occasional appearance in non-acidic habitats.



Figure 112. *Fontinalis antipyretica*, a characteristic community in springs where *Aneura chamedryfolia* also characterizes one of the communities. Photo by Bernd Haynold, through Creative Commons.

Riccardia chamedryfolia (Figure 102-Figure 108) occurred in rock crevices near water leakage (Ivanova 2009). In river gorges in Norway, *Ctenidium molluscum* (Figure 113), *Hylocomiastrum umbratum* (Figure 114), and *Trichocolea tomentella* (Figure 115) are characteristic companion species of *Riccardia chamedryfolia* (Rydgren *et al.* 2012). Frahm (2005) reported *R. chamedryfolia* from the wet lava rocks in the dark interior of a crater in the Azores. *Riccardia chamedryfolia* fo. *major* (syn. = *Aneura major*) occurs on banks with frequent submergence and slow water (Watson 1919).



Figure 113. *Ctenidium molluscum*, a species that occurs with *Riccardia chamedryfolia* in Norwegian gorges. Photo by David T. Holyoak, with permission.



Figure 114. *Hylocomiastrum umbratum*, a species that occurs with *Riccardia chamedryfolia* in Norwegian gorges. Photo by Hermann Schachner, through Creative Commons.



Figure 115. *Trichocolea tomentella*, a species that occurs with *Riccardia chamedryfolia* in Norwegian gorges. Photo by Li Zhang, with permission.

Riccardia chamedryfolia (Figure 102-Figure 108) is not entirely a wet habitat species. It is also known from trunks of the tree fern *Cyathea delgadoi* (Figure 116) in Brazil (Vital & Prado 2006). In Estonia, Kannukene *et al.* (1997) found it on the bank of a bomb crater on sand.

Adaptations

In the Tottori Prefecture of Japan, *Riccardia chamedryfolia* (Figure 102-Figure 108) can occur in pure mats (Figure 117), but it is more commonly mixed with other liverworts, such as *Aneura maxima* (Figure 2, Figure 3, Figure 7-Figure 10; Figure 18-Figure 26), *Conocephalum salebrosum* (Figure 118), *Heteroscyphus coalitus* (Figure 119), *Jubula hutchinsiae* (Figure 120), *Lejeunea aquatica*, *Makinoa crispata* (Figure 121), *Megaceros pellucidus* (see Figure 122), *Pallavicinia subciliata* (Figure 123), *Pellia neesiana* (Figure 124), and *Wiesnerella denudata* (Figure 125) (Bakalin *et al.* 2013). Both the mat life form and the accompanying liverworts can help *Riccardia chamedryfolia* maintain hydration.



Figure 116. *Cyathea delgadoi*, a species that sometimes has *Riccardia chamedryfolia* growing on its trunks. Photo from <powo.science.kew.org>, through Creative Commons.



Figure 118. *Conocephalum salebrosum*, a species that can occur mixed with *Riccardia chamedryfolia*. Photo by Paul Slichter, with permission.



Figure 119. *Heteroscyphus coalitus*, a species that can occur mixed with *Riccardia chamedryfolia*. Photo by Jia-Dong Yang, through Creative Commons.



Figure 117. *Riccardia chamedryfolia* forming a mat. Photo by Malcolm Storey, DiscoverLife.com, with online permission.



Figure 120. *Jubula hutchinsiae*, a species that can occur mixed with *Riccardia chamedryfolia*. Photo by Michael Lüth, with permission.



Figure 121. *Makinoa crispata*, a species that can occur mixed with *Riccardia chamedryfolia*. Photo through Creative Commons.



Figure 124. *Pellia neesiana*, a species that can occur mixed with *Riccardia chamedryfolia*. Photo from Botany Website, UBC, with permission.



Figure 122. *Megaceros* sp.; *Megaceros pellucidus* can occur mixed with *Riccardia chamedryfolia*. Photo by Scott Zona, through Creative Commons.



Figure 125. *Wiesnerella denudata*, a species that can occur mixed with *Riccardia chamedryfolia*. Photo by David Long, with permission.



Figure 123. *Pallavicinia subciliata*, a species that can occur mixed with *Riccardia chamedryfolia*. Photo by Li Zhang, with permission.

Reproduction

Riccardia chamedryfolia (Figure 102-Figure 111) is **autoicous** (Schuster 1992). Gemmae can be present on the tips of the ultimate branches.

Fungal Interactions

Vital *et al.* (2000) reported the fungus *Phellinus wahlbergii* (Basidiomycota; Figure 126) in association with *Riccardia chamedryfolia* (Figure 102-Figure 111) in undisturbed Atlantic forest in Brazil.



Figure 126. *Phellinus wahlbergii*, a bracket fungus with moss on it; it can also associate with *Riccardia chamedryfolia*. Photo by Clive Shirley, Hidden Forest, with permission.

Bidartondo and Duckett (2010) noted that **Aneuraceae** typically have basidiomycete fungi, in particular species of *Tulasnella* (Figure 89; see also Figure 49), giving them the potential to form **ectomycorrhizae** (form of symbiotic relationship between fungal symbiont, or mycobiont, and roots or rhizoids of various plant species; mycobiont is often from **Basidiomycota** or **Ascomycota**, and more rarely from **Zygomycota**). Using fungal DNA sequence data, they did not detect fungi in *Riccardia chamedryfolia* (Figure 102-Figure 111).

Biochemistry

Riccardia chamedryfolia (Figure 102-Figure 111) has 1-2 oil bodies per cell (Figure 127).



Figure 127. *Riccardia chamedryfolia* showing cells with 1-2 dark-colored oil bodies. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Some sesquiterpenoids have been isolated from *Riccardia chamedryfolia* (Figure 102-Figure 111) (Ge 2007).

Riccardia crassiretis

Distribution

Riccardia crassiretis is known from Sri Lanka, Philippines, Sumatra, Java, New Guinea, and New Caledonia (Furuki 2006).

Aquatic and Wet Habitats

In the Philippines, *Riccardia crassiretis* occurs on soil and rocks by water (Furuki 2006).

Adaptations

Although *Riccardia crassiretis* does not seem to live under water, its thick-walled thallus cells (Furuki 2006) could be of value if it is. On the other hand, they might be more important to prevent cell collapse when it dries out.

Reproduction

Riccardia crassiretis is **dioicous** (Furuki 2006). Capsules are described by Furuki (2001).

Riccardia crenulata

Distribution

Riccardia crenulata is known from Singapore, Philippines, Malaysia (Malay Peninsula and Borneo), and

Indonesia (Java and Sumatra) (Furuki & Tan 2013). It is also reported from Taiwan (Buchanan *et al.* 1997; Lai & Wang-Yang 1976).

Aquatic and Wet Habitats

Riccardia crenulata (re-identified from *Riccardia tenuicostata*) occurs at <30 cm above water level in the tropics (Ruttner 1955). Furuki and Tan (2013) reported it from wet rocks in Singapore.

Reproduction

Riccardia crenulata is dioicous; its sporophytes are unknown (Furuki 2001).

Riccardia diminuta

Distribution

Furuki (2006) reported *Riccardia diminuta* from the Philippines, Sumatra, Java, and New Caledonia. Yin *et al.* (2016) listed it as one of the species on Hainan Island, China. Shu *et al.* (2016) added Vietnam and Horing (2017) added Malaysia.

Aquatic and Wet Habitats

Ruttner (1955) reported that *Riccardia diminuta* occurs in thermal acidic spray zones in the tropics (Ruttner 1955). Furuki (2006) reported that it occurs on soil and rocks by water in the Philippines.

Reproduction

Riccardia diminuta is **dioicous** (Furuki 2006).

Riccardia elata (Figure 128-Figure 131)

Distribution

Riccardia elata (Figure 128-Figure 131) is known from Singapore, Indonesia (Java, Sumatra), Malaysia (Malay Peninsula and Borneo) and the Philippines (Furuki & Tan 2013). Singh and Singh (2007) reported it from New Sikkim, India.



Figure 128. *Riccardia elata* showing its delicate branching. Photo by Li Zhang, with permission.



Figure 129. *Riccardia elata* showing the borders on the thalli. Photo by Li Zhang, with permission.

Aquatic and Wet Habitats

Ruttner (1955) included *Riccardia elata* (Figure 128-Figure 130) as an aquatic species in the tropics. In the Philippines, it is known from wet soil along a stream (Figure 130) (Furuki & Tan 2013). In Sikkim, India, it occurs in moist, shady locations under slowly dripping water (Singh & Singh 2007).



Figure 130. *Riccardia elata* in a wet habitat. Photo by Li Zhang, with permission.

Adaptations

Riccardia elata (Figure 128-Figure 130) is one of the larger (up to 10 cm) *Riccardia* species (Singh & Singh 2007). In the Philippines, *Riccardia elata* is deep green when fresh (Furuki & Tan 2013), but Singh and Singh (2007) described it as light green to yellowish green when fresh (Figure 130). This suggests that its color may depend on the environment, possibly light intensity or state of hydration, but also it could be a result of nutritional status.

Reproduction

Riccardia elata (Figure 128-Figure 130) is **dioicous**, with sporophytes mostly absent (Singh & Singh 2007; Furuki & Tan 2013). Finally, in 2017, Singh and Singh

found and described capsules from the Himalayas in India. Furthermore, the 2-celled endogenous gemmae (Singh & Singh 2007) are rare, at least in the Philippines (Furuki & Tan 2013). Its chromosome number is $n=9$ m (Zheng & Zhu 2008).

Biochemistry

Biochemical studies on *Riccardia elata* (Figure 128-Figure 130) are rather limited. Figure 131 shows the cells with small oil bodies where one would expect secondary compounds to be stored.

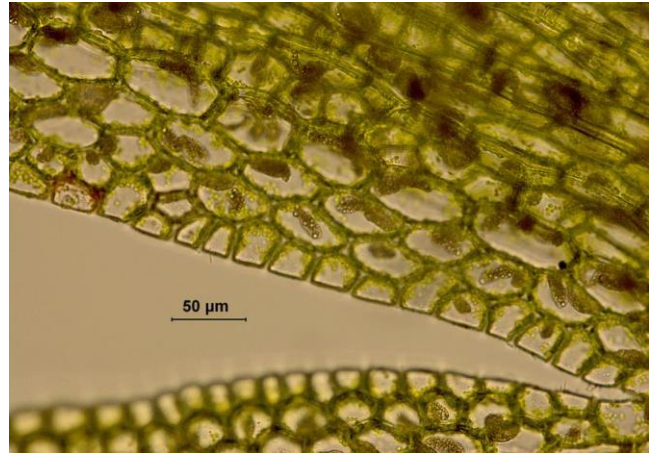


Figure 131. *Riccardia elata* showing cells with oil bodies (see cells near border) and a distinct border. Photo by Li Zhang, with permission.

From *Riccardia elata* (Figure 128-Figure 130) one stilbene and three flavonoids were isolated and their structures were determined (Ge 2007).

Riccardia graeffii (Figure 132-Figure 133)

(syn. = *Riccardia androgyna*, *Riccardia platyclada*)

In recent years, this species has gone by both *Riccardia platyclada* (Söderström *et al.* 2016) and *Riccardia graeffei* (Figure 132-Figure 133) (Furuki 1991; TROPICOS 2021). TROPICOS considers *Riccardia platyclada* to be a synonym of *Riccardia graeffei*; The Plant List considers *Riccardia platyclada* an unresolved name, while accepting *Riccardia graeffei*. In these chapters I am following the nomenclature used by Söderström *et al.* (2016) which recognizes *Riccardia graeffei* and not *Riccardia platyclada*. In any case, they are apparently accepted as the same species and I have treated them as such here.

Distribution

Riccardia graeffei (Figure 132-Figure 133) is widely distributed in tropical Asia, Australasia, and the Pacific (Furuki & Tan 2013). Its known records include India (Srivastava 1972; Sharma & Alam 2011; Gupta & Asthana 2016), Vietnam, Japan, Philippines, Malay Peninsula, Singapore, Borneo, Sumatra, Java, New Guinea, Caroline, New Caledonia, Vanuatu, Samoa, Fiji, Tonga, Tahiti, and Australia (del Rosario 1967; Furuki 2006). Singh and Singh (2015) recently reported it as new to Andaman and Nicobar Islands in the Bay of Bengal. To this list, Singh and Singh (2015) noted records from China, Indonesia, Malaysia, Taiwan, and Thailand.

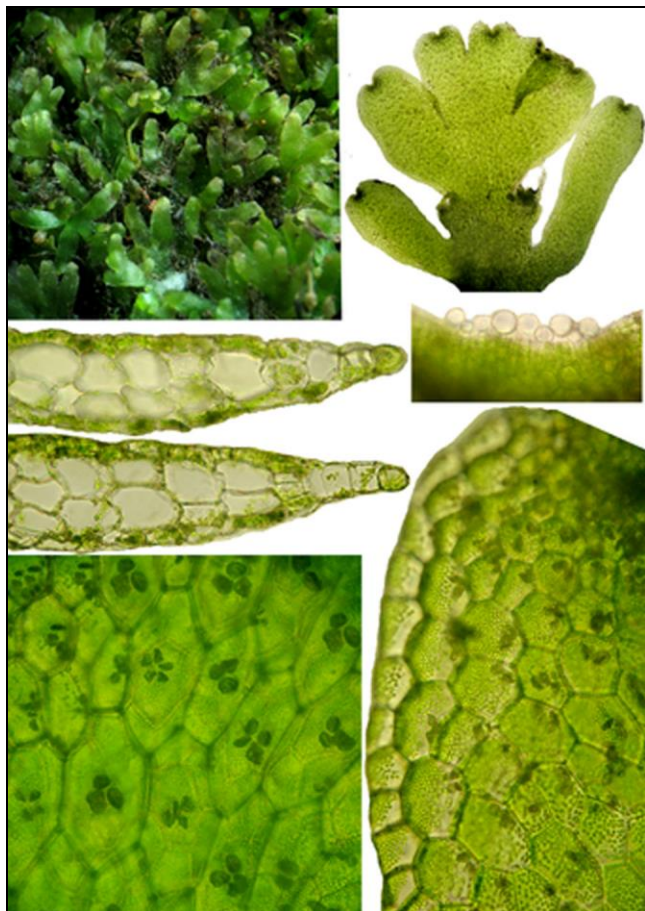


Figure 132. *Riccardia graeffei* showing growth form, cs with multi-layered cells, and oil bodies in cells. Photos from MySpecies.info, through Creative Commons.

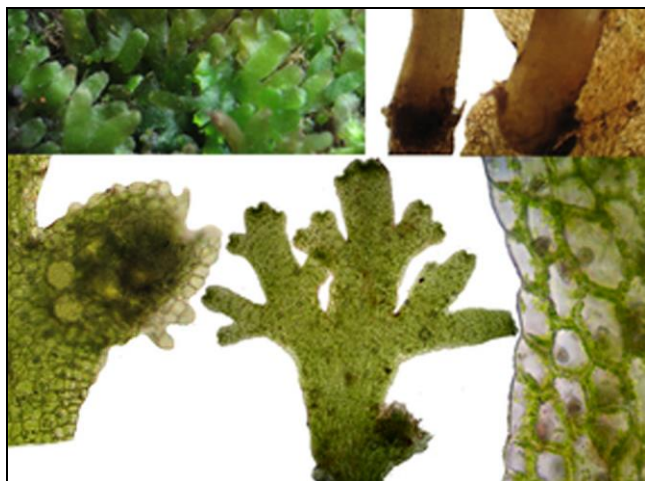


Figure 133. *Riccardia graeffei*. Photos from MySpecies.info, through Creative Commons.

Aquatic and Wet Habitats

Ruttner (1955) reported *Riccardia graeffei* (Figure 132-Figure 133) from the wall of a bay, source of pond inflow, **tuff** (light, porous rock formed by consolidation of volcanic ash) wall, <30 cm above water level, on submerged tree trunk, and overhanging water in the tropics. Ruttner also listed *Riccardia graeffei* as an aquatic inhabitant in the tropics. Furuki reported it from wet rocks,

fallen logs, and soil by water in lowland (Furuki 2006; Furuki & Tan 2013). Singh and Singh (2015) described it as terrestrial, lithophytic, or corticolous, growing in very moist places along a sheltered stream in dense tropical rainforest on the Andaman and Nicobar Islands, India. In India, Gupta and Asthana (2016) reported it from wet rocks and soil-covered rocks.

By contrast, Yamaguchi *et al.* (2005) identified *Riccardia graeffei*; Figure 132-Figure 133) in plots that had been heavily burned in tropical lowland forest of East Kalimantan, Indonesia.

Adaptations

Riccardia graeffei (Figure 132-Figure 133) has yellowish green to green thalli when fresh (Furuki & Tan 2013). It lacks rhizoids, but possesses a smooth to granulose cuticle (Singh & Singh 2015). Its color suggests an adaptation to low light.

Reproduction

Riccardia graeffei exhibits the **heteroicous** condition with male, female, and paroicous branches (Furuki 2006; Furuki & Tan 2013; Singh & Singh 2015). The capsules are blackish brown (Singh & Singh 2015). Singh and Singh (2015) reported it with 2-celled endogenous gemmae. Its chromosome number is $n=9$ m (Zheng & Zhu 2008).

Biochemistry

Riccardia graeffei has numerous botryoidal oil bodies (bottom of Figure 132) in all cells of the thallus (Furuki & Tan 2013). Ge (2007) reported riccardiphenol C and two benzoic acids from *Riccardia graeffei*.

Riccardia jackii

(syn. = *Riccardia jackii* fo. *submersa*)

Distribution

Riccardia jackii occurs in the Philippines and Java (Furuki 2006).

Aquatic and Wet Habitats

In the tropics *Riccardia jackii* is known from water spray and on volcanic tuff walls, in thermal acidic spray, and submersed in ponds (Ruttner 1955). But in the Philippines, Furuki (2006) found it on soil and humus.

Reproduction

Riccardia jackii is **dioicous** (Furuki 2006). Ono (1978) described the gemmalings of this species.

Biochemistry

Matsuo *et al.* (1982) isolated enantiomeric type sesquiterpenoids from *Riccardia jackii*. It produces ent-selinane-, ent-aromadendrane and ent-bicyclogermacrane-type sesquiterpenes together with (R)-cuparene and α -barbatene (Asakawa *et al.* 1981; Ge 2007). In addition, 3,4-dimethoxy-5-hydroxy-9,1-dihydrophenanthrene is a rare dihydrophenanthrene derivative among liverworts and was first described in *Riccardia jackii* (Salamani 1978).

Riccardia marginata

(syn. = *Aneura marginata*, *Riccardia muscoides*)

Distribution

Riccardia marginata (Figure 134) occurs in New Zealand and the north coast of Australia (DiscoverLife 2008). To these locations, Furuki and Tamura (2015) have added Japan with *Riccardia marginata* var. *pacifica*.



Figure 134. *Riccardia marginata*, a species mostly of New Zealand and Australia. Photo by Shirley Kerr, with permission.

Aquatic and Wet Habitats

The liverwort *Riccardia marginata* (Figure 134) occurs on the wet banks of running water and grows on moist soil among rushes and introduced herbs in New Zealand reserves (Macmillan 1976). Tangney (1988) reported it from permanently wet open sites in New Zealand where *Sphagnum cristatum* (Figure 135) was one of the characteristic species.



Figure 135. *Sphagnum cristatum*, a species that characterizes wet, open sites where *Riccardia marginata* occurs in New Zealand. Photo by Clive Shirley, The Hidden Forest, with permission.

Adaptations

Riccardia marginata (Figure 134) is small and brown (Pearson 1922). This coloration suggests protection against the damaging effects of high light intensity.

Reproduction

Riccardia marginata (Figure 134) is **dioicous** (Pearson 1922). Its spores are tiny, making them easily dispersed by wind, but providing it with limited resources with which to germinate and establish.

Fungal Interactions

I have seen no reports of fungi growing on or within *Riccardia marginata* (Figure 134). However, this may be a real absence based on its antibiotic activity, as discussed below, or a lack of study.

Biochemistry

It is interesting that this tiny species, *Riccardia marginata* (Figure 134), with so little ecological information has had a number of biochemical studies. Baek *et al.* (2004) isolated three new chlorinated bibenzyls from this species, the first time any simple chlorinated bibenzyl was reported from a natural source. These three compounds exhibited antimicrobial activity against *Bacillus subtilis* (bacterium; Figure 136), *Candida albicans* (yeast; Figure 137), and *Trichophyton mentagrophytes* (Ascomycota; Figure 138-Figure 139).

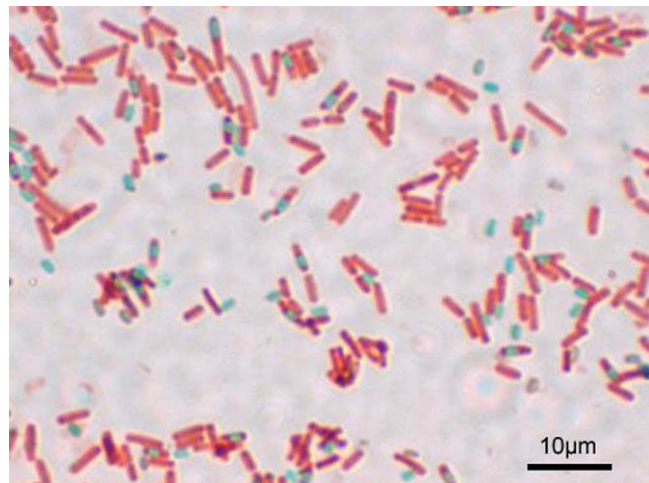


Figure 136. *Bacillus subtilis* spores, a species that is inhibited by extracts of *Riccardia marginata*. Photo by Y. Tambe, through Creative Commons.

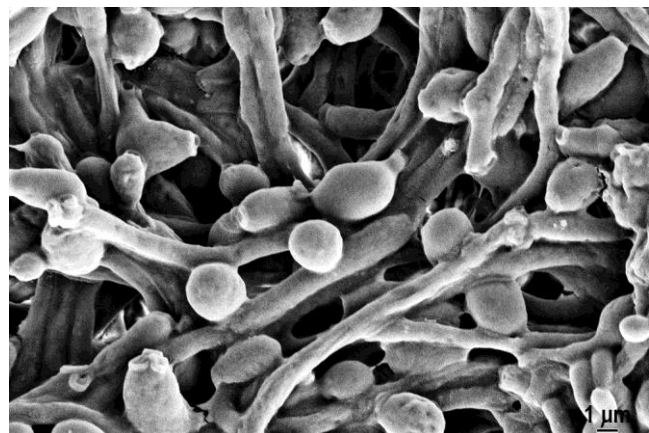


Figure 137. SEM of *Candida albicans*, a species that is inhibited by extracts of *Riccardia marginata*. Photo by Vader 1941, through Creative Commons.



Figure 138. *Trichophyton mentagrophytes* ringworm on arm, a species that is inhibited by extracts of *Riccardia marginata*. Photo through Creative Commons.

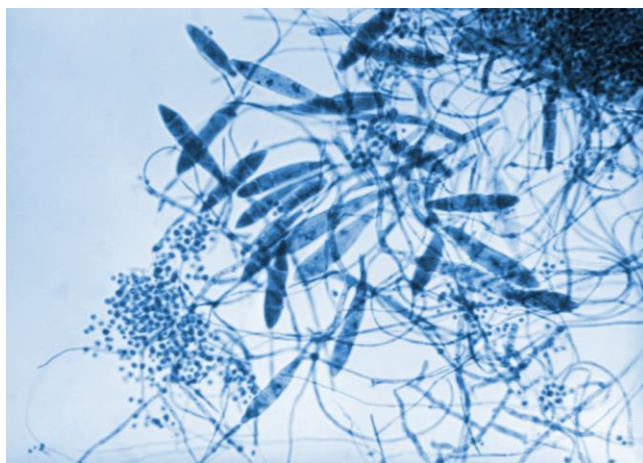


Figure 139. *Trichophyton mentagrophytes* as it appears stained under the microscope. Photo by Lucille K. Georg, through Creative Commons.

Unsinn *et al.* (2013) prepared an antimicrobial product (2,6-dichloro-3-phenethylphenol) from *Riccardia marginata* (Figure 134). Na *et al.* (2005a, b) likewise found that extracts of this species inhibited the Gram positive bacterium *Bacillus subtilis* (Figure 136), yeast (*Candida albicans*; Figure 137), and has strong action against the skin fungus *Trichophyton mentagrophytes* (Figure 138-Figure 139). It was ineffective against P388 murine leukemia cells.

***Riccardia multifida* (Figure 140-Figure 149)**

Distribution

Riccardia multifida (Figure 140-Figure 149) has a wide distribution, known from India [Western Himalaya (Uttarakhand), Eastern Himalaya (Arunachal Pradesh, Assam, Sikkim, West Bengal), Western Ghats (Kerala, Maharashtra, Tamil Nadu), Central India (Madhya Pradesh)], China, Hawaii, Micronesia, Nepal, Russia, Sri Lanka, Taiwan, Turkey, Africa, Europe, and North America (Singh & Singh 2017). Damsholt (2017) listed it as known from the Faeroe Isles. Frey and Kurschner (1983) reported it from Iran.

In North America, it occurs in the northwestern part of the continent and in the east from Newfoundland southward (Perold 2001). Kruse and Davison (2012) reported it from Texas, USA. In Europe it is reported from Greenland, Iceland, and the British Isles. It occurs in both north and south Africa, Madagascar, and west Java. Furuki (1991) reported the subspecies *R. multifida* (Figure 140-Figure 149) subsp. *decrescens* from Japan. It is likely that many more records of this species exist in the USA and elsewhere.



Figure 140. *Riccardia multifida*, a widespread species, forming a dense cushion. Photo by David T. Holyoak, with permission.



Figure 141. *Riccardia multifida* showing the branching pattern. Photo by Jan-Peter Frahm, with permission.



Figure 142. *Riccardia multifida*. Photo by Manju Nair, through Creative Commons.



Figure 143. *Riccardia multifida* showing the pale color of a well hydrated colony. Photo by Hermann Schachner through Creative Commons.



Figure 146. *Riccardia multifida*. Photo by Hermann Schachner, through Creative Commons.



Figure 144. *Riccardia multifida* showing a slightly darker phase. Photo by Jean Faubert, with permission.



Figure 147. *Riccardia multifida* growing on a vertical substrate. Photo by Michael Lüth, with permission.



Figure 145. *Riccardia multifida*. Photo by Hermann Schachner, through Creative Commons.

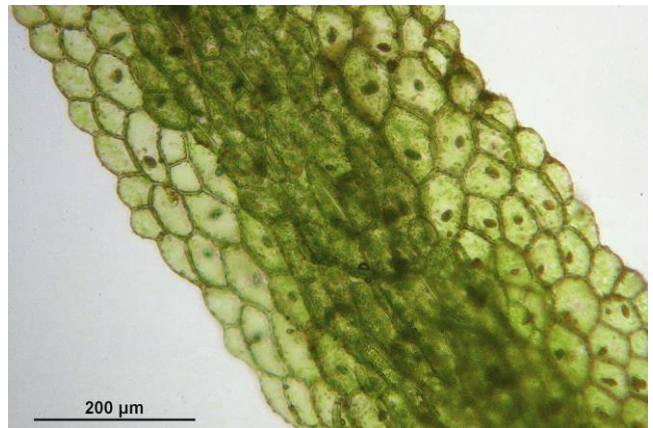


Figure 148. *Riccardia multifida* showing thallus with light-colored margins. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Riccardia multifida (Figure 140-Figure 149) occurs on streambanks with frequent submergence and slow water, wet rocks and soil near fast streams (Watson 1919), and may invade partially into the constantly submerged zone (Watson 1915). Konstantinova *et al.* (2002) found it on soil near brooks (Figure 150) in the forest of the Upper Bureya River (Russian Far East). In northwest Portugal, it occurs in mountain streams (Vieira *et al.* 2005).

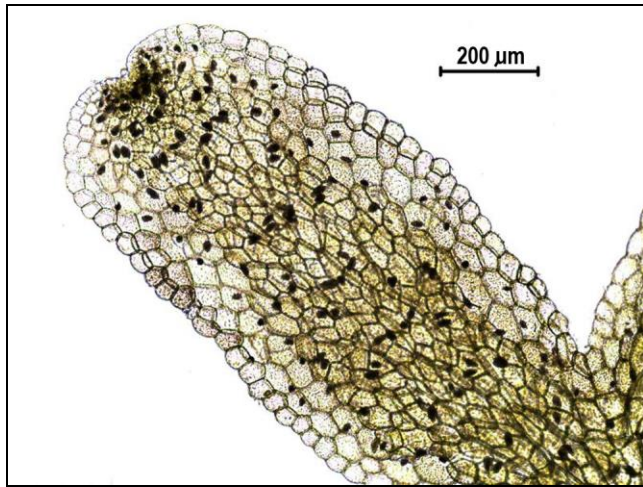


Figure 149. *Riccardia multifida* showing thallus with light-colored margins. Photo by Hugues Tinguy, with permission.



Figure 150. *Riccardia multifida* habitat. Photo by Hermann Schachner, through Creative Commons.

In the Himalayas, Singh and Singh (2017) report it from moist and shady places in dense mixed forest. Similarly, in Adjara, Georgia, on the coast of the Black Sea near the foot of the Lesser Caucasus Mountains, *Riccardia multifida* (Figure 140-Figure 149) occurs on stones and cliffs along streams in the broadleaved forest and in the waterfall spray zone, in partial shade, in broadleaved forests (Bakalin 2013).

In the Upper Peninsula of Michigan, USA, *Riccardia multifida* (Figure 140-Figure 149) occurs on gravelly bluffs along Lake Superior and on logs (Figure 151) in boggy woods (Evans & Nichols 1935). At Mountain Lake, Virginia, USA, it is "rather common" in wet sites (Sharp 1944). In West Virginia, it is one of the liverworts that occurs in McKinney's Cave (Ammons 1933). Burnham (1919) reported it from a "wet place" in the Lake George area, New York, USA. Trigoboff (2013) found that it could occur in massive clumps in Central New York on permanently wet creek rocks or dripping rocks at the sides of creeks, but nevertheless was never present at more than 2-3 spots along a creek. Fulford (1934) recorded it from shaded, swampy places in Kentucky, USA.



Figure 151. *Riccardia multifida* habitat where part of it is growing on decaying wood. Photo by Rick Ballard, through Creative Commons.

Few liverworts seem able to live in rich fens. In northwestern Europe, Kooijman and Westhoff (1995) found only two liverworts: *Aneura pinguis* (Figure 52-Figure 57) and *Riccardia multifida* (Figure 140-Figure 149), in these fens. Albinsson (1997) suggested that most liverworts require acidic, nutrient-poor sites.

Watson (1915) described zonation patterns in a Somerset heath (Figure 71). *Riccardia multifida* (Figure 140-Figure 149) occurs immediately above the zone of *Aneura pinguis* (Figure 52-Figure 57) and *Pellia epiphylla* (Figure 152). It sometimes extends downward into the latter zone. It also creates a definite zone in the furrows just at the water line.



Figure 152. *Riccardia multifida* on *Pellia epiphylla*, an occurrence that can happen where it occurs adjacent to the *Aneura pinguis* and *Pellia epiphylla* zone in wet heath. Photo by Hermann Schachner, through Creative Commons.

In Arkansas, USA, Wittlake (1950) found it under and around the springs on the slope, accompanied by *Aneura pinguis* (Figure 52-Figure 57). On the Mahogany Hammocks, Everglades National Park, Florida, USA, *Riccardia multifida* (Figure 140-Figure 149) occurs on the low hammocks, but not on the high hammocks (Zona & Sadle 2017). These low hammocks have relatively continuous moisture in the soil. On the other hand, Haynes (1915) and McFarlin (1940) found *Riccardia multifida* on logs in wet places in Florida. Clebsch (1947) found it on a limestone face above Bellamy's Cave, Kentucky, USA.

In the Western Ghats, *Riccardia multifida* (Figure 140-Figure 149) occurs on tree buttresses near streams (Jyothilakshmi *et al.* 2016). Konstantinova *et al.* (2002) reported it from soil near a brook in the forest zone of the Upper Bureya River in the Russian Far East. Michael Lüth photographed it in a grass-sedge mire with other bryophytes (Figure 153-Figure 154).



Figure 153. *Riccardia multifida* occurring on soil amid grass. Photo by Michael Lüth, with permission.



Figure 154. *Riccardia multifida* with *Scapania* amid sedges. Photo by Michael Lüth, with permission.

Adaptations

In some wet habitats *Riccardia multifida* (Figure 140-Figure 149) forms dense **mats** (Figure 155-Figure 156). These seem to be able to change colors (Figure 155-Figure 156), but we need studies to show the environmental parameters that can cause these color changes and if they offer any advantage.

Riccardia multifida (Figure 140-Figure 149) does not seem to be well adapted to drying out. At 20°C for 12 hours, only a few cells of *R. multifida* remained alive at 84% relative humidity (Clausen 1964). At 93% relative humidity about 3/4 of the cells remained alive.

Reproduction

Riccardia multifida (Figure 140-Figure 149) is **monoicous** (Singh & Singh 2017). The male and female

branches are rarely **synoicous** (Perold 2001). Although Perold states that gemmae are unknown, Yang and Hsu had already described the germination of spores and gemmae of *Riccardia multifida* in 1967.



Figure 155. *Riccardia multifida* with pale green portions and pinkish portions. Photo by Michael Lüth, with permission.



Figure 156. *Riccardia multifida* showing two clumps with one brownish pink and one pale pink-green. Photo by Michael Lüth, with permission.

Benson-Evans (1964) found that gametangial production in *Riccardia multifida* (Figure 140-Figure 149) was a long-day response. Light intensities above 16 lux in the field also correlated with gametangial production.

Steil (1923) described the structure of the antherozoid in *Riccardia multifida* (Figure 140-Figure 149). Rushing *et al.* (1995) have described the blepharoplast of the spermatid.

Presence of sporophytes is known from a number of locations (Figure 157-Figure 159).



Figure 157. *Riccardia multifida* with young sporophyte. Photo by Paul G. Davison, with permission.

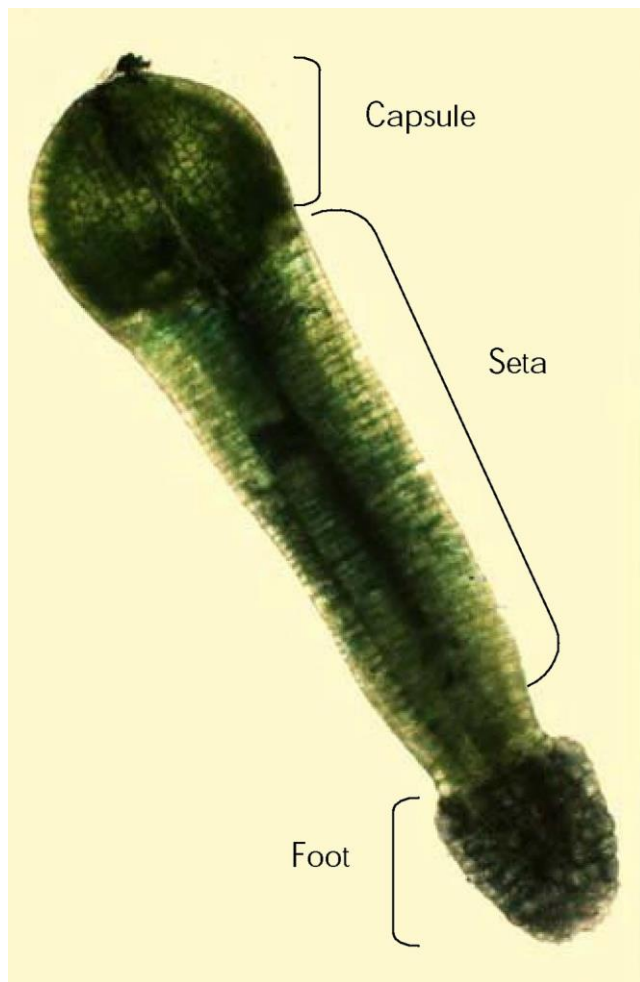


Figure 158. *Riccardia multifida* sporophyte before elongation. Image by Karen Renzaglia, with permission.

The chromosome number in the genus is $n=9 + m$ (Zheng & Zhu 2008).

Fungal Interactions

In *Riccardia multifida* (Figure 140-Figure 149), Krause *et al.* (2011) were unable to find any fungal hyphae of tulasnelloid (**Basidiomycota**) fungi in living liverwort host cells. However, fungi had colonized dead cells. More commonly, the fungi occurred outside the thallus and on the adjacent substrate. In the liverwort, uncolonized living cells exhibited thick-walled cortical cells and ovoid, starch-filled chloroplasts. These chloroplasts were absent in the colonized cells. The hyphae on the dead cells proved to be those of **Ascomycetes**. Krause *et al.* (2011) found that the differences in colonization patterns among species in the genus differed from each other, supporting the hypothesis that the host regulates the pattern of colonization by the fungus.



Figure 159. *Riccardia multifida* with capsules and fully elongated setae. Photo from Botany Website, UBC, with permission.

Jiao *et al.* (2013) determined the chemical structures of compounds obtained from *Penicillium* sp. (Figure 160-Figure 161) that lived endophytically in *Riccardia multifida* (Figure 140-Figure 149). When tested, these compounds showed significant **allelopathic** effects (phenomena by which organisms produce one or more biochemicals that influence germination, growth, survival, and reproduction of other organisms) that retarded germination of *Arabidopsis thaliana* seeds (Figure 162-Figure 163). It would be interesting to test the allelopathic effects of this liverwort-fungus combination in nature. For a tiny plant this could provide a powerful competitive advantage against the larger tracheophytes.



Figure 160. *Penicillium italicum* and *Penicillium digitatum* growing on an orange. A species of *Penicillium* lives in cells of *Riccardia multifida*. Compounds made by the fungus during this association can inhibit germination of *Arabidopsis thaliana*. Photo by George Barron, with permission.

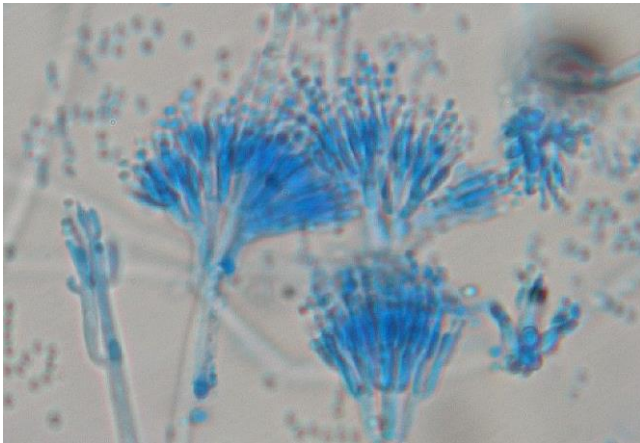


Figure 161. *Penicillium* sp. as seen under the microscope. Photo by Carlos de Paz, through Creative Commons.



Figure 162. *Arabidopsis thaliana* seeds, a species whose germination is inhibited by the *Penicillium* species that lives in cells of *Riccardia multifida*. Photo by Stefan Lefnaer, through Creative Commons.



Figure 163. *Arabidopsis thaliana*. Photo by Brona, through Creative Commons.

Biochemistry

The oil bodies are not evenly distributed, being absent or rare in the dorsal and ventral epidermal cells, absent in as much as 70% of the marginal cells, but present in internal cells (Perold 2001). They are mostly single, but occasionally two per cell.

Yoshida *et al.* (1997; Ge 2007) reported bisbibenzyls and other compounds from *Riccardia multifida* (Figure 140-Figure 149). They were able to isolate a new cyclic bisbibenzyl dimer from the variety *decreescens*.

The aromatic ethers riccardin A and riccardin B have been isolated from *Riccardia multifida* (Figure 140-Figure 149) (Salamani 1978; Asakawa *et al.* 1983). These compounds, isolated from *R. multifida*, have cytotoxic properties (Asakawa *et al.* 1983; Chandra *et al.* 2017).

Tori *et al.* (1985) used NMR spectra to identify new macrocyclic bis(bibenzyls) in *Riccardia multifida* (Figure 140-Figure 149).

Riccardia multifidoides

Distribution

Riccardia multifidoides is a tropical species that seems to be either rare or poorly known.

Aquatic and Wet Habitats

In the tropics, Ruttner (1955) reported *Riccardia multifidoides* as submersed in ponds and on the wall of a

bay. But in the Philippines, Furuki (2006) reported it only from fallen logs.

Reproduction

Riccardia multifidoides is **monoicous** (Furuki 2006).

Riccardia parvula

Distribution

Riccardia parvula is known from the Philippines, Malay Peninsula, Borneo, Sumatra, and Java.

Aquatic and Wet Habitats

Riccardia parvula occurs in waterfalls in the tropics (Ruttner 1955). In the Philippines, this species is known only from rotten logs (Furuki 2006). Nevertheless, rotten logs hold moisture longer than early stage logs, thus suggesting its preference for moisture.

On Mount Patuha, West Java, Indonesia, *Riccardia parvula* occurs on soil in disturbed forest adjacent to Situ (Lake) Patenggang, 1500 m asl (Gradstein *et al.* 2010).

Reproduction

Riccardia parvula is **dioicous** (Furuki 2006). Furuki (2001) has described the capsules and spores. The spores are 12.5-15 µm in diameter.

Riccardia singaporensis

The status of this species is controversial (Furuki & Tan 2013).

Distribution

Riccardia singaporensis occurs in Singapore (Zhu *et al.* 2018) and Australia (North Queensland) (Furuki & Tan 2013). It is rather common in Malesia and adjacent regions (Furuki & Tan 2013). Horing (2017) added it to the flora of Malaysia.

Aquatic and Wet Habitats

Riccardia singaporensis occurs on wet rocks and fallen logs in forests or along streams (Furuki & Tan 2013).

Adaptations

Thalli of *Riccardia singaporensis* are small, green to brownish green when fresh. Geotropic stolons give it a structure to survive unfavorable conditions and help the colony to spread (Furuki & Tan 2013). Rhizoids are scattered on the ventral surface of the prostrate thallus, providing a means of cementing itself to rocks.

Reproduction

Riccardia singaporensis is **heteroicous** with male and **paroicous** branches, but male branches are rare and female branches are unknown (Furuki & Tan 2013). However paroicous branches are common. Gemmae are rare.

Biochemistry

Oil bodies of *Riccardia singaporensis* are pale brownish, composed of granules, globose to elliptical (Furuki & Tan 2013). The species lacks biochemical studies.

Riccardia subexalata

(syn. = *Aneura subexalata*)

Distribution

The only record I found for this species was the report by Ruttner (1955) that it occurs in the tropics.

Aquatic and Wet Habitats

This is one of those species listed as aquatic in the tropics by Ruttner (1955).

Riccardia tenuis

(syn. = *Aneura tenuis*)

Distribution

Riccardia tenuis is known from the tropics (Ruttner 1955). But otherwise, little seems to be known about it.

Aquatic and Wet Habitats

Riccardia tenuis occurs in waterfalls in the tropics (Ruttner 1955).

Riccardia tjiobodensis

Distribution

Like the previous species, little is known about this species except the report by Ruttner (1955) that it occurs in the tropics.

Aquatic and Wet Habitats

Riccardia tjiobodensis occurs in waterfalls in the tropics (Ruttner 1955).

Riccardia wettsteinii

Several varieties are known for this species.

Distribution

Riccardia wettsteinii is known from its type specimen from Java (Pócs 1976-77).

Aquatic and Wet Habitats

Riccardia wettsteinii occurs on the wall of a bay in the tropics (Ruttner 1955), presumably in Java.

Summary

The **Aneuraceae** has a number of members that live in wet habitats, but few that live submersed. The most remarkable member is *Aneura mirabilis*, a completely parasitic species that partners with a fungus (*Tulasnella* sp.) and a tree, especially birch trees. Other members of the genus can have fungal partners or epiphytic fungi, but *Aneura mirabilis* is the only liverwort that totally lacks chlorophyll.

Members of *Aneura* often differ in thickness of the thallus that within the species can represent different cryptic species.

Lobatiriccardia is a much less known genus, but its separation from *Aneura* seems justified. It occurs in the Southern Hemisphere and the tropics. Its wetland species are mostly not submersed, occurring in bogs, streambanks, decaying logs, but occasionally submersed.

Riccardia can be found from the tropics to both polar regions. Some species occur in cold alpine streams; others occur at stream margins and on emergent rocks. The genus occupies a wide range of wet habitats.

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CHAPTER 1-12: AQUATIC AND WET MARCHANTIOPHYTA, ORDER METZGERIALES: METZGERIACEAE AND CALYCULARIACEAE

TABLE OF CONTENTS

SUBCLASS METZGERIIDAE.....	1-12-2
Metzgeriales: Metzgeriaceae.....	1-12-2
<i>Metzgeria</i>	1-12-2
<i>Metzgeria conjugata</i>	1-12-2
<i>Metzgeria furcata</i> / <i>Metzgeria setigera</i>	1-12-9
<i>Metzgeria litoralis</i>	1-12-15
<i>Metzgeria pubescens</i>	1-12-15
Metzgeriales: Calyculariaceae.....	1-12-18
<i>Calycularia crispula</i>	1-12-18
<i>Calycularia laxa</i>	1-12-20
Summary.....	1-12-21
Acknowledgments	1-12-21
Literature Cited.....	1-12-21

CHAPTER 1-12: AQUATIC AND WET MARCHANTIOPHYTA, ORDER METZGERIALES: METZGERIACEAE AND CALYCULARIACEAE



Figure 1. *Metzgeria conjugata*, a widespread species that includes damp and humid locations such as gorges and ravines among its habitats. Photo by Bernd Haynold, through Creative Commons.

SUBCLASS METZGERIIDAE

Metzgeriales: Metzgeriaceae

Metzgeria (Figure 1-Figure 14; Figure 38-Figure 41; Figure 58, Figure 60-Figure 63)

Some members of the genus *Metzgeria* (Figure 1-Figure 14; Figure 38-Figure 41; Figure 58, Figure 60-Figure 63) can be submersed in the tropics (Ruttner 1955).



Figure 2. *Metzgeria conjugata*, North American clade. Photo from UBC Botany Website, with permission.

Metzgeria conjugata (Figure 1-Figure 14)

Using molecular data, Fuselier *et al.* (2009) identified three morphologically cryptic clades of *Metzgeria conjugata* (Figure 1-Figure 14): northern North America (Figure 2), Europe (Figure 3), and south-eastern North America. These molecular differences, however, were not manifest in any morphological differences.

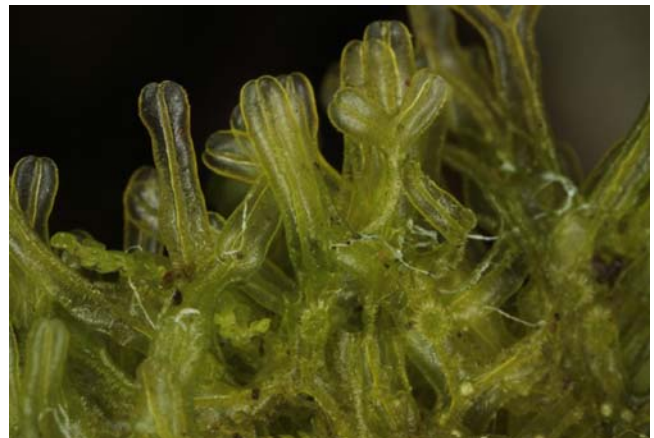


Figure 3. *Metzgeria conjugata*, European clade. Photo by Jan-Peter Frahm, with permission.

Distribution

Distribution of *Metzgeria conjugata* (Figure 1-Figure 14) is a widespread amphi-Atlantic disjunct (Schofield, 1988). It occurs in most of Europe, eastward to the Caucasus, eastward in Asia to Japan, south to Burma, Java, Sumatra, and the Celebes, eastward to New Zealand, Africa from Mozambique to Natal, Tanganyika, and Madagascar. In North America it extends from Quebec and Ontario west to Alaska, southward to California, New Mexico, and in South America it is known from Brazil south to Colombia, Chile, and Argentina. Frey (1974) reported it from Iran.



Figure 4. *Metzgeria conjugata*, a widespread amphi-Atlantic species. Photo by Jan-Peter Frahm, with permission.



Figure 5. *Metzgeria conjugata* showing a dense, pure colony. Photo by Štěpán Koval, with permission.



Figure 6. *Metzgeria conjugata* showing a growth form that extends away from the substrate. Photo by Michael Lüth, with permission.



Figure 7. *Metzgeria conjugata* showing the translucent nature of the hydrated thallus. Photo by Štěpán Koval, with permission.



Figure 8. *Metzgeria conjugata* growing flat in a wet habitat. Photo by Štěpán Koval, with permission.



Figure 9. *Metzgeria conjugata* showing the strong midrib and translucent (1 cell thick) thallus. Photo by Štěpán Koval, with permission.



Figure 10. *Metzgeria conjugata* showing 1-cell-thick thallus. Photo from UBC Botany Website, with permission.

Fuselier *et al.* (2009) considered that different forms of *Metzgeria conjugata* (Figure 1-Figure 14) may exhibit both Amphi-Atlantic and Western Europe-Western North America disjunctions.

Aquatic and Wet Habitats

Metzgeria conjugata (Figure 1-Figure 14) occurs in cool boreal forests worldwide (Schuster, 1992). Its habitats are as varied as its range, with both bark (Figure 11-Figure 12) and rocks serving as substrata, usually in damp and humid locations such as gorges and ravines (Figure 13). On rocks it usually occurs in large, pure mats. It seems to prefer calcareous sites, but it is not restricted to them.



Figure 11. *Metzgeria conjugata* on bark, Nara, Japan. Photo by Janice Glime.



Figure 12. *Metzgeria conjugata* on bark. Photo by Bernd Haynold, through Creative Commons.



Figure 13. *Metzgeria conjugata* stream bank habitat in Europe. Photo by Michael Lüth, with permission.

Metzgeria conjugata (Figure 1-Figure 14) occurs in crevices or surface of drier cliffs (Figure 14) in ravines in Connecticut, USA (Nichols 1916). It is occasionally

submerged (Watson 1919) or occurs on rock and in communities associated with streams near Lacko, Western Carpathians (Mamczarz 1970); it is rare in aquatic habitats of eastern Odenwald and southern Spessart (Philippi 1987); In Thuringia, Germany, it occurs in the *Platyhypnidium-Fontinalis antipyretica* association (Figure 15) (Marstaller 1987). Ferreira *et al.* (2008) described it from rivers; it occurs on limestone rock in the Tara River Canyon and Durmitor area, Montenegro (Papp & Erzberger 2011). In the eastern United States it occurs in Adirondack Mountain streams (Slack & Glime 1985).



Figure 14. *Metzgeria conjugata* on rock face. Photo by Michael Lüth, with permission.



Figure 15. *Platyhypnidium riparioides* on emergent rocks with *Fontinalis antipyretica* submerged. Photo by J. C. Schou, with permission.

In Brazil it usually occurs on shaded wet rocks and is rare on tree trunks (da Costa & Machado 1992).

In North Wales *Metzgeria conjugata* (Figure 1-Figure 14) grows on rocks (Figure 16) in the spray of waterfalls and on boulders by mountain streams (Rhodes 1916). In the Caucasus, Russia, this species occurs on soil, rocks, and cliffs along stream banks (Konstantinova *et al.* 2009). In Hungary, it is not rare and occurs in mountains in the western part in ravines and along streams on wet rocks (Ódor 2000).



Figure 16. *Metzgeria conjugata* on rock. Photo by Michael Lüth, with permission.

Philippi (1987) reported that *Metzgeria conjugata* (Figure 1-Figure 14) occurred occasionally in streams of eastern Odenwald and southern Spessart, where the streams are weakly acid, having little limestone, and the bryophyte substrate is red sandstone. Fulford (1934) reported it from moist sandstone cliffs in Kentucky, USA (Figure 17). Wagner (1952) suggested that its rarity in Indiana was the scarcity of deep canyons that provide the needed moist microclimate, and that light might also be a factor. Ódor (2000) supported this suggestion in Hungary, where in the Kékes North Forest Reserve in Mátra Mountains it occurs only in the wet fissures of high, shaded rock walls. In Hungary, it is not rare and occurs in mountains and in the western part in ravines and along streams on wet rocks (Ódor 2000). It also occurs on cavern ceilings – a habitat that is likely to have constant moisture levels (Norris 1967).



Figure 17. Red sandstone cliffs in Red River Gorge, Kentucky, USA, where one might find *Metzgeria conjugata*. Photo by Jarekt, through Creative Commons.

In North Carolina, USA, *Metzgeria conjugata* (Figure 1-Figure 14) occurs on moist rocks, soil, and trees (Blomquist 1936). Šoltés and Zubaľová (2015) reported *Metzgeria conjugata* (Figure 1-Figure 14) from shaded limestone rocks in the Eastern Carpathians of Slovakia.

Metzgeria conjugata (Figure 1-Figure 14) is more typically not aquatic or in wetlands. In the Polish Carpathians, *Metzgeria conjugata* seems to occur primarily at 600-800 m asl on rocks or trees, rarely on wet soil (Zubel

et al. 2011). These mostly afforested places account for the lower percentage on trees. It rarely occurs on mineral soil and rotten wood. In Korea *Metzgeria conjugata* occurs in forests that have been protected by their owners, on both rocks and trees (Hong 1960). *Metzgeria conjugata* can be epiphyllous in India (Singh *et al.* 2007) and China (Luo 1990).

Adaptations

Metzgeria conjugata (Figure 1-Figure 14) can occur in pure mats (Figure 18) or with other bryophytes (Figure 19) (Konstantinova *et al.* 2009). Both of these habits help to conserve water in habitats that become periodically dry.



Figure 18. *Metzgeria conjugata* growing in a pure mat. Photo by Štěpán Koval, with permission.



Figure 19. *Metzgeria conjugata* occurring with other bryophytes. Photo by Štěpán Koval, with permission.

Metzgeria conjugata (Figure 1-Figure 14) is pale green (Figure 20) to green-yellowish (Figure 21) and prostrate (da Costa & Machado 1992). The cell walls are thickened with small trigones – a character that needs study to determine possible adaptive value. I am guessing it makes the thin thallus stronger while maintaining flexibility. The thallus is **hirsute** (hairy; Figure 22-Figure 23), a trait in liverworts that might help to take up and conserve water. Ono (1977) has described these hairs as well as rhizoids.



Figure 20. *Metzgeria conjugata* showing its pale green color form. Photo by Michael Lüth, with permission.



Figure 21. *Metzgeria conjugata* thallus showing its yellowish-green color form. Photo by Hugues Tinguy, through Creative Commons.



Figure 22. *Metzgeria conjugata* ventral view showing hirsute thallus. Photo by Norbert Stapper, with permission.

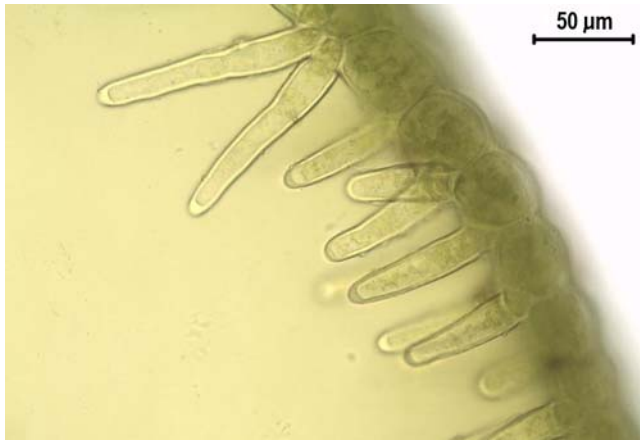


Figure 23. *Metzgeria conjugata* thallus hairs. Photo by Hugues Tinguy, through Creative Commons.

One of the characteristics I have surmised by looking at images of *Metzgeria conjugata* (Figure 1-Figure 14) from the web is that upon drying, the thallus margins curl under. The hydrated thallus is flat (Figure 18). The incurvation ultimately gives the thallus a tubular form (Figure 24-Figure 28) that reduces surface area and provides an internal chamber (Figure 28) that can help to maintain moisture.



Figure 24. *Metzgeria conjugata* fully hydrated. Photo from British Bryological Society, with permission per Barry Stewart.



Figure 25. *Metzgeria conjugata* beginning to dehydrate, showing the margins of the thallus beginning to curl under. Photo by David T. Holyoak, with permission.



Figure 26. *Metzgeria conjugata* showing a further stage of dehydration with thalli beginning to form tubes. Photo by Martin Hutten, with permission.



Figure 27. *Metzgeria conjugata* thallus dry, showing reduced surface area and tubular configuration of thalli. Photo by Hugues Tinguy, through Creative Commons.



Figure 28. *Metzgeria conjugata* showing hairs on the ventral surface. The margins are beginning to curl under, indicating that the thallus is drying. Photo by Hugues Tinguy, through Creative Commons.



Figure 30. *Metzgeria conjugata* with sporophyte. Photo from UBC Botany website, with permission.

Reproduction

Metzgeria conjugata (Figure 1-Figure 14) is **monoicous** (Figure 29) and frequently fertile (Schuster 1992; Fuselier *et al.* 2009). Capsules are common (Figure 30-Figure 31) (Schuster 1992). Frye and Clark (1937) described gemmae, but Schuster (1992) described this species as lacking gemmae. Evans (1910) also considered reports of gemmae in *Metzgeria conjugata* to be in error. Rather, he considered these marginal gemmae to be normal outgrowths of the thallus (Figure 32). In the same year as Schuster described the absence of gemmae, da Costa and Machado (1992) described gemmae from populations in Brazil as lamellar at the thallus margin.



Figure 31. *Metzgeria conjugata* with dehiscent capsule. Photo by Hermann Schachner, through Creative Commons.

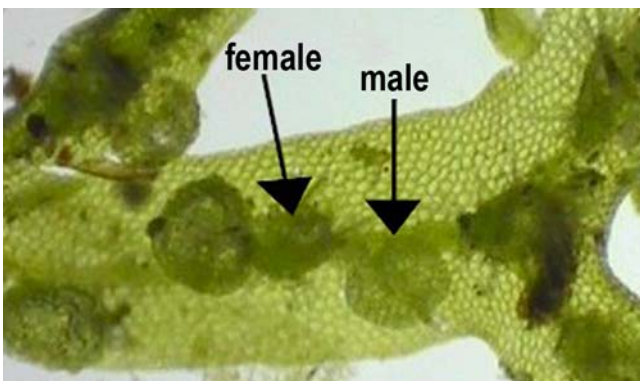


Figure 29. *Metzgeria conjugata* male and female. Modified from photo by Paul G. Davison, with permission.

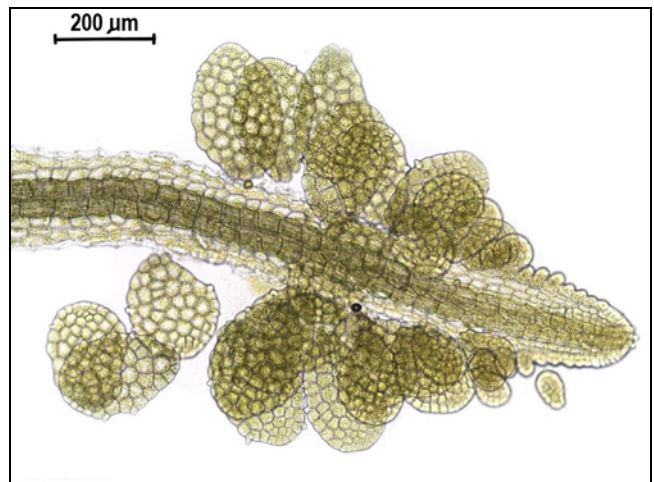


Figure 32. *Metzgeria* thallus with lobes that can serve as asexual reproductive structures. Photo by Hugues Tinguy, through Creative Commons.

Fungal Interactions

I have been unable to find any records of mycorrhizal or other fungal associations with *Metzgeria conjugata*.

Biochemistry

Schuster (1992) reports that *Metzgeria conjugata* (Figure 1-Figure 14) lacks oil bodies. Suire (2000) affirmed this again in specimens from southwest France.

Metzgeria conjugata (Figure 1-Figure 14) is one of the species used to determine that RNA editing from genomic sequences in bryophytes is predictable, based on cDNA analysis (Steinhauser *et al.* 1999).

Theodor *et al.* (1981a) identified six already known tricin and apigenin di-c-glycosides, including 2"-oferulylisoschaftoside in the gametophyte thallus of *Metzgeria conjugata* (Figure 1-Figure 14).

Some of the compounds produced by *Metzgeria conjugata* (Figure 1-Figure 14) are effective against *Paenibacillus larvae* (Figure 33) isolates (Sevim *et al.* 2017). This bacterial species causes American foulbrood diseases in honeybee larvae. The newly hatched honey bee larvae are infected through ingestion of brood honey containing *P. larvae* spores (Figure 34). After germination and multiplication, the infected bee larvae die within a few days and decompose into a ropy mass (Figure 35). The bacteria release millions of spores after desiccation.



Figure 33. *Paenibacillus larvae* with Gram-positive stain, showing spore-forming, rod-shaped bacteria. Image modified from Sevim *et al.* 2017.



Figure 34. American-foulbrood-diseased bee larvae are beige or brown in color and have diminished segmentation. Image modified from Sevim *et al.* 2017.

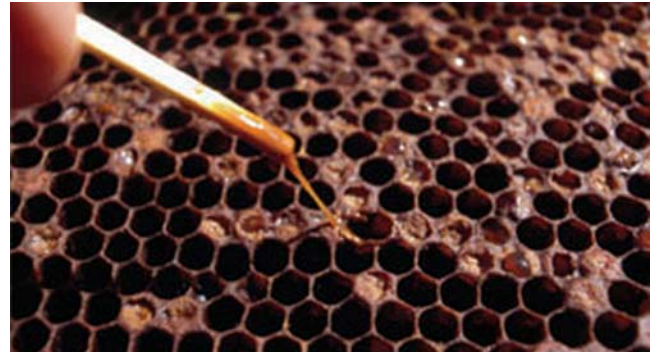


Figure 35. American foulbrood disease can be diagnosed by a matchstick test, demonstrating the viscous, glue-like larval remains adhering to the hive wall. Image modified from Sevim *et al.* 2017.

Metzgeria furcata/*Metzgeria setigera* (Figure 36, Figure 38-Figure 41)

Fuselier *et al.* (2009) demonstrated that within the broadly defined *Metzgeria furcata* (Figure 36), there are three very well-supported lineages, one from eastern North America and the other two widespread in Europe. Söderström *et al.* (2015) put the North American clade into *Metzgeria setigera* (Figure 37) as a new species.



Figure 36. *Metzgeria furcata* showing hairs on the thallus and long lobes. Photo by Shirley Kerr, with permission.



Figure 37. *Metzgeria cf. setigera*, a representative of the North American clade that is now recognized as a separate species. Photo by Oskar Gran, through Creative Commons.

Distribution

The distribution of *Metzgeria furcata* (Figure 38-Figure 41) is worldwide (So 2002, 2004), but is mostly circumboreal (Schuster 1992). So (2002) listed countries from which specimens have been examined: Australia, Tasmania, Hawaii, Micronesia, New Caledonia, Papua New Guinea, New Zealand. Later So (2004) listed a number of African localities and Phephu and van Rooy (2015) reported it from southern Africa.



Figure 38. *Metzgeria furcata* growing in a tight, pure mat. Photo by Michael Lüth, with permission.



Figure 39. *Metzgeria furcata* with a somewhat more erect growth form. Photo by Michael Lüth, with permission.



Figure 40. *Metzgeria furcata* showing its translucent thallus. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

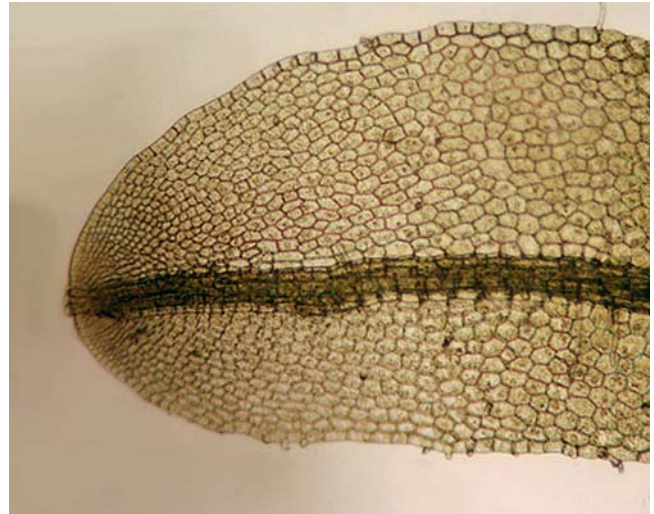


Figure 41. *Metzgeria furcata* thallus showing one-cell thickness. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Aquatic and Wet Habitats

Metzgeria furcata (Figure 38-Figure 41) occurs in rivers (Ferreira *et al.* 2008) and other aquatic habitats. It is part of the rock community in streams near Lacko, Western Carpathians (Mamczarz 1970). One of these is the *Platyhypnidium-Fontinalis antipyretica* association (Figure 15) in Thuringia, Germany (Marstaller 1987). In the Cool Temperate Victorian Rainforest it occurs in streams (Carrigan 2008).

Despite these aquatic records, Heylen and Hermý (2008) consider *Metzgeria furcata* (Figure 38-Figure 41) to be an obligate epiphyte. In the Tara River canyon and Durmitor area of Montenegro, it occurs on the bark of *Fagus* (Papp & Erzberger 2011). Although *Metzgeria furcata* is an epiphyte, it does often occur in wetlands and swamps, but still on typically bark (Schuster 1992).

Metzgeria furcata (Figure 38-Figure 41) var. *ulvula* is small and lives where there is high humidity, including along streams, but also 1-2 m high on tree trunks of older deciduous trees (Figure 42) or in the shade of rock faces or

steep banks along wooded creeks, and especially on big, steep ravines with high humidity and lots of rock face (Trigoboff 2013). It is especially common on rocks covered with *Metzgeria conjugata* (Figure 1-Figure 14). Newton (2012) reported *Metzgeria furcata* from bark of *Sambucus* spp. (Figure 43) and *Salix* sp. (Figure 44), species that often occur in wet habitats. *Metzgeria furcata* is useful as a biodiversity indicator (Heylen & Hermý 2008; Heylen & Hermý, in prep.).



Figure 42. *Metzgeria furcata* on bark. Photo by Michael Becker, through Creative Commons.



Figure 43. *Sambucus nigra* in Austria; *Metzgeria furcata* often occurs on the bark of *Sambucus* species. Photo by Franz Xaver, through Creative Commons.

In the Eurosiberian alder swamps of Latvia, *Metzgeria furcata* (Figure 38-Figure 41) occurs on decorticated logs (Madžule & Brūmelis 2008), a habitat that is typically moist longer than the surrounding habitat. On the other hand, in some areas *Metzgeria furcata* is an indicator species for logs in decay stage 1 (Madžule & Brūmelis 2008).

Metzgeria furcata (Figure 38-Figure 41) is typically an epiphyte in forests in a stream valley in the Carpathian Basin (Szövényi *et al.* 2004). In northwest Latvia it is one of the indicator species for old-growth forests, where it occurs as an epiphyte (Mežaka & Znotiņa 2006).



Figure 44. *Salix alba*; *Metzgeria furcata* often occurs on the bark of *Salix* species. Photo by Willow, Creative Commons.

However, *Metzgeria furcata* (Figure 38-Figure 41) is not completely restricted to being an epiphyte. Dobrescu and Soare (2015) reported it among the saxicolous species in the Vâlsan Keys. It is of interest to note one unusual habitat for this widely distributed species: Koppe (1969) reported it from dry whale bones on Isle Borkum, in northwestern Germany.

(in South Africa) a steep-sided, wooded ravine or valley

Productivity

Photosynthesis of *Metzgeria furcata* (Figure 38-Figure 41) was measured as $4.2 \pm 0.2 \text{ nmol CO}_2 \text{ mg}^{-1} \text{ Chl s}^{-1}$ in air (Smith & Griffiths 2000).

Adaptations

Plants of *Metzgeria furcata* is yellowish green (Figure 45), thalli 1-2 cm long (So 2004). The thallus is one cell thick and translucent (Figure 45), perhaps adapting it to low light levels by permitting easy transmission of light.



Figure 45. *Metzgeria furcata* showing yellowish-green color and translucent thallus. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Metzgeria furcata (Figure 38-Figure 41) is quite desiccation tolerant (Schuster 1992). Clausen (1964) supported this concept with her experiments. At 20° C for

12 hours, all cells survived at 33% relative humidity; at 15% rh, only about 1/4 of the cells survived. All but undeveloped apical cells survived 2-4 days of freezing at -10°C; after 30-34 days, only 3/4 of the apical cells survived. This tolerance explains its ability to live on the vertical trunks of trees, where it might have a **fan** form (Figure 46), giving it more exposed surface area, but possibly giving it more light exposure in forests. It can also grow with other bryophytes that could potentially help it to retain moisture (Figure 47).



Figure 46. *Metzgeria furcata* showing the shelf-like **fan** form. Photo by Michael Lüth, with permission.



Figure 47. *Metzgeria furcata* growing with other bryophytes, a potential way to maintain moisture longer. Photo by Shirley Kerr, with permission.

Reproduction

Schuster (1992) considered *Metzgeria furcata* (Figure 38-Figure 41) to be **dioicous**, but So (2002) described it as **autoicous**. Schuster notes that only gynoeceia have been found in eastern North America (hence *Metzgeria setigera*), and then only at higher elevations. Fuselier *et al.* (2011) likewise considered it to be dioicous. Perhaps it is **monoicous**, but conditions to stimulate production of antheridia do not occur in most of its locations. Yeates (1908) noted that typically one could only find females of

Metzgeria furcata. Plants that had developed calyptras had no embryos. Sporophytes were only found in colonies that also had male plants (Figure 48); antheridial abundance varied greatly even at the same location.



Figure 48. *Metzgeria furcata* with globular antheridia on midrib and potential propagules on the margin. Are these marginal structures gemmae or early stages of lobes? Photo by Tom Thekathyl, with permission.

Schuster (1992) describes *Metzgeria furcata* (Figure 38-Figure 41) as having plane, linear gemmae (maybe Figure 49), arising from the margin of the thallus (So 2004); in North America they are abundant (Schuster 1992). Gemma-bearing thalli (Figure 50) are typically more slender and less highly differentiated compared to non-gemma-bearing plants (Figure 45) (Evans 1910). Evans provides a detailed description of the development, separation, and subsequent germination of these structures.



Figure 49. *Metzgeria furcata* showing lobes, possibly considered gemmae in some descriptions. Could these be the linear gemmae described by Schuster (1992)? Photo by Kristian Peters, with permission.

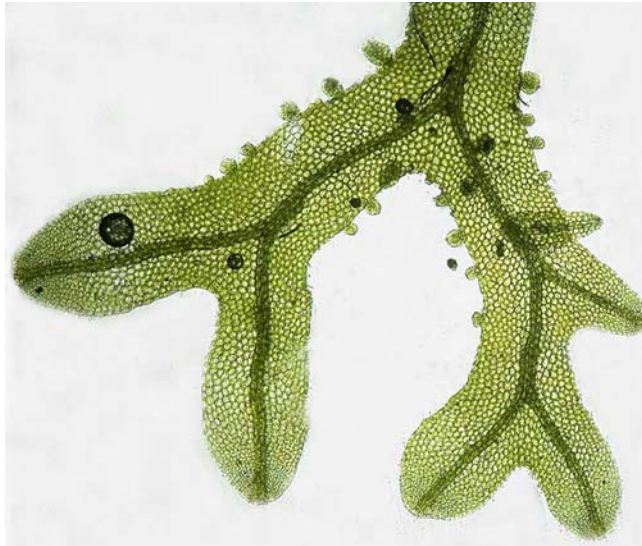


Figure 50. *Metzgeria furcata* with gemmae on margins and lobe arising from midrib. Photo by Walter Obermayer, with permission.

A discussion on Bryonet on 3 March 2021 did not really solve the problem of the definition of gemmae in *Metzgeria furcata*. Dave Kofranek summarized a number of sources that defined gemmae as simply vegetative reproductive structures. Tom Thekathyl suggested that those structures on the margin in Figure 50 might be gemmae, whereas the one arising from the midrib might be just a thallus lobe. Sorin Stefanut challenged the gemma interpretation in *Metzgeria furcata*, following the definition that gemmae are "uni- or multicellular, filamentous, globose, ellipsoidal, cylindrical, stellate, or discoid brood bodies, relatively undifferentiated, serving in vegetative reproduction," a definition found in the *Glossarium Polyglottum Bryologiae*. Stefanut contends that these are not true gemmae because they are only a small thallus having a midrib. Louis Thouvenot similarly suggested that the presence of a midrib would make them a thallus lobe. Jeff Duckett reminded us that in *Metzgeria consanguinea* and *M. violacea* the gemmae are endogenous and leave conspicuous holes in the thallus when they detach; such does not seem to be the case in *M. furcata*. Arno van der Pluijm and Jacques van Rooy both considered *Metzgeria* to have both lobes and gemmae. In South African populations, gemmae occur as outgrowths along the margins of *M. furcata* (Phephu & van Rooy 2015). I have concluded that these outgrowths at the edge of the thallus are transitional structures that act like gemmae but retain the developmental pattern of thallus branching. Hence, I agree with Sean Edwards (Bryonet 5 March 2021) that gemmae don't evolve overnight, making this a semantic question. In the words of Sanna Laaka-Lindberg (Bryonet 5 March 2021), "we often look for evidence to categorize phenomena even in cases no clear limits perhaps exist."

Metzgeria furcata seems to be the great compromiser. In some cases the marginal bits of thalli fall off at an early stage, but others remain longer, developing into much larger lobes before falling off (Arno van der Pluijm, Bryonet 3 March 2021). In either case, these marginal structures can serve as propagules. Perhaps this is one of the places where bryophytes invented gemmae?

An additional potential means of reproduction in *Metzgeria furcata* (Figure 38-Figure 41) is the development of thalli from the female involucre (Kuwahara 1973). These are not rare occurrences in northwestern Europe, and they have been observed developing into thalli. These may be the same structures described by Yeates (1908) as thallidia; Yeates concluded that these seemed to provide most of the reproduction.

Heylen and Hermý (2008) suggested that the strongly aggregated distribution of *Metzgeria furcata* (Figure 38-Figure 41) indicates local dispersal (rather than regional dispersal). This is consistent with their apparent lack of sexual reproduction and spores, but instead the dispersal of larger bits of thalli.

Slime Molds and Fungal Interactions

Some slime molds are usually associated with *Metzgeria furcata* (Figure 38-Figure 41). Isabelle Mazaud photographed *Diacheopsis synspora* (Figure 51) with this species where it was growing on *Quercus robur* bark (Figure 52-Figure 53). Ing (1994) reported *Hemitrichia minor* (Figure 54-Figure 55) in association with this species.

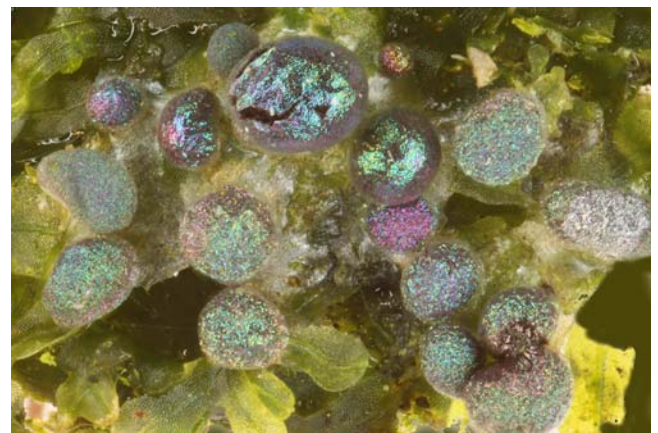


Figure 51. *Diacheopsis synspora* on *Metzgeria* in North Wales. Photo by Janet Graham, through Creative Commons.



Figure 52. *Quercus robur* in Devon, England, where one can find *Metzgeria furcata*. Photo by Alex Jane, through Creative Commons.



Figure 53. *Quercus robur* bark, a suitable substrate for *Metzgeria furcata* in Essex, England. Photo by Acabashi, through public domain.



Figure 54. *Hemitrichia minor*, a slime mold species known to associate with *Metzgeria furcata*. Photo by G. Moreno and J. Francisco, micobotanicajaen.com, with online permission.

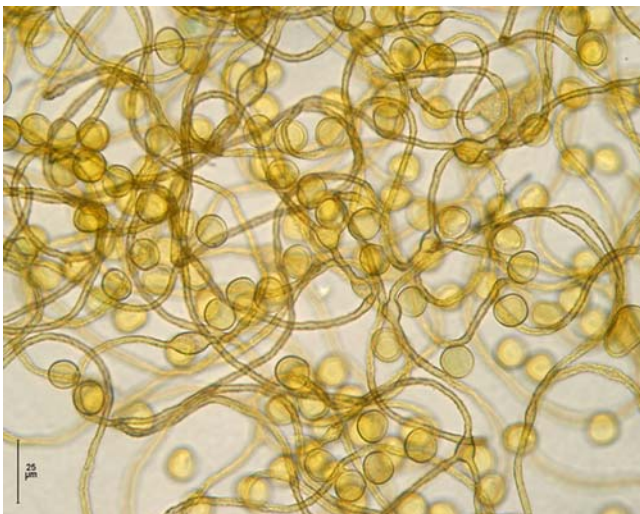


Figure 55. *Hemitrichia minor* microscopic view. Photo from Eumycetozoa Project, through DiscoverLife.org, with online permission.

Nordén *et al.* (2015) described the new *Ascomycete* fungus *Bryocentria hypothallina* from *Metzgeria furcata* (Figure 38-Figure 41). This fungus is indicated by bleached, necrotic patches on the liverwort. It produces ascumata on the under side of the thallus, perforating its surface. This parasitic fungus has a known distribution of France, Norway, and Spain – considerably less than the distribution of *Metzgeria furcata*.

Biochemistry

Members of the genus *Metzgeria* lack oil bodies (Figure 56-Figure 57) (Suire 2000). Nevertheless, Theodor *et al.* (1983) identified 12 different flavone C-glycosides in *Metzgeria furcata* (Figure 38-Figure 41) and its variety *ulvula*. Only four of these biochemicals are common to both the typical and the variety.

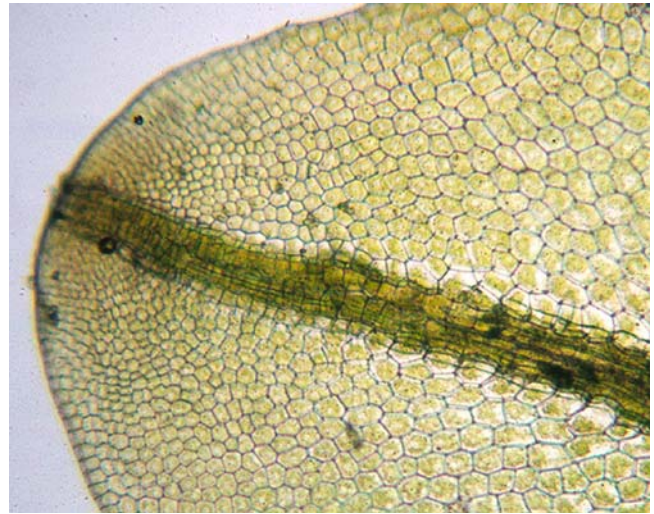


Figure 56. *Metzgeria furcata* showing absence of oil bodies in the thallus cells. Photo by Malcolm Storey, DiscoverLife.org, with online permission.



Figure 57. *Metzgeria furcata* lamina showing lack of oil bodies in thallus cells. Photo by Kristian Peters, with permission.

Werner *et al.* (2002) discovered that for *Metzgeria furcata* (Figure 38-Figure 41), thallus fragments longer than 1 mm inhibited the preparation of DNA for the polymerase chain reaction. They found that the optimal length was 0.5 mm. They suggested that the secondary

substances produced and stored in oil bodies might be responsible for this inhibition by bryophytes, but this does not explain the behavior in *Metzgeria* species because oil bodies are unknown.

The isolation of 6-C-a-L-rhamnopyranosylapigenin (isofurcatain) 7-O- β -D-glucopyranoside, from *Metzgeria furcata* (Figure 38-Figure 41) var. *ulvula*, the common variety reported in North America (Schuster 1992), is described and identified (Markham *et al.* 1982). This is a new natural product, as also is isofurcatain.

Metzgeria litoralis

Distribution

Metzgeria litoralis is known only from Chile in southern South America (Engel & Kuwahara 1973).

Aquatic and Wet Habitats

Metzgeria litoralis occurs on coastal rocks that are continuously exposed either to tidal action or ocean water spray (Engel & Kuwahara 1973). This is a highly unusual habitat for any bryophyte. The bryophytes have no mechanism for tolerating exposure to salt water. But Engel and Schuster (1973) suggest that in this case, drainage from forested areas directly above these beaches, along with high rainfall, provide sufficient fresh water for these liverworts to survive. They argue that these conditions do not allow for dispersal of bryophytes by tidal water along the shoreline.

Adaptations

Metzgeria litoralis has a yellow-green thallus that is convex, giving the appearance of a tube (Engel & Kuwahara 1973). But it is also flaccid, most likely due to the thin cell walls of the lamina.

Reproduction

Metzgeria litoralis is **dioicous** and lacks gemmae (Engel & Kuwahara 1973). However, females and sporophytes are unknown, so it is possible it is monoicous but has not experienced the environmental conditions necessary for female gametangia to develop.

Metzgeria pubescens (Figure 58, Figure 60-Figure 63)

(syn. = *Apometzgeria pubescens*)

The Southern Hemisphere populations are morphologically similar plants to the northern Holarctic ones but form a divergent lineage (often treated as *Apometzgeria frontipilis*) in South America (Fuselier *et al.* 2011). But Engel and Kuwahara (1973) found both *Metzgeria pubescens* (Figure 58) and *Metzgeria (Apometzgeria) frontipilis* (Figure 59) growing together in southern South America. Thus, Fuselier *et al.* (2011) and others have considered *Metzgeria pubescens* to be bipolar, occurring throughout Europe, China, Russia, Korea, and North America (rather sparsely), as well as Chile (Engel 1978; Schuster 1992). In any case, it appears that there are distinct genetic differences in the species between the hemispheres, suggesting that there are new species in progress.



Figure 58. *Metzgeria pubescens* growing on bark. Photo by Štěpán Koval, with permission.



Figure 59. *Metzgeria frontipilis*, a separate species that sometimes grows together with *Metzgeria pubescens*. Photo by Blanka Agüero, with permission.

Results by Fuselier *et al.* (2011) indicate that *Metzgeria pubescens* (Figure 58) in South America forms a divergent lineage that shares a closer phylogenetic history with *M. frontipilis*. As such, *M. pubescens* should be considered a Holarctic species.

Distribution

Metzgeria pubescens (Figure 60-Figure 63) occurs in Europe, Asia, and North America (So 2003). This known distribution has been expanded to a bipolar range with populations across the Holarctic and in southern South America (Fuselier *et al.* 2011). Blockeel (2020) reported it for the first time from Greece.



Figure 60. *Metzgeria pubescens* forming a nearly pure clump, but arranged to provide spaces between plants. Photo by Štěpán Koval, with permission.



Figure 62. *Metzgeria pubescens* showing the opaque thalli projecting away from the substrate. Photo by Štěpán Koval, with permission.



Figure 61. *Metzgeria pubescens* looking dry because of its covering of hairs. Photo by Štěpán Koval, with permission.

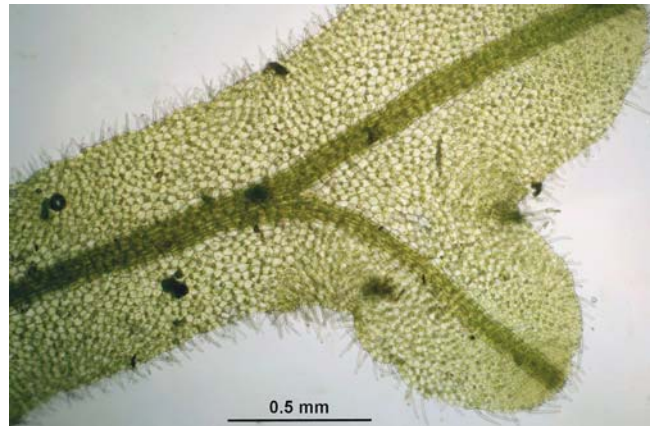


Figure 63. *Metzgeria pubescens* showing the thin (1-cell-thick) thallus and numerous hairs. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

For Romania (Ștefănuț & Goia 2012) and Slovakia (Mišíková *et al.* 2021) *Metzgeria pubescens* (Figure 60-Figure 63) is listed as a liverwort of "Least Concern" in the Red List.

Metzgeria pubescens (Figure 60-Figure 63) is known from an intermittent stream (Dhien 1978). *Metzgeria pubescens* occurred on stones beside the water at Jumog Waterfall in Indonesia (Sidiq *et al.* 2019) and in Yakutia (Sofronova 2015). Chamberlain (1972) likewise reported it from **Breccia rock** (broken fragments of minerals or rock cemented together by fine-grained matrix; Figure 64) faces by the river and upstream on limestone. Lorenz (1910) similarly reported it from a limestone ravine in Switzerland, and Papp and Sabovljević (2002) in western Serbia.



Figure 64. Breccia rock at Titus Canyon Narrows, Death Valley National Park, California, USA. Photo from NPS, through public domain.

In the Vologda Region of Russia, *Metzgeria pubescens* (Figure 60-Figure 63) grew in the beds of mosses in a boggy spruce forest (Dulin *et al.* 2009). It is critically endangered in this region due to a scarcity of suitable habitats.

But *Metzgeria pubescens* (Figure 60-Figure 63) often occurs in habitats that would not be considered aquatic or wetland. In the Algama River basin of Yakutia, Russia, it occurs on stones, stones covered with humus, and rock outcrops in the forest belt (Sofronova 2013). Horikawa (1934) reported similar habitat in Japan, where it grew with mosses on rocky soil. Photographs also show that it can occur on bark (Figure 65).



Figure 65. *Metzgeria pubescens* on bark. Photo by Štěpán Koval, with permission.

One habitat that seems to be relatively common for bryophyte species tolerant of wetlands is that of wet, rotting logs. Such is the case also for *Metzgeria pubescens* (Figure 60-Figure 63) (Sofronova 2015).

Adaptations

Metzgeria pubescens (Figure 60-Figure 63), as indicated by its name, is a densely hairy species (Figure 66-Figure 68) on its ventral side, an uncommon character in the genus and used by some systematists to create a separate genus for it. This character would seem to protect

it from drying out and also aid in providing capillary spaces that facilitate water uptake.



Figure 66. *Metzgeria pubescens* that is dry, but still green, with its hairs showing prominently. Photo by Štěpán Koval, with permission.



Figure 67. *Metzgeria pubescens* showing dense hairs. Photo by Štěpán Koval, with permission.

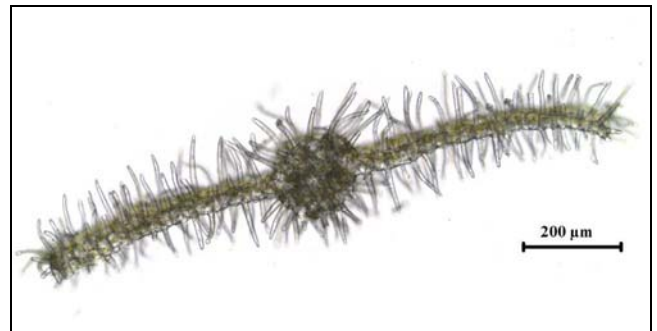


Figure 68. *Metzgeria pubescens* showing dense hairs. Photo by Hugues Tinguy, with permission.

Growth forms vary (Figure 69-Figure 70), presumably dependent on the habitat, but they could also represent different crypto species.



Figure 69. *Metzgeria pubescens* exhibiting a cluster growth form. Photo by Hugues Tinguy, with permission.



Figure 70. *Metzgeria pubescens* in a mat form. Photo by Štěpán Koval, with permission.

Reproduction

Metzgeria pubescens (Figure 60-Figure 63) is **dioicous** and rarely produces sporophytes. It furthermore apparently does not produce gemmae (Schuster 1992). Hence, it would be interesting to determine how it has become so widespread and common. These limiting reproductive strategies also help to explain the genetic divergence (Fuselier *et al.* 2011) seen for the species between the hemispheres.

M'Ardle (1896) suggested that *Metzgeria pubescens* (Figure 60-Figure 63), lacking females – at least in Ireland, was able to reproduce through a type of budding, adventitious branches that at some point could break away from the parent plant. I was unable to find any images that showed budding, at least not with the constricted bases of the branches seen in some of the above species (*e.g.* Figure 32, Figure 49).

Fungal Interactions

Glomeromycotean fungi are becoming well known in bryophytes. Ligrone *et al.* (2007) examined a large number of endophytic fungal associations in liverworts. They failed to discover any glomeromycotean fungi in *Metzgeria pubescens* (Figure 60-Figure 63).

Biochemistry

Markham *et al.* (1987) reported the existence of rotational isomerism in flavone-6,8-di-C-glycosides isolated from *Metzgeria pubescens* (Figure 60-Figure 63). Theodor *et al.* (1980, 1981b) reported five such flavone-C-glycosides.

Metzgeriales: Calyculariaceae

Calycularia crispula (Figure 71-Figure 72)

Distribution

Davison and Smith (1992) listed *Calycularia crispula* (Figure 71-Figure 72) from Asia (Himalaya, Burma, Thailand, Taiwan, Korea, Japan), Africa (Ethiopia, Tanzania, Malawi), and Mexico. When Daniels *et al.* (2014) reported it for the first time from the Western Ghats in India (see also Manju *et al.* 2015), they also included Bhutan, China, Myanmar, and Nepal. In 2010, Konstantinova and Mamontov (2010) excluded it from Russia, Canada, Japan, and Korea based on re-examination of the specimens. They instead contend that *Calycularia crispula* (Figure 71-Figure 72) is restricted to mountains of the tropics and subtropics, adding records from Zambia, China, and Costa Rica. They determined specimens from more northern collections to be *Calycularia laxa*.



Figure 71. *Calycularia crispula* showing pale green and almost translucent thallus. Photo by Shanxiong Lin, Taiwan Mosses Color Illustrations, through Creative Commons.



Figure 72. *Calycularia crispula* in Sichuan, growing with mosses and exhibiting a medium green color with slightly reddish areas. Photo by David Long, with permission.



Figure 74. *Plagiochila arbuscula* as it would appear in a humid montane forest. Photo by Peter de Lange, through online permission.

Aquatic and Wet Habitats

Calycularia crispula (Figure 71-Figure 72) occurs in moist or foggy mountain locations on soil, tree bases, logs, stumps, and rocks (Davison & Smith 1992). Daniels *et al.* (2014) describe it as occurring in upland areas in the tropics of Asia, Africa, and Central America. The broad habitat descriptions may in some cases be based on the segregate northern species *C. laxa*.

In the Western Ghats of India, *Calycularia crispula* (Figure 71-Figure 72) occurs at 1,540 m asl in montane wet temperate forests and also from 950 m asl in moist deciduous forest, attached to the bark of trees and on rocks; it also occurs on decaying logs, moist soil, in deep crevices and on shaded humus covered cliffs in river valleys.

In Thailand, *Calycularia crispula* (Figure 71-Figure 72) occurs on the bases of tree trunks, decaying wood, and humus rich rocks in humid montane forests at 1,200-2,550 m asl (Printarakul *et al.* 2019). *Bazzania* (Figure 73) and *Plagiochila* (Figure 74) often occur with it.



Figure 73. *Bazzania tricrenata*; *Calycularia crispula* can occur with species of *Bazzania* in humid montane forests of Thailand. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Daniels *et al.* (2014) describe *Calycularia crispula* (Figure 71-Figure 72) as translucent green (Figure 71). It is multilayered (Figure 75), thus not as translucent as the members of *Metzgeria* in this chapter. Konstantinova and Mamontov (2010) provide a more robust coloration, from "pale to yellowish (Figure 71) or deep green (Figure 72) often with secondary goldish, fuscous, reddish to purplish red or red-brown pigmentation." This broader description may be a better reflection of its pigmentation adaptations to various levels of light throughout its range and seasons.

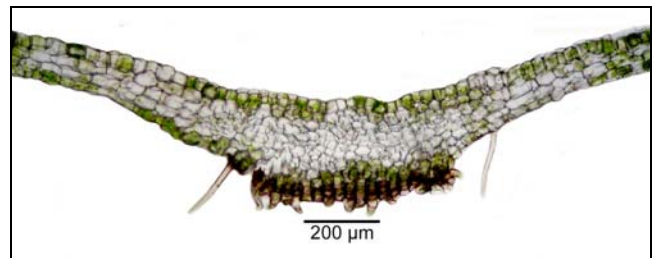


Figure 75. *Calycularia crispula* thallus cs. Photo by N. Printarakul, through Creative Commons.

Reproduction

Calycularia crispula (Figure 71-Figure 72) is **dioicous** (Konstantinova & Mamontov 2010). Both sexes are known and sporophytes are fairly common (Figure 76-Figure 77). Konstantinova and Mamontov suggest that the ventral shoots that arise from the midrib are likely to provide a means of vegetative propagation.



Figure 76. *Calycularia crispula* with capsules. Photo by N. Printarakul, through Creative Commons.

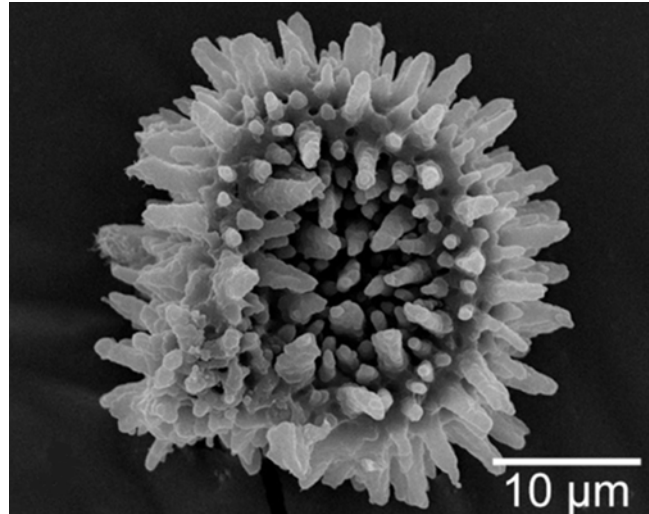


Figure 79. *Calycularia crispula* spore. Photo by N. Printarakul, through Creative Commons.



Figure 77. *Calycularia crispula* capsule in Sichuan. Photo by David Long, with permission.

The spores are endowed with large, somewhat cylindrical projections (Figure 78-Figure 79) (Konstantinova & Mamontov 2010). Experimentation is needed to determine if these facilitate flotation and subsequent dispersal of the spores.

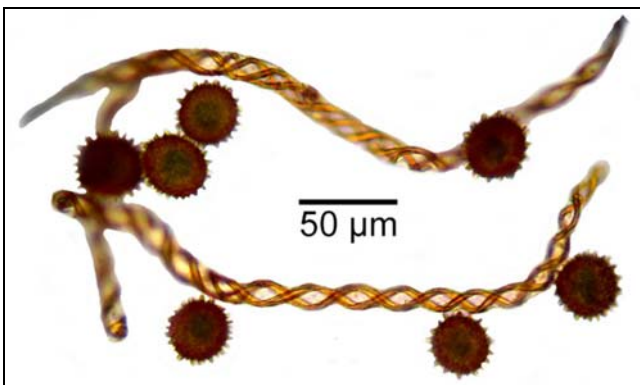


Figure 78. *Calycularia crispula* spores and elaters. Photo by N. Printarakul, through Creative Commons.

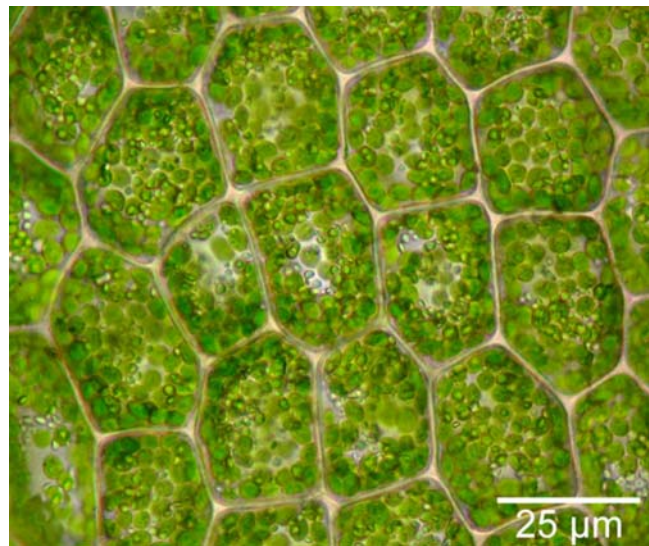


Figure 80. *Calycularia crispula* cells showing the numerous tiny oil bodies. Photo by N. Printarakul, through Creative Commons.

Biochemistry

Calycularia crispula (Figure 71-Figure 72) has 6-34 minute (1.5-4.9 μm) oil bodies per cell (Figure 80) that are presumably the source of the cedar-oil-like smell that is distinct when dried specimens are moistened (Konstantinova & Mamontov 2010).

Calycularia laxa

Distribution

Apparently the report by Davison and Smith (1992) for *Calycularia crispula* from the Aleutian Islands and Pacific Northwest (British Columbia, SE Alaska) of North America is really *Calycularia laxa*. When Konstantinova and Mamontov (2010) revised the genus, they excluded *C. crispula* from Russia, Canada, Japan, and Korea based on re-examination of the specimens and treated these collections as the northern species *Calycularia laxa*. It is

widespread and relatively common in Siberia. It is more difficult to distinguish when sterile, so there may be a more widespread distribution in the North American tundra.

Daniels *et al.* (2014) further explained that the two species are separated by habitat and distribution. *Calycularia crispula* (Figure 71-Figure 72) occurs predominantly in upland areas of the tropics in Asia, Africa, and Central America, whereas *Calycularia laxa* occurs in temperate to Arctic regions in the Northern Hemisphere.

Aquatic and Wet Habitats

Calycularia laxa (originally reported as *C. crispula*) occurs on wet cliffs of Upper Bureya River (Russian Far East) (Konstantinova *et al.* 2002). In northwestern North America it occurs on boulders and soil of moist banks of alpine streams (Davison & Smith 1992). Davison & Smith (1992) characterize its environment as having even moisture conditions and subdued light.

In the tundra zone *Calycularia laxa* occurs in moist habitats of river and lake valleys, where it grows on damp sandy soil, peat and humus-covered rocks along banks of streams, in dried river beds, in depressions between peat hillocks, in crevices of cliffs, or among boulders in rock fields (Konstantinova & Mamontov 2010). It also occurs on spots of bare soil in different types of tundra, on nival slopes, among boulders in rocky lichen tundra, on bare soil in sedge-lichen tundra, and occasionally in sedge-moss bogs. In mountains at the southern limit of its distribution the species is restricted to valleys of rivers on wet, often moss-covered, cliffs and rocks along streams in deep humid ravines, near waterfalls, on fine-grained and sandy soil or peat between rocks, in shaded crevices on wet cliffs, at the bottom of cliffs and rock outcrops, both in subalpine and forest zones, including broad-leaved forests, mixed and coniferous forests. It typically grows with other liverworts in these habitats.

Adaptations

The plants of *Calycularia laxa* are yellowish or deep green to reddish and purplish red and red-brown (Konstantinova & Mamontov 2010). Tundra plants are typically pigmented, exhibiting purple-reddish or green with "fuscous, reddish to purplish red or red-brown colored margins." This coloration is especially typical of the mouth of the pseudoperianth. This range of color potential may permit it to survive the often intense UV light in its northern locations. On the other hand, when plants occur in shaded depressions they often lack all secondary pigmentation.

Tundra plants of *Calycularia laxa* tend to be smaller, seldom exceeding 6 mm width and 15 mm length (Konstantinova & Mamontov 2010). This contrasts with plants from mountains in South Siberia, southern Alaska, and British Columbia, Canada, where plants can be as much as 12 mm wide and 50 mm long.

Calycularia laxa usually forms **mats** or grows as single plants among other bryophytes (Konstantinova & Mamontov 2010). Both of these characteristics can help to conserve moisture.

Reproduction

Calycularia laxa is **dioicous** (Konstantinova & Mamontov (2010). At least in North America, the two

sexes have not been found in the same location, and females are much more common than males. *Calycularia laxa* lacks the ventral shoots that could potentially serve as a means of vegetative propagation (Konstantinova & Mamontov 2010). This combination bodes for poor reproduction.

Biochemistry

Oil bodies of *Calycularia laxa* are 1.0-3.7 µm long, numbering 12-58 per cell (Konstantinova & Mamontov 2010). These are presumably the source of an odor that is distinct when dried specimens are moistened.

Summary

Metzgeria (Metzgeriaceae) species are not true aquatic species, but some of them are occasionally submerged, and the one included here often occur in damp or wet places, especial riverine canyons. They often form mats, and with their ribbon-like thallus this can help to conserve moisture during drier periods. *Metzgeria furcata* is very desiccation tolerant. The thalli are often translucent, permitting light to reach greater depths. Hairs and curving under can help to retain moisture in some species. Thallus lobes contribute to asexual reproduction.

Slime molds are often associated with *Metzgeria furcata*. While some species of *Metzgeria* have fungal partners, others have no known fungal associates (*Metzgeria conjugata*). *Metzgeria furcata* can have the Ascomycete fungal parasite *Bryocentria hypothallina*. Some species have known antibiotic properties, perhaps accounting for a lack of fungi.

Calycularia crispula (Calyculariaceae) occurs in humid locations, but is not aquatic. The more northern *Calycularia laxa* occurs on wet cliffs and moist stream banks.

Acknowledgments

Lars Söderström helped me find the current acceptable names for a number of older taxa.

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CHAPTER 1-13

AQUATIC AND WET MARCHANTIOPHYTA, ORDER FOSSOMBRONIALES, PART 1

TABLE OF CONTENTS

SUBCLASS PELLIIDAE	1-13-2
Fossombroniales: Fossombroniaceae	1-13-2
<i>Fossombronia</i>	1-13-2
<i>Fossombronia angulosa</i>	1-13-2
<i>Fossombronia australis</i>	1-13-9
<i>Fossombronia caespitiformis</i> subsp. <i>multispira</i>	1-13-11
<i>Fossombronia cristula</i>	1-13-16
<i>Fossombronia delgadilloana</i>	1-13-19
<i>Fossombronia foveolata</i>	1-13-21
<i>Fossombronia incurva</i>	1-13-29
<i>Fossombronia isaloensis</i>	1-13-31
<i>Fossombronia jostii</i>	1-13-34
Summary	1-13-36
Acknowledgments.....	1-13-36
Literature Cited	1-13-36

CHAPTER 1-13

AQUATIC AND WET MARCHANTIOPHYTA, ORDER FOSSOMBRONIALES, PART 1



Figure 1. *Fossombronia caespitiformis* subsp. *multispira* with capsules on bank. Photo by Michael Lüth, with permission.

Nomenclature for this chapter is based primarily on Söderström *et al.* (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. Information on these unverifiable taxa has been included in the species.

To develop this list, I used my own bibliography, collected over the past 56 years, and Google Scholar. These papers soon led me to others. I do not pretend that this is complete. It includes streams, lakes, and other wetlands, but also other wet habitats such as waterfall spray and stream and river banks. I have not discussed or searched bog and fen habitats, but I nevertheless include a number of these species because they were found in a wetland study. Bogs and poor fens have been treated in whole books and provide an extensive literature; intermediate and rich fens seem somewhat less studied. They would require considerably more review and time. Thus I felt that less-reviewed topics, particularly the aquatic habitats with which I am most familiar, should be given priority.

SUBCLASS PELLIIDAE

Fossombroniales: Fossombroniaceae

Fossombronia (Figure 1)

Fossombronia has been a troublesome genus, and many parts remain so. For example, in her revision of the genus in Mexico, the Caribbean, Central and South America, Freire (2004) reduced the 30 species described to 13.

Many of the species of *Fossombronia* can live in wet or moist habitats. Some of these could even be considered aquatic. Toivonen and Huttunen (1995) reported species of *Fossombronia* in small lakes of southern Finland. The genus has a relatively wide range of habitats, including both terrestrial and aquatic.

Fossombronia angulosa (Figure 2-Figure 5)

The name *Fossombronia angulosa* (Figure 2-Figure 5) has met with confusion. Its use in publications appears frequently to be different from the species that was

originally described. Stotler *et al.* (2005) argued that the concept used for 200 years should be retained, following the basionym *Jungermannia angulosa*. It has become the type species for the split off genus *Fossombronia*, based on the name *Fossombronia angulosa*, and was conserved following the 200-year concept of the species.



Figure 2. *Fossombronia angulosa*. Photo by Jan-Peter Frahm, with permission.



Figure 3. *Fossombronia angulosa*. Photo by Jan-Peter Frahm, with permission.



Figure 4. *Fossombronia angulosa* in moist condition. Photo by Jan-Peter Frahm, with permission.

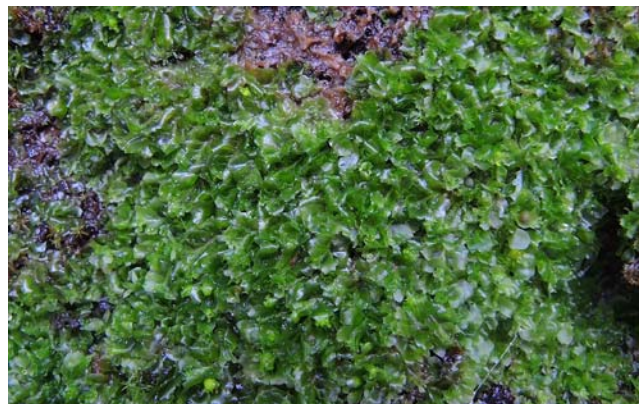


Figure 5. *Fossombronia angulosa* covering its substrate. Photo by Michael Lüth, with permission.

Distribution

Schuster (1992) considered all North American records to belong to *Fossombronia brasiliensis*, now considered to be *Fossombronia porphyrorhiza* (Figure 6), describing the distribution of *Fossombronia angulosa* (Figure 2-Figure 5) as European oceanic and Mediterranean. This included southern Ireland and southwestern England to coastal France, Spain, Portugal, southern Switzerland, Italy, eastward to Greece and Turkey, south to North Africa, the Canary Islands, Madeira, and the Azores.



Figure 6. *Fossombronia porphyrorhiza*, considered by Schuster to be a North American species. Photo courtesy of Denilson Peralta.

Fossombronia angulosa (Figure 2-Figure 5) is a Northern Hemisphere species (Sabovljević & Natcheva 2006; Milner *et al.* 2011). Dia *et al.* (2007) consider it to be oceanic-Mediterranean and Jovet-Ast (1946) to be Mediterranean-Atlantic.

The 2019 edition of the Catalog of life reports *Fossombronia angulosa* (Figure 2-Figure 5) from Norway, Britain, Ireland, Netherlands (see also du Mortier 1874), Belgium, Switzerland (see also Meier *et al.* 2013), Czech Republic, France, Portugal (see also Sérgio 1974), Spain (see also Elias Rivas & Rupidera Giraldo 1991; Elías Rivas *et al.* 2001; Pericàs Mestre *et al.* 2010), Balears, Corsica,

Sardinia, Sicily (see also Dia *et al.* 2007; Privitera *et al.* 2008), Italy (see also Puglisi & Privitera 2009; Pedrotti & Aleffi 2011), Croatia (see also Sabovljević 2003), Montenegro, Bulgaria, Albania, Greece, Crete, Turkey (see also Ezer *et al.* 2009; Oren *et al.* 2012) in Europe, Krasnodar, Morocco, Algeria, Tunisia, Azores (see also Frahm 2005), Madeira, Canary Islands, Cape Verde, South Africa, Azerbaydzhan, Turkey, Cyprus, Lebanon, Sinai, Palestine, Yemen, and Java. It most likely also includes Germany (du Mortier 1874). Ganeva (1997) notes that most of the Mediterranean-Atlantic liverworts in Bulgaria, including *Fossombronia angulosa*, are mostly in the southern part of the country, along the Black Sea coast, but also in lowland areas in northern parts.

Despite the conclusions of Schuster (1992) regarding North American populations, a number of recent authors still recognize *Fossombronia angulosa* (Figure 2-Figure 5) as a species in the western hemisphere, including Söderström *et al.* (2020). Theirs and others include records in Canada: Ontario; USA: Rhode Island, New Jersey, Texas (see also Underwood 1896), South Carolina, Alabama (see also Underwood 1896), Louisiana, Florida (see also Underwood 1896; Redfearn 1952); Mexico; Cuba; Rio Grande do Sul; and Uruguay (Söderström *et al.* 2020), as well as Brazil (Bordin & Yano 2010).

Aquatic and Wet Habitats

Ezer *et al.* (2009) consider *Fossombronia angulosa* (Figure 2-Figure 5) to be a hygrophyte-mesophyte (Figure 7). Guerra (1982) likewise treats it as a mesophyte and earthbound. Saadi *et al.* (2020) describe it as terricolous, sub-aquatic, and aquatic in Morocco; along with *Fontinalis antipyretica* (Figure 8) and *Cinclidotus riparius* (Figure 9), it can be totally immersed, but it can also grow on a water-soaked forest floor. They consider *Fossombronia angulosa* to be very rare, at least in Morocco. But in Galicia, Reinoso (1985) considers it frequent, forming extensive mats.



Figure 7. *Fossombronia angulosa* in a terrestrial, mesic habitat. Photo by Michael Lüth, with permission.

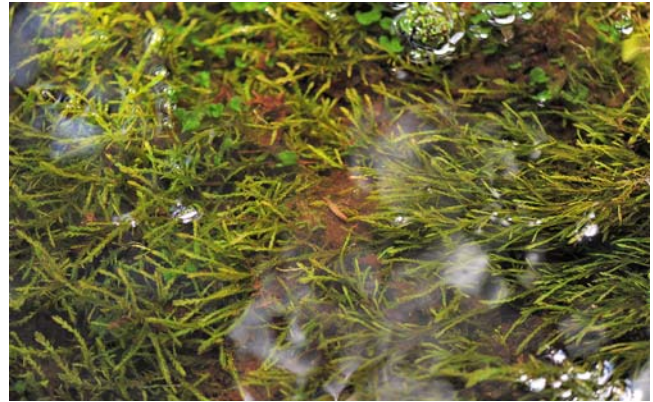


Figure 8. *Fontinalis antipyretica*, a species that occurs under water in some of the same situations as *Fossombronia angulosa* in Morocco. Photo by Dick Haaksma, with permission.



Figure 9. *Cinclidotus riparius*, a species that occurs under water in some of the same situations as Hermann Schachner, through Creative Commons.

Ferreira *et al.* (2008) reported *Fossombronia angulosa* (Figure 2-Figure 5) from rivers. Earlier, Armitage (1918) reported it from the wetter rocks and stones of streams in Madeira, but it was also found on bare earth, banks, and shady mountain ground. Özenoğlu Kiremit *et al.* (2007) found it on soil in the stream bed, but also on the soil of stream banks, frequently with other liverwort species. These habitats are consistent with what seems to be a more frequent habitat on stream banks.

In the Izarine Massif of Morocco, *Fossombronia angulosa* (Figure 2-Figure 5) occurs on wet clay soil next to a water gully and on small rocks (Laouzazni *et al.* 2021). On Tenerife in the Canary Islands, it frequents damp soil on the slopes of ravines and is again considered mesophilic (Losada Lima & Beltrán Tejera 1987). On Madeira, it occurs in the spray zone along stream margins, where it is often associated with the hygrophytic moss *Brachythecium rivulare* (Figure 10) and liverwort *Scapania undulata* (Figure 11) (Luís *et al.* 2008). In Spain it occurs on slopes close to a ravine (Figure 12) (Fuertes & Mendiola 1984; Gil Garcia & Castro 1987). Campisi *et al.* (2008) found it on soil slopes near water courses in Calabria, Italy. On the Greek Island of Crete, Blockeel (2012) found *Fossombronia angulosa* on the steep, heavily shaded banks of streams and gullies. In Ireland, where it is rare, M'Ardle (1894) found it on rocks at the mouth of the river at Pulleen Cove.



Figure 10. *Brachythecium rivulare* by stream, a common associate of *Fossombronia angulosa* in the spray zone on Madeira. Photo by Kim Nicole, through Creative Commons.

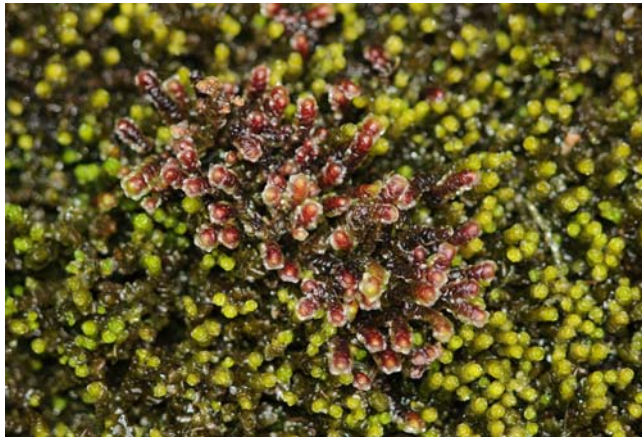


Figure 11. *Scapania undulata* with *Marsupella emarginata* surrounding it. *Scapania undulata* is a common associate of *Fossombronia angulosa* in the spray zone on Madeira. Photo by Jeremy Berker, through Creative Commons.



Figure 12. *Fossombronia angulosa* in a damp location by a stream. Photo by Michael Lüth, with permission.

Where the substrate is wet, *Fossombronia angulosa* (Figure 2-Figure 5) is able to venture away from streams and other water bodies. It occurs on humid soil (Cros *et al.* 1995), in humid areas of southeastern Spain (Casas *et al.* 1999) and on "shady slopes with a certain degree of humidity" (Jiménez *et al.* 1986). Likewise, it occurs on damp soil in the Küre Mountains in Turkey (Ören *et al.* 2012). In southern Europe it occurs on clayey moist shady

soil and also lives in wetlands in Italy, England, and the Netherlands (du Mortier 1874). Sotiaux *et al.* (2008) listed it on the ground of a slope in Corsica, but made no reference to moisture.

Despite these wet sites, there is evidence that *Fossombronia angulosa* (Figure 2-Figure 5) is drought tolerant. It is able to live in temporary water courses (Jiménez *et al.* 1986; Mundo 1986). In Morocco, Fadel *et al.* (2020) found it on shale that is soaked with water in the winter, but is dry in summer. In Sierra del Calar, it also occurs in temporary water (Mundo 1986).

Puglisi *et al.* (2015) found *Fossombronia angulosa* (Figure 2-Figure 5) in Mediterranean temporary ponds in Italy. Puglisi and Privitera (2009) described the *Fossombronia anglosae-Phaeocerotetum bulbiculosi*, now *Phymatocerotetum bulbiculosi* (Figure 13), from moist but not humified soil with a steep slope (60°-80°) on talus along the margin of a coastal lake in Italy. This association was previously only known from the Iberian Peninsula. In the British Isles, Preston *et al.* (2011) found a similar association of *Fossombronia angulosa* with *Phaeoceros laevis* (Figure 14) in locations that were very well-illuminated and relatively dry in summer.



Figure 13. *Phymatoceros bulbiculosus*, a species that forms an association with *Fossombronia angulosa* in Italy. Photo by David H. Wagner, with permission.



Figure 14. *Phaeoceros laevis*, a species that forms an association with *Fossombronia angulosa* in the British Isles. Tomás Curtis, through Creative Commons.

Pericàs Mestre *et al.* (2010) described its habitat in temporary ponds of Menorca. They considered that this habitat favored colonization, establishment, and succession of plant groups that have water requirements that are higher than in other environments.

Blockeel (2017) reported *Fossombronia angulosa* (Figure 2-Figure 5) from earthy rock crevices. Whereas rock is a common substrate for this species, it also occurs on soil (Losada Lima & Beltrán Tejera 1987) and bark (Özenoğlu & Gökler 2002), although the bark was covered with soil. It appears that the limiting factor for substrate is its pH because all the records that mention acidic or basic refer to it as acidic.

Fossombronia angulosa (Figure 2-Figure 5) occurs on sandstone rocks in Turkey (Papp & Sabovljevic 2003), a substrate that is typically acidic due to high silica content. Mundo (1986) reported that *Fossombronia angulosa* is often found with *Epipterygium tozeri* (Figure 15) and *Anthoceros punctatus* (Figure 16) on acidic vertical substrata. It occurs on acidic substrata in Spain (Fuertes & Mendiola 1984; Jiménez *et al.* 1986; Casas *et al.* 1999), and Guerra (1982) described it as acidophilic in Spain, as did Papp *et al.* 1999 in Greece and Puglisi and Privitera (2009) in Italy. In the Ibérica Peninsula the pH where it grew was 5.9 (Gil Garcia & Castro 1987).



Figure 15. *Epipterygium tozeri*, a species that often occurs with *Fossombronia angulosa*. Photo by David T. Holyoak, with permission.

Fossombronia angulosa (Figure 2-Figure 5) is one of the few bryophytes with any salt tolerance (Smith 1990; Perold 1999). Rilstone (1949) reported it from near the sea in Cornwall. Blockeel (1991) found it on a sandy coastal bank. While these are not immersed in salt water, salt in the air can accumulate on the bryophytes. Hill *et al.* (2007) reported that it occurs in both saline and non-saline situations in the British Isles. Perhaps its greatest salt tolerance is shown in salt marshes, where it can be found frequently in early spring in Kansas, USA (Smyth & Smyth 1911).

In almost all of these habitats, *Fossombronia angulosa* (Figure 2-Figure 5) appears to be **sciaphilous** (shade-loving or shade tolerant) (du Mortier 1874; Armitage 1918; Guerra 1982; Jiménez *et al.* 1986; Losada Lima & Beltrán Tejera 1987; Puglisi & Privitera 2009; Blockeel 2012; Osman *et al.* 2019).



Figure 16. *Anthoceros punctatus*, a species that often occurs with *Fossombronia angulosa*. Photo from Proyecto Musgo through Creative Commons.

In surprising contrast, Preston *et al.* (2011) report the *Fossombronia angulosa*-*Phaeoceros laevis* (Figure 2-Figure 5; Figure 14) association from a "very well-illuminated" habitat in relatively dry places. These locations have higher January and July temperatures than those of any other species cluster, as well as experiencing relatively low annual precipitation. Some occur on waste by copper mines and in china-clay quarries.

Fossombronia angulosa (Figure 2-Figure 5) is rare in many countries. Pedrotti and Aleffi (2011) attributed its disappearance or threatened state to human activity and industrialization, especially exploitation of areas such as peatlands in the Alps.

Adaptations

Fossombronia angulosa has horizontal to patent leaves that are usually nearly plane (Figure 17) (Stotler *et al.* 2005). This form minimizes surface exposure and thus should contribute to reducing moisture loss.



Figure 17. *Fossombronia angulosa* growing horizontally. Photo by Jan-Peter Frahm, with permission.

Reproduction

Fossombronia angulosa (Figure 2-Figure 5) is a robust, **dioicous** plant (Stotler *et al.* 2005) with clearly visible antheridia (Figure 18). Reinoso (1985) reported that *Fossombronia angulosa* was a frequent species in parts of Galicia, where it formed extensive lawns that were fertile most of the times it was collected. It has been the subject of several studies related to its reproduction. Vian (1969, 1970) published observations on the evolution of intercellular substances during spermatogenesis. Bajon-Barbier (1997) made ultrastructural studies on the maturation of the egg cell.



Figure 18. *Fossombronia angulosa* with antheridia. Photo by Jan-Peter Frahm, with permission.

Showalter (1927) described cytology involved in fertilization. He gave detailed descriptions of the sexual organs and observed that sexual organs occurred in almost any season, but were most common in autumn and early winter. The egg is apparently viable for fertilization for "a considerable length of time." Following artificial insemination, several to 12 eggs were fertilized on a thallus. It required 6-9 days for the zygote to undergo its first division, following an increase in size. Sperm from the moss *Funaria hygrometrica* (Figure 19-Figure 20) were also able to penetrate the eggs, but these did not initiate development of an embryo. *Sphaerocarpus donnellii* (Figure 21) sperm were likewise able to penetrate and they were able to begin, but not complete, embryonic cell division. More than one *Fossombronia angulosa* (Figure 2-Figure 5) sperm can penetrate the same egg, but there is no evidence that more than one male nucleus ever penetrates the egg nucleus. Even in fully fertilized eggs, when multiple zygotes are formed on the same thallus, some of the zygotes do not undergo further development. Even so, 4-8 embryos may develop and become mature sporophytes (Figure 22-Figure 23) on one female thallus.



Figure 19. *Funaria hygrometrica*, a species whose sperm can penetrate the eggs of *Fossombronia angulosa*. Photo by Bob Klips, with permission.

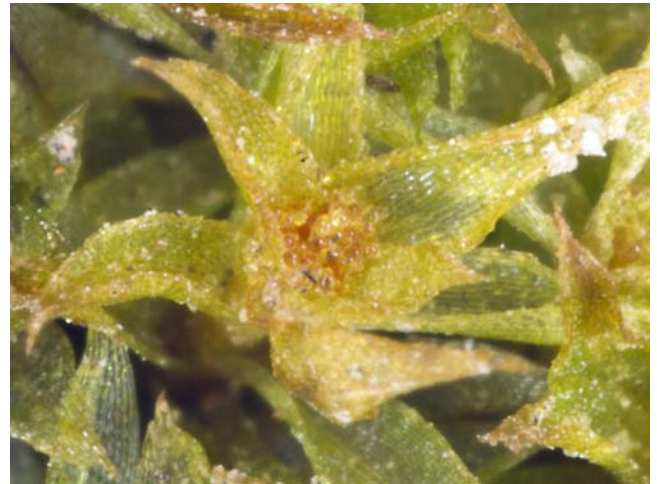


Figure 20. *Funaria hygrometrica* antheridia, source of sperm that can penetrate the eggs of *Fossombronia angulosa*. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 21. *Sphaerocarpus donnellii*, a species whose sperm can penetrate the eggs of *Fossombronia angulosa* and initiate embryo development. Photo by Belinda Lo through Creative Commons.



Figure 22. *Fossombronia angulosa* with capsule. Photo by Des Callaghan, with permission.

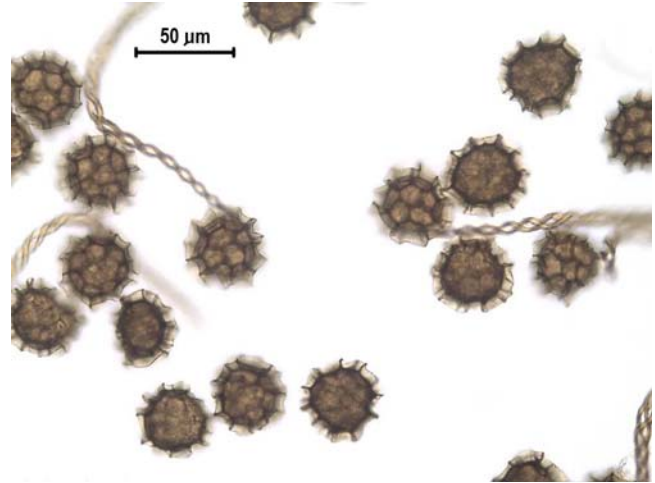


Figure 24. *Fossombronia angulosa* spores and elaters. Photo by Hugues Tinguy, with permission.



Figure 23. *Fossombronia angulosa* with capsules, some of which are dehiscent (brown). Photo by David T. Holyoak, with permission.

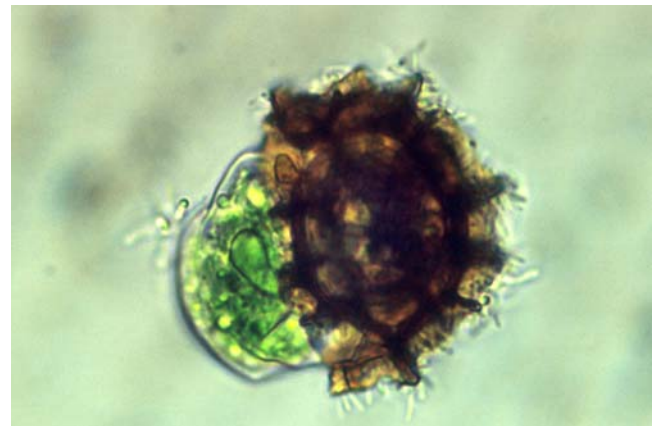


Figure 25. *Fossombronia angulosa* germinating spore. Photo from Plant Actions, with permission.

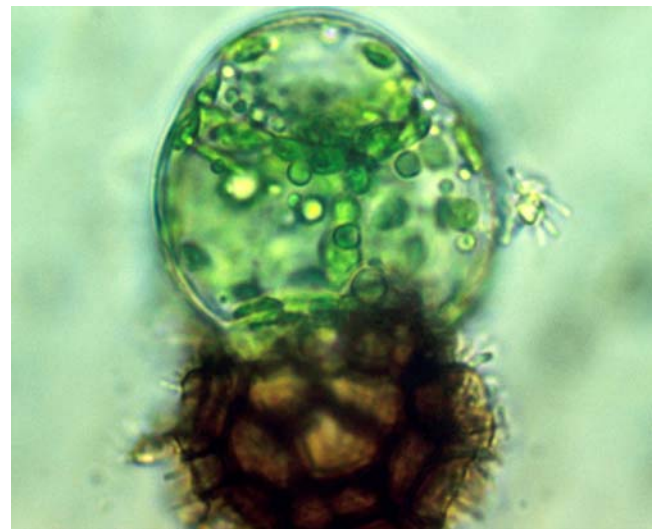


Figure 26. *Fossombronia angulosa* young protonema. Photo from Plant Actions, with permission.

Leforestier (1975) described the spores (Figure 24) of *Fossombronia angulosa* (Figure 2-Figure 5) under both light and scanning microscopy and later described the germ tube (Figure 25-Figure 26) (Leforestier 1979). Castaldo-Cobianchi and Giordano (1986) further described the spore wall morphology. Gambardella (1987) described the surface features in detail, based on both SEM and TEM microscopy. Spores are produced in spring (Schuster 1992). Chromosome numbers have been reported as $n = 9$ (Mehra 1938; Newton 1975).

Biochemistry

I have been unable to find any information on oil bodies in *Fossombronia angulosa*. Figure 27 suggests that they might be tiny and diffuse, difficult to detect.

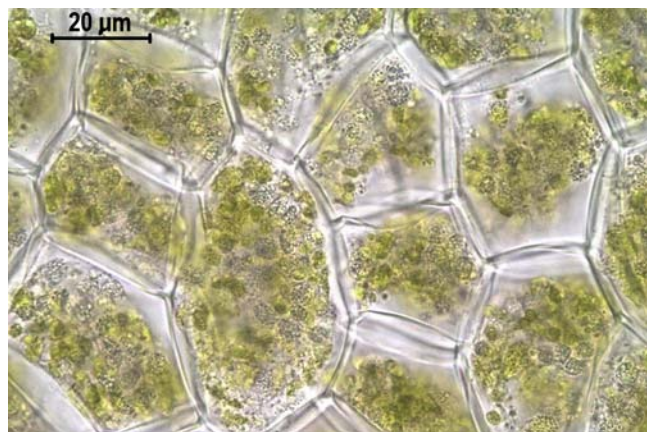


Figure 27. *Fossombronia angulosa* cells with what might be oil bodies. Photo by Hugues Tinguy, with permission.

Fossombronia angulosa (Figure 2-Figure 5) has been the subject of biochemical evolution. Based on the Greek populations studied, it has some of the same compounds [dictyotene, the main compound of the volatile fraction (14.1%), (Z)-multifidene, and dictyopterene] as that found in the brown algae (Ludwiczuk *et al.* 2008; Asakawa & Ludwiczuk 2017). Dictyotene is the major volatile compound (Asakawa & Ludwiczuk 2017). *Fossombronia angulosa* emits a seashore odor that is caused by dimethyl sulfide. Other identified compounds include biosynthesized cyathane-type diterpenoids, 2-tridecanone (13.0%), and β -sabinene (11.7%). Von Reuß (2009) found C11 hydrocarbons, dictyopterene A, ectocarpene, and dictyotene, compounds that are known as brown algal **pheromones** (chemical substances produced by organism and serves especially as stimulus to other individuals of the same species for one or more behavioral responses, often as attractants for opposite sex). Von Reuß also identified a new pentylbenzene.

Fossombronia australis (Figure 28-Figure 29)

Distribution

Fossombronia australis (Figure 28-Figure 29) occurs in Australia, New Zealand, and the sub-Antarctic Kerguelan and Prince Edward Islands (Crandall-Stotler & Gradstein 2017).



Figure 28. *Fossombronia australis*. Photo by Bruce Fuhrer, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.



Figure 29. *Fossombronia australis* showing purple rhizoids. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.

Aquatic and Wet Habitats

Fossombronia australis (Figure 28-Figure 29) occurs in low elevation wetlands in regions near the Antarctic (Crandall-Stotler & Gradstein 2017). Campbell (1988) considered its partial submersion to be sufficiently diagnostic to include the character in her key to Australian species. She reported it for wet, shady banks or as dense, partially submerged colonies in freshwater swamps and *Sphagnum* mires (Figure 30). Glenny (1995) reported it from a flush next to a stream in New Zealand.



Figure 30. *Sphagnum cristatum* mire in Australia. Photo by M. Fagg, ©ANBG (Australian National Botanic Gardens), <<http://www.anbg.gov.au/photo/image-collection.html>>, with online permission.

Carcaillet (1993) reported *Fossombronia australis* (Figure 28-Figure 29) with *Azorella selago* (Figure 31) in peat bogs of Crozet Island in the Southern Ocean. Vána and Gremmen (2005) found it on all parts of nearby Heard Island, often associated with *Azorella* or *Poa cookii* (Figure 32). The area was influenced by birds and seals that are possible dispersal agents. On the same island, Bergstrom and Selkirk (2000) found it on gravel at the edge of *Azorella selago* cushions or growing between branches of *A. selago*. Its rhizoids were anchored in a mixture of humic material typically consisting of abscised leaves and accumulated wind-blown sediment. At the margins of pools it grew with species of the moss *Brachythecium*

(Figure 10) in moist or wet areas. They considered *Fossombronia australis* to be a species of wide ecological amplitude.



Figure 31. Cushions of *Azorella selago* in the Kerguelen Islands, a flowering plant species that may have *Fossombronia angulosa* growing with it in peat bogs of Crozet Island in the Southern Ocean. Photo from Creative Commons.



Figure 32. *Poa cookii*, a grass species that may have *Fossombronia angulosa* growing with it in peat bogs of Crozet Island in the Southern Ocean. Photo M. Grun, through Creative Commons.

In the sub-Antarctic islands, Smith and Mucina (2006) found *Fossombronia australis* (Figure 28-Figure 29) among submerged and floating macrophytes in the lakes and tarns, as well as in fernbrakes.

Reproduction

Fossombronia australis (Figure 28-Figure 29) is **dioicous** (Campbell 1988), producing spherical antheridia on separate plants (Figure 33), perhaps explaining its lack of abundance despite being widespread within its distribution. Nevertheless, capsules are known (Figure 34), so dispersal by spores is possible (Figure 35).



Figure 33. *Fossombronia australis* antheridia. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.



Figure 34. *Fossombronia australis* capsule. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.

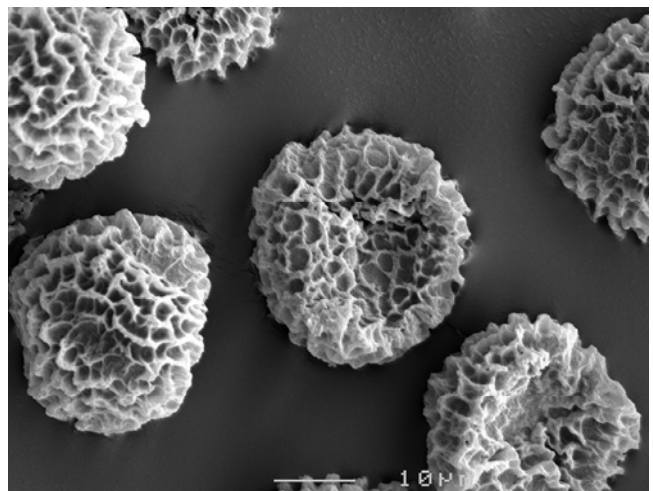


Figure 35. *Fossombronia australis* spores, SEM. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.

Role

For such a little known species, it is surprising to learn that Chown and Scholtz (1989) have documented that *Fossombronia australis* (Figure 28-Figure 29) is consumed by the curculionid beetles *Mesembriorrhinus brevis* and *Dusmoecetes marioni* on the sub-Antarctic Prince Edward Islands. Few records of herbivory by specific insects are available on liverworts.

Fossombronia caespitiformis subsp. *multispira* (Figure 37-Figure 39)

(syn. = *Fossombronia husnotii*)

Fossombronia caespitiformis (Figure 36-Figure 39) is highly variable. Stotler *et al.* (2005) considered it to comprise two subspecies: *F. caespitiformis* subsp. *caespitiformis* (Figure 36) and *F. caespitiformis* subsp. *multispira* (Figure 37-Figure 39). I have found records of the latter from wet habitats.



Figure 36. *Fossombronia caespitiformis*, a highly variable Mediterranean species. Photo by Des Callaghan, with permission.



Figure 37. *Fossombronia caespitiformis* subsp. *multispira* in Europe. Photo by Michael Lüth, with permission.



Figure 38. *Fossombronia caespitiformis* subsp. *multispira*. Photo by Jan-Peter Frahm, with permission.



Figure 39. *Fossombronia caespitiformis* subsp. *multispira*. Photo by Michael Lüth, with permission.

Distribution

Like so many of the liverworts, confusion in the taxonomy of *Fossombronia caespitiformis* subsp. *multispira* (Figure 37-Figure 39) (Lockhart *et al.* 2012) has made it difficult to describe the distribution of this variety (Pononessi *et al.* 2016). It is known from most of the Mediterranean countries as well as Madeira in the Canary Islands (González Mancebo *et al.* 2007; Ros *et al.* 2007), but is rare in Italy (Aleffi *et al.* 2008) and Critically Endangered there (Pononessi *et al.* 2016). Sérgio *et al.* (2011) recorded it from Portugal and Pericàs *et al.* (2016) as new from Minorca, Spain. Sotiaux *et al.* (2009) extended its known range to Belgium. It is also known from Ireland, but is listed as "data deficient" regarding its rarity (Kingston 2012). Blockeel (2020) verified its occurrence in Greece. But it is apparently even more widespread than indicated by these authors; Fischer (1993) reported it from Rwanda.

It is very rare in the cork oak forest of Morocco (El Harech *et al.* (2020) and on the Montseny Massif of the Iberian Peninsula (Sáez *et al.* 2018).

Aquatic and Wet Habitats

Although *Fossombronia caespitiformis* subsp. *multispira* (Figure 37-Figure 39) is quite rare in most of Italy, Pononessi *et al.* (2016) found it to be moderately abundant on water-logged soil (Figure 40-Figure 41) associated with temporary ponds in central Italy,

accompanied by *Isoetes hixrix* (a lycopod; Figure 42). Puglisi *et al.* (2015) similarly found it associated with temporary ponds in Italy. In fact, Poponessi *et al.* (2018) found it to be one of the two bryophyte communities in these habitats. It was the dominant species in one, accompanied by *Riccia sorocarpa* (Figure 43) on waterlogged, clayey-sandy soil in heathland clearings (Figure 44). Hugonnot and Simont (2018) found a similar habitat for *Fossombronia caespitiformis* subsp. *multispira* in temporarily wet lawns in Corse-du-Sud, France, a habitat where grazing contributes to its ecology. It is also known from rivers (Ferreira *et al.* 2008). Cogoni *et al.* (2016) described the species as hygro-xerophytic, noting its presence in temporary ponds, where it had a frequency greater than 30%.



Figure 40. *Fossombronia caespitiformis* on mud. Photo by Michael Lüth, with permission.



Figure 41. *Fossombronia caespitiformis* subsp. *multispira* on muddy soil in Europe. Photo by Michael Lüth, with permission.



Figure 42. *Isoetes hixrix*, a species that accompanies *Fossombronia caespitiformis* subsp. *multispira* in temporary ponds. Photo by Ralph Mangelsdorff, through Creative Commons.



Figure 43. *Riccia sorocarpa*, a species that accompanies *Fossombronia caespitiformis* subsp. *multispira* in temporary ponds. Photo by Hugues Tinguy, with permission.



Figure 44. Heathland, a habitat where one can find *Fossombronia caespitiformis* subsp. *multispira* in Italy. Photo from <mdpi.com>, through Creative Commons.

Substrata of *Fossombronia caespitiformis* subsp. *multispira* can include litter (Figure 45), as well as soil and rocky mixes. They also be a part of hummocks (Figure 46).



Figure 45. *Fossombronion caespitiformis* subsp. *multispira* on litter in Europe. Photo by Michael Lüth, with permission.



Figure 46. *Fossombronion caespitiformis* subsp. *multispira* in a hummock. Photo by Michael Lüth, with permission.

Sotiaux *et al.* (2009) found that *Fossombronion caespitiformis* subsp. *multispira* (Figure 37-Figure 39) is typical of intensive **arable** (describes land used or suitable for growing crops) fields (Figure 47). This habitat is often similar to that of temporary ponds, in particular requiring species with short life cycles.



Figure 47. *Fossombronion caespitiformis* subsp. *multispira* appearing as it could in arable fields. Photo by Michael Lüth, with permission.

Fossombronion caespitiformis subsp. *multispira* (Figure 37-Figure 39) is able to inhabit rocky areas (Figure 48). Blockeel (2012) reported it from schistose banks as well as thin soil in western Crete. Blockeel (2020) also found it on phyllite rocks on the sheltered gravelly track in a stream valley in Greece.



Figure 48. *Fossombronion caespitiformis* subsp. *multispira* on rocky bank. Photo by Michael Lüth, with permission.

As noted by Gabriel *et al.* (2011), approximately one-fourth of European bryophytes are under actual or potential threat. Gabriel and coworkers used geographical distribution, abundance, and habitat specificity to develop a list of such bryophytes in the Azores. *Fossombronion caespitiformis* subsp. *multispira* (Figure 37-Figure 39) is present in the Azores, where it grows in coastal wetlands (Gabriel *et al.* 2019), but its threat status was not listed by Gabriel *et al.* (2011), presumably due to insufficient data.

Adaptations

Cogoni *et al.* (2016) reported that *Fossombronion caespitiformis* subsp. *multispira* (Figure 37-Figure 39) is typically solitary and creeping. In the temporary ponds where it lives in parts of the Mediterranean, a **pauciennial/perennial** life strategy permits it to take advantage of the periods of adequate moisture (Puglisi *et al.* 2016). In the Mediterranean temporary ponds, it is a **short-lived shuttle** species. In that location, its sexual reproduction is abundant, but asexual reproduction is absent or rare. Despite its frequent sexual reproduction, its dispersal is short-range, most likely due to the large size of its spores, but assuring that most of the spores will fall on a suitable habitat. Furthermore, the somewhat large spores (32-35 μm) (Sotiaux *et al.* 2009) provide it with the resources to be more successful upon germination.

Fossombronion caespitiformis subsp. *multispira* (Figure 37-Figure 39) sometimes grows with other bryophytes (Figure 49), possibly benefitting from their presence to help in retaining moisture.

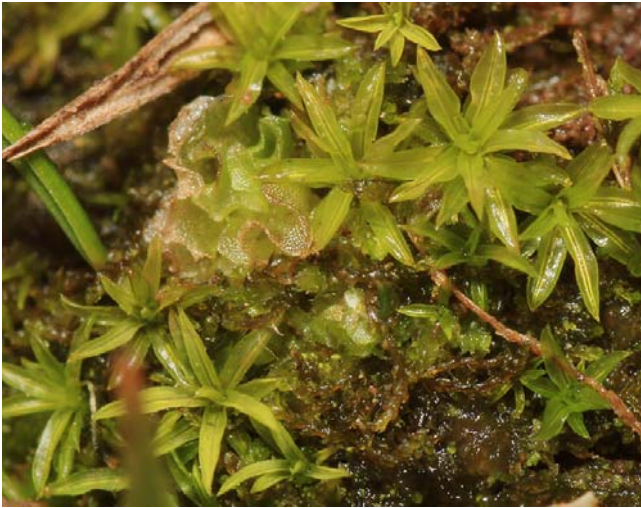


Figure 49. *Fossombronia caespitiformis* subsp. *multispira* growing with mosses. Photo by Barry Stewart, with permission.

Like many species of *Fossombronia*, *F. caespitiformis* subsp. *multispira* (Figure 37-Figure 39) has violet rhizoids (Figure 50). It would be interesting to follow the evolutionary pathway to this unusual character, perhaps permitting us to determine why they have persisted in the genus.



Figure 50. *Fossombronia caespitiformis* with violet rhizoids. Photo by Tom Thekathiyil, with permission.

Reproduction

Several authors (Mansion 1905; Puglisi *et al.* 2016) have noted that *Fossombronia caespitiformis* subsp. *multispira* (Figure 37-Figure 39) is abundantly fertile (Figure 51-Figure 60). Its spores (Figure 61) are relatively large (Sotiaux *et al.* 2009), partially compensating for the absence of specialized asexual reproduction by increasing the success of short-distance dispersal. The spores germinate to form a thalloid protonema (Figure 62).



Figure 51. *Fossombronia caespitiformis* developing sporophyte in archegonium. Photo by Tom Thekathiyil, with permission.



Figure 52. *Fossombronia caespitiformis* in habitat showing nearly mature capsules before seta elongation. Photo by Michael Lüth, with permission.



Figure 53. *Fossombronion caespitiformis* showing capsules mostly before seta elongation. Photo by Michael Lüth, with permission.



Figure 56. *Fossombronion caespitiformis* with capsules and elongated setae. Photo by Jonathan Sleath, BBS, with permission.



Figure 54. *Fossombronion caespitiformis* before seta elongation. Photo by Andras Keszei, with permission.



Figure 55. *Fossombronion caespitiformis* as setae begin to elongate. Photo by Jan-Peter Frahm, with permission.



Figure 57. *Fossombronion caespitiformis* capsules with elongated seta. Photo by Andras Keszei, with permission.



Figure 58. *Fossombronion caespitiformis* capsule showing surface. Photo by Andras Keszei, with permission.

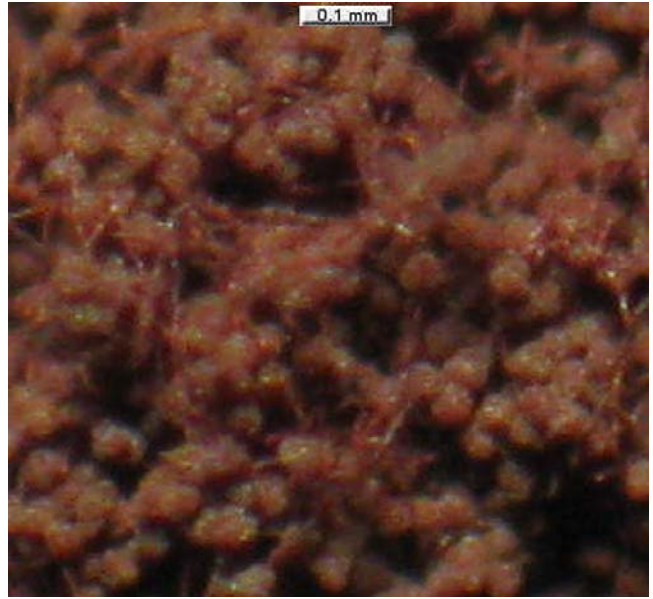


Figure 61. *Fossombronion caespitiformis* spores and elaters. Photo by Tom Thekathyl, with permission.



Figure 59. *Fossombronion caespitiformis* subsp. *multispira* with dehiscent capsules. Photo by Michael Lüth, with permission.

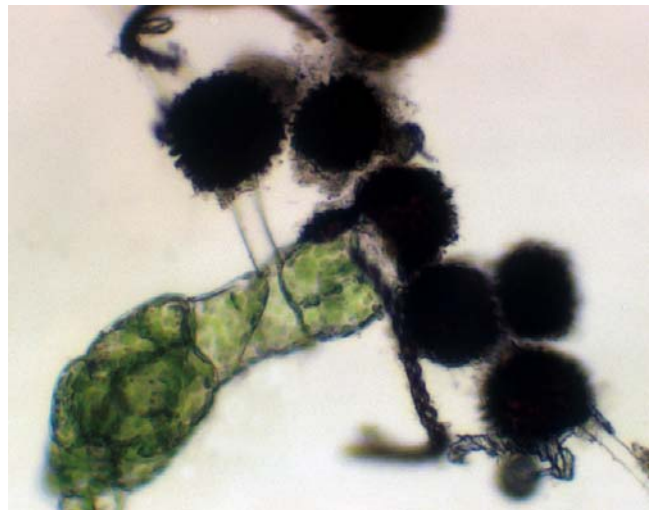


Figure 62. *Fossombronion caespitiformis* protonema. Photo from Plant Actions, with permission.



Figure 60. *Fossombronion caespitiformis* capsule opening, showing the irregular breakage of the capsule. Photo by Tom Thekathyl, with permission.

Fossombronion cristula (Figure 63-Figure 65)

Distribution

Fossombronion cristula (Figure 63-Figure 65) is endemic to the eastern United States and has been reported from Connecticut, Illinois, Indiana, Massachusetts, Maryland, Michigan, New Jersey, New York, North Carolina, Ohio, Tennessee, and West Virginia (Crandall-Stotler & Bray 2019).



Figure 63. *Fossombronia cristula*, an endemic species in eastern USA. Photo by Kochibi, through Creative Commons.



Figure 64. *Fossombronia cristula*. Photo by Kochibi, through Creative Commons.



Figure 65. *Fossombronia cristula*. Photo by Kochibi, through Creative Commons.

Aquatic and Wet Habitats

Fossombronia cristula (Figure 63-Figure 65) occurs on moist, denuded soils (Figure 66-Figure 68), often in disturbed habitats such as paths or ditches, and on lake or stream banks, typically at low to moderate elevations (Crandall-Stotler & Bray 2019).



Figure 66. *Fossombronia cristula* among graminoids. Photo by Kochibi, through Creative Commons.



Figure 67. *Fossombronia cristula* on disturbed soil. Photo by Kochibi, through Creative Commons.



Figure 68. *Fossombronion cristula* on disturbed soil. Photo by Kochibi, through Creative Commons.

Reproduction

Fossombronion cristula (Figure 63-Figure 65) is **monoicous** (Crandall-Stotler & Bray 2019). The antheridia (Figure 69-Figure 70) are intermixed with archegonia and develop simultaneously with them. The seta expands to about 3.4 mm and the capsule (Figure 71) "splits, expanding by depression" (Claassen 1904).



Figure 69. *Fossombronion cristula* with yellow antheridia. Photo by Kochibi, through Creative Commons.

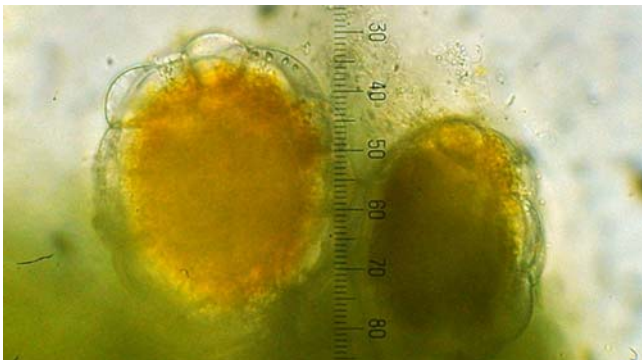


Figure 70. *Fossombronion cristula* antheridia. Photo by Kochibi, through Creative Commons.

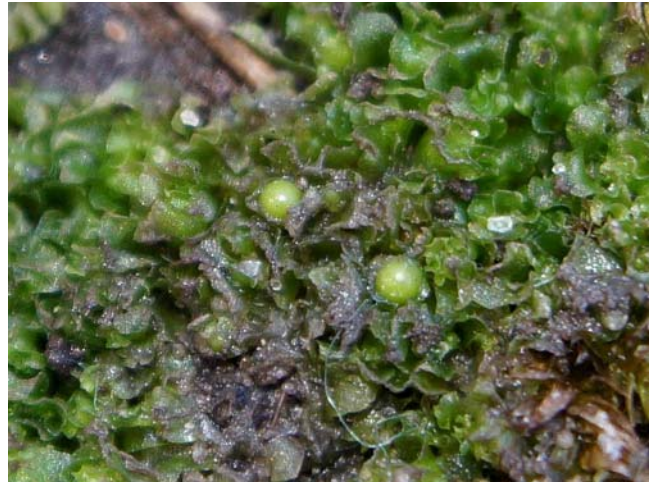


Figure 71. *Fossombronion cristula* with developing capsules before seta elongation. Photo by John Bunch, through Creative Commons.

Spores (Figure 72) have a wide size range, tending on the large size (36-50 μm). Renzaglia and Bartholomew (1985) described sporeling development and its implications for phylogenetic relationships.



Figure 72. *Fossombronion cristula* spores. Photo by Tom Wiebolt, through Creative Commons.

Biochemistry

It appears that oil bodies have not been found in many species of *Fossombronion*. Based on Figure 73, there appear to be small oil bodies in the cells of *Fossombronion cristula* (Figure 63-Figure 65).



Figure 73. *Fossombronia cristula* leaf cells, showing oil bodies. Photo by Kochibi, through Creative Commons.



Figure 75. *Fossombronia delgadilloana* male with young antheridia. Photo by Barbara Crandall-Stotler, modified, with permission.

Aquatic and Wet Habitats

Fossombronia delgadilloana occurs submerged in high elevation mires of Latin America (Figure 76-Figure 78) (Crandall-Stotler *et al.* 2019). In Ecuador, it occurs in partly burned *Polylepis* forest, in streaming water, deeply shaded, at 3750 m (Gradstein 2021).

Fossombronia delgadilloana (Figure 74-Figure 75)

Distribution

Fossombronia delgadilloana (Figure 74-Figure 75) is a recent species known only from the Latin American area – Mexico, high Andes of Venezuela, and Ecuador (Crandall-Stotler *et al.* 2019; Gradstein 2021).



Figure 74. *Fossombronia delgadilloana*, a species of high elevations in Mexico, Venezuela, and Ecuador. Photo by Barbara Crandall-Stotler, with permission.



Figure 76. *Fossombronia delgadilloana* general habitat. Photo by Barbara Crandall-Stotler, with permission.



Figure 77. *Fossombronia delgadilloana* habitat. Photo by Barbara Crandall-Stotler, with permission.



Figure 78. *Fossombronia delgadilloana* habitat at high elevation in Andes. Photo by Barbara Crandall-Stotler, with permission.

Reproduction

Fossombronia delgadilloana (Figure 74-Figure 75) has "widely dispersed antheridia" (Figure 79-Figure 80) (Crandall-Stotler *et al.* 2019). Capsules are known (Figure 81); spores are $> 40 \mu\text{m}$ in diameter (Figure 82-Figure 83).

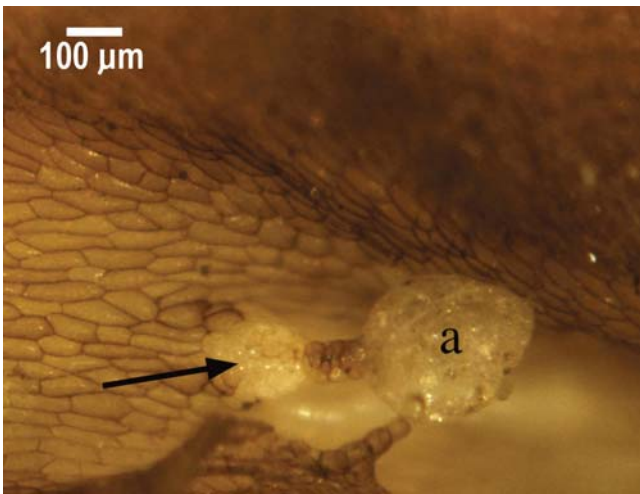


Figure 79. *Fossombronia delgadilloana* with young antheridia. Photo by Barbara Crandall-Stotler, modified, with permission.

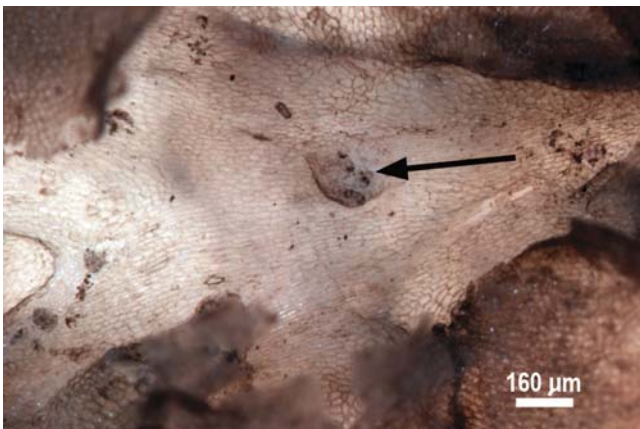


Figure 80. *Fossombronia delgadilloana* with dehiscent antheridia (at arrow). Photo by Barbara Crandall-Stotler, modified, with permission.



Figure 81. *Fossombronia delgadilloana* with sporophyte, arrow at foot. Photo by Barbara Crandall-Stotler, modified, with permission.

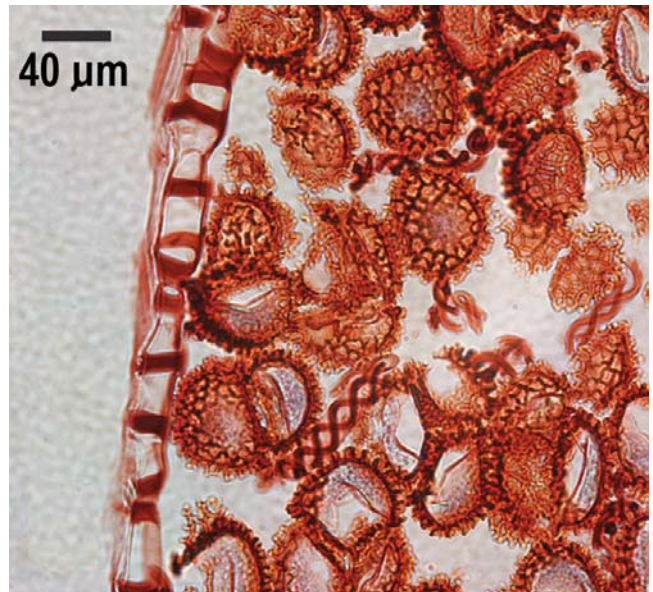


Figure 82. *Fossombronia delgadilloana* capsule and spores. Photo by Barbara Crandall-Stotler, with permission.

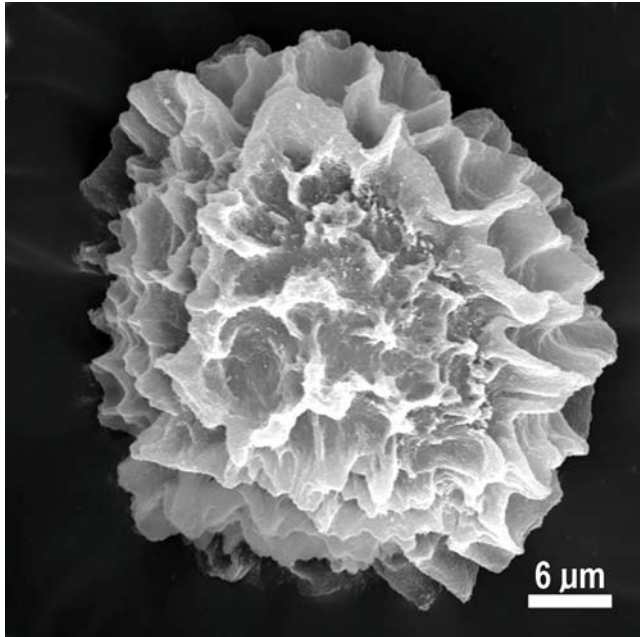


Figure 83. *Fossombronia delgadilloana* spore SEM. Photo by Barbara Crandall-Stotler, modified, with permission.

Biochemistry

Fossombronia delgadilloana has small (15-20 μm diameter) oil bodies (Figure 84). We can expect these to have secondary compounds that help to protect the plant from pathogens or herbivory, but no studies have been done on them.

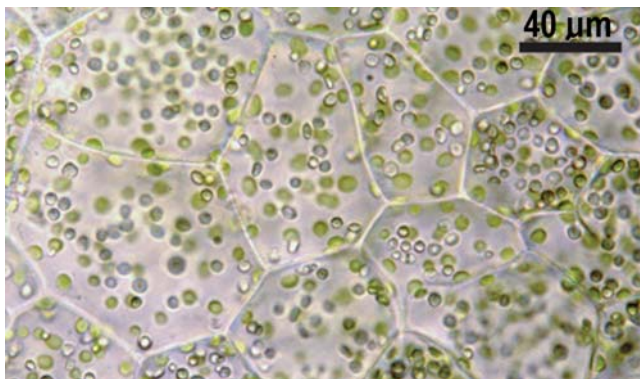


Figure 84. *Fossombronia delgadilloana* leaf cells showing small oil bodies and scattered chloroplasts. Photo by Barbara Crandall-Stotler, modified, with permission.

Fossombronia foveolata (Figure 85-Figure 90)

Fossombronia foveolata (Figure 85-Figure 90) has been variously considered and is perhaps best treated as a complex. Among the names I have encountered in aquatic and wet habitat studies, I here include *Fossombronia salina*, a species that recent authors have placed in *F. foveolata* (Scott & Pike 1987). Species determination is often complicated by the absence of one or the other sexual organs in monoicous plants, causing some researchers to treat them dioicous and therefore not belonging to *F. foveolata*.



Figure 85. *Fossombronia foveolata*, a Holarctic species. Photo by Des Callaghan, with permission.



Figure 86. *Fossombronia foveolata* habit. Photo by Kristian Peters, with permission.



Figure 87. *Fossombronia foveolata*. Photo by Jouko Rikkinen, through Creative Commons.



Figure 88. *Fossombronionia foveolata*. Photo by Jouko Rikkinen, through Creative Commons.



Figure 89. *Fossombronionia foveolata* forming a dense turf. Photo by Jouko Rikkinen, through Creative Commons.



Figure 90. *Fossombronionia foveolata*. Photo by Dick Haaksma, with permission.

Distribution

Schuster (1992) describes *Fossombronionia foveolata* (Figure 85-Figure 90) as widespread temperate and cooler

Holarctic in Europe and North America, but apparently absent from Asia, a content that is included in later reports. It is often a pioneer on bare soil, but also occurs on sandy or rocky margins of lakes and occasionally in bogs.

ITIS (2021) lists its distribution as Africa, Caribbean, Europe, Northern Asia, North America, Central America, and South America. Müller (2000) reported it from the East African Islands of Réunion and Mauritius.

Konstantinova (2000) considered *Fossombronionia foveolata* (Figure 85-Figure 90) to be a North Holarctic liverwort. In Asia, it is known from Russia (Dulin 2015). In Europe, it is known from Estonia (rare) (Ingerpuu *et al.* 2014; Vellak *et al.* 2015), Romania (Ștefănuț & Maria 2018), Poland (vulnerable) (Staniaszek-Kik 2014; Klama & Górski 2018), and the British Isles (Smith 1978).

In North America it extends from Alaska southward to Mexico and the Caribbean islands. Evans (1916) reported *Fossombronionia foveolata* (Figure 85-Figure 90) from Quebec, Canada. Crandall-Stotler and Bray (2019) added British Columbia, Newfoundland, Nova Scotia, and Ontario to its Canadian locations. Andrew (1931) reported it from New York, Sharp (1939) from Tennessee, and Miller (1964) found reports from Indiana, Michigan, New York, West Virginia, and Ohio in the USA. Spencer (1993) added Maine and Wheeler *et al.* (1983) added Minnesota. Crandall-Stotler and Bray (2019) added Arkansas, Connecticut, Delaware, Illinois, Kentucky, Louisiana, Maryland, Massachusetts, Mississippi, Missouri, New Hampshire, New Jersey, North Carolina, Oklahoma, Oregon, Pennsylvania, Rhode Island, South Carolina, Texas, Vermont, Washington, and Wisconsin, attesting to its widespread distribution. Yet, some states imbedded among these are missing, suggesting a lack of collecting in places like Pennsylvania.

In addition to North America, it is known from Europe and from the African locations of Azores, Madagascar, Morocco, South Africa, Tanzania, and Zaïre (Crandall-Stotler & Bray 2019).

Aquatic and Wet Habitats

Nichols (1918) reported *Fossombronionia foveolata* (Figure 85-Figure 90) from rocks (Figure 91) on ravine streambanks (Figure 92), Cape Breton Island, Canada. Cain and Fulford (1948) similarly found it along river banks, but also on wet soil along lake shores in Ontario. Steere (1934) found it on the clay shore of Carp Lake in Michigan, USA. McFarlin (1940) found it in a low hammock along a creek in Florida. In Kentucky, USA, Norris (1967) found it on a grassy stream bank. Blomquist (1936) reported it from bare clayey soils in forests, stream edges, springs, and ponds. Andreas and Moosbrugger (2021) found it on moist clay soil in Ohio. Saadi *et al.* (2020) reported it from both aquatic and sub-aquatic soil in Morocco, occurring in the ravine of a river and from shady siliceous soil, and as in most places, it is very rare. Simons and Jansen (2018) found it in oligotrophic ponds in The Netherlands. Bosanquet *et al.* (2018) reported it from reservoirs, lakes, ponds, and lowland heath (Figure 44) in the British Isles.



Figure 91. *Fossombronia foveolata* on rock of a stream bank. Photo by Jouko Rikkinen, through Creative Commons.

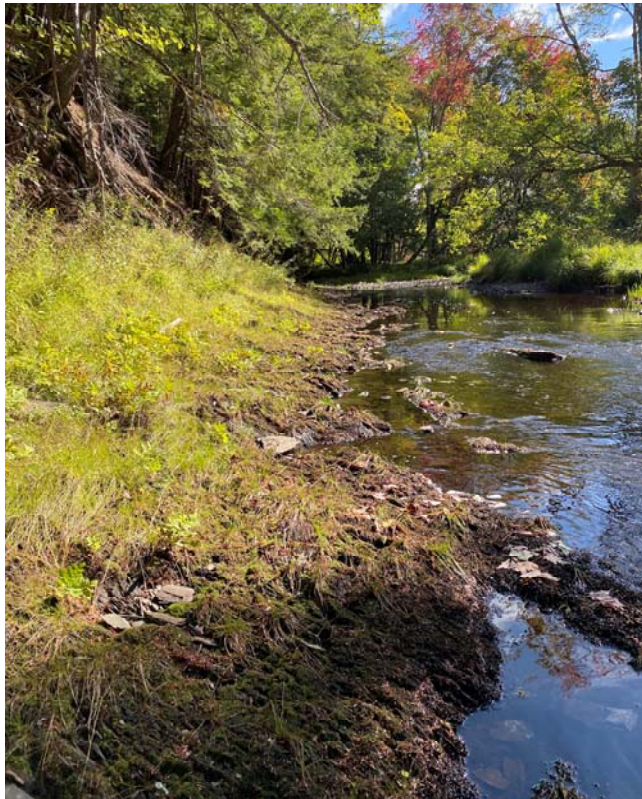


Figure 92. *Fossombronia foveolata* habitat on a stream bank. Photo by Tom Neily, through Creative Commons.

Jacobs (1949) reported *Fossombronia foveolata* (Figure 85-Figure 90) from seasonally moist clay in locations that become periodically dry. Similarly, it is a species that finds the margins of ponds (Figure 93) to be a suitable habitat (Maine, USA – Taylor 1921; New York – Burnham 1929; Dorset – Aquilina 2010; France – Bardet & Douchin 2017). In such habitats, the liverworts can be immersed in winter, abruptly being exposed out of water again in the spring (Bardet & Douchin 2017). Such exposure also occurred at Sindor Lake in Russia (Dulin 2015) and at the wet edge of Aughnagurgan Lough in Ireland (Fitzgerald & Fitzgerald 1967). Rikkinen (1992) noted its presence on peat (Figure 94), mineral soil, and well-decayed wood on the periodically flooded margins of ponds in Finland.



Figure 93. *Fossombronia foveolata* on a pond margin. Photo by Dick Haaksma, with permission.



Figure 94. *Fossombronia foveolata* with *Sphagnum*. Photo by Jouko Rikkinen, through Creative Commons.

Sharp (1939) described the habitat of *Fossombronia foveolata* (Figure 85-Figure 90) in Tennessee, USA, as moist open soil (Figure 95), where it was uncommon. Barringer (2011) noted that it prefers clay soils, occurring on exposed clay (Figure 96) and moist sand in New Jersey. Sabovljevic *et al.* (2010) reported it from mud in southeastern Europe. Preston *et al.* (2011) characterized it as preferring damp, acidic (see also Crandall-Stotler & Bray 2019) habitats as a pioneer in the British Isles. Its range of habitats also includes open, sloping sandstone among scrub oaks and very thin sandy soil mixed with woody debris (Wittlake 1954). It also seems able to inhabit ditches, as seen in Figure 97 by Kobichi.

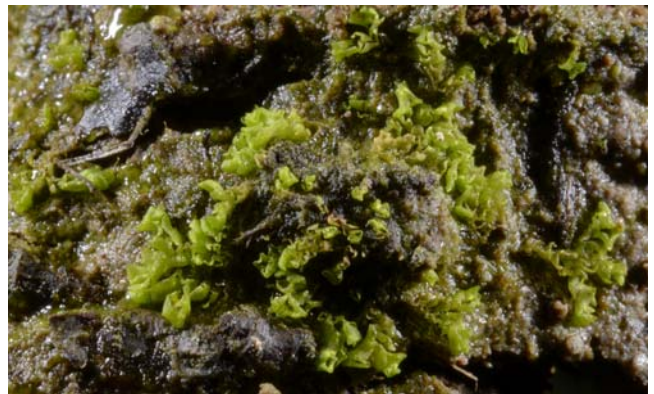


Figure 95. *Fossombronia foveolata* on moist soil. Photo by Jouko Rikkinen, through Creative Commons.



Figure 96. *Fossombronia foveolata* on open clay soil. Photo by Dick Haaksma, with permission.



Figure 97. *Fossombronia foveolata* habitat along ditch. Photo by Kochibi, through Creative Commons.

Its habitats include swamps, fens, and bogs. Ingerpuu *et al.* (2014) considered *Fossombronia foveolata* (Figure 85-Figure 90) to be a vulnerable species occurring rarely in Estonian fens. Staniaszek-Kik (2014) reported it from peat bogs and swamp forest depressions. In Minnesota, USA, it occurs in the Red Lake Peatland (Wheeler *et al.* 1983). Bradáčová *et al.* (2015) reported it from peaty and sandy soil along water-filled depressions in rich fens of Bohemia, as well as on bare soil of a wet, shaded path. In a somewhat similar habitat, Paton (1974) reported it from a dried out wet hollow on heath (Figure 44) in the British Isles. In Lithuania, *Fossombronia foveolata* occurred on bare peat in a swampy black alder forest (Jukonienė *et al.* 2013). In another seasonally wet habitat it occurs on the edges of snowbanks in the tundra of Alaska (Hermann 1973).

Fossombronia foveolata (Figure 85-Figure 90) also occurs in grasslands in the western Ghats of India (Manju & Rajesh 2009). Its occurrence in grassy cemeteries in the Interior Highlands of Arkansas might ensure that it is wet at times, perhaps seasonally, but we have no indication of that (Kyzer & Marsh 1999).

As noted earlier, *Fossombronia salina* may be a synonym of *Fossombronia foveolata* (Figure 85-Figure 90). This variant is known from saline situations, but it has also been collected from a swamp in Connecticut, USA (Evans 1901). Nevertheless, that location was less than 1 km from salt water.

Adaptations

Fossombronia foveolata (Figure 85-Figure 90) forms small patches (Figure 98-Figure 102) or tight **mats** (Figure 103-Figure 104), the latter helping to conserve water during dry periods (Crandall-Stotler & Bray 2019). This helps to extend the growing season long enough for reproduction.



Figure 98. *Fossombronia foveolata* patches on mud. Photo by Dick Haaksma, with permission.



Figure 99. *Fossombronia foveolata* patch on mud. Photo by Dick Haaksma, with permission.



Figure 100. *Fossombronia foveolata* in patches on mud. Photo by Dick Haaksma, with permission.



Figure 101. *Fossombronia foveolata* patches on mud. Photo by Dick Haaksma, with permission.



Figure 102. *Fossombronia foveolata* in patches on mud. Photo by Dick Haaksma, with permission.



Figure 103. *Fossombronia foveolata* forming a tight mat. Photo by Jouko Rikkinen, through Creative Commons.



Figure 104. *Fossombronia foveolata* dense turf. Photo by Jan-Peter Frahm, with permission.

Fossombronia foveolata (Figure 85-Figure 90) is pure green, but cell walls rarely become brown in the sun (Figure 105) (Schuster 1992). On the other hand, Evans (1901) observed that *Fossombronia salina*, considered by most to be synonymous with *F. foveolata*, is dark green, becoming paler or brownish with age. The *Fossombronia foveolata* thallus is flat to strongly wavy, with purple rhizoids (Figure 106). This raises the question of the role of habitat in determining the degree of waviness – and the rhizoid coloration.



Figure 105. *Fossombronia foveolata* that is green, but older parts have become brown. Photo by Jouko Rikkinen, through Creative Commons.



Figure 106. *Fossombronia foveolata* with purple rhizoids. Photo by Paul Davison, with permission.

Wood (2007) found that *Fossombronia foveolata* (Figure 85-Figure 90) is desiccation tolerant (Figure 107) down to 30% relative humidity. In Central Europe, it occurs in moderately low nutrient sites, with an Ellenberg (see Hill *et al.* 2007) nitrogen value of 3 (Simmel *et al.* (2021).



Figure 107. *Fossombronia foveolata* in dry state. Photo by Tim Faasen, with permission.

Reproduction

Fossombronia foveolata (Figure 85-Figure 90) is an annual (Schuster 1992). It is **monoicous** [**paroicous** or **synoicous** (Scott & Pike 1987; Crandall-Stotler & Bray 2019)], usually producing predominantly archegonia with few antheridia (Figure 108-Figure 109) intermixed, but mostly spatially separated. Bray (1997) explored the life history and reproduction of *F. foveolata* for his doctoral dissertation. The species is **protandrous** (antheridia produced before archegonia) (Crandall-Stotler & Bray 2019). Sporophytes (Figure 110-Figure 117) are produced in summer and fall (Schuster 1992).



Figure 108. *Fossombronia foveolata* with a few yellow antheridia. Photo by J. C. Schou, with permission.



Figure 109. *Fossombronia foveolata* with yellow antheridia. Photo by J. C. Schou, with permission.



Figure 110. *Fossombronia foveolata* with young capsules. Photo by Kochibi, through Creative Commons.



Figure 111. *Fossombronia foveolata* young capsule. Photo by J. C. Schou, with permission.



Figure 112. *Fossombronia foveolata* with young capsule. Photo by Manju Nair, through Creative Commons.



Figure 113. *Fossombronia foveolata* with capsule as seta begins to elongate. Photo by Hugues Tinguy, with permission.



Figure 114. *Fossombronia foveolata* with capsule with an elongating seta. Photo by Bob Klips, with permission.



Figure 115. *Fossombronia foveolata* with developing capsules among a few mature ones. Photo by J. C. Schou, with permission.

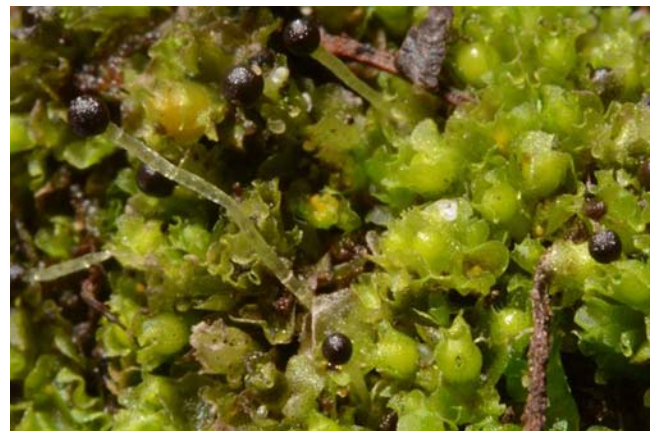


Figure 116. *Fossombronia foveolata* with elongated setae and mature capsules. Photo by J. C. Schou, with permission.



Figure 117. *Fossombronia foveolata* with maturing, mature, and dehiscing capsules. Photo by J. C. Schou, with permission

Evans (1901) found that the unusual *Fossombronia salina*, which is currently considered a likely form or variety of *Fossombronia foveolata* (Figure 85-Figure 90), had not yet produced mature sporophytes in late summer or early autumn in New Jersey, USA. On the other hand, numerous, somewhat immature, capsules were present in late May in a more northern coastal swamp population in Connecticut, USA. As further testament to the variability in sporophyte production, Suragina *et al.* (2002) reported

that few of the plants they found in the Volgograd Province in Russia had sporophytes with mature spores.

Scott and Crandall-Stotler (2002) demonstrated a high degree of homozygosity in the sporophytes of *Fossombronia*. Within *Fossombronia foveolata* (Figure 85-Figure 90) in southern Illinois, the genetic differentiation exhibited low levels. This resulted in little polymorphism among the southern Illinois populations. The species furthermore exhibited short-distance sperm and spore dispersal, indicating that the populations there were probably the result of a single founder population that has spread through inbreeding and vegetative propagation.

Spores (Figure 118-Figure 120) of *Fossombronia foveolata* (Figure 85-Figure 90) are brown to dark brown, and relatively large (38-54 μm) (Crandall-Stotler & Bray 2019).



Figure 118. *Fossombronia foveolata* spores and elaters. Photo by David T. Holyoak, with permission.



Figure 119. *Fossombronia foveolata* spores and elater. Photo by Hugues Tinguy, with permission.



Figure 120. *Fossombronia foveolata* SEM of spore. Photo by Barbara Crandall-Stotler, with permission.

Thomas *et al.* (1979) explored the sporophyte (Figure 110-Figure 117) nutrition in *Fossombronia foveolata* (Figure 85-Figure 90). They found that the sporophyte (separated from the gametophyte) was capable of fixing CO_2 . In fact, the ratio of the ability to fix CO_2 per mg fresh weight ranged 0.13 to 0.39 in the five liverworts tested.

Fungal Interactions

Hoysted *et al.* (2019) reported that **Mucoromycotina** fungi colonized the gametophytes of *Fossombronia foveolata* (Figure 85-Figure 90). Field and Pressel (2018) reported that this liverwort has both **Glomeromycota** and **Mucoromycota** fungi (Figure 121). Rimington *et al.* (2018) determined at least some of these to be arbuscular mycorrhizal fungi.

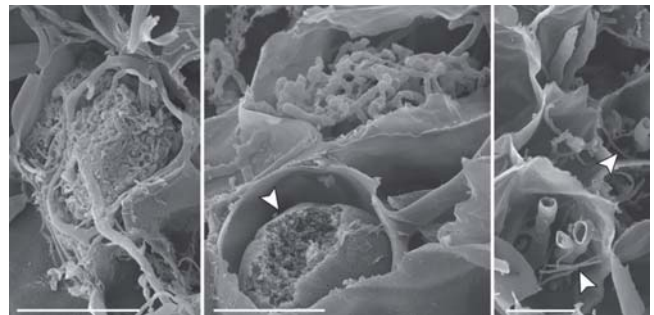


Figure 121. *Fossombronia foveolata* with **Mucoromycotina** and **Glomeromycotina**. Photo by Katie Field and Silvia Pressel, with permission.

Biochemistry

Fossombronia foveolata (Figure 85-Figure 90) typically has 6-9 oil bodies (Figure 122) per cell (Schuster 1992).

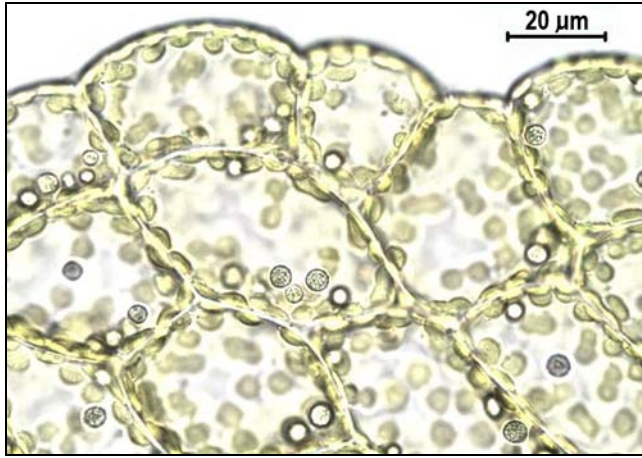


Figure 122. *Fossombronia foveolata* leaf cells and what appear to be oil bodies. Photo by Hugues Tinguy, with permission.

Basile and Basile (1987) demonstrated the presence of arabinogalactan-proteins (AGP's) in bryophytes, including *Fossombronia foveolata* (Figure 85-Figure 90) (see also Classen *et al.* 2019). These occur in the extracellular matrix of plants and are a class of hydroxyproline-containing glycoproteins. They suggested that AGP's are widespread in bryophytes. Their components and description help us understand the evolution of the plant cell wall.

Fossombronia foveolata (Figure 85-Figure 90) also is among the bryophytes for which the mitochondrial genome has been sequenced (Myszczyński *et al.* 2019).

***Fossombronia incurva* (Figure 123-Figure 124)**

Distribution

Fossombronia incurva (Figure 123-Figure 124) occurs at low to moderate elevations in Oregon, USA, and in northwestern Europe (Britain, Ireland, Poland, Finland, Sweden) (Crandall-Stotler & Bray 2019). Despite its somewhat wide distribution, it is a rare species.



Figure 123. *Fossombronia incurva*, a species with mostly northwestern European distribution. Photo by Dick Haaksma, with permission.



Figure 124. *Fossombronia incurva* growing in small clumps. Photo by Dick Haaksma, with permission.

Aquatic and Wet Habitats

Fossombronia incurva (Figure 123-Figure 124) occurs on moist sandy or gravelly soils, often along streams, lakes (Figure 125), or in dune slacks (Crandall-Stotler & Bray 2019). On a stream terrace along Sutton Creek in Oregon, USA, the species was growing with the also rare *Haplomitrium hookeri* (Figure 126), forming a community of mixed liverworts and hornworts.



Figure 125. *Fossombronia incurva* habitat. Photo by Barry Stewart, with permission.



Figure 126. *Haplomitrium hookeri*, a leafy liverwort that sometimes grows with *Fossombronia incurva* in Oregon, USA. Photo by Des Callaghan, with permission.

Adaptations

Fossombronia incurva (Figure 123-Figure 124) can grow isolated or in small **tufts** (Figure 124) (Crandall-Stotler & Bray 2019). In some cases, it is surrounded by other bryophytes (Figure 127) that could help it to retain moisture. We need experimentation to see how these forms survive in their moist habitats, especially when they experience dry seasons.



Figure 127. *Fossombronia incurva* growing with other bryophytes. Photo by Barry Stewart, with permission.

Reproduction

Fossombronia incurva (Figure 123-Figure 124) is **dioicous**, with male plants smaller than females (Crandall-Stotler & Bray 2019). The antheridia are clustered near the shoot apices (Figure 128-Figure 129), protected in dorsal leaf axils. Capsules are black at maturity, with variable shape (obovoidal, ellipsoidal, to spheroidal) (Figure 130-Figure 132). Their dehiscence is irregular fracturing (Figure 133). The spores (Figure 134) are 20-24(-28) μm . These smaller spores, nevertheless, might limit their dispersal because they often remain in tetrads (Figure 134), thus being larger and dispersed shorter distances. This bet-hedging strategy should permit some (single) spores (Figure 135) to disperse long distances, while keeping others (tetrads) close to home in a known suitable habitat.



Figure 128. *Fossombronia incurva* males with yellow antheridia. Photo by David T. Holyoak, with permission.

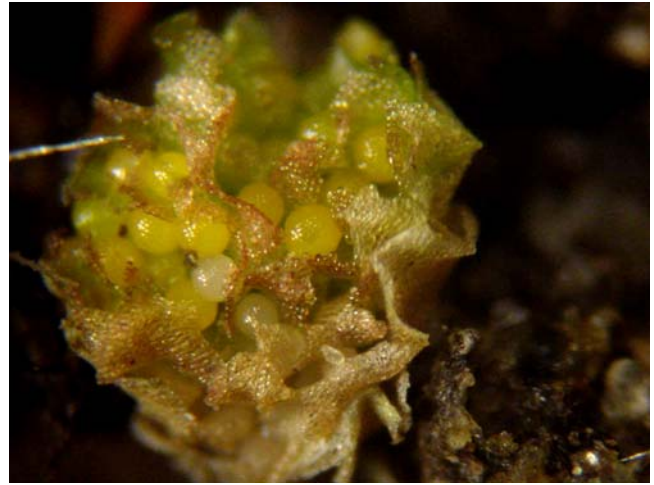


Figure 129. *Fossombronia incurva* with antheridia. Photo by Dick Haaksma, with permission.



Figure 130. *Fossombronia incurva* female plants with immature capsules. Photo by Dick Haaksma, with permission.



Figure 131. *Fossombronia incurva* with immature capsules. Photo by Dick Haaksma, with permission.



Figure 132. *Fossombronia incurva* with capsules and elongated setae. Photo by David T. Holyoak, with permission.



Figure 133. *Fossombronia incurva* dehiscing sporangium. Photo courtesy of David H. Wagner.

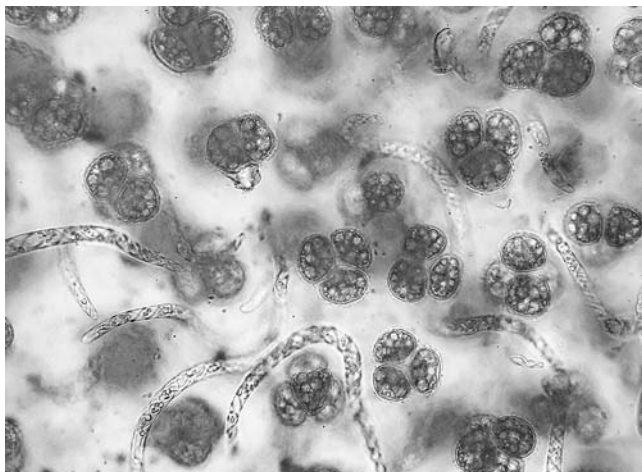


Figure 134. *Fossombronia incurva* spore tetrads and elaters. Photo by Barry Stewart, with permission.

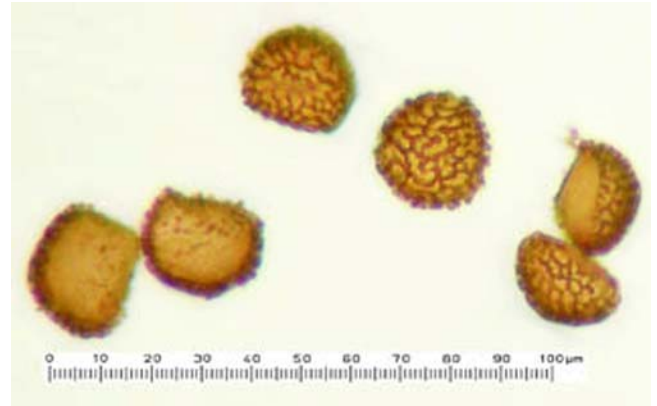


Figure 135. *Fossombronia incurva* spores. Photo courtesy of David H. Wagner.

Fossombronia incurva (Figure 123-Figure 124) apparently has no gemmae, and no other asexual structures seem to have been described, but it has a persistent, subterranean rhizome that can contribute to local spreading (Crandall-Stotler & Bray 2019).

Fossombronia isaloensis (Figure 136-Figure 138)

Distribution

Fossombronia isaloensis (Figure 136-Figure 138) is thus far endemic to Madagascar (Cargill *et al.* 2020).



Figure 136. *Fossombronia isaloensis*. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.



Figure 137. *Fossombronia isaloensis* in dry condition. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.



Figure 138. *Fossombronia isaloensis* showing "maroon" margins. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.

Aquatic and Wet Habitats

Fossombronia isaloensis (Figure 136-Figure 138) occurs at 1010 m asl, on damp, soft, acidic sandstone beside a small stream (Figure 139-Figure 141) that is shaded by dry native scrub, growing with the tiny liverwort *Cephaloziella* (Figure 142) (Cargill *et al.* 2020).



Figure 139. Massif where *Fossombronia isaloensis* type specimen was found. Photo by Des Callaghan, with permission.



Figure 140. Base of canyon habitat where *Fossombronia isaloensis* type specimen was found. Photo by Des Callaghan, with permission.



Figure 141. *Fossombronia isaloensis* at base of canyon where type specimen was found. Photo by Des Callaghan, with permission.



Figure 142. *Cephaloziella*; a member of this genus can grow with *Fossombronia isaloensis*. Photo by Ken-Ichi Ueda, through Creative Commons.



Figure 144. *Sphagnum magellanicum* showing green color as seen in shade or immediately after snowmelt. Photo by Blanka Agüero, with permission.

Adaptations

Like many other *Fossombronia* species, *Fossombronia isaloensis* (Figure 136-Figure 138) has dark red-purple rhizoids (Cargill *et al.* 2020) – a character that is unusual in bryophytes (but not in *Fossombronia*), but perhaps not adaptive. The margins of leaves and ventral surfaces of stems are maroon (Figure 138) (Cargill *et al.* 2020), but the color can extend into depths of the lobes, a character suggesting too much light, as seen on house plants that are placed outside on a sunny day after a winter indoors. This is seen in such species as *Sphagnum magellanicum* (Figure 143-Figure 144) that are red (Figure 143) in the sun but green (Figure 144) in the shade. The most intense purplish red coloring occurs when the sun is bright but the temperature is cold.



Figure 143. *Sphagnum magellanicum* showing red color that is especially intense when it is cold and sunny. Photo by Michael Lüth, with permission/

Reproduction

Fossombronia isaloensis (Figure 136-Figure 138) is **dioicous** (Figure 145-Figure 146) (Cargill *et al.* 2020), but at least produces some sporophytes (Figure 147). These are non-emergent or emergent on short setae. The spores (Figure 148-Figure 149) are medium to large [(37.5– 57.5 μm); Figure 148-Figure 149]. It does, however, produce tubers, formed as geotropic swollen apices.

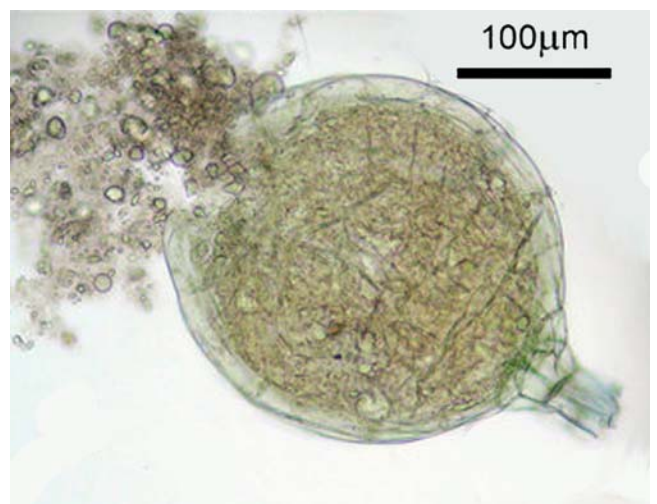


Figure 145. *Fossombronia isaloensis* antheridium. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.

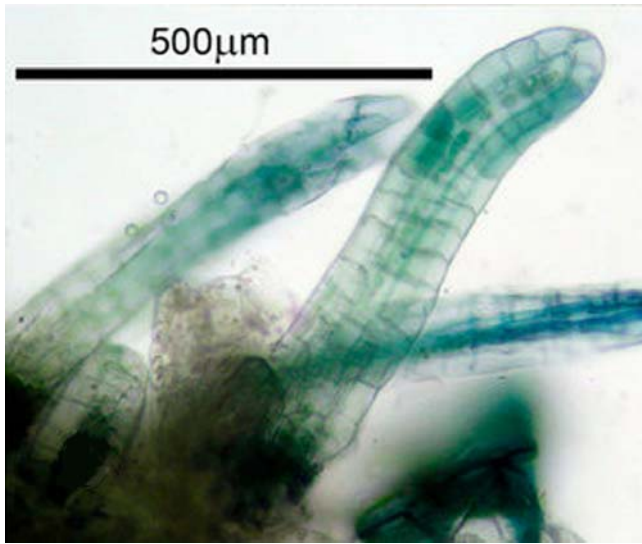


Figure 146. *Fossombronia isaloensis* archegonia. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.

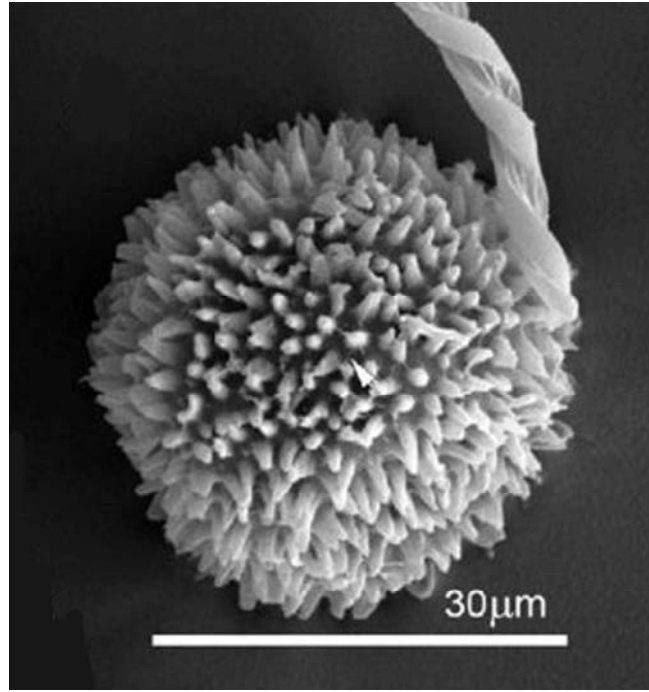


Figure 149. *Fossombronia isaloensis* spore and elater. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.



Figure 147. *Fossombronia isaloensis* sporophyte foot and seta. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.



Figure 148. *Fossombronia isaloensis* spores. Photo by D. Christine Cargill, ©CANBR (Centre for Australian National Biodiversity Research, <<http://www.cpbr.gov.au/cpbr/>>, with permission.

Biochemistry

Thus far, oil bodies have not been observed in *Fossombronia isaloensis* (Figure 136-Figure 138) (Cargill *et al.* 2020). It also lacks biochemical studies.

Fossombronia jostii (Figure 150-Figure 151)

Distribution

Fossombronia jostii (Figure 150-Figure 151) is known only recently, from Ecuador (Crandall-Stotler & Gradstein 2017).



Figure 150. *Fossombronia jostii*, a species endemic to Ecuador. Photo by Lou Jost, with permission from S. Robbert Gradstein.

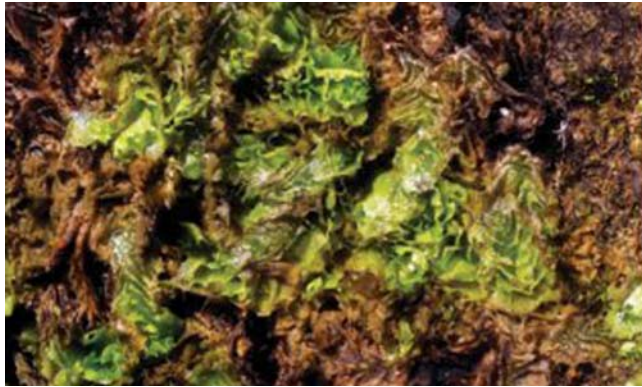


Figure 151. *Fossombronia jostii* in Rio Anzu Canyon, Ecuador. Photo by Lou Jost, with permission from S. Robbert Gradstein.

Aquatic and Wet Habitats

In Ecuador, *Fossombronia jostii* (Figure 150-Figure 151) occurs on limestone boulders along the Rio Anzu (Figure 152-Figure 153) where it flows through a narrow gorge (Crandall-Stotler & Gradstein 2017). The rocks are moist and periodically inundated in the riverbed. The Rio Anzu is periodically flooded and otherwise remains moist.



Figure 152. *Fossombronia jostii* on limestone rocks in Rio Anzu Canyon, Ecuador. Photo by S. Robbert Gradstein, with permission.



Figure 153. *Fossombronia jostii* in Rio Anzu Canyon, Ecuador, showing limestone rocks that serve as substrate. Photo by S. Robbert Gradstein, with permission.

Adaptations

Fossombronia jostii (Figure 150-Figure 151) forms large, light green, mats (Crandall-Stotler & Gradstein 2017).

Reproduction

Fossombronia jostii (Figure 150-Figure 151) is **dioicous** and sexually dimorphic (Crandall-Stotler & Gradstein 2017). Male plants are narrower, with smaller leaves, than the female. Antheridia occur at the apices of the male shoots. The spores (Figure 154-Figure 155) are relatively small (28-32 μm in diameter across distal face, 24-26 μm in polar diameter).

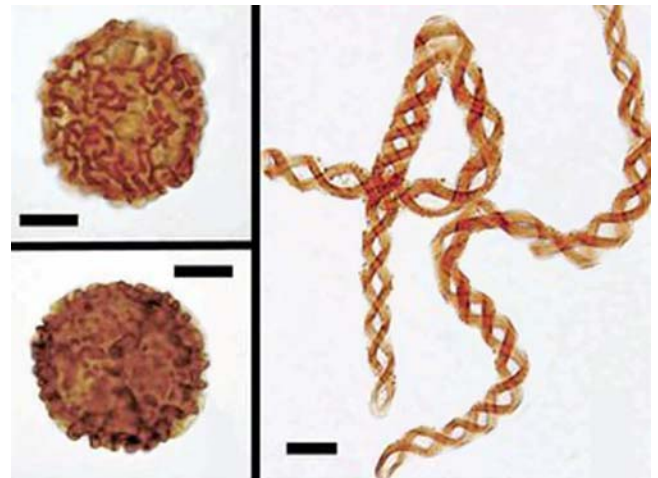


Figure 154. *Fossombronia jostii* spores (left) and elaters (right). Photo by Lou Jost, with permission from S. Robbert Gradstein.

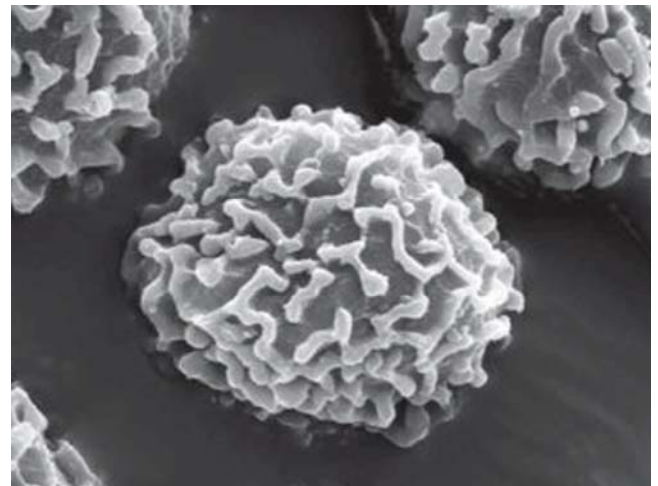


Figure 155. *Fossombronia jostii* SEM of spores. Photo by S. Robbert Gradstein, with permission.

It thus far is not known to produce any type of asexual reproductive or perennating structure, including a noted absence of tubers and gemmae (Crandall-Stotler & Gradstein 2017).

Summary

The wet habitat members of *Fossombronina* often occur in habitats that receive splash or that become inundated periodically, a habitat consistent with their presence in disturbed habitats. This suggests that they are poor competitors. Some are dioicous and others monoicous. Some produce abundant capsules. They quickly re-appear when disturbed conditions become favorable, some from spores, some from persistent tubers. Some benefit from moisture conservation derived by growing with other bryophytes, while others grow in solitary patches that look like green carnations. Some are annuals and others are perennials.

Members of the genus *Fossombronina* were the subject of a number of early studies on development in liverworts. The presence of arabinogalactan-proteins (AGP's) was identified in bryophytes for the first time in *Fossombronina foveolata*.

Acknowledgments

Thank you to Lars Söderström for his continued help in sorting out nomenclature changes.

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CHAPTER 1-14

AQUATIC AND WET MARCHANTIOPHYTA, ORDER FOSSOMBRONIALES, PART 2

TABLE OF CONTENTS

SUBCLASS PELLIIDAE	1-14-2
<i>Fossombronía mylioides</i>	1-14-2
<i>Fossombronía peruviana</i>	1-14-4
<i>Fossombronía porphyrorhiza</i>	1-14-4
<i>Fossombronía pusilla</i>	1-14-6
<i>Fossombronía renateae</i>	1-14-14
<i>Fossombronía texana</i>	1-14-15
<i>Fossombronía wondraczekii</i>	1-14-15
<i>Fossombronía wrightii</i>	1-14-19
Summary	1-14-20
Acknowledgments	1-14-20
Literature Cited	1-14-20

CHAPTER 1-14

AQUATIC AND WET MARCHANTIOPHYTA, ORDER FOSSOMBRONIALES, PART 2



Figure 1. *Fossombronion pusilla*, a cosmopolitan species of moist soil and temporary ponds. Photo by Hugues Tinguy, with permission.

SUBCLASS PELLIIDAE, Fossombroniales part 2

Fossombronion mylioides (Figure 2-Figure 3)

Distribution

Thus far, *Fossombronion mylioides* (Figure 2-Figure 3) is known only from Iriomote Island, Japan (Higuchi 2016; Crandall-Stotler & Gradstein 2017), making it a narrow endemic.

Figure 2. *Fossombronion mylioides*, an endemic of Iriomote Island, Japan. Photo by Masanabu Higuchi, National Museum, Japan, with permission.





Figure 3. *Fossombronia mylioides*. Photo by Masanabu Higuchi, National Museum, Japan, with permission.

Aquatic and Wet Habitats

Fossombronia mylioides (Figure 2-Figure 3) is a riverine species, growing on open boulders covered with sandy soil, along the Urauchi and Nakama Rivers of Japan (Krayesky *et al.* 2005; Higuchi 2016; Crandall-Stotler & Gradstein 2017).

Fossombronia mylioides (Figure 2-Figure 3) also grows directly on moist rocks and stones in river beds and along streams (Figure 4-Figure 5) (Krayesky *et al.* 2005; Higuchi 2016). In these habitats it is sometimes submerged. It can also grow on vertical rock faces near the streams. In areas that flood, it may be mixed with *Riccardia* (Figure 6) (Higuchi 2016).



Figure 4. *Fossombronia mylioides* on rock in Japan. Photo by Masanabu Higuchi, National Museum, Japan, with permission.



Figure 5. *Fossombronia mylioides* on rock in Japan. Photo by Masanabu Higuchi, National Museum, Japan, with permission.



Figure 6. *Riccardia multifida*; *Riccardia* is mixed with *Fossombronia mylioides* in areas that flood in Japan. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Fossombronia mylioides (Figure 2-Figure 3) is light green, with dense, deep purple rhizoids that attach it firmly to its substrate (Higuchi 2016). The color suggests bright sun, but there are no data to suggest protection from high light.

Reproduction

Fossombronia mylioides (Figure 2-Figure 3) is **monoicous**, with archegonia and antheridia scattered on the dorsal surface of the stem (Higuchi 2016). Setae are quite short (2-3 mm). Sporophytes mature in March (Krayesky *et al.* 2005; Higuchi 2016).

The capsule dehiscence is somewhat unusual among bryophytes. Once the capsules dry, they dehisce irregularly from apex downward, lacking sutures or other weakened area for splitting (Figure 7) (Higuchi 2016). Instead the capsule walls form irregular fragments. The spores and elaters tend to clump together and fall as a group. Higuchi observed that the time required from the beginning of dehiscence to the spore dispersal is about 22 minutes. If you are able to observe it, consider yourself lucky.

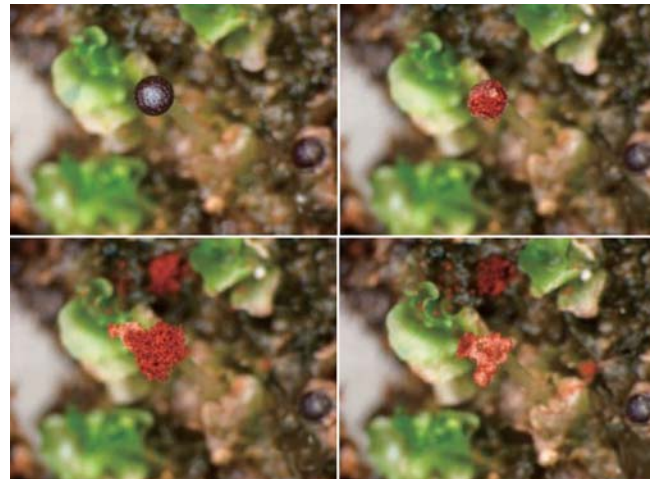


Figure 7. *Fossombronia mylioides* dehiscence and dispersal, shown here over 23 minutes. Photos by Masanabu Higuchi, National Museum, Japan, with permission.

Fossombronia peruviana

(syn. = *Fossombronia herzogii*; *Austrofossombronia peruviana*) (Crandall-Stotler *et al.* 1999)

Distribution

Fossombronia peruviana occurs in high elevation locations in the páramos and punas of the Andes (Crandall-Stotler & Gradstein 2017). Gradstein (2020) included it in the checklist for Ecuador; Müller (2016) reported it from Chile. Gradstein and Arbe (2003; Villagrán Moraga 2020) listed it for Bolivia and Villagrán Moraga (2020) for Venezuela and Peru.

Aquatic and Wet Habitats

Fossombronia peruviana occurs in consistently wet and aquatic habitats at high elevations in the Andean páramos and punas (Crandall-Stotler & Gradstein 2017), including high elevation mires in Latin America (Crandall-Stotler *et al.* 2019). Villagrán Moraga (2020) found it in the Chilean Altiplano wetlands. Gradstein and Pócs (2021) found the species to be characteristic of peaty soil along small streams and in mires of the páramo and puna, where it is sometimes submerged. Gradstein *et al.* (2016) reported it as usually submerged in pure, extensive mats in northern Chile. Although it is widespread, it is far from common.

Adaptations

Fossombronia peruviana is polymorphic, changing its form in response to its habitat (Crandall-Stotler *et al.* 2010). When submerged, it forms **mats**, but forms **turfs** rather than mats on soil. In the water they lack the purple rhizoids and are usually **sterile** (lacking reproductive organs).

Reproduction

Gradstein *et al.* (2016) found that most of the Chilean plants of *Fossombronia peruviana* were sterile. However, one plant was male with several groups of 10-12 naked antheridia on the midrib near the apex, where it is protected by strongly folded leaves. Capsules (Figure 8) are known, and the spores (Figure 9) resemble those of *Fossombronia foveolata* (Figure 10).

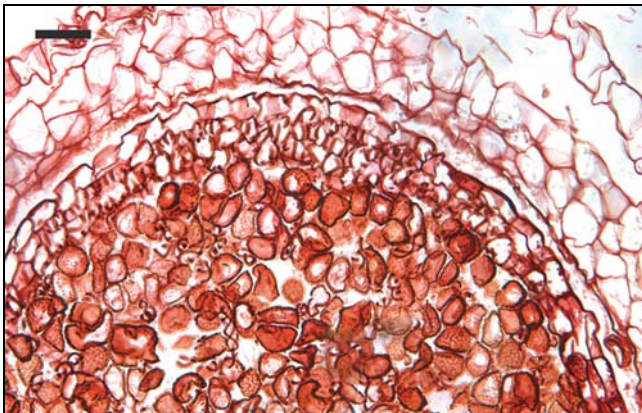


Figure 8. *Fossombronia peruviana* spore SEM. Photo by Barbara Crandall-Stotler, modified, with permission.

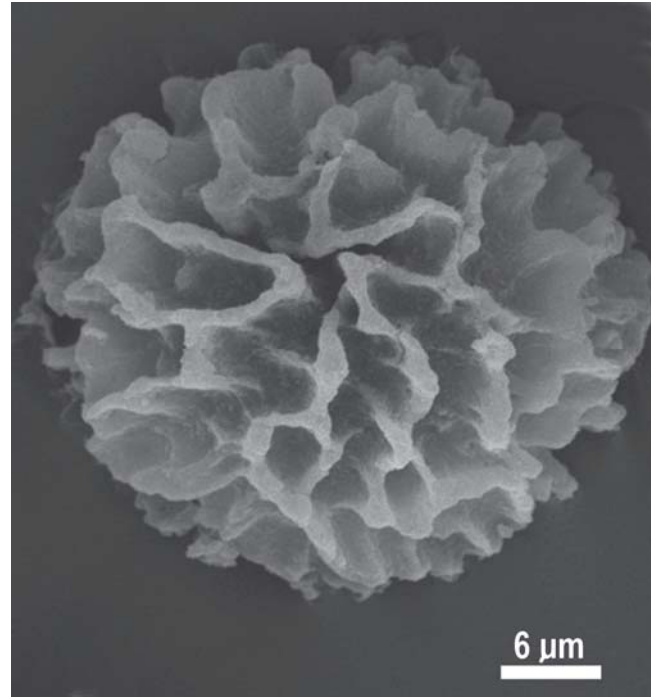


Figure 9. *Fossombronia peruviana* spore SEM. Photo by Barbara Crandall-Stotler, modified, with permission.



Figure 10. *Fossombronia foveolata* SEM of spore, showing its similarities to spores of *Fossombronia peruviana*. Photo by Barbara Crandall-Stotler, with permission.

***Fossombronia porphyrorhiza* (Figure 11)**

[syn. = *Fossombronia brasiliensis*, *Fossombronia salina*(?)]

With this species we suffer from confused taxonomy. My original introduction to it was through *Fossombronia salina* (Evans 1901), but that narrowly distributed species

was named as a synonym of *F. brasiliensis* (Evans 1914). Later, *F. brasiliensis* was considered a synonym of *F. porphyrorhiza* (Figure 11) (Schäfer-Verwimp 2010; TROPICOS 2021), but *F. salina* was considered more related to *F. foveolata* (Figure 12) by the Stotler's (Lars Söderström, pers. comm. March 2021). Hence I shall try to keep the published name intact as I discuss these three taxa under the umbrella of *Fossombronia porphyrorhiza*.



Figure 11. *Fossombronia porphyrorhiza*, Chapada dos Guimaraes, Brazil. Photo courtesy of Denilson Peralta.



Figure 12. *Fossombronia foveolata*. Photo by Kochibi, through Creative Commons.

Distribution

Fossombronia porphyrorhiza (Figure 11) is both common and widespread in the Neotropics (Mexico, West Indies, Central America, South America) (Crandall-Stotler

& Bray 2019). But it also extends into the southeastern United States. Other publications place it as far north as Rhode Island and Connecticut, USA.

Fossombronia porphyrorhiza (Figure 11) extends from coastal regions of Connecticut and Rhode Island, USA, southward to the southeastern US, Puerto Rico, Cuba, Haiti, Dominican Republic, Isle of Pines near Cuba, and Trinidad, through Mexico and Central America to Brazil (Schuster 1992). Schäfer-Verwimp (1999) reported this species (as *Fossombronia brasiliensis*) from Dominica, Gradstein and Hekking (1979) from Colombia, and Schäfer-Verwimp and Reiner-Drehwald (2009) from Guadeloupe, West Indies. Söderström *et al.* (2013) listed it from Paraguay.

Aquatic and Wet Habitats

Peralta and Yano (2008) considered *Fossombronia porphyrorhiza* (Figure 11) to be both **rupicolous** (living among, inhabiting, or growing on rocks) and **terricolous** (living on soil or ground). Pereira Correia *et al.* (2015) likewise considered it to be rupicolous. But those substrate classifications can place it in both terrestrial and aquatic habitats.

Schuster (1992) considers *Fossombronia porphyrorhiza* (as *F. brasiliensis*; Figure 11) to be one of wide ecological distribution. It occurs on moist exposed soil along ditches, exposed sandy-clayey soil in broken ground of old fields, on moist rocks, and as is common among liverworts of such moist but not submersed habitats, it can occur on dead wood.

Guerke (1971) found *Fossombronia porphyrorhiza* (as *F. brasiliensis*; Figure 11) on moist ditch banks along a dirt road in Louisiana, USA, Pôrto *et al.* in a similar habitat in Brazil, and Schäfer-Verwimp (1999) in Dominica, West Indies. Hermann (1959) found it on the open clay bank of a pond in the eastern USA. Redfearn (1979) found it in the Ozarks of Arkansas, USA, on moist vertical sandstone along creek margins. Haupt (1942) found it on a moist humus bank along a road in Costa Rica. Yano and Bastos (2004) found it on a river bank in Brazil.

Sometimes *Fossombronia porphyrorhiza* (Figure 11) satisfies its moisture needs by living near waterfalls on shaded rocks (Schäfer-Verwimp 1999). Redfearn (1980) reported *Fossombronia porphyrorhiza* from calcareous cedar glades in Missouri, Tennessee, and Texas, USA.

Breil (1996) reported a greater variety of habitats in the Virginia Piedmont, USA. Here *Fossombronia porphyrorhiza* (Figure 11) occurred in swamps, along streams, and both single and as mats on moist, clayey, compact soil of old fields. It often accompanies other species of seasonal habitats such as *Riccia* (Figure 13) or *Sphaerocarpos* (Figure 14). Gradstein and Weber (1982) likewise reported it from terrestrial habitats in the Galapagos Islands, and Stotler *et al.* (1998) reported it from an exposed soil bank where it was intermixed with mowed grass in Panama.



Figure 13. *Riccia sorocarpa* on wet soil, a species that occurs in the same seasonal habitats as *Fossombronionia porphyrorhiza*. Photo by Hermann Schachner, through Creative Commons.



Figure 14. *Sphaerocarpos donnellii*; *Sphaerocarpos* species of seasonal habitats often accompany *Fossombronionia porphyrorhiza* there. Photo by Belinda Lo through Creative Commons.

Reproduction

Although the species has been confused with *Fossombronionia angulosa* (Figure 15), *F. porphyrorhiza* (Figure 11) is **monoicous** (Breil 1996), contrasting with the dioicous condition of *F. angulosa*. Despite this monoicous condition, Haupt (1942) reported that whereas it had numerous antheridia and archegonia on a roadside in Costa Rica, it had few sporophytes. On the other hand, Schäfer-Verwimp (1999) found it with mature sporophytes in Dominica, West Indies. Its brown to yellow-brown spores have a wide size range of 38-55 μm (Crandall-Stotler & Bray 2019).

Could this lack of sporophytes be due to the collecting season, or to the wrong photoperiod or other environmental conditions for fertilization? Chin *et al.* (1987) explored the influence of photoperiod, temperature, and inorganic nitrogen source on reproduction and growth in *Fossombronionia porphyrorhiza* (Figure 11). They found that at 18°C it behaved as a short-day plant, requiring 6-12 hours of night for development of archegonia and antheridia. At 10°C it was a quantitative short-day plant, producing more female gametangia, whereas at 18°C it produced more male gametangia. Nitrate was more favorable to the production of gametangia than was

ammonium. This may explain incomplete development of the reproductive structures, but the scarcity of sporophytes in Haupt's (1942) collections remains without explanation.



Figure 15. *Fossombronionia angulosa*, a dioicous species often confused with *Fossombronionia porphyrorhiza*. Photo by Jan-Peter Frahm, with permission.

Fossombronionia typically produces tubers for asexual reproduction (Paton 1974, Schuster 1992), with leafy propagules being rare (Pôrto *et al.* 1999). But in Brazil Pôrto and coworkers found that *Fossombronionia porphyrorhiza* (Figure 11) produced numerous fleshy green propagules with small leaves on the dorsal sides of stems.

Fungal Interactions

There seem to be no records of fungal associations with *Fossombronionia porphyrorhiza* (Figure 11).

Biochemistry

I found a surprising absence of biochemical information on this species.

Fossombronionia pusilla (Figure 16-Figure 20)

Fossombronionia pusilla (Figure 16-Figure 20) has been included in *Fossombronionia angulosa* (Figure 15) by a number of authors (Stotler *et al.* 2005). I have maintained the two taxa separately here.

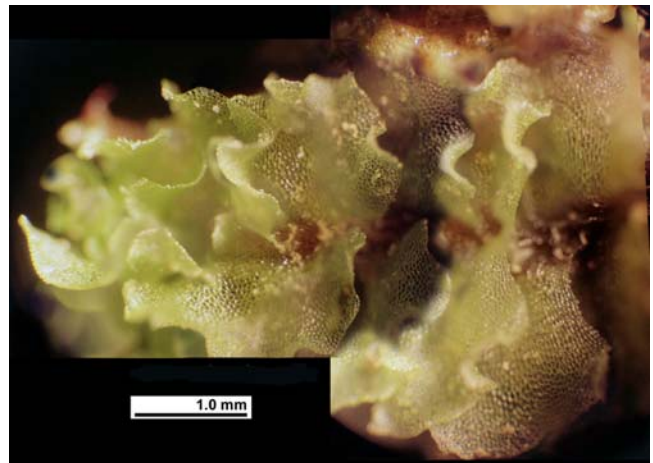


Figure 16. *Fossombronionia pusilla*. Photo by David H. Wagner, with permission.



Figure 17. *Fossombronia pusilla* var. *pusilla* whole plant. Photo by Malcolm Storey, DiscoverLife.org, with online permission.



Figure 19. *Fossombronia pusilla* forming dense clumps. Photo by Andras Keszei, with permission.



Figure 20. *Fossombronia pusilla* var. *pusilla*. Photo by Malcolm Storey, DiscoverLife.org, with online permission.



Figure 18. *Fossombronia pusilla*. Photo by Štěpán Koval, with permission.

Distribution

Fossombronia pusilla (Figure 16-Figure 20) is a cosmopolitan species (Crandall-Stotler & Bray 2019). In North America it is restricted to the west coast (California and Oregon). But it also occurs in South America (Chile); Europe: Germany (Schultze-Motel 1968), England (Callaghan & Ashton 2008), Ireland, Denmark, Italy, France (Gökler 1998), Bulgaria, Croatia, Greece, Macedonia, Romania, Serbia, Slovenia, Turkey (Blockeel *et al.* 2002, Papp & Erzberger 2007), Belgium, Czech Republic, Portugal, Sicily, Spain, Switzerland (Sérgio 1974), Russia (Borovichev & Bakalin 2017), Maltese Islands (Gradstein 1972), Madeira (Sérgio 1974); Asia: Japan (Higuchi 2016), India (Singh & Singh 2007; Alam 2011 – at > 2100 m); and Africa: Algeria (Gökler 1998), Tunisia (Sérgio 1974). Frahm (2005) reported it from the Azores. It also occurs in Papua New Guinea (Krayesky *et al.* 2005).

Aquatic and Wet Habitats

Fossombronia pusilla (Figure 16-Figure 20) occupies a variety of habitats on open soil (Crandall-Stotler & Bray 2019). It frequently grows over moist soil (Çetin 1999),

remaining moist longer due to shade from nearby vegetation (Figure 21) (Crandall-Stotler & Bray 2019). Rilstone (1949) described it as frequent on bare, moist soil in Cornwall, UK. This is an apparent contrast with those colonies found by Osman *et al.* (2019) in Tunisia. They found that *F. pusilla* grew strictly on humus and litter there. Schultze-Motel (1968) found it on a loamy slope in Germany with *Fissidens bryoides* (Figure 22) and *Brachythecium velutinum* (Figure 23).



Figure 21. *Fossombronion pusilla* habitat in the shade of grass. Photo by Štěpán Koval, with permission.



Figure 22. *Fissidens bryoides* with capsules, a species that accompanies *Fossombronion pusilla* on loamy slopes in Germany. Photo by Dick Haaksma, with permission.



Figure 23. *Brachythecium velutinum* with capsules, a species that accompanies *Fossombronion pusilla* on loamy slopes in Germany. Photo by Michael Lüth, with permission.

Özenoğlu Kiremit *et al.* (2007) reported soil banks (Figure 24), stream banks, cave entrance, wet rocks, and stream beds as habitats for *Fossombronion pusilla* (Figure 16-Figure 20) in Antalya, Turkey. Casas *et al.* (1983) found it at the edges of a ravine in Spain.



Figure 24. *Fossombronion pusilla* habitat on a soil bank. Photo by Štěpán Koval, with permission.

In Italy, temporary ponds seem to be the best known habitat for *Fossombronion pusilla* (Figure 16-Figure 17-Figure 20) (Puglisi *et al.* 2015 and others). In Sardinia, Italy, Cogoni *et al.* (2015) found it in temporary ponds, but it is critically endangered in Sardinia. In central Italy, Poponessi *et al.* (2016, 2018) found it associated with temporary ponds, where it was moderately abundant. It occurred on clayey-sandy waterlogged soil with *Isoetes histrix* (Figure 25) and in partially shaded pool systems along the borders of small ponds. It is, nevertheless, considered to be near threatened in Italy because of its scarcity in the country.



Figure 25. *Isoetes histris*, a species that accompanies *Fossombronia pusilla* on clayey-sandy, waterlogged soil in central Italy. Photo by Michel Garner, through Creative Commons.

In another study, Filippino (2018) reported *Fossombronia pusilla* (Figure 16-Figure 20) from Mediterranean temporary ponds, describing the ponds as small and shallow bodies of water isolated from permanent water bodies and undergoing periodic flooding and drought. *Fossombronia pusilla* is one of the bryophyte species found there, but it is considered critically endangered.

In Oregon, USA, it grows on moist soil in disturbed sites like road cuts, along trail cuts, but also in open natural habitats (Wagner 2006).

Fadel *et al.* (2020) found that in the Benslimane region of Morocco *Fossombronia pusilla* (Figure 16-Figure 20) was mostly present in wet crevices of limestone blocks, but also occurred in wetlands where the soil is humid (Figure 26) for a large part of the year and has a rich alluvium. In the Michlifien crater, they found it on shaded rock.

Gradstein (1972) similarly reported *Fossombronia pusilla* (Figure 16-Figure 20) from sheltered crevices in limestone rock of the Maltese Islands, where it was accompanied by *Tortella inflexa* (Figure 27). Papp and Erzberger (2007) found it on base-rich rock in Turkey. On the other hand, Hill *et al.* (2007) note that *Fossombronia pusilla* occurs on moderately acid soil that is constantly moist or damp, but not permanently waterlogged.

In addition to its wet habitats, it has been found on bark in Ohio, USA (Austin 1869).

Adaptations

Fossombronia pusilla (Figure 16-Figure 20) is a hygrophytic, solitary, creeping shuttle species (Filippino 2018). This life cycle strategy is suitable in particular for its temporary pond habitats. In Oregon, USA, it is a winter ephemeral that disappears in the summer (David H. Wagner, pers. comm. 18 April 2021).

In some cases it grows with other bryophytes (Figure 28) that may help it to hold moisture, but it is also possible that they can outcompete it.



Figure 26. *Fossombronia pusilla* var. *pusilla* on moist soil. Photo by Malcolm Storey, DiscoverLife.org, with online permission.



Figure 27. *Tortella inflexa*, a species that grows with *Fossombronia pusilla* in crevices of limestone rock on the Maltese Islands. Photo by Dick Haaksma, with permission.



Figure 28. *Fossombronia pusilla* var. *pusilla* mixed with other bryophytes. Photo by Malcolm Storey, <DiscoverLife.org>, with online permission.

It has purple rhizoids (Figure 29), but their adaptive value, if any, is unknown.

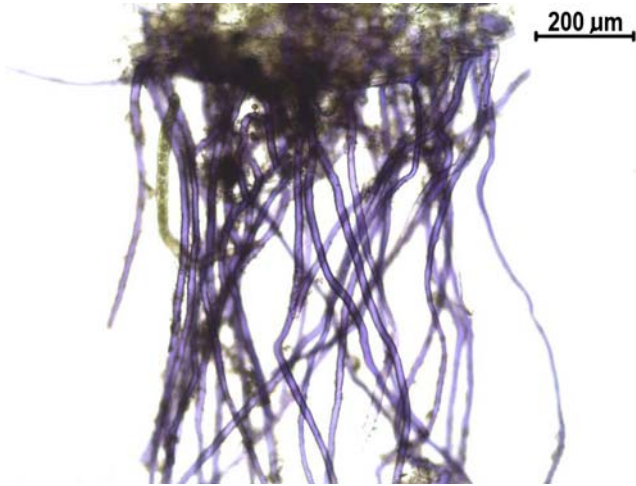


Figure 29. *Fossombronion pusilla* purple rhizoids. Photo by Hugues Tinguy, with permission.

Reproduction

Fossombronion pusilla (Figure 16-Figure 20) is **monoicous** (Crandall-Stotler & Bray 2019). The antheridia (Figure 30-Figure 32) and archegonia are intermixed. Wilson (1911) noted that the first mention of spermatozooids in plants was that of Schmiedel in 1747, for this species, accompanied by a description of their movement. The images I have found of the capsules show both immersed capsules and capsules with elongated setae. In both cases, one can find both brown (Figure 33-Figure 36) and black (Figure 37-Figure 43) capsules. Dehiscence is an irregular pattern of cell breakup (Figure 44-Figure 45). The spores (Figure 46-Figure 47) have a wide size range (38-58 μm) and are yellowish brown to dark brown (Crandall-Stotler & Bray 2019). The chromosome number is $n=8$ (Mehra 1938).



Figure 30. *Fossombronion pusilla* with small yellow antheridia showing. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 31. *Fossombronion pusilla* var. *pusilla* with antheridia. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

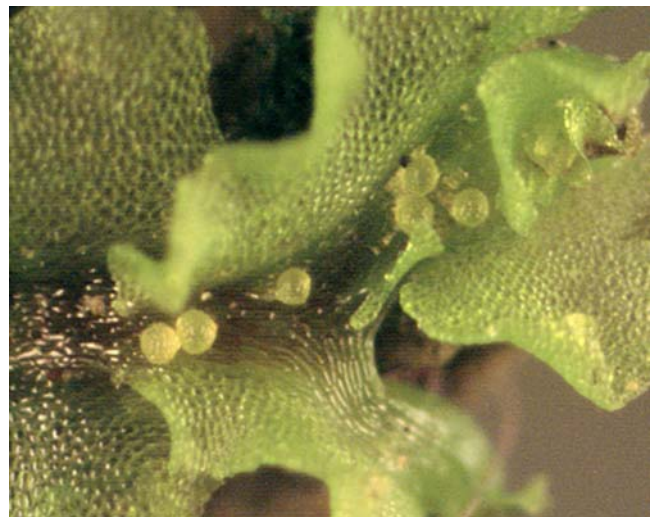


Figure 32. *Fossombronion pusilla* var. *pusilla* with antheridia. Photo by Malcolm Storey, DiscoverLife.org, with online permission.



Figure 33. *Fossombronion pusilla* with capsules. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 34. *Fossombronion pusilla* var. *pusilla* with capsules. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

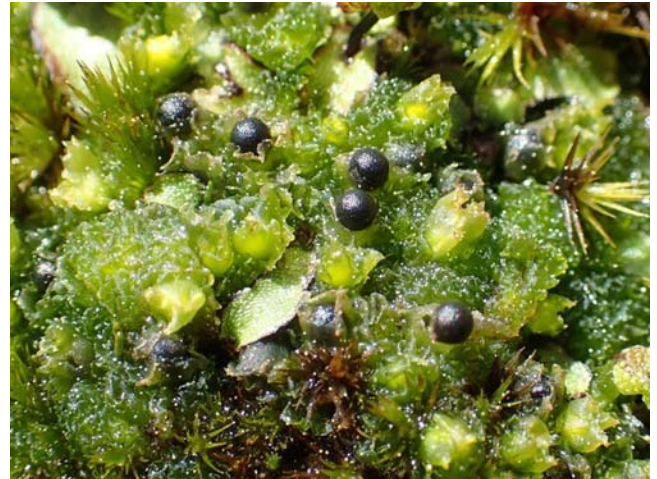


Figure 37. *Fossombronion pusilla* with capsules. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 35. *Fossombronion pusilla* var. *pusilla* with capsules. Photo by Malcolm Storey, DiscoverLife.org, with online permission.



Figure 38. *Fossombronion pusilla* with capsules. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 36. *Fossombronion pusilla* var. *pusilla* with capsules. Photo by Malcolm Storey, DiscoverLife.org, with online permission.



Figure 39. *Fossombronion pusilla* with capsules. Photo by David T. Holyoak, with permission.



Figure 40. *Fossombronia pusilla* with capsules, growing with *Dieranella varia* and *Trichodon cylindrica*. Photo by Barry Stewart, with permission.



Figure 41. *Fossombronia pusilla* perianth and capsules. Photo by Štěpán Koval, with permission.



Figure 42. *Fossombronia pusilla* capsules with elongated seta. Photo by Štěpán Koval, with permission.



Figure 43. *Fossombronia pusilla* var. *pusilla* capsule. Photo by Malcolm Storey, DiscoverLife.org, with online permission.



Figure 44. *Fossombronia pusilla* with dehiscent capsules. Photo by Heino Lepp, with online permission.



Figure 45. *Fossombronia pusilla* var. *pusilla* with dehiscent capsules. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

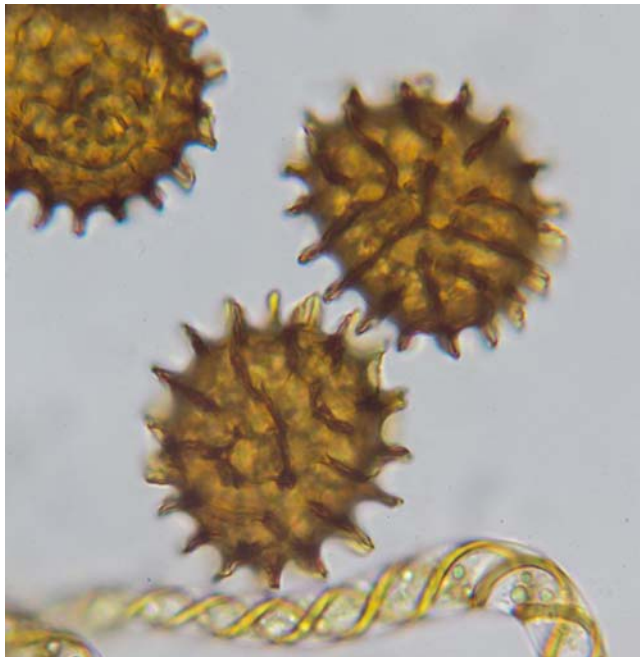


Figure 46. *Fossombronia pusilla* spores and elater. Photo by Štěpán Koval, with permission.

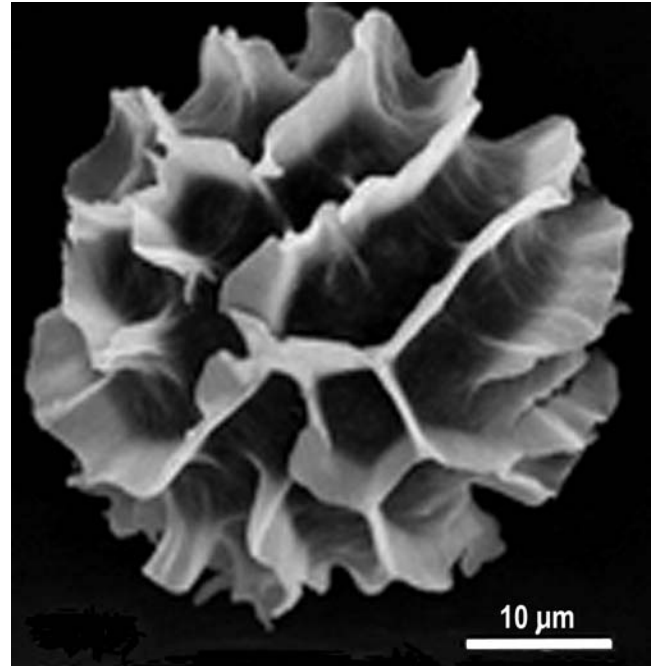


Figure 47. *Fossombronia pusilla* SEM of spore. Photo by Piyanart Suankeaw, through Creative Commons.

In California and Oregon, *Fossombronia pusilla* is **perennial** by means of fleshy, persistent tuberous stems (Figure 48) (Crandall-Stotler & Bray 2019). Otherwise, it appears that no specialized asexual reproductive structures exist.

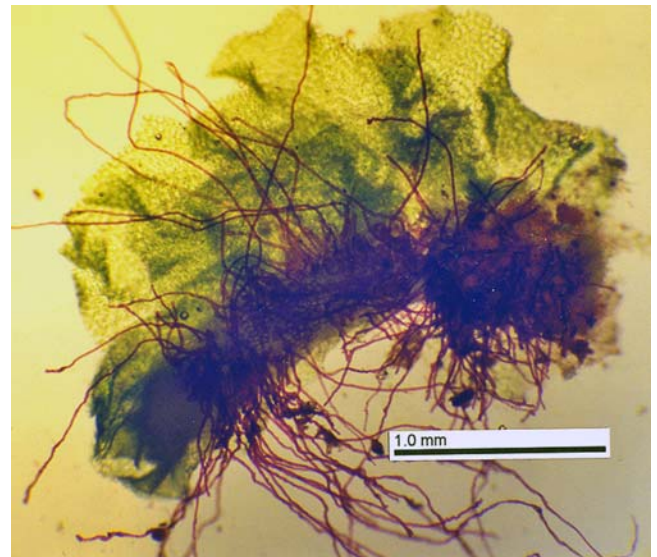


Figure 48. *Fossombronia pusilla* thallus showing purple rhizoids and perennial fleshy stem. Photo by David H. Wagner, with permission.

Ono (1973) reported the induction of callus formation in cultured *Fossombronia pusilla*.

Fungal Interactions

Christie *et al.* (1985) used soluble carbohydrates of ten axenically cultured liverwort species to demonstrate that these are synthesized by the liverworts and not by fungal hyphae that are present with the field populations. They were unable to rule out the fungal production of hexitol by

fungus endophytes of the liverworts tested, but none was found in *Fossombronia pusilla* (Figure 16-Figure 20). Vesicular-arbuscular endophytic fungi were present in the field where *F. pusilla* was collected, but a symbiotic or parasitic relationship remained to be demonstrated.

Rimington *et al.* (2019) examined evolution and symbiotic networks in symbioses between **Mucoromycotina** fungi and liverworts. Network analysis permits us to visualize and quantify how network members interact, showing which plants interact with which fungi. The researchers found that these networks are dominated by specialists, not generalists. *Fossombronia pusilla* (Figure 16-Figure 20) was the only connector hub in all three networks and was the most important member of all three symbiotic networks. They suggested that many of the liverwort associations might be facultative.

Biochemistry

I have found no descriptions of the oil bodies, but Figure 49 has what appear to be spherical oil bodies.

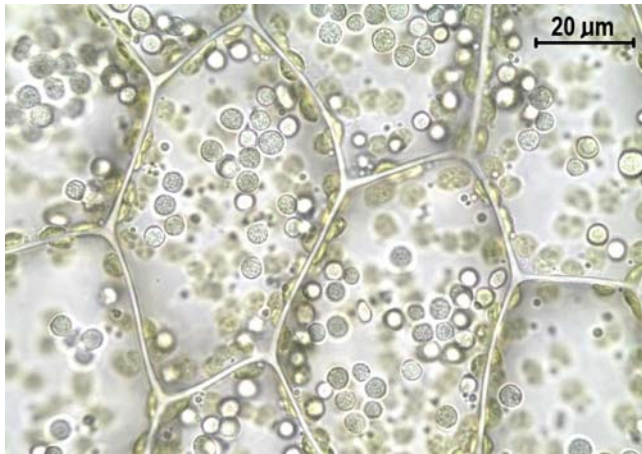


Figure 49. *Fossombronia pusilla* cells with what appear to be oil bodies. Photo by Hugues Tinguy, with permission.

Sauerwein *et al.* (1992) noted the difficulty in investigating secondary compounds in small liverworts such as *Fossombronia pusilla* (Figure 16-Figure 20). It is difficult to collect sufficient material, so they cultured it in the lab. They found that it grew well on Gamborg B5 solid medium, but the liverworts died in liquid media. When the researchers added vitamin B₁₂ to the liquid media, growth was stimulated and the liverwort produced terpenes. These included diterpenedialdehydes perrottetianal A, B and 8-hydroxyperrottetianal A. They also reported santonin for the first time in a bryophyte. Grammes *et al.* (1994) identified three new terpenes, again using cultured gametophytes.

When Sauerwein and Becker (1990) cultured *Fossombronia pusilla* (Figure 16-Figure 20) from spores, they produced the same secondary substances as those measured in collected material. They identified perrottetianal A and B and α -(-)-santonin. They also identified seven terpenes and found that terpenes isolated from a petrol ether extract exhibited antibacterial activity.

Spiteller *et al.* (2002) found that whereas both the bacterium *Streptomyces* sp. and liverwort *Fossombronia pusilla* (Figure 16-Figure 20) produced geosmin, they used different pathways. Dickschat *et al.* (2005) also found that

geosmin was manufactured by the Myxobacteria *Myxococcus xanthus* and *Stigmatella aurantiaca*. These likewise followed a different pathway from that used by *Fossombronia pusilla*.

Fossombronia renateae

Distribution

Fossombronia renateae has a narrow distribution in southern Africa, where there are only two known locations (Perold 1999).

Aquatic and Wet Habitats

At Lone Creek Falls in southern Africa, *Fossombronia renateae* grows between rocks on soil that is kept moist by spray from the waterfalls (Perold 1999). It is accompanied there by *Bryum alpinum* (Figure 50) and *Entosthodon limbatus* (as *Funaria limbata*).



Figure 50. *Bryum alpinum*, a species that accompanies *Fossombronia renateae* in the spray of waterfalls in southern Africa. Photo by David T. Holyoak, with permission.

Adaptations

Fossombronia renateae forms creeping, dense, crowded stands or is intimately to loosely mixed with mosses (Perold 1999). Both habits could help to conserve moisture during dry periods and permit slow drying that is more likely to prepare the liverwort for surviving the dry conditions.

Reproduction

Fossombronia renateae is **dioicous** (Perold 1999). Nevertheless, both sexes were seen and Perold was able to find a few dehiscent capsules retained from the previous season.

Biochemistry

Oil bodies in *Fossombronia renateae* are few (4-6 per cell, 5 μ m diameter) (Perold 1999).

***Fossombronia texana* (Figure 51)**

(syn. = *Fossombronia mexicana*)

Distribution

Fossombronia texana (Figure 51) is known from Texas, Oklahoma, Missouri, and Arkansas (Timme & Redfearn 1997; Atwood & Brinda 2019), but its distribution is poorly known, causing its endangered status to be "no status rank" (NatureServe Explorer 2021). In addition to these USA sites, it occurs in Mexico, Cuba, and Bermuda (Crandall-Stotler & Bray 2019).

Aquatic and Wet Habitats

Atwood and Brinda (2019) reported *Fossombronia texana* (Figure 51) from a bridge over a creek. It also occurs on shaded dolomite ledges along the creek and generally is a calciphile on limestone near streams.

Fossombronia texana (Figure 51) forms loose to dense mats over calcareous boulders (limestone, marl, or travertine) in or next to rivers, where they are frequently inundated (Crandall-Stotler & Gradstein 2017). Crandall-Stotler and Bray (2019) consider it to be restricted to calcareous substrata. On loose marl it can form dense carpets. Its sites are often in shaded riverine habitats. Others are on drip walls of the Interior Highlands at low to moderate elevations.

Among north temperate *Fossombronia* species, only *Fossombronia texana* (Figure 51) forms mats directly on rocks along waterways, which at times become submerged (Bray 2001).



Figure 51. *Fossombronia texana*. Photo by Bob O'Kennon, through Creative Commons.

Adaptations

The **mat** life form (Crandall-Stotler & Gradstein 2017) of *Fossombronia texana* (Figure 51) most likely helps it to conserve water in its streamside habitat where moisture can become less available in the summer. It may also help to reduce drag during times when it becomes inundated.

Reproduction

Fossombronia texana (Figure 51) is **monoicous** (Atwood & Brinda 2019) with antheridia scattered along with archegonia (Crandall-Stotler & Bray 2019).

Therefore, production of capsules (Figure 52) is not limited by distance between the sexes. The spores are large (42-57 μm). It lacks tubers at the stem apices (Atwood & Brinda 2019), an asexual reproductive means known in some other species of *Fossombronia*.



Figure 52. *Fossombronia texana* with capsules. Photo by Bob O'Kennon, through Creative Commons.

Fossombronia wondraczekii* (Figure 53-Figure 54)*Distribution**

Fossombronia wondraczekii (Figure 53-Figure 54) is widely circumboreal (Aleffi & Esposito 2005; Poponessi *et al.* 2015), scattered in North America (Crandall-Stotler & Bray 2019) and elsewhere, but widespread (Poponessi *et al.* 2015). It extends from eastern Greenland, south to the Appalachians, and west to Ohio and Indiana in North America. It is also present in Iceland, Europe, northern Africa, Australia, and New Zealand. Poponessi *et al.* (2015) added Cyprus, Mauritius, Réunion, Siberia, and Sri Lanka. Ștefănuț and Goia (2012) listed it for Romania. It is usually not common, and in the Western Carpathians of Poland it is in the protected and threatened category (Stebel & Vončina 2017).



Figure 53. *Fossombronia wondraczekii*, a species that occurs in both hemispheres. Photo by Hugues Tinguy, with permission.



Figure 54. *Fossombronionia wondraczekii* with capsule before seta elongation. Photo by Dick Haaksma, with permission.

Aquatic and Wet Habitats

Aleffi and Esposito (2005) characterized *Fossombronionia wondraczekii* as mesohygrophilous, photosciaphilous, and terricolous. *Fossombronionia wondraczekii* (Figure 53-Figure 54) is mostly restricted to moist soil habitats in low to moderate elevations (Crandall-Stotler & Bray 2019). These are often disturbed habitats. It typically grows intermixed with other bryophytes or forms small rosettes on moist soil where it is shaded by nearby vegetation. Ștefănuț and Maria (2018) found it with other bryophytes near a slow-flowing stream and Stebel (2015) found it on wet soil near a ditch, both in Poland. Sotiaux *et al.* (2007) reported it from ground along a streamlet in Corsica, France, growing with *Bryum alpinum* (Figure 50).

In the Nilgiri Hills of India, *Fossombronionia wondraczekii* (Figure 53-Figure 54) grows in dense patches on moist and exposed rocks and soil-covered rocks along with other terrestrial mosses (Figure 55) (Alam 2011). *Fossombronionia wondraczekii* occurs on calcareous stony soil (Figure 56) in the Balearic Islands (Sáez *et al.* 2006).



Figure 55. *Fossombronionia wondraczekii* growing with mosses. Photo by Michael Lüth, with permission.



Figure 56. *Fossombronionia wondraczekii* growing on stony soil. Photo by Tom Neily, through Creative Commons.

Like a number of other members of *Fossombronionia*, *Fossombronionia wondraczekii* (Figure 53-Figure 54) occurs along the edge of ponds, especially in Italy, giving it a spotty and local distribution (Poponessi *et al.* 2016).

It is not unusual to find members of *Fossombronionia* in temporary habitats. In the Western Carpathians, *Fossombronionia wondraczekii* (Figure 53-Figure 54) occurs with other rare species in fallow fields (Armata 2005). Klama and Górski (2018) similarly found it in wet fields, stubble fields, and fallow fields (Figure 57) in Poland, as well as moderately used forest ground roads. Sotherton and Self (2000) reported it from lowland farmland in the UK. These records suggest that it benefits, for a short period of time at least, from the lack of competition in disturbed habitats. This suggestion is further supported by its ability to colonize burned soil in moist depressions in southern Italy (Aleffi & Esposito 2005). Its rapid maturation and high level of spore dispersal aid in its colonization of such disturbed areas.



Figure 57. *Fossombronionia wondraczekii* on dry mud, typical of seasonally flooded habitats. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission.

Adaptations

The habit of *Fossombronia wondraczekii* to grow among other bryophytes (Figure 58) (Crandall-Stotler & Bray 2019) most likely keeps this moisture-loving species moist longer, reducing both frequency and duration of desiccation.



Figure 58. *Fossombronia wondraczekii* habitat on soil, growing with mosses that may help to conserve moisture. Photo by Hugues Tinguy, with permission.

The dense patches are yellowish-green to green (Figure 59). In patches no bigger than a dime it grows "like a bunch of unkempt, light green, Victorian ruffles" (Figure 60) with distinctive bright violet rhizoids growing from the undersides of horizontal stems" (Trigoboff 2012). Because of its small areas of growth, Hill *et al.* (2007) distinguish it as a "patch" rather than a mat.



Figure 59. *Fossombronia wondraczekii*, showing yellowish-green color and small patch. Photo by Bernd Heynold, through Creative Commons.



Figure 60. *Fossombronia wondraczekii* habitat on calcareous soil, showing patchy growth pattern. Photo by Bernd Heynold, through Creative Commons.

Reproduction

Fossombronia wondraczekii (Figure 53-Figure 54) is **monoicous** with its antheridia (Figure 61) scattered among and intermixed with the archegonia (Alam 2011; Crandall-Stotler & Bray 2019). It apparently lacks asexual reproductive structures and regenerates by spores (Figure 62-Figure 68) (Aleffi & Esposito 2005). One of its advantages toward arriving in disturbed habitats and in spreading somewhat rapidly is its high dispersal ability (Sotiaux *et al.* 2006). Brown and Lemmon (1993) described the development of the spores in detail.



Figure 61. *Fossombronia wondraczekii* with a few visible yellow antheridia. Photo by Štěpán Koval, with permission.



Figure 62. *Fossombronionia wondraczekii* patch with capsules. Photo by Michael Lüth, with permission.



Figure 65. *Fossombronionia wondraczekii* capsules with collapsed setae, showing how numerous they can be. Photo by Shaun Pogacnik, through Creative Commons.



Figure 63. *Fossombronionia wondraczekii* with nearly mature capsules. Photo by Michael Lüth, with permission.



Figure 66. *Fossombronionia wondraczekii* open sporangium exposing spores and elaters. Photo by Michael Lüth, with permission.



Figure 64. *Fossombronionia wondraczekii* with capsules in multiple stages of maturity and dehiscence. Photo by Bob Klips, through Creative Commons.



Figure 67. *Fossombronionia wondraczekii* spores and elaters. Photo by Shaun Pogacnik, through Creative Commons.



Figure 68. *Fossombronia wondraczekii* spore and elater. Photo by Bob Klips, through Creative Commons.

Trigoboff (2012) reported ripe capsules on 5 December in Central New York, UA. There were shed spores, and many plants were bleached, with a "ghostly" appearance. On 10 January, he considered the plants to be "legally dead." Despite this unseemly condition, there were bits of green tissue, some unripe capsules, and a few unopened capsules with mature spores. The usual time for capsule (Figure 62-Figure 65) production of *Fossombronia wondraczekii* in central New York is 15 September to 15 October, with peak spore discharge 25 September to 5 October (Schuster 1949).

Srivastava and Sharma (1995) described the development and morphology of the *Fossombronia wondraczekii* sporelings. There were three types of development, with the most common one being filamentous, septate germ-tubes.

Biochemistry

Feld *et al.* (2005) identified five new sacculatane diterpenoids in *Fossombronia wondraczekii* (Figure 53-Figure 54).

Fossombronia wrightii (Figure 69)

Distribution

Fossombronia wrightii (Figure 69) occurs in the Caribbean (ITIS 2021).

Aquatic and Wet Habitats

Like *Fossombronia texana* (Figure 51), *Fossombronia wrightii* (Figure 69) forms mats over calcareous boulders in or next to rivers, where they are frequently inundated (Crandall-Stotler & Gradstein 2017). Freire and Stotler (2007) reported it to be riparian on rocks in Cuba.

Adaptations

As do most of the wet habitat *Fossombronia* species included in this chapter, *F. wrightii* (Figure 69) forms **mats**, in this case on calcareous boulders. Once again, we can assume that it helps to conserve water during dry periods, but it would also reduce drag during periods of

high water when it becomes inundated. At such times, the flow of rivers is likely to be rapid.

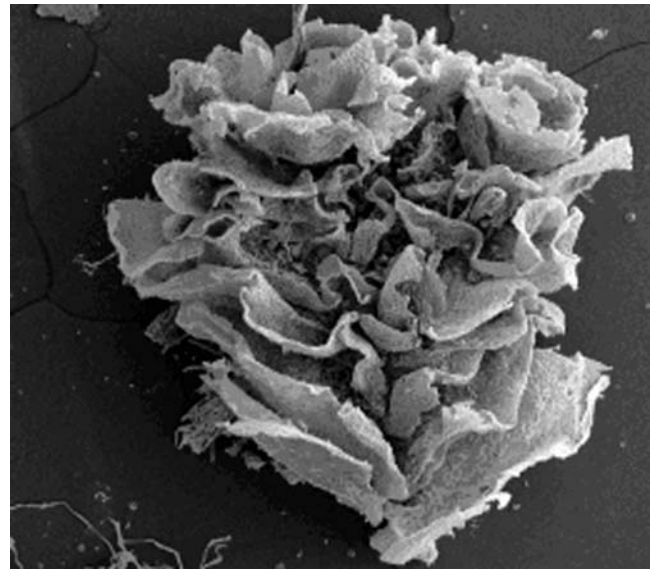


Figure 69. *Fossombronia wrightii* SEM, a riparian Caribbean species. Photo courtesy of Virginia Freire.

Reproduction

Fossombronia wrightii (Figure 69) has known sporophytes (Figure 70) and produces spores without tubercles (Figure 71), but it is not known if it is **dioicous** or **monoicous** because no antheridia have been found (Virginia Freire, pers. comm. 24 April 2021). It forms fleshy tubers (Figure 72) that undoubtedly help it to spread where it has become established. They could also serve as dispersal agents at times of inundation, having a greater likelihood of survival than the leafy plant.



Figure 70. SEM of *Fossombronia wrightii* with sporophyte and tuber. Photo courtesy of Virginia Freire.

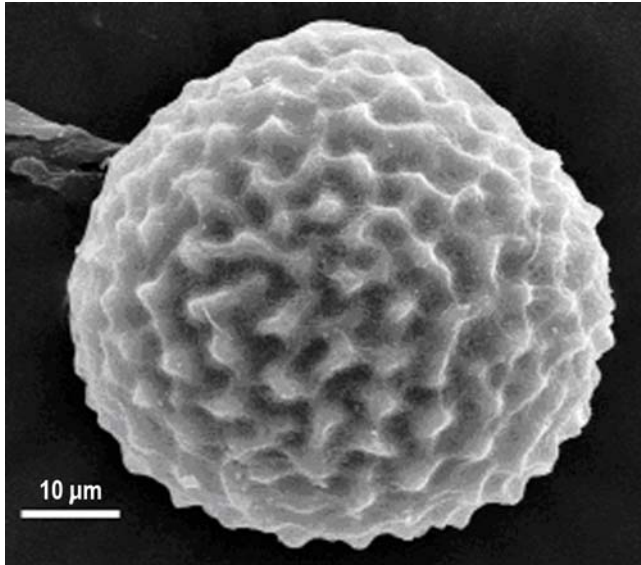


Figure 71. *Fossombronia wrightii* spore SEM. Photo courtesy of Virginia Freire.

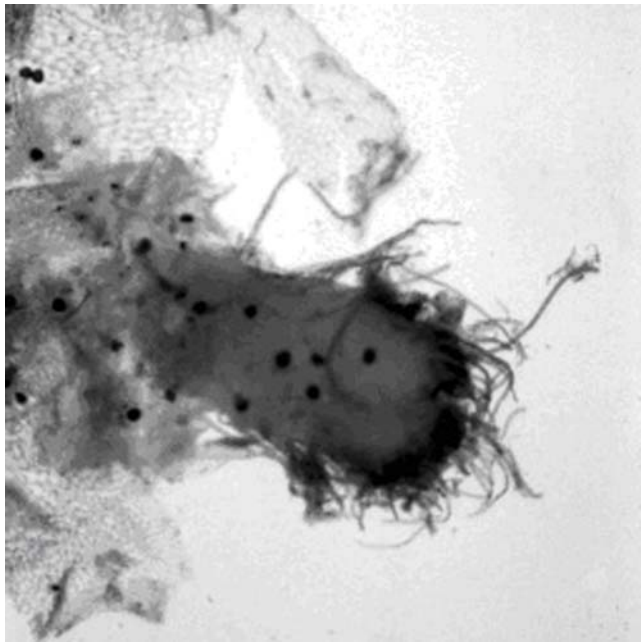


Figure 72. SEM of *Fossombronia wrightii* tuber. Photo courtesy of Virginia Freire.

Summary

Some of the species in this subchapter are at least periodically submerged (e.g. *Fossombronia mylioides*), but most of the species can occur in wet habitats that can dry out. The adaptations seem to be physiological, permitting it to survive both submersion and drying out. For example, *Fossombronia pusilla* grows in temporary ponds. Some grow with other bryophytes, thus benefitting from reduced water loss; others benefit from forming large, closely overlapping mats. Some of the aquatic species are confined to high elevations in the Andes.

Acknowledgments

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CHAPTER 1-15

AQUATIC AND WET MARCHANTIOPHYTA, PALLAVICINIALES

TABLE OF CONTENTS

SUBCLASS PELLIIDE	1-15-2
Pallaviciniales: Hymenophytaceae	1-15-2
<i>Hymenophyton flabellatum</i>	1-15-2
Pallaviciniales: Pallaviciniaceae	1-15-6
<i>Jensenia decipiens</i>	1-15-6
<i>Pallavicinia</i>	1-15-7
<i>Pallavicinia indica</i>	1-15-7
<i>Pallavicinia levieri</i>	1-15-7
<i>Pallavicinia lyellii</i>	1-15-8
Summary	1-15-16
Acknowledgments	1-15-16
Literature Cited	1-15-16

CHAPTER 1-15

AQUATIC AND WET MARCHANTIOPHYTA, PALLAVICINIALES



Figure 1. Wetland habitat with *Betula pubescens*, a habitat suitable for *Pallavicinia lyellii*. Photo by Ingo2802, through Creative Commons.

Nomenclature for this subchapter is based primarily on Söderström *et al.* (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species.

SUBCLASS PELLIIDAE

Pallaviciniales: Hymenophytaceae

Hymenophyton flabellatum (Figure 2, Figure 4-Figure 6)

(syn. = *Symphogyna flabellata*)

Hymenophyton flabellatum (Figure 2, Figure 4-Figure 6) has been treated variously by different researchers. Pfeiffer (2000) reviewed these differences in perspective and suggested that at least two distinct taxa of *Hymenophyton* exist in New Zealand and Tasmania. Pfeiffer *et al.* (2004) used molecular analysis to determine

differences in populations and recognized four taxa in *Hymenophyton*. Because of the differences in treatment through time, I have included all literature related to *Hymenophyton flabellatum*, even if it has since been placed in a different species.



Figure 2. *Hymenophyton flabellatum*, a species from Australia, New Zealand, and Tasmania. Photo by Ken Harris, EntSocVic, through Creative Commons.

Distribution

Hymenophyton flabellatum s.l. (Figure 2, Figure 4-Figure 6) has a Palaeoaustral distribution pattern, with populations known from Tasmania, New Zealand, and Australia. Pfeiffer (2000) recognized *H. flabellatum* and *H. leptopodum* (Figure 3) in New Zealand and *H. mulleri* collected from a river (Evans 1925) in Australia. *Hymenophyton mulleri* (*H. muelleri*) is not recognized by Söderström *et al.* (2016); TROPICOS (2021) includes it in *Hymenophyton flabellatum*. The Tasmanian taxon might also be recognized as *H. leptopodum*. The segregate *Hymenophyton pedicellatum* is known from South America (Pfeiffer *et al.* 2004). Segregates of *H. flabellatum* from New Caledonia, Fiji Islands, Colombia, and Chile (Evans 1925) have been variously treated as a member of *H. flabellatum* and as separate taxa (Pfeiffer 2000).



Figure 3. *Hymenophyton leptopodum*, a segregate recognized in New Zealand. Photo by TePapa, through Creative Commons.



Figure 4. *Hymenophyton flabellatum*. Photo by Niels Klazenga, with permission.



Figure 5. *Hymenophyton flabellatum* wet, growing on soil. Photo by Jan-Peter Frahm, with permission.



Figure 6. *Hymenophyton flabellatum* showing stipe and leafy plant. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

Hymenophyton flabellatum (Figure 2, Figure 4-Figure 6) occurs in Cool Temperate Victorian Rainforest streams (Downes *et al.* 2003; Carrigan 2008) found it in an unregulated creek in Australia. In New Zealand, Frogley and Glennie (2020) found it in a small creek bed. Braggins (1987) found it in a Tasmanian stream on clay and humus. Suren (1996) considered it to be obligately or facultatively aquatic in streams.

But *Hymenophyton flabellatum* (Figure 2, Figure 4-Figure 6) is not restricted to streams. In their biochemical study, Asakawa *et al.* (2001) noted that *Hymenophyton flabellatum* occurred on shaded wet soil (Figure 7), humus, and old logs in forests, usually in shade, and on banks beside streams and waterfalls (Figure 8). In *Eucalyptus regnans* forest (Figure 9) at Wallaby Creek, Victoria, Australia, *Hymenophyton flabellatum* occurred on very wet, sodden, white-rot logs sheltered on south sides of logs (Ashton 1986). Gibson (2006) reported it to be common in wet forests in Australia.



Figure 7. *Hymenophyton flabellatum* growing on soil. Photo by Jan-Peter Frahm, with permission.



Figure 8. *Hymenophyton flabellatum* on a vertical substrate. Such growth forms of shelves can occur in the splash of waterfalls. Photo from Manaaki Whenua – Landcare Research, with online permission.



Figure 9. *Eucalyptus regnans* forest in Australia, where one can find *Hymenophyton flabellatum* on very wet logs. Photo by Patche99z, through Creative Commons.

Adaptations

It is interesting that *Hymenophyton flabellatum* (Figure 2, Figure 4-Figure 6) has water-conducting elements (Figure 10-Figure 11) in its gametophytes (Burr *et al.* 1974; Campbell *et al.* 1975). These are axially elongated cells with no living contents and numerous perforations in their walls, making them unique among land plants. Héban (1978) identified endoplasmic-reticulum cisternae associated with the differentiating pores and compared them to developing sieve pores in phloem of tracheophytes.



Figure 10. *Hymenophyton flabellatum* showing ribs made of water-conducting elements. Photo by Arthur Chapman, through Creative Commons.



Figure 11. *Hymenophyton flabellatum* wet plants showing the prominent rib. Photo by Devaprayaga, through Creative Commons.

The plants of *Hymenophyton flabellatum* (Figure 2, Figure 4-Figure 6, Figure 14) are olive-green with fan-shaped fronds (Figure 12), crowded chloroplasts, small cells, and thick cell walls. The aquatic and wet habitat affiliations of this species puzzle me because they would seem to be adapted to drier habitats with their small cells, thick walls, and conduction system. Nevertheless, the fan-

shaped fronds would most likely lose water easily (Figure 12-Figure 13), and they seem to handle both wet (Figure 11-Figure 12) and dry conditions (Figure 13).



Figure 12. *Hymenophyton flabellatum* showing signs of drying. Photo by Paul George, through Creative Commons.



Figure 13. *Hymenophyton flabellatum* dry plants. Photo by Robert Pergl, through Creative Commons.

Reproduction

The genus *Hymenophyton* (Figure 2, Figure 4-Figure 6-Figure 14), as far as known, is **dioicous** (Figure 14) (Campbell *et al.* 1975; Crandall-Stotler *et al.* 2005). This image from Karen Renzaglia shows that at least sporophytes are known (Figure 15).

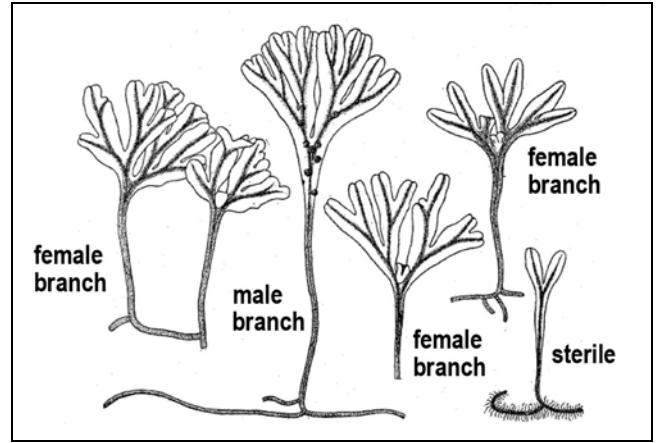


Figure 14. *Hymenophyton flabellatum* male, female, and sterile branches. Image modified from Evans 1925.

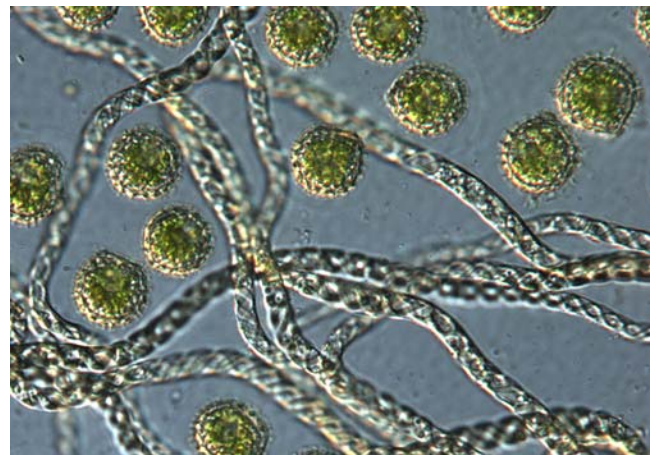


Figure 15. *Hymenophyton* spores and elaters. Photo by Karen Renzaglia, with permission.

Fungal Interactions

Johnson (1977) reported mycorrhizal infections of rhizoids in *Hymenophyton flabellatum* (Figure 2, Figure 4-Figure 6). Ligrone *et al.* (2007) identified **Glomeromycotean** endophytes in New Zealand specimens. They concluded that **Glomeromycota** (Figure 16) lineages that form arbuscular mycorrhizae in a wide range of liverwort taxa have been derived by "host-shifting" from tracheophyte taxa (Figure 17) to liverworts.



Figure 16. *Glomus coremioides* (Glomeromycota); some members of this phylum form arbuscular mycorrhizae in liverworts such as *Hymenophyton flabellatum*. Photo by Damon Tighe, through Creative Commons.

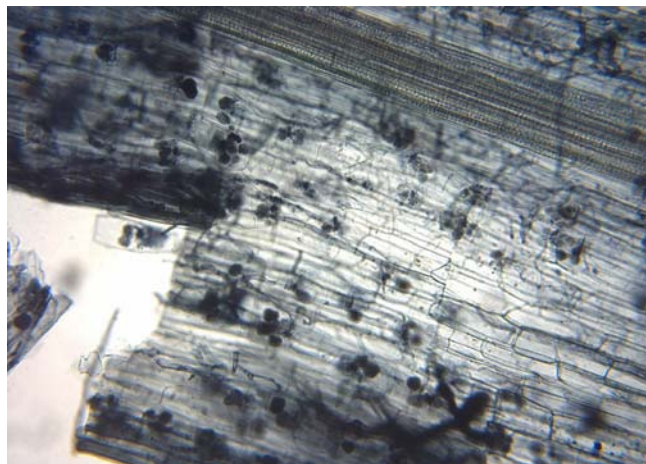


Figure 17. *Glomeromycota* arbuscular mycorrhiza in root of a tracheophyte. Photo by M. Sturm, through public domain.

Biochemistry

Campbell *et al.* (1975) used chemical constituents to distinguish between *Hymenophyton flabellatum* (Figure 2, Figure 4-Figure 6) and *H. leptopodium* (Figure 3), concluding that they were both valid species. One of these differences is the presence of kaempferols in the latter but not in *H. flabellatum*. Both species have flavone C-glycosides. Markham *et al.* (1976) further supported this conclusion based on flavonoid constituents.

Classen *et al.* (2019) reported arabinogalactan-proteins, compounds found in the extracellular matrix of *Hymenophyton flabellatum* (Figure 2, Figure 4-Figure 6) plants. These proteins have a small protein moiety that is usually rich in **hydroxyproline** (found in plant cell walls; serve as attachment points for glycan chains which are added as post-translational modifications). **Hydroxyproline** seems to have a major evolutionary role in liverworts, by regulating leaf and branch development (Basile 1990).

Toyota *et al.* (2009) identified 1-(2, 4, 6-trimethoxy-phenyl)-but-2 (E)-en-1-one, a known compound, as the cause of the hot-tasting, strongly pungent substance released when fragments of *Hymenophyton flabellatum* (Figure 2, Figure 4-Figure 6) are chewed. It is possible that this compound serves to discourage herbivores, but do the likely herbivores – arthropods – taste things the same way we do? In fact, Numata *et al.* (1984) demonstrated that its compound 1-(2, 4, 6-trimethoxy-phenyl)-but-2 (E)-en-1-one has antifeedant activity against the larvae of the yellow butterfly *Eurema hecabe mandarina* (Figure 18), although for that test it was extracted from *Arachniodes standishii* (Figure 19), a fern (see also Asakawa *et al.* 2001; Asakawa 2015).

Asakawa (2004) considered *Hymenophyton flabellatum* (Figure 2, Figure 4-Figure 6) to be one of the most chemically isolated liverworts so far examined. It was the only liverwort known to contain phenyl butanone. phenyl butanone in some fruits is used in perfumery and cosmetics (PubChem 2021).

It is not surprising that a liverwort so well endowed with noxious chemicals should offer protection against infections. Earl (2010) reported that *Hymenophyton flabellatum* (Figure 2, Figure 4-Figure 6) is commonly used medicinally.



Figure 18. *Eurema hecabe* on *Lespedeza bicolor*, a butterfly whose larvae are repelled by a compound that is present in *Hymenophyton flabellatum*. Photo by Alpsdake, through Creative Commons.



Figure 19. *Arachniodes standishii*, a fern that produces the same antifeedant 1-(2, 4, 6-trimethoxy-phenyl)-but-2 (E)-en-1-one as that in *Hymenophyton flabellatum*. Photo by Ecelan, through Creative Commons.

Pallaviciniales: Pallaviciniaceae

Jensenia decipiens

(syn. = *Pallavicinia zollingeri*)

Schaumann *et al.* (2004) investigated DNA relationships in the genus *Jensenia* (Figure 20). They found a low level of variation both within and between taxa in the genus. On the other hand, the molecular data do support the separation of the genus *Jensenia* (Figure 20) from *Pallavicinia* (Figure 21-Figure 27). Forrest *et al.* (2005) further supported this separation and using cladistic methods concluded that *Jensenia* is monophyletic, thus a natural group. They considered its distribution to be the product of dispersal, not vicarious similarities.

Distribution

Jensenia decipiens is tropical, known from Sri Lanka (Farmer 1894; Long & Rubasinghe 2014), the Philippines, Malaysia (Grolle & Piippo 1986; Piippo & Tan 1992), Indonesia (Sumatra, Java, and Celebes) (Grolle & Piippo 1986; Piippo & Tan 1992; Gradstein *et al.* 2005), and

Papua New Guinea (Grolle & Piippo 1986; Enroth 1990; Piippo & Tan 1992), and more recently it has been reported from Malesia (Arianti & Gradstein 2007) and Japan (Schaumann *et al.* 2005).



Figure 20. *Jensenia connivens*; *Jensenia decipiens* occurs on muddy stream banks. Photo by Bill Malcolm, with permission.

Aquatic and Wet Habitats

Jensenia decipiens in Ceylon occurs on muddy streambanks at 6200' (Farmer 1894). At lower elevations it outcompetes other plants with its profuse growth.

Ruttner (1955) reported *Jensenia decipiens* from the wall of a bay in the tropics. Piippo and Tan (1992) reported it from wet crevices of a trail in very deep shade in the Philippines.

Adaptations

Jensenia decipiens grows erect from a creeping rhizome. Its branches are thus tree-like (van der Gonde 1980). This would be a disadvantage in locations that dry, but in a moist environment it could provide greater access to CO₂ and possibly to light for photosynthesis.

Reproduction

Jensenia decipiens and all members of the genus thus far described are **dioicous** (van der Gonde 1980). Farmer (1894) described details of its development, including the gametophyte, archegonia, sporophyte, and spores.

Moore (1906) questioned the account of sporogenesis provided by Farmer (1894) and suggested that it was not unique, as suggested by the Farmer account, but was instead consistent with that known for other plants, including other liverworts.

The branching pattern of *Jensenia decipiens* is rather unusual. It appears to be dichotomous, but on closer inspection, the terminal bud occurs between the paired branches, and remains and grows, as in **monopodial** branching (having a central axis from which other branches arise, as in a spruce tree).

Pallavicinia

Pallavicinia can occur as a **rheophyte** (plant that lives in fast-moving water currents in environment where few other organisms can survive) in the wet tropics of SE Asia (Akiyama 1992).

Pallavicinia indica

Distribution

Pallavicinia indica is known from India, Java, Nepal, Sri Lanka, Sumatra, and Tahiti (Campbell 1908; Herzog 1942; Pradhan & Joshi 2009; Long & Rubasinghe 2014; Lavate *et al.* 2015; Manju *et al.* 2015). Specimens reported from China appear to belong to *Pallavicinia levieri* (Mamontov *et al.* 2015).

Aquatic and Wet Habitats

Pallavicinia indica occurs on **tuff** (porous volcanic rock) wall, waterfalls in tropics (Ruttner 1955). This species does not seem to prefer wet habitats. Nair and Prajitha (2016) reported the habitat of *Pallavicinia indica* as "land cuttings."

Pallavicinia levieri (Figure 21)

Distribution

Pallavicinia levieri (Figure 21) is an Asian temperate-tropical mountain species. It is known from Cambodia, China, Japan, Vietnam, Indonesia, Philippines, and Papua New Guinea (Grolle & Piippo 1984, 1986; Mamontov *et al.* 2015).



Figure 21. *Pallavicinia levieri* with leafy liverworts, from Guangdong, China. Photo by Li Zhang, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported *Pallavicinia levieri* (Figure 21) as aquatic from the tropics (Ruttner 1955). Mamontov

et al. (2015) reported that it occurs along river beds of primeval forests, along stream beds and slopes in secondary mixed evergreen forests, and in deep gorges. In Cambodia it occurs on wet cliffs near waterfalls.

Reproduction

Pallavicinia levieri (Figure 21) is **dioicous** (Figure 22-Figure 23) (Mamontov *et al.* 2015). Campbell and Williams (1914) provide a morphological study.



Figure 22. *Pallavicinia levieri* with perianths and young sporophytes, from Hainan, China. Photo by Rui-Liang Zhu, with permission.



Figure 23. *Pallavicinia levieri* with perianth and other bryophytes. Photo by Li Zhang, with permission.

Biochemistry

Hashimoto *et al.* (1993, 1995) reported that the major component of *Pallavicinia levieri* (Figure 22-Figure 23) is sacculatal, a pungent diterpene dialdehyde (Asakawa 1982). It also produces pallavicinol and a rare chettaphanin-type diterpenoid. It has a pungent (-)-polygodial that is a strong piscicide (Asakawa 1990). Furthermore, killie-fish (*Oryzia latipes*) die within 2 hours when exposed to a solution of 0.4 ppm of sacculatal, and within 20 minutes at 1 ppm of sacculata and 1/3 1/3-hydroxysacculatal (Asakawa 1998).

Pallavicinia lyellii (Figure 24-Figure 27)

(syn. = *Pallavicinia radiculosa*)

Distribution

Pallavicinia lyellii (Figure 24-Figure 27) is a subcosmopolitan, temperate-tropical species (Stebel *et al.* 2018). It occurs in western and central parts of Europe, Asia, North, Central, and South America, northern and central Africa, and some areas in the Southern Hemisphere. Nevertheless, it is rare in Europe. Lavate *et al.* (2015) detailed its country locations, including Bermuda, Brazil, Cuba, England, Europe, Jamaica, Japan, Java, Kansaie, Moluccas, New Zealand, Philippines, Ryukya (Ryukyu?), Singapore, Sri Lanka, and West Indies.



Figure 24. *Pallavicinia lyellii* showing its typical life form. Photo by Jan-Peter Frahm, with permission.



Figure 25. *Pallavicinia lyellii* showing the ribbon-like life form. Photo by Jan-Peter Frahm, with permission.



Figure 26. *Pallavicinia lyellii* with narrow ribbons that suggest low light. Photo by Clive Shirley, Hidden Forest <hiddenforest.co.nz>, with permission.



Figure 28. Marshy habitat where *Pallavicinia lyellii* occurs. Photo by Des Callaghan, with permission.



Figure 27. *Pallavicinia lyellii* mat. Photo by Clive Shirley, Hidden Forest <hiddenforest.co.nz>, with permission.



Figure 29. *Pallavicinia lyellii* among grasses in marshy habitat. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Pallavicinia lyellii (Figure 24-Figure 27) occurs in thermal acidic sprays in the tropics (Ruttner 1955). In northwest Portugal it occurs on steep, water-dripping schist surfaces or moist clayey streambanks between herbs, in shaded or moderately exposed places in low altitudes (Vieira *et al.* 2005). It can also occur in marshes, as photographed by Des Callaghan (Figure 28-Figure 29), where the grasses and sedges provide protection from moisture loss. It forms small patches mixed with other bryophytes such as *Aneura pinguis* (Figure 30), *Solenostoma hyalinum* (Figure 31), and *Fissidens polyphyllus* (Figure 32) in mountain streams.



Figure 30. *Aneura pinguis*, a species that occurs with *Pallavicinia lyellii* in small patches in mountain streams. Photo by Hermann Schachner, through Creative Commons.



Figure 31. *Solenostoma hyalinum*, a species that occurs with *Pallavicinia lyellii* in small patches in mountain streams. Photo by Michael Lüth, with permission.



Figure 32. *Fissidens polyphyllus*, a species that occurs with *Pallavicinia lyellii* in small patches in mountain streams. Photo by David T. Holyoak, with permission.

Stebel *et al.* (2018) found that in Poland *Pallavicinia lyellii* (Figure 24-Figure 27) prefers damp or considerably wet habitats (Figure 33-Figure 37) and even grows in semi-aquatic conditions (Düll 1992). It grows on acidic to moderately acidic substrata and can live in moderately bright habitats (Stebel *et al.* 2018), but it is also very shade tolerant, as exemplified by its growth **under** a carpet of *Sphagnum* spp. (Figure 34) (Düll 1992; Dierßen 2001; Ellenberg & Leuschner 2010). Its light tolerance permits it to grow in open "bogs (Figure 35)," bog alder (*Alnus glutinosa*, Figure 36) or birch (*Betula pubescens*, Figure 37) forests, and beside wooded acid streams on moist soil (Figure 38), leaf litter, decaying wood (Figure 39), damp rocks (Figure 40), and rarely on exposed tree roots (Smith 1990; Dierßen 2001; Lavate *et al.* 2015; Mamontov *et al.* 2015). It doesn't seem to tolerate competition and thus is well-served by disturbed habitats with the right moisture.



Figure 33. *Pallavicinia lyellii* habitat at Cadnam Bog. Photo by Des Callaghan, with permission.



Figure 34. *Pallavicinia lyellii* under *Sphagnum*. Photo by Gill Stevens, with permission from BBS website.



Figure 35. Bohemia bog with *Sphagnum cuspidatum* and *S. denticulatum*. Photo by Jonathan Sleath, with permission.



Figure 36. *Alnus glutinosa* habitat where there is a suitable light level for *Pallavicinia lyellii* to grow. Photo by Sten Porse, through Creative Commons.



Figure 38. *Pallavicinia lyellii* in a wet habitat. Photo by Michael Lüth, with permission.



Figure 39. *Pallavicinia lyellii* on wet, rotting log. Photo by Richard Orr, with permission.



Figure 37. *Betula pubescens* habitat where there is a suitable light level for *Pallavicinia lyellii* to grow. Photo by Ingo2802, through Creative Commons.



Figure 40. *Pallavicinia lyellii* habitat. Photo by Michael Lüth, with permission.

Lavate *et al.* (2015) described the thallus of *Pallavicinia lyellii* (Figure 24-Figure 27) as **terricolous** (growing on soil or on ground) and **rupicolous** (growing on or among rocks), listing its habitats in India as moist soil on rocks, banks of freshwater streams (Figure 41), and cut surfaces as an associate with other liverworts. The relative humidity in these locations is typically 70-80%.



Figure 41. *Pallavicinia lyellii* growing streamside in Spain. Photo by Michael Lüth, with permission.

In Maryland, USA, *Pallavicinia lyellii* (Figure 24-Figure 27) occurs on soil, rotten wood (Figure 39), and tree bases in a stream valley (Glime 1966). In Florida, USA, White and Judd (1985) found it among the most conspicuous bryophytes at a ravine and adjacent uplands.

Sometimes *Pallavicinia lyellii* (Figure 24-Figure 27) seems to benefit from the shade of grasses, as observed by Gill Stevens at Wimbledon Downs (Figure 42-Figure 43).

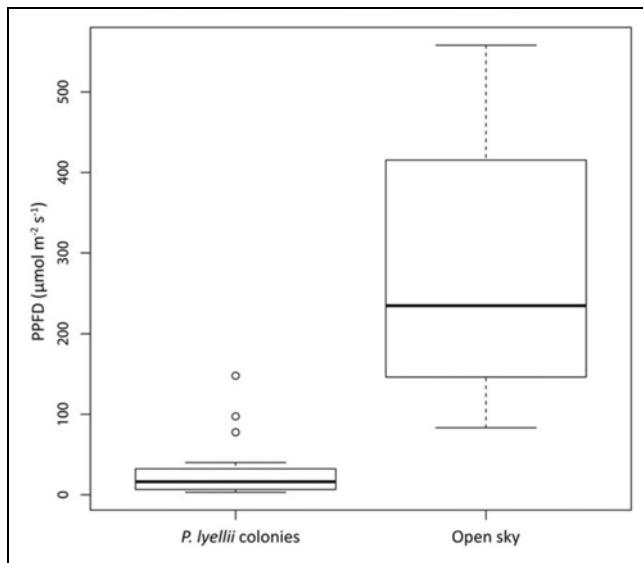


Figure 42. *Pallavicinia lyellii* photosynthetic photon flux density (PPFD), beneath canopies of *Molinia caerulea* and 1 m above (open sky), demonstrating the effect of cover on the liverwort. $n = 20$. Image by Des Callaghan, with permission.

Adaptations and Physiology

Pallavicinia lyellii (Figure 24-Figure 27) is a **short-lived shuttle** species (Smith 2006). This strategy permits it to inhabit the disturbed sites where it can enjoy the lack of competition.

Stebel *et al.* (2018) consider *Pallavicinia lyellii* (Figure 24-Figure 27) to be a **hemicryptophyte** (perennial plant having overwintering buds located at soil surface). It is sensitive to dehydration, but it has a prominent midrib that conducts water and that Stebel *et al.* and others (Dierßen 2001; Pence *et al.* 2005) suggest may serve as a buffer against the rapid loss of water. In some habitats it

grows with other bryophytes (Figure 44) (Vieira *et al.* 2005; Lavate *et al.* 2015), another potential mechanism for conserving water (Stebel *et al.* 2018). But it can also grow in solitary, dense mats, as seen in Figure 45.



Figure 43. *Pallavicinia lyellii* at base of *Molinia caerulea* at Wimbledon Commons, UK. Photo by Gill Stevens, from BBS website, with permission.



Figure 44. *Pallavicinia lyellii* with mosses and other plants. Photo by Blanka Agüera, with permission.



Figure 45. *Pallavicinia lyellii* on stream bank, North Carolina. Photo by Janice Glime.

Charissou and Hugonnot (2020) note that *Pallavicinia lyellii* (Figure 24-Figure 27) pioneers moist clods but it is especially sensitive to desiccation. Pence *et al.* (2005) found that a pretreatment for one week with 10 μ M ABA improved survival of desiccation in *Pallavicinia lyellii*. *Pallavicinia lyellii* was less responsive to ABA treatment than the aquatic *Riccia fluitans* (Figure 46), but more responsive than the more terrestrial *Marchantia polymorpha* (Figure 47). Untreated *Pallavicinia lyellii* took 120 minutes to reach the same level of desiccation as that reached by *Riccia fluitans* in 45 minutes (11%). ABA did not change the rate of drying in these two species, but it slowed the drying rate significantly in *Marchantia polymorpha*. Treated plants also exhibited an increase in total soluble carbohydrates.



Figure 46. *Riccia fluitans*, a species that more commonly floats in ponds and other quiet waters. Photo by Christian Fischer, through Creative Commons.

Reproduction

Pallavicinia lyellii (Figure 24-Figure 27) is **dioicous** (Figure 48) (Stebel *et al.* 2018). Sex distribution varies between populations (Figure 49). Both males and females often occur together (Figure 48-Figure 57). Vieira *et al.* (2005) reported that the species was fertile in a Portuguese stream habitat in March. These plants had mature

perigonia (Figure 52-Figure 57) and sporophytes (Figure 58-Figure 59).



Figure 47. *Marchantia polymorpha*, a species that usually does not occur under water. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 48. *Pallavicinia lyellii* showing inter-mixed female (red arrows) and male (white arrows), black fertilized. Photo by Des Callaghan, with permission.

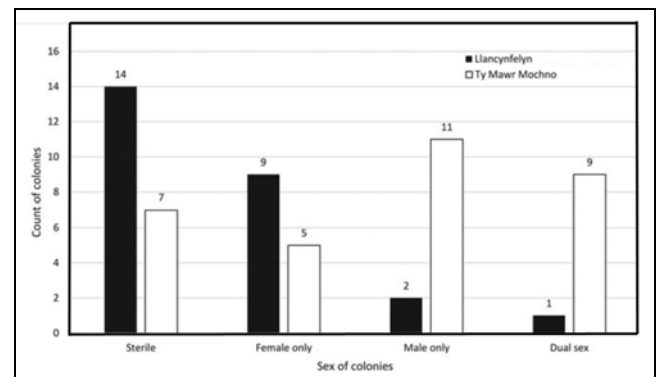


Figure 49. *Pallavicinia lyellii* sex distribution in 2 populations in Wales, showing differences in two locations. Modified from Des Callaghan, with permission.



Figure 50. *Pallavicinia lyellii* male. Photo by Blanka Aguera, with permission.



Figure 53. *Pallavicinia lyellii* female with lacinate scales that surround a group of archegonia. Photo by Des Callaghan, with permission.



Figure 51. *Pallavicinia lyellii* male with antheridia. Photo by Tom Thekathyl, with permission.



Figure 54. *Pallavicinia lyellii* with lacinate scales surrounding an emerging perianth. Photo by Jan-Peter Frahm, with permission.

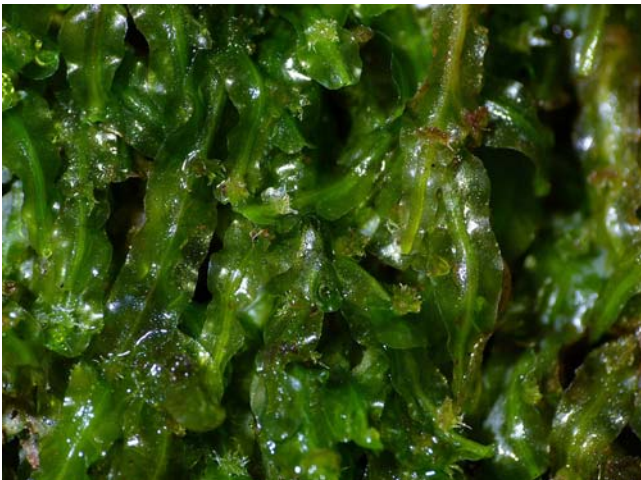


Figure 52. *Pallavicinia lyellii* wet, with archegonia. Photo by Shyamal L, through Creative Commons.



Figure 55. *Pallavicinia lyellii* with senescing branches. Photo by Jeremy Collison, through Creative Commons.



Figure 56. *Pallavicinia lyellii* perianths. Photo by Blanka Aguero, with permission.



Figure 57. *Pallavicinia lyellii* young sporophyte still inside perianth (arrow). Photo courtesy of Des Callaghan.



Figure 58. *Pallavicinia lyellii* with emerging sporophytes. Photo by Jan-Peter Frahm, with permission.



Figure 59. *Pallavicinia lyellii* with dehiscent capsule. Photo by John Bradford, with permission.

Biochemistry

The oil bodies (Figure 60) of *Pallavicinia lyellii* (Figure 24-Figure 27) are small, numerous per cell, and very variable in shape (Juslén *et al.* 2021). Ebner (2016) expressed surprise that despite the great variety of natural products in liverworts, he was only able to find already known compounds, including terpenes, fatty acids, and sterols in *Pallavicinia lyellii*.

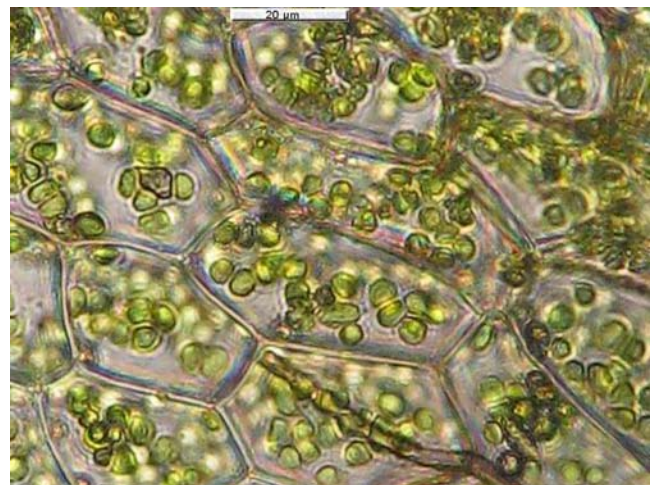


Figure 60. *Pallavicinia lyellii* thallus cells, showing the difficulty of observing oil bodies. Photo by Tom Thekathiyil, with permission.

Adler (1983) identified the 4-desmethylsterol fraction in *Pallavicinia lyellii* (Figure 24-Figure 27). Rajan and Murugan (2010) extracted ascorbate peroxidase from

Pallavicinia lyellii. This enzyme performed optimally at 40°C. The authors suggested that this pathway may contribute to desiccation tolerance in *P. lyellii*.

Williams *et al.* (2016) found that ***Pallavicinia lyellii*** (Figure 24-Figure 27) has remarkable inhibitory activity against bacterial pathogens. Subhisha and Subramoniam (2005) reported antifungal activity by a steroid from this species. Extracts of ***Pallavicinia lyellii*** inhibited ***Pseudomonas aeruginosa*** (bacterium; Figure 61) and exhibited the greatest antibacterial activity against ***Escherichia coli*** (Figure 62) among the nine liverworts tested (Linde *et al.* (2016).

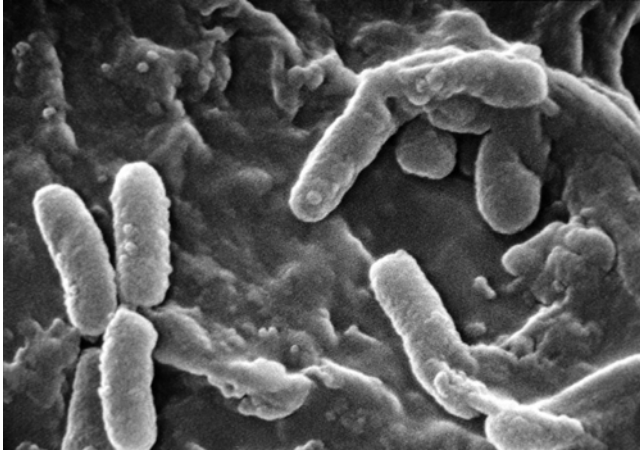


Figure 61. ***Pseudomonas aeruginosa*** SEM. Photo by Janice Haney Carr, CDC, through public domain.



Figure 62. ***Escherichia coli*** SEM with color added. Photo by Niaid, through Creative Commons.

Summary

These members of the **Pallaviciniales** are at best facultatively aquatic. On the other hand, they like moist habitats such as stream banks, wet cliffs, and the spray of waterfalls. ***Hymenophyton flabellatum*** is able to form a mycorrhizal relationship with fungi in **Glomeromycota**. No fungal relationships seem to be known in the **Pallaviciniaceae** included here.

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CHAPTER 1-16

AQUATIC AND WET MARCHANTIOPHYTA, PELLIALES

TABLE OF CONTENTS

SUBCLASS PELLIIDAE	1-16-2
Pelliales: Pelliaceae	1-16-2
<i>Pellia</i>	1-16-2
<i>Pellia appalachiana</i>	1-16-3
<i>Pellia endiviifolia</i>	1-16-5
<i>Pellia epiphylla</i>	1-16-12
<i>Pellia neesiana</i>	1-16-25
Summary	1-16-33
Acknowledgments	1-16-33
Literature Cited	1-16-33

CHAPTER 1-16

AQUATIC AND WET MARCHANTIOPHYTA, PELLIALES



Figure 1. *Pellia endiviifolia* by stream. Photo by J. Claude, through Creative Commons.

Nomenclature for this subchapter is based primarily on Söderström *et al.* (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species.

SUBCLASS PELLIIDAE

Pelliales: Pelliaceae

Pellia (Figure 1Figure 3-Figure 4, Figure 19-Figure 20, Figure 49-Figure 52, Figure 96-Figure 103)

Pellia sp. occurs at the base of the Flume wall and on ledges of the Flume at Franconia Notch, New Hampshire, USA (Figure 2) (Glime 1982), an environment that is always humid. In West Virginia, USA, mountain streams, members of this genus preferred pH 6.6 (Stephenson *et al.* 1995).



Figure 2. Flume, Franconia Notch, New Hampshire, USA, a habitat where one can find *Pellia* on the ledges and the base of the cliffs. Photo by Janice Glime.

Pellia appalachiana* (Figure 3-Figure 4)*Distribution**

Pellia appalachiana (Figure 3-Figure 4) is endemic to the southeastern USA (Alabama, Georgia, Kentucky, North Carolina, South Carolina, Tennessee) (Southern Appalachian Bryophytes 2019).



Figure 3. *Pellia appalachiana* female with involucre. Photo by Paul G. Davison, with permission.



Figure 4. *Pellia appalachiana* forming a large rosette, suggesting it originated from a single spore. **Arrows** indicate female with involucre. Photo by Paul G. Davison, with permission.

Aquatic and Wet Habitats

The species of *Pellia* included here have similar habitats. *Pellia appalachiana* (Figure 3-Figure 4) is intolerant of desiccation, so its habitats are ones that are constantly moist (Southern Appalachian Bryophytes 2019). It thrives where the habitat has periodic disturbance, especially stream banks (Figure 5-Figure 7) that experience episodes of scouring or muddy-rocky shelves associated with waterfalls. When it grows on vertical walls, mats may slough off, providing a bare surface for spores to

germinate. Such habitats are available in **rockhouses** (shallow cave-like opening at the base of a bluff or cliff; Figure 8). Zartman and Pittilo (1998) found it in spray cliff communities of the Chattooga Basin in the southern Blue Ridge.



Figure 5. *Pellia appalachiana* on soil that is periodically inundated at edge of stream. Photo by Paul G. Davison, with permission.



Figure 6. *Pellia appalachiana* habitat at edge of stream. Photo by Paul G. Davison, with permission.



Figure 7. *Pellia appalachiana* habitat on stream bank. Photo by Paul G. Davison, with permission



Figure 8. *Pellia appalachiana* rock house habitat, Alabama. Photo by Paul G. Davison, with permission.

Adaptations

Pellia appalachiana (Figure 3-Figure 4) can grow with other bryophytes that are not too aggressive, most likely benefitting from greater moisture-holding ability. The ribbon-like structure also helps to minimize the effects of abrasion in their streamside habitat where inundation can bring mud and sand or small stones (Southern Appalachian Bryophytes 2019).

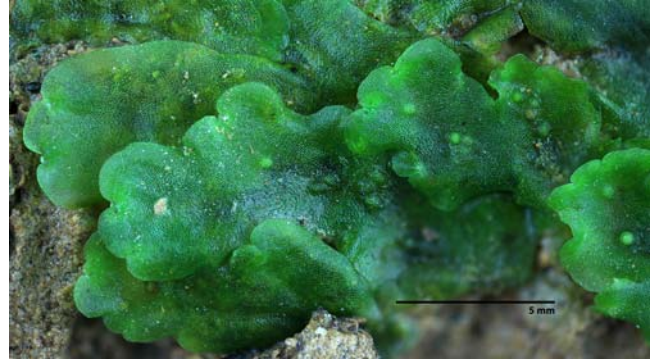


Figure 10. *Pellia appalachiana* with young antheridial pustules. Photo by Paul Davison, with permission.



Figure 11. *Pellia appalachiana* with maturing antheridia. Photo by Paul G. Davison, with permission.



Figure 9. *Pellia appalachiana* growing with *Pellia epiphylla*, *Pallavicinia lyellii*, *Nardia lescurii*, and *Sphagnum* sp. Photo by Paul Davison, with permission.

Reproduction

Pellia appalachiana (Figure 3-Figure 4) is **dioicous** (Southern Appalachian Bryophytes 2019). Its antheridia (Figure 10- Figure 11) are sunken in dorsal pustules that are scattered along the midrib area. The archegonia (Figure 12-Figure 18) are at the base of a lobed involucre. The reproductive organs are typically absent on the new spring growth, but can often be located on older thalli hidden by the new growth.



Figure 12. *Pellia appalachiana* female showing involucres (arrows). Photo by Paul G. Davison, with permission.



Figure 13. *Pellia appalachiana* female involucres (arrows). Photo by Paul G. Davison, with permission.



Figure 14. *Pellia appalachiana* female involucres (arrows). Photo by Paul G. Davison, with permission.

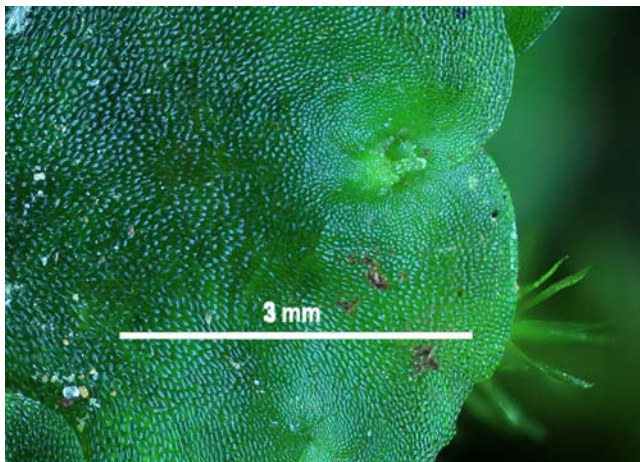


Figure 15. *Pellia appalachiana* female involucre with tip of archegonium protruding. Photo by Paul G. Davison, with permission.

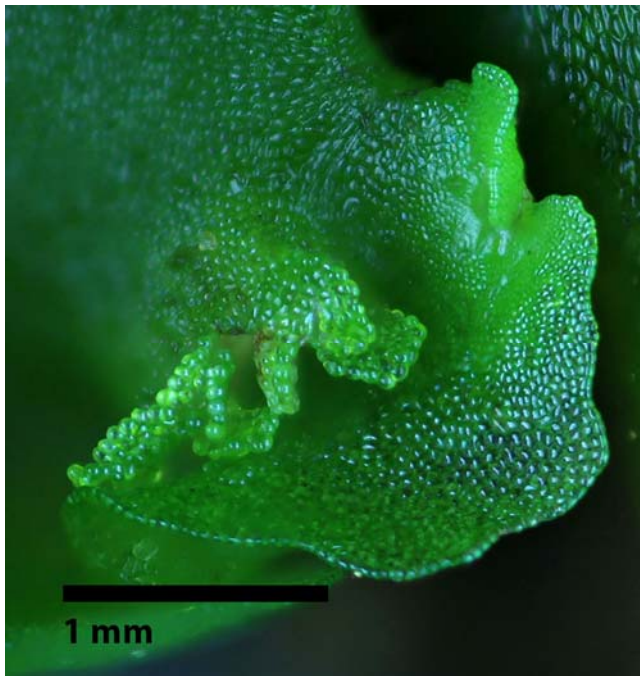


Figure 16. *Pellia appalachiana* female involucre showing lobes. Photo by Paul G. Davison, with permission.



Figure 17. *Pellia appalachiana* lobed female involucre. Photo by Paul G. Davison, with permission.

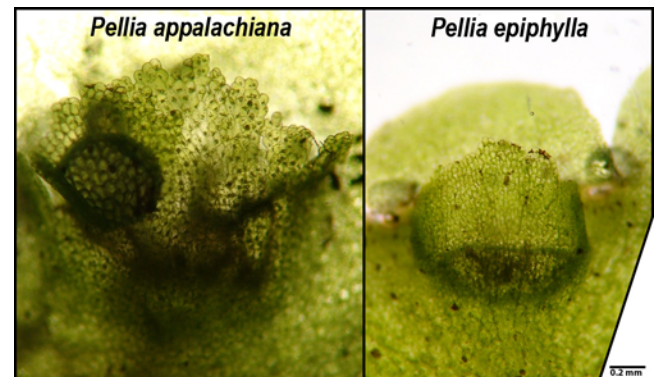


Figure 18. Comparison of the lobed involucre of *Pellia appalachiana* with the unlobed involucre of *Pellia epiphylla*. Photo modified from Paul G. Davison, with permission.

Pellia endiviifolia (Figure 19-Figure 20)

(syn. = *Pellia calycina*, *Pellia endivifolia*, *Pellia fabroniana* var. *lorea*)

Distribution

Pellia endiviifolia (Figure 19-Figure 20) is widely distributed in the Northern Hemisphere (Parzych *et al.* 2018). Dhien (1983) considers it to be circumboreal. It occurs through a large portion of Europe from Denmark and Belgium, southward to Italy, Spain, and Portugal, and further to North Africa (Schuster 1992). In Asia it is known from Japan, Siberia, Taiwan, China, and possibly India. Schuster disallows reports from North America, instead considering these to be *Pellia epiphylla* (Figure 49-Figure 51), *P. neesiana* (Figure 96-Figure 103), and *P. megaspora* (Figure 21).



Figure 19. *Pellia endiviifolia*. Photo from Snappy Goat, through public domain.



Figure 20. *Pellia endiviifolia* with dark coloration that suggests exposure to bright light. Photo by Des Callaghan, with permission.



Figure 21. *Pellia megaspora*, one of the species Schuster accepted as occurring in North America. Photo by Jean Faubert, with permission.

Aquatic and Wet Habitats

Szoszkiewicz *et al.* (2006) listed *Pellia endiviifolia* (Figure 19-Figure 20) among the river species. It is among the most common bryophytes in the River Tweed, UK (Holmes & Whitton 1975). It is scattered in the River Swale, Yorkshire, UK (Holmes & Whitton 1977b). The species occurs on travertine in the *Cratoneuron* association of Lorraine River, Belgium (de Sloover & Goossens 1984) and in the *Fissidens grandifrons* (Figure 22) community in calcareous water (Gil & Ruiz 1985). In Thuringia,

Germany, it can be found in the *Platyhypnidium* (Figure 23)-*Fontinalis antipyretica* (Figure 24) association (Marstaller 1987). The streams are typically oligotrophic (Trempl 2003), as in the Alsatian Rhine valley (Vanderpoorten & Palm 1998; Vanderpoorten *et al.* 1999), in Belgian streams (Vanderpoorten & Tignon 2000), and in Iskur River and its main tributaries in Bulgaria (Papp *et al.* 2006).



Figure 22. *Fissidens grandifrons* wet at stream edge where it might occur with *Pellia endiviifolia*. Photo by Scot Loring, through Creative Commons.



Figure 23. *Platyhypnidium riparioides* in water, inhabiting the type of stream where one might find *Pellia endiviifolia*. Photo by Hermann Schachner, through Creative Commons.



Figure 24. *Fontinalis antipyretica*, a species that may indicate habitat suitability for *Pellia endiviifolia*. Photo by Matt Goff (www.sitkanature.org), with permission.

Papp (1998) found *Pellia endiviifolia* (Figure 19-Figure 20) to be common in streams (Figure 1) in Greece. Likewise, Scarlett and O'Hare (2006) reported that it is among the commonest species in English and Welsh rivers. It has a wide ecological amplitude, at times being exposed and other times inundated during periods of high flow (Pentecost & Zhang 2006; Pentecost & Zhaohui 2006).

Pellia endiviifolia (Figure 19-Figure 20) is among the most frequent species in Europe in association with rivers and streams, typically occurring on travertines (Pentecost & Zhang 2006). In Montenegro, it occurs at springs, rivers, and streams in Tara River canyon and the Durmitor area (Papp & Erzberger 2011). It occurs in poorly mineralized and basic waters in the Tiber River basin of Italy, where it does not seem to be influenced by phosphate concentrations (Ceschin *et al.* 2012).

In Ireland Weekes *et al.* (2018) found *Pellia endiviifolia* (Figure 19-Figure 20) in association with *Fontinalis antipyretica* (Figure 24) or *Hygroamblystegium fluviatile* (Figure 25), as described also by Bailly (2012). It typically was submerged or in the splash zone of shady, calcareous rivers, especially with overhanging trees or bridges. Although it has a high presence in these areas, it has low cover values. In Portugal, Vieira *et al.* (2005) included it among the threatened bryophytes.



Figure 25. *Hygroamblystegium fluviatile*, an associate of *Pellia endiviifolia*. Photo by Michael Lüth, with permission.

Some populations of *Pellia endiviifolia* (Figure 19-Figure 20) occur in river beds and brook beds, as reported by Konstantinova *et al.* (2009) for *Pellia endiviifolia* from the valley of the Bushujka River in the western Caucasus, Russia. It even occurs in artificial waterways with flowing water. Dhien (1983) reported it from canal water and on its banks.

But many populations of *Pellia endiviifolia* (Figure 19-Figure 20) seem to meet their needs out of the water (Figure 26), on stream banks and river banks. It occurs on the river bank of the River Tees, UK (Holmes & Whitton 1977b) and is similarly associated with the River Wear, England (Birch *et al.* 1988). In the Caucasus, it occurs on the bank of a Zakan River tributary and on rocks on stream banks, especially those rich in calcium and receiving splash (Konstantinova *et al.* 2009). Some of these bank locations are on soil on the banks of subalpine streams and the edges of forest streams. Weekes *et al.* (2018) similarly found it

either submerged or in the splash zone of streams and rivers in Ireland, preferring calcareous conditions and shade. But in contrast to many studies, these researchers reported it from margins of fast-flowing **mesotrophic** water. In some locations it grew on clay banks in the shade of *Petasites hybridus* (Figure 27), the latter protecting it from competition.



Figure 26. *Pellia endiviifolia* habitat out of water in India. Photo by Michael Lüth, with permission.



Figure 27. *Petasites hybridus* along river, a plant that often occurs in dense patches that can provide shade for *Pellia endiviifolia*. Photo through Creative Commons.

There seem to be few records of the association of *Pellia endiviifolia* (Figure 19-Figure 20) with lakes. It occurs in wet places around lakes in Scotland, especially in the shade (West 1910). In the Caucasus, Russia, it can occur on the banks of pools.

Watson (1919) reported *Pellia endiviifolia* (Figure 19-Figure 20) from waterfalls (Figure 28). Hazrat *et al.* (2020) found it in association with waterfalls in deep shade in Pakistan. Konstantinova *et al.* (2009) found that on streambanks in the Caucasus, it was especially associated with areas near waterfalls.



Figure 28. *Pellia endiviifolia* near Swallow Falls, Wales, where the habitat remains humid. Photo by Janice Glime.

In Ireland, Pilkington (2003) found it on wet rock faces that are continually irrigated by water trickling down, typically with large, mossy tufts.

Pakalne and Čakare (2001) documented the presence of *Pellia endiviifolia* (Figure 19-Figure 20) on steep river ravine slopes at the springs in the Gauja National Park, Latvia. This was often a marginal zone between the spring and mire vegetation. In the Netherlands it can be among the dominant bryophytes of cold springs (Sýkora 2006).

Some populations of *Pellia endiviifolia* (Figure 19-Figure 20) thrive in bogs and boggy habitats. In the Caucasus, Russia, it occurs in boggy meadows and bogs of subalpine meadows. Weekes *et al.* (2018) reported it from vertical peat banks associated with fast-flowing water in Ireland. Lewis (1976) described it as "creeping over the wet, peaty surfaces" in the northern isles of Shetland, where it can achieve high cover values.

Even moist cliffs can satisfy the needs of *Pellia endiviifolia* (Figure 19-Figure 20). Konstantinova *et al.* (2009) found it on moist cliffs in the western Caucasus, Russia, often associated with streams. Milliken and Pendry (2002) found it in cliff flushes where it occurs in continuous water flow on the rock face, usually in small patches.

Other occurrences take advantage of muddy soils, both wet and dry, and even on tree trunks (Figure 29) in Pakistan, but these don't seem to be preferred habitats (Hazrat *et al.* 2020). On Mount Boranja, West Serbia, *Pellia endiviifolia* (Figure 19-Figure 20) occurs on humid soil (Pantović & Sabovljević 2013).

Lo Giudice and Cristaudo (2004) note that in the mountains of Sicily *Pellia endiviifolia* (Figure 19-Figure 20) occurs on wet calcarenite rocks where it is mostly shaded by herbaceous plants. Boucard *et al.* (2013) noted that most of the low-shore bryophytes, including *Pellia endiviifolia*, have been neglected in studies, whereas those associated with active tuffs, also including *Pellia endiviifolia*, have been included in phytosociological surveys. It forms an association there with *Cratoneuron filicinum* (Figure 30).



Figure 29. *Pellia endiviifolia* on bark in a moist habitat. Photo by Martin Hutten, with permission.

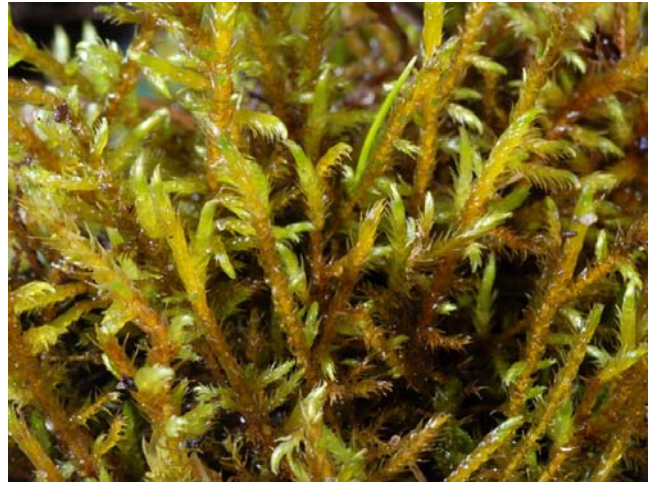


Figure 30. *Cratoneuron filicinum*, a species that accompanies *Pellia endiviifolia* in low-shore environments. Photo by J. C. Schou, with permission.

Physiology

It has been difficult to understand how facultative aquatic bryophytes, such as *Pellia endiviifolia* (Figure 19-Figure 20), in calcareous waters are able to obtain sufficient CO₂ for photosynthesis and subsequent growth. In these high pH waters, CO₂ is readily converted to bicarbonates and carbonates. This understanding has been complicated by the assumption that all bryophytes are C₃ plants (Smith & Griffiths 1996), requiring free CO₂. For whatever reason, the pyrenoids that help many algae to concentrate CO₂ did not continue in any bryophyte lines except for the hornworts.

Pellia endiviifolia (Figure 19-Figure 20) lacks the internal ventilation (Figure 31) present in some thallose liverworts, such as *Marchantia* spp (Figure 32-Figure 33) (Meyer *et al.* 2008). This imposes limitations on the internal storage of free CO₂ needed for photosynthesis. Instead, species of *Pellia* are diffusion limited (Griffiths *et al.* 2004). *Pellia* has a simple thallus with no pores and a C₃ pathway of photosynthesis (Meyer *et al.* 2008). It is furthermore desiccation intolerant, thus requiring that CO₂ must enter the plants through water when it is submersed or in high humidity or splash. It in fact has "an extremely narrow" range of optimal water content" during maximal electron transport.

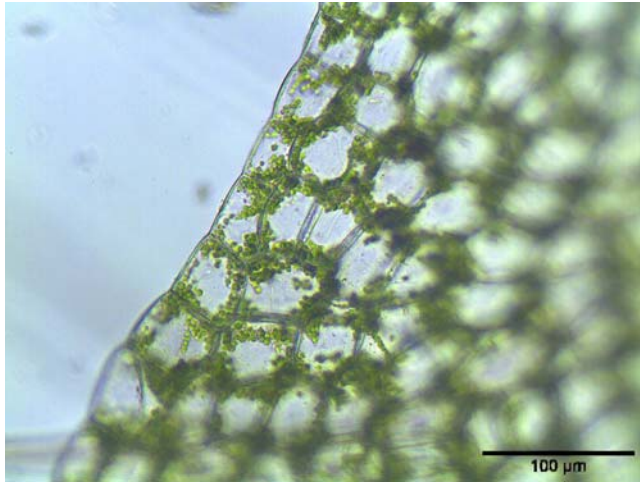


Figure 31. *Pellia endiviifolia* thallus showing lack of air chambers. Photo by Christian Fischer, through Creative Commons.



Figure 32. *Marchantia polymorpha* with isopod. Photo by Walter Obermayer, with permission.



Figure 33. *Marchantia polymorpha* thallus section through pore, showing internal chamber. Photo by Jennifer Steele, with permission through Botany Website.

Griffiths *et al.* (2004) suggested that understanding of the genes and regulatory processes related to pyrenoids and multiple plastids is necessary to understand the selective pressures that have shaped the evolutionary changes in bryophytes. For example, in the hornwort genus *Megaceros* (Figure 34), there is a gradual loss of the pyrenoid associated with the development of the multiplastidic condition. At the same time, it appears that the thalli of liverworts went from the simple, non-porous types like those of *Pellia* (Figure 19-Figure 20, Figure 31) to the chambered type in *Marchantia* (Figure 32-Figure 33) with access to the atmosphere through pores. But this advantage for CO₂ acquisition creates a more rapid loss of water from the thallus.



Figure 34. *Megaceros* with capsules, a genus in which pyrenoids diminished as multiplastidic species evolved. Photo by David Tng <www.davidtng.com>, with permission.

Because bryophytes take in water directly through the gametophyte tissues, in this case through the thallus, they tend to reflect the concentrations of minerals in the water. Satake *et al.* (1987) determined the elemental concentrations of selected nutrients and heavy metals in *Pellia endiviifolia* (Figure 19-Figure 20). The mean concentrations of major essential elements in the liverwort thalli were 49,600 $\mu\text{g g}^{-1}$ K, 9,140 $\mu\text{g g}^{-1}$ Na, 6,740 $\mu\text{g g}^{-1}$ Ca, 3,840 $\mu\text{g g}^{-1}$ P, and 3,060 $\mu\text{g g}^{-1}$ Mg. When the field sites were polluted with the heavy metals Cu, Zn, and Pb, these appeared in high concentrations in the thalli of *Pellia endiviifolia* (maxima 0.88% Cu, 0.55% Zn, and 0.36% Pb in the older thalli).

Parzych *et al.* (2018) again assessed the accumulative possibilities of *Pellia endiviifolia* (Figure 19-Figure 20) for N, P, K, Mg, Ca, Zn, Fe, Cu, Ni, Mn, Al, and Sr. The nutrients normally considered to be macronutrients accounted for 96% of this pool. Nitrogen constituted 40% of this sum, phosphorus 4.9%, potassium 38%, magnesium 5%, calcium 12%, and trace elements 3.8% of this sum. Among the trace elements, iron was dominant (56.3%), manganese 24.8%, and aluminum 17%; other elements comprised less than 1%. *Pellia endiviifolia* accumulated high concentrations of iron and manganese, thus suggesting its usefulness as a bioaccumulator and a purification agent. Their research indicated that accumulation of Mg, Fe, and Cu was influenced by the environmental conditions, whereas N, P, K, Ca, Zn, Ni, Mn, Al, and Sr were determined by the species itself. Staniszewski (2001) used

Pellia endiviifolia as a bioindicator in the Kujawskie Lakeland, Poland.

Adaptations

Pellia endiviifolia (Figure 19-Figure 20) can form pure **mats** (Figure 1) (Konstantinova *et al.* 2009). These help to conserve water and to reduce drag during times of flooding. At other locations, it might exist with other liverworts, especially *Conocephalum* (Figure 35) and *Chiloscyphus* (Figure 36), or mosses (Figure 37), again having the potential to conserve moisture.



Figure 35. *Conocephalum salebrosum*; *Pellia endiviifolia* sometimes grows with a member of this genus. Photo by Richard Draker, through Creative Commons.



Figure 36. *Chiloscyphus polyanthos*, a species that often accompanies *Pellia endiviifolia*. Photo by Hermann Schachner, through Creative Commons.



Figure 37. *Pellia endiviifolia* growing with mosses. Photo by Jean Faubert, with permission.

Reproduction

Pellia endiviifolia (Figure 19-Figure 20) is **dioicous** (Sierocka *et al.* 2014). Sierocka *et al.* identified a female-specific gene expression in *Pellia endiviifolia* (Figure 38) and determined its developmental regulation and connection to the production of archegonia. They recognized three genes that are expressed only in females. The archegonial tissue exhibited a 10-fold increase in transcript level for all three of these genes compared to the vegetative parts of the same female thalli. These genes appear to be developmentally regulated. Male plants are recognizable by their often red blisters scattered around the middle of the thallus (Figure 38-Figure 45). Female plants are recognizable by the collar-like involucre that surrounds the archegonia (Figure 38, Figure 46). Sporophytes are known (Figure 47).



Figure 38. *Pellia endiviifolia* males with reddish antheridial cavities and females in center. Photo by David T. Holyoak.



Figure 39. *Pellia endiviifolia* males. Photo by Hermann Schachner, through Creative Commons.



Figure 40. *Pellia endiviifolia* with antheridia. Photo by Hugues Tinguy, with permission.

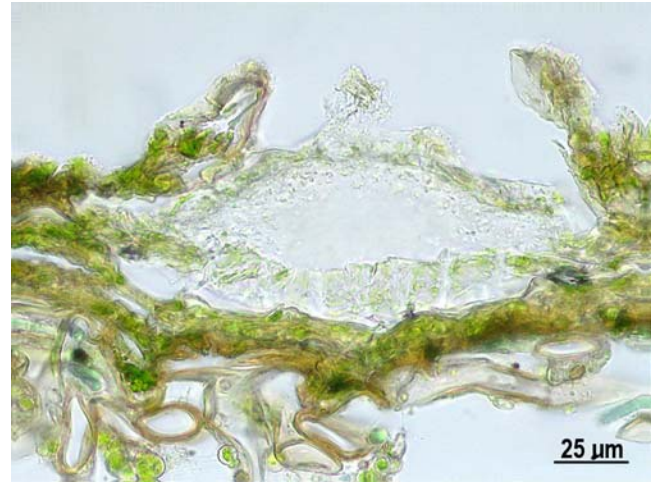


Figure 43. *Pellia endiviifolia* thallus cross section through antheridium. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 41. *Pellia endiviifolia* with antheridia. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

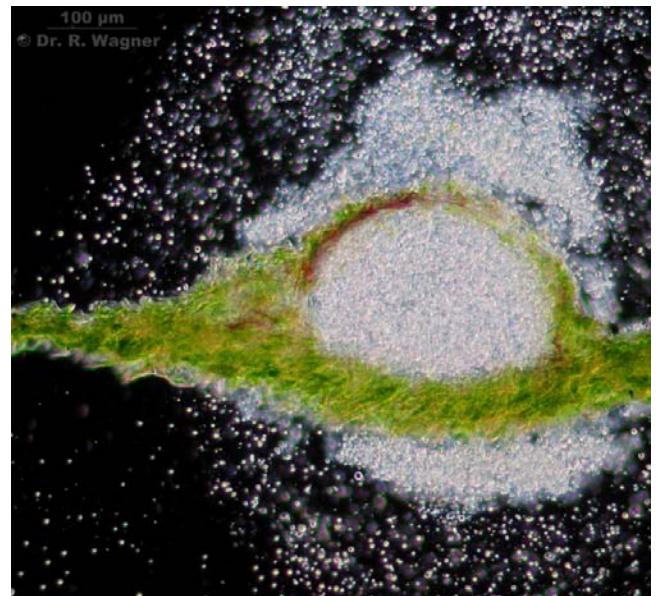


Figure 44. *Pellia endiviifolia* cross section with antheridium and escaping spermatocytes. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

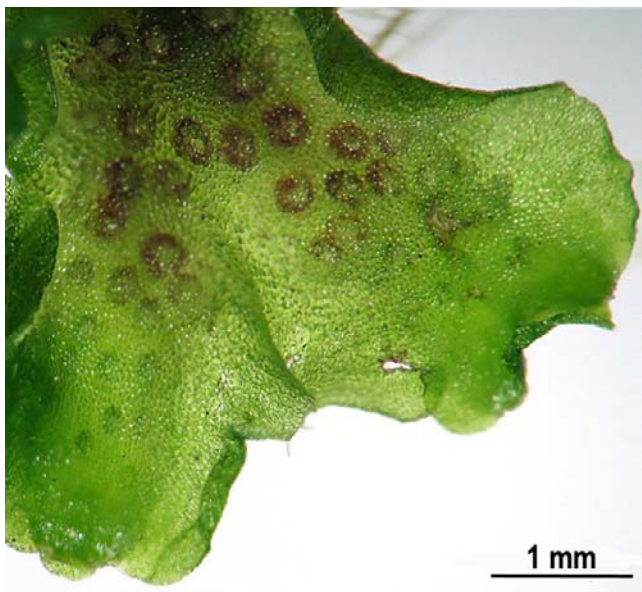


Figure 42. *Pellia endiviifolia* with antheridia. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

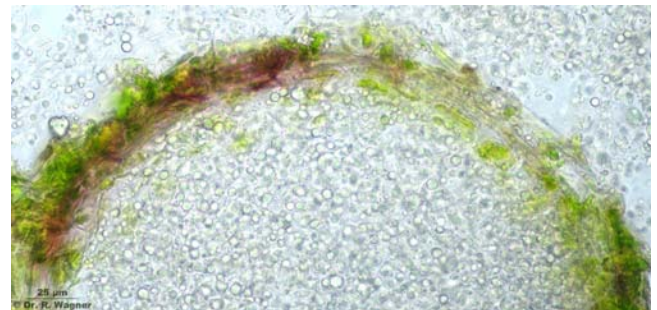


Figure 45. *Pellia endiviifolia* antheridium cross section and spermatocytes. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 46. *Pellia endiviifolia* females showing involucre. Photo by David T. Holyoak, with permission.



Figure 47. *Pellia endiviifolia* nearly mature capsules. Photo from Snappy Goat, through public domain.

Vojtkó (1993) described spore morphology in 29 liverwort species. The only elliptic spores in the study were in *Pellia endiviifolia* (Figure 19-Figure 20). At the same time, this was also the largest spore (80x65 µm). The spore also had "surprisingly" thin walls compared to the other spores studied.

Biochemistry

Ono *et al.* (1992) confirmed the presence of the pungent diterpene dialdehyde, sacculatal in *Pellia endiviifolia* (Figure 19-Figure 20). Later, Mehmeti (2009), using GCMS-GC, likewise found sacculatal and several derivatives to be the predominant components of the volatiles in this pungent liverwort in Tokushima, Japan. Asakawa (2004) suggested a lack of oil bodies in *Pellia* might explain the paucity of volatiles in the species tested. However other authors have noted the presence of oil bodies (Pihakaski 1972; Pihakaski & Pihakaski 1979, 1980), although at least in *Pellia neesiana* they are tiny (Figure 136) (Schuster 1992).

Hashimoto *et al.* (1995) found that the pungent 1,β-hydroxysacculatal and sacculatal in *Pellia endiviifolia* (Figure 19-Figure 20) exhibit piscicidal activity by killing killie-fish in 20 min at 1 ppm.

Alaba *et al.* (2015) attempted to show microRNA relationships between green algae and liverworts, using the green alga *Chlamydomonas reinhardtii* (Figure 48) and liverwort *Pellia endiviifolia* (Figure 19-Figure 20). Until this study, no microRNA sequences were known from liverworts, but gene expression had only been studied in *Marchantia polymorpha* (Figure 32). They discovered an impressive array of 311 conserved microRNAs known from plant families in addition to 42 new liverwort-specific microRNAs. Nevertheless, degradome analysis revealed that target mRNAs of only three microRNAs (miR160, miR166, and miR408) have been conserved between liverworts and other land plants. Three of the liverwort microRNAs show high similarity to previously reported microRNAs from *Chlamydomonas reinhardtii*.



Figure 48. *Chlamydomonas reinhardtii*, a green alga species that shares three microRNAs with *Pellia endiviifolia*. Photo by Yuuji Tsukii, with permission.

Pellia epiphylla (Figure 49-Figure 51)

(syn. = *Pellia fabbroniana*)

Distribution

Pellia epiphylla (Figure 49-Figure 51) is known from North America, Europe, North Africa, and nearby areas of Asia (Boll 2020).



Figure 49. *Pellia epiphylla* mat with a few mosses mixed in. Photo by Kristian Peters, with permission.



Figure 50. *Pellia epiphylla* forming tight layers that can help to conserve water. Photo by Michael Lüth, with permission.



Figure 52. *Pellia epiphylla* that is at least partially submersed. Photo by Ken McFarland and Paul Davison, with permission.



Figure 51. *Pellia epiphylla* on soil at Cwm Idwal National Nature Reserve 357 in Wales. Photo by Janice Glime.



Figure 53. *Pellia epiphylla* habitat under grass bank of flush at Cwm Idwal National Nature Reserve 39, Wales. Photo by Janice Glime.

Aquatic and Wet Habitats

Boll (2020) described *Pellia epiphylla* (Figure 49-Figure 51) as a liverwort that "loves very humid places," growing close to rivers and other watercourses (Figure 52). Watson (1919) described it from margins of fast streams, on banks with frequent submergence and slow water, submerged in slow water with poor mineral salts, waterfalls, wet rocks and soil near fast streams, and margins of fast streams on wet rocks or soil. Coroi *et al.* (2004) considered *Pellia epiphylla* to be a wetland indicator in streamside forests. Ferreira *et al.* (2008) attributed it to rivers. Marczonek (1984) investigated the ecology of *Pellia epiphylla* populations. In Wales, I found it growing on the sides of flushes, shaded by overhanging grasses (Figure 53).

In the British Isles, *Pellia epiphylla* (Figure 49-Figure 51) is among the most common bryophytes in the River Tweed (Holmes & Whitton 1975). It occurs on the river bank of the River Tees (Holmes & Whitton 1977a) and the upper to midstream of the River Swale (Holmes & Whitton 1977b). In the River Tyne, it occurs throughout (Holmes & Whitton 1981). Scarlett & O'Hare (2006) considered it to be among the commonest species in English and Welsh rivers.

Elsewhere in Europe, in the Sudeten Mountains of Poland and the Czech Republic, *Pellia epiphylla* (Figure 49-Figure 51) occurs in streams (Samecka-Cymerman & Kempers 1998), especially in waters affected by mineralization zones (Samecka-Cymerman & Kempers 1993). In Germany, it occurs in slow-flowing water in Westfalens, northwestern Germany (Koppe 1945), in the upper and middle reaches in the Harz Mountains (Bley 1987), and submersed or above water in the *Platyhypnidium* (Figure 23)-*Fontinalis antipyretica* (Figure 24) association, Thuringia, Germany (Marstaller 1987). It often occurs just above *Platyhypnidium riparioides* (Figure 23) (Gimingham & Birse 1957). In northwest Portugal, it occurs in mountain streams (Vieira *et al.* 2005). It likewise occupies streams in the northeastern part of Finland (Heino & Virtanen 2006). On Madeira Island, it occurs at low altitudes, in a narrow stream, and where there is low flow in mountainous streams (Luis *et al.* 2015).

Most North American findings of *Pellia epiphylla* (Figure 49-Figure 51) have been above the water on stream banks rather than submersed, although the plants can be submersed for a short time in spring or other times when

the streams and rivers experience flooding. Steinman and Boston (1993) report only a small amount present at most of their research sites in Walker Branch, Tennessee.

Sørensen (1948) reported *Pellia epiphylla* (Figure 49-Figure 51) at a water pH of 7.7 in streaming water in Denmark. However, in West Virginia mountain streams its preferred pH was 4.17 (Stephenson *et al.* 1995).

Pellia epiphylla (Figure 49-Figure 51) can also occupy irrigation ditches (Beaucourt *et al.* 1987).

But *Pellia epiphylla* (Figure 49-Figure 51) seems to occur most commonly on stream banks, especially in North America. In the Western Carpathians near Lacko, Mamczarz (1970) attributed it to rocks and water communities associated with streams. In the Komi Republic of Russia it occurs on soil on river banks. Leclercq (1977) reported it from earthy and gravelly substrates of river banks in Haute Ardenne rivers, Belgium.

Greenwood (1911) commented that *Pellia epiphylla* (Figure 49-Figure 51) is common in some locations, growing on the ground in damp shaded places and preferring stream banks where it can be submerged or just above the water line, often extending a meter or more from the water's edge.

In North America, *Pellia epiphylla* (Figure 49-Figure 51) might be restricted to stream and river banks. In my own meanderings, I have never seen it submersed, but it is common on the banks immediately adjacent to streams. These locations can, of course, be submerged during high flows, but typically not for more than a few days.

In Connecticut, USA, Nichols (1916) reported *Pellia epiphylla* (Figure 49-Figure 51) from moist rock surfaces or springy banks of ravines, wet, sandy streambanks, and along calcareous rivers. Greenwood (1923) found it on moist, shaded banks, accompanied by *Conocephalum conicum* (Figure 54) and *Bazzania trilobata* (Figure 55) in Center County, Pennsylvania, USA.



Figure 54. *Conocephalum conicum* at a stream edge where it is often accompanied by *Pellia epiphylla*. Photo by David Holyoak, with permission.

There seem to be few records of *Pellia epiphylla* (Figure 49-Figure 51) specifically from springs. Sørensen (1948) recorded it at pH 7.1 in springs in Denmark.



Figure 55. *Bazzania trilobata*, a species that often accompanies *Pellia epiphylla* on stream banks. Photo by Bernd Haynold, through Creative Commons.

Similarly, it appears to be much less common in association with lakes than with streams and rivers. Toivonen and Huttunen (1995) reported *Pellia epiphylla* (Figure 49-Figure 51) from small lakes in southern Finland. It occurs in wet places around lakes, especially in shade, in Scotland (West 1910). Mallik and Wein (1986) reported that it could be found on the flooded side of a *Typha* marsh (Figure 56), but not on the drained side.



Figure 56. Flooded side of cattail (*Typha*) marsh, a potential site for *Pellia epiphylla*. Photo by David Hoffman, through Creative Commons.

Some collectors have reported *Pellia epiphylla* (Figure 49-Figure 51) from wet cliffs and bluffs. Vitt (1967) reported finding it on the upper portions of sandstone bluffs in southeastern Missouri, USA, typically in wet, shaded areas (Figure 57).

Proctor *et al.* (1992) used *Pellia epiphylla* (Figure 49-Figure 51) from moist, shady clay banks near a stream gully to measure $\delta^{13}\text{C}$ values from a wet heath in East Devon. Watson (1915) indicated zonation patterns of plants in a Somerset, UK, heath, noting that *Pellia epiphylla* occurred just above the water line of the channels

(Figure 58) in locations where it would remain constantly moist. Otherwise, I have found no reports of this species from peaty habitats.



Figure 57. Sandstone bluff in Missouri, USA, where *Pellia epiphylla* can be found in moist places. Photo by V. Smith, through Creative Commons.

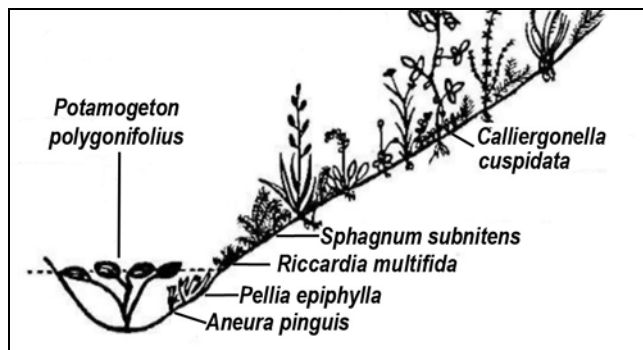


Figure 58. *Pellia epiphylla* zonation in a heathland water channel. Drawing modified from Watson 1915.

Clapham (1940) commented on the occurrence of the acidophilic *Pellia epiphylla* (Figure 49-Figure 51) in calcareous fens in the Oxford District of the UK. Clapham contended that the liverwort was able to grow there because of mats of fen mosses and the bases of woody plants that provided suitable substrata.

Physiology

Proctor *et al.* (1992) compared $\delta^{13}\text{C}$ in nine *Sphagnum* species and several liverworts. That of *Pellia epiphylla* (Figure 49-Figure 51) was typical for that of the two Marchantian liverworts.

One of the problems that aquatic bryophytes in particular must solve is obtaining CO_2 for photosynthesis. Evolutionarily, they have had the selective choice to concentrate it with such structures as pyrenoids, or to ventilate so that CO_2 can easily enter the plant and reach the photosynthetic tissue (Meyer *et al.* 2008). Tracheophytes have generally followed the latter evolutionary pathway. But *Pellia* lacks both pyrenoids and internal air chambers accessible through pores (Figure 31, Figure 59-Figure 60). In fact, *Pellia* has a simple thallus lacking pores and is diffusion limited. *Pellia epiphylla*

(Figure 49-Figure 51) is more desiccation tolerant than *Pellia endiviifolia* (Figure 19-Figure 20). *Pellia epiphylla* exhibited a wider operating range of the mean total water content (88-142%) than did *P. endiviifolia*. Meyer *et al.* concluded that it was this wider operating range that permitted *Pellia epiphylla* to maintain net gain in photosynthesis in drier habitats.

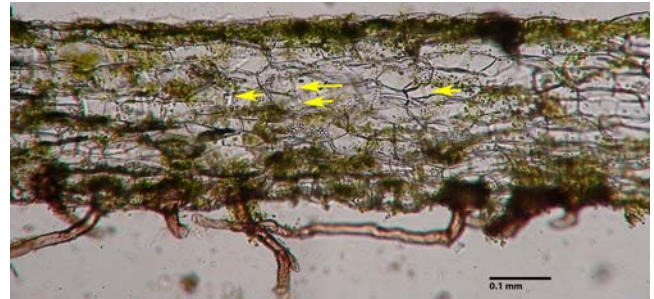


Figure 59. *Pellia epiphylla* longitudinal section, showing bands in some midrib cells (arrows) and rhizoids. Photo by Ken McFarland and Paul Davison, with permission.

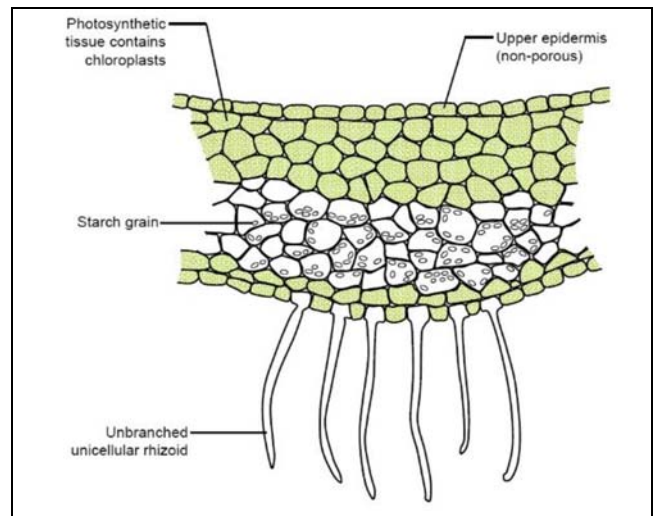


Figure 60. *Pellia epiphylla* cross section drawing. Photo from <Crondon.com>, with online permission for educational use.

Dilks and Proctor (1979) showed that species such as *Pellia epiphylla* (Figure 49-Figure 51) from moist habitats have increasing photosynthesis as water content increases in the range of 500 to 1000% of dry weight. Furthermore, its photosynthesis is affected at much lower water deficits than is respiration as the plant dries.

Proctor (1982) determined that the photosynthetic rate in the attached sporophyte of *Pellia epiphylla* (Figure 49-Figure 51) is very low when compared with that of its gametophyte. Using labelled CO_2 , he found that the photosynthetic uptake of CO_2 by the sporophyte is only a few percent of the labelled C translocated from the gametophyte. It appears that this translocation from gametophyte to sporophyte is most active when the sporophyte has reached its full size but is still green, subsequently declining as the capsule matures through its final stages.

Samecka-Cymerman *et al.* (1997) investigated the ability of *Pellia epiphylla* (Figure 49-Figure 51) to serve as bioindicators of heavy metals in soil. They reported that in liverworts such as *P. epiphylla* the ionic balance is

disturbed by elevated concentrations of microelements, especially iron, copper, cobalt, and lead. Marczonek (1984) found a close correlation between the average thallus surface of *Pellia epiphylla* and the calcium to magnesium ratio in the soil, establishing the existence of relations between these liverworts and their substratum. For example, there is a significant relationship between lead and barium in the soil and that found in the liverwort (Samecka-Cymerman *et al.* 1997). But the relationships are not always simple. In *Pellia epiphylla*, there is a negative correlation between manganese content of the soil and nitrogen, phosphorus, and potassium content in the liverworts. This relationship had already been established for tracheophytes and probably relates to competition for cation exchange sites on the liverwort surface. They suggested that the same competition probably applies to potassium. Mg^{++} can occupy two exchange sites, giving it a tighter hold, than can K^+ that can occupy only one exchange site. On the other hand, *Pellia epiphylla* is a good biomonitor for nickel, chromium, copper, and barium.

Water in *Pellia epiphylla* (Figure 49-Figure 51) travels in capillary films between the rhizoids (Figure 59) and the lower surface, where it is partly absorbed (Clee 1939). What remains travels over the surface and is retained around the antheridia by the incurved and wavy thallus margins.

Those bryophytes, including most populations of *Pellia epiphylla* (Figure 49-Figure 51), that live out of the water must experience the freeze-thaw regimen of winter and early spring. Rütten and Santarius (1992) found that this species exhibits a distinct increase in cold tolerance from summer to winter. Nevertheless, compared to that of the mosses in the study, the hardening capacity of the liverwort was relatively low. All but one of the mosses experienced an increase in sucrose concentration in the cells, but no significant changes in glucose or fructose contents.

Pihakaski and Pihakaski (1979) examined the effects of chilling on the ultrastructure and net photosynthesis of *Pellia epiphylla* (Figure 49-Figure 51). Naturally frozen plants were thawed, revealing thallus margins that were brownish; cells were plasmolyzed. Chilling for 20 hours at -22°C resulted in death of the thallus cells and disruption of the organelles. On the other hand, the apical growth region and the nerve with its surrounding cells were normal and green. Using various lengths of time at -22°C , they determined that vacuoles of the dead cells were empty. Electron-dense particles appeared on the tonoplast and, in some cells, inside the vacuole; the nucleus also exhibited a granular appearance. Healthy cells that had been kept at 3°C exhibited no granularity. At -22°C lipid-like substances were apparent, but not at 3°C . The oil bodies had either become more dense or were in various stages of disruption. Some appeared to have lost their contents.

Using *Pellia epiphylla* (Figure 49-Figure 51) that had been frost-hardened at 3°C , Pihakaski and Pihakaski (1979) determined that both respiration and photosynthesis can continue below freezing (Figure 61). At -10°C respiratory loss of CO_2 is greater than that gained by photosynthesis, but photosynthetic gain is greater in the range of -10 to -2°C . As the plants thaw up to 5°C , they reach a respiratory peak. At temperatures above 5°C , photosynthesis increases slowly, then rapidly, then tapers off or decreases,

approximating a sigmoid pattern as the temperature increases. Maximal photosynthesis in all plants occurs at $15\text{--}20^{\circ}\text{C}$.

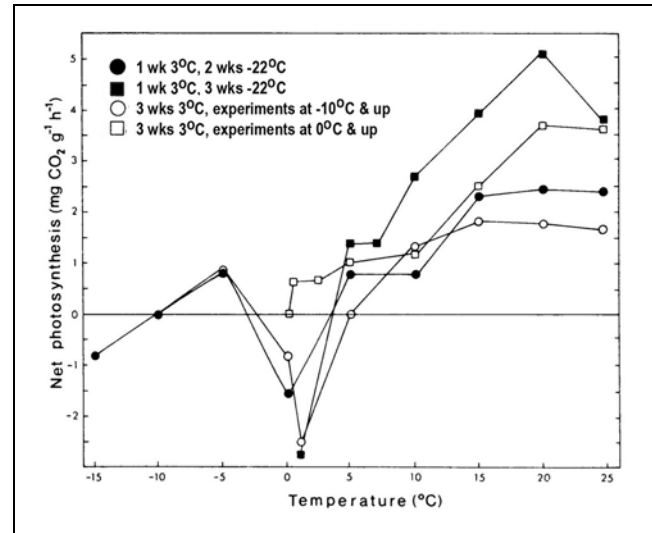


Figure 61. Net photosynthetic responses to temperature at 9000 lux for *Pellia epiphylla*. Modified from Pihakaski and Pihakaski 1979.

Pihakaski and Pihakaski (1979) also noticed that the starch grains in the chloroplasts and the results of photosynthetic experiments indicate that chloroplasts of *Pellia epiphylla* (Figure 49-Figure 51) are able to photosynthesize at very low temperatures. Nevertheless, after 20 hours at -22°C the starch-degrading is unable to perform and the plastids continue to contain large starch grains. In summary, cold-hardened *Pellia epiphylla* can recover very rapidly after a chilling period at -15°C and even after long-term storage at -22°C . Rapid chilling, however, is detrimental to CO_2 uptake. The researchers suggested that oil bodies may help in the survival of liverworts at low temperatures.

Dilks and Proctor (1975) noticed that leafy liverworts that withstood rapid cooling to -5°C for 6 h are protected from intracellular freezing at normal rates of cooling by the withdrawal of water to form extracellular ice. On the other hand, they found that *Pellia epiphylla* (Figure 49-Figure 51) was killed by rapid cooling to -5°C .

Adaptations

In the right circumstances, *Pellia epiphylla* (Figure 49-Figure 51) can achieve great masses and may cover a meter or more of soil (Greenwood 1911). One would expect such large clumps to provide more protection against desiccation than small patches.

The thalli of *Pellia epiphylla* (Figure 49-Figure 51) are typically completely green, but when they grow too far from water they can have a purplish or reddish tinge (Figure 62) along the middle (Greenwood 1911; Boll 2020). Their growth form changes from horizontal with close attachment to the substrate when the substrate is horizontal, but on vertical substrata they take on a more ruffled (Figure 63) habit (Boll 2020).



Figure 62. *Pellia epiphylla* with red coloration typical of populations growing too far from water. The mat habit and associated mosses can help it to retain water in these conditions. Photo by Michael Lüth, with permission.



Figure 63. *Pellia epiphylla* forming overlapping layers. Photo by Andrew Spink, with permission.

The ends of *Pellia epiphylla* (Figure 49-Figure 51), plants can overlap like shingles (Figure 63, Figure 66), providing at least some reduction in moisture loss. The gametophyte absorbs water primarily through its under surface (Figure 60, Figure 63) and the lower midrib is important in the retention of water (Boll 2020). Dry plants are thinner and have a more solid texture than that of plants from very moist locations (Greenwood 1911). The species furthermore produces more luxuriant growth near the water, which Greenwood attributes to having less compact cell structure in moist conditions.

It appears that *Pellia epiphylla* (Figure 49-Figure 51), lacks mechanisms to protect it from UV-B radiation. Takaács *et al.* (1999) report that the protective mechanism is "rapidly exhausted" in this species, making it intolerant of increased UV-B.

Pellia epiphylla (Figure 49-Figure 51) does respond to light in another way. It exhibits positive phototropism of the sporophyte (Thomas *et al.* 1987). The entire length of the seta responded to 6 W m^{-2} . Curvature toward the light occurred within 10-15 minutes of continuous illumination. The growth rate of the shaded side of the seta increased significantly (from 0.50 to 0.96 mm hr^{-1}) and decreased on the lighted side (to 0.26 mm hr^{-1}).

Reproduction

Pellia epiphylla (Figure 49-Figure 51), is **monoicous** (Zielinski 1984). It was one of the first liverworts to have its development described. Hutchinson (1915) described development not only of growth, but also antheridia (Figure 64) and archegonia. As in most liverworts, fertilization requires that the plants be wet (Boll 2020).



Figure 64. *Pellia epiphylla* with antheridia. Photo by Des Callaghan, with permission.

Antheridia, archegonia, and sporangia are largely supplied with water from the exterior (Clee 1939). Capillary spaces retain the water in the narrow crevices between the antheridial cavity and antheridium, between the flaps of the involucre (Figure 66), and between these and the long necks of the archegonia. Antheridia absorb water until they burst, thus releasing the sperm cells that must swim to the archegonia for fertilization (Boll 2020). The antheridia absorb their water from the upper surface, probably ensuring that there is enough water to complete the fertilization process.

The water travels down the neck of the archegonium to the egg, thus facilitating entry of the sperm, and is there, available, for the developing embryo (Clee 1939). Films of water are retained between the sporophyte foot of the dividing embryo and the severed archegonium that now forms the calyptra. The sporophyte obtains water that is absorbed by the foot primarily from external sources. This water travels up the seta and eventually reaches the spores. Clee suggested that, therefore, the sporophyte is not very dependent on the gametophyte for its supplies of water or nutrients.

Walton (1943) described the sperm reaching the archegonium in greater detail. Noting that the archegonia are at the plant apex and that antheridia are 10-15 mm away on the dorsal surface, he questioned the feasibility of swimming between them. Showalter (1926) had found that it takes several hours for the sperm of a close relative, *Aneura* (Figure 65), to swim 10 mm. In fact, in many mosses and liverworts, it is the spermatocytes that are freed from the antheridia, and these are carried rapidly by water surface tension over the free water surface of the plants at $\sim 20 \text{ mm per minute!}$ When experimenting with *Pellia epiphylla* (Figure 49-Figure 51), Walton found that the spermatocytes broke loose from ripe antheridia, extruding in grey masses into the water. These masses quickly broke apart at the surface and dispersed rapidly across the wet

surface. It did not take hours, but only 15 seconds for the spermatocytes to reach the archegonial involucre (Figure 66). The free-swimming sperm required only 15 minutes to emerge from the spermatocytes and arrive at the archegonium.



Figure 65. *Aneura pinguis*, in a genus in which sperm require several hours to swim 10 mm. Photo by Hugues Tinguy, with permission.



Figure 66. *Pellia epiphylla* with involucres (arrow) and overlapping lobes. Photo by Rob Cutis, through Creative Commons.

Various stages of capsule development of *Pellia epiphylla* (Figure 49-Figure 51) are shown in Figure 67 to Figure 82. Greenwood (1911) reported that plants of this species in moist conditions are more likely to be sterile than those in drier situations, with abundant capsules appearing in drier conditions (Figure 75-Figure 76). Interestingly, in April the maturity of capsules increases as plants occur nearer the water. New shoots were appearing at this time on the edges of the old plants (Figure 70-Figure 71), and antheridial beginnings were already visible as dots. Figure 84 shows a cross section of the capsule wall with spores inside.



Figure 67. *Pellia epiphylla* young capsules emerging from perianths. Photo from Biopix, through Creative Commons.



Figure 68. *Pellia epiphylla* young capsule emerging. Photo from Biopix, through Creative Commons.



Figure 69. *Pellia epiphylla* perianth inside involucre with seta extended. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 70. *Pellia epiphylla* from Illinois, USA, with senescing older parts and new green branches from the tips. Photo by Li Zhang, with permission.



Figure 71. *Pellia epiphylla* with emerging sporophyte. Note the old thalli that are brown and the new growth from the tips. Photo by Li Zhang, with permission.



Figure 72. *Pellia epiphylla* with nearly mature capsules. Photo by Michael Lüth, with permission.



Figure 73. *Pellia epiphylla* with elongating setae emerging from involucres at base. Photo by Malcolm Storey, <DiscoverLife.com>, with online permission.



Figure 74. *Pellia epiphylla* capsules nearing maturity. Photo by Allen Norcross, with permission.



Figure 75. *Pellia epiphylla* with abundant sporophytes in drier conditions. Photo by Michael Lüth, with permission.



Figure 76. *Pellia epiphylla* with numerous nearly mature capsules on elongated setae. Photo by Michael Lüth, with permission.

Despite the ease of having sperm reach the archegonia in this monoicous species, Zielinski (1984) found electrophoretic evidence of *Pellia epiphylla* (Figure 49-Figure 51) achieving cross-fertilization. In fact, Prus-Glowacki and Zielinski (1987) reported 93% cross fertilization, citing it as support of the hypothesis that this species might be self-incompatible. But it is also possible that a timing difference in maturity of antheridia and archegonia on the same plant might reduce self-fertilization. This needs further exploration.



Figure 77. *Pellia epiphylla* with both elongating setae and nearly dehiscing capsules. Photo by Jan-Peter Frahm, with permission.



Figure 78. *Pellia epiphylla* dehiscing sporophytes. Photo by Kristian Peters, with permission.

Slade (1965) found that temperature and soil water tension affected both the rate of seta elongation and its final length in *Pellia epiphylla* (Figure 85). Daytime temperature is apparently more important than nighttime temperature. Day length has no effect, but low light intensity stimulates greater elongation, a seta version of etiolation.



Figure 79. *Pellia epiphylla* capsules with deliquescent setae after spores are shed. Photo by Jutta Kapfer, with permission.



Figure 80. *Pellia epiphylla* with numerous dehiscent capsules. Photo by Allen Norcross, with permission.



Figure 81. *Pellia epiphylla* dehiscent capsule. Photo by Allen Norcross, with permission.



Figure 82. *Pellia epiphylla* capsule dehiscent. Photo by Ralf Wagner, <www.dr-ralf-wagner.de>, with permission.



Figure 83. *Pellia epiphylla* with dehiscent capsule and mass of elaters. Photo by Malcolm Storey, <www.discoverlife.org>, with online permission.

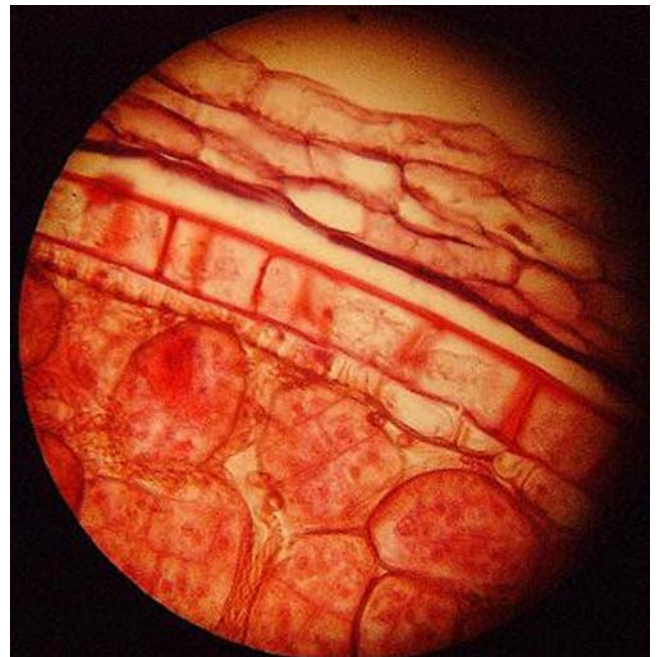


Figure 84. *Pellia epiphylla* capsule cross section showing capsule wall and spores. Photo from <Crondon.com>, with online permission for educational use.



Figure 85. *Pellia epiphylla* with emerging sporophytes. Photo by Michael Lüth, with permission.

Slade's observations are consistent with those of Asprey *et al.* (1958) for *Pellia epiphylla* (Figure 49-Figure 51). They reported that the sporangium, foot, and seta reach full differentiation by the end of September in Great Britain. However, in natural conditions, the seta does not elongate until the following year, usually starting in late February. Spores mature first, as indicated by the darkening of the capsule wall. The seta can elongate from 1 mm to as much as 80 mm in 3-4 days.

When capsules were treated with gibberellin (as 100 ppm potassium gibberellate) and maintained in culture at 18°C and natural daylight and day length in January, full seta elongation occurred in *Pellia epiphylla* (Figure 49-Figure 51) and reached an average length of 57 mm after 5 days (Asprey *et al.* 1958). The control capsules exhibited no elongation. When a solution of 1.0 ppm IAA was added to the gibberellic acid treatment, setae experienced full elongation. The researchers suggested that dormant setae of intact sporophytes may react to either potassium gibberellate or IAA to stimulate elongation of the seta. In isolated sporophytes, the potassium gibberellate produces only slight elongation (7-10 mm), whereas if that treatment is followed by IAA, full elongation (~63 mm) occurs. If only IAA is applied, elongation is attenuated at ~37 mm.

Thomas *et al.* (1983) demonstrated the presence of ~2.5-2.9 µg per gram fresh weight of putative free IAA in *Pellia epiphylla* (Figure 49-Figure 51) sporophytes. They also found that ethylene released by the setae increases during growth from 0.027 to 0.035 nanoliters per seta per hour (Figure 86). Applied ether (5 µL per liter) inhibits IAA-stimulated elongation of the seta. Thomas and coworkers postulated that IAA and ethylene act in tandem to modulate the elongation of the seta in this species. The further role of lunularic acid, a liverwort hormone similar to ABA, needs exploration.

Ellis and Thomas (1985) found that the shaded sides of sporophytes of *Pellia epiphylla* (Figure 49-Figure 51) became more acidic than the lighted sides. This change occurred before curvature occurred and could be produced also by the application of IAA or FC to one side of the seta. This response suggests that IAA mediates phototropism in *Pellia epiphylla*.

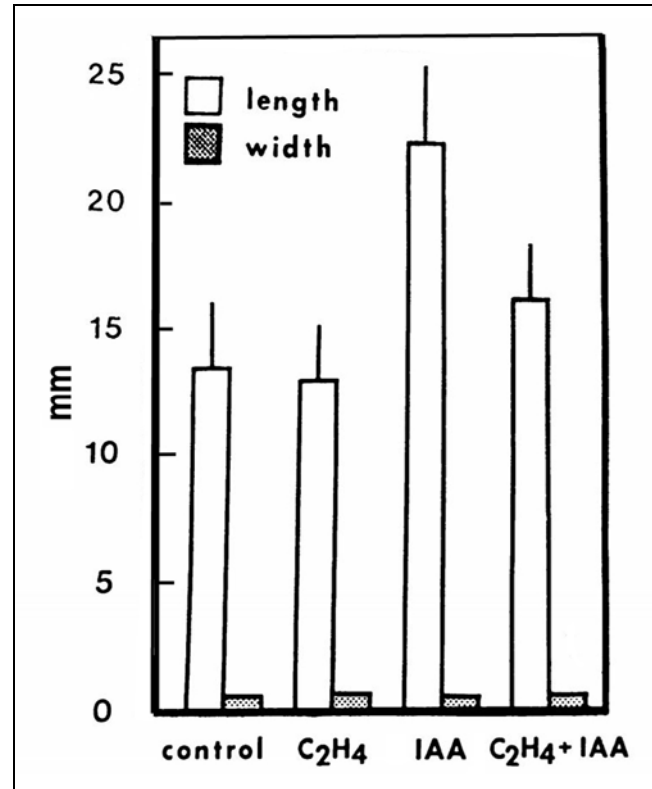


Figure 86. Effect of ethylene (C₂H₄ at 5 µL L⁻¹) and IAA (10 µM) on growth of *Pellia epiphylla* setae. Vertical line indicates standard error. Modified from Thomas *et al.* 1983.

Cromble and Paton (1958) found that there seems to be an age effect on sporophyte maturation. They suggest that a gradual change occurs during the winter months so that setae are ready for rapid elongation in spring when the temperature rises.

Schnepf *et al.* (1979) timed the growth of setae in *Pellia epiphylla* (Figure 49-Figure 51). The intact plants had a seta elongation rate of ~0.6 mm h⁻¹. Excised setae provided with 0.1 mM IAA exhibited a steady-state growth rate of 0.7-1.2 mm h⁻¹. A number of inhibitors altered the elongation rate. They interpreted the greater rate of elongation in excised sporophytes to indicate that this is not a passive thinning of auxin-loosened walls, but instead is dependent on maintenance of organized structure and macromolecule synthesis.

Poli *et al.* (2003) found that the IAA seems to move by simple diffusion in the liverworts, using *Pellia epiphylla* (Figure 49-Figure 51) as one of the model organisms. This contrasts with the bipolar transport that was operational in *Polytrichum ohioense* (Figure 87). Thomas *et al.* (2002) used radioactive labelling of IAA in *Pellia epiphylla* to trace the upward gravitropic curvature of horizontal sporophytes, showing response within 50-60 minutes. They furthermore showed that applied IAA moved preferentially to the lower side of the setae in horizontally oriented sporophytes. This mechanism provides a gravitropism that works to make sporophytes upright.



Figure 87. *Polytrichum ohioense*, trail through virgin spruce, *Picea rubra*, Gaudineer Park, WV. Photo by Janice Glime.

Farmer (1894b) found that the spores of *Pellia epiphylla* (Figure 49-Figure 51) don't germinate until after they leave the capsule, while noting that in some species of liverworts they germinate within the capsule. The *P. epiphylla* spores are "crowded" with starch grains. Willis (1957) described spore formation in the species.

Wolfson (1928) found that sporelings of *Pellia epiphylla* (Figure 49-Figure 51) have little capacity to resist desiccation, and they cannot resist drying for even one week. Wolfson describes early cell divisions in the sporelings.

Bartholomew-Began (1996) found the spores in *Pellia epiphylla* (Figure 49-Figure 51) to be **endosporic** (having 1 or more cell divisions within the spore wall; Figure 88) and **precocious** (developing early, sometimes within capsule). She describes the development of the protonema, noting that at the 23-24-cell stage rhizoid initiation occurs.

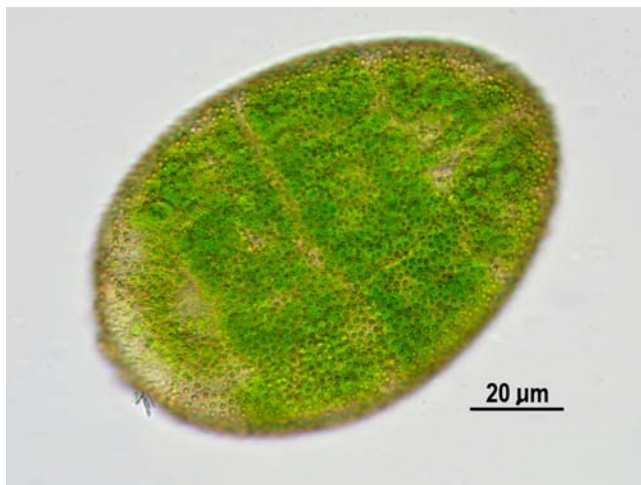


Figure 88. *Pellia epiphylla* spore showing divisions within the spore (**endosporic**). Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Interactions with Fungi and Slime Molds

Fungi have been observed in *Pellia epiphylla* (Figure 49-Figure 51) for more than a century. Ellis (1897)

reported *Trichoderma* (Figure 89) as a parasite on the species. Ridler (1922) noted that every plant he inspected was infected with fungi. These appeared on both the gametophyte and sporophyte and the fungus seemed closest to a species of *Phoma* (Figure 90). Hadden (1921) reported the very rare *Elaeomyxa cerifera* (Figure 91), a slime mold, as occurring primarily on *Pellia epiphylla* (see also Ing 1994). But the role of fungi in the life of this and other liverworts have been largely ignored.



Figure 89. *Trichoderma harzianum*, member of a fungal genus that is parasitic on *Pellia epiphylla*. Photo from USDA, through public domain.

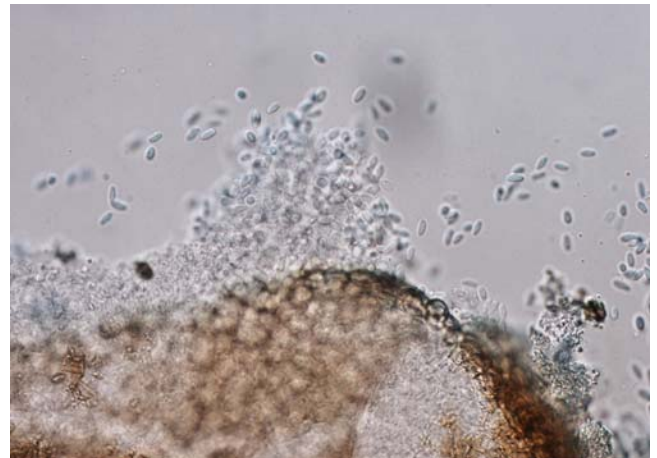


Figure 90. *Phoma*, a genus that might be one that infects large numbers of *Pellia epiphylla* plants. Photo by Cesar Felderon, through Creative Commons.



Figure 91. *Elaeomyxa cerifera*, a slime mold that occurs primarily on *Pellia epiphylla*. Photo by Sarah Lloyd, with permission.

Magrou (1925) considered the relationship of fungi with *Pellia epiphylla* (Figure 49-Figure 51) to be **commensal** (describing relationship in which members of one species gain benefits while those of other species are neither benefitted nor harmed). Pressel *et al.* (2014) noted the use of molecular data and TEM (Figure 92-Figure 93) to understand the relationship between the two. Read *et al.* (2000) reported that glomalean fungi could form typical VA mycorrhizae in the flowering plant *Plantago lanceolata* (Figure 94), but also can colonize *Pellia epiphylla*, where they produced arbuscules and vesicles in the thallus (Figure 92-Figure 93).

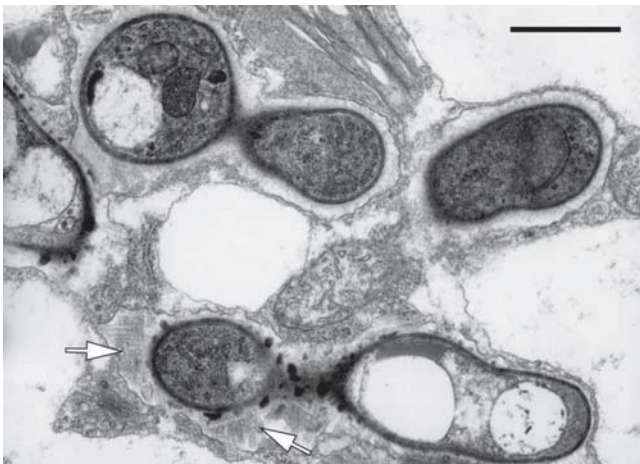


Figure 92. *Pellia epiphylla* cells with arbuscular fungi. Photo from Pressel *et al.* 2014, with permission.

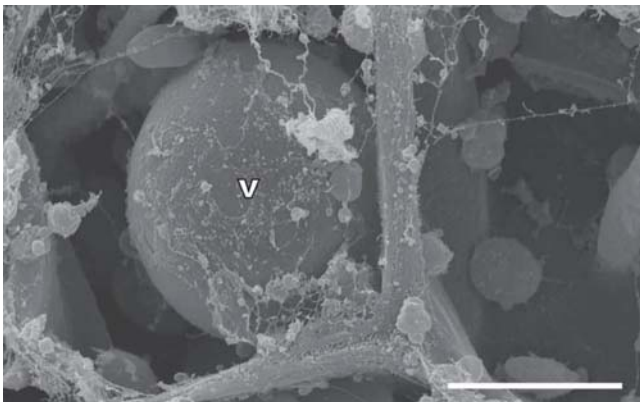


Figure 93. *Pellia epiphylla* with arbuscular fungi. Photo from Pressel *et al.* 2014, with permission.



Figure 94. *Plantago lanceolata*, a species that has some of the same glomalean fungi as those in *Pellia epiphylla*. Photo by Forest and Kim Starr, through Creative Commons.

Biochemistry

Pihakaski (1972) reported that proteins appeared to be present in the oil bodies (Figure 95) of *Pellia epiphylla* (Figure 49-Figure 51). Using electron microscope techniques, he showed that these proteins occur in the stroma, but not in the globules embedded in that stroma. Instead, the globules are comprised of unsaturated neutral lipids, forming the bulk of the total stainable lipids in the cell. These occur entirely in the oil bodies in *Pellia epiphylla*.

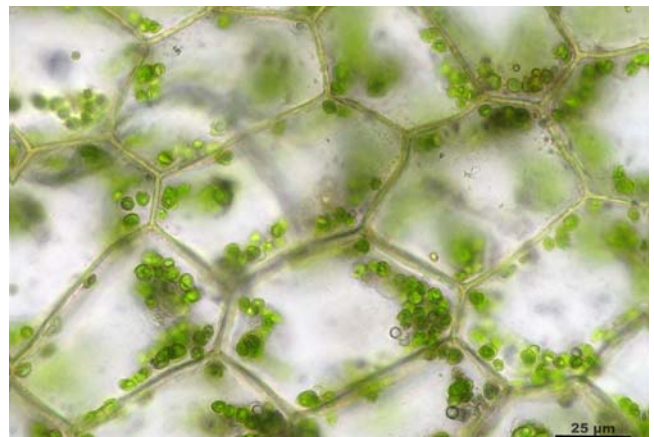


Figure 95. *Pellia epiphylla* lamina cells showing chloroplast and few small oil bodies. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Prus-Glowacki *et al.* (1998) found that two sibling species could be identified within *Pellia epiphylla* (Figure 49-Figure 51) based on differences in activity of malate dehydrogenase, esterase, and aspartate aminotransferase. Ono *et al.* (1992) demonstrated the closeness of *P. epiphylla* to *P. neesiana* (Figure 96-Figure 103) based on the presence of the pungent diterpene dialdehyde, sacculatal in both. Pacak *et al.* (1998) used RAPD to support the distinction between the northern and southern **allopatric** (having non-overlapping distributions) populations of *Pellia epiphylla* in Poland and that the polyploid *Pellia borealis* is a hybrid of these two.

Cullmann *et al.* (1996) isolated a new macrocycle of lignan, caffeic acid, and an aliphatic C₈ moiety from *Pellia epiphylla* (Figure 49-Figure 51). Cullmann *et al.* (1997) identified phenolic constituents, naming pellepiphyllin, 7-hydroxypellepiphyllin, perrottetin E, perrottetin E-11-methyl ether, 14'-hydroxyperrottetin E, 10'-hydroxyperrottetin E, 10'-hydroxyperrottetin E-11-methyl ether, 10,10'-dihydroxyperrottetin E and 13', 13''-bis (10'-hydroxyperrottetin E). Mukhia *et al.* (2015) confirmed the presence of the phenolic compounds coumarin, alkaloid, anthraglycoside, arbutin, phenol, and flavonoids and demonstrated significant anti-diabetic activity. Phenolic compounds often serve as herbivore deterrents, but to my knowledge this has not been tested in *Pellia epiphylla*. Cullmann and Becker (1998a) extracted eight sesquiterpenoids from *Pellia epiphylla*, three of which were new. Six diterpenes, several sterols, betulin, and δ -tocopherol were present. Pellialactone was present, and loliolide was shown in a liverwort for the first time. Rischmann *et al.* (1989) isolated a new naphthalene derivative from the gametophyte of *Pellia epiphylla* and defined its structure. Li *et al.* (2019) continued to isolate sacculatanes, describing eight that were not previously known from *Pellia epiphylla*. Two of the epiphyllins exhibited antioxidant effects.

Cullmann and Becker (1998b) did an unusual study by examining secondary compounds in the sporophytes and spores of *Pellia epiphylla* (Figure 67-Figure 85). They identified five africanane-type sesquiterpenes, *epi*-swartzianin A, 9(15)-africanene, isoaficanol, leptographiol, and the new 10 β -hydroxy isoaficanol, the new humulane derivative 1,8-humuladien-5-ol, caryophyllene oxide, phytol, and (1,2)-bis-nor-phytone. They also found palmitic acid, linolic acid methyl ester, 7, 10, 13-hexadecatriene acid methyl ester, octadecanol and three bisbibenzyls: perrottetin E, 10'-hydroxy perrottetin E, 10'-hydroxy perrottetin E-11-methyl ether, caffeic and ferulic acid methyl esters, and four flavones: luteolin, luteolin-7-methyl ether, luteolin-7,3'-dimethyl ether and the new luteolin-5,7,3'-trimethyl ether. In addition, spores contained isoaficanol and 1,8-humuladien-5-ol.

Pihakaski and Pihakaski (1980) demonstrated that in *Pellia epiphylla* (Figure 49-Figure 51) the herbicide glyphosate caused a rapid decrease in photosynthetic activity and also in its ability to react quickly to changes in light intensity. Nevertheless there appeared to be some sort

of acclimation to the glyphosate. The net photosynthetic inhibition was strong for the week following exposure, but that reversed during the following weeks. After 4-5 weeks following glyphosate treatment, net photosynthesis increased again. On the day following treatment, a number of cytological changes occurred, including structural changes to the chloroplast surface, deterioration of oil bodies, endoplasmic reticulum, and ribosomes, increase of lipid spherules, and vacuolation of cytoplasm. After two weeks the grana formation was deteriorated, the plasmalemma was disconnected, and the length of mitochondrial cristae had decreased.

Pellia neesiana (Figure 96-Figure 103)

Distribution

Pellia neesiana (Figure 96-Figure 103) is widely distributed in the northern part of the Northern Hemisphere (Schütz *et al.* 2016). It occurs in Europe, Asia, North America, Greenland, and Iceland, particularly at higher elevations.



Figure 96. *Pellia neesiana* in a tight, single-species colony. Photo by C. and C. Johnson <www.ohbr.org.uk>, with permission.



Figure 97. *Pellia neesiana* showing a typical yellow-green thallus. Photo by David T. Holyoak, with permission.



Figure 98. *Pellia neesiana* thallus. Photo by Des Callaghan, with permission.



Figure 101. *Pellia neesiana* female with involucre. Photo by Jan-Peter Frahm, with permission.



Figure 99. *Pellia neesiana* with scattered antheridia. Photo by J. C. Schou, with permission.



Figure 102. *Pellia neesiana* showing transparency of the thallus. Photo by Ken McFarland and Paul Davison, with permission.



Figure 100. *Pellia neesiana* showing transparency of the thallus. Photo by Ken McFarland and Paul Davison, with permission.



Figure 103. *Pellia neesiana* in a wet habitat. Photo by J. C. Schou, with permission.

Aquatic and Wet Habitats

Pellia neesiana (Figure 96-Figure 103) occurs on grassy ground or on rocks by fast streams (Watson 1919). In the Alps, it is not common, with *Trichophorum cespitosum* (Figure 104) (Geissler & Selldorf 1986). It occurs on soil in the flood valley of the Upper Bureya River (Russian Far East) (Konstantinova *et al.* 2002). In northeastern Finland it occurs in streams (Heino & Virtanen 2006).



Figure 104. *Trichophorum cespitosum*, a sedge species that is sometimes accompanied by *Pellia neesiana* in the Alps. Photo by Hermann Schachner, through Creative Commons.

Basile *et al.* (2017) considered *Pellia neesiana* (Figure 96-Figure 103) to be a species living submerged along the rivers in cool and temperate areas of the northern hemisphere. But based on the records I have found, *Pellia neesiana* is less of a river species, and the records suggest it might spend most of its life above water. Sharp (1944) reported that it could attain local abundance on boulders in a creek in Virginia, USA. Steere (1937) found it on a rotten log in a small stream in Michigan, USA. But it is not clear if these latter two finds were submersed.

Wet soil and habitats close to water are much more common for *Pellia neesiana* (Figure 105) than submersed habitats. Nichols (1922) reported that it was locally abundant along muddy river shores in Michigan, USA. Lepage (1953) reported a similar habitat in northern Québec, Canada. Hong (2007) reported it from moist soil near a stream in the Queen Charlotte Islands, British Columbia, Canada. Across the ocean in the Western Caucasus of Russia, *Pellia neesiana* occurs on dry river beds, on bare soil among grasses in wet areas (Figure 106), on rocks and soil on banks of streams in subalpine meadows, and at edges of streams in forests (Konstantinova *et al.* 2009). Dulin (2015) likewise found it on river banks in the Komi Republic of Russia. Schütz *et al.* (2016) included stream banks in their summary of its habitats.



Figure 105. *Pellia neesiana* at the edge of a stream. Photo by C. and C. Johnson <www.ohbr.org.uk>, with permission.



Figure 106. *Pellia neesiana* habitat on bank. Photo by Michael Lüth, with permission.

It appears that the best place to search for *Pellia neesiana* (Figure 96-Figure 103) might be on soil near pools and lakes (Figure 107). Bartholomew-Began (1999) found it on thin, fine soil over rocks at the edge of a pool in the Hawk Mountain Sanctuary, Pennsylvania, USA. Dulin (2015) reported it from the banks of lakes in the Komi Republic of Russia. Schütz *et al.* (2016) reported that it tolerates seasonal flooding, including along lake margins.



Figure 107. *Pellia neesiana* at the edge of water. Photo from Botany Website, UBC, with permission.

Haynes (1909) identified *Pellia neesiana* (Figure 96-Figure 103) from the side of a decaying log as well as on wet ground. The species occurs on moist, sandy soil in Kentucky, USA (Fulford 1934). Papp *et al.* (2013) reported it from a wet meadow in western Croatia. Dulin (2015) reported it from soil in hollows and on butts of trees in a grass-*Sphagnum* (Figure 108) habitat as well as in birch forests (Figure 109). Schütz *et al.* (2016) considered it to prefer soils that were moderately acid to sub-neutral.

Schütz *et al.* (2016) included springs, marshes, ditches, and damp tracks among the habitats of *Pellia neesiana* (Figure 96-Figure 103). These are typically shaded, sub-neutral to moderately acid clayey to sandy loams with poor nutrient content.



Figure 108. Grass-*Sphagnum* habitat where one might find *Pellia neesiana* in soil hollows. Photo by Janice Glime.



Figure 109. *Pellia neesiana* large patch on forest floor. Photo by Michael Lüth, with permission.

Wet cliffs (Figure 110) can at times be suitable for colonization. Bakalin (2015) reported *Pellia neesiana* (Figure 96-Figure 103) from moist crevices in cliffs, moist to wet cliffs, and gravelly barrens in open places, particularly in the alpine belt of the Tardoki-Yani Range in Pacific Russia.

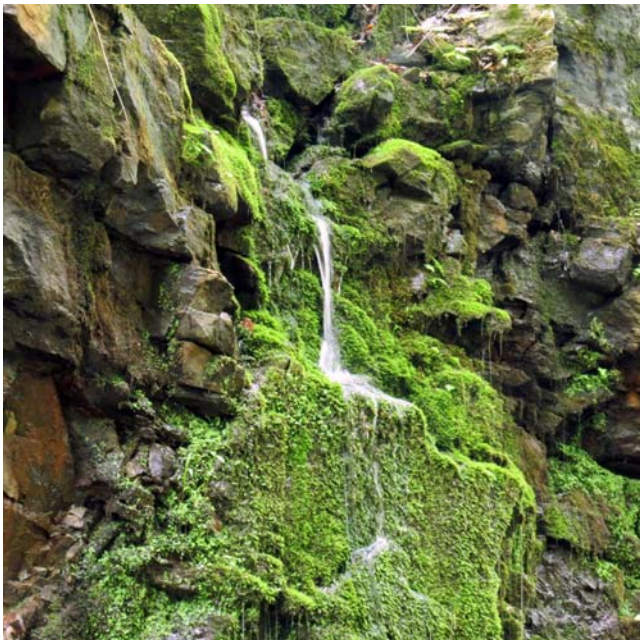


Figure 110. Rock wall and waterfall on cliff that could be a habitat for *Pellia neesiana*. Photo by Allen Norcross, with permission.

So far I have found only one report of boggy habitats. Konstantinova *et al.* (2009) report *Pellia neesiana* (Figure 96-Figure 103) on hillocks among *Sphagnum* and in grass-*Sphagnum* bogs (Figure 108). Dulin (2015) similarly attributed it to grass-*Sphagnum* and herb-*Sphagnum* habitats. He also reported it in waterside boggy grass willow-birch communities.

Hugonnot (2011) described *Pellia neesiana* (Figure 96-Figure 103) fens (Figure 111) in the Massif of central France. Lenz (2011) found it in a sloping shrub fen of Bighorn National Forest in Wyoming, USA.



Figure 111. Fen habitat dominated by bryophytes. Photo through Creative Commons.

Although late snowbeds (Figure 112) are neither aquatic nor wetlands, they do provide an extended period of available water as they melt. *Pellia neesiana* (Figure 96-Figure 103) can be dominant in such areas (Górski 2015).



Figure 112. Alpine snowbed that can provide water well into summer, creating a habitat suitable for *Pellia neesiana*. Photo by Alpandino, through Creative Commons.

Physiology

Like so many of the aquatic bryophytes, *Pellia neesiana* (Figure 96-Figure 103) has been the subject of the effects of pollution on bryophytes. Basile *et al.* (2017) examined the liverwort to determine the effect

contaminated water from the Sarno River in South Italy in consideration of its potential as a biomonitor. They floated the liverwort in the river in nylon bags for one week. They observed severe alterations to the chloroplasts and modified cell ultrastructure from samples exposed to the highest levels of Cd and Pb both in the lab and in the river. Interestingly, heat shock proteins (HSP70) increased as the pollution gradient increased. They attributed the ultrastructural changes to those heat shock proteins, noting that at the same time, histological changes were not evident after a 7-day exposure in the river.

Adaptations

Pellia neesiana (Figure 96-Figure 103) has an undifferentiated thallus (Figure 113-Figure 114) where photosynthesis occurs. Thus, it lacks air chambers and must exchange oxygen and CO₂ through its non-porous epidermis.

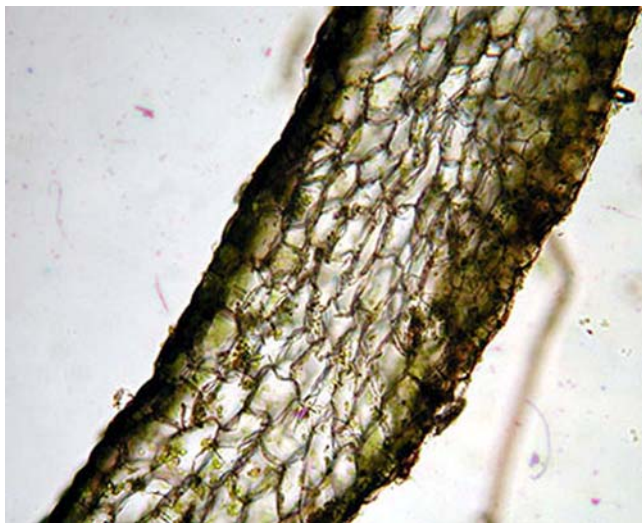


Figure 113. *Pellia neesiana* thallus cross section showing lack of internal air chambers. Photo from Botany Website, UBC, with permission.

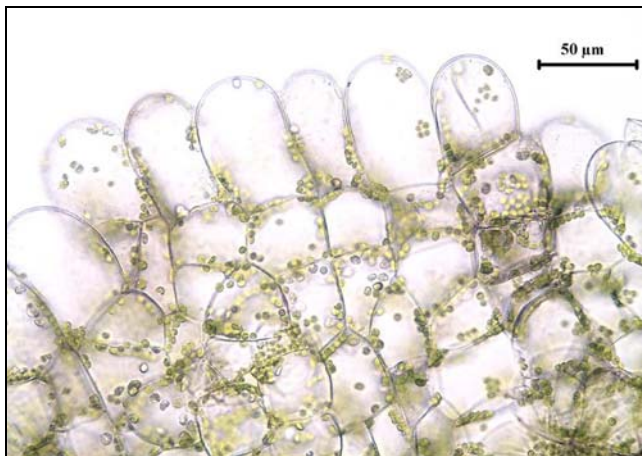


Figure 114. *Pellia neesiana* thallus cells, creating papillae on the margin. Photo by Hugues Tinguy, with permission.

Pellia neesiana (Figure 96-Figure 103) occurs in pure mats (Figure 115-Figure 116) or with *Scapania spitsbergensis* (Figure 117), *Schistochilopsis opacifolia* (Figure 118), *Trilophozia quinqueidentata* (Figure 119) in

the alpine belt of the Tardoki-Yani Range in Russia (Bakalin 2015).



Figure 115. *Pellia neesiana* forming a nearly pure mat with a few mosses. Photo by Bernd Haynold through Creative Commons.



Figure 116. *Pellia neesiana* showing dark-color form. Photo by Hermann Schachner, through Creative Commons.



Figure 117. *Scapania spitsbergensis* with pink coloration, species that occurs with *Pellia neesiana* in alpine belt of Russia. Photo by S. S. Choi <portal.kgilk.ru>, with online permission.



Figure 118. *Schistochilopsis opacifolia*, species that occurs with *Pellia neesiana* in alpine belt of Russia. Photo by Hermann Schachner, through Creative Commons.



Figure 119. *Trilophozia quinquedentata*, species that occurs with *Pellia neesiana* in alpine belt of Russia. Photo by Hermann Schachner, through Creative Commons.

Pellia neesiana is typically yellowish green (Figure 120), but it often develops red to reddish-purplish coloration (Figure 115) (Schütz *et al.* 2016). The color change could be a response to light exposure, but it can also be an indicator of other types of stress.

Reproduction

Pellia neesiana (Figure 96-Figure 103) is **dioicous** (Schuster 1992). Antheridia occur in the mid region of the thallus (Figure 120-Figure 125). Schütz *et al.* (2016) reported that *Pellia neesiana* can produce up to 30 archegonia from the vertical flat receptacle and the bottom of the gynoeceum (Figure 126-Figure 127).



Figure 120. *Pellia neesiana* antheridia. Photo by C. and C. Johnson <www.ohbr.org.uk>, with permission.



Figure 121. *Pellia neesiana* with antheridia. Photo by Michael Lüth, with permission.



Figure 122. *Pellia neesiana* antheridia. Photo by Hugues Tinguy, with permission.



Figure 123. *Pellia neesiana* antheridia. Photo by Hugues Tinguy, with permission.

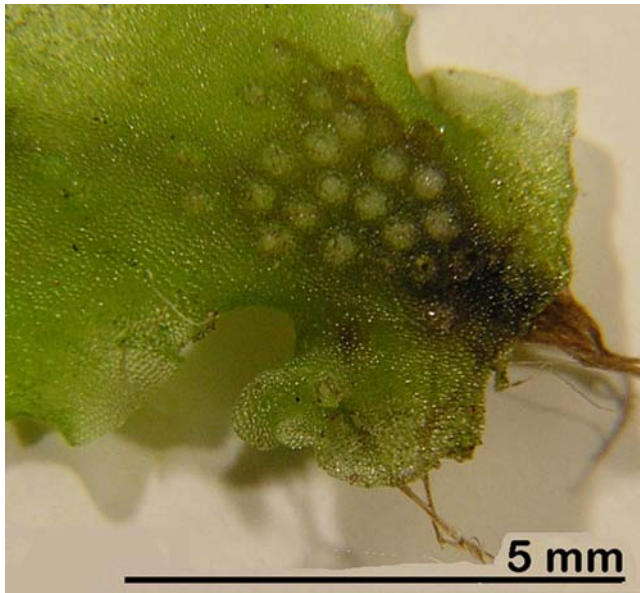


Figure 124. *Pellia neesiana* with opened antheridia. Photo courtesy of David H. Wagner.

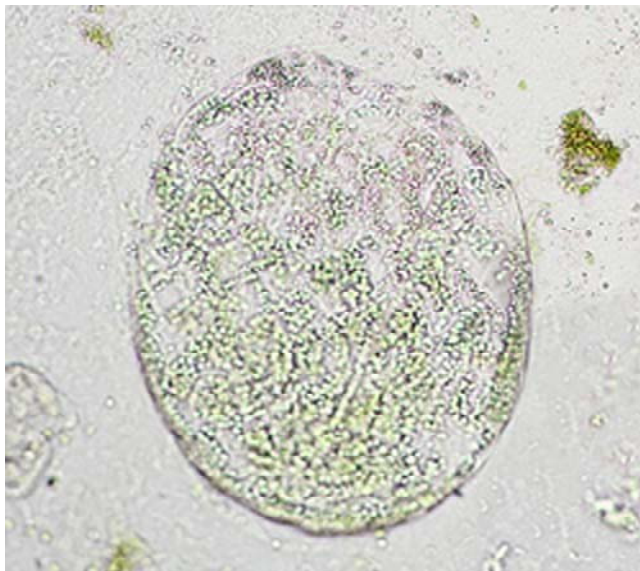


Figure 125. *Pellia neesiana* antheridium. Photo by C. and C. Johnson <www.ohbr.org.uk>, with permission.



Figure 126. *Pellia neesiana* females, showing yellowish green color and involucre. Photo by David T. Holyoak, with permission.



Figure 127. *Pellia neesiana* with female involucre. Photo by Jan-Peter Frahm, with permission.

Despite its **dioicous** condition, *Pellia neesiana* (Figure 96-Figure 103) has produced enough sporophytes (Figure 128-Figure 131) for two researchers to study the germination and development of spores and sporelings. Wolfson (1928) described the cell division as the spore germinated and found that the sporelings have little tolerance for desiccation. Bartholomew-Began (1996) made further investigations into the divisions of the protonema, comparing them with those of *Pellia epiphylla* (Figure 49-Figure 51). Like *P. epiphylla* (Figure 49-Figure 50), *Pellia neesiana* is precocious and endosporic. Rhizoid initiation occurs after the protonema reaches 23 or 24 cells. The protonema develops into a thalloid form, but its pattern of division in both species differs from that of metzgerialian liverworts.



Figure 128. *Pellia neesiana* with young sporophyte. Photo from Botany Website, UBC, with permission.



Figure 130. *Pellia neesiana* with nearly mature capsules and elongated setae. Photo by Dale Vitt, with permission.

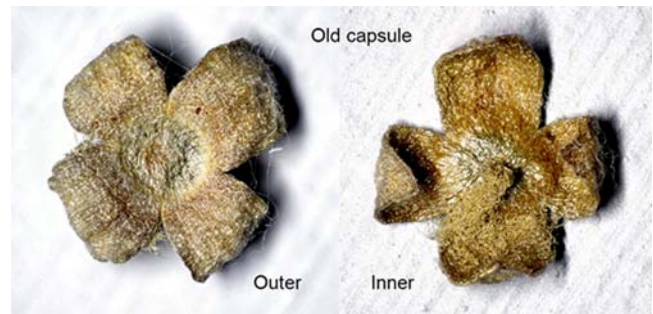


Figure 131. *Pellia neesiana* dehiscent capsule. Photo by C. and C. Johnson <www.ohbr.org.uk>, with permission.

Role

Wilkinson *et al.* (2005) discovered that labelled nitrogen decreased in *Pellia neesiana* (Figure 96-Figure 103) with distance from the salmon stream into the forest. The researchers noted that bears catch fish, then transport them to land to consume them (Figure 132). This activity distributes the N from the salmon into the forest. *Pellia neesiana* also was in far greater abundance below the falls, and the researchers suggested that the liverwort was exploiting nutrients available from salmon carcasses and other wildlife activity.



Figure 129. *Pellia neesiana* with capsules and elongating setae. Photo by Janice Glime.



Figure 132. *Ursus americanus* (black bear) carrying fish to land. Photo by Aaron Huelsman, through Creative Commons.

Pellia neesiana (Figure 96-Figure 103) has experienced several studies on its faunal relationships. However, Grimaldi (2018) reports that the leaf mining fly *Spania nigra* (Figure 133-Figure 135) uses *Pellia neesiana* as a home and food for its larvae and a place for pupation (see also (Mik 1896; Nartshuk 1995).



Figure 133. *Spania* sp. eggs (arrows) on *Pellia endiviifolia*. Photo by Yume Imada and Makoto Kato, with permission.



Figure 134. *Spania* sp. first instar larva mining *Pellia endiviifolia*. Photo by Yume Imada and Makoto Kato, with permission.



Figure 135. *Spania* sp. final instar larva and posterior spiracle closeup. Photo by Yume Imada and Makoto Kato, with permission.

Biochemistry

Pellia neesiana (Figure 96-Figure 103) has tiny oil bodies (3.6-6.5 μm across; Figure 136), numbering from 8 up to 32 (Schuster 1992).

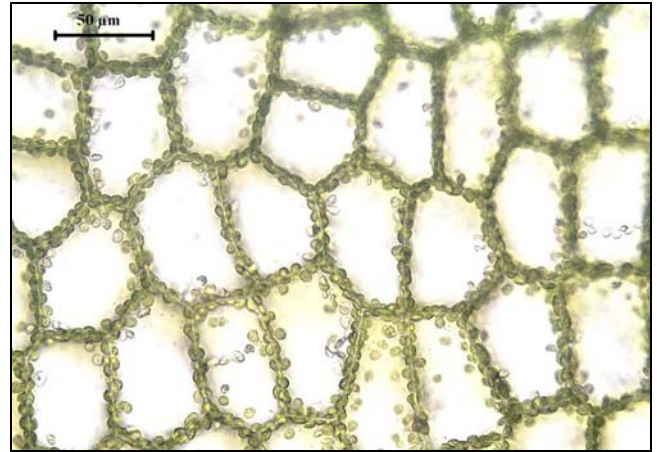


Figure 136. *Pellia neesiana* thallus cells. Chloroplasts confined to margins of cell indicate presence of large vacuole. Mostly colorless oil bodies are scattered. Photo by Hugues Tinguy, with permission.

Ono *et al.* (1992) detected the pungent diterpene dialdehyde, sacculatal in *Pellia neesiana* (Figure 96-Figure 103), suggesting its close relationship to *P. endiviifolia* (Figure 19-Figure 20).

Summary

These members of the **Pelliales** are at best facultatively aquatic. On the other hand, they like moist habitats and *Pellia* in particular can be found on stream banks, especially under overhanging grasses where it is moist and shaded. Others tolerate temporary ponds where they are submerged part of the year and out of water part of the year. *Pellia epiphylla* had both slime molds and fungi that find it a suitable place to live, whereas *Pellia neesiana* provides a home for the leaf-mining fly *Spania*.

Acknowledgments

Thank you to Lars Söderström for his continued help in sorting out nomenclature changes. David Wagner helped me sort out the stages of antheridial development in *Pellia neesiana* and provided me with an image of open ostioles.

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Add *Blasia pusilla* slime papillae image

CHAPTER 1-17

AQUATIC AND WET MARCHANTIOPHYTA, ORDER BLASIALES

TABLE OF CONTENTS

MARCHANTIOPSIDA	1-17-2
Blasiidae – Blasiales	1-17-2
Blasiaceae	1-17-2
<i>Blasia pusilla</i>	1-17-2
Distribution	1-17-2
Aquatic and Wet Habitats	1-17-3
Physiology.....	1-17-9
Adaptations	1-17-10
Reproduction.....	1-17-10
Role.....	1-17-17
Symbiotic Interactions	1-17-17
Interactions with Fungi	1-17-22
Biochemistry	1-17-23
Summary.....	1-17-23
Acknowledgments	1-17-24
Literature Cited	1-17-24

CHAPTER 1-17

AQUATIC AND WET MARCHANTIOPHYTA, ORDER BLASIALES



Figure 1. *Blasia pusilla* forming a rosette on wet soil. Photo by Dale Vitt, with permission.

Nomenclature for this chapter is based primarily on Söderström *et al.* (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species.

To develop this list, I used my own bibliography, collected over the past 56 years, and Google Scholar. These papers soon led me to others. I do not pretend that this is complete. It includes streams, lakes, wetlands, and other wet substrata. It mostly ignores bogs and ignores fens, but nevertheless includes a few of these species because they were found in a wetland study. Bogs and poor fens have been treated in whole books and provide an extensive literature; fens seem somewhat less studied. They would require considerably more review and time. Thus I felt that less-reviewed topics, particularly the aquatic habitats with which I am most familiar, should be given priority.

The species in this subchapter are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study. Their relative frequency can be noted based on the number of references cited.

MARCHANTIOPSIDA

Blasiidae – Blasiales

Blasiaceae

Blasia pusilla

Distribution

Blasia pusilla is a boreal-montane species (Dia & Not 1991). It occurs in Europe, West Greenland, North America, Asia (India, Kamchatka, China, Korea, Japan) (Rohret 1916; Schuster 1992). Schuster (1992) considers the Australian records to be errors.

It tends to form rosettes on its substrate (Figure 1-Figure 3).



Figure 2. *Blasia pusilla* habit on soil. Photo by Štěpán Koval, with permission.



Figure 3. *Blasia pusilla* habit, Mt. Robson, BC, Canada, 26 July 1980. Photo by Janice Glime.

Aquatic and Wet Habitats

Blasia pusilla (Figure 1-Figure 6) is not typically a submersed species. Holmes and Whitton (1975) considered it to be an "uncommon" member of the flora in the River Tweed. Jonsgard and Birks (1995) reported it from small streams in the Krakenes, Norway. In the Caucasian State Nature Reserve, Russia, it occurred in the dry river bed of the Bushujka River on silting rocks (Konstantinova *et al.* 2009).

Schuster (1992) comments that when *Blasia pusilla* (Figure 1-Figure 6) does occur in stream beds, it is almost always seasonal. Erosion and slippage seem to destroy most of the plants.

Nevertheless, the usual habitat of *Blasia pusilla* seems to be near water (Figure 6), occasionally submerged in some locations, but only facultatively aquatic.



Figure 4. *Blasia pusilla* rosette on sand, showing conspicuous ribs. Photo by Štěpán Koval, with permission.



Figure 5. *Blasia pusilla* on sand, with stellate gemmae. Photo by Štěpán Koval, with permission.



Figure 6. *Blasia pusilla* on wet soil. Photo by Kristian Peters, with permission.

River and stream banks seem to be among the most suitable habitats for *Blasia pusilla* (Figure 1-Figure 6). Sampson (1905) reported it from the bank of the River Dee in the UK. Paton (1967, 1971) reported it from gravelly detritus by a river and a clay stream bank in the UK. Rilstone (1949) found it on wet banks (Figure 1) in Cornwall, UK, but considered it to be rare. Fitzgerald and Fitzgerald (1966) reported it from schist detritus on rocks by the Glenedra River in northeast Ireland. Similarly, M'Ardle (1909) noted that it occurred among wet rocks in Ireland. Schumacher and Sivertsen (1987) found it on the banks of rivers, brooks, and rivulets in Norway, and Damsholt *et al.* (1984) reported it from along rills, along with *Scapania paludosa* (Figure 7) and *Pellia neesiana* (Figure 8).



Figure 7. *Scapania paludosa*, a species that occurs with *Blasia pusilla* along rills in Norway. Photo by Hermann Schachner, through Creative Commons.



Figure 8. *Pellia neesiana*, a species that occurs with *Blasia pusilla* along rills in Norway. Photo from Botany Website, UBC, with permission.

Vána and Ignatov (1995) reported *Blasia pusilla* (Figure 1-Figure 6) from ravine slopes and on logs covered by alluvium in flood valleys, as well as creek bars, in the Altai Mountains of Asia. In the Komi Republic, Dulin (2014) found *Blasia pusilla* on inundated soil along the river bank, in pure patches (Figure 9) or with other liverworts. Sofronova reported it from banks of water courses in the Upper Course of the Indigirka River, East Yakutia (Sofronova 2018), and on stones near the Tipton River as well as rock outcrops there, sustaining in both river and stream banks that experience occasional floods (Sofronova 2017). In South Siberia it can be found in

willow thickets along river and stream banks, sometimes mixed with *Jungermannia pumila* (Figure 10) and *Scapania mucronata* (Figure 11) (Czernyadjeva *et al.* 2013).

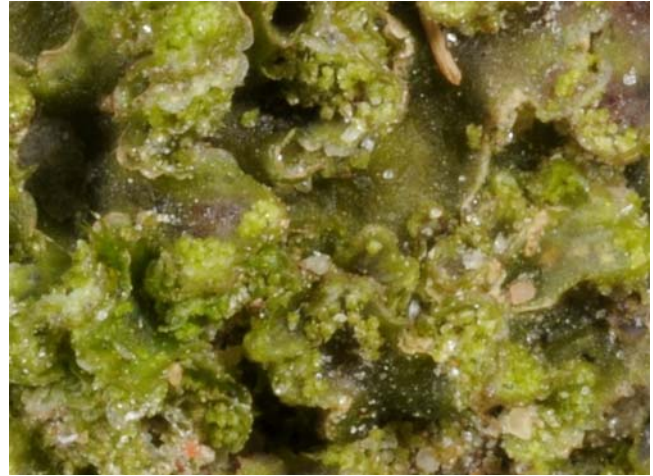


Figure 9. *Blasia pusilla* growing in pure patch on sand. Photo by Jouko Rikkinen, through Creative Commons.



Figure 10. *Jungermannia pumila*, a species that occurs mixed with *Blasia pusilla* in South Siberia willow thickets. Photo by Michael Lüth, with permission.



Figure 11. *Scapania mucronata*, a species that occurs mixed with *Blasia pusilla* in South Siberia willow thickets. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

In North America, Blomquist (1939) found *Blasia pusilla* (Figure 1-Figure 6) along the west branch of the New River in the Appalachian Mountains, USA. In the Arctic, it develops extensive cover, up to 75%, in the area flooded by glacial streams (Slack & Horton 2010). Skorepa (1968) found it on moist, shaded sandstone near a stream in southern Illinois, USA. Wagner (2009) reported it from moist sand (Figure 12-Figure 14) next to a creek in Oregon, USA, both solitary and mixed with other liverworts and with hornworts. It seems to like clay, occurring on clayey stream banks in Ohio, USA (Hall 1958). Hong (1978, 1980) reported it from wet rocks and soil in the North Cascades Range of Washington, USA.

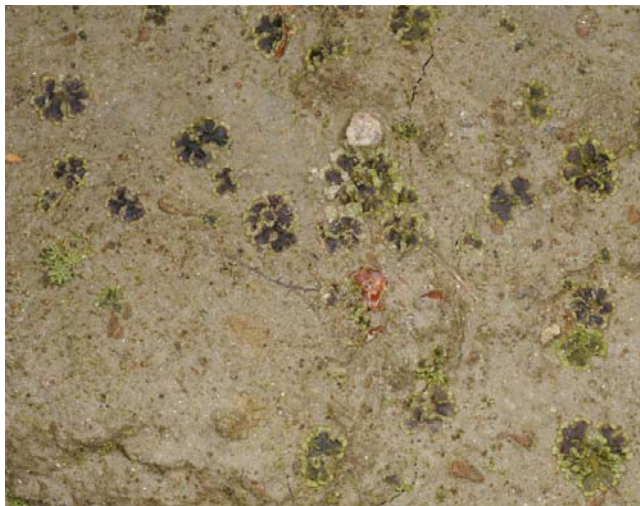


Figure 12. *Blasia pusilla* in aging small, pure patches on sand. Photo by Jouko Rikkinen, through Creative Commons.



Figure 13. *Blasia pusilla* habit on sand. Photo by Jouko Rikkinen, through Creative Commons.



Figure 14. *Blasia pusilla* habit on sand with older thallus dying. Photo by Jouko Rikkinen, through Creative Commons.

Ditches (Figure 15) can offer similar conditions to streams, so the presence of *Blasia pusilla* (Figure 1-Figure 6) there might be expected. Taylor (1921) reported it from the sides of a ditch in Mount Desert, Maine, USA. Paton (1971) similarly found it on a ditch bank in the UK.



Figure 15. Drainage ditch in Germany, a habitat where one might find *Blasia pusilla* along the sides. Photo by Dirk Ingo Franke, through Creative Commons.

Waterfalls provide moist habitats where moisture-loving liverworts are able to survive (Figure 16). On Bering Island, Russia, *Blasia pusilla* (Figure 1-Figure 6) occurs on wet boulders in a waterfall canyon (Bakalin 2005). Gruber *et al.* (2005) found that in the area near Krimml Waterfalls of Austria, *Blasia pusilla* grows best in locations receiving spray from the waterfalls. Odland *et al.* (1991) found that following regulation of a river in Aurland, western Norway, cover by *Blasia pusilla* increased near the waterfall in the spray zone. The regulation reduced the spray precipitation by 98-100%, but there is still considerable spray near the waterfall.



Figure 16. Waterfalls such as these create a constantly moist environment suitable for liverworts such as *Blasia pusilla*. Photo by Fabian Michelangeli, through public domain.

Slopes often provide moist, shaded habitats (Figure 17-Figure 18). Rose (1950) found that *Blasia pusilla* was "plentiful" on a damp, north-facing bank on clayey sand in the UK. Dulin (2014) found it on "slightly matted loamy soil at a slope ledge" and on the vertical surface of a ground wall in the Komi Republic. Bakalin *et al.* (2016) found it on the moist soil or mineral ground of eroded slopes, where it typically occurred with *Anthelia juratzkana* (Figure 19), *Calypogeia muelleriana* (Figure 20), and *Solenostoma hyalinum* (Figure 21).



Figure 17. *Blasia pusilla* habitat on slope. Photo by Hermann Schachner, through Creative Commons.



Figure 18. *Blasia pusilla* habitat on slope. Photo by Hermann Schachner, through Creative Commons.



Figure 19. *Anthelia juratzkana*, a species that occurs with *Blasia pusilla* on slopes in Russia. Photo by Hermann Schachner, through Creative Commons.



Figure 20. *Calypogeia muelleriana*, a species that occurs with *Blasia pusilla* on slopes in Russia. Photo by Hugues Tinguy, with permission.



Figure 21. *Solenostoma hyalinum* with capsule, a species that occurs with *Blasia pusilla* on slopes in Russia. Photo by Michael Lüth, with permission.



Figure 22. *Blasia pusilla* on wet soil. Photo by Bernd Haynold, through Creative Commons.

In the Mt. Greylock region of Massachusetts, USA, Andrews (1904) found only a small specimen on a wet bank in the Notch. Lanfear (1933) found *Blasia pusilla* (Figure 1-Figure 6) on clay banks and shale in western Pennsylvania, USA. Conard (1940) likewise reported it from moist, shaded clayey banks, where it was rare, in Iowa, USA. Breil (1996) found it on moist, eroding loamy slopes in the Virginia Piedmont, USA.

The suitable slopes include a number of records along trails. Váňa and Ignatov (1995) reported it from wet clayish soil along both trails and roads in the Altai Mountains of eastern Asia. Czernyadjeva *et al.* (2017) found it, albeit rare, on a railway embankment, as did Dulin (2014, 2015) in the Komi Republic. Bakalin *et al.* (2013) found it on a moist clayish road rut, occurring in pure mats, in Adjara, Georgia. Ören *et al.* (2015) found it on a damp, steep, roadside slope in Turkey, where it was the most common bryophyte on the slope. Rikkinen (1992) reported it from shaded roadside banks and other disturbed sites in Finland. Blomquist (1939) reported *Blasia pusilla* (Figure 1-Figure 6) from a moist clay road bank in North Carolina, USA. Greenwood (1915) found it on damp soil by roadsides in Massachusetts, USA.

Springs are not often mentioned as habitats for *Blasia pusilla* (Figure 1-Figure 6), but then springs are less common habitats. Paton (1961) found it in the UK on a sandy track that remained moist by water from small springs. Wittlake (1950) found it under and around springs on a slope in Arkansas, USA. Similarly, seepage areas sometimes provide suitable habitats. Blockeel (2020) reported it from moist soil by a seepage in Greece.

Damp or wet soil is suitable, but few reports seem to identify that habitat for *Blasia pusilla* (Figure 1-Figure 6) (Macvicar 1902; Lanfear 1933; Paton 1967; Hong 1977, 1978). In their survey of the upper course of the Indigirka River in East Yakutia, Sofronova (2018) reported it from soil in the horsetail, moss shrub post-ice community. Among its damp soil habitats (Figure 22-Figure 24), Rilstone (1949) found it on clayey moors in Cornwall, UK, but it is rare.



Figure 23. *Blasia pusilla* large population on soil. Photo by Hermann Schachner, through Creative Commons.



Figure 24. *Blasia pusilla* on soil. Photo by Bernd Haynold, through Creative Commons.

Bogs don't seem to be a usual habitat for *Blasia pusilla* (Figure 1-Figure 6). The only record I have seen is that of

Macvicar (1902) for Meiller Bog in the Ben Lawers District, UK (Figure 25).



Figure 25. View from summit of Ben Lawers, UK, where *Blasia pusilla* occurs in a "bog" habitat. Photo by Scott Holland, through public domain.

Some plants of *Blasia pusilla* (Figure 1-Figure 6) are able to inhabit dune slacks (Figure 26) (Swann 1982; Persson & Pleijel 2008). These habitats occur between foredunes in low-lying depressions (Geographyinaction 2021). In the winter the plants can be close to or below the water level. Organic matter is slow to develop in slacks, but there is usually an impervious layer. Mosses (and possibly some liverworts) help to retain moisture. Other dune slacks remain as pools (Wikipedia 2021).



Figure 26. Dune slack in UK, a habitat where *Blasia pusilla* can occur. Photo by Gary Rogers, through Creative Commons.

The ability of *Blasia pusilla* (Figure 1-Figure 6) to colonize disturbed substrata has made it a successful pioneer species. When a former peat moor became agricultural land, bryophytes were able to colonize. For example, *Blasia pusilla* was among the pioneers in a maize field (Figure 27) when it remained untilled due to extremely wet weather (van den Bosch & Kersten 2004).



Figure 27. Muddy field in the UK, a potential site for the occurrence of *Blasia pusilla*. Photo by Ian Peterson, through Creative Commons.

Drawdown of a lake in western Norway exposed a floodplain system with artificial islands (Odland 1997). During the first three years following construction, *Blasia pusilla* (Figure 1-Figure 6) was among the dominants able to colonize, but they disappeared or were greatly reduced after 8 years. The colonization by *B. pusilla* was not immediate, as *Subularia aquatica* (Figure 28) and small acrocarpous mosses dominated after one month, but this soon shifted to one in which *Blasia pusilla* was one of the dominants (Odland 1997; Odland & del Moral 2002).



Figure 28. *Subularia aquatica*, a species that is a primary colonizer in a drawdown lake, preceding the colonization by *Blasia pusilla*. Photo by J. C. Schou, with permission.

Blasia pusilla (Figure 1-Figure 6) is also present as a pioneer in the early successional stages of the Arctic tundra (Figure 29, where it reaches 75% in areas flooded by a glacial stream (Slack & Horton 2010). In even harsher conditions of a gold mining area of northeast Yakutia, *Blasia* was the only liverwort present (Sofronova 2019).



Figure 29. Arctic tundra, a habitat where *Blasia pusilla* can cover 75% of the ground in glacial melt areas. Photo by A. Diallya, through Creative Commons.

Various Russian records indicate that *Blasia pusilla* (Figure 1-Figure 2-Figure 6) is tolerant of more terrestrial, drier habitats as well (Figure 30). Sofronova found it on sand between rocks (Sofronova 2013), few plants on soil among *Salix* shrubs (Figure 31) (Sofronova 2015), and on decaying wood (Sofronova 2017), summarizing it as occurring in two main types of habitats in Yakutia: decaying wood and rocks. Dulin (2014) describes terrestrial habitats in the Komi Republic: matted loamy soil at slope ledge between inundated shrublet-moss spruce forest and pebbly bar; on slightly matted soil of roadside wall.



Figure 30. *Blasia pusilla* habitat on soil and roots. Photo by Michael Lüth, with permission.

Physiology

Nordhorn-Richter (1984) explored the presence of fluorescence in bryophytes, as seen with a compound microscope under UV light, including *Blasia* in her studies. She found that the receptacular gemmae (Figure 32) fluoresced yellow in UV light.

Smith (2002) examined rapid chlorophyll fluorescence induction in a number of bryophytes. *Blasia pusilla* (Figure 1-Figure 6) did not have outstanding values; its highest yield of PSII Fv/Fm was 0.78 ± 0.01 .

Blasia pusilla (Figure 1-Figure 6) extends into the Arctic, surviving, for example, in the mountain tundra belt of Northeast Yakutia, Russia (Sofronova 2019). This area

has permafrost, yet the liverwort is able to survive the long winters (Figure 33), probably mostly as gemmae.



Figure 31. *Salix* habitat, which can provide suitable habitat for *Blasia pusilla*. Photo by Dennis Kalma, FEIS, through public domain.

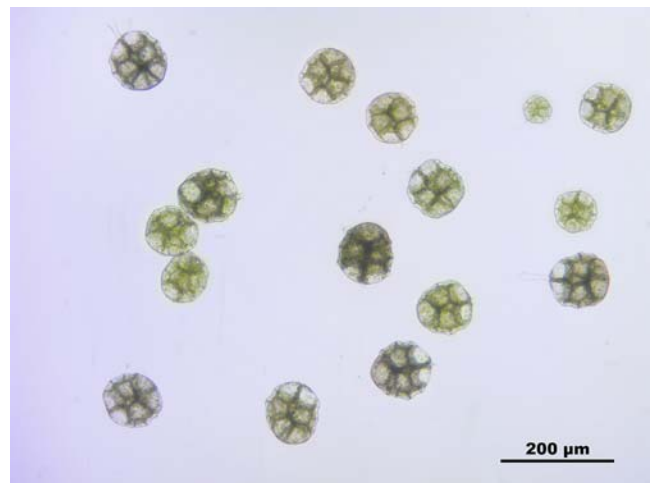


Figure 32. *Blasia pusilla* gemmae from flask. Photo by Hermann Schachner, through Creative Commons.



Figure 33. *Blasia pusilla* frozen. Photo by Bernd Haynold, through Creative Commons.

Adaptations

Blasia pusilla can dry out (Figure 34). This seems to be common at the end of the growing season, but gemmae are able to carry it over to the next spring. But it also has some adaptations to help it in its water relations.



Figure 34. *Blasia pusilla* with flasks, somewhat dry. Photo by Bob Klips, with permission.

Blasia pusilla (Figure 1-Figure 6) develops strands of thick-walled cells (Figure 35) that provide both mechanical support and conducting tissue (Rohret 1916). The plants can grow in pure mats (Figure 36) or with other liverworts (Wagner 2009; Dulin 2014; Sofronova 2017), both providing a reduction in water loss.



Figure 35. *Blasia pusilla* discolored, probably due to aging or sun exposure, and showing the strands that provide mechanical support and conduits for water. Photo by Štěpán Koval, with permission.



Figure 36. *Blasia pusilla* large population on soil. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Allsopp and Ilahi (1971) described the morphology of *Blasia pusilla* (Figure 1-Figure 6). *Blasia pusilla* is typically seasonal, resulting from considerable dieback (Figure 37) in the winter months (Schuster 1992). This occurs both in submersed locations and out of water. Its reappearance in the spring results from its prolific production of gemmae (two types) and spores from its numerous sporophytes.

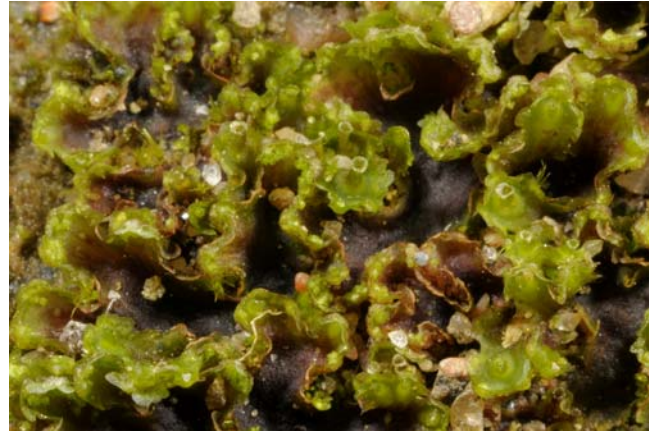


Figure 37. *Blasia pusilla* with older thallus dying. Photo by Jouko Rikkinen, through Creative Commons.

Blasia pusilla (Figure 1-Figure 6) is **dioicous**. Rohret (1916) describes the male plants as being more slender and deeply lobed than the female plants. Antheridia occur in a row on each side of the midrib in small lobes of the thallus (Figure 38). Ten to twelve archegonia (Figure 39) are produced near the tip, but the continued growth of the apex causes them to eventually reside near the middle of the thallus length. Ultimately, the sex organs are imbedded in the thallus (Figure 39) due to overgrowth by the thallus. Despite the numerous archegonia, typically only one sporophyte develops on a single thallus. Despite its dioicous condition, it can produce abundant sporophytes (Figure 40-Figure 46) in at least some locations (Rohret 1916; Schuster 1992; Breil 1996).

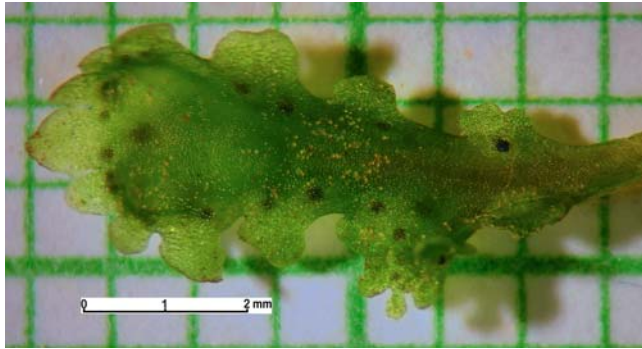


Figure 38. *Blasia pusilla* male thallus with small antheridial lobes at bottom. Photo courtesy of David H. Wagner.



Figure 41. *Blasia pusilla* capsules. Photo by Rafael Medina, with permission.



Figure 39. *Blasia pusilla* archegonium imbedded in thallus. Photo courtesy of David H. Wagner.



Figure 42. *Blasia pusilla* with mature capsules. Photo by Jouko Rikkinen, through Creative Commons.



Figure 40. *Blasia pusilla* with emerging capsules. Photo by Kristian Peters, with permission.



Figure 43. *Blasia pusilla* with mature capsules. Photo by Jouko Rikkinen, through Creative Commons.



Figure 44. *Blasia pusilla* with mature and dehiscent capsules. Photo by Jouko Rikkinen, through Creative Commons.



Figure 45. *Blasia pusilla* with dehiscent capsules, showing tangled elaters. Photo by Jouko Rikkinen, through Creative Commons.



Figure 46. *Blasia pusilla* with open capsules. Photo by Rafael Medina, with permission.

Wagner (2009) reported the presence of male plants and females with sporophytes near Sutton Creek in Oregon, USA. Rohret (1916) reported that sex organs of *Blasia pusilla* are formed in the summer in Iowa, USA. But it

appears that this timing differs by location, probably relating to factors associated with latitude. Fertilization of *Blasia pusilla* (Figure 1-Figure 6) occurs in the spring in England, Scotland, Wales, and North Carolina, USA (Duckett & Renzaglia 1993). Sporophytes develop during the summer months and the parent gametophytes die (Figure 42) (Duckett & Renzaglia 1993). Spores are shed in the spring, indicating that the sporophyte must overwinter on the dead gametophyte (Rohret 1916; Duckett & Renzaglia 1993; Shimamura *et al.* 2006). The death of the gametophyte before the sporophyte matures is unique to *Blasia*. The cell division in the seta is completed by early autumn and the cells are packed with amylochloroplasts (Duckett & Renzaglia 1993). The capsule produces sporocytes with abundant protein bodies. These researchers suggest that day length probably controls the initiation of the sex organs in spring and dormancy of sporophytes in autumn. On the other hand, they suggest that it is higher temperatures that govern the sporophyte maturation. Both sporogenesis and seta elongation occur in early spring in Japan (Shimamura *et al.* 2006). Spores are large (35-50 μm). Udar and Srivastava (1983) provide SEM micrographs of the spores of *Blasia* and discuss the reproductive biology.

Van Zanten (2005) noted the rarity of sporophytes on *Blasia pusilla* (Figure 1-Figure 6) in The Netherlands. But when he was able to find ripe capsules, it was not spring, but November. He attributed the increase in plants with capsules to a greater search intensity. He also noted that the increase in capsules did not affect the production of gemmae.

Renzaglia and Duckett (1987) described the spermatogenesis of *Blasia pusilla* (Figure 1-Figure 6) in detail. Bartholomew (1986) described the sporeling development of *Blasia pusilla*, noting that the spores are endosporic, but not precocious. Germination is initiated by imbibition of water, causing the spores to swell to 50-60 μm . Differences in temperature and light regimes (18°C, 18:6 light dark & 3000-3500 lux; 18°C, 12:12 light dark & 500 lux; 10°C & 18:6 light dark, 1300 lux) had no effect on spore germination or development except to alter the rate. Bartholomew-Began (2009) explored the development of the sporeling in another member of Blasiales (*Cavicularia*; Figure 47) and found that the pattern of development is unique to *Cavicularia* and *Blasia*.

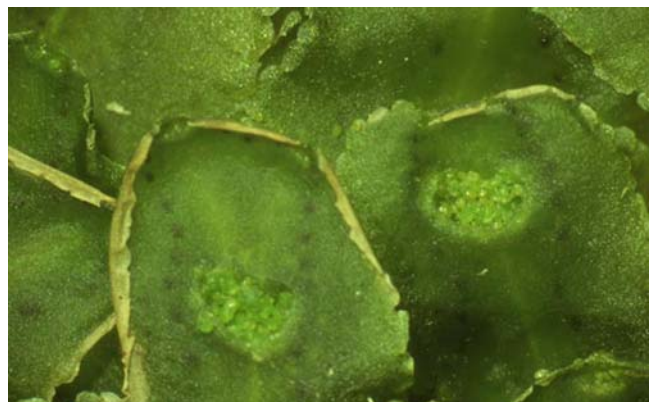


Figure 47. *Cavicularia densa* with *Nostoc* colonies forming a row on each side of the gemmae cups. Photo from Digital Museum Hiroshima University, with permission.

It is possible for *Blasia pusilla* (Figure 1-Figure 6) to reproduce aposporously in culture (Matzke & Raudzens 1968; Raudzens & Matzke 1968). Particular cells of the elongating seta can remain alive. After 3.5-6 weeks these can at times in the right conditions give rise to diploid gametophytes. These gametophytes develop in appearance like those with only one set of chromosomes. Normal gametophytes have $n=9$; the ones produced by apospory have $n=18$. They can produce archegonia, but not antheridia. Matzke and Raudzens consider that this type of apospory could not occur in the field.

Allsopp and Ilahi (1971) described regeneration in *Blasia pusilla* (Figure 1-Figure 6). An early description of the asexual reproduction in *Blasia pusilla* was provided by Buch in 1907. *Blasia pusilla* produces two types of gemmae in addition to spores (During 2001a). The stellate gemmae (Figure 48-Figure 55) form on the dorsal side of the thallus and the globose gemmae (Figure 56-Figure 68) are produced in receptacles (Buch 1907; Duckett & Renzaglia 1993; Paton 1999; Laaka-Lindberg *et al.* 2003). Those produced in the flask-like receptacles exhibit a yellow fluorescence in UV light (Nordhorn-Richter 1984)



Figure 48. *Blasia pusilla* with stellate gemmae. Photo by David T. Holyoak, with permission.



Figure 49. *Blasia pusilla* with stellate gemmae. Photo by Martin Hutten, with permission.



Figure 50. *Blasia pusilla* with stellate gemmae. Photo by Shaun Pogacnik, through Creative Commons.

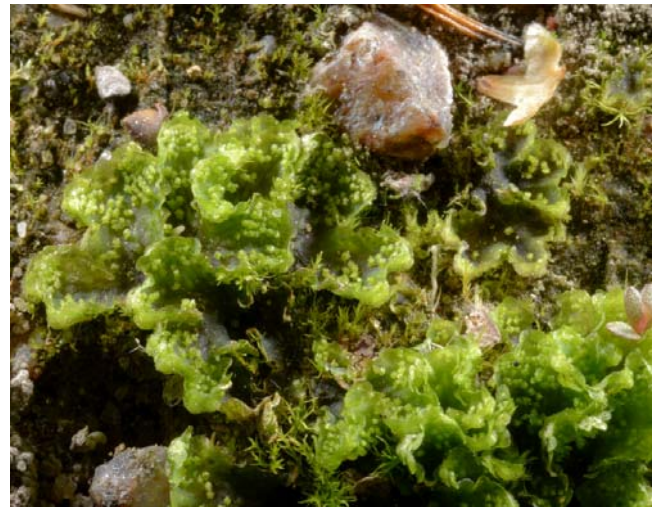


Figure 51. *Blasia pusilla* with stellate gemmae. Photo by Jouko Rikkinen, through Creative Commons.



Figure 52. *Blasia pusilla* with stellate gemmae (arrow) on surface and *Pellia* on left (arrow). Photo by Paul Davison, with permission.



Figure 53. *Blasia pusilla* with stellate gemmae, habit on sand. Photo by Jouko Rikkinen, through Creative Commons.



Figure 54. *Blasia pusilla* showing stellate gemmae arranged on the thallus margins. Photo courtesy of David H. Wagner.

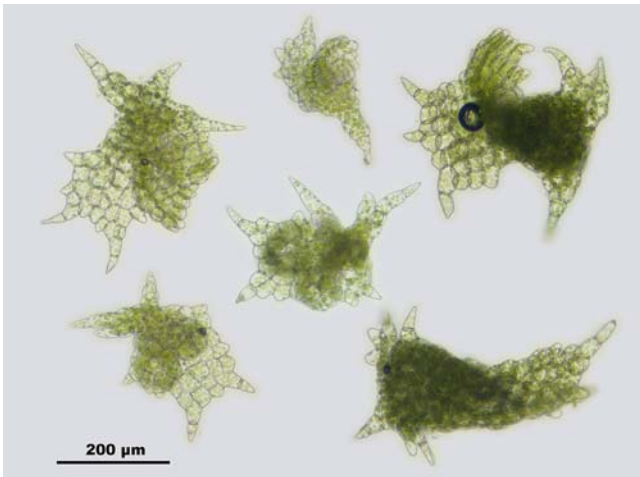


Figure 55. *Blasia pusilla* stellate gemmae. Photo by Hermann Schachner, through Creative Commons.

The globose gemmae (Figure 56-Figure 68) from the receptacles are able to persist in diaspore banks. Both kinds of gemmae of *Blasia pusilla* (Figure 1-Figure 6) are multicellular, with each cell containing a large nucleus and many oil bodies (Rohret 1916). I have been unable to find any other report of oil bodies in the gemmae of *Blasia pusilla*.



Figure 56. *Blasia pusilla* with numerous flask-like receptacles containing gemmae. Photo by Dick Haaksma, with permission.



Figure 57. *Blasia pusilla* side view of gemmae flasks. Photo by Jouko Rikkinen, through Creative Commons.



Figure 58. *Blasia pusilla* side view of habit with gemmae flasks. Photo by Jouko Rikkinen, through Creative Commons.



Figure 61. *Blasia pusilla* habit with moisture. Photo by Jouko Rikkinen, through Creative Commons.



Figure 59. *Blasia pusilla* showing numerous gemmae flasks. Photo by Hermann Schachner, through Creative Commons.



Figure 62. *Blasia pusilla* with flasks of gemmae and gemmae exuding from flask. Photo by Hermann Schachner, through Creative Commons.



Figure 60. *Blasia pusilla* with flask-like gemmae receptacles and exuding gemmae. Photo by Tim Faasen, with permission.

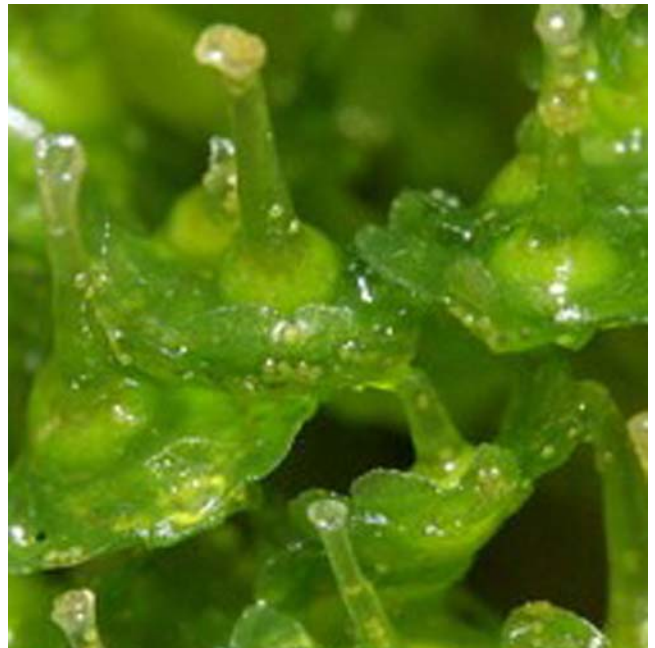


Figure 63. *Blasia pusilla* with gemmae in flask and mucilage exuding from tips. Photo by Hermann Schachner, through public domain.



Figure 64. *Blasia pusilla* gemmae on flask. Photo by Štěpán Koval, with permission.

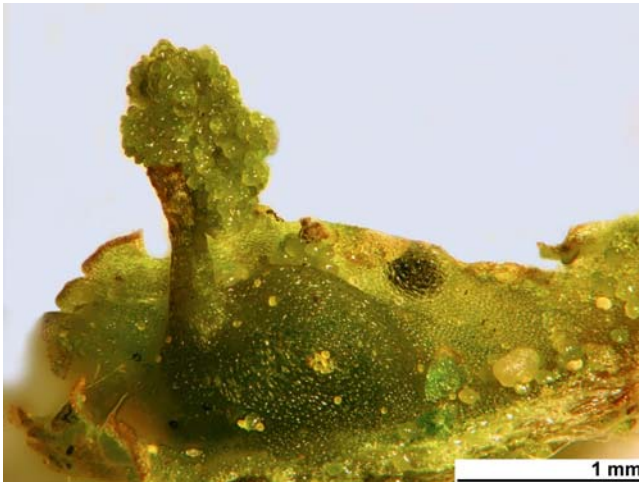


Figure 65. Gemmae flask of *Blasia pusilla* with gemmae exuding from the opening. Photo courtesy of David Wagner.

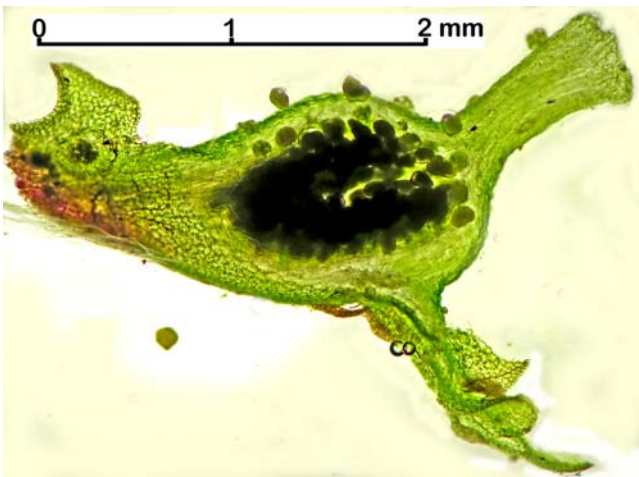


Figure 66. View of gemmae flask of *Blasia pusilla*, showing globose gemmae inside and on its surface. Photo courtesy of David Wagner.



Figure 67. *Blasia pusilla* with gemmae in neck of flask. Photo by Hermann Schachner, through Creative Commons.

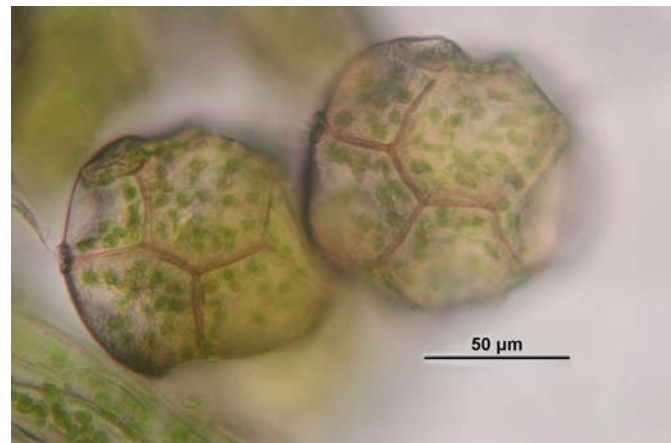


Figure 68. *Blasia pusilla* gemmae from flask. Photo by Hermann Schachner, through Creative Commons.

As the globose gemmae (Figure 56-Figure 68) in the flask-like receptacles of *Blasia pusilla* (Figure 1Figure 2-Figure 6) develop, the mucilage papillae secrete a slimy substance that enters the flask cavity (Rohret 1916). As the mature gemmae break from their stalks, they become imbedded in the viscid liquid. Pressure of the growing gemmae, and probably entrance of water into the flask, causes the mucilage to swell and exude from the flask neck (Figure 63-Figure 67). When the gemma begins to grow, the young plant benefits from the energy stored in the gemma (Figure 68). As the old thalli die, the gemmae and young plants are permitted to reach the soil. The gemmae can be shed during most of the year. These globose gemmae of *Blasia pusilla* have large oil droplets, and these may help the gemmae survive the winter to replace winter-damaged plants.

Bartholomew-Began and Jones (2005) described the receptacular gemma (Figure 56-Figure 68) development of *Blasia pusilla* (Figure 1Figure 2-Figure 6). These discoid to ellipsoid, stalked gemmae are produced within the flask-shaped receptacle. The gemma has distinct tiers of thick-walled cells with margins of lateral column of thin-walled cells. Germination does not occur until the gemmae are free from the receptacle. In fact, During (2001b) found that the disc-like gemmae do not seem to be able to germinate right away after they are dispersed, a condition that permits them to find their way into diaspore banks.

The globose receptacular gemmae (Figure 56-Figure 68) of *Blasia pusilla* (Figure 1-Figure 6) are present on both male and female plants (CRB 1908). However they are rare if the female is developing embryos. The apical brood-buds are common in summer; gemmae do not seem to germinate in summer or autumn, but instead are dormant until spring, when they can form new plants. Shoots arise from one side of the gemma, not both.

During (2001c) considers the production of two kinds of gemmae to be beneficial for ruderal species such as *Blasia pusilla* (Figure 1-Figure 6). The stellate gemmae (Figure 48-Figure 55) bring along their own nitrogen-fixing *Nostoc* symbiont in the two auricles (Duckett & Renzaglia 1993). These gemmae are also in possession of large amylochloroplasts (During 2001c). They are produced throughout the growing season, but are unable to survive the cold of winter. The more globose receptacular gemmae (Figure 56-Figure 68) are filled with starch, proteins, and lipids, but no *Nostoc*. Unlike the stellate gemmae, they are not released until late summer or autumn, survive the winter, and germinate in spring. These cold-resistant gemmae are suitable for diaspore banks. When they are brought to the surface, they do not germinate right away. This could cause them to be missed in some diaspore studies since identification is usually based on germination. Perhaps they are waiting for the right combination of temperature, day length, and light intensity, or maybe requiring a cold period first.

Role

In the Mt. Kurikoma district of Japan, Chiba and Kato (1969) explored the testacean (protozoa) community associated with bryophytes. They found that these communities related to the habitat of the bryophytes, with *Blasia pusilla* (Figure 1-Figure 2-Figure 6) among those that formed a suitable substrate for the protozoans.

Symbiotic Interactions

Most of the cyanobacterial symbiotic associations in the bryophytes are with the genus *Nostoc* (Watts *et al.* 1999). Although *Nostoc* partners are common in the **Anthocerotophyta**, this is not the case among the **Marchantiopsida**. Only two species of **Marchantiopsida** are known to harbor *Nostoc* (Figure 69) symbionts: *Blasia pusilla* (Figure 1-Figure 2-Figure 6; Figure 70) and *Cavicularia densa* (Figure 47), both in **Blasiidae** (Rikkinen & Virtanen 2008). It is interesting that these species lack fungal symbionts (Adams & Duggan 2008; Rikkinen & Virtanen 2008; Liepiņa 2012), although they can have non-symbiotic fungal inhabitants.



Figure 69. *Nostoc punctiforme*, a Cyanobacterium that can live symbiotically in *Blasia pusilla*. Photo by Eduardo Zuñiga, through Creative Commons.



Figure 70. *Blasia pusilla* showing *Nostoc* colonies. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

The *Nostoc* (Figure 69-Figure 70) of *Blasia pusilla* occurs extracellularly (Jackson *et al.* 2012) in auricles on the ventral surface (Figure 71-Figure 77) along the midrib (Adams 2002), thus receiving some protection from bright light and from desiccation. These *Nostoc* colonies cause areas of dark spots visible along the thallus (Adams *et al.* 2006). The assurance of transfer of these symbionts to the next generation is accomplished by the occurrence of the *Nostoc* in the lobes of the stellate gemmae (Figure 48-Figure 55) (Duckett & Renzaglia 1993; Rikkinen & Virtanen 2008). Rodgers and Stewart (1977) found that this symbiosis works well under moist conditions, but not in waterlogged or desiccated conditions. In their experiments, Rikkinen and Virtanen (2008) found that 95 out of 100 of the stellate gemmae produced cyanobacterial colonies within 3 months in culture.



Figure 71. *Blasia pusilla* side view of habit showing *Nostoc* colonies on ventral side. Photo by Jouko Rikkinen, through Creative Commons.

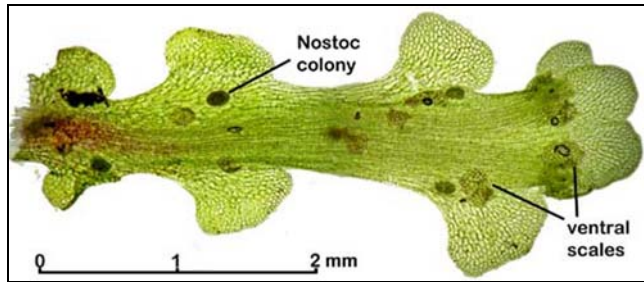


Figure 72. *Blasia pusilla* labelled to show location of *Nostoc*. Photo by David H. Wagner, with permission.



Figure 73. *Blasia pusilla* showing *Nostoc* as darker patches on the lobes. Photo by Bernd Haynold, through Creative Commons.

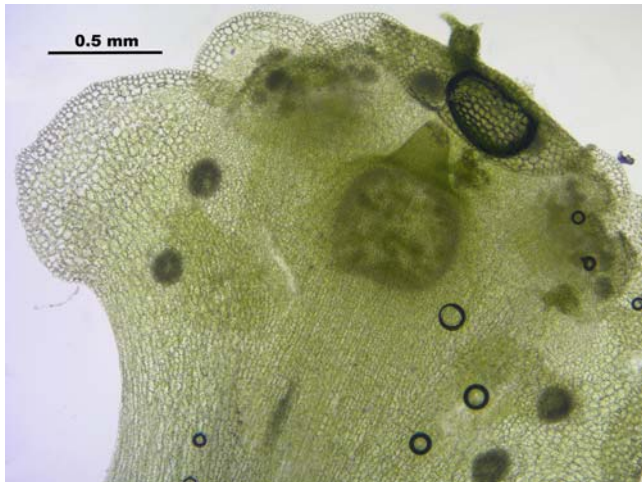


Figure 74. *Blasia pusilla* with *Nostoc* colonies. Photo by Hermann Schachner, through Creative Commons.

Duckett and Renzaglia (1993) found that viability differed between the non-symbiotic receptacular gemmae (Figure 78) and the symbiotic stellate gemmae (Figure 79). The stellate gemmae contain starch, but are short-lived. The receptacular gemmae, on the other hand, contain proteins and lipids and remain viable for a long time. The stellate gemmae, with their symbionts and starch, are able to secure their initial development and produce plants with symbiotic nitrogen fixation in a short time. The receptacular gemmae, by surviving longer, had more opportunity to obtain a *Nostoc* partner from the soil (Figure 80-Figure 82).

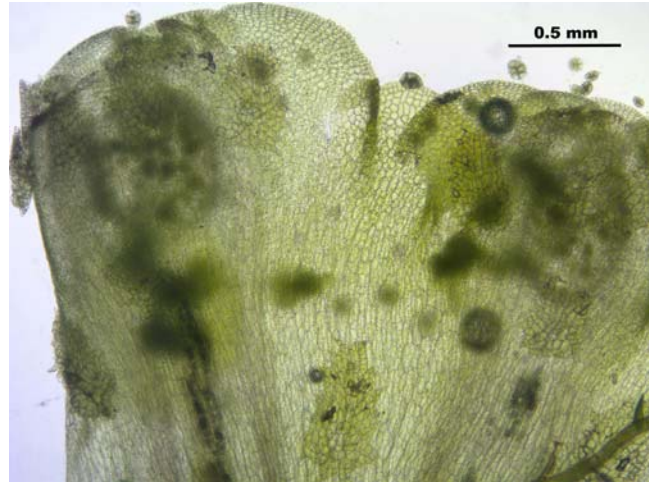


Figure 75. *Blasia pusilla* with *Nostoc* colonies and gemmae (globose especially at margins of thallus). Photo by Hermann Schachner, through Creative Commons.

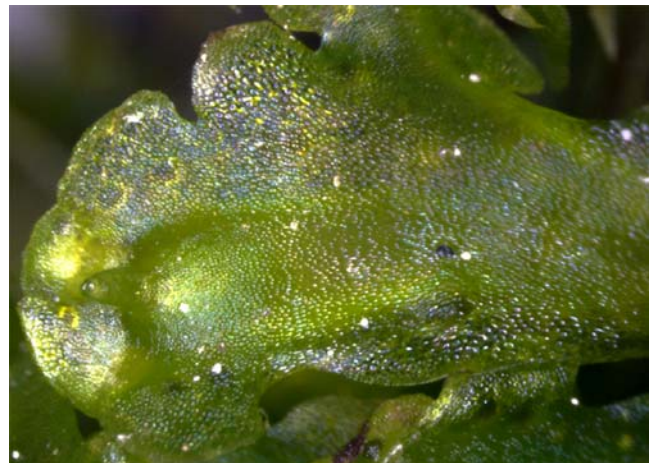


Figure 76. *Blasia pusilla* showing *Nostoc* in dark patches. Photo by Jouko Rikkinen, through Creative Commons.

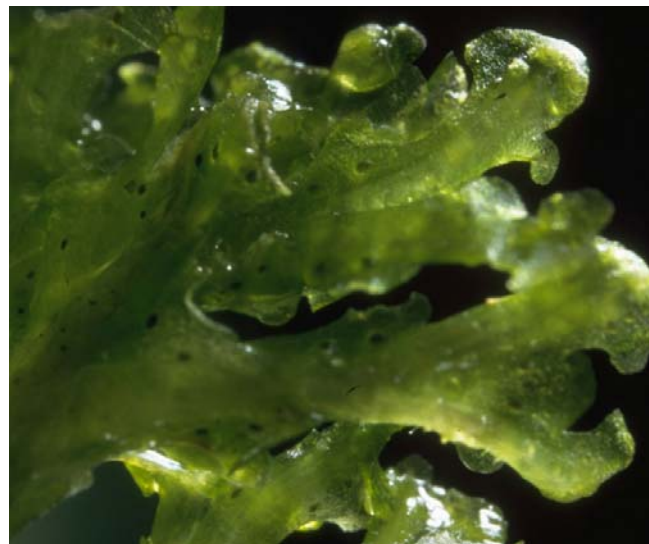


Figure 77. *Blasia pusilla* showing *Nostoc* colonies. Photo by Jan-Peter Frahm, with permission.



Figure 78. *Blasia pusilla* with flasks of gemmae. Photo by Hugues Tinguy, through Creative Commons.



Figure 79. *Blasia pusilla* with stellate gemmae. Photo by Jouko Rikkinen, through Creative Commons.



Figure 80. *Nostoc commune* on soil, a potential source for symbionts for *Blasia pusilla*. Photo by Yamamaya, through Creative Commons.

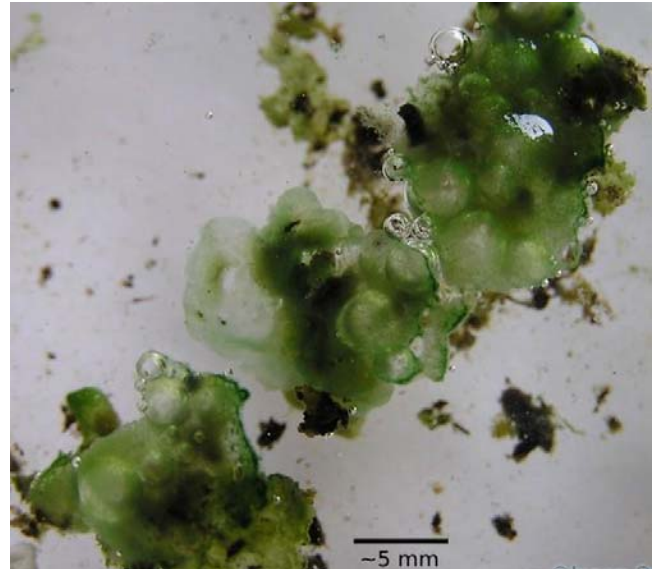


Figure 81. *Nostoc* free-living colonies. Photo by Jason Oyadomari, with permission.



Figure 82. Free-living *Nostoc* colonies. Photo by Jason Oyadomari, with permission.

Meeks (1990) described the colonization and establishment of *Nostoc* in *Blasia pusilla* (Figure 73-Figure 77), including both structural and metabolic changes that result from the symbiosis. There has been some controversy over the location of the *Nostoc* in pits (Davison 2009), attributing them to pits on the thallus. However, Davison argues that pits and open holes do not exist in *Blasia pusilla*. The *Nostoc* actually occurs in the cavities formed by the slime papillae (Adams 2002; Solheim *et al.* 2004). These occur in auricles – as almost spherical structures.

Kimura and Nakano (1990) found that the *Nostoc* is only invasive when it is in its motile, hormogonial (describing mobile filaments) stage (Figure 83, Figure 84). Knight and Adams (1996; Adams 2002) found that when *Blasia pusilla* is deprived of N, it releases extracellular signals that trigger hormogonia to form; at the same time, these signals serve as a highly effective attractant to facilitate the hormogonia in finding the thallus. The ability of these shorter hormogonia to glide makes it possible for them to move to the sites where they can become symbionts (Adams 2002). This invasion induces morphological changes in the cavities it invades.

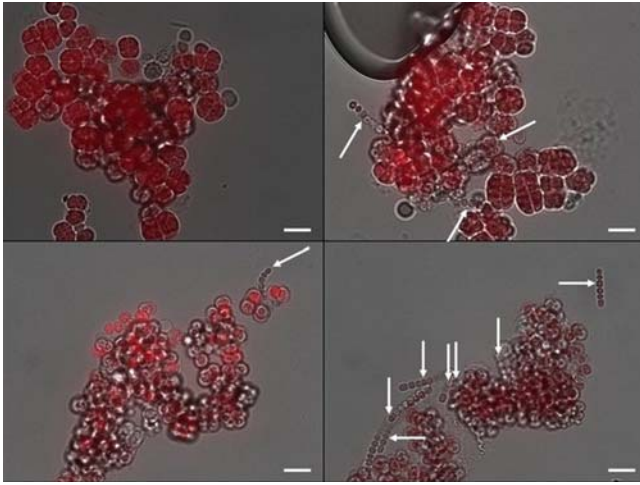


Figure 83. *Chlorogloeopsis fritschii* forming hormogonia, the mobile stage that is able to invade the thallus of liverworts such as *Blasia pusilla*. Photo by Benjamin L. Springstein, Fabian Nies, and Tal Dag, through Creative Commons.

Nilsson *et al.* (2006) found that the extracts of both symbiotic plants such as *Blasia pusilla* (Figure 73-Figure 77) and non-symbiotic plants such as rice all elicited positive **chemotaxis** (directional movement in response to chemical) by the two *Nostoc* strains tested. The chemotaxis is reduced by increased temperature and darkness but stimulated by phosphorus and iron starvation or elevated salt concentrations. Sugars also stimulated chemotaxis, but flavonoids and amino acids had no effect. Díaz *et al.* (2011) suggested that **lectins** could be expected to promote the symbiont cellular dispersal. They demonstrated that it causes *Nostoc* to differentiate mobile cells that are attracted to the lectins. However, the *Nostoc* does not form filaments (Figure 82) before its chemotropic movement in response to lectins.

Once infection of the *Blasia pusilla* (Figure 73-Figure 77) thallus has occurred, the developmental pathway of the symbiont must switch from hormogonia development (Figure 83) to heterocyst (Figure 84) differentiation (Adams 2002). That means it must have a mechanism for repressing further hormogonia formation, which is genetically programmed. Once the symbiotic association has formed, the *Nostoc* produces **heterocysts** (Figure 84-Figure 85) (Herrero *et al.* 2004), which are the sites of the extensive nitrogen fixation. Gorelova *et al.* (1996) provided protocol that made it possible to study this symbiont development.



Figure 84. *Nostoc* with heterocysts (arrow). Photo by Jason Oyadomari, with permission.

Rodgers and Stewart (1977) reported that in *Blasia pusilla* (Figure 73-Figure 77) the 2-week-old colonies had a 20% heterocyst (Figure 84) frequency, whereas by six weeks this had increased to 48%. Production of heterocysts in symbiotic conditions can be 10-20 times that found free-living *Nostoc* (Adams 2002). Rodgers and Stewart (1977) found a heterocyst frequency of the free-living isolates to be 3-6%, but in their study this increased to 30% or more when they were symbiotic in *Blasia*. *Nostoc* colonies develop in the slime cavities of the *Blasia* thallus within 72 hours. These colonies stretch the cells of the cavities. Filamentous protrusions develop on the liverwort cavity wall and penetrate the *Nostoc* colonies, forming a labyrinth of wall ingrowths in the *Nostoc* cells (Duckett *et al.* 1977), thus increasing the surface area of contact with the host by about 30% within 4 weeks (Rodgers & Stewart 1977), presumably facilitating transfer of the nitrogen compounds.

In *Blasia pusilla* (Figure 73-Figure 77), these specialized cells are formed as a response to limiting nitrogen conditions in the cell and are initiated by specialized genes (Herrero *et al.* 2004). In the *Nostoc* the **heterocysts**, as their name implies, are different from the other cells. They are able to reduce atmospheric nitrogen by providing an oxygen-free environment in which the nitrogenase enzyme can function (Wolk *et al.* 1994). This anoxic condition is achieved by both increased respiration and lack of photosynthesis in the heterocyst. The heterocyst loses the ability to fix CO₂, but products needing additional carbon can be supplied by the bryophyte (Duckett *et al.* 1977; Herrero *et al.* 2004). The heterocysts are unable to divide, but they perform an important function for the *Nostoc*, and in turn, for the liverwort partner. They reduce N₂, readily available from the atmosphere, to ammonium (Figure 85) (Adams 2002) that is then incorporated into amino acids, particularly glutamine (Stewart & Rodgers 1978; Wolk *et al.* 1994). The symbiotic colonies of *Nostoc* in *Blasia pusilla* (Figure 73-Figure 77) are more effective at converting the nitrogen to a usable form (ammonia) than those that are free-living. This is rapidly transferred to the liverwort thallus, increasing the liverwort yield by 300-500% in 30 days.

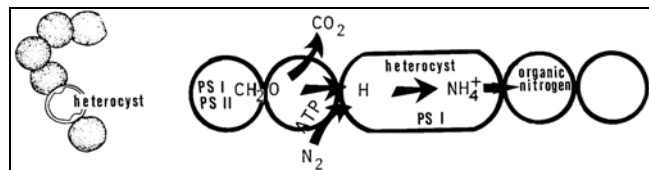


Figure 85. Heterocyst of *Anabaena*, a member of the **Cyanobacteria**, showing the nitrogen fixation pathway. Drawing by Janice Glimme.

Although ammonia (NH₃) is the immediate product of the nitrogen reduction, it is toxic and is quickly converted to harmless amino acids (Figure 85). It is unclear if the transfer to the photosynthetic cells of the *Nostoc* filaments (and probably the liverwort) is by ammonia or by glutamine (derived from the glutamate) and possibly other amino acids – or both (Stewart & Rodgers 1978; Wolk *et al.* 1994). It appears that the *Nostoc* is dependent on the *Blasia* for its fixed carbon. Stewart and Rodgers (1977) found that excised *Nostoc* colonies had only a negligible ability to fix CO₂, but that in the cavities of *Blasia pusilla*

(Figure 73-Figure 77) they receive fixed carbon from the thallus of the liverwort. Further details of the biochemical pathway are provided by Chapman *et al.* (2008) and Duggan *et al.* (2013).

The mechanism of transfer of reduced nitrogen from the heterocyst is a source-sink relationship (Wolk *et al.* 1994; Meeks 2009). The carbohydrate serves as the reductant and the abundant reduced nitrogen (NH_4) is transferred to other cells due to a concentration gradient. Once the reduced nitrogen is incorporated into biological compounds, those compounds and the cells that contain them become sinks.

Rodgers (1978) described the conditions favorable to the *Nostoc* symbiosis in *Blasia pusilla* (Figure 73-Figure 77). As an endophyte, *Nostoc* has greater nitrogenase activity at lower pH levels than those suitable for the free-living form. On the other hand, the symbiont requires a higher light level than the free living form. Below 10°C, the *Nostoc* has low activity in either growth condition, but the free-living form has high activity above 12°C, whereas the endophyte requires 17°C for such levels of activity. The free-living form is also more tolerant of desiccation, although both have protective mucilage.

Rodgers and Stewart (1977) identified *Nostoc sphaericum* (Figure 86) in the populations of *Blasia pusilla* (Figure 73-Figure 77) they examined. Although *Nostoc punctiforme* (Figure 69) is able to inhabit both *Blasia pusilla* and *Anthoceros* (Figure 87-Figure 89) species in the lab, different strains occupy *Blasia* and *Anthoceros* in the field (Leizerovich *et al.* 1990). In the lab, a strain of *Nostoc punctiforme* is able to colonize and form a symbiont with *Blasia pusilla*, but the lab strain of this *Nostoc* species has not been identified from any of these liverworts in the field (Rikkinen & Virtanen 2008). Further studies indicate that there is a "moderate level of spatial and temporal continuity" by some of the *Nostoc* strains in the *Blasia pusilla*-*Nostoc* symbioses (Costa *et al.* 2001). Jackson *et al.* (2012) demonstrated that three arabinogalactan proteins (AGP) were common to widely diverse cyanobacterial partnerships.



Figure 86. *Nostoc sphaericum*, "the caviar of the Andes" and also a symbiont of *Blasia pusilla*. Antonio W. Salas, through Creative Commons.



Figure 87. *Anthoceros*, NZ, showing bluish green color that suggests the presence of *Cyanobacteria*. Photo by Clive Shirley, Hidden Forest <hiddenforest.co.nz>, with permission.

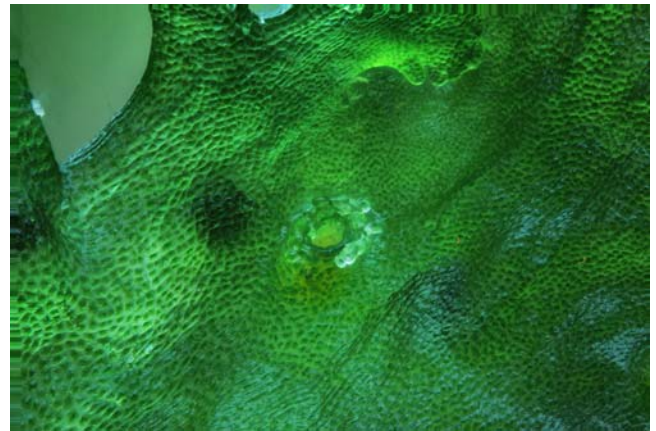


Figure 88. *Anthoceros punctatus* pore and *Nostoc* colony. Photo by Des Callaghan, with permission.

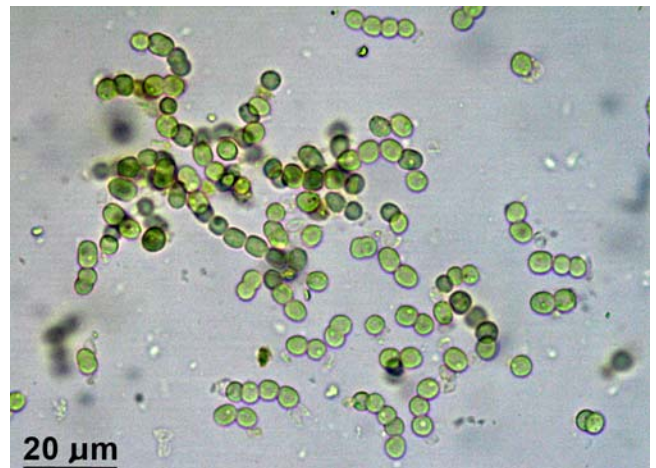


Figure 89. *Nostoc* from *Anthoceros agrestis*, showing the breakup of hormogonia and scarcity of heterocysts during early colonization. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.

In axenic cultures, all but one of the free-living *Calothrix* spp. (Figure 90), *Chlorogloeopsis* spp. (Figure 83), and *Nostoc* spp. (Figure 69, Figure 84, Figure 86) (all *Cyanobacteria*) were able to join in a symbiotic relationship with both *Blasia pusilla* (Figure 73-Figure 77) and *Phaeoceros* sp. (Figure 91) (West & Adams 1997). By

contrast, the strains of *Cyanobacteria* found as symbionts in the field where not found free-living in those locations. Furthermore, none of the symbiotic strains were found at more than one sample site.



Figure 90. *Calothrix parietina*, a *Cyanobacterium* in a genus that can inhabit *Blasia pusilla*. Photo from Algae Base, through Creative Commons.



Figure 91. *Phaeoceros laevis* with a bluish-green color suggesting the presence of its *Nostoc* partner. Photo by Oliver S., through Creative Commons.

Liaimer *et al.* (2016) further elaborated on the diversity of *Cyanobacteria* strains. They claimed that *Blasia pusilla* (Figure 1Figure 2-Figure 6) recruits its symbiotic *Nostoc* partner from the soil nitrogen-fixing strains. They found that those from an agricultural community exhibited negative allelopathic interactions, but such was not the case in an undisturbed site. The *Cyanobacteria* did not exhibit antimicrobial activity, but four of the isolates were cytotoxic to human cells. Interestingly, the symbiotic recruits commonly produced microcystin, a toxic compound, but it was not commonly produced in the free-living community. Could this be an additional herbivore deterrent for the liverwort?

The bryophyte-*Cyanobacteria* symbiosis, by providing usable nitrogen compounds, is an important contributor to the environment (Solheim *et al.* 2004).

Interactions with Fungi

As already noted, *Blasia pusilla* (Figure 1Figure 2-Figure 6) is not known to have any fungal endophytes (Liepiņa 2012). On the other hand, they do have parasitic

inhabitants. Redhead (1981) reported *Blasiphalia pseudogrisella* (Basidiomycota; Figure 92) from the rhizoids. Hallgrímsson (1981) found this fungus to be frequent on river banks in Iceland and concluded that it is probably always associated with *Blasia pusilla*.

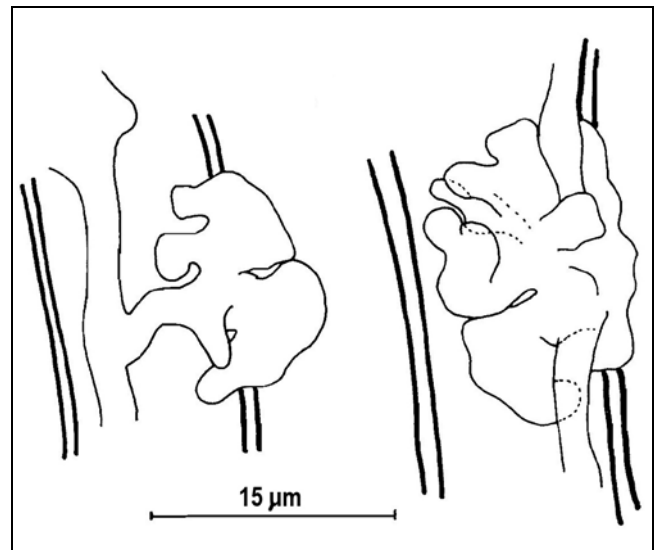


Figure 92. Appressoria of *Blasiphalia pseudogrisella* on rhizoids of *Blasia pusilla*. Drawing modified from Scott Redhead 1981.

Persson and Pleijel (2008) reported the rare species *Bryoscyphus marchantiae* (discomycete; Figure 93) as a parasite on *Blasia pusilla* (Figure 1Figure 2-Figure 6) in dune slacks (Figure 26).



Figure 93. *Bryoscyphus marchantiae* on liverwort; this species is able to parasitize *Blasia pusilla*. Photo by Iain Munro, through Creative Commons.

The mushroom *Blasiphalia pseudogrisella* (Figure 94) in the Arctic and alpine Northern Hemisphere is known only from *Blasia pusilla* (Figure 1Figure 2-Figure 6) (Antonin & Noordeloos 2001). Hyphae appearing to be identical to those of this mushroom formed clasping pads (appressoria) on the rhizoids of *Blasia pusilla*.

Furthermore, gemmae of the liverwort had a sparse covering of fungal spores matching those of the mushroom. Some of these seemed to have infected the gemmae. In other cases, dispersed gemmae had short rhizoids covered with fungal appressoria. Antonin and Noordeloos suggested that the gemmae could be vectors for dispersing the fungus.



Figure 94. *Blasiphalia pseudogrisella* growing with bryophytes. Photo by R  nee Lebeuf, through public domain.

Biochemistry

Blasia pusilla (Figure 1Figure 2-Figure 6) is one of those liverworts that apparently lacks oil bodies (Figure 95-Figure 96) (Schuster 1992; Millar *et al.* 2007; He *et al.* 2013). On the other hand, Rohret (1916) reported numerous oil bodies from the gemmae. Whether they are in the oil bodies or not, a number of compounds have been recognized from this species, but their antibiotic activity is limited (Millar *et al.* 2007).

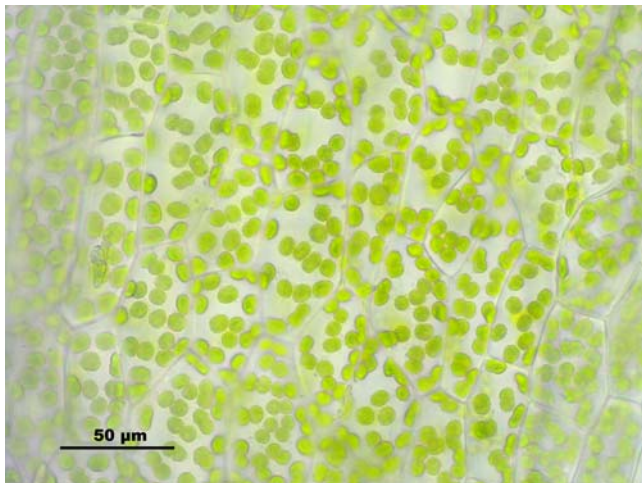


Figure 95. *Blasia pusilla* cells with chloroplasts, but lacking oil bodies. Photo by Hermann Schachner, through Creative Commons.

Hashimoto *et al.* (1993) reported riccardin C, riccardin F, and orsellinic acid methyl ester from *Blasia pusilla* (Figure 1-Figure 6). Viennois *et al.* (2011) found that riccardins from this species are natural antagonist compounds.

Four phenolic novel cyclic bisbibenzyl dimers, six bibenzyl derivatives, apigenin 7-O-  -d-glucoside, shikimic

acid, and five orsellinic acid derivatives were isolated from *Blasia pusilla* (Figure 1Figure 2-Figure 6) (Hashimoto *et al.* 1994; Yoshida *et al.* 1996). Asakawa (1994) reported that the cyclic bis-bibenzyl dimers of this species exhibit inhibitory activity against plant growth. Could this help maintain a habitat with limited competition for this species that seems to thrive best in disturbed habitats and as a pioneer?

Axenic *Blasia pusilla* (Figure 1Figure 2-Figure 6) extract is able to produce bioactive compounds. These retard fungal sporulation, but thus far there is no indication that they are able to inhibit bacterial growth (Millar *et al.* 2007). Furthermore, Asakawa (2008) reported moderate cytotoxicity against KB cells and only weak activity against HIV-RT. Millar *et al.* (2007) suggest that antimicrobial activity is greater in taxa with oil bodies; this would limit the medicinal value of *Blasia pusilla*.

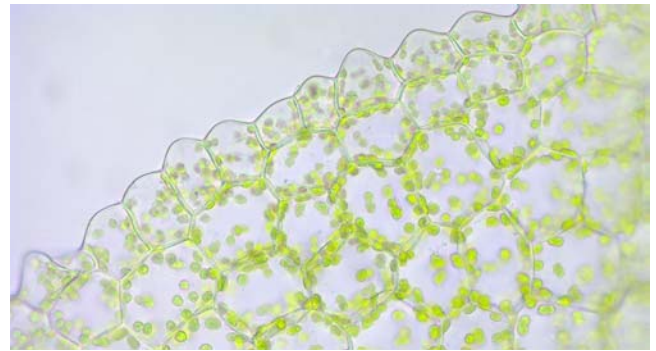


Figure 96. *Blasia pusilla* marginal cells with chloroplasts and no oil bodies. Photo by Hermann Schachner, through Creative Commons..

Summary

Blasia pusilla is the only species representing the **Blasiales** on wet substrates. It is rarely submerged, but can live in mires, streambanks, spray of waterfalls, fens, bogs, and similar wet habitats. It does well on disturbed substrata and is often an early pioneer. In these habitats, it benefits from persistent ovoid gemmae that can remain in the diaspore bank. Its *Nostoc* partner helps it to meet its fixed nitrogen needs. It is also able to spread through use of its stellate gemmae that get a head start with their own *Nostoc* colonies. The ovoid gemmae get their *Nostoc* partner from the soil.

Blasia pusilla is dormant through dieback in winter, the attached sporophyte is dormant in winter, and gemmae remain dormant while on the thallus. Both gemma germination and production of sexual structures are dependent on signals from the environment. Water triggers spore germination, but day length and temperature seem unimportant. Day length may affect initiation of sex organs and dormancy of sporophytes, but higher temperatures seem to affect sporophyte maturation.

Blasia pusilla has no symbiotic fungal partners, but they do harbor surface fungi and parasitic fungi. The absence of antibiotic effects against bacteria may be the result of lacking oil bodies.

Acknowledgments

Lars Söderström helped me find the current acceptable names for a number of older taxa. I have also benefitted from discussions with him on conventions in naming of some structures. David Wagner provided me with important images of reproductive structures.

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CHAPTER 1-18

AQUATIC AND WET MARCHANTIOPHYTA, ORDER LUNULARIALES

TABLE OF CONTENTS

MARCHANTIOPSIDA	1-18-2
Marchantiidae – Lunulariales	1-18-2
Lunulariaceae	1-18-2
<i>Lunularia cruciata</i>	1-18-2
Distribution	1-18-2
Aquatic and Wet Habitats	1-18-5
Physiology	1-18-11
Pollution	1-18-14
Adaptations	1-18-15
Reproduction	1-18-16
Uses	1-18-23
Herbivory	1-18-24
Interactions	1-18-25
Biochemistry	1-18-29
Summary	1-18-33
Acknowledgments	1-18-33
Literature Cited	1-18-33

CHAPTER 1-18

AQUATIC AND WET MARCHANTIOPHYTA, ORDER LUNULARIALES



Figure 1. *Lunularia cruciata* with nearly mature gemmae cups, clearly showing the crescent shape of the cup. Photo by James Dickson, with permission.

MARCHANTIOPSIDA

Marchantiidae – Lunulariales

Lunulariaceae

Lunularia cruciata (Figure 1-Figure 13)

(syn. = *Lunularia thaxteri*)

Although *Lunularia cruciata* (Figure 1-Figure 13) and *L. thaxteri* can be morphologically distinct, these differences are due to environmental expressions (Bischler & Boisselier 1998). Their genetic markers indicate that they are the same species. Itouga *et al.* (2000) further described the genetic structure.

Distribution

Lunularia cruciata (Figure 1-Figure 13) is a common species in western Europe, being native around the Mediterranean (NBNatlas 2021). But it has spread through a wide range due to its propensity for growing in gardens and flower pots. It is easily spread by gemmae through horticultural watering regimes. Hence, one can also find it in California, USA (Whittemore 1982), in greenhouses in Australia, and in New Zealand (NBNatlas 2021). Not surprisingly, it is most common in urban areas and seems to be spreading northeastward in Europe with climate warming (Essl & Lambdon 2009; Skudnik *et al.* 2013a). Nevertheless, it is considered to be a rare liverwort away from the Mediterranean area. Skudnik *et al.* (2013b) reported that it had been considered rare or under threat in Slovenia, but their discovery of new locations suggested that instead it was a matter of under-recording.



Figure 2. *Lunularia cruciata* on soil. Photo from <www.aphotofauna.com>, with permission.



Figure 5. *Lunularia cruciata* showing numerous gemmae cups with gemmae beginning to disperse. Photo by Michael Lüth, with permission.



Figure 3. *Lunularia cruciata* habitat in Bhutan. Photo by David Long, with permission.



Figure 6. *Lunularia cruciata*, almost entirely lacking gemmae cups. Photo from <www.aphotofauna.com>, with permission.



Figure 4. *Lunularia cruciata* with young gemmae cups. Photo by George Shepherd, through Creative Commons.



Figure 7. *Lunularia cruciata* in Europe. Photo by Michael Lüth, with permission.



Figure 8. *Lunularia cruciata* habitus. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 9. *Lunularia cruciata* in rock crevice, showing large pores in the thallus. Photo by Alexis Orion, through Creative Commons.



Figure 10. *Lunularia cruciata* with gemmae beginning to disperse. Photo by Hermann Schachner, through Creative Commons.



Figure 11. *Lunularia cruciata* with tiny gemmae cup sitting piggyback on another gemmae cup. Photo by Luis Nunes Alberto, through Creative Commons.



Figure 12. *Lunularia cruciata* with gemmae. Photo by Michael Lüth, with permission.



Figure 13. *Lunularia cruciata* with gemmae cups and lots of still-attached gemmae. Photo by Fotis Samaritakis, through Creative Commons.

This same horticultural transportation most likely accounts for the presence of *Lunularia cruciata* (Figure 1-

Figure 13) in Japan (Noguchi 1977; Taoda 1980). Taoda used it as a species indicating the degree of urbanization. It has also appeared in Kashmir of the Himalayas (Ismail *et al.* 2018). Other localities include Botswana and it is common in most of the southern African countries (Steel *et al.* 2004), Slovakia (Janovicova & Somogyi 1996), Germany (Frahm 1973), where it was fertile (Kirschner *et al.* 2010), Benslimane Region of Morocco where it is one of the two most common liverwort species (Elharech *et al.* 2018; Fadel *et al.* 2020), Nepal (Karki & Ghimire 2019), northeastern USA [Uva *et al.* (1997) considered it a weed], New York (Trigoboff 2000), British Columbia, Canada (Schofield 1997), and Central Chile (Gradstein & Cuvertino 2015).

Aquatic and Wet Habitats

Lunularia cruciata (Figure 1-Figure 13) has a relatively wide range of habitats (Yeates (1908). Ferreira *et al.* 2008) list it as a river species. It occurs midstream in the River Swale, Yorkshire, UK (Holmes & Whitton 1977a) and is mostly in the mid to lower River Tyne, UK (Holmes & Whitton 1981). It is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006). In Thuringia, Germany, it is known in the *Platyhypnidium* (Figure 14)-*Fontinalis antipyretica* (Figure 15) association, (Marstaller 1987). Özenoğlu Kiremit *et al.* (2007) found it on rocks and tree roots in a stream bed in Turkey. Konstantinova *et al.* (2009) found it on the bank of the Khosta River in the Caucasus of Russia. On Madeira Island, it occurs in mountain streams (Luis *et al.* 2015).



Figure 14. *Platyhypnidium riparioides*, a species that is often an indicator of suitable habitat for *Lunularia cruciata*. Photo by Hermann Schachner, through Creative Commons.



Figure 15. *Fontinalis antipyretica*, an aquatic moss species that is often an indicator of suitable habitat for *Lunularia cruciata*. Photo from Botany Website, UBC, with permission.

Yeates (1908) considers *Lunularia cruciata* (Figure 1-Figure 13) to be less hygrophilous than *Marchantia polymorpha* (Figure 16). The former is a suitable indicator of rich nutrients or eutrophic conditions in aquatic habitats (Werner 2001).



Figure 16. *Marchantia polymorpha* by water, a species that is more hygrophilous than *Lunularia cruciata*. Photo by Hugues Tinguy, with permission.

But it is more likely that *Lunularia cruciata* (Figure 1-Figure 13) occurs near water, rather than in it, often wet or periodically inundated. It occurs on wet ground at the edge of waterfalls (Figure 17) in Morocco, as well as what Fadel *et al.* (2020) called small water surfaces.



Figure 17. Waterfall in Ireland, showing the effects of moisture from the falls that makes a suitable habitat for *Lunularia cruciata*. Photo by Phil Armitage, through Wikimedia Commons.

Lunularia cruciata (Figure 1-Figure 13) occurs in damp places, on banks with frequent submergence and slow water (Figure 18-Figure 27) (Watson 1919), including the river bank of the River Tees, UK (Holmes & Whitton 1977b). In Germany it occurs increasingly in such natural habitats as brook banks (Borsdorf 1987; Bergl & Meinunger 1988). In Morocco, Saadi *et al.* (2020) found it both underwater and on soil and rocks near running water.



Figure 20. *Lunularia cruciata* on rock in stream. Photo by Andrew Melton, through Creative Commons.



Figure 18. *Lunularia cruciata* on stream bank. Photo by Tom Kaye, through Creative Commons.



Figure 21. *Lunularia cruciata* on stream bank. Photo by Gerrit Öhm, through Creative Commons.



Figure 19. *Lunularia cruciata* forming shelves on rock by water. Photo by David Claro, through Creative Commons.



Figure 22. *Lunularia cruciata* at base of log. Photo by Geerah, through Creative Commons.



Figure 23. *Lunularia cruciata* by water. Photo by S. Bushes, through Creative Commons.



Figure 24. *Lunularia cruciata* by water. Photo by Susan Marley, through Creative Commons.



Figure 25. *Lunularia cruciata* on rock by water. Photo by Thomas Koffel, through Creative Commons.



Figure 26. *Lunularia cruciata* by water. Photo by Ulysses M., through Creative Commons.



Figure 27. *Lunularia cruciata* on tree root near water. Photo by Maddi Song, through Creative Commons.



Figure 28. *Lunularia cruciata* with other bryophytes by water. Photo by Susan Marley, through Creative Commons.

Sometimes damp walls and slopes (Figure 29-Figure 31) provide suitable habitat. Armitage (1918) found *Lunularia cruciata* (Figure 1-Figure 13) on damp walls and bare earth banks on Madeira. Konstantinova *et al.* (2009) reported it at the base of limestone cliffs in the valley of the Khosta River, Caucasus, Russia. Garcia-Rowe and Saiz-Jimenez (1991) found it on vertical wet surfaces on Spanish cathedrals, where it could make it easier for tracheophytes to invade and damage the buildings with their roots.



Figure 29. *Lunularia cruciata* zone on slope. Photo by Stephen Thorpe, through Creative Commons.



Figure 30. *Lunularia cruciata* on clay bank. Photo by Susan Marley, through Creative Commons.



Figure 31. *Lunularia cruciata* habitat where it forms a zone on the substrate, probably related to water levels. Photo by Kate McCombs, through Creative Commons.

Springs are less common habitats. The only record I found was *Lunularia cruciata* (Figure 1-Figure 13) growing around a spring in Halstead, England (Lorenz 1910).

Wet soil in other locations is a more common habitat. Fadel *et al.* (2020) reported *Lunularia cruciata* (Figure 1-Figure 13) from rocky walls and wet soil (Figure 32-Figure 34) in Morocco. It was able to occupy limestone, schistose, and quartzite substrata. It was among the four most common species in wetlands. Salisbury (1962) considers it the commonest species on wet ground of gardens in the UK.



Figure 32. *Lunularia cruciata* with antheridial discs (dark brown) and gemmae cups, on wet soil. Photo by Michael Keogh, through Creative Commons.



Figure 35. *Lunularia cruciata* on rock. Photo by <www.aphotofauna.com>, with permission.



Figure 33. *Lunularia cruciata* on clay. Photo by Mattia Manchetti, through Creative Commons.



Figure 36. *Lunularia cruciata* on thin soil on rock. Photo by Zoltán Nagy, through Creative Commons.



Figure 34. *Lunularia cruciata*, on soil, Waikite Pools Recreation Area, NZ, 16 July 1988. Photo by Janice Glime.

Karki and Ghimire (2019) reported *Lunularia cruciata* (Figure 1-Figure 13) as saxicolous (Figure 35-Figure 37) in Central Nepal, and locally rare. In some locations one can find it tucked into wet crevices (Figure 38-Figure 40) or on shale that is soaked with water (Figure 41) in the winter (Fadel *et al.* 2020).



Figure 37. *Lunularia cruciata* on thin soil on rock. Photo by Zoltán Nagy, through Creative Commons.



Figure 38. *Lunularia cruciata* with gemmae cups (left) + *Marchantia polymorpha* (right) among rocks. Photo by Michael Lüth in Europe, with permission.



Figure 41. *Lunularia cruciata* on wet rock. Photo by Loverworts, through Creative Commons.



Figure 39. *Lunularia cruciata* in rock crevice. Photo by Attila Oláh, through Creative Commons.



Figure 40. *Lunularia cruciata* in rock crevice. Photo by Alexis Orion, through Creative Commons.

Based on its other habitats, it is not surprising that *Lunularia cruciata* (Figure 1-Figure 13) is able to occupy the rich alluvium associated with temporary ponds (Fadel *et al.* 2020).

This opportunistic liverwort also lives by paths and roadsides. Skudnik *et al.* (2013b) found it on damp soil by paths and roadsides in Slovenia. Likewise, Yeates (1908) noted its presence on the banks of roadside water channels, but also on boulders in deep-seated valley beds, at the bottom of old walls and outhouses, and even on shaded banks where it was often hidden by brambles. Özenoğlu Kiremit *et al.* (2007) found it on soil banks along the road in Antalya, Turkey.

It appears that the most common habitat for the introduced populations is related to horticulture. *Lunularia cruciata* (Figure 1-Figure 13) is common in greenhouses (Figure 42) and gardens, where sprinkling systems and garden hose water facilitate dispersal of gemmae from the gemmae cups. Perold (1993) reported the species from old gardens, nurseries, and forested areas in southern Africa, where it is most likely introduced. Bergl and Meinunger (1988) reported that it was introduced to Central Europe through greenhouse cultures used to supply market gardens, churchyards, and parks (Frahm 1973). Schofield (1997) noted that in British Columbia, Canada, it occurs almost exclusively in gardens. Similarly, in Chile, it occurs in urban areas (Gradstein & Cuvertino 2015). A picture by Merav Vonshak suggests that it might occur in spruce forests (Figure 43).

Salisbury (1962) lists *Lunularia cruciata* (Figure 1-Figure 13) as a troublesome weed in gardens of the UK. Its frequency in such habitats is 40%! It does well in sunken paths and greenhouses as well (Augier 1966; Coudreuse *et al.* 2005).



Figure 42. *Lunularia cruciata* on soil in a flower pot in greenhouse in Ripley, Michigan, USA, with mosses. Photo by Janice Glime.



Figure 43. *Lunularia cruciata* amid spruce needles. Photo by Merav Vonshak, through Creative Commons.

Armitage (1918) found *Lunularia cruciata* (Figure 1-Figure 13) on open ground and bare earth banks as well as shady mountain ground, on Madeira. Gradstein (1972) reported it from the Maltese Islands on the thin soil layer of a sheltered floor enclosure of a temple. Steel *et al.* (2004) considered it to be one of the world's commonest liverworts and a common inhabitant of man-made and disturbed environments in Botswana. Lo Giudice *et al.* (1997) found it to be common in urban areas and relatively indifferent to substrate hardness. It can also occur on soil under shrubs and small trees (Özenoğlu Kiremit *et al.* 2007; Saadi *et al.* 2020).

Physiology

Lunularia cruciata (Figure 1-Figure 13) was the subject of a number of early physiological studies. Crocker (1912) evaluated its tropisms and concluded that, contrary to the conclusions of Weinert (1909), the rhizoids of growing gemmae are positively gravitropic, as are those of the thallus. Bischoff (1912) supported this argument by concluding that the absence of motile starch in the rhizoids does not negate the statolith theory and suggests that other bodies in the cell could accomplish this role of sensing the direction of gravity.

Temperature effects on *Lunularia cruciata* (Figure 1-Figure 13) could benefit from more study. It appears that not only is *Lunularia cruciata* spreading to more northern habitats, perhaps as a result of global warming, but it seems to be attaining more frost tolerance. Bergl and Meinunger (1988) contend that its expansion to the north is due to the establishment of frost-resistant types. In Japan, plants in cultivated locations are likewise frost-resistant (Fletcher 1982). Warming temperatures also can play a role in gemma germination (Schwabe 1990).

Lunularia cruciata has both rhizoids (Figure 44) and scales that contribute to its external capillary movement of water (McConaha 1941). This species has two types of rhizoids (Figure 45). The smooth rhizoids are partially enclosed by the ventral scales and may contact the substrate. The tuberculate rhizoids originate beneath the scales and create numerous connected capillary strands that parallel the thallus, creating a "rapid" distribution system for water uptake throughout the thallus.



Figure 44. *Lunularia cruciata* ventral side showing rhizoids clinging to soil. Photo by Pat Enright, through Creative Commons.

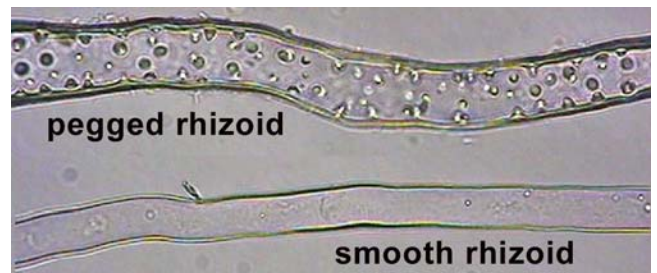


Figure 45. Pegged and smooth rhizoids of *Conocephalum conicum*; *Lunularia cruciata* has the same two types. Photo by Paul Davison, with permission.

By contrast, the upper surface of *Lunularia cruciata* (Figure 1-Figure 13) is designed to keep water out, at least through the pores (Figure 46-Figure 47) (Schönherr & Ziegler 1975). The air pores are surrounded by hydrophobic ledges (Figure 48) that constrict the entrance. This permits only liquids with a contact angle of zero° with the hydrophobic ledge to enter.



Figure 46. *Lunularia cruciata* showing pores. Photo by Steven Bodzin, through Creative Commons.



Figure 47. *Lunularia cruciata* showing pores. Photo by Mike, through Creative Commons.



Figure 48. *Lunularia cruciata* thallus and pore longitudinal section. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Giordano *et al.* (1985, 1989) reported the presence of a hyaline parenchyma in the thallus of *Lunularia cruciata* (Figure 1-Figure 13). These have wall thickenings with large primary pit fields between them and numerous plasmodesmata-derived pores. These differ from the parenchymatous cells of the midrib, where the plasmodesmata-derived pores occur in small, sparse groups. The researchers suggest that the reticulate pattern has a role in the water-holding capacity and lateral distribution of water, using both **symplastic** (inside cell

membrane) and **apoplastic** (space outside plasma membrane) pathways.

Deltoro *et al.* (1998) listed *Lunularia cruciata* (Figure 1-Figure 13, Figure 49) as a desiccation-intolerant bryophyte. At low water content they showed low efficiency of photosynthetic conversion, closed down their photosystem II reaction centers, and exhibited weak nonphotochemical quenching. They were unable to restore photochemical activity after desiccation. The large leakage of potassium suggests membrane damage.



Figure 49. *Lunularia cruciata* with gemmae, growing in a flower pot in a greenhouse where it gets watered regularly. Photo by Janice Glime.

Nevertheless, *Lunularia cruciata* (Figure 1-Figure 13) responds to long days by increasing its resistance to drought (Valio *et al.* 1969; Schwabe 1990, 2019). When moved from moist conditions to relative humidity levels of 90%, the liverwort dies (Figure 50). However, after long-day treatment, it can be dried for years and still survive. The rapidity of drying is likely to be important.



Figure 50. *Lunularia cruciata* dieback. It may still have some living tissue that will come back. Photo by Jon Sullivan, through Creative Commons.

Fredericq (1966) first examined the effects of photoperiod on growth in *Lunularia cruciata* (Figure 1-Figure 13). Lunularic acid increases with long-day treatment of *Lunularia cruciata* (Valio & Schwabe 1970). Its concentration changes rapidly in response to day-length change. The inhibition of growth in this species is linearly related to the concentration of the acid, with very high

concentrations being lethal. Sabovljević and Marka (2009) verified these day-length relationships in the field. Absciscic acid could not be detected in the species (Valio & Schwabe 1970), but lunularic acid appears to have the same functions (Yoshikawa *et al.* 2002).

Wilson and Schwabe (1964) found that red light induces dormancy and far-red reverses it. This suggests that phytochrome is involved in the response. But this is contradicted by the effect of short exposures (15 seconds) of far-red light that alone causes significant growth inhibition. They surmised that the far-red light could elicit the formation of some of the P 730 form of phytochrome. In experiments, *Lunularia cruciata* (Figure 1-Figure 13) exhibited photoreversibility like that in *Marchantia polymorpha* (Figure 16), but with a weaker response to far-red light than that of *M. polymorpha* (Fredericq 1966). Huault (1980) found that phytochrome was involved in the germination of propagules in *Lunularia cruciata*.

The optimum day length for growth in *Lunularia cruciata* (Figure 1-Figure 13) is 8 hours (Schwabe & Valio 1970b). Continuous light causes growth to cease, with a rapid onset of dormancy. The effects of red vs far-red light depended on the duration and frequency and intervening light quality. Furthermore, growth promoters of tracheophytes generally inhibit *Lunularia*, or have little effect.

Liverworts use lunularic acid where other plants use ABA as a dormancy hormone and, apparently, to help prepare them for drying, as shown in *Lunularia cruciata* (Figure 1-Figure 13) (Schwabe 1990). Schwabe and Nachmony-Bascomb (1963) found that long days induce dormancy and short days break it in this species. All parts of the thallus are able to register day length, including the young gemmae (Figure 51) in the cup. However, temperature interacts strongly with the photoperiod, making it difficult to determine the critical day length. High temperature (24°C) in continuous light rapidly induces dormancy – within 6 days. During this dormancy, the plants have a greater capacity to resist drought; actively growing thalli die in a reduction to 80% relative humidity.



Figure 51. *Lunularia cruciata* with gemmae; the thallus and gemmae both respond to day length. Photo by Damon Tighe, through Creative Commons.

Thomas and Silcox (1983) explored the effects of various biological compounds on IAA effects and proton

efflux in *Lunularia cruciata* (Figure 1-Figure 13). They suggested that **lysis** (breakage by rupture of cell wall or membrane) of cells may be caused by conversion of starch reserves to solutes that create greater osmosis, rather than protoplast swelling.

LaRue and Narayanaswami (1955, 1957; Narayanaswami 1957) determined that IAA inhibits the germination of gemmae of *Lunularia cruciata* (Figure 1-Figure 13) in the lab. They also demonstrated that if the gemmae remained in the thallus cups, they did not germinate (Figure 52), but if the thallus was cut close to the cup, germination could occur. Removal of the upper half of the thallus, above the gemma cup, caused the gemmae in the cups to germinate. Mutilations elsewhere on the thallus did not cause the gemmae to germinate. Hence, it appears that the apical growing region produces the growth inhibitors. This would be an ecologically advantageous trait, permitting resources to promote growth until unfavorable conditions stopped it. Lack of further production of the inhibitor would then permit the gemmae to germinate and provide a means of surviving such conditions as drying out.



Figure 52. *Lunularia cruciata* with dormant gemmae resting on thallus. Photo by Martin Hutten, with permission.

Schwabe and Valio (1970a) later demonstrated that the gemmae themselves exhibit self-inhibition through a substance produced in the growing tip. This inhibitor has greater production in short days compared to that in long-day dormancy conditions. Furthermore, the growing conditions determine how much inhibitor diffuses away. Dry conditions, for example, can elicit the morphological changes of incipient dormancy.

There are three life cycle stages that can become dormant in *Lunularia cruciata* (Figure 1-Figure 13): mature thallus, gemma, and spore. Plants from Israel that have dried in the air produce adventitious branches ventrally from the region immediately behind the meristem. That meristem fails to resume growth. Dormant gemmae, on the other hand, resume growth when removed from the cup.

Lunularia cruciata (Figure 1-Figure 13) succeeds and maintains growth at very low light intensities (Nachmony-Bascomb & Schwabe 1963). The gemmae are also able to grow at the same low light intensities. Initial growth of the gemmae is due only to the expansion of the cells. It would be interesting to learn whether they take advantage of sunflecks (Figure 53).



Figure 53. *Lunularia cruciata* with sunflecks that might give it bursts of photosynthesis. Photo by Siznax, through Creative Commons.

Gemmae cup production is markedly diminished by high temperatures above 12°C (Nachmony-Bascomb & Schwabe 1963). Thallus growth is severely limited by lack of P; N can also restrict growth to a very low level.

The first sign of growth from dormant gemmae of *Lunularia cruciata* (Figure 1-Figure 13) is development of rhizoids (Valio & Schwabe 1969). Temperature and light are important in controlling this development. As long as the days are long, a wide range of temperatures is suitable. When gemmae have been illuminated for 2 hours in white light, then transferred to darkness, about 50% of the gemmae produce rhizoids, and only at 20-25°C. No rhizoid production occurs in total darkness, but the gemmae remain alive for at least 6 months.

Fernández-Marín *et al.* (2009) found that darkness induced the xanthophyll cycle in *Lunularia cruciata* (Figure 1-Figure 13) as a response to dehydration.

Pollution

Lunularia cruciata (Figure 1-Figure 13) is known as a toxitolerant species (Daly 1970; Gilbert 1970). Gilbert (1971) found that it is SO₂-resistant. It has the advantage of being able to transform quickly from its more susceptible protonema stage to the more protected and resistant thallus stage (LeBlanc & Rao 1975).

Vieira *et al.* (n.d.) found that *Lunularia cruciata* (Figure 1-Figure 13) was among the most tolerant liverworts to water pollution and increased pH and conductivity. In their study, this species occurred at a mean height of 30 cm above the water. Basile *et al.* (2017) similarly found the species to be very tolerant of air pollution.

Other studies have examined the effects of heavy metals on *Lunularia cruciata* (Figure 1-Figure 13). Basile (1993) examined the localization of lead in the cells and tissues. Carginale *et al.* (2004) found that cadmium accumulation in this species was both dose and time dependent. This metal accumulated preferentially in hyaline parenchyma and at the base of the gemmae cups. In the cells, it accumulated in the vacuoles and cell walls. These accumulations were accompanied by an increase of sulfur in the vacuoles of the stressed cells. The researchers suggested that the excess sulfur in the vacuoles may have

been facilitated by stress-induced phytochelatins. Ultrastructural changes also occurred at sublethal levels of cadmium: alteration of the fine structure of cells and induced alterations of the chloroplast structure. Both apical thallus growth and gemma germination were inhibited, following a dose-dependent response.

Basile *et al.* (2017) reported that in the Land of Fires, *Lunularia cruciata* (Figure 1-Figure 13) exhibited high values of Al, Cd, Cr, Cu, Hg, Ni, Pb in its tissues. Reactive Oxygen Species (ROS) were high and the plants exhibited antioxidant activity and DNA damage. Basile and coworkers likewise found that phytochelatins served as good biomarkers of metal pollution. Further exploration indicated that detrimental pollution was indicated by a significant increment in heat shock protein (Hsp70) expression and occurrence and modifications in the chloroplast ultrastructure. Basile *et al.* (2005) found that accumulation of cadmium, one of the most toxic metals in the environment, affected DNA expression. The enzyme cystathionine γ -synthase is upregulated by Cd. Three other genes are downregulated.

Nothing is ever simple in biology. Alam and Sharma (2012) found that responses could change. Nevertheless, the responses indicated an increase in heavy metal air pollutants in the summer, a change that could be missed by ordinary pollution monitoring.

Lower exposures to radiation elicited damage to gemmae apical cells (Miller 1968). Apical cells of gemmae of *Lunularia cruciata* (Figure 1-Figure 13) are larger than other cells. However, radiation exposure had no different effect on energy absorption per chromosome in gemmae apices than it did in vegetative cells.

Degola *et al.* (2014) questioned why the phytochelatin synthase enzyme evolved long before pollution became a problem. This pre-adaptive enzyme would seemingly not be needed in ancient organisms to sequester excess cadmium or arsenic. Therefore, they looked for essential functions. They hypothesized that there was a need to regulate trace element homeostasis and to minimize the risk of exposure to toxic concentrations of certain metals even in pre-plant organisms such as **Charophyta** (*Nitella mucronata*; Figure 54).



Figure 54. *Nitella mucronata*, an alga species that is likely to regulate trace element homeostasis. Photo by Kristian Peters, through Creative Commons.

Adaptations

Thalli of *Lunularia cruciata* (Figure 1-Figure 13) are large and flat, forming overlying patches (Figure 55) or even extensive turfs (Perold 1993; Steel *et al.* 2004). Or they can grow with other mosses and liverworts (Figure 56-Figure 61) that help to maintain moisture. Such growth arrangements can help to conserve water. They have numerous rhizoids that help them remain attached in the disturbed habitats they frequent. As already noted the scales and rhizoids also move water to all locations on the thallus, and pores facilitate the movement of water between cells both apoplastically and symplastically.



Figure 55. *Lunularia cruciata* on soil, forming overlapping patches. Photo by George Shepherd, with permission.



Figure 56. *Lunularia cruciata* with mosses. Photo by Duarte Frade, through Creative Commons.



Figure 57. *Lunularia cruciata* with mosses on soil. Photo by Martin Hutten, with permission.



Figure 58. *Lunularia cruciata* with mosses. Photo from <www.aphotofauna.com>, with permission.



Figure 59. *Lunularia cruciata* with mosses. Photo from <www.aphotofauna.com>, with permission.



Figure 60. *Lunularia cruciata* with mosses. Photo from <www.aphotofauna.com>, with permission.



Figure 61. *Lunularia cruciata* with mosses. Photo from <www.aphotofauna.com>, with permission.

Reproduction

It appears that *Lunularia cruciata* (Figure 1-Figure 13) relies primarily on gemmae. It is a **dioicous** perennial (Perold 1993; Steel *et al.* 2004) and its spread through horticultural shipments seems to have created populations with only one sex. In fact, it rarely has sexual reproduction in the UK (Benson-Evans & Hughes 1955; Blackstock 2018). One factor seemed to be the cold winters, which were tolerable to female plants (Figure 62), but male-expressing plants (Figure 63-Figure 66), and consequently sporophytes (Figure 67), were restricted to the southern parts of England and Wales.



Figure 62. *Lunularia cruciata* developing archegoniophores. Photo by Fotis Samaritakis, through Creative Commons.



Figure 63. *Lunularia cruciata* male plants with antheridial discs (dark patches) and splash cups. Photo from <www.aphotofauna.com>, with permission.



Figure 64. *Lunularia cruciata* with antheridial discs. Photo by Rutger Barendse, Saxifraga, through Creative Commons.



Figure 65. *Lunularia cruciata* with antheridial discs. Photo by Ricardo Ferreiro Sanjurjo, through Creative Commons.



Figure 66. *Lunularia cruciata* with antheridial discs. Photo by Tricia Stewart, through Creative Commons.



Figure 67. *Lunularia cruciata* female plants with developing sporophytes in the archegoniophore receptacle lobes. Photo by Stavros Apostolou, through Creative Commons.

Benson-Evans and Hughes (1955) reported that *Lunularia cruciata* (Figure 1-Figure 13) requires a low temperature regime before the production of sexual organs, a physiological function similar to **vernalization** (cooling process that facilitates initiation of growth stage, such as initiation of sexual organs or gemma germination) in tracheophytes. Nevertheless, as Blackstock (2018) notes, both genders are known in more northern localities. Even sporophytes have a wider distribution than previously thought. The limited sporophyte production is in part due to the dioicous condition, but also to a female-biased sex ratio. Since warmer conditions have arrived, it appears that fertility has increased. In northwest Wales, sexual reproduction has benefitted from prolonged and synchronous production of archegonia and antheridia (Figure 63-Figure 66). Yeates noted in 1908 that it seems to reproduce best in the even temperatures of greenhouses, with most of its reproduction by gemmae. In fact, the thalli disappear in winter and reappear in spring, whereas the gemmae survive through winter, presumably accounting for most of the reappearance in spring.

But vernalization does not seem to be the only factor. Benson-Evans (1964) found that *Lunularia cruciata* (Figure 1-Figure 13) grew best and produced gametangia at 21°C in long days (18 hours), but not at either 10°C or in short days (6 hours).

Sporophyte production (Figure 67-Figure 80) in *Lunularia cruciata* (Figure 1-Figure 13) is so rare outside the Mediterranean that finding it is often considered worthy of publication. Such records include Chalaud (1931), Rousseau (1955), Goodman (1956) for South Wales, and Ahayoun *et al.* (2008) for Morocco. The sporophytes are elevated on an **archegoniophore** (stalk that elevates archegonia), with four occurring on each **receptacle** (expanded portion of archegoniophore bearing sporangia).



Figure 68. *Lunularia cruciata* with emerging archegoniophores and developing capsules. Photo by Ken-Ichi Ueda, with permission.

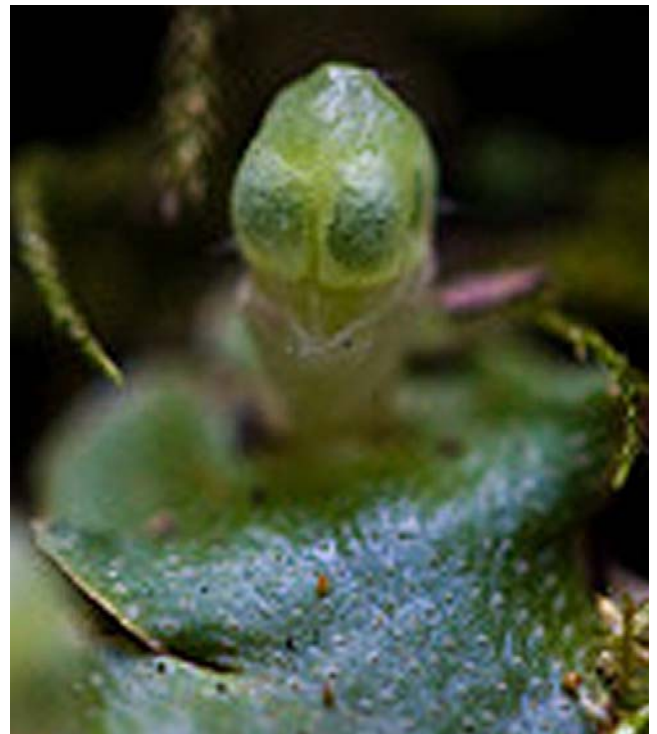


Figure 69. *Lunularia cruciata* with archegoniophore with developing sporophytes. Photo by Ken-Ichi Ueda, with permission.



Figure 70. *Lunularia cruciata* with archegoniophores, showing how common the archegoniophores can be in some locations. Photo by Stephen Thorpe, through Creative Commons.



Figure 73. *Lunularia cruciata* with archegoniophores, in Israel. Photo by Jael Orgad, with online permission.



Figure 71. *Lunularia cruciata* with mature archegoniophore. The few plants provide limited opportunity for fertilization. Photo by Loverworts, through Creative Commons.



Figure 74. *Lunularia cruciata* with archegoniophores growing on vertical wall. Note the thallus dieback. Photo by Debbi Brusco, through Creative Commons.



Figure 72. *Lunularia cruciata* with fully elongated archegoniophore and nearly mature capsules. Photo by loverworts, through Creative Commons.



Figure 75. *Lunularia cruciata* archegoniophore with four nearly mature capsules. Photo by loverworts, through Creative Commons.

Perold (1995) noted that *Lunularia cruciata* (Figure 1-Figure 13) responded to photoperiod in its native Israel, but this could not be determined in the field for New Zealand plants because of the much lower winter temperatures in New Zealand. On the other hand, Sérgio and Viana (1973) considered the availability of water as a possible limiting factor for development of sporophytes, based on the distribution of plants producing sporophytes. This would also explain the greater incidence of sexual reproduction in the Mediterranean climate.

Saxton (1931) described the archegoniophore and sporophyte (Figure 67-Figure 80) of *Lunularia cruciata* (Figure 1-Figure 13). I note here that many authors have avoided the term **archegoniophore** for this species, referring instead to the **receptacle**, which should be the expanded top portion of the archegoniophore. Kirschner *et al.* (2010) recorded the first sighting of sporophytes in Germany in the botanical garden in Main. They were able to observe all developmental stages, beginning with antheridial receptacles in early spring, followed by archegonial receptacles somewhat later in spring. Sporophytes developed in late summer.

Shinn (1902) presented a rather different picture of sexual reproduction of *Lunularia cruciata* (Figure 1-Figure 13) in California, USA. The first fertile plants appeared in April on the drier parts of shaded soil on the greenhouse floor. These bore many small, white, tuft-like sheaths (Figure 76) covering the young archegonial receptacles. Unlike most bryophytes (antheridia usually develop first), the antheridia developed two weeks later. These were on the same plants of this "dioicous" thallus! But they did occur on different divisions of the thallus. By 9 May, capsules appeared, while others were just beginning to emerge from the scales of the sheaths.



Figure 77. *Lunularia cruciata* with mature capsules, three of which are dehiscing. Photo by Fotis Samaritakis, through Creative Commons.



Figure 76. *Lunularia cruciata* with white sheaths where archegoniophores will emerge. Note the adjacent male plants. Carminda Santos, through Creative Commons.

Spores (Figure 77-Figure 80) of *Lunularia cruciata* (Figure 1-Figure 13) are "very small" (Perold 1993), a feature that should facilitate their long-distance dispersal but that would carry with it little reserved food to give the germinating a boost. They are either green or brown and smooth, so perhaps photosynthesis helps them to get a start. Kumar and Kapila (2003) reported a chromosome number of $n=9$.



Figure 78. *Lunularia cruciata* dehiscing capsules showing masses of spores and elaters. Photo by Fotis Samaritakis, through Creative Commons.



Figure 79. *Lunularia cruciata* dehisced capsules. Photo by Ken-Ichi Ueda, with permission.



Figure 80. *Lunularia cruciata* with sporophytes dispersing spores. Photo by Ken-Ichi Ueda, with permission.

The gemmae of *Lunularia cruciata* (Figure 1-Figure 13) occur in pocket-like gemmae cups (Figure 81) (Brodie 1951). The gemmae themselves are **lenticular** (lens-shaped; Figure 82), a common shape for gemmae in cups, and can be splashed for about 60 cm.

Yeates (1908) noted that gemmae are coated with an adhesive mucilage that could readily attach to the coats of animals, hence accomplishing dispersal. Furthermore, rats disperse them to gullies and sewers that further disperse them by moving water. They could also attach to bird's feet, but there are no data on their survival as the birds fly through the cooler atmosphere.

Sussman (1965) attributed the success of many bryophytes, especially *Lunularia cruciata* (Figure 1-Figure 13), to the resistant nature of their tissues and gemmae (Figure 83-Figure 96). Such bryophyte species have high regenerative capacity and gemmae have good desiccation resistance. This permits them to spread widely around the world without the production of spores. And for this species, they often spread as hitchhikers in horticultural shipments.



Figure 81. *Lunularia cruciata* with gemmae firmly tucked into the cups. Photo from Botany Website, UBC, with permission.



Figure 82. *Lunularia cruciata* showing the lenticular shape of the gemmae. Photo by Martin Hutten, with permission.



Figure 83. *Lunularia cruciata* with young gemmae cups, showing how quickly they can appear on a young thallus that is still small. Photo by Ken-ichi Ueda, through Creative Commons.



Figure 84. *Lunularia cruciata* with crescent-shaped gemmae cups. Photo by David T. Holyoak, with permission.



Figure 87. *Lunularia cruciata* gemmae in cup, showing collected water and suggesting that the gemmae are not ready for dispersal. Photo by Bernard De Cuyper, with permission.



Figure 85. *Lunularia cruciata* gemmae tightly arranged in crescent-shaped cup. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 88. *Lunularia cruciata* thallus section through gemmae cup. Arrow indicates one of the gemmae. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 86. *Lunularia cruciata* gemmae cup with discoid gemmae. Photo by Andras Keszei, with permission.



Figure 89. *Lunularia cruciata* gemmae cup cross section. **Arrow** indicates one of the gemmae. Note that the gemmae are attached and must break loose prior to dispersal. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 90. *Lunularia cruciata* with a few gemmae that have broken loose. Photo by Michael Lüth, with permission.



Figure 93. *Lunularia cruciata* with some gemmae resting on the thallus, but not germinating. Photo by Michael Lüth, with permission.



Figure 91. *Lunularia cruciata* gemmae cup with one escaped gemma. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 94. *Lunularia cruciata* showing many dormant gemmae resting on the thallus, away from the gemmae cup. Photo by Jan-Peter Frahm, with permission.



Figure 92. *Lunularia cruciata* with mature gemmae ready for dispersal. Those on the thallus will not germinate there. Photo by Jan-Peter Frahm, with permission.



Figure 95. *Lunularia cruciata* gemmae that have broken loose and are ready for dispersal. Photo by Walter Obermayer, with permission.



Figure 96. *Lunularia cruciata* and young plants, probably from gemmae. Photo by S. Bush, through Creative Commons.

Itouga *et al.* (2002) compared genetic differentiation in four species of East Asian liverworts. They found that the highest gene flow occurred in *Conocephalum japonicum* (Figure 97), a dioicous species that relies on spores, and was lowest in *Lunularia cruciata* (Figure 1-Figure 13), a dioicous species that relies on gemmae. *Lunularia cruciata* showed strong population differences, whereas *Conocephalum japonicum* showed little, further supporting the greater gene flow in the latter. In general, however, it was the monoicous species that exhibited the greatest population differences.

Following these, studies appeared on factors affecting the sexual cycle (Longton 1990) and morphology of the sporophyte of *Lunularia cruciata* (Figure 1-Figure 13) (Shimamura & Deguchi 2002).



Figure 97. *Conocephalum japonicum* with antheridial discs. Photo by David Long, with permission.

The persistence of gemmae permits the species to appear in disturbed areas. Biggs and Wittkuhn (2006) found diaspores of *Lunularia cruciata* (Figure 1-Figure 13) in litter samples, but not in soil samples. Disturbance can bring diaspores such as gemmae to the surface, where they can get light and germinate (Figure 98).



Figure 98. *Lunularia cruciata* germinating gemma. Photo from Plant Actions, with permission from Eugenia Ron Alvarez and Tomas Sobota.

Longton (1990) summarized the sexual reproduction problems in *Lunularia cruciata* (Figure 1-Figure 13). It readily produces both sexes and sporophytes in its native Mediterranean area. However, in areas where it has more recently become established, most likely by human dispersal through horticulture, sporophytes are rare. In Europe and California, USA, this is apparently due to insufficient moisture in summer to facilitate fertilization or sporophyte development. In temperate regions, it appears that climatic conditions are unsuitable for gametangial formation. Gametangia may occasionally appear in such temperate areas as southern Britain, but this may be due to aberrant weather that more closely resembles that of the Mediterranean area. It is also possible that the required long-day stimulation for gametangial development is not coupled with the right temperature (15-21°C) or moisture availability. Based on observations, it appears that a warm period is needed to initiate antheridia in Britain, thus initiating them in late summer, followed by a cool period of winter when they become dormant. It also appears that the conditions needed to stimulate growth and reproduction differ geographically. In Israel, short days (winter) stimulate growth, during the more humid time of year, and the plants become dormant in the dry summer. But in Britain it is long days that stimulate growth. Clearly there are physiological races among these scattered populations. It appears that it has survived despite the mismatched timing because of its production of gemmae.

Uses

Aside from sometimes being welcome in a garden (but more likely considered a weed), *Lunularia cruciata* (Figure 1-Figure 13) has been used in making maize beer (Franquemont *et al.* 1990; Harris 2008).

Pande *et al.* (2004) found that extracts of *Lunularia cruciata* (Figure 1-Figure 13) inhibited germination of seeds of the legume *Indigofera heterantha* (Figure 99) and non-legume *Impatiens scabrida* (Figure 100). The inhibition was greater at lower concentrations than at higher ones. Initiation of germination was also delayed more in lower concentrations. Likewise, seedling growth was suppressed. As in most of these allelopathic studies, we need to demonstrate that the same inhibition occurs in the presence of whole plants of *Lunularia cruciata* and that the solvent alone does not contribute to the inhibition.

Or perhaps dying plants could leach the inhibitors in concentrations similar to those from the macerated plants. A further question is the ability of the soil to bind the inhibitor in the field, rendering it useless against these tracheophytes.



Figure 99. *Indigofera heterantha*, a species whose seed germination is inhibited in the lab by extracts from *Lunularia cruciata*. Photo by Dinesh Valke, through Creative Commons.



Figure 100. *Impatiens scabrida*, a species whose seed germination is inhibited in the lab by extracts from *Lunularia cruciata*. Photo by Paganum, through Creative Commons.

Schwabe (1990) found that an internal accumulation of lunularic acid could inhibit the growth of *Lunularia cruciata* (Figure 1-Figure 13). Schwabe also suggested that lunularic acid from the parent plant served to inhibit the germination of gemmae while still residing on the parent (Figure 101-Figure 102). As already noted, IAA could serve this function. On the other hand, despite leakage of lunularic acid to the soil, evidence suggests that it is not accumulated there, thus permitting gemmae to germinate once leaving the parent plant surface.



Figure 101. *Lunularia cruciata* with dormant gemmae on thallus. Photo by Martin Hutten, with permission.



Figure 102. *Lunularia cruciata* with dormant gemmae on thallus. Photo by Martin Hutten, with permission.

Herbivory

It is clear from some of the images posted that *Lunularia cruciata* (Figure 1-Figure 13) experiences herbivory (Figure 103). This could be from slugs, pillbugs, or insects. And perhaps even birds might nibble the edges.



Figure 103. *Lunularia cruciata* showing herbivory (lower right). Photo by Des Callaghan, with permission.

Interactions

Bacteria most likely play a larger role in bryophyte development than we have supposed. *Methylobacterium* (Figure 104) is able to inhabit the surfaces of plants, including *Lunularia cruciata* (Figure 1-13) (Kutschera & Koopmann (2005). While there, they secrete cytokinins that are able to promote growth of gemmae on agar plates. There seemed to be no effect on the seed plants tested, and Kutschera and Koopmann hypothesized that these bacteria have a role in normal development and regulation in *Lunularia cruciata* in nature.

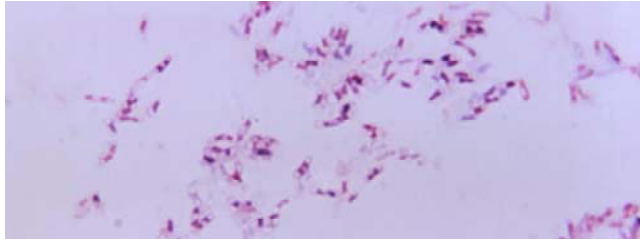


Figure 104. *Methylobacterium*, a bacteria species that can live on the surfaces of *Lunularia cruciata*. Photo by R. E. Weaver, CDC, through public domain.

Sahu *et al.* (2013) observed that the green alga *Stichococcus bacillaris* (Figure 105) occurred as a contaminant on laboratory cultures of *Lunularia cruciata* (Figure 1-13) on soil in growth chambers. They found that presence of the alga suppressed the growth of the liverwort, an example of algal allelopathy.



Figure 105. *Stichococcus bacillaris* on rotting wood, a green alga species that can be allelopathic to *Lunularia cruciata*. Photo by James K. Lindsey, with permission.

Bukvicki *et al.* (2021) determined that bis-bibenzyl perrottetin F was isolated from *Lunularia cruciata* (Figure 1-13) by the fungus *Aspergillus niger* (Figure 106). This compound exhibits inhibitory activity against the bacteria *Pseudomonas aeruginosa* (Figure 107) PAO1 and *Staphylococcus aureus* (Figure 108) at concentrations of 100 μ m to 450 μ m. It also has "remarkable ability" to inhibit the synthesis of bacterial quorum-sensing signal molecules. These results suggest that this biological combination could provide a fast and effective way of producing bioactive substances.



Figure 106. *Aspergillus niger*, a fungus that is able to isolate bis-bibenzyl perrottetin F from *Lunularia cruciata*. Photo through public domain.

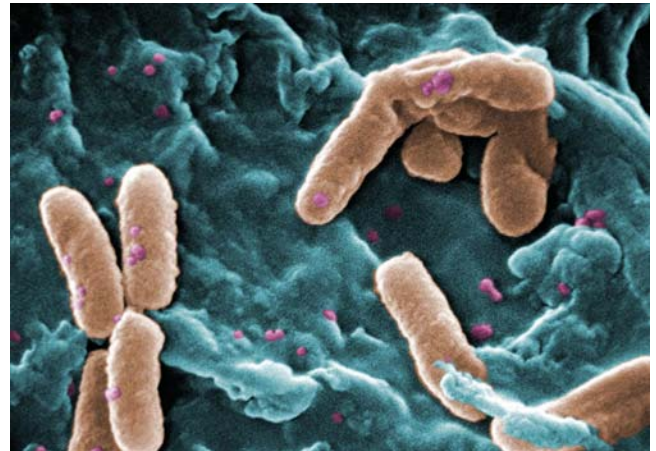


Figure 107. *Pseudomonas aeruginosa*, colorized SEM. This is a bacterial species that is inhibited by bis-bibenzyl perrottetin F isolated by *Aspergillus niger* from *Lunularia cruciata*. Photo by Janice Haney Carr, CDC, through public domain.

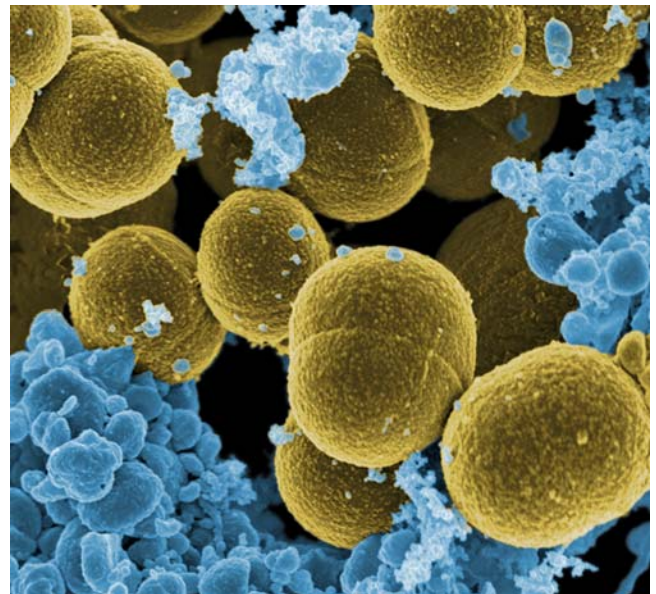


Figure 108. *Staphylococcus aureus*, colorized SEM. This is a bacterial species that is inhibited by bis-bibenzyl perrottetin F isolated by *Aspergillus niger* from *Lunularia cruciata*. Photo by Frank DeLeo, NIH, through public domain.

Lunularia cruciata (Figure 1-Figure 13) can be colonized by the oomycete pathogenic fungus *Phytophthora palmivora* (Figure 109) (Carella & Schornack 2018). The hyphae colonize the air chambers in the dorsal photosynthetic layer, and they may sometimes be associated with ventral epidermal cells and rhizoids (Figure 110). However, the fungus is never associated with the central storage region.



Figure 109. *Phytophthora palmivora* mycelia on papaya that has been damaged by herbivory. Photo by Scot Nelson, through Creative Commons.

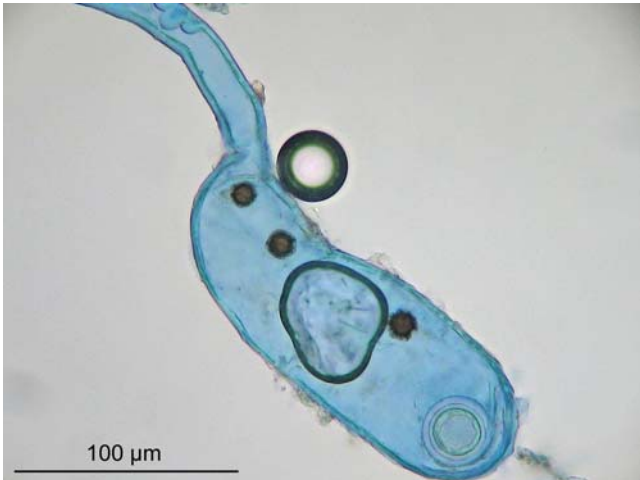


Figure 110. *Lunularia cruciata* inflated rhizoid. Photo by Jan Eckstein, with permission.

One of the most common groups of fungi in association with bryophytes is the **Glomeromycota**, a phylum of fungi that produce arbuscular mycorrhizal associations almost exclusively with bryophyte plants and tracheophyte roots. Among their habitats, they include wetlands and salt marshes.

Rhizophagus irregularis (Figure 111) is a symbiotic fungus in **Glomeromycota** that can colonize the thalli of *Lunularia cruciata* (Figure 1-Figure 13) (Carella & Schornack 2018). During the symbiosis, the fungus acts to up-regulate the transcriptome genes of the liverwort (Delaux *et al.* 2015). Delaux *et al.* conclude that the green alga ancestor of land plants was preadapted for symbiotic associations. This was followed in early land plants by gene duplication that permitted additional pathways,

enabling a fully functional arbuscular mycorrhizal symbiosis.



Figure 111. *Rhizophagus irregularis* in the roots of the bean *Vicia faba*; it is a symbiotic fungus that can colonize the thalli of *Lunularia cruciata*. Photo by Mylène Durant, through Creative Commons.

Lunularia cruciata (Figure 1-Figure 13) is one of the bryophyte species in which the **Glomeromycota** mycorrhizae develop (Fonseca *et al.* 2006). Fonseca and coworkers cultured *Rhizophagus irregularis* (syn.=*Glomus intraradices*; Figure 111) and *Glomus proliferum* (see Figure 112), then introduced them to *Lunularia cruciata*. The fungi produced external hyphae and spores similar to those found associated with roots.



Figure 112. *Glomus* sp.; *Glomus* species are all obligate arbuscular mycorrhizal (AM) fungi; *G. proliferum* forms this relationship with *Lunularia cruciata*. Photo by Reiner Richter, through Creative Commons.

But that is not evidence of a symbiotic relationship, so Fonseca and Berbara (2008) used Koch's postulates to determine if they formed a symbiotic relationship. They found that fungi in cultured liverwort thalli were able to extend into a compartment of the Petri dish where they obtained phosphorus and to translocate that phosphorus

into the liverwort. The liverwort responded with increased dry weight, greater AM fungi spore production, and higher liverwort total phosphorus content. However, the researchers suggested that the energy requirements to maintain the symbiosis may limit its symbiotic advantage in the field. Fonseca and Berbara considered the relationship of endophytic *Rhizophagus irregularis* (Figure 111) and *Glomus proliferum* (see Figure 112) with *Lunularia cruciata* (Figure 1-Figure 13) to be a parasitic/opportunistic partnership rather than a mutualistic symbiosis.

The thalli of *Lunularia cruciata* (Figure 1-Figure 13) reveal major anatomical traits of mycorrhizal associations (arbuscules, coils, arbusculate coils and vesicles) when infected with *Glomus proliferum* (Figure 112) (Fonseca & Berbara 2008; Fonseca *et al.* 2009a). But colonized liverwort thalli exhibited a reduction in biomass in comparison with axenic thalli, supporting the conclusion that the relationship is parasitic (Fonseca *et al.* 2009a, b; Figueiredo 2010). Fonseca *et al.* 2009a) determined that those liverwort plants that did not fare well already had sufficient phosphorus, thus giving all the benefit to the fungus. This does not rule out the possibility of benefit to the liverwort in conditions where phosphorus is limiting because of the ability of the fungus to scavenge phosphorus from a much larger area than that available to the liverwort alone. Furthermore, significant reductions in growth of infected compared with uninfected cultured plants did not arise until 86 and 106 days of infection (Figueiredo 2010).

Fonseca *et al.* (2013) introduced laboratory methods for culturing *Rhizophagus clarus* (Figure 113) (syn.=*Glomus clarum*) and *Gigaspora margarita* (also in the *Glomeromycota*; Figure 114) with *Lunularia cruciata* (Figure 1-Figure 4-Figure 13). *In vitro* cultures of *Rhizophagus clarus* and *Gigaspora margarita* were grown with *Lunularia cruciata* on macro and micronutrients with a layer of activated charcoal in the upper agar layer (Fonseca *et al.* 2014). Both fungal species reached maturity in less than 150 days and were still viable after more than 500 days. Container size was the only limiting factor for growth of the liverwort. Both fungal species colonized the midrib parenchyma. *Gigaspora margarita* developed relatively small, shallow colonies, apparently limited by its distribution within the plant. Penetration by this species occurs mainly through new entry points by its external hyphae from neighboring thalli and not by invasion from cell to cell. The higher level of colonization by *Rhizophagus clarus* most likely resulted from the internal growth of the fungi along the midrib parenchyma toward the thallus apical meristem. The production of spores occurred primarily among the rhizoids, developing between overlapping thalli and over the thalli (Fonseca *et al.* 2013). The pattern of development was similar to that seen in *Rhizophagus irregularis* (Figure 111) and *Glomus proliferum* (see Figure 112).

Nobre *et al.* (2013) found that inoculated thalli of *Lunularia cruciata* (Figure 1-Figure 13) achieved their peak absolute growth rate at 39 days after inoculation with *Glomus proliferum* (Figure 112), whereas those not inoculated required 42 days, suggesting a benefit to the liverwort under the growing conditions of the experiment. The liverwort exhibited a relative growth rate of 0.074 and 0.387 cm² cm⁻² d⁻¹, respectively. Addition of 20 and 80

mg carbon L⁻¹ of humic acid had a positive influence on the growth of *L. cruciata*.



Figure 113. *Rhizophagus clarus*, a fungus that is able to colonize the midrib parenchyma of *Lunularia cruciata*. Photo by Silvani Vanesa, Fernández Bidondo Laura, and Fracchia Sebastián, BGIV, through Creative Commons.



Figure 114. *Gigaspora margarita*, a fungus that is able to form small colonies in the thallus of *Lunularia cruciata*. Photo by Mike Geuther, through Creative Commons.

Desirò *et al.* (2013) renewed the story of big fleas have little fleas by demonstrating that the *Glomeromycota* inhabiting *Lunularia cruciata* (Figure 1-Figure 13) in a botanical garden were themselves inhabited by coccoid Gram-positive parasitic endobacterium related to the class *Mollicutes* (Figure 115).

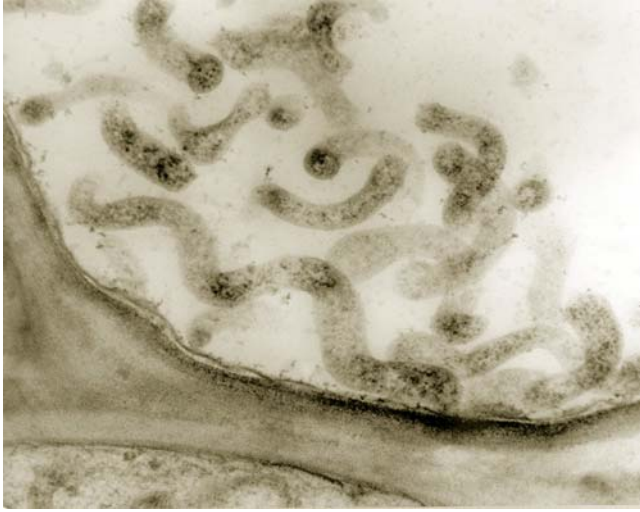


Figure 115. TEM image of *Spiroplasma* sp. (in class **Mollicutes**) from corn phloem. Photo through Creative Commons.

Auret (1930) first reported an endophytic fungus in *Lunularia cruciata* (Figure 1-Figure 13) in South Africa (only females were present). The fungi resided below the assimilating tissue and in the rhizoids. The mycelium exhibited branched, septate hyphae with granular contents, and they formed vesicles, arbuscules, and sporangioles, but none of the cells of the field-grown plants exhibited fructifications. However, when grown on glucose or protein agar, the fungus produced thin, hyaline hyphae that began to form pycnidia by the tenth day. These matured into flask-shaped structures with a beak or neck. Auret described this as a new species, *Phoma lunulariicola* (Figure 116-Figure 117). The relationship did not appear to harm the liverwort beyond the cells that were infected.

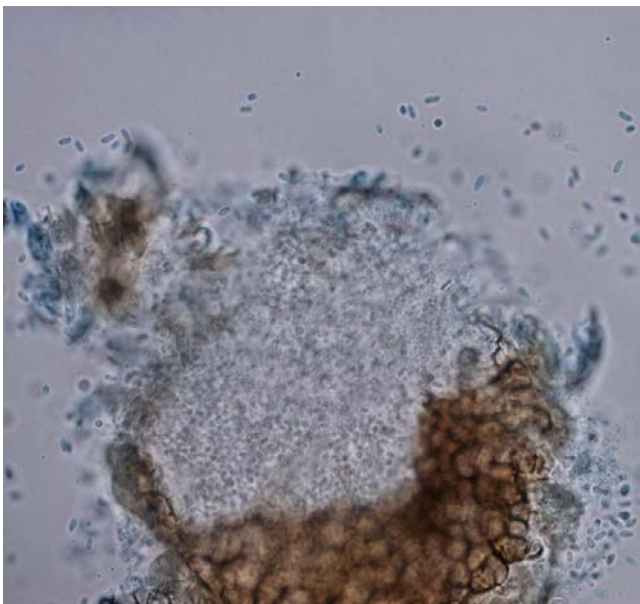


Figure 116. *Phoma herbarum*; *Phoma lunulariicola* is an endophytic fungus in *Lunularia cruciata*. Photo by Cesar Calderon, through Creative Commons.

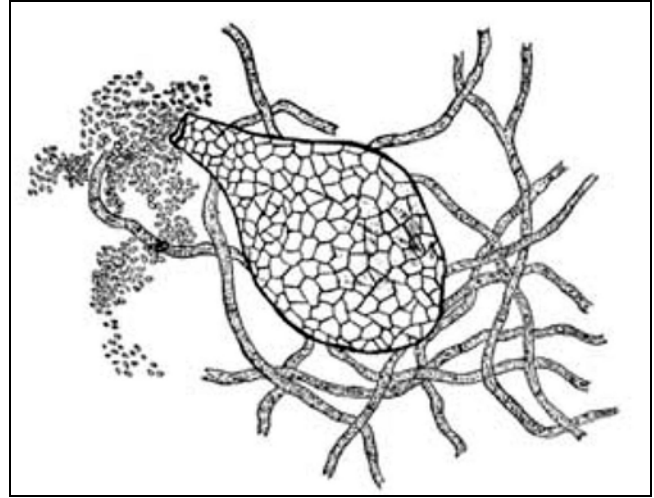


Figure 117. *Phoma lunulariicola* from *Lunularia cruciata*, showing flask of spores. Modified from Auret 1930.

Ridler (1923) also observed the relationship. The fungus occurred in a single strand of cells along the thickened midrib area toward the surface of *Lunularia cruciata* (Figure 1-Figure 13). The liverwort partially digests the fungus, causing the fungus to form arbuscules and sporangioles. Its growth is restricted henceforth. The liverwort starch disappears after the fungus enters, benefitting the fungus. The liverwort does not seem to be harmed, agreeing with the description given by Auret (1930). Ridler also concluded that it was a species of *Phoma* (Figure 116-Figure 117).

Giordano *et al.* (1999) recorded the interactions between the lichen *Cladonia foliacea* (Figure 118) and *Lunularia cruciata* (Figure 1-Figure 13). The interaction by the lichen caused a delay in protonemal growth and reduction in the number of thallose plants produced. Internally, the cytoplasm obtained a granular appearance with many microvesicles in the protonema, enlarged periplasmic space, and changes in chloroplast shape.



Figure 118. *Cladonia foliacea*, a lichen that causes a delay of protonemal growth and reduces the number of thalli produced in *Lunularia cruciata*. Photo by J. C. Schou, with permission.

Basile *et al.* (2011) tested the effect of essential oils from the flowering plant *Sideritis italica* (**Lamiaceae**; Figure 119) on thallus and rhizoid growth and gemma development of *Lunularia cruciata* (Figure 1-Figure 13). Leaf oil was more active than was flowerhead oil, causing

inhibition of gemma development and browning, and inhibiting apical growth of the thallus of *L. cruciata*.



Figure 119. *Sideritis italica*, a species from which the essential oils inhibit gemma development and browning, and they inhibit apical growth in the thallus of *Lunularia cruciata*. Photo by Andrea Moro, through Creative Commons.

Biochemistry

Lunularia cruciata (Figure 1-Figure 13) exhibits "conspicuous oil bodies" (Lepp & Lawson 1984). These are susceptible to damage from pollutants. In elevated vanadium levels, they change color from light brown to black.

Lunularia cruciata (Figure 1-Figure 13) has been the subject of many physiological studies, so it is no surprise that it has been a subject of many biochemical studies as well. As early as 1940, Lugg determined that the amide tyrosine and tryptophan contents of the proteins of the main photosynthesizing tissues of *Lunularia cruciata* presented the same magnitude as those in seed plants.

Because of the micro-organisms that inhabit the surfaces of bryophytes, it is necessary to make certain that compounds identified actually were produced by the bryophyte and not the inhabitants. Christie *et al.* (1985) determined that the carbohydrates produced by axenically cultured *Lunularia cruciata* (Figure 1-Figure 13) were the same as those identified from field populations, especially alditols.

Lunularic acid, an ABA-like inhibitor and stress hormone, was named for its discovery in *Lunularia cruciata* (Figure 1-Figure 13) (Pryce & Kent 1971). Thus far, this hormone is almost unique to liverworts, and is notably absent from mosses (Pryce 1972). Yoshikawa *et al.* (2002) demonstrated the similarity of lunularic acid to

ABA in both the physiological responses it elicits and in its apparent ability to bind to the same receptor in tracheophytes.

One of the early reports is the presence of sucrose phosphatase in *Lunularia cruciata* (Figure 1-Figure 4-Figure 13) (Hawker & Smith 1984). This is evolutionarily significant because in all species tested it has been absent in red and brown algae and from fungi.

Markham and Porter (1974) identified luteolin 3',4'-O- β -d-glucuronide as the major flavonoid in *Lunularia cruciata* (Figure 1-Figure 13) and at that time unique to this species. They also found luteolin 3'-O- β -d-glucuronide. James *et al.* (2020) reported the presence of carbohydrates, proteins, diterpenes, phytosterols, and anthocyanin, but flavonoids did not appear in the alcoholic or acetonetic extracts.

Jocković *et al.* identified luteolin-7-O-glucoside and quercetin from extracts of *Lunularia cruciata* (Figure 1-Figure 13). Quercetin is a common plant flavonol in fruits, vegetables, leaves, seeds, and grains. It is reputed to bolster the immune system, to reduce hot flashes, and to serve as an antioxidant in humans. However, it is short-lived in humans, with a half life of only 1-2 hours, and the FDA warns that many of the claims for its beneficial effects to humans have not been validated.

Bryophytes present unique problems for biochemical analysis. Many species are quite small and it is difficult to get enough plants for analysis (Mukhia *et al.* 2019). Some are only available in a particular season; others have restricted geographic distribution or are rare. Hence, Mukhia *et al.* propagated *Lunularia cruciata* (Figure 1-Figure 13) for this purpose, using gemmae. This was a good choice because of its ability to grow in gardens over a large portion of the planet. They validated this approach by comparing its pharmacological properties with those of naturally grown plants. This endeavor revealed nine key compounds present in both lab-grown and field-grown plants. This verified that both *in vitro* and naturally grown plants produced antioxidant and anti-diabetic activity, thus making it feasible to culture this species for both experimental and clinical use.

The antibiotic activities of many liverworts against bacteria are well known. Joshi (1993) investigated antibacterial properties of *Lunularia cruciata* (Figure 1-Figure 13). Basile *et al.* (1993) explored the effects of a-D-oligogalacturonides on the production of antibiotic substances. Basile *et al.* (1998a) determined the minimum concentrations of extracts needed to illicit antibiotic activity against 13 bacterial strains and compared these with standard antipharmaceutical antibiotics. The extracts were effective against both Gram-positive and Gram-negative bacteria.

Sorbo *et al.* (2004) found significant antibacterial activity by *Lunularia cruciata* (Figure 1-Figure 13) extracts against the Gram-positive *Staphylococcus aureus* (Figure 108), *Streptococcus* sp. (Figure 120), and *Enterococcus* sp. (Figure 121). The activity against Gram-negative *Proteus mirabilis* (Figure 122), *Pseudomonas aeruginosa* (Figure 107), *Escherichia coli* (Figure 123), *Salmonella* sp. (Figure 124), and *Klebsiella* sp. (Figure 125) was especially good. The extracts also exhibited antioxidant activity, apparently due to A catechin and its derivatives. By contrast, Russell (2010) found no visible

antibiotic activity against the Gram-negative *Escherichia coli* (Figure 123) or *Klebsiella pneumoniae* (Figure 125). Nevertheless, *Lunularia cruciata* exhibited the most significant antibacterial activity among the 14 bryophyte species tested.

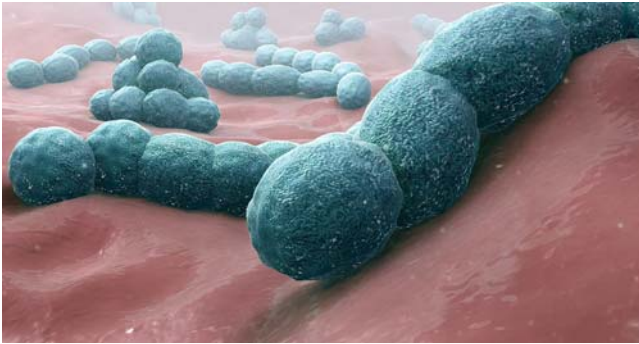


Figure 120. *Streptococcus pneumoniae*; *Lunularia cruciata* exhibits significant antibacterial activity against *Streptococcus* sp. Photo from <www.scientificanimations.com>, through Creative Commons.



Figure 121. *Enterococcus faecalis*; *Lunularia cruciata* exhibits significant antibacterial activity against *Enterococcus* sp. Photo by Janice Haney Carr, CDC, public domain.



Figure 122. *Proteus mirabilis* suffering from Penicillin exposure. In early stages the bacteria are thickened in the middle (**lower left**). Later they fold into a V shape (**upper right**) just before lysis. Extracts from *Lunularia cruciata* are especially good at inhibiting the bacterium *Proteus mirabilis*. Photo by Geoman3, through Creative Commons.



Figure 123. *Escherichia coli* colored SEM image, a species that does not seem to be affected by extracts from *Lunularia cruciata*. Photo from NIAID, through Creative Commons.



Figure 124. Colored SEM image of *Salmonella* invading cells; at least some members of this genus are unaffected by extracts from *Lunularia cruciata*. Photo from NIAID, through Creative Commons.



Figure 125. *Klebsiella pneumoniae* colored SEM image, a species that does not seem to be affected by extracts from *Lunularia cruciata*. Photo from NIAID, through Creative Commons.

Dhondiyal *et al.* (2013) reported "substantial" antibiotic activity by *Lunularia cruciata* (Figure 1-Figure 13) extracts against five pathogenic species of bacteria [*Agrobacterium tumefaciens* (Figure 126), *Xanthomonas phaseoli* (Figure 127), *Escherichia coli* (Figure 123), *Bacillus subtilis* (Figure 128), and *Dickeya dadantii* (Figure 129)]. This occurred in all four crude organic extracts against all five bacteria species. The extracts proved to be very effective against these bacteria when compared to the standard antibiotic ampicillin. But these results must be viewed with caution. While they provide evidence that the liverwort has medicinal properties, the aqueous extracts had no antibiotic effects, suggesting that the plants may not be protected by these natural compounds in nature. Furthermore, based on conflicting reports discussed above, we need to assess the role of the solvents as well as temperature, light, and nutrient conditions in altering the antibiotic effectiveness.



Figure 126. *Agrobacterium tumefaciens* causing a gall at the tree base. Photo by Jerzy Opiola, through Creative Commons.



Figure 127. *Xanthomonas phaseoli* infecting leaves of the bean *Phaseolus vulgaris*; *Lunularia cruciata* exhibits significant antibiotic activity against this bacterial species. Photo by Howard F. Schwartz, through Creative Commons.

Lunularia cruciata (Figure 1-Figure 13) alcoholic and acetic extracts are very active against *Klebsiella pneumoniae* (Figure 125) (James *et al.* 2020). *Escherichia coli* (Figure 123) is inhibited by both acetone and alcohol extracts. *Staphylococcus aureus* (Figure 108) is inhibited only by acetone extracts, whereas alcohol extracts elicit no inhibition. The researchers suggested that lunularic acid

may be the reason for greater inhibitory responses to *Lunularia cruciata* extracts than to *Marchantia emarginata* (Figure 130) extracts.

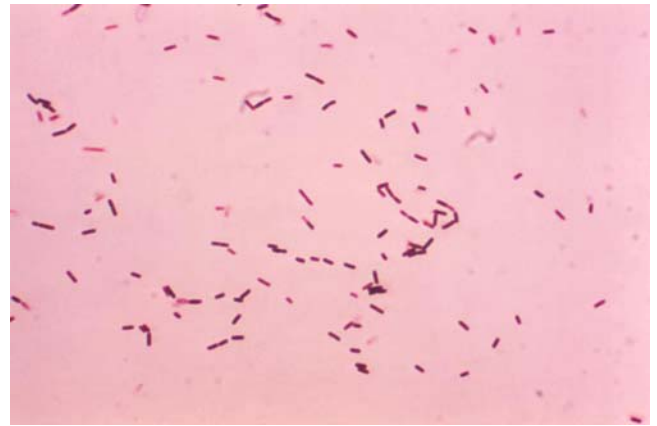


Figure 128. *Bacillus subtilis* with Gram stain; *Lunularia cruciata* exhibits significant antibiotic activity against this species. Photo by W. D. Clark, CDC, through public domain.



Figure 129. *Dickeya dadantii* infecting *Allium cepa* (onion); *Lunularia cruciata* exhibits significant antibiotic activity against this bacterial species. Photo by Scot Nelson, through Creative Commons.



Figure 130. *Marchantia emarginata*, a species that elicits less inhibitory response than does *Lunularia cruciata*. Photo by Li Zhang, with permission.

Basile *et al.* (1998a) tested the minimum concentrations of extracts of *Lunularia cruciata* (Figure 1-Figure 13) needed to illicit antibiotic activity against 2 fungal species, but they found no antifungal activity among the strains tested.

Although extracts of *Lunularia cruciata* (Figure 1-Figure 13) in organic solvents proved to be very effective on the tested bacteria, none of the extracts had any effect against the three pathogenic fungi [*Alternaria alternata* (Figure 131), *Sclerotinia sclerotiorum* (Figure 132), and *Pyricularia oryzae* (Figure 133)] tested (Dhondiyal *et al.* 2013).

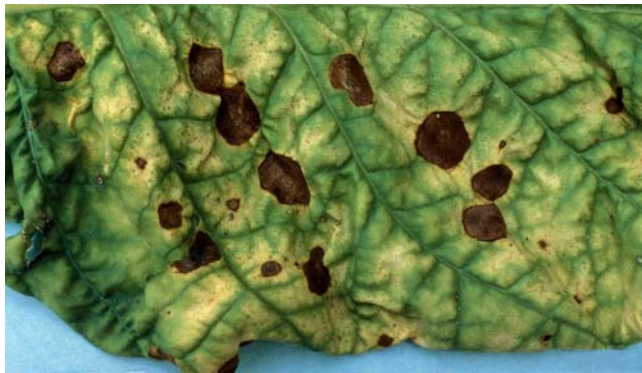


Figure 131. *Alternaria alternata* on tobacco leaf (*Nicotiana tabacum*), a species of fungi that is immune to extracts of *Lunularia cruciata*. Photo by R. J. Reynolds Tobacco Company, through Creative Commons.



Figure 132. *Sclerotinia sclerotiorum* on bean, *Phaseolus vulgaris*, a fungus species that is immune to extracts of *Lunularia cruciata*. Photo by Jymm, through Creative Commons.



Figure 133. *Pyricularia oryzae* from rice, a fungus species that is immune to extracts of *Lunularia cruciata*. Photo by Donald Groth, USDA Forest Service, through public domain.

Basile *et al.* (1991, 1993, 1998b) tested the ability of α -d-oligogalacturonides (OG) to induce antibiotic activity, using the fern *Nephrolepis* sp. (Figure 134) as a model system. This compound can occur naturally in the soil as a product of biological components. The experiments demonstrated that indeed the antibiotic activities can be induced, at least in the fern. Further testing indicated that extracts from wild-grown *Lunularia cruciata* (Figure 1-Figure 13) likewise inhibited the growth of all bacterial strains tested, whereas extracts from the axenically grown plants in the presence of α -d-oligogalacturonides were able to inhibit only three of the tested bacterial strains. Basile and coworkers concluded that the OG mixture induces the production of fewer antibiotic compounds compared to inducing compounds typically found in the soil. This does not rule out the possibility of more specific compounds being produced in response to OG.



Figure 134. *Nephrolepis exaltata*, in a genus that produces the same α -d-oligogalacturonides (OG) as those of *Lunularia cruciata*, compounds that can induce production of antibiotic compounds. Photo by Mokkie, through Creative Commons.

Sorbo *et al.* (2004) showed allelopathic activity by 7 pure flavonoids of *Lunularia cruciata* (Figure 1-Figure 13). In this case, they inhibited root development of the radish, *Raphanus sativus* (Figure 135). These same flavonoids presented severe allelopathic activity against spore germination and growth of the moss *Tortula muralis* (Figure 136).



Figure 135. *Raphanus sativus* (radish), a species whose roots are inhibited by flavonoids from *Lunularia cruciata*. Photo by Rasbak, through Creative Commons.



Figure 136. *Tortula muralis*, a moss species for which both spore germination and growth are severely inhibited by flavonoids from *Lunularia cruciata*. Photo by Björn S., through Creative Commons.

Compounds from *Lunularia cruciata* (Figure 1-Figure 13) have other potential medical applications. An acetone extract is effective, causing significant changes in light emissions from whole blood phagocytes and polymorphonuclear leukocytes, providing inhibitory activity (Ielpo *et al.* 1998). The researchers postulated that the activity could be caused by compounds such as flavonoids or sesquiterpenes. In further experiments, Ielpo *et al.* (2000) demonstrated that both raw extracts and purified flavonoids exhibited activity against leukocytes.

Novakovic *et al.* (2019) isolated seven new bisbibenzyls from *Lunularia cruciata* (Figure 1-Figure 13), some of which are rare in nature. They demonstrated that riccardin G exhibited cytotoxic activity against the A549 cell line for lung cancer.

Summary

Lunularia cruciata is primarily a Mediterranean species, but it has spread to many places in the world through the horticulture trade. In many of these places sexual reproduction is rare or non-existent and gemmae provide the primary means of spread. It occurs in wet habitats, but is sometimes known from streams. Such moist habitats are provided by waterfalls, stream and river banks, moist slopes and dripping cliffs, springs, mires, seepage, wet soil, dune slacks, and roadside ditches. But it can in some circumstances venture farther from water, especially in gardens and greenhouses. It does especially well in greenhouses and gardens, perhaps due to dispersal gemmae by the watering regime.

Lunularia cruciata was the subject of a number of early physiological studies – finding positive gravitropism, conduction in midrib cells and between scales and rhizoids, hydrophobic pores, greater growth in response to short day length, desiccation hardening in long days, high temperatures and continuous light induce dormancy, lunularic acid protects against drought, inhibition of gemma germination by the

thallus, and effects of higher temperatures on inhibiting gemmae.

Lunularia cruciata is highly resistant to pollution, but it can accumulate heavy metals and thus serves as a biological monitor. Flat, overlapping thalli and accompanying other bryophytes help to maintain moisture.

Various compounds in *Lunularia cruciata* are effective in inhibiting growth of bacteria. Fungi form various relationships from surface colonies to beneficial to parasitic. *Lunularia cruciata* has allelopathic properties against some seeds.

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CHAPTER 1-19

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: AYTONIACEAE

TABLE OF CONTENTS

Aytoniaceae	1-19-2
<i>Asterella africana</i>	1-19-2
<i>Asterella khasyana</i>	1-19-5
<i>Mannia fragrans</i>	1-19-6
<i>Mannia triandra</i>	1-19-12
<i>Reboulia hemisphaerica</i>	1-19-17
Summary	1-19-34
Acknowledgments	1-19-34
Literature Cited	1-19-34

CHAPTER 1-19

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: AYTONIACEAE



Figure 1. A steep stream bank where one might find liverworts in the **Aytoniaceae**. Photo by Michael Lüth, with permission.

Many of the species in this subchapter are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study or other wet habitat.

Marchantiidae – Marchantiales

Aytoniaceae

***Asterella africana* (Figure 2-Figure 3)**

(syn. = *Fimbriaria africana*)

This species can exhibit a large variability in spore and elater dimensions, but other morphological characters seem to be relatively constant (Figueiredo *et al.* 2006).

Distribution

Asterella africana (Figure 2-Figure 3) is known from southern Europe, Macaronesia, and Africa (Long 2005), with widespread distribution in northern Macaronesia, but rare in Europe and North Africa (Blockeel 2012). Casas (1998) listed it for Spain and the Balearic Islands. Rupidera Giraldo and Elias Rivas (1996) reported it from the Iberian Peninsula. Blockeel (2012) reported it from

Crete as new to Greece. It occurs on Madeira and mainland Portugal (Sérgio *et al.* 2001; Figueiredo *et al.* 2006; Sim-Sim *et al.* 2010; Luís *et al.* 2015). Frahm (2005) found it on 5 of the 9 islands of the Azores. Van Dort and Nieuwkoop (2003) reported it from the laurel forests of the Canary Islands. Aleffi (2005) listed it from Italy.



Figure 2. *Asterella africana* thallus. Photo by Jan-Peter Frahm, with permission.



Figure 3. *Asterella africana* on soil. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

Long (2005) considered *Asterella africana* (Figure 2-Figure 3) to have hygromorphic characters, but Losada Lima and Beltran Tejera (1987) considered it mesophytic in the Canary Islands. On the Iberian Peninsula Sérgio and García (2009) found that *A. africana* was associated with moderate temperatures and high humidity.

Luís *et al.* (2010) consider *Asterella africana* (Figure 2-Figure 3) to be riparian in Madeira (Figure 4), where it occurs in mountain streams (Luís *et al.* 2015). Luís and coworkers (2010) found that riparian bryophytes are affected by the habitat and position in the stream, but not by the main aspect (northern versus southern slope).



Figure 4. Fog among the mountains on Madeira Island. Photo courtesy of Michael Stech.

In the Adelantado Forest on Tenerife, wet habitats and shady areas permit the establishment of bryophytes that are scarce elsewhere (Cedr s-Perdomo *et al.* 2017). Among these, *Asterella africana* (Figure 2-Figure 3) occupies slopes near the ravine, taking advantage of the wet conditions. It is also frequent on shady humid slopes of ravines on Tenerife (Losada Lima & Beltran Tejera 1987). Pati o *et al.* (2010) considered anthropogenic disturbances such as water pollution and canalization to be a threat to this species along streams on the Canary Islands.

With these moisture requirements, it is not surprising to find *Asterella africana* (Figure 2-Figure 3) in association with waterfalls. Gonz lez-Mancebo and Hern ndez-Garc a (1996) found *Asterella africana* to be abundant on rocks and soil near continuously flowing springs and waterfalls in the Canary Islands. Capelo *et al.* (2005) reported a similar habitat on basalt in a waterfall on Madeira Island.

In Crete, one can find *Asterella africana* (Figure 2-Figure 3) on wet schistose rock ledges near a stream, where it seems to be always saturated (Blockeel 2012). Dirkse (1995) reported that on the Canary Islands it prefers sheltered rocks with dripping water, especially laurel and pine forests. Van Dort and Nieuwkoop (2003) similarly found it in the laurel forests of the Canary Islands. In particular, they found it at the foot of damp walls, where it was accompanied by *Bryum donianum* (Figure 5).



Figure 5. *Bryum donianum*, a species that accompanies *Asterella africana* at the base of damp walls in the Canary Islands. Photo by Michael L th, with permission.

S rgio *et al.* (2010) found *Asterella africana* (Figure 2-Figure 3) on wet slopes on Macaronesia, again in laurel forests. Dirkse and Bouman (1996) found *A. africana* in the wettest and darkest places on the Canary Islands. Hern ndez-Garc a *et al.* (1995) considered it to be hydrophilic on the Islands, occurring in areas with low light and abundant drip.

Lava tube and pit cave entrances can provide interesting habitats for bryophytes. In the Azores, *Asterella africana* (Figure 2-Figure 3) seems to do well in such cave entrance habitats (Gabriel *et al.* 2008, 2011). It is possible that this habitat is a refugium because all recent records for *Asterella africana* are from cave entrances (Gabriel *et al.* 2008).

Physiology

Few studies discuss any aspect of the physiology of *Asterella africana*. Pedrotti (1996) considers the species to have "thermophilic tendencies."

Adaptations

Long (2005) compared the hygromorphic *Asterella africana* (Figure 2-Figure 3) to the xeromorphic *Asterella persica*. In *A. africana*, the thallus is thin with large air chambers, whereas in the xeromorphic *A. persica* the thallus is thick and leathery with spongy assimilation tissue that has small, irregular air chambers. This is consistent

with the conclusion that air chambers in bryophytes provide for better gas exchange, but are a source of water loss.

On the Canary Islands, humidity conditions, substrate dynamics, and vegetation disturbance are important in influencing the life strategies present (González-Mancebo & Hernández-García 1996). These researchers report that *Asterella africana* (Figure 2-Figure 3) is a long-lived species, a strategy they consider typical around continuously flowing springs and waterfalls on both rocks and soil. In the Canary Islands, they found that the perennial life strategy is best represented in the more humid forests.

By contrast, Lloret and González-Mancebo (2011) considered *Asterella africana* (Figure 2-Figure 3) to be a short-lived shuttle species in the Canary Islands. These differences are likely the result of sampling two different habitat conditions, with the Lloret and González-Mancebo study being an altitudinal study.

Reproduction

On the Canary Islands, from which one can find many records of the presence of *Asterella africana* (Figure 2-Figure 3), the breeding systems, climatic conditions, and rarity can have considerable influence on the fertility of the species.

Asterella africana (Figure 2-Figure 3) is **monoicous** (Figure 6) (Long 1999, 2005). More specifically, it is **paroicous** (with archegonia and antheridia on same branch or stem) (Bischler-Causse & Long 1993). Losada Lima and Beltran Tejera (1987) found it fertile with archegonial heads (Figure 6-Figure 9) in the Canary Islands from February to July, and occasionally in November.



Figure 6. *Asterella africana* with young archegoniophores. Photo by Tim Waters, through Creative Commons.

Biochemistry

Although this species has a restricted distribution and is rare in many areas, the essential oils have been elucidated. The species of *Asterella* commonly produce intense scents (Ludwiczuk & Asakawa 2015). These odors are products of essential oils. Figueiredo *et al.* (2006) found that the essential oils were dominated by the monoterpene fraction (79-84%). These were

predominantly myrtenyl acetate (30-42%) and α -pinene (10-17%). Sesquiterpene and non-terpenoid fractions amounted to only 1-2% and 4-8%, respectively (see also Asakawa *et al.* 2013).



Figure 7. *Asterella africana* on Tenerife with young archegoniophores. Photo by Jonathan Sleath, with permission.



Figure 8. *Asterella africana* archegonial heads. Photo by Jan-Peter Frahm, with permission.



Figure 9. *Asterella africana* archegonial head with capsules. Photo by Jan-Peter Frahm, with permission.

***Asterella khasyana* (Figure 10-Figure 15)**(syn. = *Fimbriaria khasyana*; *Rhacotheca azorica*)**Distribution**

Asterella khasyana (Figure 10-Figure 15) is distributed in southeast Asia and tropical Africa (Long 2005). Its records include India, Pakistan, Nepal, Indochina, Indonesia, Bhutan, China, Philippines, and Thailand (Piippo 1990; Kaul *et al.* 1995; Piippo *et al.* 1997; Boonkerd *et al.* 2007; Singh & Singh 2008a; Daniels 2010; Piippo 2010; Singh *et al.* 2010; Piippo & Koponen 2013). It is common in the Great Himalayan National Park (Singh & Singh 2008a). Matcham (2000) found it in Uganda, Africa. Piippo and Koponen (2013) considered it to be present but very rare in Hunan Province, China.

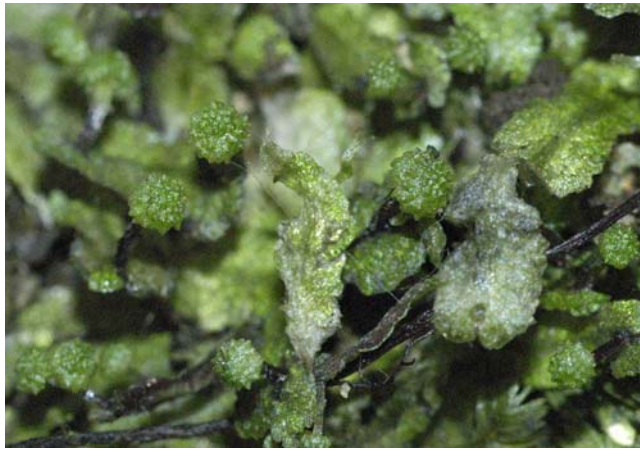


Figure 10. *Asterella khasyana* with archegoniophores and drying thalli. Photo by Manju Nair, through Creative Commons.



Figure 11. *Asterella khasyana* with archegoniophores. Photo by David Long, with permission.

Aquatic and Wet Habitats

Habitats for *Asterella khasyana* (Figure 10-Figure 11) vary. Karki and Ghimire (2019) consider it to be terricolous and saxicolous in Central Nepal, where it is locally rare. Dixit and Kerketta (2019) likewise consider it terricolous in the Lafa Hills, Chhattisgarh, India. But it seems to be predominantly reported from wet habitats.

Matcham (2000) reported *Asterella khasyana* from a very wet cliff in Uganda.

For bryophytes such as *Asterella khasyana* (Figure 10-Figure 11) that tend to be moisture loving, waterfalls offer a suitable habitat. Not many species can withstand being in the strong flow of the falls themselves, but the moist stream or river bank that is in the spray zone is a suitable habitat for many of these moisture loving species. Long (2006) reported *Asterella khasyana* from wet rocks by a waterfall in the Himalayas.

In the Himalayas, *Asterella khasyana* (Figure 10-Figure 11) occurs on damp rocky banks by the road (Long 2006). It has a sufficiently wide moisture tolerance to be found in dry habitats as well as wet ones. Long (2006) found it in a steep valley with patches of evergreen broad-leaved forest in the Himalayas in areas that are not wet. Singh and Singh (2008a) even classify it as terrestrial in the Great Himalayan National Park, where it is common, but state that it grows in moist and shady places.

For those species that are tolerant of higher humidity, stream and river banks are suitable and often preferred habitats. Piippo and Koponen (2013) reported *Asterella khasyana* (Figure 10-Figure 11) from sand on a wet brook side in Hunan Province, China. But also in China, in Hunan, Piippo and Koponen (2013) report *A. khasyana* from secondary forests and on sandy forest slopes. Piippo and Koponen (2013) also reported it from a cliff in China, where it has a humus substrate. Its rarity in the province may reflect a lack of suitable habitat, but it is more likely the result of not having arrived yet.

Boonkerd *et al.* (2007) reported *Asterella khasyana* (Figure 10-Figure 11) on moist, sandy soil slopes and rocks in exposed areas of the lower montane forests in Thailand. Paudel (2019) found it commonly in terrestrial habitats in Kailali in the Far West Nepal, where it was among the few species found in both acidic and basic pH.

Adaptations

Asterella khasyana (Figure 10-Figure 11) seems to cope with its somewhat wide range of habitats by several adaptive strategies. Long (2005) considers its thin, delicate thallus with large air chambers in overlapping layers to be hygromorphic characters. It lacks photosynthetic filaments in these chambers. It would be interesting to compare these characters among a large number of populations from varying degrees of moisture.

In some terricolous habitats *A. khasyana* grows in association with leafy liverworts (Dixit & Kerketta 2019), most likely affording it a greater water retention in its habitat. Sreenath and Rao (2020) found that in Andhra Pradesh, India, the species forms irregular rosettes that are often associated with *Fissidens jungermannioides* and other acrocarpous mosses, again a habit that is likely to conserve moisture.

Reproduction

Asterella khasyana (Figure 10-Figure 11) is **monoicous**, with its androecia on the main thallus just behind the base of the archegoniophore (**paroicous**) (Boonkerd *et al.* 2007). The archegonial heads (Figure 12-Figure 14) have distinct projections that may help in conservation of moisture, but we must also consider the possibility of light scattering to prevent damage to sporogenous tissue and developing spores.



Figure 12. *Asterella khasyana* with archegonial heads. Photo by David Long, with permission.



Figure 13. *Asterella khasyana* archegonial heads. Photo by Jan-Peter Frahm, with permission.



Figure 14. *Asterella khasyana* archegoniophores showing maturing sporangia looking like beaks. Photo by Jan-Peter Frahm, with permission.

The spores in *Asterella khasyana* (Figure 10-Figure 11) are large, ranging 65-78 μm in some Indian populations (Singh & Singh 2008b) and 80-90 μm in the Andhra Pradesh, India (Sreenath & Rao 2020). In Thailand, Boonkerd *et al.* (2007) reported a range of 75-90 μm . Alam *et al.* (2020) report spores that are 85-100 μm in southern India. Naveen *et al.* (2014) described the morphology spores of the species in India. It would be

interesting to know how the spore size relates to habitat and to dispersal ability in this species.

No specialized asexual reproductive structures are known in *Asterella* (Schuster 1992), but Chaturvedi and Eshuo (2012) described abnormal asexual reproduction in *Asterella khasyana* (Figure 10-Figure 11). This was accomplished by the development of new thalli from the archegonial head (Figure 15), a type of regeneration.

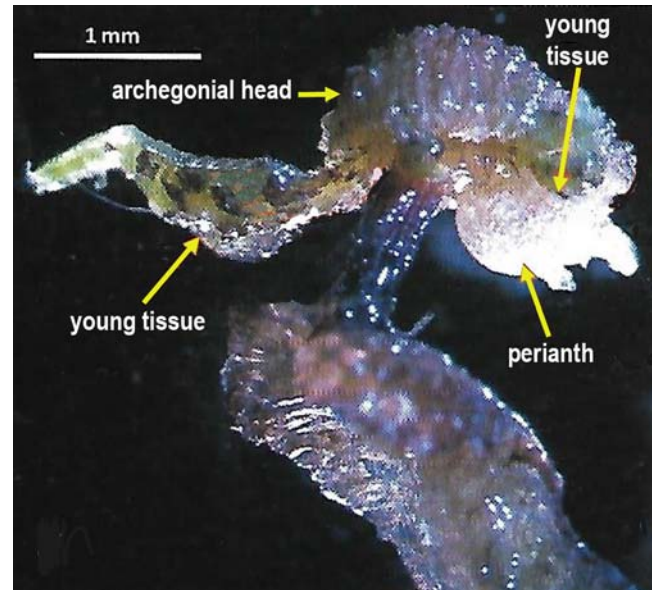


Figure 15. *Asterella khasyana* regeneration of archegonial head. Photo by Sunil Chaturvedi, with permission.

***Mannia fragrans* (Figure 16-Figure 18)**

(syn. = *Grimaldia fragrans*)

Distribution

Mannia fragrans (Figure 16-Figure 18) is widely distributed, but its distribution is disjunct (Schuster 1992). Portions of its distribution are relict. It is known in Asia (Himalayan Mountains, Korea, China, Japan), Europe, and scattered locations in North America (Schuster 1992; Choi *et al.* 2020), but it is relatively rare, despite its widespread distribution.



Figure 16. *Mannia fragrans* thallus with scales. Photo by Martin Hutten, with permission.



Figure 17. *Mannia fragrans* growing on the ground. Photo by Michael Lüth, with permission.



Figure 18. *Mannia fragrans* showing curling dry thalli. Photo by Michael Lüth, with permission.

When Oesau (2010) investigated the current presence of *Mannia fragrans* (Figure 16-Figure 18) in the lower valley of the River Nahe, Germany, they were able to confirm its previously known locations in conservation areas, but they warned that it is nevertheless endangered due to natural succession and damage by game animals.

Aquatic and Wet Habitats

Schuster (1992) describes both xeromorphic and mesomorphic ecotypes for *Mannia fragrans* (Figure 16-Figure 20). Conard (1940) refers to Iowa, USA, populations as distinctly xerophytic, growing in wooded areas or on stony hills in the prairie, but it is also frequent on rocks in half shade. Oesau (2010) found it in the arid region of the River Nahe in Germany.

Nevertheless, *Mannia fragrans* (Figure 16-Figure 20) occurs along calcareous rivers in Connecticut, USA (Nichols 1916).

Bakalin *et al.* (2019) reported a number of locations in Amur Province in Russia, but none of these was wet. Only mesic sandstone cliffs and crevices were somewhat moist.

In Poland *Mannia fragrans* (Figure 16-Figure 20) has been considered an endangered species (Piwowarczyk & Stebel 2012). Nevertheless, while it is threatened by succession of tracheophytes (Figure 21), it has been

released from the damage due to former grazing. The researchers describe it as "almost all over the slope above the Kamienna River in the village of Podgrodzie."



Figure 19. *Mannia fragrans* soil habitat. Photo by Michael Lüth, with permission.



Figure 20. *Mannia fragrans* on bank. Photo from Gencat, with online permission.



Figure 21. *Mannia fragrans* showing competing tracheophytes and lichens. Photo by Michael Lüth, with permission.

One habitat that seems to favor *Mannia fragrans* (Figure 16-Figure 20) is wind holes (Figure 22). Choi *et al.* (2020) report its presence on shaded rocks near the wind hole in broad-leaved deciduous forests in Korea. Bakalin *et al.* (2017) describe these as formations where the wind enters large holes tens of meters above, then goes underground, where it passes among wet stones and cliffs in areas with much lower temperatures due to evaporation of water from the stones. Therefore, at the exit hole, the air temperature may be about 10°C below that of the surrounding environment. This provides suitable habitat for several *Mannia* species.



Figure 22. Wind hole in Bihor Mts. in Transylvania, Romania. Note cryptogams growing on the interior walls. Photo courtesy of Tamás Pócs.

Physiology

In *Mannia fragrans* (Figure 23-Figure 24) all cells survived 12 hours at 20°C and 15% humidity, making it the most desiccation-tolerant species among the 33 species reported (Clausen 1964). When in ice at -10°C, it was unable to survive for even two days, but when partly desiccated it did survive 2 days at -10°C. This suggests that when it is hydrated, there is likely to be membrane damage due to formation of crystals or cell expansion.



Figure 23. *Mannia fragrans* on soil in a dry state. Photo by Michael Lüth, with permission.



Figure 24. *Mannia fragrans* dry and curled. This might reduce moisture loss, but it could also reduce light damage in the dormant cells. Photo by Janice Glime. The dark color also helps to prevent light damage.

Adaptations

Sometimes *Mannia fragrans* grows with other bryophytes (Figure 25-Figure 26). This behavior can take advantage of the capillary water held by the adjoining bryophytes to maintain its own moisture longer.



Figure 25. *Mannia fragrans* with emerging archegoniophores and accompanying mosses. Photo by Angus Mossman, through Creative Commons.



Figure 26. *Mannia fragrans* with mosses, where it could benefit from their moisture retention. Michael Lüth, with permission.

In other cases, its own thalli tightly cover the ground (Figure 27), reducing evapotranspiration. This is probably useful in some habitats in preventing erosion and protecting soil organisms.



Figure 27. *Mannia fragrans* showing overlapping and tightly adhering thalli of a nearly pure colony. Photo by Michael Lüth, with permission.

One potential adaptation to obtaining and maintaining moisture is the presence of ventral scales (Figure 28). In other liverworts, these are known to provide capillary spaces that facilitate the uptake of water throughout the thallus.



Figure 28. *Mannia fragrans* ventral scale with transparent appendages. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Reproduction

The genus *Mannia* can be **dioicous** or **monoicous** (Choi *et al.* 2020). *Mannia fragrans* (Figure 29) is **polyoicous** (species being both monoicous and dioicous) (Schuster 1992). Hock *et al.* (2009) noted that colonizers that produce both sex organs are favored in selection because they ensure sexual reproduction when no partner is present. This is especially important for species like *Mannia fragrans* that have no specialized means of asexual reproduction.



Figure 29. *Mannia fragrans* with antheridial patches (dark brown) and young archegoniophores (pinkish red with scales, but it is hard to determine if they are on the same plant or on different plants. Photo by Jan-Peter Frahm, with permission.

The male branches or plants (Figure 30-Figure 31) produce patches of antheridia on the thallus surface. The phenology of these sexual structures, including the conditions that trigger their initiation, need to be studied.



Figure 30. *Mannia fragrans* on soil in NW Iowa, USA, with a few brown antheridial patches. Photo by Janice Glime.



Figure 31. *Mannia fragrans* with brown patches of antheridia. Photo by Janice Glime.

In *Mannia fragrans* (Figure 29), there is a strong female-biased sex ratio (Figure 32-Figure 35); sexual expression is high (Hock *et al.* (2008b). This high expression contributes to high fertilization rates and may account for its widespread distribution. But its relative rarity suggests that most arrival sites do not provide the conditions needed for establishment.



Figure 32. *Mannia fragrans* thalli with developing archegoniophores. Photo by Michael Lüth, with permission.



Figure 33. *Mannia fragrans* with beginning stages of archegoniophores and scales. Photo by Štěpán Koval, with permission.

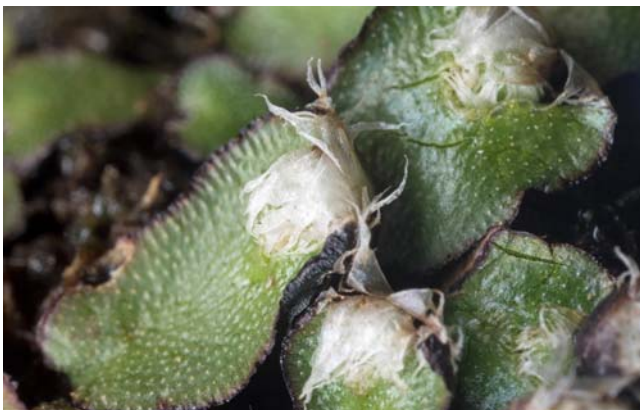


Figure 34. *Mannia fragrans* showing archegoniophore scales. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 35. *Mannia fragrans* archegonial heads with scales. Note the browning thalli that can leave small apical portions for potential dispersal. Photo by Aaron Carlson, through Creative Commons.

The archegoniophore is surrounded by white scales (Figure 34-Figure 38) that remain at the base when it elongates. Perhaps these help to maintain the proper moisture levels at the time of fertilization. Following sexual reproduction, there is further growth in male plants, but not in female plants/branches (Hock *et al.* 2009).



Figure 36. *Mannia fragrans* young archegonial head with scales. Photo by Aaron Carlson, through Creative Commons.



Figure 37. *Mannia fragrans* archegonial head with scales as it emerges from the thallus. Photo by Botanicalwanderer, through Creative Commons.



Figure 38. *Mannia fragrans* female lobes with only small apical portions of the thallus remaining. Photo by Samuel Brinker, through Creative Commons.

Despite the elevation of the sporangia on the extended archegoniophore (Figure 39), the large spores [60.0-82.0 μm (Figure 40) (Choi *et al.* 2020)] will mostly fall back to the same population. This results in significant differences between distant populations and signals negligible gene flow between them. There are numerous rare alleles and unique recombinations, indicating that at least occasional recombination and mutation do occur (Hock *et al.* 2009). In Japan, mature spores occur in early winter (Furuki 1992).



Figure 39. *Mannia fragrans* mature archegonial heads with dehiscent sporangia. Photo by Václav Dvořák, through Creative Commons.

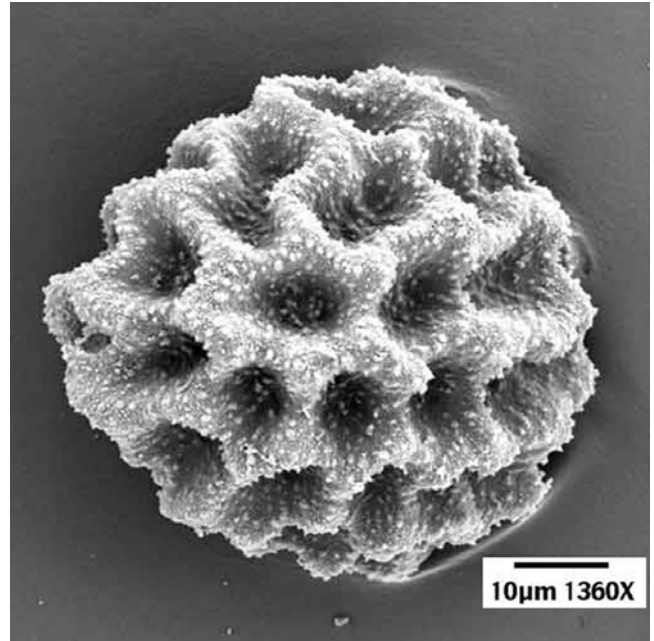


Figure 40. *Mannia fragrans* distal spore wall SEM. Photo by William T. Doyle, with permission.

Asexual reproduction in *Mannia fragrans* occurs commonly by fragmentation of thalli (Figure 41) (Hock *et al.* 2008b). But despite the high frequency of spore production, the genetic diversity within populations is low, suggesting that fragmentation is an important source of new plants (Hock *et al.* 2008b, 2009). Even when sexual reproduction occurs within the population, it is likely to occur between two identical genomes that have arisen through fragmentation.



Figure 41. *Mannia fragrans* with what appear to be dying older thalli with green apices and early stages of sexual structures. As these older parts of thalli die, they provide a means of fragmentation. During rain events, these smaller pieces of thalli could become dislodged, facilitating dispersal. This dispersal mechanism needs to be documented.

Hock *et al.* (2008a, b) used *Mannia fragrans* (Figure 41) to demonstrate that a diaspora bank can conserve genetic variability over generations and seasons. Propagules can remain in the soil for extended periods of time, then come to the surface following a disturbance, and grow, expressing the gene pool of previous points in time.

Fungal Interactions

De (2017) found that the **Glomeromycota** fungus *Planticonsortium tenue* (= *Glomus tenue*) grows in association with the gametophyte of *Mannia fragrans* (Figure 41). It primarily colonizes the smooth rhizoids, but can also live among the scales (Figure 28) and tuberculate rhizoids. From there, the fungus grows upward into the parenchyma cells of the thallus midrib and crosses the cell walls through the plasmodesmata. It is interesting that vesicles are able to develop in the smooth rhizoids and in the scales, but fail to develop in the tuberculate rhizoids. Within the thallus, the fungus occurs mostly intracellularly, forming vesicles and arbuscules in the midrib cells. Young cells are fungus free.

Biochemistry

As its name implies, *Mannia fragrans* (Figure 41) is usually aromatic, with the odor of cedar oil, although there seem to be some population variants (Choi *et al.* 2020). Schuster (1992) describes it as "oil cells frequent." Asakawa (2007) attributes the strong, sweet mossy odor to the cuparene-type sesquiterpene ketone, grimaldone.

Huneck *et al.* (1988a) reported pakynol as a macrocyclic bisbibenzyl diether from *Mannia fragrans* (Figure 41). Nogradi *et al.* (1990) later elaborated the synthesis of the compound in this species and Böcskei and Keserü (1994) described its crystal structure.

Huneck *et al.* (1988b) described the structure of the tricyclic sesquiterpenoid grimaldone in this species. Odrzykoski and Szwejkowski (1981) found that *Mannia fragrans* (Figure 41) has only one form of glutamate dehydrogenase, but has two forms for glutamate-oxaloacetate transaminase.

Mannia triandra (Figure 42-Figure 43)

(syn. = *Mannia rupestris*)

There is a surprising number of publications on this species. Schill (2006) wrote a dissertation on the taxonomy and phylogeny of the genus *Mannia*.

Distribution

Mannia triandra (Figure 42-Figure 43) is a disjunct, circumpolar, subcontinental species from subarctic and subalpine regions (Müller *et al.* 2014), *i.e.* **arctomontane** (Borovichev & Bakalin 2016). Its distribution includes Europe [Montenegro (Duda 1965) and Albania, Austria, Bosnia, Bulgaria, Croatia, Czech Republic, France, Germany, Hungary, Italy, Macedonia, Poland, Romania, Russia, Slovakia, Slovenia, Sweden, Switzerland, Ukraine (Hugonnot & Offerhaus 2005; Sabovljević & Natcheva 2006; Müller *et al.* 2014)], North America (Greenland, Canada, USA), and Asia (China, Japan, Russia) (Müller *et al.* 2014). Schuster (1992) questions the Japanese record as probably another species. Furthermore, there seemed to be no recent records in Bosnia, Macedonia, or Slovenia (Sabovljević & Natcheva 2006; Ros *et al.* 2007; Alegro *et al.* 2019). However, in 2017, Krajšek and Martinčič reported several localities for it in Slovenia and cautioned that it is only visible in spring due to its ephemeral life cycle. Records for Spain appear to be based on problems of incorrect synonymy and Brugués *et al.* (2011) therefore excluded it from the flora there.



Figure 42. *Mannia triandra* on soil in Europe. Photo by Michael Lüth, with permission.



Figure 43. *Mannia triandra* thalli amid other bryophytes. Photo by Michael Lüth, with permission.

Mannia triandra (Figure 42-Figure 43) is a calcicole, concentrated mostly at low elevations in the Alps (Schuster 1992). Shershen *et al.* (2018) reported *M. triandra* from the Loud Thunder Forest Preserve in Illinois, USA. Conard (1940) reported it as rare in Iowa, USA.

Mannia triandra (Figure 42-Figure 43) is red-listed (threatened or endangered) in many of the countries where it occurs (Schumacker & Matriny 1995; Kučera & Váňa 2003; Colacino & Sabovijevec 2006; Martinčič 2009; Németh & Papp 2011; Dulin 2013; Zechmeister & Köckinger 2014; Borovichev & Bakalin 2016; Hodgetts *et al.* 2019).

Aquatic and Wet Habitats

Mannia triandra (Figure 42-Figure 43) is a species that occurs on Ca-rich or other basic substrata (Borovichev & Bakalin 2016). Hugonnot (2010) considers it to be a temporary hygrophile. Philippe (2013) says it is "absolutely not rupicolous," *i.e.*, it does not grow on rocks. Conard (1940) states that it is strictly xeric in Iowa, USA.

But this xerophytic habit is not universally true. In Hungary, Németh (2011) found *Mannia triandra* (Figure 42-Figure 43) growing with *Clevea* (= *Athalamia*) *hyalina* (Figure 44), *Myurella julacea* (Figure 45), and *Plagiobryum zieri* (Figure 46) on north-facing slopes

where it is shaded, humid, and "rather cool" (see also Németh & Papp 2011). It is mesothermophilic (Dierßen 2001). Philippe (2013) describes its habitat of Bonneille, France, as one that has a misty escarpment with a high spring humidity and dry summer. But none of the colonies occurred in habitats that were even temporarily oozing.



Figure 44. *Clevea hyalina*, a species that accompanies *Mannia triandra* in cavities of vertical rocks. Photo by Hugues Tinguy, with permission.



Figure 45. *Myurella julacea*, a species that accompanies *Mannia triandra* in cavities of vertical rocks. Photo by Michael Lüth, with permission.



Figure 46. *Plagiobryum zieri*, a species that accompanies *Mannia triandra* in cavities of vertical rocks. Photo by Tomas Hallingbäck, with permission.

Dürhammer (2017) finds *Mannia triandra* (Figure 42-Figure 43) on permanently humid substrata of calcareous rocks that are adequately lit. It is endangered in the damp cracks in the rock due to the rock climbers who tend to rest there or use them as footholds. It does especially well in humid rock overhangs, but that habitat is particularly fragile. Meinunger (1992) found that the same problems face populations in Germany. These habitats contrast with Philippe's (2013) assertion that it is not rupicolous, suggesting again that it may have population differences.

Borovichev and Andreeva (2009) found *Mannia triandra* (Figure 42-Figure 43) on limestone outcrops on the river bank in the Lapland Nature Reserve, Murmansk, Russia, where it was moist and shady.

Borovichev (2014) found that in the Murmansk Province of Russia, *Mannia triandra* (Figure 42-Figure 43) grows exclusively on calcareous substrates. Philippe (2013) describes *M. triandra* as *chasmophilic*, living in crevices of limestone escarpments. Alegro *et al.* (2019) reported it from small, earthy pits and cavities of vertical rocks, often accompanied by *Preissia quadrata* (Figure 47).



Figure 47. *Preissia quadrata* with archegoniophores, a species that often accompanies *Mannia triandra* in cavities on rocks. Photo by Oskar Gran, through Creative Commons.

Papp (1980) reported the only known location for *Mannia triandra* (Figure 42-Figure 43) in Hungary to be the base of a large limestone rock wall. Németh and Papp (2011) found it in cool, humid microhabitats of north-facing calcareous slopes in the Bükk Mountains of Hungary. Papp *et al.* (2007) reported it from limestone cliffs. In the Komi Republic of Russia, Dulin (2013) found it on ledges of southeast-facing outcrops (Figure 48-Figure 50).



Figure 48. *Mannia triandra* on rock in a large crevice. Photo by Renzo Salvo, through Creative Commons.



Figure 49. *Mannia triandra* in limestone rock crevice. Photo by Hugues Tinguy, with permission.



Figure 50. *Mannia triandra* on rock ledge. Photo by Oliver Dürhammer, through Creative Commons.

In the Korean Peninsula, *Mannia triandra* (Figure 42-Figure 43) occurs in wind holes (Figure 22) (Borovichev & Bakalin 2016). These cooler locations serve as refugia for rare alpine plants.

But often, *Mannia triandra* (Figure 42-Figure 43) occupies habitats that are not moist (Németh & Papp 2011). In the Bükk Mountains of Hungary, these include rock crevices on dolomite, soil (Figure 51) at the base of near vertical rock walls, and humus containing dolomite fragments between surface roots of small *Fagus sylvatica* (Figure 52) and *Fraxinus ornus* trees. Conard (1940) reported it from exposed dry rocks in wooded areas and on stony hills in the prairie in Iowa, USA.



Figure 51. *Mannia triandra* on soil. Photo by Hugues Tinguy, with permission.



Figure 52. *Fagus sylvatica* roots, providing a habitat where one might find *Mannia triandra*. Photo by Vegetator, through Public Domain.

Physiology

Dierßen (2001) described the ecological amplitude of European bryophytes, including *Mannia triandra* (Figure 42-Figure 43). Simmel *et al.* (2021) assigned an Ellenberg Indicator Value (EIV) for N of only 3, an indicator that it occurs on sites that are more or less infertile.

The range of habitats known for *Mannia triandra* (Figure 42-Figure 43) suggest that it has a relatively wide moisture tolerance (Figure 53). Its presence on rock surfaces indicate that it will get dried out at times (Figure 53).



Figure 53. *Mannia triandra* in a dry condition. Photo by Hermann Schächner, through Creative Commons.

Adaptations

Mannia triandra (Figure 42-Figure 43) is a **short-lived shuttle species** (Orbán 1984; Németh & Papp 2011), permitting it to occupy transient habitats.

Mannia triandra (Figure 42-Figure 43) has well developed aerenchyma in the thallus (Figure 54), occupying 2-3 layers in the middle of the thallus and completely filling the wings (Borovichev & Bakalin 2016). These are, however, empty, having no photosynthetic filaments. Hence, they serve as reservoirs for CO₂, but can also increase evapotranspiration.

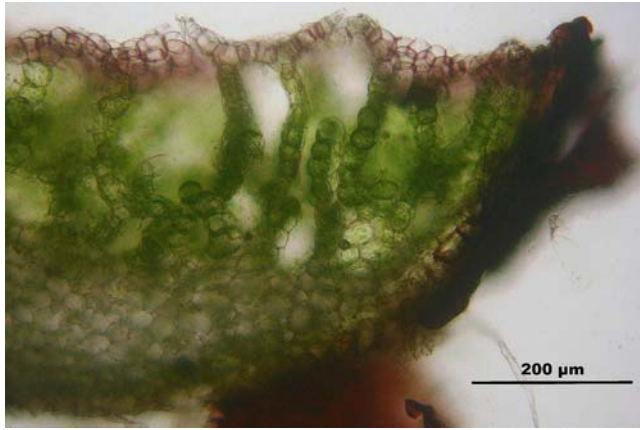


Figure 54. *Mannia triandra* thallus section showing air chambers and pores. Photo by Hermann Schachner, through Creative Commons.

Based on images I have seen, *Mannia triandra* (Figure 42-Figure 43) can grow with densely intermingled other bryophytes (Figure 55-Figure 56). Such a growth habit can help to maintain moisture for longer periods of time.



Figure 55. *Mannia triandra* with mosses, showing their dense growth that can help to retain water. Photo by Michael Lüth, with permission.



Figure 56. *Mannia triandra* with closely associated mosses and producing young archegoniophores. Photo by Michael Lüth, with permission.

Reproduction

Schuster (1992) describes *Mannia triandra* (Figure 42-Figure 43) as **dioicous**. However, Borovichev and Bakalin (2016) describe the androecia and gynoecia (Figure 57) as physically separated, with the androecia on the main thallus and not on the same branch as the female receptacle (Borovichev & Bakalin 2016).



Figure 57. *Mannia triandra* with brown androecia and a separate thallus or branch with one young archegoniophore (lower left). Photo by Štěpán Koval, with permission.

Hugonnot *et al.* (2017) found *Mannia triandra* fertile in May (Figure 57-Figure 60) in Saint-Maurin, France. Németh and Papp (2011) describe the life cycle of *M. triandra* in Hungary as thalli appearing in spring, producing spores in early spring, at which time its "small blue-green thalli" typically disappear during the dry season. The population size in any given year is very dependent on rainfall during its growing season. Müller *et al.* (2014) similarly found fluctuations in the population size from year to year. In 2008, one population occupied approximately 0.25 m². In 2009, it occupied only 5 dm². Then, in 2013, a rock was demolished and its area increased to at least 0.5 m². Similarly, Dürhammer (2017) found that the sporangia (Figure 61-Figure 67) numbers fluctuate considerably from year to year, perhaps driven by fluctuating weather conditions.



Figure 58. *Mannia triandra* with young archegoniophores showing the surrounding dense scales. Photo by Michael Lüth, with permission.



Figure 59. *Mannia triandra* with emergent archegoniophores and dead thalli. Photo by Štěpán Koval, with permission.



Figure 60. *Mannia triandra* young emergent archegoniophores and dying thallus. Photo by Hermann Schachner, through Creative Commons.



Figure 61. *Mannia triandra* archegoniophores with disintegrating thalli. Photo from Earth.com, with permission.



Figure 62. *Mannia triandra* archegoniophores with sporangia beginning to push scales surrounding them outward. Photo by Hugues Tinguy, with permission.



Figure 63. *Mannia triandra* archegoniophores beginning to elongate and sporangia beginning to emerge. Photo by Hugues Tinguy, with permission.



Figure 64. *Mannia triandra* with young capsules and elongated archegoniophores. Photo by Štěpán Koval, with permission.



Figure 65. *Mannia triandra* archegoniophores with mature capsules. Photo by Hermann Schachner, through Creative Commons.



Figure 66. *Mannia triandra* with mature sporangia. Photo by Paul G. Davison, with permission.



Figure 67. *Mannia triandra* underside of archegonial head showing mature sporangia. Photo by Paul G. Davison, with permission.

Spores (Figure 68) of *Mannia triandra* (Figure 42-Figure 43) are large [(55-)60-70(-75) μm] (Borovichev & Bakalin 2016). This is probably a major factor in its distribution. Since it is an annual species with no special asexual reproductive structures, it must rely on its spores, but being large, their dispersal is limited (Hugonnot & Celle 2012). As a result, it is not surprising that it is a poor competitor (Philippe 2013).

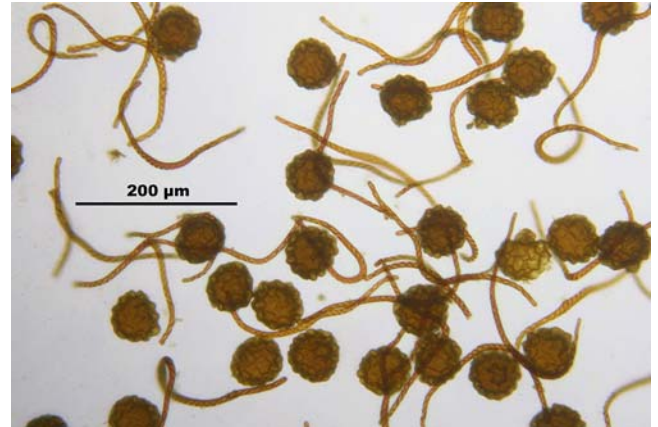


Figure 68. *Mannia triandra* spores and elaters. Photo by Hermann Schachner, through Creative Commons.

biochemistry

Mannia triandra (Figure 42-Figure 43) has numerous oil cells and has oil bodies that range 10-25 μm in diameter (Borovichev & Bakalin 2016). It nevertheless lacks the scent of cedar oil known in *Mannia fragrans* <<http://e-coddb.bas.bg/rdb/en/vol1/Mantrian.html>>.

Reboulia hemisphaerica (Figure 69-Figure 76)

Stephani (1899) recognized *Reboulia hemisphaerica* (Figure 69-Figure 76) as a polymorphic species. It seems to have at least four genetically distinct races (Boisselier-Dubayle *et al.* 1998). Nevertheless, it exhibits less polymorphism than that generally attributed to mosses.

Hicks (1992) reported that three subspecies had been described for *Reboulia hemisphaerica* (Figure 69-Figure 76), differing in distribution of sex organs.



Figure 69. *Reboulia hemisphaerica* rosettes. Photo by Janice Glime.



Figure 70. *Reboulia hemisphaerica* in Europe. Photo by Michael Lüth, with permission.



Figure 71. *Reboulia hemisphaerica*. Photo by Michael Lüth, with permission.



Figure 72. *Reboulia hemisphaerica* in Europe. Photo by Michael Lüth, with permission.



Figure 73. *Reboulia hemisphaerica*. Photo by Janice Glime.



Figure 74. *Reboulia hemisphaerica* in Europe, with archegoniophores. Photo by Michael Lüth, with permission.



Figure 75. *Reboulia hemisphaerica* with purple edges. Photo by Allen Norcross, with permission.



Figure 76. *Reboulia hemisphaerica* in North America. Photo by Paul G. Davison, with permission.

Distribution

Reboulia hemisphaerica (Figure 69-Figure 76) is cosmopolitan (Piippo *et al.* 1997; Kürschner 2008) and is especially distributed in subtropical and temperate regions (Nieuwkoop 1996). *Reboulia hemisphaerica* is distributed in China, India, Japan, Korea, Nepal, Afghanistan, Pakistan, Java, Boning, New Zealand, Australia, Europe, Africa, Tahiti, North America, and South America (Singh & Singh 2002; Nair & Prajitha 2016).

Janovicová and Kubinská (2001) considered *Reboulia hemisphaerica* (Figure 69-Figure 76) to be both rare and threatened in the Biele Karpaty Mountains of Slovakia.

Aquatic and Wet Habitats

Reboulia hemisphaerica (Figure 69-Figure 76) is occasionally submerged (Watson 1919) and can occur in rivers (Ferreira *et al.* 2008). Konstantinova (2011) reported it from sandy soil between rocks in a dry stream bed in Dagestan, Russia. In the Uşak province of western Turkey it occurs on wet rocks (Gökler 2017). Hong (1977) found it on wet rocks in Montana, USA.

Reboulia hemisphaerica (Figure 69-Figure 76) occurs on the bank of the Banaz stream in the Uşak province of western Turkey (Gökler 2017). In the Izarene Massif of Rocco, it occurs on clayey soil on slopes (Figure 77) beside flowing water (Laouzazni *et al.* 2021). In Cyprus, it occurs under shrubs on the bank of a gully and on a steep bank by a stream in a deep valley (Blockeel 2003). Sharp (1939) found it on moist banks (Figure 1) in eastern Tennessee, USA. Konstantinova (2011) reported that *Reboulia hemisphaerica* subsp. *australis* occurs in Dagestan, Russia, in the gorge at the source of the Gunibka River on the bank. Some of its habitats on rocks and soil banks are shown in Figure 77-Figure 82.



Figure 77. *Reboulia hemisphaerica* with elongating archegoniophores on soil of a steep bank, Europe. Photo by Michael Lüth, with permission.



Figure 78. *Reboulia hemisphaerica* habitat on rocks. Photo by Michael Lüth, with permission.



Figure 79. *Reboulia hemisphaerica* on limestone cliff in Ohio, USA. Photo by Robert Klips, with permission.



Figure 80. *Reboulia hemisphaerica* on vertical face of rock. Photo by Michael Lüth, with permission.



Figure 81. *Reboulia hemisphaerica* habitat on steep soil bank with tree roots. Photo by Michael Lüth, with permission.



Figure 82. *Reboulia hemisphaerica* habitat on a soil bank. Photo by Michael Lüth, with permission.

Both streams and rivers can have floodplains. Many species have life cycles timed to take advantage of these ephemeral habitats. In the Virginia Piedmont, USA, the presence of *Reboulia hemisphaerica* (Figure 69-Figure 76) can indicate such a habitat where most of the species appear in late fall after leaf drop, regrowing from spores and dying soon after dispersing their spores (Breil 1977). These indicator species are sensitive to drying, yet typically require high light intensities.

Reboulia hemisphaerica (Figure 69-Figure 76) seems to have a preference for steep slopes (Figure 83-Figure 84). In the Netherlands, it is nearly always found on slopes up to 90° (Nieuwkoop 1996). Martin (1943) reported it from a cliff face in Ledges State Park, Iowa, USA. Miller and Thomson (1959) reported it from moist sandstone cliffs in Indiana, USA.



Figure 83. *Reboulia hemisphaerica* on a vertical face with soil over rock. Photo by Barry Stewart, with permission.



Figure 84. *Reboulia hemisphaerica* with archegoniophores on steep rocky slope. Photo by Michael Lüth, with permission.

Slopes and cliffs often have water trickling down them, or occur in canyons that remain humid. These provide suitable habitat for moisture-loving species of liverworts. In particular, cracks and crevices (Figure 85) provide protection and tend to remain moist longer than bare rock. *Reboulia hemisphaerica* (Figure 69-Figure 76) can occur in such locations (Sharp 1939; Crundwell & Nyholm 1979; Konstantinova 2011).



Figure 85. *Reboulia hemisphaerica* on rock ledge. Photo by Michael Lüth, with permission.

In the Netherlands, Nieuwkoop (1996) found that *Reboulia hemisphaerica* (Figure 69-Figure 76) preferred a loamy substrate (Figure 86), even if growing on a rock. These usually were on moist, loamy walls with light shade. Like the above members of the family Aytoniaceae, *Reboulia hemisphaerica* takes advantage of the cooler temperatures and greater moisture of wind holes (Figure 22) (Bakalin *et al.* 2017).



Figure 86. *Reboulia hemisphaerica* on soil. Photo by Štěpán Koval, with permission.

Reboulia hemisphaerica (Figure 69-Figure 76) exhibits a wide range of moisture tolerance, growing on slopes of ditches, on roadside banks, and along roads (Brown 1924). Jerath and Pujá (2006) reported it as xeromorphic in the Shivalik Ecosystem of Punjab, India, but also growing in moist and exposed places. Nair and Prajitha (2016) found it on cut earth in the western Ghats of India. Singh and Singh (2002) found it on rocks in partially exposed places in India.

Province (2011) reported it in particular from basic schists and slate on rock outcrops among scrub vegetation in South-west Sichuan, China. Piippo and Koponen (2013) similarly found it in both primeval and secondary evergreen forests in northwestern Sichuan, China, in both open and shaded sites, on humus over rock (Figure 87) or stone, on cliffs, clay, and soil (Figure 88).



Figure 87. *Reboulia hemisphaerica* on soil over rock, Europe. Photo by Michael Lüth, with permission.



Figure 88. *Reboulia hemisphaerica* on soil. Photo by Jan-Peter Frahm, with permission.

Konstantinova *et al.* (2018) considered *Reboulia hemisphaerica* (Figure 69-Figure 76) to be a calcicole. It occurs in Russia on bare soil on mossy rock outcrops, on ledges (Figure 89-Figure 91) and in crevices, and even under rocks. Aleffi *et al.* (2005) listed it from rocks and escarpments in Italy. It finds similar habitats to be suitable in Morocco, including rock ledges with accumulated soil and bases of rocks (Ros *et al.* 2000), but Saadi *et al.* (2020) found it on siliceous soil in Morocco. Piippo and Tan (1992) found it on an abandoned wall in a shaded garden in the Philippines.



Figure 89. *Reboulia hemisphaerica* on rock ledges. Photo by Michael Lüth, with permission.



Figure 90. *Reboulia hemisphaerica* with archegoniophores on rock ledge. Photo by Michael Lüth, with permission.



Figure 91. *Reboulia hemisphaerica* with archegoniophores on rock ledge. Photo by Barry Stewart, with permission.

In Oklahoma, USA, *Reboulia hemisphaerica* (Figure 69-Figure 76) is the most frequent species of liverwort on dry rock outcrops (Little 1936) and also occurs on sandy soil (Sharp 1930). In Illinois, USA, it occurs on rocks, walls, and soil, including a sandstone wall (Spessard 1972; Simon 1977). Conard (1940) found it to be common on dry earth or rocks in Iowa, USA. At Mountain Lake, Virginia, USA, it similarly occurs on calcareous rocks and crevices (Sharp 1944).

In Myvatn, Iceland, *Reboulia hemisphaerica* (Figure 69-Figure 76) occurred as a pioneer on Krafla following the 1984 eruption (pers. obs. 1987). In just three years, it reached large populations (Figure 92-Figure 93).



Figure 92. *Reboulia hemisphaerica* in abundance during early succession on Krafla, Myvatn, Iceland, 3 years after 1984 eruption. Photo by Janice Glime.



Figure 93. *Reboulia hemisphaerica* succession on Krafla, Myvatn, Iceland, three years after the 1984 eruption. Photo by Janice Glime.

Physiology

Reboulia hemisphaerica (Figure 69-Figure 76) apparently has a wide moisture tolerance. Crundwell and Nyholm (1979) considered it to be one of the most drought-tolerant of the Turkish liverworts.

Reboulia hemisphaerica (Figure 69-Figure 76) exhibits growth and branching at moisture levels ranging 40-90%, with optimum growth at 70-80% (Vishvakarma & Kaul 1988a).

Xiang *et al.* (2010a) found that water stress affects the soluble sugar and proline, but has negligible effect on MDA. Calcium stress has even greater effects on sugar and proline. Low calcium results in a reduction in the accumulation of proline and soluble sugar, but as low calcium stress worsens their content gradually increases.

Hoffman and Gates (1970) demonstrated, using *Reboulia hemisphaerica* (Figure 69-Figure 76), that water loss proceeds rapidly in moist plants, with very low resistance. But as the water loss decreases, both convection and reradiation of energy become more important. At the same time, resistance increases in proportion to water loss. *Reboulia hemisphaerica* transpired for 2 hours under a radiation regime of 2.6 to 2.8 cal cm⁻² min⁻¹.

Reboulia hemisphaerica (Figure 69-Figure 76) has a mean water conductive rate of ~0.5 mm s⁻¹ (McConaha

1941). The areolation of its thallus greatly increases the surface through which water can be lost through the atmosphere by pores. A high phlobaphene content on the ventral surfaces helps to maintain a capillary film there among the tuberculate rhizoids and prevents water loss from the upturned thallus margins. McConaha demonstrated that a single water drop at one end of the thallus became distributed through the length of the thallus by its external capillary system. This water was immediately available to all absorptive surfaces. This external system provides a much more rapid transport than any known internal system. This seems to compensate successfully for the increased water loss due to areolation. In contrast to the description of McConaha, O'Hanlon (1928) describes the species with only a mere suggestion of air chambers and no air pores.

Takio *et al.* (1990) examined the chlorophyll content and photosynthetic rate in *Reboulia hemisphaerica* (Figure 69-Figure 76). They found that it possessed high levels of chlorophyll when cultured in light ($4\text{--}34\ \mu\text{g mg}^{-1}$ dry weight). These plants likewise had a high photosynthetic rate of $10\text{--}94\ \mu\text{mol O}_2\ \text{mg}^{-1}\ \text{chlorophyll h}^{-1}$. Dark-grown cells exhibited these same high levels of chlorophyll and photosynthesis, contrasting sharply with the low chlorophyll levels in dark-grown *Barbula unguiculata* (Figure 94).



Figure 94. *Barbula unguiculata*. Photo by Kristian Peters, through Creative Commons.

Rao *et al.* (1979) reported on the assimilation of labelled carbon into amino acids for *R. hemisphaerica*. The CO_2 assimilation rate was lower than that of seed plants. The chlorophyll content of these populations (from moist locations in the Ooty Hills, India) was low, as was the chlorophyll *a:b* ratio, parameters that are typical of shade-loving species. Rao *et al.* (1979) reported that the Hill reaction rates of *R. hemisphaerica* was lower than that typically reported for seed plants.

Both dark-grown and light-grown cells of *Reboulia hemisphaerica* (Figure 69-Figure 76) exhibited high chlorophyll content ($4\text{--}34\ \mu\text{g mg}^{-1}$ dry weight) after one year of culture on 2% glucose medium (Takio *et al.* 1990). Photosynthetic activity was likewise high in both ($10\text{--}84\ \mu\text{mol O}_2\ \text{mg}^{-1}\ \text{chlorophyll h}^{-1}$).

Lei *et al.* (2010) explored the responses of photosystem II in *Reboulia hemisphaerica* (Figure 69-Figure 76) to nitrogen deposition. Increased N concentrations (40 and $60\ \text{kg h m}^{-2}\ \text{a}^{-1}$) caused changes in chlorophyll fluorescence and reduced the energy-trapping capacity per unit area. It furthermore changed the redox states, destroyed electron flow especially beyond the Q-A, disabling that energy absorption and necessitating its consumption by fluorescence and heat. Liu *et al.* (2009) also explored N effects on this species and found both photosynthetic rate and starch concentration were lower at N concentrations of 20 and $40\ \text{kg h}^{-1}\ \text{m}^{-2}$ than at the control levels or at $60\ \text{kg h}^{-1}\ \text{m}^{-2}$. On the other hand, the total N in the tissue changed inversely. Both the inducible and constituted nitrate reductase activity were very low in all treatments, suggesting that it is unable to use nitrates. Potassium ion leakage increased significantly when the N addition increased to $60\ \text{kg N h}^{-1}\ \text{m}^{-2}$, suggesting membrane damage.

Vishvakarma and Kaul (1986) explored the temperature tolerance of *Reboulia hemisphaerica* (Figure 69-Figure 76). Morais and Becker (1991) cultured *Reboulia hemisphaerica* and found that it grew best on agar with 0.5% sucrose and an 18 h light: 6 h dark regime. Callus could be induced by phytohormones ($2\ \text{mg L}^{-1}$ α -naphthylacetic acid + $1\ \text{mg L}^{-1}$ kinetin) or by 4% glucose. Once cultures differentiated, there was a tenfold increase in sesquiterpene production. No sesquiterpenes were produced in dark cultures, but 5-hydroxy-7,8,4'-trimethoxyflavone was present. In light cultures, apigenin n -7,4'-dim ethylether was the only flavonoid produced.

Xiang *et al.* (2010b) evaluated the effects of heavy metals on *Riccardia hemisphaerica* (Figure 69-Figure 76) from cavern rock and soil on walls. They found that *R. hemisphaerica* actually exhibited depletion levels of Ca in the Three Gorges karst region, whereas some mosses exhibited either strong or relative enrichment in their tissues. It exhibited no enrichment of Mg, whereas the moss *Thuidium cymbifolium* (Figure 95) did. *Reboulia hemisphaerica* did, however, show a strong enrichment by Zn.



Figure 95. *Thuidium cymbifolium*, a species that can experience Mg enrichment. Photo by Chris Alice Kratzer, through Creative Commons.

Adaptations

One aspect that may account for the wide range of habitats for *Reboulia hemisphaerica* (Figure 69-Figure 76) is its ability to form pure mats or to grow with other bryophytes (Figure 96-Figure 97) (Konstantinova *et al.* 2018). The accompanying bryophytes can act like a sponge to retain moisture that could maintain suitable conditions for *R. hemisphaerica*, whereas pure mats can completely cover the substrate and reduce evapotranspiration.



Figure 96. *Reboulia hemisphaerica* growing over mosses. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.



Figure 97. *Reboulia hemisphaerica* with mosses and archegoniophores. Photo by Michael Lüth, with permission.

Reboulia hemisphaerica (Figure 69-Figure 76) has air chambers (Figure 98-Figure 100) that form an extensive system of air spaces separated by thin partitions (Dupler 1921; Haupt 1921a). These have air pores (Figure 99-Figure 101) on the upper surface, but no filaments, and thus serve primarily for gas exchange. Dupler (1921) describes them as very elongated air chambers that extend lengthwise along the midrib region. They radiate from there toward the thallus margins. They are in a single layer just below the surface and presumably facilitate CO₂ exchange in internal photosynthetic cells.

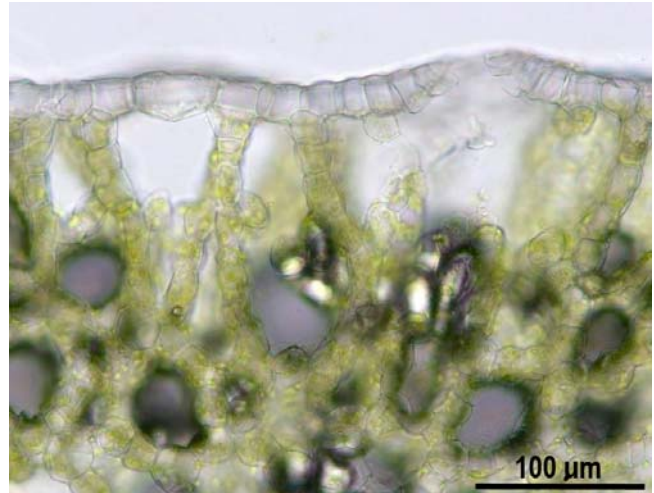


Figure 98. *Reboulia hemisphaerica* section showing air chambers. Photo by Jia-Dong Yang, through Creative Commons.



Figure 99. *Reboulia hemisphaerica* air chambers and pore. Photo by Hugues Tinguy, with permission.

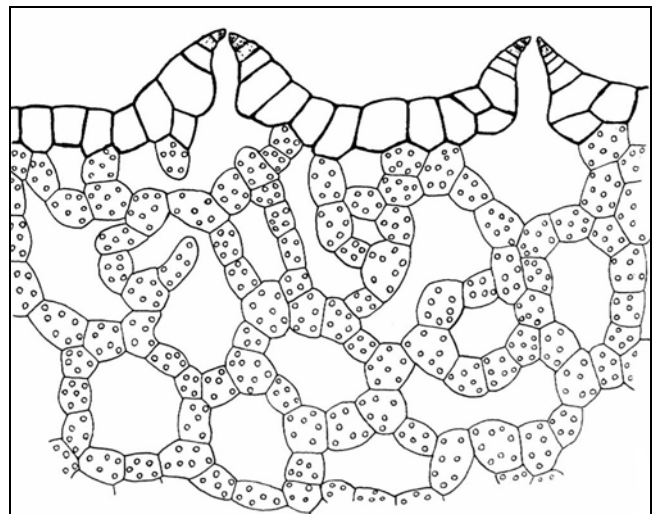


Figure 100. *Reboulia hemisphaerica* air chambers and pores. From Haupt 1921a.

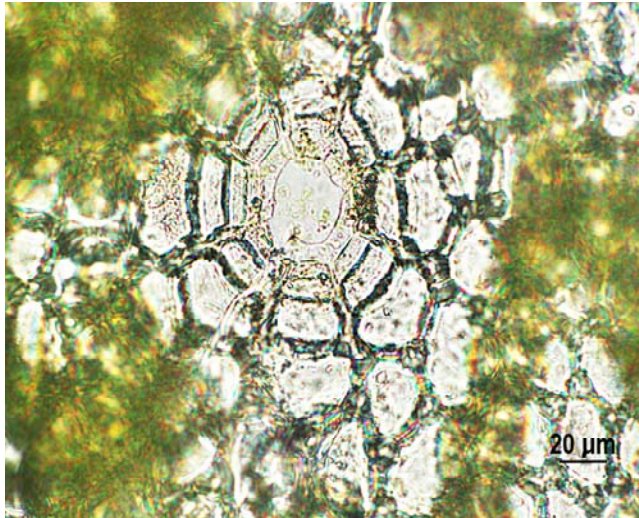


Figure 101. *Reboulia hemisphaerica* thallus pore. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Having pores (Figure 99-Figure 101) presents its own set of problems. They are advantageous for gas exchange, but not only do they allow water to leave the thallus, they also can allow water to enter. In species like *Reboulia hemisphaerica* (Figure 69-Figure 76), these pores have hydrophobic ledges that not only constrict the size of the pore, but that also repel water, preventing water from entering the plant during downpours or other water events Schönherr & Ziegler (1975). For water to enter, it must have a contact angle of 0° with the ledge. It would be interesting to see the difference in photosynthetic rate if these chambers were injected with water to fill the spaces.

Watson (1919) noted that when *Reboulia hemisphaerica* (Figure 69-Figure 76) grows on wet ground it has fewer rhizoids than when it grows in drier situations. This suggests that more rhizoids help to facilitate the movement and uptake of water, as noted above for other members of the family. Daniels (1998) cites the complex morphology along with tuberculate and smooth rhizoids, scale leaves (Figure 102), and well defined assimilatory and storage zones as xerophytic adaptations in *R. hemisphaerica*.

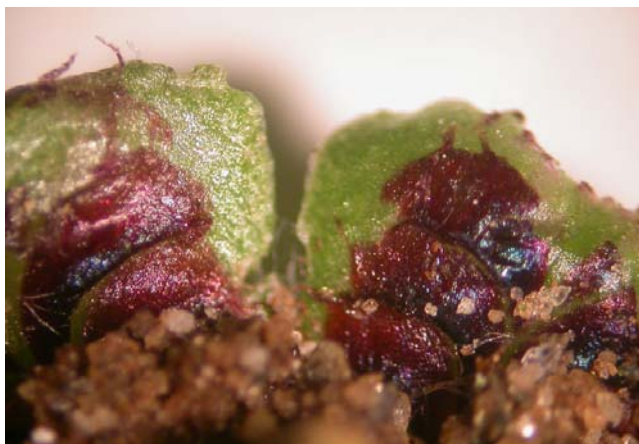


Figure 102. *Reboulia hemisphaerica* ventral side with scales (reddish). Photo by Blanka Aguero, through Creative Commons.

Reproduction

Haupt (1921a) described *Reboulia hemisphaerica* (Figure 69-Figure 76) as **monoicous** (Figure 103-Figure 107) in Midwestern USA. It is **protandrous** (antheridia develop before archegonia; Figure 105-Figure 106). Generally, 2-3 antheridial groupings develop in succession before the archegonia develop. The antheridia and archegonia occur in separate groups on the dorsal thallus surface.



Figure 103. *Reboulia hemisphaerica* male and female reproductive structures. Photo by Bob Klips, with permission.



Figure 104. *Reboulia hemisphaerica* with sexual structures. Photo by Ed Leathers, with permission.



Figure 105. *Reboulia hemisphaerica* with antheridia but no visible archegoniophores. Photo by Michael Lüth, with permission.



Figure 106. *Reboulia hemisphaerica* with male (brown) and female (green) sex organs. Photo by Ed Leathers, with permission.



Figure 109. *Reboulia hemisphaerica* young archegoniophores in Europe. Photo by Michael Lüth, with permission.



Figure 107. *Reboulia hemisphaerica* with young archegoniophores and mosses that probably help in moisture retention. Photo by Barry Stewart, with permission.

Dupler (1922a) considered the male receptacle and antheridium to be plastic, including both primitive and advanced characteristics. It is typically dorsal and posterior to the female receptacle (Figure 108-Figure 118) that terminates the branch. It is sessile or on a very short stalk, a feature that places it close to the archegonial head before elongation of the latter on its stalk.



Figure 108. *Reboulia hemisphaerica* young archegoniophores in Europe. Photo by Michael Lüth, with permission.



Figure 110. *Reboulia hemisphaerica* archegoniophores in Europe. Photo by Michael Lüth, with permission.



Figure 111. *Reboulia hemisphaerica* with young archegoniophores. Photo by Li Zhang, with permission.



Figure 112. *Reboulia hemisphaerica* archegonial heads. Photo by Heino Lepp, Australian National Botanic Gardens <www.anbg.gov.au>, with online permission.



Figure 115. *Reboulia hemisphaerica* with elongated archegoniophores. Photo by Michael Lüth, with permission.



Figure 113. *Reboulia hemisphaerica* archegonial heads. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.



Figure 116. *Reboulia hemisphaerica* with emerging archegoniophores. Photo by Štěpán Koval, with permission.



Figure 114. *Reboulia hemisphaerica* with emerged archegoniophores in Europe. Photo by Michael Lüth, with permission.



Figure 117. *Reboulia hemisphaerica* with emerging archegoniophores and still green thalli. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.



Figure 118. *Reboulia hemisphaerica* with archegoniophores and dying thalli. Photo by Štěpán Koval, with permission.

Udar and Chandra (1964) reported anomalous female receptacles in *Reboulia hemisphaerica* (Figure 69-Figure 76). One aberrant type produced branch stalks of the archegoniophores. A second aberrant type was just the opposite, producing no stalks or nearly sessile archegonial heads. Furthermore, Chandra (1963) reported compound female receptacles.

Miduno (1937) described the spermatozooids of *Reboulia hemisphaerica* (Figure 69-Figure 76). These typically had two cilia, although they also found five with three cilia. Other variations in size of the spermatozoid and relative length of the cilia were present.

Among the variations in the life cycle of *Reboulia hemisphaerica* (Figure 69-Figure 76) are differences in oicy. Since Haupt (1921a) published his descriptions of Midwestern, USA, populations, differences among populations have led to the description of subspecies. The subspecies of *R. hemisphaerica* differ in the distribution of their sexual organs (Hicks 1992). The typical variety is **paroicus**, whereas the three more recent subspecies are **dioicus** and two **autoicus** ones with differences in male receptacle size. Konstantinova (2011) reported that populations in the eastern Caucasus of Russia were **autoicus**. However in the entire country of Russia, one can find **paroicus**, **autoicus**, and **dioicus** populations (Bakalin 2008). Schuster (1992) considered all these to be one species, but Bakalin (2008) considers them to need further study. Itouga *et al.* (2005) noted that *R. hemisphaerica* had been subdivided into seven subspecies based on sexual condition, a strong indicator of genetic diversity. They recognized three subspecies in Japan, including the autoicus subsp. *orientalis*, subsp. *acrogyna*, and a new to Japan **paroicus** subsp. *hemisphaerica*. In addition to differences in oicy, spore maturation times differed. In subsp. *acrogyna* spores matured in summer, whereas in subsp. *hemisphaerica* and subsp. *orientalis*, they matured in spring.

The emergence of the archegoniophore of *Reboulia hemisphaerica* (Figure 69-Figure 76) does not occur until the sporophytes are nearly mature (Haupt 1921a). Archegonia appear in autumn and fertilization occurs then. The embryo develops immediately, but the sporophyte

(Figure 119-Figure 123) does not mature until the following spring, necessitating survival through the winter.



Figure 119. *Reboulia hemisphaerica* with immature capsules. Photo by Jiří Kameníček (BioLib, Obázek), with permission.



Figure 120. *Reboulia hemisphaerica* with archegoniophores and emergng sporangia. Photo by Jan-Peter Frahm, with permission.



Figure 121. *Reboulia hemisphaerica* with mature black sporangia. Photo by Michael Lüth, with permission.



Figure 122. *Reboulia hemisphaerica* archegoniophores with young capsules and mature capsules. Photo by Adolf Ceska, with permission.



Figure 123. *Reboulia hemisphaerica* archegonial head with scales and capsules that have shed their spores. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Allsopp (1964) found that whereas male gametangiophores developed on media with 1% glucose, female gametangiophores developed on sugar-free media. Could these differences in energy needs serve to induce their formation at different times?

Rao and Das (1968) found a sharp rise in the respiratory rate and a doubling of the C:N ratio as *Reboulia hemisphaerica* (Figure 69-Figure 76) transformed from the vegetative to female reproductive phase. At that time, the plants exhibited enhanced levels of endogenous IAA (indole-3-acetic acid), RNA, and protein. During antheridial formation the plants exhibited a reverse trend and exhibited no appreciable change in the C:N ratio (see also Hartmann & Weber 1990).

As noted by Haupt (1921a), *Reboulia hemisphaerica* (Figure 69-Figure 76) is fertilized in autumn in southern Wisconsin and northern Illinois, USA (O'Hanlon 1928); Dupler (1922b) likewise reported fertilization in October. In early spring (8 March) the plants are still dormant (O'Hanlon 1928). Woodburn (1919) determined that both egg and sperm nuclei are in a resting condition in the early stages of fusion. When transplanted indoors on 29 October, *R. hemisphaerica* regenerated new branches but failed to exhibit elongation of the archegoniophore (O'Hanlon 1928). The plants exhibited an inverse relationship between amount of regeneration and development within the receptacle. Most thalli produce fewer than three mature sporophytes per head, but can produce up to nine.

As one might expect, *Reboulia hemisphaerica* (Figure 69-Figure 76) has a lower gene flow with increasing distance ($Nm = -0.0009 \times \text{km}^{1.1}$) (Itouga *et al.* 2002). The mean value for populations in East Asian populations was only 0.609. Thus, the genetic variation was high, as would be predicted for species that reproduce only by spores. Slatkin (1985) considers that Nm values <1 usually imply that genetic drift has been a major contributor to the distribution of genetic variation. Itouga and coworkers found that the break point for Nm values <1 was 125 km. Dispersal of spores beyond 100 km was negligible. Itouga and coworkers agree that the degree of genetic differentiation within monoicous marchantialean species is correlated with dispersal distances of sperm and rates of self-fertilization. Nevertheless, the dioicous *Asterella wallichiana* (Figure 124) and monoicous *R. hemisphaerica* showed similar levels of gene flow in this study.



Figure 124. *Asterella wallichiana*, a dioicous liverwort with gene flow levels similar to those of the monoicous *Reboulia hemisphaerica*. Photo by Forestowlet, through Creative Commons.

Woodburn (1919) described the union of egg and sperm and the early developmental stages of the ensuing sporophyte. Dupler (1922b) also described the early embryogeny of *Reboulia hemisphaerica* (Figure 69-Figure 76). The embryo begins immediate development following fertilization. There is considerable variation in the development of the early embryo, with accompanying variations in habitat, archegoniophore, and other morphological variations. By winter, the sporogenous tissue is becoming differentiated. However, the sporophyte does not mature until the following May or June. Brown found *Reboulia hemisphaerica* fruiting "profusely" in a variety of places in Georgia (in the Caucasus region).

Haupt (1921b) found that the archegoniophore begins to elongate in early spring (Figure 125), about the last week of March, in Indiana, USA. The sporogenous tissue resumes development, but there is no indication at that time as to which will become spores and which elaters. By the first part of May, these cells break apart from each other, form an abundance of mucilage, and spore mother cells and elaters are clearly distinguishable.



Figure 125. *Reboulia hemisphaerica* with developing archegoniophores and dying older thalli. Photo by Štěpán Koval, with permission.

Blair (1926) describes meiosis in *Reboulia hemisphaerica* (Figure 69-Figure 76). She notes only 16 chromosomes arriving at each pole. However, several authors (Sha *et al.* 2003; Itouga *et al.* 2005) have since determined the chromosome number for *R. hemisphaerica* to be $n=9$, a typical number in liverworts.

Patidar *et al.* (1987) reported 2410 spores (Figure 126-Figure 127) per capsule in *Reboulia hemisphaerica* (Figure 69-Figure 76). Schuster (1966) earlier reported 2500 per capsule (see also O'Hanlon 1930). These large (70-80 μm) spores germinate in about five days when in suitable conditions of fairly good light and plenty of moisture (O'Hanlon 1930). They remain completely viable for at least five months.

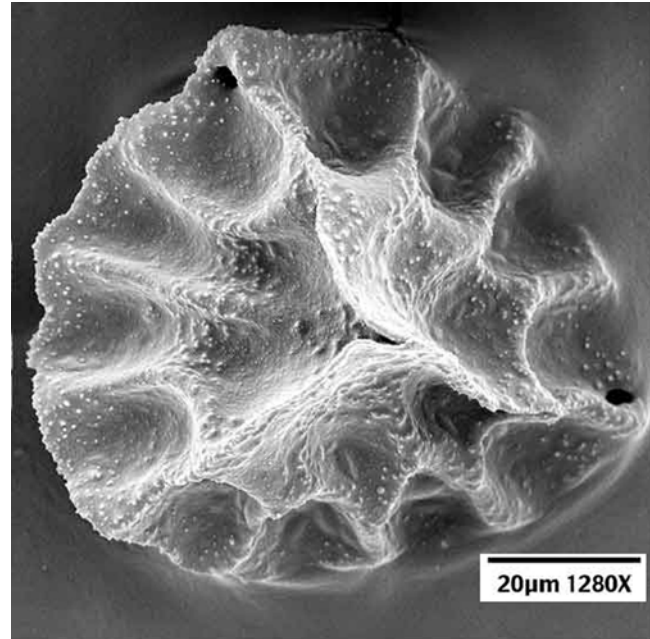


Figure 126. *Reboulia hemisphaerica* spore SEM. Photo by William T. Doyle, with permission.

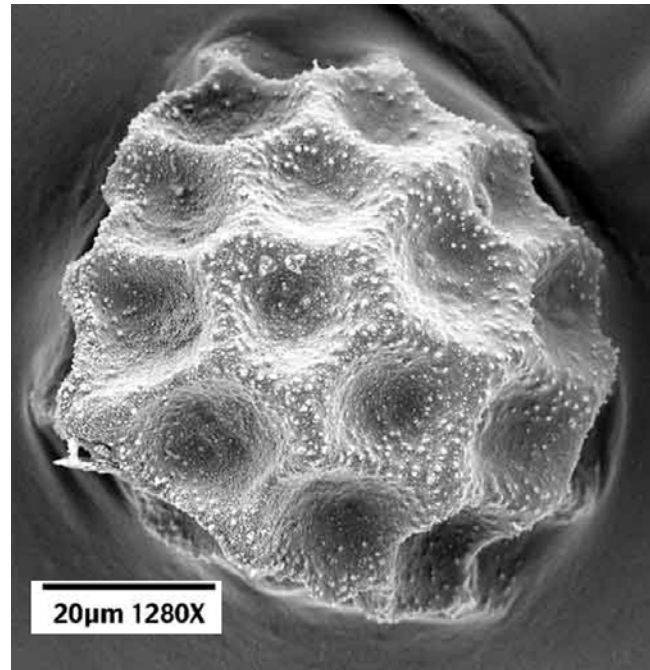


Figure 127. *Reboulia hemisphaerica* distal spore wall SEM. Photo by William T. Doyle, with permission.

Reboulia hemisphaerica (Figure 69-Figure 76) produces a tangle of white, sticky filaments (Figure 128) below the capsule (Frank 2015). These appear to aid in spore dispersal in a rather unusual way. They make a bryophyte version of masking tape. The springtail *Bourletiella hortensis* (Figure 129) peruses the capsule area and comes away with bits of the sticky filaments on its body. And to these, spores are attached. Frank suggests that not only do springtails aid dispersal through these adhered filaments, but that other animals could easily contribute as well.



Figure 128. *Reboulia hemisphaerica* archegoniophores with mature sporangia in Europe. Note the white filaments hanging below the capsules. Photo by Michael Lüth, with permission.



Figure 129. *Bourletiella hortensis*, a springtail that facilitates spore dispersal in *Reboulia hemisphaerica* by getting sticky filaments with adhering spores stuck to its body. Photo by Andy Murray, through Creative Commons.

Vishvakarma and Kaul (1987) studied the effects of such conditions as duration, quality, and intensity of light on spore germination in *Reboulia hemisphaerica* (Figure 69-Figure 76). Inoue (1960) reported that blue and red light were the most effective in promoting rhizoid development, and far-red and green caused less activity. However, germ tube development was just the opposite of rhizoid development, being relatively short in blue and red light but elongating remarkably in far-red and green.

Vishvakarma and Kaul (1988b) found that the optimum pH for both germination and thallus growth was 6, but vegetative growth occurred in the range of 3.0-7.0. Germination was more restricted at pH 5-7. Differences between germination requirements and growth tolerances could explain the absences of species in some areas where we expect them.

O'Hanlon (1930) noted that the first stage in spore germination of *Reboulia hemisphaerica* (Figure 69-Figure 76) is the emergence of a germ tube and a single rhizoid. The author provides details of subsequent cell divisions

leading up to bud formation. Rhizoids form on the ventral side of the protonema, establishing its dorsiventrality. Low intensity causes the germ tubes to be extremely long or to give rise to secondary and even tertiary germ tubes. Hartmann and Weber (1990) reviewed the literature on control of germination in this and other species of liverworts.

Vishvakarma *et al.* (1987) showed that percentage spore germination of *Reboulia hemisphaerica* (Figure 69-Figure 76) was enhanced by the addition of Mg in the liquid culture medium.

Not all bryophytes are known to produce callus tissue. Allsopp (1957) reported the first success in obtaining unlimited callus-like growth in liverworts, one of which was *Reboulia hemisphaerica* (Figure 69-Figure 76). This technique is often useful for mass producing desired chemical from bryophyte tissues.

Koevenig (1973) investigated reproductive physiology of *Reboulia hemisphaerica* (Figure 69-Figure 76). Archegoniophores elongate in late spring in Kansas. Under long days (12 hr light, 12 hr dark, or 16 hr light, 8 hr dark), pre-elongation archegoniophores elongated completely within two weeks at both 15 and 25°C. But in short days (8 hr light, 16 hr dark) no elongation occurred. Cold temperature (5°C) slowed elongation. Adding plant growth hormones (IAA, NAA, BA, GA) to heads failed to stimulate to normal lengths in short days. Koevenig suggested that perhaps the hormones could facilitate elongation but could not initiate it. (See also Sztein *et al.* 1997).

Brown and Lemmon (1990) elucidated the mitotic apparatus of *Reboulia hemisphaerica* (Figure 69-Figure 76). They concluded that the mitotic apparatus in this species demonstrates a transition between algae and land plants.

Nehira and Nakagoshi (1987) reported that after removal of bryophytes in an urban environment, the same community became re-established in 1-2 years. Pleurocarpous mosses and thalloid liverworts such as *Reboulia hemisphaerica* (Figure 69-Figure 76) regenerated faster than did acrocarpous mosses. This regrowth occurred primarily in spring and autumn, but there was little seasonal variation in the amount of available airborne diaspores.

Role

Bryophytes such as *Reboulia hemisphaerica* (Figure 69-Figure 76) often serve as substrates for algae, especially diatoms (Ando 1978). These algae and other micro-organisms provide food for visiting invertebrates. But the bryophytes themselves can serve as food (Konstantinov *et al.* 2019). The flea beetle *Distigmoptera borealis* (Figure 130) was recently discovered eating *R. hemisphaerica*. Imada and Kato (2016) reported on larvae of the fly *Litoleptis* on bryophytes and described six new species, all thallus-miners of liverworts. *Litoleptis kiiensis* (Figure 131), *L. niyodoensis*, *L. himukaensis*, and *L. izuensis* are all thallus miners on *Reboulia hemisphaerica* and only that species.



Figure 130. *Distigmoptera borealis*, a beetle that consumes *Reboulia hemisphaerica* thalli. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.



Figure 131. *Litoleptis kiiensis* larva, an inhabitant of *Reboulia hemisphaerica*. Photo courtesy of Yume Imada.

Biochemistry

Reboulia hemisphaerica (Figure 69-Figure 76) was an early subject of biochemical studies. Furusawa *et al.* (2006) isolated and described structures of new cyclomylytayne and ent-chamigrane-type sesquiterpenoids from *Reboulia hemisphaerica* subsp. *australis*. Morais *et al.* (1988, 1991) described a gymnomitrane-type sesquiterpenoid and two derivatives from cultures of this species. Keserü and Nogradi (1995) reported riccardins. Warmers and König (1999, 2000) reported gymnomitrone from plants in nature and described its synthesis. Wei *et al.* (1995) described five new sesquiterpenoids and three new marchantin-type compounds and elucidated their structures. Sakai *et al.* (1999) were able to describe the synthesis (+)-cyclomylytayne-5 α -ol from *Reboulia hemisphaerica* from Taiwan.

Toyota *et al.* (1999) found and described the structure of four new sesquiterpenes from *Reboulia hemisphaerica* (Figure 69-Figure 76), as well as isolating nine compounds that were already known. Warmers and König (2000) identified the biosynthesis of the gymnomitrane-type sesquiterpene in this species.

Reboulia hemisphaerica (Figure 69-Figure 76) has chemotypes (Ludwiczuk *et al.* (2008). The researchers found two "totally different chemical compositions" in two different locations in Tokushima, Japan, whereas those from the same location had very similar chemical composition, indicating genetic isolation of the two populations. They noted that *R. hemisphaerica* has sesquiterpenoids and acetogenins.

Asakawa and Matsuda (1982) isolated riccardin C from *Reboulia hemisphaerica* (Figure 69-Figure 76) – a secondary compound that appears to be widespread among thallose liverworts. Wang *et al.* (2011a) found four new phenolic glycosides in this species in China and described their structures as rebousides. Wang *et al.* (2011b) described the configuration of isoriccardin C and riccardin D isolated from this species.

Kwon *et al.* (2019) were able to describe the entire chloroplast genome of *Reboulia hemisphaerica* with its 122,596 base pairs with 87 protein-coding genes, eight rRNAs, and 36 tRNAs. These indicated a close relationship to *Dumortiera hirsuta* (Figure 132).



Figure 132. *Dumortiera hirsuta*, a close relative of *Reboulia hemisphaerica*, based on chlorophyll DNA. Photo by Lin Kyan, with permission.

There have been at least some traditional medical uses of bryophytes (Du 1997). Sabovljević *et al.* (2016) noted that *Riccardia hemisphaerica* (Figure 69-Figure 76) is sold in Chinese markets. It has been cited numerous times related to potential medicinal uses of its compounds. Belcik and Wiegner (1980) reported good antibacterial activity in culture, reinforcing the findings of Banerjee and Sen (1979), who considered it to be one of the most active bryophytes against bacteria.

Becker (1990) pointed out the need for *in vitro* plant cultures when the desired plant product has a high price or conventional production of the plant causes problems. Liverwort culture meets the second criterion, but the science is new and although many medicinally active compounds are known, development of their commercial use is negligible. Kandpal *et al.* (2016) further noted the need for new antibiotic compounds because of the increasing evolution of antibiotic-resistant bacterial strains.

While one extract may inhibit bacteria or have other medicinal properties, a different extract solvent of the same compound(s) may exhibit no activity (Zehr 1990). Although this is a serious consideration in making ecological interpretations, it is usually not a serious problem for medicinal applications. Furthermore, effectiveness differs among bacteria species. Zehr showed that *Bacillus subtilis* (Figure 133-Figure 134) and *Escherichia coli* (Figure 135) were the most susceptible bacteria tested while *Enterococcus faecalis* (Figure 136) experienced the least inhibition.

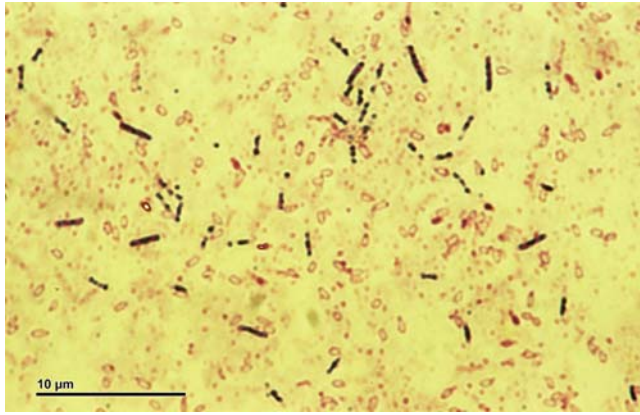


Figure 133. *Bacillus subtilis*, a bacterial species that is inhibited by extracts of *Reboulia hemisphaerica*. Photo by Josef Reischig, through Creative Commons.

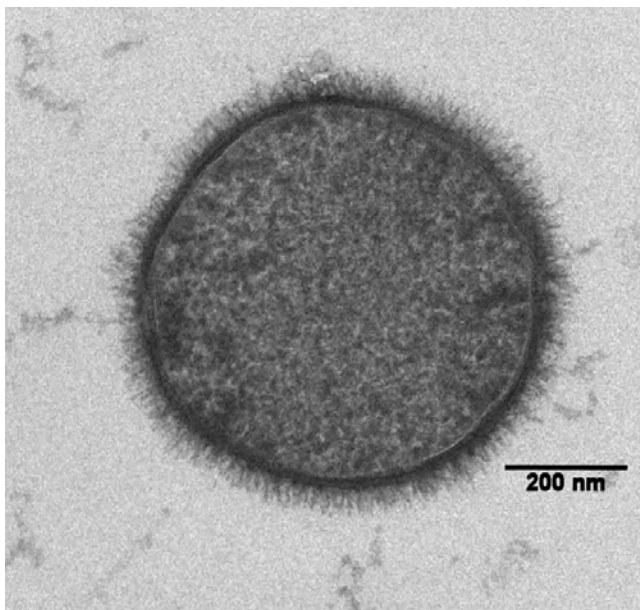


Figure 134. *Bacillus subtilis*, a bacterial species that is inhibited by extracts of *Reboulia hemisphaerica*. Photo by Allonweiner, through public domain.

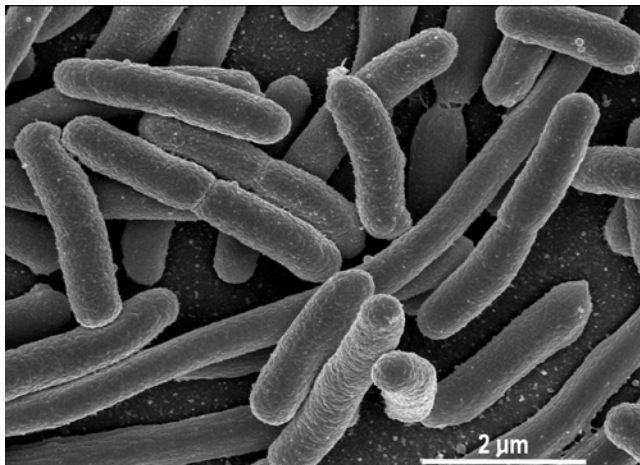


Figure 135. *Escherichia coli*, a bacterial species that is inhibited by extracts of *Reboulia hemisphaerica*. Photo from Rocky Mountain Laboratories, through public domain.

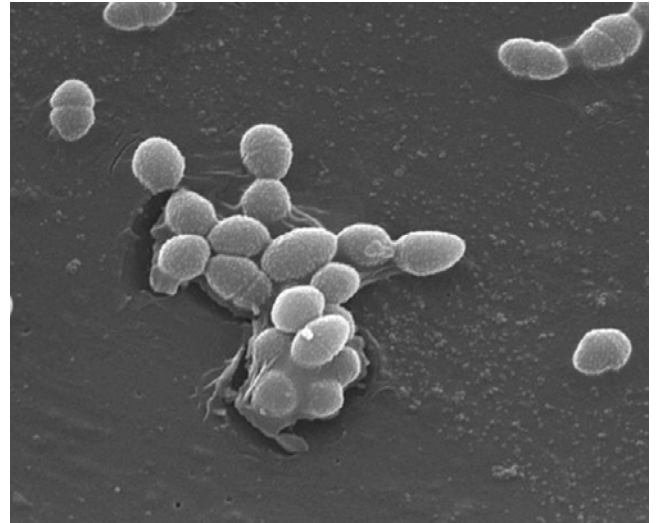


Figure 136. *Enterococcus faecalis* SEM, a species of bacteria that is more resistant than others in study to extracts of *Reboulia hemisphaerica*. Photo from CDC, through public domain.

Following these early studies, a number of additional studies confirmed antibacterial and medicinal activity in *Reboulia hemisphaerica* (Figure 69-Figure 76) (Joshi 1995; Ko *et al.* 1995; Du 1997).

Ko *et al.* (1995) isolated marchantinquinone, from *Reboulia hemisphaerica* (Figure 69-Figure 76), a compound known to inhibit lipid peroxidation and to serve as a free radical scavenger. Liao *et al.* (2000) reported that marchantinquinone from *R. hemisphaerica* inhibited platelet aggregation and ATP release stimulated by thrombin. Harrowven *et al.* (2005) found that Riccardin C, manufactured by *Reboulia hemisphaerica* exhibited cytotoxicity against nasal epidermoid carcinoma cells in culture as well as inhibiting HIV-1 reverse transcriptase.

Asakawa (1998; 2007) cited a number of potential medical uses for *Reboulia hemisphaerica* (Figure 69-Figure 76), including treatment of blotches, external wounds, and bruises, and hemostasis. Tosun *et al.* (2016) and Chandra *et al.* (2017) expanded on this list, including uses to cure cuts, burns, wounds, bacteriosis, pulmonary tuberculosis, neurasthenia, fractures, convulsions, scalds, uropathy, inflammation, fever, and pneumonia. Tosun *et al.* (2016) further elaborated on the specific means of wound healing. Önder and Özenoğlu (2019) found that extracts of *R. hemisphaerica* were effective against three different cancer cell lines.

A variety of potential uses emerged in laboratory cultures of *Reboulia hemisphaerica* (Figure 69-Figure 76) (Gao *et al.* 2009; Asakawa 2013; Tosun *et al.* 2013). Harada *et al.* (2013) reported its potential for the treatment of cardio-vascular diseases, including arteriosclerosis. Even pet treatments are possible, with *R. hemisphaerica* inhibiting carrageenan-induced paw edema (Tosun *et al.* 2013).

Kandpal *et al.* (2016) found the extract of *R. hemisphaerica* (Figure 69-Figure 76) to be the most effective bryophyte species tested against *Escherichia coli* (Figure 135), *Bacillus cereus* (Figure 137), and *Pseudomonas aeruginosa* (Figure 138). The researchers found a correlation between total phenol and flavonoid contents and the antioxidant activity.

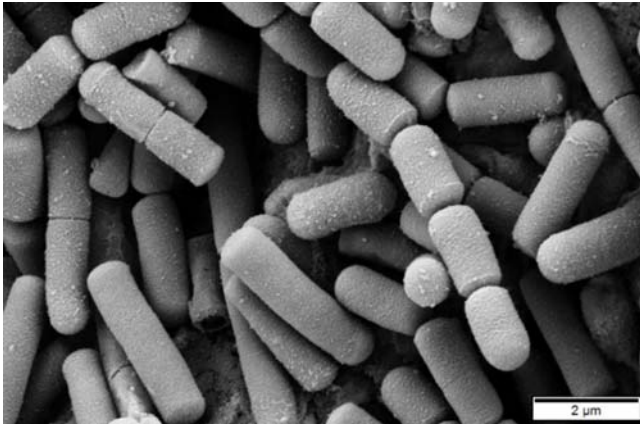


Figure 137. *Bacillus cereus* SEM, a bacterial species that is inhibited by extracts of *Reboulia hemisphaerica*. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.



Figure 138. *Pseudomonas aeruginosa*, a bacterial species that is inhibited by extracts of *Reboulia hemisphaerica*. Photo from CDC, through public domain.

Summary

The Aytoniaceae does not have members that are typically submersed, but several species are at least tolerant of being constantly wet from water spray or other source of water. Their habitats include waterfall spray, streamside, dripping cliffs and ledges, wet soil and wind holes, but also various substrata in mesic forests. The latter habitat provides cool, moist air that permits Arctic species to survive in temperate regions. On the other hand, many of these species occur in the mountains, especially in Macaronesia.

The members of Aytoniaceae included here tend to endure a wide range of habitats, including a wide range of moisture conditions. They have air spaces that permit CO₂ exchange and rhizoids and scales that facilitate water uptake. Sexual condition varies, even within a species, but no gemmae or other specialized asexual reproductive structures are present. Most of the species die from the posterior end after fertilization, but grow from the apex.

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CHAPTER 1-20

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CONOCEPHALACEAE, PART 1

TABLE OF CONTENTS

Conocephalaceae.....	1-20-2
<i>Conocephalum conicum</i>	1-20-2
Distribution.....	1-20-5
Aquatic and Wet Habitats.....	1-20-5
Stream and River Banks.....	1-20-7
Springs.....	1-20-10
Waterfalls.....	1-20-10
Non-Aquatic Habitats.....	1-20-10
Physiology.....	1-20-10
Adaptations.....	1-20-13
Reproduction.....	1-20-16
Fungal Interactions.....	1-20-18
Animal Interactions.....	1-20-19
Biochemistry.....	1-20-30
<i>Conocephalum orientale</i>	1-20-22
Distribution.....	1-20-25
Aquatic and Wet Habitats.....	1-20-25
Physiology.....	1-20-26
Adaptations.....	1-20-27
Reproduction.....	1-20-28
Biochemistry.....	1-20-30
Summary.....	1-20-30
Acknowledgments.....	1-20-31
Literature Cited.....	1-20-31

CHAPTER 1-20

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CONOCEPHALACEAE, PART 1



Figure 1. *Conocephalum conicum* s.l. habitat on emergent rock. Photo from <www.aphotofauna.com>, with permission.

Conocephalaceae

Conocephalum conicum (Figure 1-Figure 11)

Recently, genetic determinations and usable morphological characters have led to the division of *Conocephalum conicum* (Figure 1-Figure 2-Figure 11) into several species (Szweykowski *et al.* 2005; Akiyama 2022). Therefore, one must read the research attributed to this species with caution because it might actually refer to

Conocephalum salebrosum (Figure 12-Figure 13) in North America, or several species in Japan. When I can't be sure which species it is, I shall denote the species as *Conocephalum conicum* s.l. (the abbreviation s.l. refers to *sensu lato* and means in the broad sense; s.s. refers to *sensu stricto* and means in the narrow sense) (Figure 1-Figure 2-Figure 11).

Conocephalum conicum s.s. (Figure 1-Figure 11) is a smaller plant than *C. salebrosum* (Figure 12); *C. salebrosum* plants are dull, with more conspicuous thallus grooves that are more conspicuous than the air pores (Figure 13) (Stotler & Crandall-Stotler 2017).



Figure 2. *Conocephalum conicum* showing conspicuous pores. Photo by Li Zhang, with permission.



Figure 3. *Conocephalum conicum* from Scotland, showing conspicuous pores. Photo courtesy of David Long.



Figure 4. *Conocephalum conicum* showing distinct pores and weaker thallus sections. Photo by Hermann Schachner, through Creative Commons.



Figure 5. *Conocephalum conicum* with conspicuous pores. Photo by Ralf Wagner, with permission.



Figure 6. *Conocephalum conicum* from Wales, showing distinct pores. Photo courtesy of Jonathan Sleath.

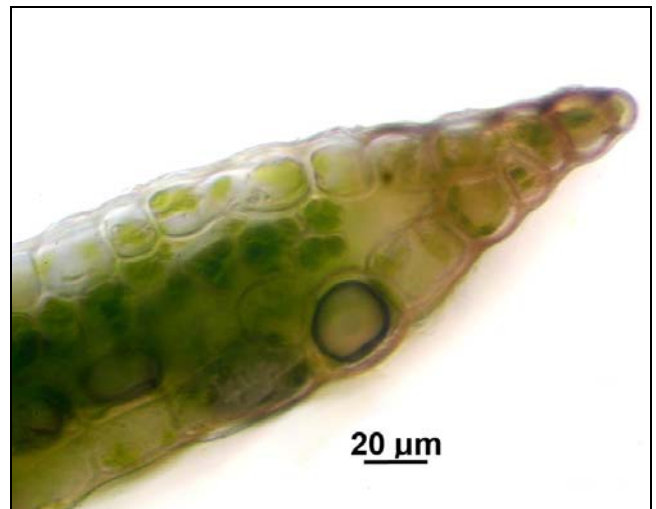


Figure 7. *Conocephalum conicum* thallus margin section, from Céret, France. Photo courtesy of Louis Thouvenot.



Figure 8. *Conocephalum conicum* s.l. showing conspicuous pores. Photo by Li Zhang, with permission.

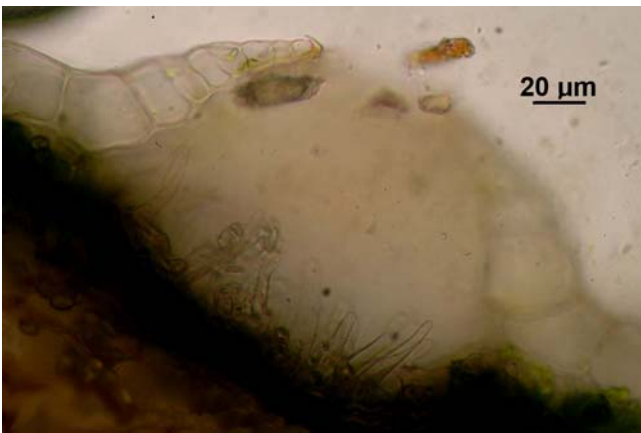


Figure 9. *Conocephalum conicum* from Céret, France, showing pore section. Photo courtesy of Louis Thouvenot.

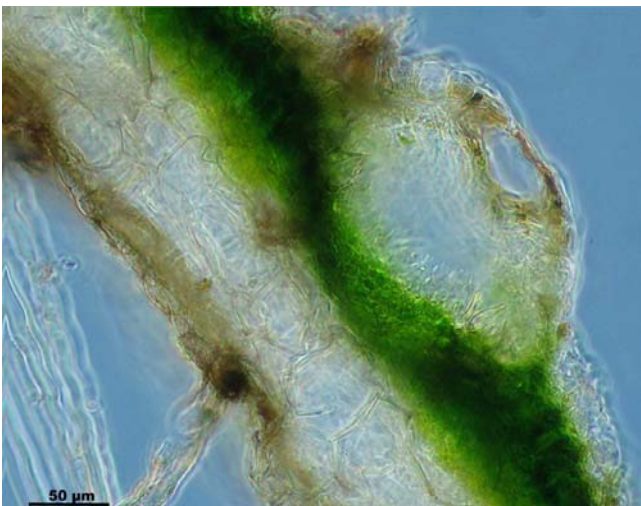


Figure 10. *Conocephalum conicum* showing pore section. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.



Figure 11. *Conocephalum conicum* s.l. pore wall. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.



Figure 12. *Conocephalum salebrosum* on left with conspicuous thallus grooves and dull thallus and *C. conicum* on right and center with conspicuous pores and shiny thallus. Photo courtesy of Jonathan Sleath.



Figure 13. *Conocephalum salebrosum* showing dull thallus, conspicuous grooves, and pores less conspicuous than thallus grooves. Photo by Jouko Rikkinen, through Creative Commons.

Distribution

Sérgio *et al.* (2011) surmised that *Conocephalum salebrosum* (Figure 12-Figure 13) has a more scattered and wider distribution than does *C. conicum* (Figure 1-Figure 11). Stotler and Crandall-Stotler (2017) concluded that *Conocephalum conicum* does not occur in North America and that all of the specimens previously identified as *C. conicum* are instead aligned with *C. salebrosum*. In Russia Borovichev *et al.* (2009) found *C. conicum* to be more widespread than *C. salebrosum*. The overall distribution of *C. conicum* appears to be restricted to Europe. The photos below illustrate its presence in a number of European countries (Figure 14-Figure 18).



Figure 14. *Conocephalum conicum*, Wales. Photo courtesy of David Long.



Figure 15. *Conocephalum conicum*, Scotland. Photo courtesy of David Long.



Figure 16. *Conocephalum conicum*, Céret, France. Photo courtesy of Louis Thouvenot.



Figure 17. *Conocephalum conicum*, Sardoia, Italy. Photo courtesy of Michael Lüth.



Figure 18. *Conocephalum conicum*, Czech Republic. Photo by Vita Plasek, with permission.

Aquatic and Wet Habitats

Borovichev *et al.* (2009) found that *Conocephalum conicum* (Figure 1-Figure 11) and *C. salebrosum* (Figure 12-Figure 13) have similar ecological preferences and that they can even grow intermingled (Figure 19). Both form extensive mats on streambanks and at the bases of moist rocks and cliffs. *Conocephalum conicum* tends to be more hygrophytic than *C. salebrosum*. Both species seem to specialize in colonizing spring and river micro-habitats close to running or standing water. The photographs below illustrate some of the habitats where *Conocephalum conicum* has been found in Europe (Figure 20-Figure 22).



Figure 19. *Conocephalum conicum* (left) and *C. salebrosum* (right). Photo courtesy of Michael Lüth.



Figure 21. *Conocephalum conicum* in wet limestone cave, Traeth Glaslyn Nature Reserve, Wales. Photo by Janice Glime.

Conocephalum conicum s.l. (Figure 1-Figure 11) occurs in wet places around lakes, especially in shade in Scotland (West 1910); in ground, rock, spring, and water communities associated with streams near Lacko, Western Carpathians (Mamczarz 1970); in association with the River Wear, England (Birch *et al.* 1988); associated with rivers (Ferreira *et al.* 2008). Its habitat seems to be primarily from rivers, streams, and stream banks (Figure 26). Nevertheless, it occurs often on rocky walls above streams (Figure 20) and in caves (Figure 21-Figure 22).



Figure 20. *Conocephalum conicum* growth habit on wall s.l. Photo by Allen Norcross, with permission.



Figure 22. *Conocephalum conicum* in wet, limestone cave, Traeth Glaslyn Nature Reserve, Wales. Photo by Janice Glime.

There are many reports of *Conocephalum conicum* (Figure 1-Figure 11) from streams and rivers. It is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006). It is among the most common bryophytes in the River Tweed, UK (Holmes & Whitton 1975) and occurs throughout the River Swale, Yorkshire, UK (Holmes & Whitton 1977b). In the River Tyne, UK, it occurs mostly in mid to lower reaches (Holmes & Whitton 1981). It is part of the *Platyhypnidium-Fontinalis antipyretica* (Figure 23-Figure 24) association in Thuringia, Germany (Marstaller 1987). It occurs both in the Iskur River, Bulgaria, and its main tributaries (Papp *et al.* 2006). In Greece it is common in streams (Papp 1998). It occurs on moist stones and rocks in the streambed (Figure 1, Figure 25) in streams of Gory Stolowe Mountains, Poland (Szweykowski 1951). It is also found in mountain streams of northwestern Portugal (Vieira *et al.* 2005) and in mountainous streams on Madeira Island (Luis *et al.* 2015).



Figure 23. *Platyhypnidium riparioides* of the *Platyhypnidium-Fontinalis antipyretica* association that may also include *Conocephalum conicum*. Photo by Hermann Schachner, through Creative Commons.



Figure 24. *Fontinalis antipyretica* of the *Platyhypnidium-Fontinalis antipyretica* association that may also include *Conocephalum conicum*. Photo from Botany Website, UBC, with permission.



Figure 25. *Conocephalum conicum* s.l. on emergent rock in stream. Photo from <www.aphotofauna.com>, with permission.

Stream and River Banks

Conocephalum conicum (Figure 1-Figure 11) is able to live on banks with frequent submergence (Figure 26) and slow water, usually on rocks just above water (Figure 27-Figure 31) (Watson 1919). It occurs in a zone above *Cratoneuron filicinum* (Figure 32-Figure 33), up to 0.9 m above the water (Gimingham & Birse 1957). Holmes and Whitton (1977a) found it on the river bank of the River Tees, UK.



Figure 26. *Conocephalum conicum* habitat along a stream in France. Photo courtesy of courtesy of Leica Chavoutier.

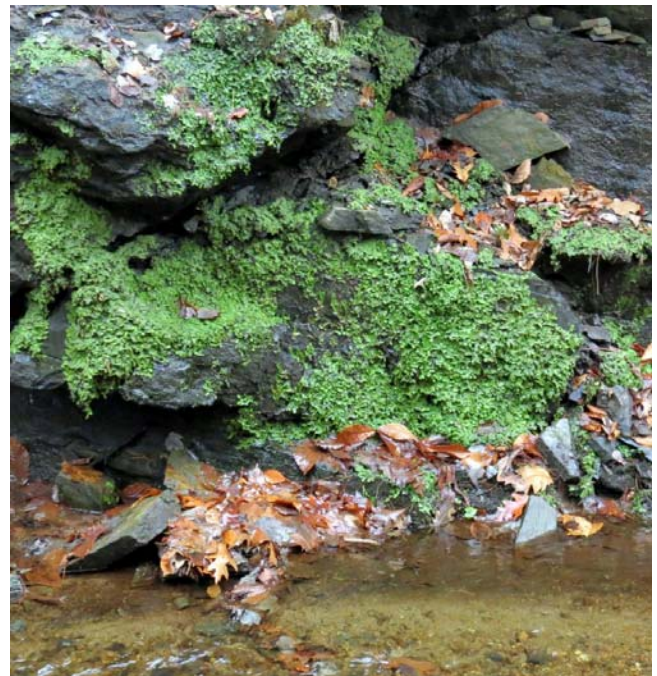


Figure 27. *Conocephalum conicum* s.l. on rock wall at stream edge. Photo by Allen Norcross, with permission.



Figure 28. *Conocephalum conicum* s.l. on rock wall of stream. Photo by Allen Norcross, with permission.



Figure 29. *Conocephalum conicum* s.l. on rock at stream edge. Photo by Allen Norcross, with permission.



Figure 30. *Conocephalum conicum* on wet rock, Sardinia, Italy. Photo courtesy of Michael Lüth.



Figure 31. *Conocephalum conicum* s.l. on rock wall. Photo by Allen Norcross, with permission.



Figure 32. *Cratoneuron filicinum*; *Conocephalum conicum* s.l. lives in a zone above this species in Europe. Photo by Claire Halpin, with permission.



Figure 33. *Cratoneuron filicinum*, a species that lives in a zone closer to the water than that of *Conocephalum conicum* s.l. Photo by Tigrente, through Creative Commons.

Luis *et al.* (2008) reported *Conocephalum conicum* s.s. (Figure 1-Figure 11) along the lower reaches of Ribeira Brava in Madeira in disturbed areas dominated by the great

reed *Arundo donax* (Figure 34). It was associated there with the mosses *Bryum dichotomum* (Figure 35), *Pohlia melanodon* (Figure 36), *Ptychostomum capillare* (Figure 37), and *Scorpiurium circinatum* (Figure 38-Figure 39) and the liverwort *Lunularia cruciata* (Figure 40).



Figure 34. *Arundo donax*, a grass that sometimes is accompanied by *Conocephalum conicum* s.l. along the lower reaches of the Ribeira Brava in Madeira. Photo by Forest and Kim Starr, through public domain.



Figure 37. *Ptychostomum capillare*, an associate of *Conocephalum conicum* along the Ribeira Brava in Madeira. Photo by Michael Becker, through Creative Commons.



Figure 35. *Bryum dichotomum*, an associate of *Conocephalum conicum* along the Ribeira Brava in Madeira. Photo by David T. Holyoak, with permission.



Figure 38. *Scorpiurium circinatum* moist, an associate of *Conocephalum conicum* along the Ribeira Brava in Madeira. Photo by Hugues Tinguy, with permission.



Figure 36. *Pohlia melanodon*, an associate of *Conocephalum conicum* along the Ribeira Brava in Madeira. Photo by David T. Holyoak, with permission.



Figure 39. *Scorpiurium circinatum* dry. Photo by David T. Holyoak, with permission.



Figure 40. *Lunularia cruciata*, an associate of *Conocephalum conicum* along the Ribeira Brava in Madeira. Photo by Michael Langeveld, through Creative Commons.

Springs

There seem to be few reports of *Conocephalum conicum* (Figure 1-Figure 11) in or around springs. It is known at a spring in the Tara river canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).

Waterfalls

Watson (1919) reported *Conocephalum conicum* (Figure 1-Figure 11) from waterfalls, but others don't seem to attribute it to this habitat. This is often a lack of detail in reporting, with the splash zone of a waterfall included with "streambank."

Non-Aquatic Habitats

Although *Conocephalum conicum* (Figure 1-Figure 11) is usually associated closely with water, it can be found on slopes (Figure 41), perhaps getting water from seepage, or occurring on canyon walls where it is shaded and humid (Figure 42).



Figure 41. *Conocephalum conicum* s.l. habitat. Photo by Michael Lüth, with permission.



Figure 42. *Conocephalum conicum* s.l. on rock of stream canyon. Photo by Michael Lüth, with permission.

Physiology

Conocephalum conicum (Figure 1-Figure 11) is more easily stressed by **desiccation** than its sibling species *C. salebrosum* (Figure 12-Figure 13) (Szweykowski *et al.* 2005; Borovichev *et al.* 2009). This explains its more aquatic habitats.

Like *C. salebrosum*, *C. conicum* (Figure 1-Figure 11) has scales (Figure 43-Figure 44) and rhizoids (Figure 45-Figure 46) that provide **capillary spaces** on the ventral surface. We can assume that like the case of *C. salebrosum*, water moves through these spaces along the thallus and is delivered to all points on the thallus where it is taken in and distributed.



Figure 43. *Conocephalum conicum* s.l. from Italy showing scales on the ventral thallus surface. Photo courtesy of Anna di Palma.

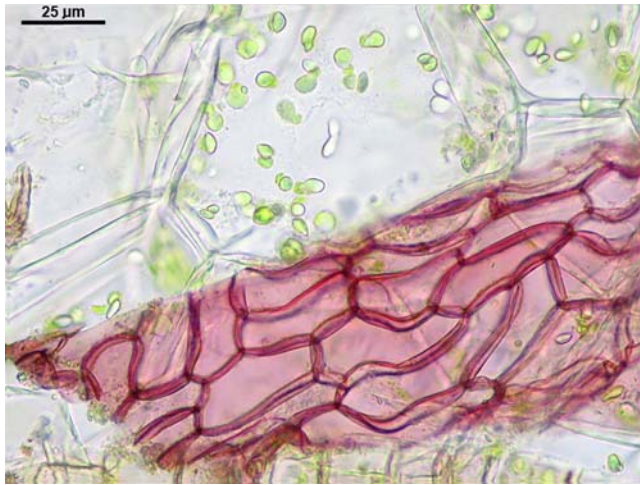


Figure 44. *Conocephalum conicum* s.l. ventral scale that aids in movement of water across the ventral side of thallus. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.



Figure 45. *Conocephalum conicum* s.l. thallus with rhizoids and thallus; rhizoids help to move water across the ventral side of the thallus and facilitate uptake. Photo by Ralf Wagner at <www.dr-ralf-wagner.de>, with permission.



Figure 46. *Conocephalum conicum* rhizoids showing the capillary spaces where they are massed. Photo by Paul Davison, with permission.

The shade habitat of *Conocephalum conicum* s.l. (Figure 1-Figure 11) is supported by its reaction to supplemented **UV-B radiation** (Ihle & Laasch 1995; Ihle 1997). This radiation causes a drastic decrease in the reaction center proteins D1 and D2 as well as the outer light-harvesting antenna. Streptomycin inhibited the repair process of PS II, indicating that only chloroplastic protein synthesis is needed for recovery. A specimen from India suggests that under the right conditions this species can produce protective pigments (Figure 47).



Figure 47. *Conocephalum conicum* from India showing brown pigmentation. Photo courtesy of Muhammet Ören.

At the other end of the light intensity range, **low light** causes **etiolation**. Ken Adams (pers. comm.) demonstrated this by growing *Conocephalum conicum* in the dark (Figure 48).



Figure 48. *Conocephalum conicum* etiolation (3 weeks in dark). Photo by Ken Adams, with permission.

The **pH** seems to be important in the distribution of *Conocephalum*, but most reports of preference can only be applied to *Conocephalum conicum* s.l. (Figure 1-Figure 11). Trębacz (1992) found that **pH** is also important within the cells of *Conocephalum conicum* s.l. It responds to the onset of **light** by decreasing its internal **pH** by about 0.15 units, followed by a slow increase. Respiration also can exhibit up to a 100% increase in response to excitation, but

the pH seems not to be involved. Dziubińska *et al.* (1989) found that cutting the thallus or providing an electrical stimulus elicited a transient rise in the rate of respiration. If the stimulation fails to produce any excitation, the respiration does not increase. The differences in response depend on the character of the excitation and the area of the thallus stimulated. Erdtmann and Mueller Stoll (1983) investigated the relationship between respiration and regeneration in *Conocephalum conicum* s.l.

Trębacz and Fensom (1989) found that in *Conocephalum conicum* s.l. (Figure 1-Figure 11) labelled carbon travelled cell to cell at a rate of $\sim 2.0\text{--}1.7\ \mu\text{m}\ \text{s}^{-1}$, a rate that is the same as that of cytoplasmic streaming. **Photosynthesis** occurs in the thallus cells (Figure 49); CO_2 is obtained from the air through the pores on the thallus surface (Figure 50-Figure 51) and oxygen is released there. Below these openings are chambers with chlorophyllous cells where photosynthesis occurs (Figure 51). Starch can be stored in the cells and can be densely clumped in the stalk portion of the archegoniophore (Figure 52).



Figure 49. *Conocephalum conicum* photosynthetic cells in thallus. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 50. *Conocephalum conicum* s.l. showing pore openings on the thallus surface in the UK. Photo by Dick Haaksma, with permission.

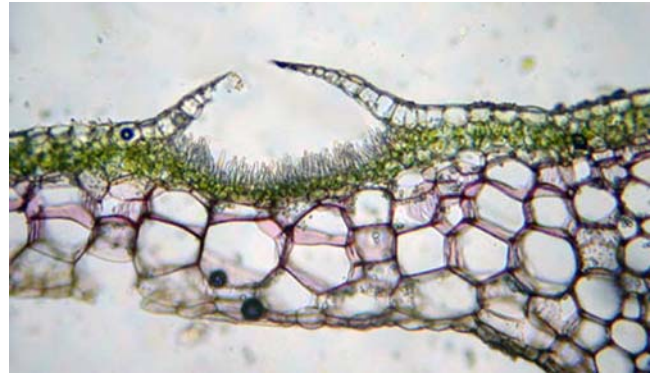


Figure 51. *Conocephalum conicum* s.l. showing longitudinal section of pore. Photo from Botany Website, UBC, with permission.



Figure 52. *Conocephalum conicum* s.l. archegoniophore stalk section showing stained dense starch grains. Photo from Botany Website, UBC, with permission.

In addition to whatever benefit may be derived from neighbors, *Conocephalum conicum* s.l. (Figure 1-Figure 11) has anatomical adaptations that may permit it to live where it can become inundated with water. The **air pores** (Figure 50), which are quite large in this genus, have hydrophobic cuticular ridges (Figure 51) surrounding them (Schönherr & Ziegler 1975). This allows only liquids with a contact angle of zero degrees with the ledges to enter the air pore. This presumably permits the internal air chambers of the species to maintain the air space needed to obtain CO_2 . One would assume that this is necessary for rapid recovery once the water recedes and to allow continued photosynthesis when kept wet on the exterior by splash.

Dilks and Proctor (1975) found that *Conocephalum conicum* s.l. (Figure 1-Figure 11) was killed by **rapid cooling** to -5°C , whereas many of the bryophytes tested could withstand such rapid cooling. Nevertheless, it certainly can survive freezing temperatures in caves, where the temperature is not likely to drop suddenly (Figure 53). Dilks and Proctor surmised that the ability to survive long periods at low temperatures, as exhibited by many species, seems to relate to desiccation resistance.



Figure 53. *Conocephalum conicum* s.l. on wet cave roof with ice. Photo by Allen Norcross, with permission.

Krol *et al.* (2003) found that *Conocephalum conicum* (Figure 1-Figure 11) s.l. exhibits all-or-none action potentials in response to **sudden temperature drops**. Calcium is important in these potentials, with its inhibition or decrease resulting in the inhibition of voltage transients. The researchers concluded that the temperature drop causes a change in membrane potential due to calcium influx from both internal and external stores.

Conocephalum conicum s.l. (Figure 1-Figure 11) produces **Heat Shock Protein 70** in response to atmospheric pollution (Basile *et al.* 2013). The **heavy metals** accumulate in cell walls, accompanied by a strong increment in the Heat Shock Protein 70. Cadmium and lead accumulate in the parenchyma and are absorbed to cell walls or concentrated in vacuoles. The pollutants result in severe alterations to the organelles. The researchers concluded that *C. conicum* s.l. is tolerant of heavy metals and can serve as a bioindicator (see also Maresca *et al.* 2020). Nevertheless, Iqbal *et al.* (2011b) expressed concern that it was threatened by changes in the environment in Bhaderwah as well as in the Kumaon Himalaya.

Trębacz *et al.* (1994) compared the activities of Ca^{2+} , K^+ , Cl^- , and NO_3^- in *Conocephalum conicum* (Figure 1-Figure 11). The free cytosolic Ca^{2+} did not exhibit any light-dependent changes when no action potential was triggered. However, action potentials typically caused a 2-fold increase in free cytoplasmic Ca^{2+} concentration. Action potentials cause little change in K^+ activity. For both Cl^- and NO_3^- the vacuolar activity was 5 to 6 times that of the cytoplasmic activity. Changes in illumination had little effect on the concentrations of the two ions.

Samecka-Cymerman *et al.* (1997) found that the ecological differentiation between the liverwort species *Conocephalum conicum* (Figure 1-Figure 11), *Marchantia polymorpha* (Figure 54), and *Pellia epiphylla* (Figure 55) correlates closely with the soil chemistry. They found a high correlation between the soil concentrations of heavy metals as well as macroelements and the thalli of these liverworts. *Conocephalum conicum* s.l. proved to be a good biomonitor of chromium and cobalt.



Figure 54. *Marchantia polymorpha* with gemmae cups. Photo by Hermann Schachner, through Creative Commons.



Figure 55. *Pellia epiphylla*, a species of similar locations near stream water, but differs in soil chemistry from that of *Conocephalum conicum*. Photo by Hermann Schachner, with permission.

Adaptations

Gimingham and Birse (1957) concluded that thalloid mats such as those in *Conocephalum* occur at the most moist end of the spectrum. *Conocephalum conicum* s.l. (Figure 1-Figure 11) often occurs in **association** with other liverworts, such as *Chiloscyphus kashyapii*, *Dumortiera hirsuta* (Figure 56), *Marchantia* spp. (Figure 54), *Pellia endiviifolia* (Figure 57), *Preissia quadrata* (Figure 58), *Reboulia hemispherica* (Figure 59), and occasionally with *Aneura pinguis* (Figure 60), *Clevea hyalina* (Figure 61), *Mannia triandra* (Figure 62), and as well as the mosses *Myurella sibirica* (Figure 63) and *Thuidium delicatulum* (Figure 64) (Iqbal *et al.* 2011a). *Conocephalum conicum* is also associated with fungi, ferns, flowering plants, and even insects. These associations might prove to be beneficial, perhaps by maintaining moisture or in helping the liverworts to obtain it. They could also result in competition.



Figure 56. *Dumortiera hirsuta*, a liverwort that often occurs in association with *Conocephalum conicum* s.l. Photo by George Shepherd, through Creative Commons.



Figure 59. *Reboulia hemisphaerica*, a liverwort that often occurs in association with *Conocephalum conicum* s.l. Photo by Michael Lüth, with permission.



Figure 57. *Pellia endiviifolia*, a liverwort that often occurs in association with *Conocephalum conicum* s.l. Photo by Hermann Schachner, through Creative Commons.



Figure 60. *Aneura pinguis*, a liverwort that often occurs in association with *Conocephalum conicum* s.l. Photo by Hermann Schachner, through Creative Commons.



Figure 58. *Preissia quadrata*, a liverwort that often occurs in association with *Conocephalum conicum* s.l. Photo by Bernd Haynold, through Creative Commons.



Figure 61. *Clevea hyalina*, a liverwort that sometimes occurs in association with *Conocephalum conicum* s.l. Photo by Hugues Tinguy, with permission.



Figure 62. *Mannia triandra*, a liverwort that sometimes occurs in association with *Conocephalum conicum* s.l. Photo courtesy of Guido Brusa.



Figure 63. *Myurella sibirica*, a moss that often occurs in association with *Conocephalum conicum* s.l. Photo by Dick Haaksma, with permission.



Figure 64. *Thuidium delicatulum*, a moss that often occurs in association with *Conocephalum conicum* s.l. Photo by Blanka Agüero, with permission.

Levine (1999) explored the "indirect facilitation" in a riparian community where *Conocephalum conicum* s.l. (Figure 1-Figure 11) (see Shevock *et al.* 2021) was a member. "Indirect facilitation occurs when the indirect positive effect of one species on another, via the suppression of a shared competitor, is stronger than the direct competitive effect." In a northern California, USA, riparian community, Levine conducted field experiments. Using a factorial design, he found three qualitatively different interactions between *Carex nudata* (Figure 65) and three target species. The *Carex* facilitated *Conocephalum conicum* s.l. in the presence of *Mimulus guttatus* (Figure 66) by suppressing the latter. On the other hand, when *M. guttatus* was absent, *Carex nudata* was a competitor with *Conocephalum conicum* s.l.



Figure 65. *Carex nudata*, a species that interacts with *Conocephalum conicum* s.l. by suppressing *Mimulus guttatus*, or to compete when *M. guttatus* is absent. Photo by Paul Slichter, with permission.

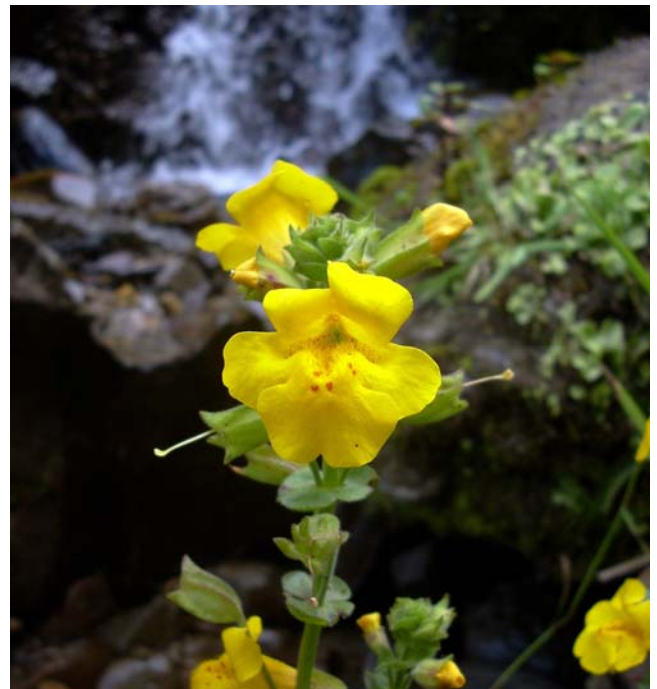


Figure 66. *Mimulus guttatus*, a species that competes with *Conocephalum conicum* s.l. Photo by Christopher M. Luna, through Creative Commons.

Reproduction

Conocephalum conicum s.l. (Figure 1-Figure 11) has been of interest to bryologists in a number of studies related to reproduction. However, some of these have been done in North America, so I must assume they actually refer to *Conocephalum salebrosum* (Figure 12-Figure 13). Thus, I have discussed them under that species in the next subchapter.

One of the mechanisms of spread of *Conocephalum* species is its ability to **overwinter** and produce new growth in spring. The overwintering buds are protected by scales (Figure 67-Figure 69). But young plants (Figure 70-Figure 71) also arise with no apparent connection to plants from a previous year.



Figure 67. *Conocephalum conicum* s.l. overwintering bud scales. Photo from Botany Website, UBC, with permission.



Figure 69. *Conocephalum conicum* s.l. overwintering bud scales. Photo by Dick Haaksma, with permission.



Figure 70. *Conocephalum conicum* s.l. young. Photo by Dick Haaksma, with permission.



Figure 68. *Conocephalum conicum* s.l. with scales covering winter buds. Photo by Allen Norcross, with permission.



Figure 71. *Conocephalum conicum* s.l. young plants. Photo by Dick Haaksma, with permission.

Benson-Evans (1964) found that *Conocephalum conicum* s.l. (Figure 1-Figure 11) from Wales grew best and produced **gametangia** (Figure 72-Figure 75) at 21°C, but not at 10°C. It grew and produced gametangia best in long days (18 hours), but not in short days (6 hours).

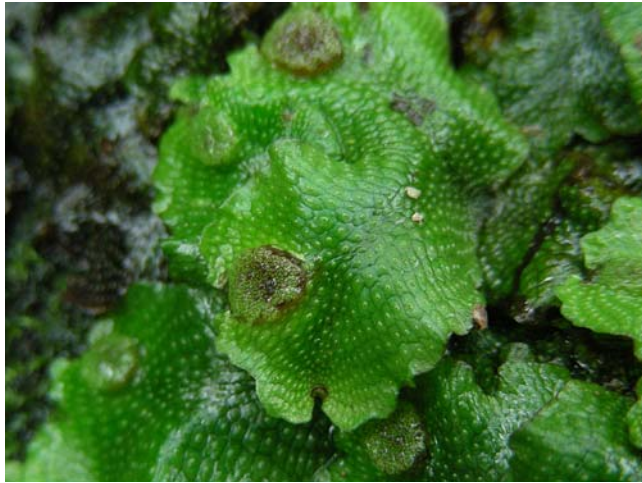


Figure 72. *Conocephalum conicum* with immature antheridial receptacles, Sardoia, Italy. Photo courtesy of Michael Lüth.



Figure 73. *Conocephalum conicum* s.l. antheridial receptacles. Photo by Malcolm Storey through Creative Commons.



Figure 74. *Conocephalum conicum* s.l. males with mature antheridial receptacles, Nichinan, Japan, June 1983. Photo by Janice Glime.

Yamazaki (1981) discovered that even within a population of *Conocephalum conicum* (Figure 1-Figure 11) the **genetic variation** was abundant, a condition that suggests that sexual reproduction predominates in the natural populations. It is not unusual to see reproductive populations (Figure 76-Figure 78), and for the most part

bryologists have not reported asexual structures. Since *C. conicum* can grow together with *C. salebrosum* (Figure 12-Figure 13), it is possible that some of the variation Yamazaki observed was really that of what we now consider to be two species.



Figure 75. *Conocephalum conicum* s.l. mature antheridial receptacle. Photo by Malcolm Storey, through Creative Commons.



Figure 76. *Conocephalum conicum* s.l. with developing archegoniophore. Photo by Li Zhang, with permission.



Figure 77. *Conocephalum conicum* s.l. mature sporangia in the cone-shaped archegonial head, a relatively frequent sight due to the frequent sexual reproduction. Photo by Hermann Schachner, through Creative Commons.



Figure 78. *Conocephalum conicum* s.l. sporangia ready to release spores. Photo from Botany Website, UBC, with permission.

More recently, **tubers** have been verified on *Conocephalum conicum* s.l. (Figure 1-Figure 11) in Sussex, England (Paton 1993). These were found so uncommonly that their presence was often omitted from descriptions of the species. They may, however, be more common than assumed because they are located on **moribund** (in terminal decline; lacking vitality or vigor; Figure 79) thalli – a part of the plant often overlooked or discarded in the preparation of specimens. Furthermore, they are on the ventral surface, hidden among the rhizoids. Nevertheless, when they become detached, they germinate to produce a new thallus.



Figure 79. *Conocephalum* cf. *salebrosum* dead and new growth on population at Hocking Hills, Ohio, USA. It is on the ventral side of such moribund tissues where tubers have been found in *Conocephalum conicum* s.l. Photo by Janice Glime.

Bhagat *et al.* (2012) suggested that sexual reproduction is a less important means of reproduction in *Conocephalum* than is asexual reproduction. They based this on the relatively constant ratio of spores to elaters (Figure 80) (0.40-0.43:1) over the past 54 years, a ratio that is much lower than that known in other **Marchantiales**.

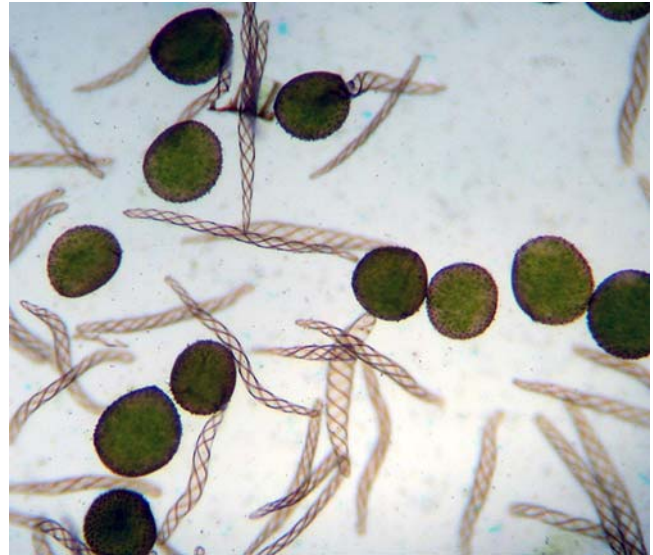


Figure 80. *Conocephalum conicum* s.l. spores and elaters at maturity. Photo from Botany Website, UBC, with permission.

Fungal Interactions

Carré and Harrison (1961) reported a species of *Pythium* (Figure 81), a parasitic fungus, invading *Conocephalum conicum* s.l. (Figure 1-Figure 11). This endophyte invades the rhizoids (Figure 82) and then the thallus, but is limited to the area adjoining the midrib. A species of *Pythium* was consistently isolated from infected rhizoids and thalli. Other fungal species were in cultures with sterile thalli, but none was able to form the typical **vesicular-arbuscular** (Figure 83) condition. Some were, however, able to penetrate the rhizoids and lower cells of the thallus.

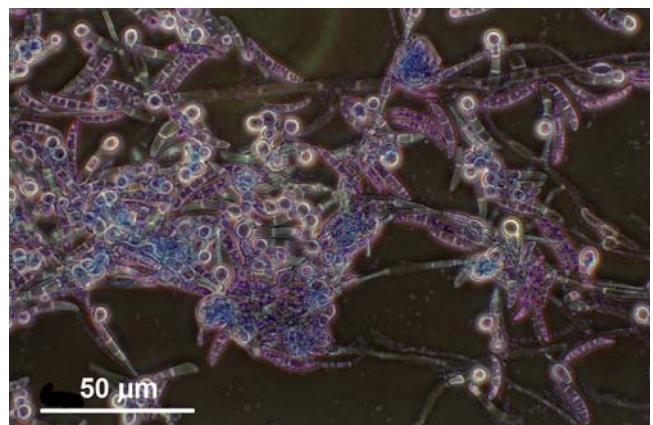


Figure 81. *Pythium* sp.; a species of *Pythium* is endophytic in *Conocephalum conicum* s.l. Photo by Josef Reischig, through Creative Commons.

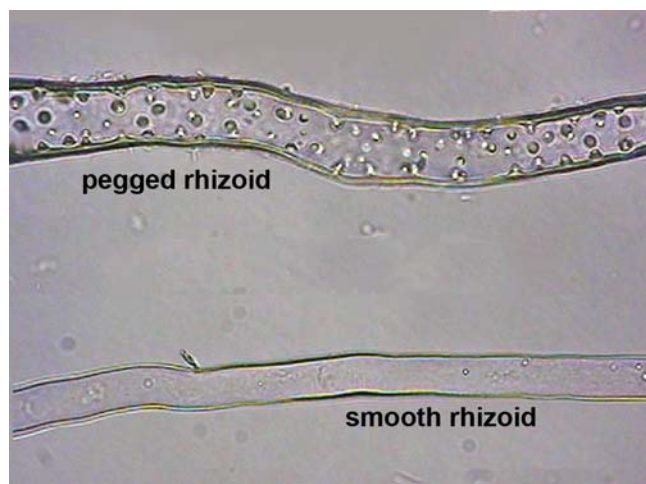


Figure 82. *Conocephalum conicum* s.l. two types of rhizoids. Photo by Paul Davison, with permission.

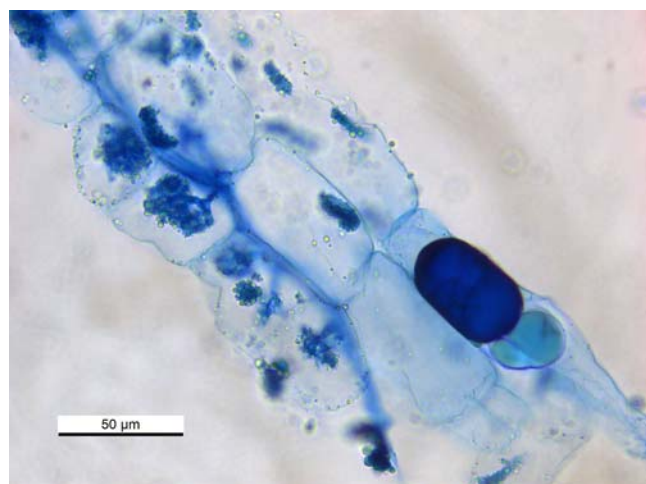


Figure 83. **Vesicular arbuscular mycorrhizae** in root cells, showing the form that might also show up in the thallus of *Conocephalum conicum*. Photo by Rit Rajarshi, through Creative Commons.

Ligrone and Lopes (1989) reported a highly branched fungus that colonizes the smooth-walled rhizoids (Figure 82) of *Conocephalum conicum* s.l. (Figure 1-Figure 11). The fungus is able to enter the thallus through these rhizoids to the parenchyma of the midrib, where it is entirely intracellular. The fungus forms vesicles (see Figure 83) in the rhizoids and a few ventral layers of the parenchyma cells. The fungal hyphae spread from cell to cell. More internal cells have prominent arbuscules (Figure 83) formed by the infecting hyphae. The infected host cells experience proliferation of the ribosomes, plastids, and mitochondria. The arbuscules ultimately degenerate, leaving clumps of collapsed hyphae, and these cells have not been observed to become reinfected.

Later, Ligrone *et al.* (2007) reported **Glomeromycotean** associates in liverworts. *Glomus mosseae* (Figure 84) was identified in axenic thalli of both *Conocephalum conicum* (Figure 1-Figure 11) and *C. salebrosum* (Figure 12-Figure 13) and produced an association with these liverworts similar to that seen in the wild. These fungi suppressed cell wall autofluorescence in Marchantialean liverworts and triggered the deposition of a

new wall layer that specifically bound the monoclonal antibody CCRC-M1 against fucosylated side groups associated with xyloglucan and rhamnogalacturonan I.



Figure 84. *Glomus mosseae* spores cultured with tomato root. Photo by Samson90, through Creative Commons.

Nevertheless, *Conocephalum conicum* s.l. (Figure 1-Figure 11) exhibited some antifungal activity. Asakawa (2007) reported antimicrobial, antifungal, antipyretic, and antidotal activity from *Conocephalum conicum* s.l.. It can be used to cure cuts, burns, scalds, fractures, swollen tissue, poisonous snake bites, and gallstones. We don't know which cryptospecies was used in the study.

Animal Interactions

Imada *et al.* (2011) found that there are ~25 East Asian endemic members of the micropterigid moths (Figure 85) that occur exclusively on *Conocephalum* (Figure 1-Figure 11, Figure 86). These moth species are separated by geographical isolation. It would be interesting to know if these moth species have any correlations with the chemical differences among cryptospecies of this liverwort.



Figure 85. *Neomicropteryx nipponensis* larva feeding on *Conocephalum conicum* s.l. Note the darkened necrotic areas where the outer cells have been removed. Photo by Yume Imada, with permission.



Figure 86. *Conocephalum conicum* s.l. that has been nibbled. Photo by Allen Norcross, with permission.

Biochemistry

Conocephalum conicum s.l. (Figure 1-Figure 11) has had more than its share of biochemical analyses. Only a few are included here. Unfortunately, most of these predate the breakup of the species into multiple species and cryptospecies.

Markham *et al.* (1976) found that flavonoids differed between a German sample and one from the USA. This difference might be the forerunner of our understanding that the North American populations are actually *Conocephalum salebrosum* (Figure 12-Figure 13). They also found that the flavonoids they identified did not change qualitatively with seasonal changes. Using 280 samples, Toyota *et al.* (1997) compared three chemotypes of *Conocephalum conicum* s.l. (Figure 1-Figure 11).

Ludwiczuk *et al.* (2013) identified cryptic species in *Conocephalum conicum* s.l. using volatile components. Using 13 samples, they identified four cryptic species of *C. conicum* and the species *C. salebrosum* (Figure 12-Figure 13). The chemical differences correlated with the geographic distribution of the samples.

Ghani *et al.* (2016) used Japanese material of Type-II *Conocephalum conicum* s.l. (Figure 1-Figure 11) to release a phenyl propanoid, trans-methyl cinnamate as a stress response. Although they used it to show that this type had this compound, only previously known from Type III, it is interesting ecologically to know that phenyl compounds can be released in response to stress. Are these similar to the herbivory responses known from many tree leaves?

Asakawa and Takemoto (1979) identified tulipinolide as the compound causing the pungency one can sense in the female gametophyte of *Conocephalum conicum* s.l. (Figure 1-Figure 11); the compound and the smell are absent in the males. The guaianolides were inhibitory toward germination and growth of roots of rice in the husk.

Castaldo-Cobianchi *et al.* (1988) reported antibiotic activity in *Conocephalum conicum* s.l. (Figure 1-Figure 11) against both Gram+ and Gram- bacteria.

Odrzykoski and Szweykowski (1991) described three new sesquiterpenoids from *Conocephalum conicum* s.l. (Figure 1-Figure 11). They found that the compounds varied in their cytotoxicity, but that they could exert immunosuppressive effects on rat splenocytes at lesser concentrations than those that were toxic. Melching and König (1999) identified three new sesquiterpenes from *Conocephalum conicum* s.l. in Germany.

Lu *et al.* (2006) identified four new monoterpene esters and elucidated a number of known compounds in *Conocephalum conicum* s.l. (Figure 1-Figure 11). Two compounds were moderately cytotoxic to human HepG2 cells and one of these also exhibited antibacterial activity against *Pseudomonas aeruginosa* (Figure 87).

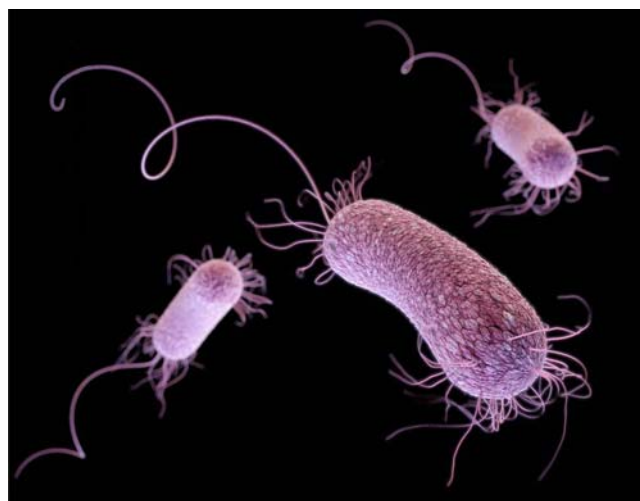


Figure 87. *Pseudomonas aeruginosa*, a bacterium that is inhibited by compounds from *Conocephalum conicum* s.l. Photo from CDC, through public domain.

Himanshu *et al.* (2007) tested several bryophytes, including *Conocephalum conicum* s.l. (Figure 1-Figure 11) for activity against the human pathogens *Escherichia coli* (Figure 88) and *Salmonella typhi* (Figure 89) and two fungi, *Aspergillus niger* (Figure 90), *Candida albicans* (Figure 91). None of the water-soluble extracts was effective on the pathogens. However, the acetone-soluble extract was inhibitory against all the pathogens. *Candida albicans* was strongly inhibited by the extract from *Conocephalum conicum* s.l.

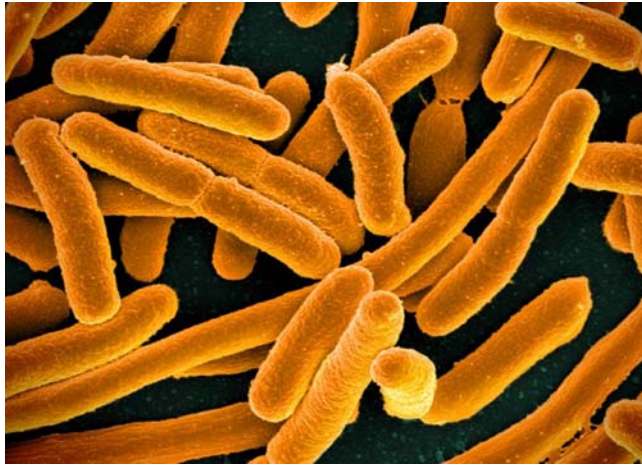


Figure 88. *Escherichia coli*, a human pathogen that is inhibited by extracts of *Conocephalum conicum* s.l. Photo from NIAID, through Creative Commons.

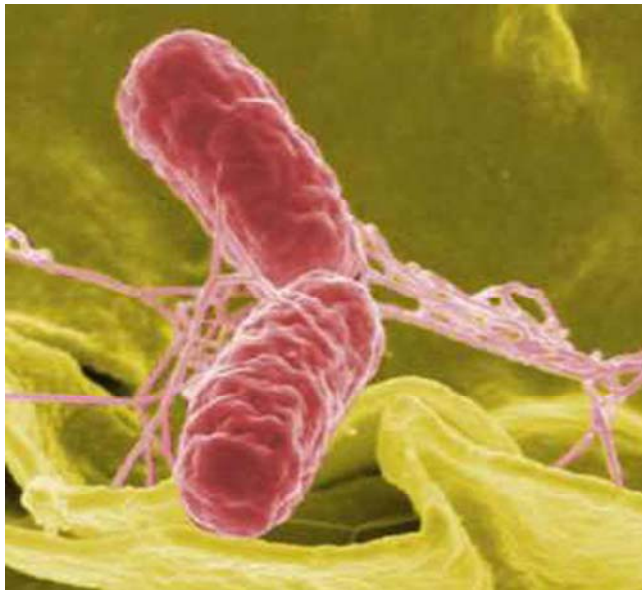


Figure 89. *Salmonella* sp., a human pathogen that is inhibited by extracts of *Conocephalum conicum* s.l. Photo by Elapied, through Creative Commons.

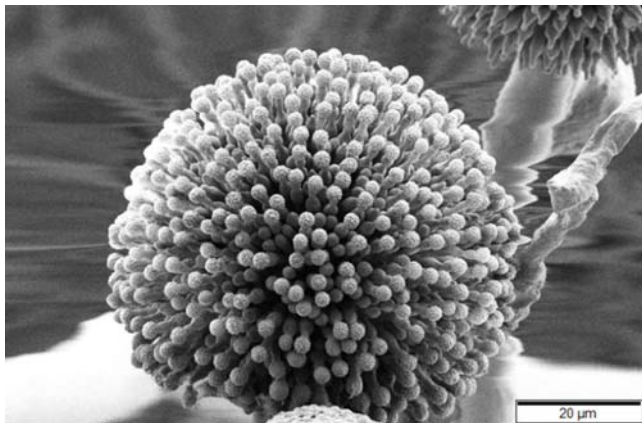


Figure 90. *Aspergillus niger* SEM, a pathogen that is inhibited by extracts of *Conocephalum conicum* s.l. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.



Figure 91. *Candida albicans* pseudohyphae in a fresh and unstained urine sediment. Photo from Controllab, through Creative Commons.

Ivković *et al.* (2021) found that methanol extracts of terpenes, oils, sugars and bis-bibenzylys were absent in *Conocephalum conicum* s.l. (Figure 1-Figure 11), whereas these are present in both *Marchantia polymorpha* (Figure 54) and *Pellia endiviifolia* (Figure 57).

Negi *et al.* (2020) found that *Conocephalum conicum* s.l. (Figure 1-Figure 11) acetone extracts were active against *Aspergillus flavus* (Figure 92) and *A. parasiticus* (Figure 93-Figure 94), with the highest activity coming from populations collected at Mukteshwar (2100 m asl). Negi and Chaturvedi (2021) further evaluated the usefulness of *Conocephalum conicum* s.l. and found that methanol extracts were highly effective against the fungal wilt disease caused by *Fusarium oxysporum* f. *lycopersici* (Figure 95-Figure 96), a disease that makes it unprofitable to grow tomatoes in the tropics. Since *C. conicum* is an "efficient" source of the Riccardin C that is active in inhibiting the fungi on tomatoes, it could be an eco-friendly alternative to the more conventional fungicides.



Figure 92. *Aspergillus flavus*, a fungus that is inhibited by extracts of *Conocephalum conicum* s.l. Photo from Medmyco, through Creative Commons.

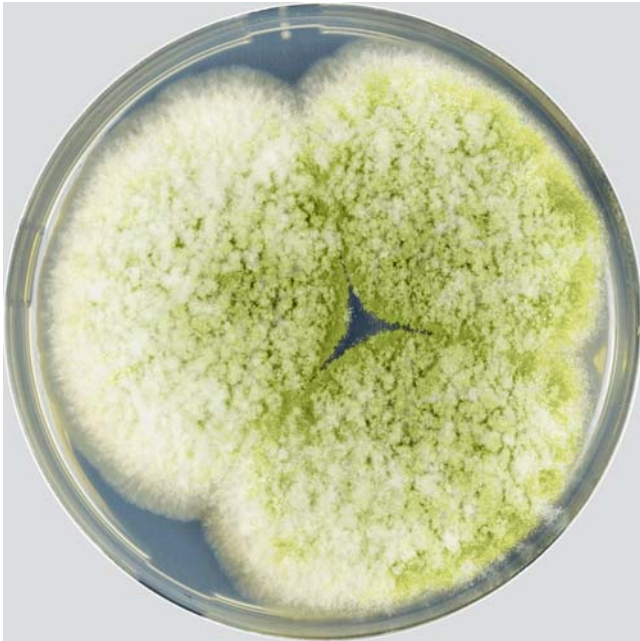


Figure 93. *Aspergillus parasiticus*, a fungus that is inhibited by extracts of *Conocephalum conicum* s.l. Photo by Line Ledsgaard Jensen, Mikael Rørdam Andersen, Ellen Kirstine Lyhne, through public domain.



Figure 95. Tomato plant infected with *Fusarium oxysporum* f. *lycopersici*. Photo by Gerald Holmes, Strawberry Center, Cal Poly San Luis Obispo, with permission.



Figure 94. *Aspergillus parasiticus*. Photo from Medmyco, through Creative Commons.



Figure 96. Culture of *Fusarium oxysporum*, a fungus that is devastating to tomato crops in the tropics; extracts of *Conocephalum conicum* s.l. inhibit its growth. Photo by Keith Weller, through public domain.

***Conocephalum orientalis* (Figure 97-Figure 100)**

In 1994, Akiyama and Hiraoka (1994a, b) noted allozyme variation in the *Conocephalum* in Japan. This

led to later studies on the differences among the Japanese forms. In 2022 Akiyama has published several new species, some of which occur in wet habitats.

One of these new species is *Conocephalum orientalis* (Figure 97-Figure 100), a segregate of *C. conicum* (Figure 1-Figure 11) previously known as J type (Figure 97) (Akiyama 2022). The thallus of *Conocephalum orientalis* is shiny and light green (Figure 98-Figure 99), but becomes yellowish when growing in the shade; the air chambers (visible as polygons at the surface) increase in size toward the center of the thallus (Figure 100) The grooves are deep (Figure 101-Figure 102), like those of *C. salebrosum* (Figure 97). It forms the largest plant bodies of any *Conocephalum* species in Japan.



Figure 99. *Conocephalum orientalis* showing thallus grooves and pores. Photo courtesy of Hiroyuki Akiyama.



Figure 97. *Conocephalum orientalis* (J) and *C. salebrosum* (S). Photo courtesy of Hiroyuki Akiyama.



Figure 100. *Conocephalum orientalis* showing thallus grooves and pores, with polygons larger toward the center. Photo courtesy of Hiroyuki Akiyama.

Thallus variation occurs within as well as between populations of *Conocephalum orientalis* (Figure 97-Figure 100) (Akiyama 2022). These can include differences in thallus size (Figure 101), degree of purplish pigments on ventral surface (Figure 102-Figure 104), wavy margins (type J2; Figure 105), and blackish thallus grooves (type J3; Figure 106-Figure 109).



Figure 98. *Conocephalum orientalis*. Photo courtesy of Hiroyuki Akiyama.



Figure 101. *Conocephalum orientalis* showing variation in single population. Photo courtesy of Hiroyuki Akiyama.



Figure 102. *Conocephalum orientalis* young thallus that is still purplish. Photo courtesy of Hiroyuki Akiyama.



Figure 105. *Conocephalum orientalis* type J2 with wavy margin. Photo courtesy of Hiroyuki Akiyama.



Figure 103. *Conocephalum orientalis* showing purplish midrib on underside. Photo courtesy of Hiroyuki Akiyama.



Figure 106. *Conocephalum orientalis* type J3 showing variation in purplish ventral side. Photo courtesy of Hiroyuki Akiyama.



Figure 104. *Conocephalum orientalis* showing red underside of older tissues. Photo courtesy of Hiroyuki Akiyama.



Figure 107. *Conocephalum orientalis* type J3 with purplish ventral side and dark thallus grooves. Photo courtesy of Hiroyuki Akiyama.



Figure 108. *Conocephalum orientale* type J3 showing blackish thallus grooves. Photo courtesy of Hiroyuki Akiyama.



Figure 109. *Conocephalum orientale* type J3 with purplish ventral side and dark grooves. Photo courtesy of Hiroyuki Akiyama.

Although the separation of the species names is new, some natives of Japan have distinguished them for some time (Akiyama 2022). The plants now known as *Conocephalum orientale* (Figure 97-Figure 100) are heated in oil and eaten like potato chips. The distinctive aroma is lost during heating. They taste similar to the dried seaweed **nori** (Figure 110).



Figure 110. Nori, a red alga used to wrap sushi; fried *Conocephalum orientale* tastes much like this alga. Photo by Kropsoq, through Creative Commons.

Distribution

Conocephalum orientale (Figure 97-Figure 100) is described as a segregate of *C. salebrosum* (Figure 111), another recent segregate from *C. conicum* (Akiyama 2022). *Conocephalum orientale* is known from Japan and Taiwan, where it is the largest of the Japanese species and is the *Conocephalum* species most likely to be encountered on stream banks.



Figure 111. *Conocephalum salebrosum* from Japan. Photo courtesy of Hiroyuki Akiyama.

Aquatic and Wet Habitats

Conocephalum orientale (Figure 97-Figure 100) forms large plants on streamsides (Figure 112) (Akiyama 2022). It occurs in slightly shaded places along streams and seepage slopes along forest trails.



Figure 112. *Conocephalum orientalis* on rock. Photo courtesy of Hiroyuki Akiyama.

Conocephalum orientalis (Figure 97-Figure 100) avoids rock surfaces with no soil, except where there is an extreme amount of rainfall (Akiyama 2022). It becomes quite succulent in areas with good moisture conditions. By contrast, populations in direct sunlight, such as concrete retaining walls along sunlit roadways, can become hard and yellowish. The J2 type becomes very thick with wavy margins in dry conditions (Figure 113). The J3 type is more common in mountain areas such as Hokkaido; these thalli can be orange to purplish on the ventral side, even in summer (Figure 114), most likely a response to higher UV light. Thalli in these mountainous areas are also larger than the streamside populations of lower elevations.



Figure 113. *Conocephalum orientalis* type J2 with wavy margin. Photo courtesy of Hiroyuki Akiyama.



Figure 114. *Conocephalum orientalis* type J3 showing variation in orange to purplish ventral side. Photo courtesy of Hiroyuki Akiyama.

Physiology

Although there has not been time for separate physiological studies to be done on the newly named species *Conocephalum orientalis*, we can infer some of its physiology from its structures and their known functions in other members of the *C. conicum* species complex. In other cases, Akiyama (2022) was able to link earlier studies with the new species through voucher specimens.

The color of *Conocephalum orientalis* (Figure 97-Figure 100) also changes with the seasons. The thallus is pale green in spring through autumn (see Figure 115), although there is a pale reddish purple coloration at the basal part of the midrib. In the shade the thallus can become dark green (Figure 116). However, in late autumn and through winter, the entire under surface becomes reddish purple.



Figure 115. *Conocephalum orientalis* pale color at one location in the sun. Photo courtesy of Hiroyuki Akiyama.



Figure 116. *Conocephalum orientalis* dark color at one location in the shade. Photo courtesy of Hiroyuki Akiyama.

Akiyama (2022) found that plants of *Conocephalum orientalis* (Figure 97-Figure 100) grown in good moisture conditions become succulent and have clear slimy contents of polysaccharides flowing from the cut across mucilage canals (Figure 117). But it often lacks mucilage cells, suggesting that it is best adapted for a wet habitat (Akiyama 2022). It does, however, have abundant rhizoids (Figure 118-Figure 119) that form capillary spaces suitable for movement of water. We can surmise that its rhizoids and scales (Figure 118-Figure 119) move water along the ventral surface, as in other *Conocephalum* species, facilitating the uptake of water. In addition, it often has symbiotic fungi that can help in obtaining nutrients.



Figure 117. *Conocephalum orientalis* from Japan showing leak of mucilage from cross section of mucilage canals. Photo courtesy of Hiroyuki Akiyama.



Figure 118. *Conocephalum orientalis* from Taiwan, ventral side showing rhizoids. Photo courtesy of Hiroyuki Akiyama.



Figure 119. *Conocephalum orientalis* type J3 rhizoids and purplish ventral side. Photo courtesy of Hiroyuki Akiyama.

Adaptations

Plants of *Conocephalum orientalis* (Figure 97-Figure 100) seem to be quite plastic in nature. When plants grow in darker places, such as the entrance of a cave, thalli become very thin and yellowish (Figure 120), resembling Japanese forms of *C. salebrosum* (Akiyama 2022). Hard, leathery thalli can form in the sun, accompanied by dense ventral scales (Figure 119); their appendages are large and strongly colored reddish purple, a color that is also seen on the upper side of the thalli. These population differences can relate to altitude and shading, but the differences seem not to be linked to any genetic differences.



Figure 120. *Conocephalum orientalis* thin thalli produced under diffuse light. Photo courtesy of Hiroyuki Akiyama.

Akiyama (2022) described the thallus of *Conocephalum orientalis* (Figure 97-Figure 100) as having a light green ventral surface (Figure 118). However, this becomes reddish purple toward late autumn. This is a pattern seen in other bryophytes, including *Sphagnum* (Figure 121) species, presumably in response to the greater light intensity due to loss of canopy leaves, and to the cold nights. The cold nights and warm days are also responsible for the red colors seen on trees in the autumn (Kyne & Diver 2012).



Figure 121. *Sphagnum capillifolium* showing a color transition from green to red. Photo by Bernd Haynold, through Creative Commons.

Akiyama (2022) noticed that smaller plants of *Conocephalum orientalis* (Figure 97-Figure 100) tended to be the most common along the lower elevation streams, whereas at higher elevations they were larger, more "normal" plants.

Reproduction

Conocephalum orientalis (Figure 97-Figure 100) is **dioicous** (Figure 125-Figure 128) and **perennial** (Akiyama 2022). The antheridia appear as clusters in antheridial receptacles on the upper surface of the thallus at the tips of the thallus branches (Figure 122-Figure 124). In the spring, these receptacles appear at tips of newly formed lobes. These antheridial receptacles may appear on stalks created by the midrib because the thallus tissue ceases growth when the receptacle forms (Figure 125). These stalks differ from those of *Marchantia* in which the thallus folds and encloses the rhizoids.



Figure 122. *Conocephalum orientalis* male with antheridial receptacles. Photo courtesy of Hiroyuki Akiyama.



Figure 123. *Conocephalum orientalis* male with immature antheridial receptacle. Photo courtesy of Hiroyuki Akiyama.



Figure 124. *Conocephalum orientalis* male showing antheridial receptacle. Photo courtesy of Hiroyuki Akiyama.



Figure 125. *Conocephalum orientalis* male with stalked thallus, a condition that can sometimes be seen in new growth. Photo courtesy of Hiroyuki Akiyama.

Shimamura *et al.* (2008) described the dispersal of sperm (Figure 126) in *Conocephalum conicum* (Figure 1-Figure 11), providing photographs of their discovery in Japan. Shimamura now considers that the species is probably the newly described *Conocephalum orientalis* (Figure 97-Figure 100). Shimamura and coworkers found that as the sperm were discharged, they became airborne (Figure 126), a phenomenon they were able to verify in the field. They postulated that this explosive behavior, along with the elevated receptacles, would increase the efficiency of fertilization in this (and probably many other) liverwort species, particularly in a drought environment.

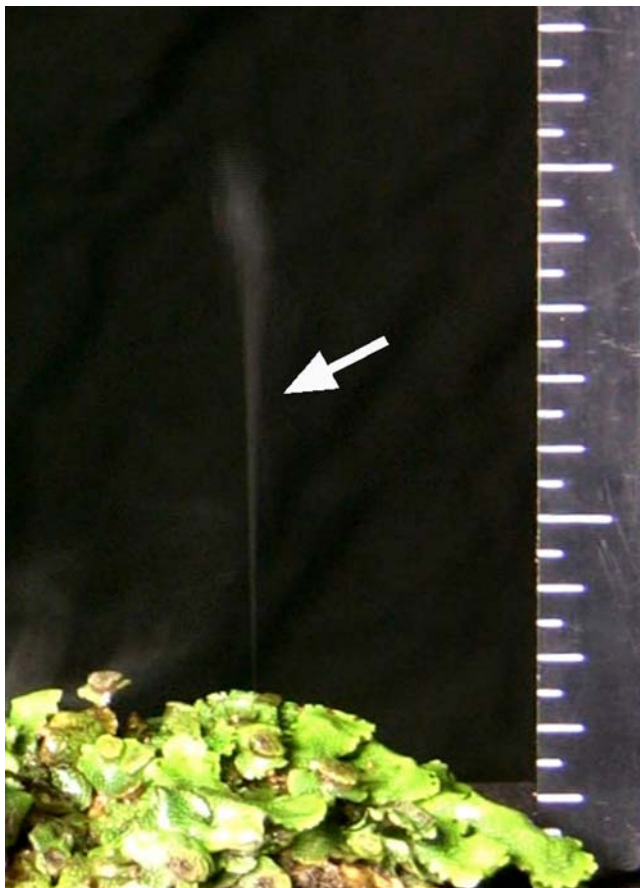


Figure 126. *Conocephalum orientalis* explosive sperm dispersal. Photo courtesy of Masaki Shimamura.

The archegonial heads begin growing near the growing tips (Figure 127). At maturity the archegonial heads are large and are perched on a stalk (Figure 128) up to 9 cm tall (Akiyama 2022).

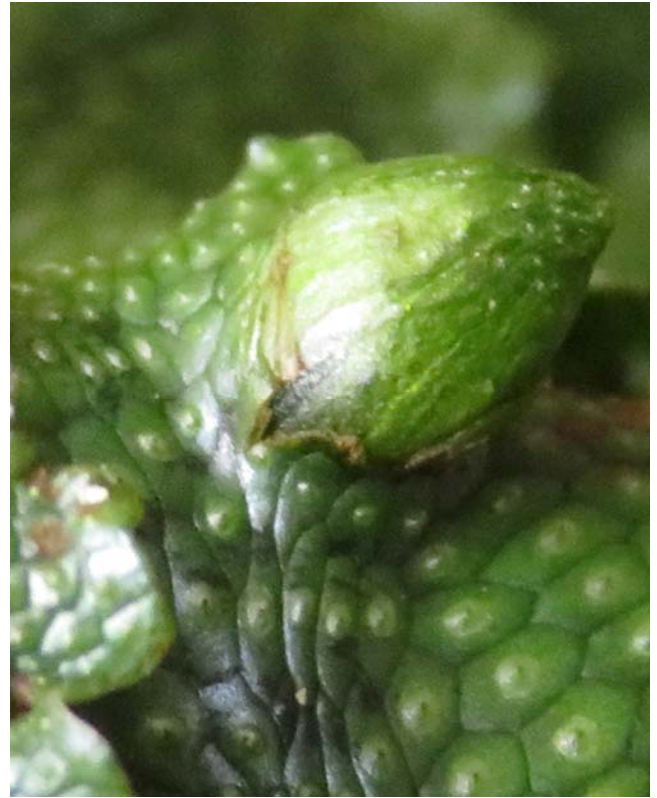


Figure 127. *Conocephalum orientalis* with young archegoniophore. Photo courtesy of Hiroyuki Akiyama.

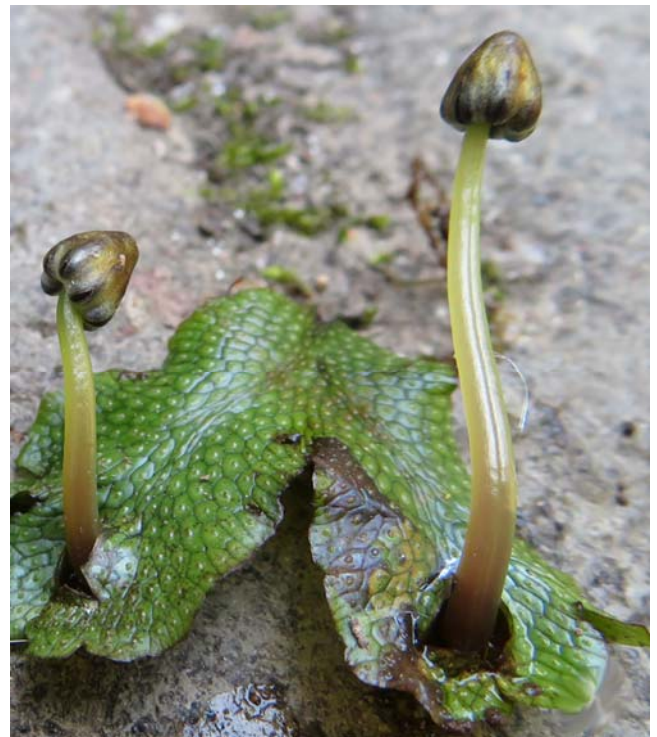


Figure 128. *Conocephalum orientalis* with mature archegoniophore. Photo courtesy of Hiroyuki Akiyama.

Conocephalum orientalis (Figure 97-Figure 100) produces spores that may be dispersed while small, or they may remain in the capsule, dividing into **endosporic** sporelings (Akiyama 2022). Spore germinability is 40-100% among the smaller spores. The remaining spores

divide within the spore walls (Figure 129) while still in the sporangium, thus increasing the number of chloroplasts. These larger spores lose their germinability within 30 days under room conditions (Inoue 1966 in Akiyama 2022). Such a two-size strategy permits immediate long distance dispersal of small spores, whereas the larger, short-lived spores have a size advantage that permits them to get a rapid start near the location of their parents. Spore sizes range 65-130 μm in longer diameter (Akiyama 2022).



Figure 129. *Conocephalum conicum* s.l. multicellular spores and elaters. Photo by Hugues Tinguy, with permission.

Conocephalum orientale (Figure 97-Figure 100) has no known asexual reproductive structures (Akiyama 2022), but presumably it can reproduce by fragments. It is able to overwinter and produces bud scales (Figure 130-Figure 131) that protect the growing points. The thallus produces winter buds at the tip of the thallus in autumn, developing new shoots in the following spring. It can afford to lose some older cells, with other cells remaining viable, but cells that give rise to new tissue are few in number and vulnerable at the tip of the plant, so the bud scales help to protect them. These scales are absent in tropical populations, where the thallus grows throughout the winter, but a few populations in more northern locations of Japan also lack the buds, and these have been aligned with unique alleles (Isono *et al.* 1999; Akiyama 2022).



Figure 130. *Conocephalum orientale* with young overwintering bud. Photo courtesy of Hiroyuki Akiyama.



Figure 131. *Conocephalum orientale* with overwintering bud. Photo courtesy of Hiroyuki Akiyama.

Biochemistry

Conocephalum orientale (Figure 97-Figure 100) produces large amounts of methyl cinnamate, giving it a pleasant odor (Toyota *et al.* 1997; Toyota 2000; Ab Ghahi *et al.* 2016; Miyatake *et al.*, 2018). It would be interesting to see if this compound has any role in discouraging herbivores.

Other biochemical studies on *Conocephalum orientale* likely exist, but the task remains to link the studies with their current species concept.

Summary

Conocephalum conicum s.l. has recently been divided into multiple species in addition to several cryptospecies. Some studies indicate that *Conocephalum* s.s. does not exist in North America or Asia and is confined to Europe. This reconfiguration of the *Conocephalum conicum* complex has made it difficult to link many published studies with the modern species concepts.

Several of these newly defined species occur in wet habitats. *Conocephalum conicum* tends to be in wetter habitats than those of *C. salebrosum*, a widespread species and possibly the only one in most of North America. Nevertheless, both of these species occur near water (streambanks, springs, splash of waterfalls, canyon walls) and can grow intermixed in Europe. *Conocephalum conicum* prefers shade and can grow in running water or on emergent rocks. It can also occur on slopes where it may get water from seepage.

Members of *Conocephalum* often occur in large mats or mixed with other bryophytes. They have scales and rhizoids on the ventral surface that aid in movement and uptake of water. Air pores have hydrophobic cuticular ridges that prevent water from entering to the internal air chambers through the pores. Rapid cooling kills the cells of *C. conicum* s.l., but apical buds of members of the genus survive winter under the

protection of bud scales. Heat Shock Proteins help to protect the cells from heavy metals, where the latter can accumulate and serve as biomonitors.

Conocephalum conicum can experience **indirect facilitation** from other species, in some cases in which another species outcompetes a species that is a strong competitor to the *C. conicum*.

Little is known about the tubers that grow among the rhizoids, but fragmentation occurs as new growth and branching occur and older parts die. Sexual reproduction is common. Gametangia of *C. conicum* s.l. are produced best at 21°C in long days.

Conocephalum conicum s.l. is often infected by vesicular-arbuscular fungi and a species of *Glomus*, but benefits and harmful effects need to be evaluated. The species does produce antifungal and antibacterial compounds, some of which could be used commercially.

There are ~25 East Asian micropterigid moths that occur exclusively on species of *Conocephalum*.

Conocephalum orientalis is a newly described species from Japan that has deep grooves unlike those of *C. conicum* s.s. It is sometimes eaten in Japan, where it is the most common *Conocephalum*, especially along streams. This species changes color with the seasons, becoming pale reddish purple in late autumn, and becoming dark green in the shade. It becomes succulent in good moisture conditions, but very thin in low light of caves.

Conocephalum orientalis expels its sperm explosively, presumably facilitating their dispersal to nearby female plants. Like other species of *Conocephalum*, some spores are small and dispersed early, whereas others are larger due to **endosporic** development.

Acknowledgments

Bryonettors provided a wonderful array of images to illustrate this chapter. Thank you to Masaki Shimamura for providing me with the image of the explosive sperm dispersal in *Conocephalum* cf. *orientalis*. And thank you to Hiroyuki Akiyama for sending me his 2022 paper on the new species in Japan and providing me with original images. I appreciate Guido Bursa's notification that one of my images was not the species indicated, and supplying me with a new, correct image.

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CHAPTER 1-21

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CONOCEPHALACEAE, PART 2

TABLE OF CONTENTS

<i>Conocephalum purpureorubrum</i>	1-21-2
Distribution	1-21-5
Aquatic and Wet Habitats	1-21-5
Non-Aquatic.....	1-21-5
Physiology	1-21-5
Reproduction.....	1-21-6
Biochemistry	1-21-7
<i>Conocephalum salebrosum</i>	1-21-8
Distribution	1-21-9
Aquatic and Wet Habitats	1-21-11
Stream and River Banks.....	1-21-12
Canyon Walls.....	1-21-12
Floodplains.....	1-21-14
Waterfalls.....	1-21-15
Non-Aquatic Habitats.....	1-21-15
Physiology	1-21-17
Adaptations	1-21-18
Reproduction.....	1-21-19
Animal Interactions.....	1-21-24
Fungal Interactions.....	1-21-24
Biochemistry	1-21-24
Summary	1-21-25
Acknowledgments	1-21-25
Literature Cited.....	1-21-25

CHAPTER 1-21

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CONOCEPHALACEAE, PART 2



Figure 1. *Conocephalum* cf. *salebrosum* at water's edge, Wahkeena Historical Preserve, Ohio, USA. Photo by Janice Glime.

***Conocephalum purpureorubrum* (Figure 2-Figure 14)**

Conocephalum purpureorubrum (Figure 2-Figure 14) was previously designated as *Conocephalum conicum* F type (Akiyama 2022). The lower surface of the thallus is reddish purple (Figure 2-Figure 4) even in summer, although this coloration may be confined to the midrib (Figure 5). The upper surface of the thallus mat is yellowish green (Figure 6-Figure 9) in western Japan or slightly shiny and blackish green (Figure 10-Figure 11) in eastern Japan. Upper epidermal cells of thalli can have thin or thick walls. The grooves outlining the **areolae** (air chambers) are deep and distinct (Figure 12-Figure 13). These air chambers do not differ in size between the margins and central portions (Figure 14).



Figure 2. *Conocephalum purpureorubrum* from Japan, showing partially purple underside. Photo courtesy of Hiroyuki Akiyama.



Figure 3. *Conocephalum purpureorubrum* ventral side showing a large portion with purplish coloration. Photo courtesy of Hiroyuki Akiyama.



Figure 4. *Conocephalum purpureorubrum* from Toyama Prefecture, Japan, showing form with entire underside purplish in color. Photo courtesy of Hiroyuki Akiyama.



Figure 5. *Conocephalum purpureorubrum* ventral surface not purple except along midrib. Photo courtesy of Hiroyuki Akiyama.



Figure 6. *Conocephalum purpureorubrum* from Japan, showing thallus grooves and pores. Photo courtesy of Hiroyuki Akiyama.



Figure 7. *Conocephalum purpureorubrum* from Japan. Photo courtesy of Hiroyuki Akiyama.



Figure 8. *Conocephalum purpureorubrum* light form typical of western Japan. Photo courtesy of Hiroyuki Akiyama.



Figure 9. *Conocephalum purpureorubrum* pale form typical in western Japan. Photo courtesy of Hiroyuki Akiyama.



Figure 10. *Conocephalum purpureorubrum* showing dark green and blackish form typical of populations in eastern Japan. Photo courtesy of Hiroyuki Akiyama.



Figure 11. *Conocephalum purpureorubrum* showing dark thalli mixed with lighter ones. Photo courtesy of Hiroyuki Akiyama.



Figure 12. *Conocephalum purpureorubrum* from Japan, showing distinct polygons formed by thallus grooves and yellowish green color typical of populations in western Japan. Photo courtesy of Hiroyuki Akiyama.



Figure 13. *Conocephalum purpureorubrum* from Japan, showing thallus grooves and pores. Photo courtesy of Hiroyuki Akiyama.



Figure 14. *Conocephalum purpureorubrum* from Japan, showing pores and distinct thallus grooves. Photo courtesy of Hiroyuki Akiyama.

Distribution

Conocephalum purpureorubrum (Figure 2-Figure 14) is known from southern China, South Korea, Taiwan, and Japan (Akiyama 2022).

Aquatic and Wet Habitats

Conocephalum purpureorubrum (Figure 2-Figure 14) can grow in drier habitats than those of *C. orientale* (Figure 15), but it can also grow intermixed with that species (Figure 16). It occurs at some waterfall sites. It tends to grow in more humid habitats when it grows with *C. salebrosum* (Figure 1, Figure 30-Figure 49) (Akiyama 2022), a behavior suggesting possible **indirect facilitation** as discussed in the previous subchapter under *C. conicum* (Figure 17). It is also possible that these behavioral differences in habitat preference relate to differences in genetic races (see Akiyama & Hiraoka 1994).



Figure 17. *Conocephalum conicum* from Scotland, with distinct thallus grooves. Photo courtesy of David Long.



Figure 15. *Conocephalum orientale* type J2 with wavy margin. Photo courtesy of Hiroyuki Akiyama.

Non-Aquatic

The eastern populations of *Conocephalum purpureorubrum* (Figure 2-Figure 14) usually occur on soil of valley slopes where they are far from water (Figure 18), but they can sometimes grow along streams (Akiyama 2022).



Figure 18. *Conocephalum purpureorubrum* from Mt. Takao, Japan, showing terrestrial habitat. Photo courtesy of Hiroyuki Akiyama.



Figure 16. *Conocephalum purpureorubrum* (FW) and *C. orientale* (J) growing intermixed in Japan. Photo courtesy of Hiroyumi Akiyama.

Physiology

Plants of *Conocephalum purpureorubrum* (Figure 2-Figure 14) tend to be thick and pale in sunny conditions (Figure 19) and thin and dark in shaded conditions (Figure 20) (Akiyama 2022). The reddish ventral condition seems to persist all year, but does its intensity relate to low light? In some flowering plants on tropical forest floors this ventral purplish coloring helps in the back-scattering of sunlight to the photosynthetic tissue (Lee *et al.* 1979). Such a role has not been explored in bryophytes. It seems likely that it would mostly work in liverworts among the bryophytes because they have a dorsiventral orientation.



Figure 19. *Conocephalum purpureorubrum* pale form typical of populations in western Japan. Photo courtesy of Hiroyuki Akiyama.



Figure 20. *Conocephalum purpureorubrum* from Japan, showing dark form typical of shade, with deep thallus grooves. Photo courtesy of Hiroyuki Akiyama.

Rhizoids are abundant on the ventral surface of *Conocephalum purpureorubrum* (Figure 21-Figure 23) (Akiyama 2022). These undoubtedly facilitate the movement and uptake of water into the thallus.



Figure 21. *Conocephalum purpureorubrum* showing rhizoids along the midrib. Photo courtesy of Hiroyuki Akiyama.



Figure 22. *Conocephalum purpureorubrum* showing numerous rhizoids. Photo courtesy of Hiroyuki Akiyama.



Figure 23. *Conocephalum purpureorubrum* showing numerous rhizoids. Photo courtesy of Hiroyuki Akiyama.

Conocephalum purpureorubrum (Figure 2-Figure 14) may have mucilage canals (Figure 24), but mucilage cells are often absent (Akiyama 2022). The mucilage may help to keep the cells moist, but experiments are needed to verify this. They are often absent in populations in dry habitats.

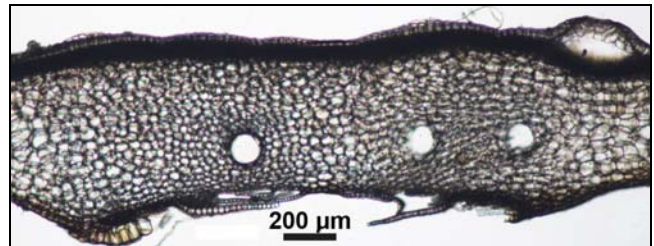


Figure 24. *Conocephalum purpureorubrum* from Japan, showing mucilage canals. Photo courtesy of Hiroyuki Akiyama.

Reproduction

Conocephalum purpureorubrum (Figure 2-Figure 14), like other species of *Conocephalum*, is **dioicous**. The antheridial receptacles form at the apex of the male thallus (Figure 25-Figure 26). Bud scales can often be seen at their margins (Figure 25).



Figure 25. *Conocephalum purpureorubrum* young antheridial receptacle. Note the remaining reddish brown bud scales. Photo courtesy of Hiroyuki Akiyama.

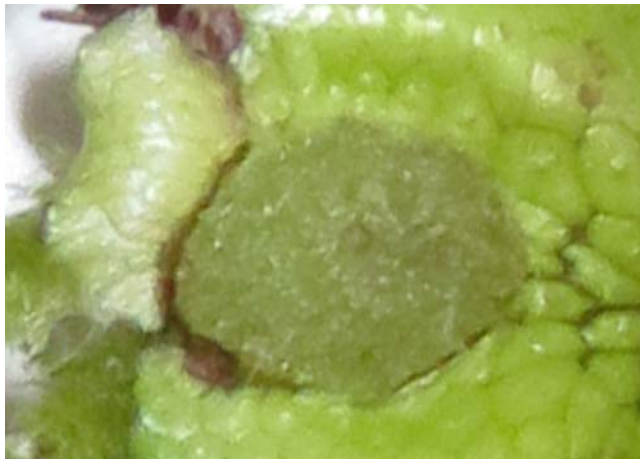


Figure 26. *Conocephalum purpureorubrum* young antheridial receptacle. Photo courtesy of Hiroyuki Akiyama.

Female plants of *Conocephalum purpureorubrum* (Figure 2-[Figure 14](#)) form archegoniophores at the apex of the female plants ([Figure 27](#)-[Figure 28](#)). When sporangia mature, the stalks elongate to 3-6 cm with bluntly conical archegonial heads ([Figure 28](#)-[Figure 29](#)). The sporangia hang down from the archegonial heads.



Figure 27. *Conocephalum purpureorubrum* with young archegoniophore. Photo courtesy of Hiroyuki Akiyama.



Figure 28. *Conocephalum purpureorubrum* with young archegoniophores beginning to elongate. Note that the black sporangia are already visible. Photo courtesy of Hiroyuki Akiyama.



Figure 29. *Conocephalum purpureorubrum* with mature archegoniophores and sporangia. Photo courtesy of Hiroyuki Akiyama.

Biochemistry

Biochemical analysis may reveal some interesting compounds in *Conocephalum purpureorubrum* ([Figure 2-](#)

Figure 14). This species has a fresh, earthy odor, usually not a mushroom odor (Akiyama 2022).

***Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49)**

Conocephalum salebrosum (Figure 1, Figure 30-Figure 49) is a relatively recently described species and is a segregate of *Conocephalum conicum* (Figure 17) (Szweykowski *et al.* 2005). It appears that many of the North American records of *Conocephalum conicum* should be placed here (Stotler & Crandall-Stotler 2017), with populations in California (Figure 50) being potential exceptions (see Shevock *et al.* 2021). The latter, for now, are best designated as *Conocephalum conicum* s.l.

In Europe, the distinction of the species in older literature is not so simple, if even possible without checking voucher specimens. Both species occur there. For example, Poponessi *et al.* (2014) have reported *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) from Italy. Sérgio *et al.* (2011) reported it from Portugal and Madeira and Azores Islands. Other records are documented in Figure 30-Figure 36. Figure 37 shows the similarities of a British Columbia, Canada, population to *Conocephalum salebrosum*.



Figure 30. *Conocephalum salebrosum* from Europe, showing distinct thallus grooves. Photo courtesy of Michael Lüth.



Figure 31. *Conocephalum salebrosum* showing distinct thallus divisions. Photo by Jouko Rikkinen, through Creative Commons.



Figure 32. *Conocephalum salebrosum* showing thallus section grooves, in Wales. Photo courtesy of Jonathan Sleath.

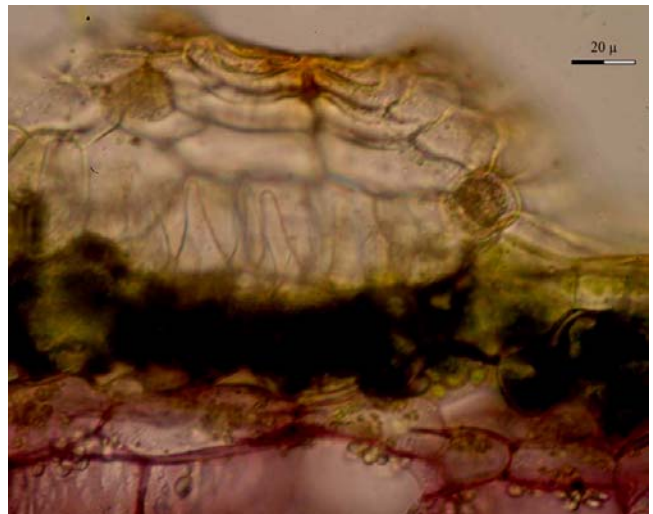


Figure 33. *Conocephalum salebrosum* from Corsav, France, showing pore section. Photo courtesy of Louis Thouvenot.



Figure 34. *Conocephalum salebrosum* from Europe, showing pore section. Photo by Norbert J. Stapper, with permission.



Figure 35. *Conocephalum salebrosum* from Corsavy, France, showing thallus margin section. Photo courtesy of Louis Thouvenot.



Figure 36. *Conocephalum salebrosum* from Wales, showing distinct section grooves. Photo courtesy of Jonathan Sleath.



Figure 37. *Conocephalum conicum* s.l. showing distinct thallus grooves and less distinct pores. These thallus grooves of a western North American population fit more closely with those of *C. salebrosum*. Photo from Botany Website, UBC, with permission.

Distribution

The distribution of *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) remains sketchy because of the long treatment of the species as part of *Conocephalum conicum* (Figure 17) (Szweykowski *et al.* 2005). It is definitely known from North America (Figure 38-Figure 41), but can also be found in Europe (Figure 42-Figure 43) (e.g. Tacchi *et al.* 2009) and eastern Asia (Figure 44-Figure 49) (Sérgio *et al.* 2011). Sérgio and coworkers consider it to be Holarctic.



Figure 38. *Conocephalum* cf. *salebrosum* habitat in Quebec, Canada. Photo by Martine Lapointe, with permission.



Figure 39. *Conocephalum salebrosum* in New York, USA. Photo courtesy of Jerry Jenkins.



Figure 40. *Conocephalum* cf. *salebrosum* from Ohio, USA. Photo by Bob Klips, with permission.



Figure 41. *Conocephalum* cf. *salebrosum*, Grand Ledge Park, Michigan, USA. Photo by Janice Glime.



Figure 42. *Conocephalum salebrosum* from the UK. Photo by Barry Stewart, with permission.



Figure 43. *Conocephalum salebrosum* from Chauderon, France. Photo courtesy of David Long.



Figure 44. *Conocephalum salebrosum* in Yunnan, China. Photo by David Long, with permission.



Figure 45. *Conocephalum salebrosum* from Sichuan, China. Photo courtesy of David Long.



Figure 46. *Conocephalum salebrosum* from Japan. Photo courtesy of Hiroyuki Akiyama.



Figure 47. *Conocephalum* males, Mt. Hiei, Japan. The prominent thallus grooves suggest this is now in the species *Conocephalum salebrosum*. The thallus sections do not get larger in the center of the thallus, as they do in *Conocephalum orientalis*. Photo by Janice Glime.



Figure 50. *Conocephalum conicum* s.l. from California, USA. Photo by R. L. Fleming, Jr., courtesy of David Wagner.

Aquatic and Wet Habitats

Conocephalum, presumably *C. salebrosum* (Figure 1, Figure 30-Figure 49), occurs on wet, sandy streambanks and on moist rock surfaces (Figure 51-Figure 53) or springy banks of ravines in Connecticut, USA (Nichols 1916). On Cape Breton Island, Canada it also occurs on streambanks (Nichols 1918).



Figure 48. *Conocephalum salebrosum* thallus from Japan, showing grooves and pores. Photo courtesy of Hiroyuki Akiyama.



Figure 51. *Conocephalum* cf. *salebrosum* with archegoniophores on canyon wall at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 49. *Conocephalum salebrosum* thallus from Japan, showing pores and distinct grooves. Photo courtesy of Hiroyuki Akiyama.

Populations in California (Figure 50), however, are similar, but not identical, to *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) (Shevock *et al.* 2021).



Figure 52. *Conocephalum* cf. *salebrosum* at Scott Falls, Michigan, USA. Photo by Janice Glime.



Figure 53. *Conocephalum* cf. *salebrosum* habitat in Quebec, Canada. Photo by Martine Lapointe, with permission.



Figure 54. *Conocephalum* cf. *salebrosum* on canyon wall at Hocking Hills, Ohio, USA. Photo by Janice Glime.

Conocephalum salebrosum (Figure 1, Figure 30-Figure 49) can be found along stream banks in the Appalachian Mountain, USA, streams (Glime 1968). In another humid environment, it is known from the base of the Flume wall and ledges in the flume at Franconia Notch, New Hampshire, USA (Glime 1982). It is likely the species that is a restricted terrestrial species in montane streams and on streambanks in western Canada (Vitt *et al.* 1986; Glime & Vitt 1987). It seems to avoid the submersion that is common for *C. conicum* (Figure 17).

Stephenson *et al.* (1995) reported its preferred pH as 7.9 in West Virginia, USA, mountain streams. Sérgio *et al.* (2011) considered *Conocephalum conicum* (Figure 17) to be less hygrophytic than *C. salebrosum* (Figure 1, Figure 30-Figure 49), being more tolerant of desiccation and preferring limestone areas.

Stream and River Banks

In North America, Porter (1933) reported *Conocephalum* (now probably *C. salebrosum* – Figure 1, Figure 30-Figure 49) from shady streambanks on soil in Wyoming, USA. Little (1936) described its habitat as constantly moist, shaded rock outcrops within a few feet of water in Oklahoma, USA. There it is one of the commonest species on moist, shaded bases of walls near water, occurring on both sandstone and limestone, as well as chert bluffs near water and especially in canyons and by springs.

In Europe, Tacchi *et al.* (2009) found it in ravines in the Apennines of Italy. Antkowiak *et al.* (2008) reported *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) synusia overgrowing high escarpments below the headstream at the River Kamionka in eastern Poland. Borovichev *et al.* (2009) found that *C. salebrosum* formed extensive mats on stream banks as well as on the bases of moist rocks and cliffs.

Canyon Walls

I have found *Conocephalum* cf. *salebrosum* (Figure 1, Figure 30-Figure 49) in extensive mats on canyon walls (Figure 54-Figure 67). These canyons were sandstone and humid.



Figure 55. *Conocephalum* cf. *salebrosum* habitat near top of canyon at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 56. *Conocephalum* cf. *salebrosum* on canyon wall at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 57. *Conocephalum* cf. *salebrosum* on canyon walls Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 60. *Conocephalum* cf. *salebrosum* and ferns on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 58. *Conocephalum* cf. *salebrosum* between ledges in damp canyon wall, Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 61. *Conocephalum* cf. *salebrosum* and ferns on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 59. *Conocephalum* cf. *salebrosum* on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 62. *Conocephalum* cf. *salebrosum* and ferns on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 63. *Conocephalum* cf. *salebrosum* on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 66. *Conocephalum* cf. *salebrosum* new growth at apices of old thalli on canyon walls, Hocking Hills, Ohio, USA, on 26 April 2015. Photo by Janice Glime.



Figure 64. *Conocephalum* cf. *salebrosum* new growth in rock shadow in the canyon at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 67. *Conocephalum* cf. *salebrosum* young plants on canyon wall at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 65. *Conocephalum* cf. *salebrosum* with new growth on canyon walls, Hocking Hills, Ohio, USA, on 26 April 2015. Photo by Janice Glime.

Floodplains

Because of its need for high humidity and tolerance of submersion, *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) commonly occurs in floodplains of streams and rivers (Figure 69-Figure 68), including periodically flooded bases of canyons (Figure 70-Figure 71).



Figure 68. *Conocephalum* cf. *salebrosum*, floodplain, Rose Lake, Michigan, USA, where the products of sexual reproduction are readily visible (8 May). Photo by Janice Glime.



Figure 69. *Conocephalum* cf. *salebrosum*, growing on floodplain, Rose Lake, Michigan, USA. Photo by Janice Glime.



Figure 70. *Conocephalum* cf. *salebrosum* on mud in the canyon at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 71. *Conocephalum* cf. *salebrosum* at base of canyon rock where it is flooded during high water, Hocking Hills, Ohio, USA. Photo by Janice Glime.

Waterfalls

Among its moist habitats, *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) can form large, dense patches on dripping rocks and wet soil where it is in close contact with water (Sérgio *et al.* 2011), including those areas wet by the splash of waterfalls (Figure 72) (personal observation).



Figure 72. *Conocephalum* cf. *salebrosum* beside Hungarian Falls at Tamarack City, Michigan, USA. Photo by Janice Glime.

Conocephalum salebrosum (Figure 1, Figure 30-Figure 49) was locally abundant at the entrance to Grotta degli Innamorati in central Italy at the Marmore Waterfalls Regional Park (Pononessi *et al.* 2020). I have seen the species in several locations in Michigan, USA, growing on a rock wall behind a waterfall (Figure 73).



Figure 73. *Conocephalum salebrosum* behind waterfall at Scott Cave, Michigan, USA. Photo by Janice Glime.

Non-Aquatic Habitats

Akiyama (2022) considered rather dry habitats (Figure 74) to be included among those of *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49). This fits with my own experience in North America. Other somewhat dry habitats are shown in Figure 75-Figure 79.



Figure 74. *Conocephalum salebrosum* from Japan, on limestone boulder. Photo courtesy of Hiroyuki Akiyama.



Figure 75. *Conocephalum salebrosum* from Japan, on limestone boulder. Photo courtesy of Hiroyuki Akiyama.



Figure 76. *Conocephalum salebrosum* from Japan, dry on thin soil on boulder. Photo courtesy of Hiroyuki Akiyama.



Figure 77. *Conocephalum salebrosum* from Japan, on moist limestone soil. Photo courtesy of Hiroyuki Akiyama.



Figure 78. *Conocephalum salebrosum* from Japan, on rock. Photo courtesy of Hiroyuki Akiyama.



Figure 79. *Conocephalum salebrosum* from Japan, small plants from moist, shaded site. Photo courtesy of Hiroyuki Akiyama.

Physiology

McConaha (1939) determined that the water absorption of *Conocephalum salebrosum* is limited to the ventral appendages, which are restricted to the underside of the midrib (Figure 80). The scales (Figure 80) increase the surface area by ~380% and the rhizoids (Figure 80-Figure 83) increase it by 5100%. The rhizoid strands and scales create an extensive capillary system (that is able to move water ventrally along the entire length of the thallus).



Figure 80. *Conocephalum salebrosum* showing rhizoids and scales that move water along ventral surfaces by capillarity. Photo by Jouko Rikkinen, through Creative Commons.



Figure 81. *Conocephalum salebrosum* from Japan showing rhizoids and purplish coloring restricted to the midrib. Photo courtesy of Hiroyuki Akiyama.



Figure 82. *Conocephalum salebrosum* from Japan showing rhizoids and purplish color extending beyond midrib. Photo courtesy of Hiroyuki Akiyama.



Figure 83. *Conocephalum conicum* s.l. showing **pegged (upper)** and **smooth (lower)** rhizoids. Photo from Botany Website, UBC, with permission.

Schott *et al.* (2021) found that *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) from west Germany had ice-nucleating proteins that differed in ice-nucleating temperature and seasonal concentration from those of *Marchantia polymorpha* subsp. *ruderalis* (Figure 84). Ice formed in the air chambers of both species, and crystals grew out of the air chamber pores (Figure 85). Crystals also formed in various locations on the ventral side of the thallus. This crystal formation resulted in dehydration of the thallus cells and permitted survival of low temperatures and frost (Figure 86). Presumably, this is a means of preventing crystal formation within the cells where it can damage membranes.



Figure 84. *Marchantia polymorpha* subsp. *ruderalis*. Photo by Michel Langeveld, through Creative Commons.



Figure 85. *Conocephalum* cf. *salebrosum* with ice crystals emanating from the thallus. Photo by Allen Norcross, with permission.



Figure 86. *Conocephalum salebrosum* and icicles, showing a habitat where it is able to survive the cold of winter with its ice-nucleating proteins, but without sudden cooling. Photo by Allen Norcross, with permission

Adaptations

Although no specific adaptations have been attributed to *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49), it is likely that many are similar to those of *Conocephalum conicum* (Figure 17). However, *C. salebrosum* does have more conspicuous pores (Akiyama 2022) that could be an advantage is gas exchange and hence, photosynthesis.

Conocephalum salebrosum (Figure 87-Figure 88) from Japan has more mucilage canals and mucilage cells

than most other members of the *Conocephalum conicum* complex there (Akiyama 2022). These most likely help it to conserve moisture in its drier habitats.

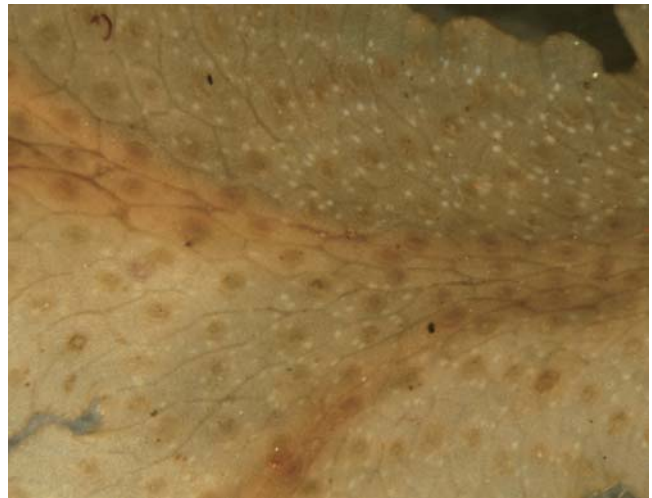


Figure 87. *Conocephalum salebrosum* from Japan, showing mucilage cells and canals. Photo courtesy of Hiroyuki Akiyama.



Figure 88. *Conocephalum salebrosum* from Japan, showing mucilage cells and canals in thallus cross section. Photo courtesy of Hiroyuki Akiyama.

In addition to its rhizoids and scales (Figure 80-Figure 83) for water movement and uptake, *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) often occurs in large mats (Figure 1) or mixed with other bryophytes (Figure 89-Figure 90) (Akiyama 2022). These closely intermingled plants can help to maintain moisture on the lower side of the plant where uptake occurs.



Figure 89. *Conocephalum* cf. *salebrosum* in Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 90. *Conocephalum* cf. *salebrosum*, *Mnium hornum*, and *Atrichum undulatum*. Photo by Bob Klips, with permission.

Reproduction

Showalter (1921) determined that the male and female chromosomes of *Conocephalum* cf. *salebrosum* (Figure 1, Figure 30-Figure 49) in Wisconsin and New York, USA, and in Copenhagen, Denmark, did not differ as they do in some **dioicous** liverworts, but that 1 of the 9 chromosomes was considerably smaller, a condition that apparently led to some earlier researchers finding only 8.

Antheridia in *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) are borne in receptacles on the thallus surface (Figure 91-Figure 94) and apparently not elevated by an elongated midrib as they are in *C. orientalis* (Figure 15) (see Conocephalaceae part 1 subchapter).



Figure 91. *Conocephalum* cf. *salebrosum* males. Photo by John Hribljan, with permission



Figure 92. *Conocephalum salebrosum* males from Canada. Photo by Jean Faubert, with permission.



Figure 93. *Conocephalum salebrosum* antheridial receptacle with bud scales at edge. Photo courtesy of Hiroyuki Akiyama.



Figure 94. *Conocephalum salebrosum* antheridial receptacle from Japan. Photo courtesy of Hiroyuki Akiyama.

Graham (1909) described the development of both the gametophyte and sporophyte of *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49). In New York, USA, the gametangiophore (Figure 95-Figure 105) begins development early in June. Archegonia are mature by the first of July. The development of the sporangia (Figure 104-Figure 105) is rather slow, with spores and elaters

maturing by the onset of winter. At that time, growth ceases. The stalk of the gametangiophore is still very short, with the conical head appearing to be sessile on the thallus. In the warmth of the following May, this archegoniophore elongates rapidly, lifting the receptacle well above the thallus surface (Figure 100-Figure 103). When the stalk of the sporangium elongates, the spores are released when the capsule ruptures. A surrounding sheath may protect the overwintering capsule from excessive radiation and transpiration.



Figure 95. *Conocephalum salebrosum* from Japan, with beginning of archegoniophore. Photo courtesy of Hiroyuki Akiyama.

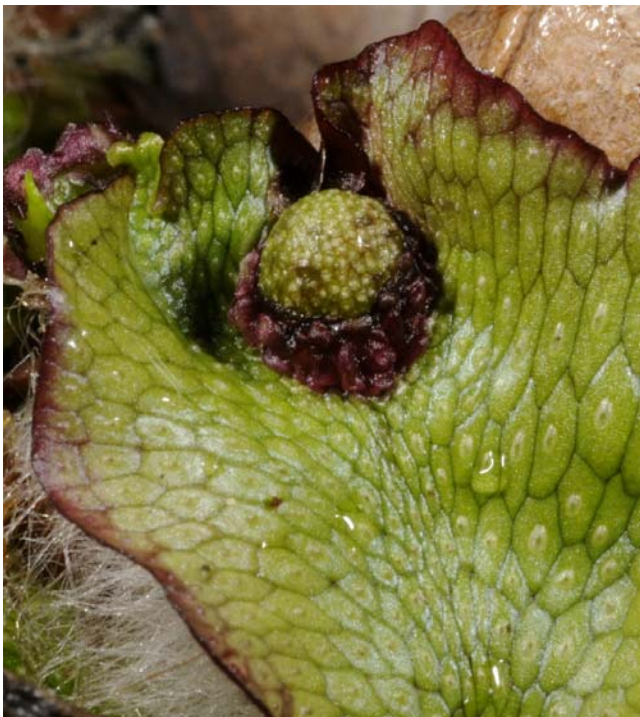


Figure 96. *Conocephalum salebrosum* with young archegoniophore. Photo by Jouko Rikkinen, through Creative Commons.



Figure 97. *Conocephalum salebrosum* with beginning archegoniophore, from Pfälzer Wald, Germany. Photo courtesy of Michael Lüth.



Figure 98. *Conocephalum* cf. *salebrosum* developing archegoniophore. Photo from Botany Website, UBC, with permission.

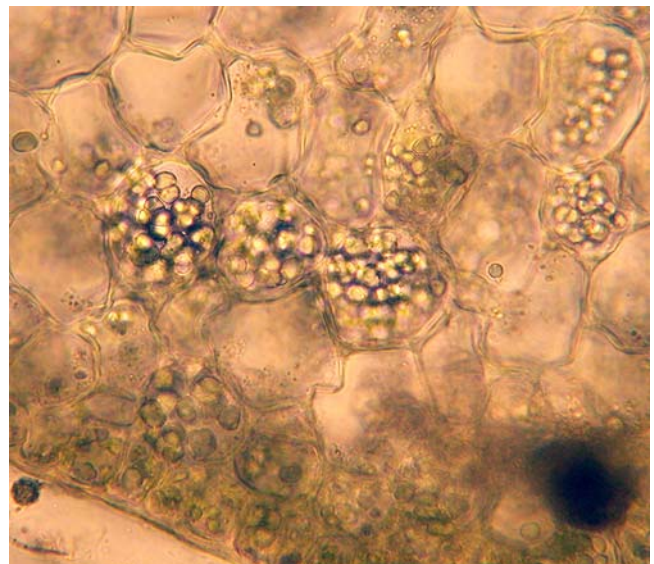


Figure 99. *Conocephalum salebrosum* archegoniophore stalk cs showing starch grains. Photo from Botany Website, UBC, with permission.



Figure 100. *Conocephalum* cf. *salebrosum* with elongating archegoniophores, floodplain, Rose Lake, Michigan, USA. Photo by Janice Glime.



Figure 103. *Conocephalum* cf. *salebrosum* with mature archegoniophores. Photo from Botany Website, UBC, with permission.



Figure 101. *Conocephalum salebrosum* with mature archegoniophores, in Merthyr Tidfyl, Wales. Photo by Des Callahan, with permission.



Figure 104. *Conocephalum salebrosum* archegoniophores with capsules.. Photo by Hermann Schachner through Wikimedia Commons.



Figure 102. *Conocephalum* c.f. *salebrosum* with archegoniophores on canyon wall, Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 105. *Conocephalum salebrosum* archegonial receptacle showing black sporangia, from Europe. Photo by Barry Stewart, with permission.

Taylor and Hollensen (1984) elaborated on this cycle for plants of *Conocephalum* cf. *salebrosum* (Figure 1, Figure 30-Figure 49) in Michigan, USA. Growth is initiated in March. The full reproductive cycle requires 21 months. Archegonia are initiated in August and fertilized the following June. The sporophyte matures in that autumn and spores are shed in the next spring. The thalli are under snow and dormant from December through February.

Ellen (1920) described the germination of the spores of *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) in Sinsinawa, Wisconsin, USA. Here, the spore mother cells are well developed before the beginning of September and the spores are freed from the mother cell walls about mid September. In Early October, growth and a heavy deposit of starch precede the cell division. Each sporeling has up to eight cells that remain in the spore wall (Figure 106). Before winter, the partition cell walls thicken, starch is deposited, and growth occurs by division of the spores. These multicellular sporelings remain through the winter. When warm weather returns, cell division resumes and continues until the stored food is gone. Cell division pauses and the cells expand, accompanied by a rapid development of chlorophyll and starch. This is followed by a second series of cell divisions until the sporelings become a spherical mass of 30-40 cells. As this mass matures, the archegoniophore elongates rapidly in 4-5 days to attain a height of 5-6 cm. At the same time, the seta on each capsule elongates and the capsule emerges through the calyptra and sheath. The capsule wall ruptures and sporelings and elaters are dispersed. Most of the sporelings are short-lived, but some survive up to 38 days of desiccation.

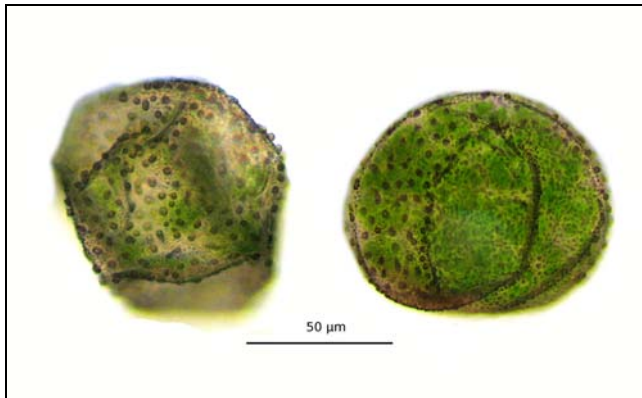


Figure 106. *Conocephalum salebrosum* multicellular spores resulting from endosporic development. Photo courtesy of Leica Chavoutier.

It appears that some spores of *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) might be dispersed while they are still small – one-celled (Ellen 1920). This strategy of multicellular spore spheres (sporelings) and single-celled spores would permit achieving a good start in the nearby habitat by dispersed spheres while permitting long-distance dispersal of the one-celled spores.

At the end of the growing season, apical buds form and older portions become moribund (Figure 107). In the spring, these buds expand and develop new plants (Figure 107-Figure 114), increasing the area covered due to branching.



Figure 107. *Conocephalum salebrosum* dead (moribund) and new growth at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 108. *Conocephalum* cf. *salebrosum* showing new growth at tips of older thalli, from Europe. Photo by Michael Lüth, with permission.



Figure 109. *Conocephalum* cf. *salebrosum* showing new growth and moribund older thalli, from Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 110. *Conocephalum* cf. *salebrosum* new growth, from Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 113. *Conocephalum* cf. *salebrosum* new growth and dead thalli at Hocking Hills, Ohio, USA. Photo by Janice Glime.

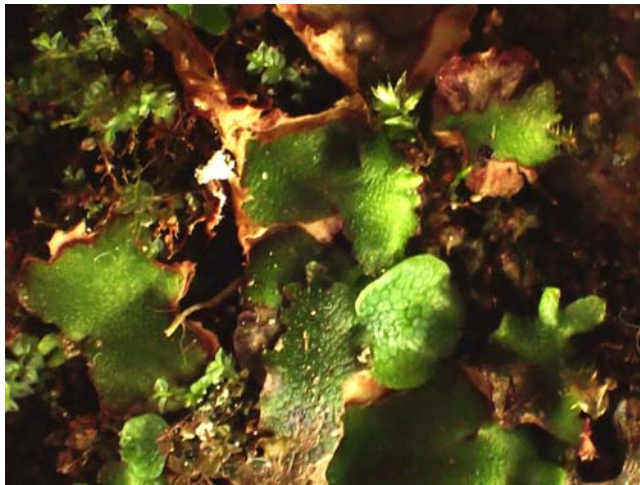


Figure 111. *Conocephalum* cf. *salebrosum* new growth on canyon walls, Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 114. *Conocephalum salebrosum* dead with new growth at Hocking Hills, Ohio, USA. Photo by Janice Glime.



Figure 112. *Conocephalum* cf. *salebrosum* new growth on canyon walls at Hocking Hills, Ohio, USA. Photo by Janice Glime.

By whatever mechanism, when *Conocephalum* cf. *salebrosum* (Figure 1, Figure 30-Figure 49) was growing in my garden room, it managed to appear in new locations around the room. It never had sexual structures. I attributed its dispersal to the movement of my box turtle, but I have no real proof. Unfortunately, I never caught anybody in the act.

Ainsworth (1965) reported bulbils in *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) from New York, USA, that had been kept in the dark for 28 days. These occur anywhere on the ventral surface, but when the midrib has bulbils still attached, these seem to inhibit the production of bulbils elsewhere on the thallus. An average of ~1.3 bulbils can occur in 1 mm² of thallus. This is not the first report of these structures. Karsten (1887) found them on thalli of *Conocephalum conicum* s.l. (Figure 17) that had been so completely overgrown by other thalli that they too, were in complete darkness.

These "bulbils" have been somewhat controversial. Paton (1993) referred to the tubers of *Conocephalum conicum* s.l. (Figure 17). that occur on the ventral surface of the midrib and become detached to form new plants, as described by MacVicar (1926) and again by Paton from Sussex, England. These likewise occurred on moribund

thalli (Figure 107). Paton noted that these dark-produced structures, termed bulbils by Ainsworth (1965), germinated in ~5 days when placed in moist conditions in the light.

Animal Interactions

When growing in my garden room, *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) had nibbles around its edges. These were triangular and best fit the hypothesis that they were eaten by the Society Finches or the Canary in the room.

In the field I have found evidence of herbivory, but in these cases the removal was not triangular. Instead, it occurred not only on the margins but also mid thallus and the eaten areas were of irregular shape (Figure 115-Figure 117). These could be the product of insects, isopods, or possibly snails.



Figure 115. *Conocephalum salebrosum* herbivory in the Upper Peninsula of Michigan. Photo courtesy of John Hribljan.



Figure 116. *Conocephalum* cf. *salebrosum* eaten in Houghton County, Michigan, USA, 6 August 2009. Photo by Janice Glime.



Figure 117. *Conocephalum* cf. *salebrosum* eaten in Houghton County, Michigan, USA. Nibbling on the edges suggests a large arthropod, perhaps an isopod. Photo by Janice Glime.

Fungal Interactions

Liepiņa (2012) reported that both *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49) and *C. conicum* (Figure 17) were "moderately" mycorrhizal. Both liverworts have Glomeromycotean endophytes and these fungi form nonseptate hyphae, vesicles, and arbuscules (see Figure 118), indicating that they created a functional symbiosis with the liverworts. The hyphae entered through the rhizoids and passed directly through the cell walls of the liverworts.

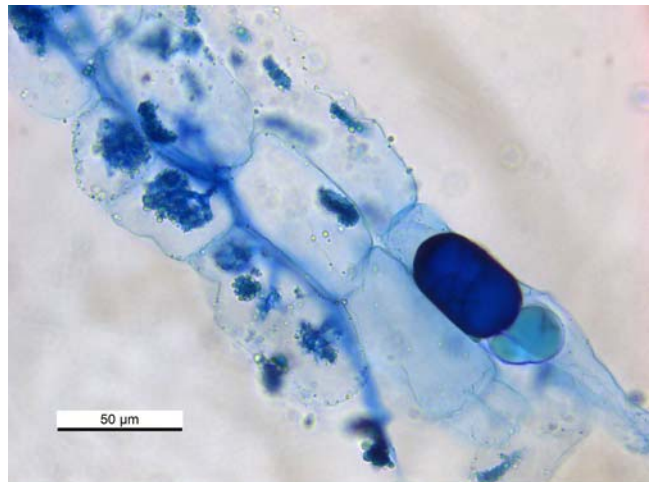


Figure 118. Vesicular arbuscular mycorrhizae in root cells, showing the form that might also show up in the thallus of *Conocephalum salebrosum*. Photo by Rit Rajarshi, through Creative Commons.

Biochemistry

It is likely that some of the biochemical work attributed to *Conocephalum conicum* (Figure 17) actually applies to *C. salebrosum* (Figure 1, Figure 30-Figure 49), but unless it is recent or in North America, voucher specimens from the study would need to be verified. Even then, since the two liverworts grow together, the assays might have included both species without having both represented in the voucher specimens.

Craft *et al.* (2016) attempted to demonstrate chemotypes in the *Conocephalum* complex in the southern Appalachian Mountains, USA. They used a common garden experiment, but found that the experiment became a common stress experiment that significantly altered the compositions of volatile compounds in *Conocephalum salebrosum* (Figure 1, Figure 30-Figure 49). This phenomenon might provide antiherbivory compounds in response to herbivory, as already known from tree leaves (see, for example, Moreira *et al.* 2012). It would also be interesting to know the cost of producing such compounds relative to the cost of herbivory.

Summary

When chemical and genetic analyses were done on the *Conocephalum conicum* complex, the researchers decided that division into multiple species was warranted. From that division, *C. salebrosum* was identified and determined to be holarctic, seemingly replacing what was known as *C. conicum* in North America. Then, in 2022, several Japanese species were segregated from *C. conicum*, including *C. purpureorubrum*.

Ecological information on *Conocephalum purpureorubrum* is scant due to its recent consideration as a different species. It occurs in both damp habitats and dry ones, sometimes occurring streamside or on steep slopes. Its life cycle seems to be the same as that of *C. conicum*, with no asexual structures known. It is unusual in always having at least some purplish color present on the ventral surface. It has mucilage canals, but it often lacks mucilage cells.

Conocephalum salebrosum occurs near water, but extends into drier habitats than those typical of *C. conicum*. Most of the North American populations may belong to this species, often occurring on rock in canyons, near waterfalls, and along stream margins. Scales and rhizoids facilitate water movement and uptake along the ventral surface. The species can suffer from herbivory, but it contains compounds that are potentially antiherbivorous. It also frequently has vesicular arbuscular mycorrhizae.

Acknowledgments

Bryonettors provided a wonderful array of images to illustrate this chapter. Thank you to Masaki Shimamura for providing me with the image of the explosive sperm dispersal in *Conocephalum cf. orientalis*. And thank you to Hiroyuki Akiyama for sending me his 2022 paper on the new species in Japan and providing me with original images.

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CHAPTER 1-22

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: CYATHODIACEAE, DUMORTIERACEAE

TABLE OF CONTENTS

Marchantiidae – Marchantiales	1-22-2
Cyathodiaceae	1-22-2
<i>Cyathodium bischlerianum</i>	1-22-4
Distribution	1-22-4
Aquatic and Wet Habitats.....	1-22-4
Reproduction	1-22-5
Biochemistry	1-22-5
<i>Cyathodium cavernarum</i>	1-22-5
Distribution	1-22-5
Aquatic and Wet Habitats.....	1-22-6
Adaptations	1-22-7
Reproduction	1-22-8
Interactions.....	1-22-9
Biochemistry	1-22-9
<i>Cyathodium foetidissimum</i>	1-22-9
Distribution	1-22-9
Aquatic and Wet Habitats.....	1-22-9
Adaptations	1-22-11
Reproduction	1-22-11
Interactions.....	1-22-12
Biochemistry	1-22-12
<i>Cyathodium spruceanum</i>	1-22-13
Distribution	1-22-13
Aquatic and Wet Habitats.....	1-22-13
Adaptations	1-22-13
Reproduction	1-22-13
Fungal Interactions.....	1-22-14
Biochemistry	1-22-14
Dumortieraceae	1-22-14
<i>Dumortiera hirsuta</i>	1-22-14
Distribution	1-22-15
Aquatic and Wet Habitats.....	1-22-27
Physiology.....	1-22-17
Adaptations	1-22-19
Reproduction	1-22-20
Role.....	1-22-23
Interactions.....	1-22-23
Fungal Interactions.....	1-22-23
Animal Interactions.....	1-22-23
Biochemistry	1-22-25
<i>Dumortiera hirsuta</i> ssp. <i>nepalensis</i>	1-22-27
Distribution	1-22-27
Aquatic and Wet Habitats.....	1-22-27
Biochemistry	1-22-27
Summary	1-22-27
Acknowledgments	1-22-28
Literature Cited	1-22-28

CHAPTER 1-22

AQUATIC AND WETLAND

MARCHANTIOPHYTA, CLASS

MARCHANTIOPSIDA – CYATHODIACEAE, DUMORTIERACEAE



Figure 1. *Dumortiera hirsuta* habitat in Europe. Photo by Michael Lüth, with permission

Marchantiidae – Marchantiales

Cyathodiaceae

There have been several taxonomic considerations of the genus *Cyathodium* (Schiffner 1938; Srivastava & Dixit 1996; Salazar Allen & Korpelainen 2006).

This family often occurs in moist habitats such as caves and stream banks. *Cyathodium* habitats are typically shaded and include river banks on soil or rocks, in waterfalls, caves, cement floors, stairs, and flowerpots, with some occurring as epiphytes (Salazar Allen & Korpelainen 2006). Large communities can occur on

unstable river banks where they can become submerged and sometimes become detached by flooding or drying. They are often associated with filamentous *Cyanobacteria* (Figure 32), but these are not endophytic. Endophytic fungi are known from wild populations of *C. spruceanum* (Figure 2) and *C. cavernarum* (Figure 3) in Panama (Salazar Allen unpublished data). Riverbank plants often provide substrate for diatoms, including *Surirella* (Figure 4), *Nitzschia* (Figure 5), *Amphora* (Figure 6), *Rhopalodia* (Figure 7), *Eunotia* (Figure 8), and possibly *Diploneis* (Figure 9) (Allen & Korpelainen 2006). The most aquatic of *Cyathodium* species is *Cyathodium bischlerianum* (Figure 10).



Figure 2. *Cyathodium spruceanum* males. Photo by José Gudiño L., courtesy of Noris Salazar Allen.



Figure 3. *Cyathodium cavernarum*, a species that grows on river and streambanks with *Cyathodium bischlerianum*. Photo by Renjusplace, through Creative Commons.

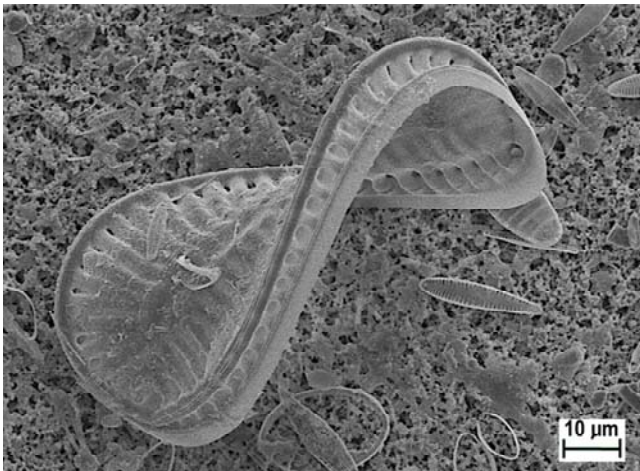


Figure 4. *Surirella spiralis*, in a genus of diatoms that often grows on species of *Cyathodium*. Photo by Nicola Angeli, through Creative Commons.

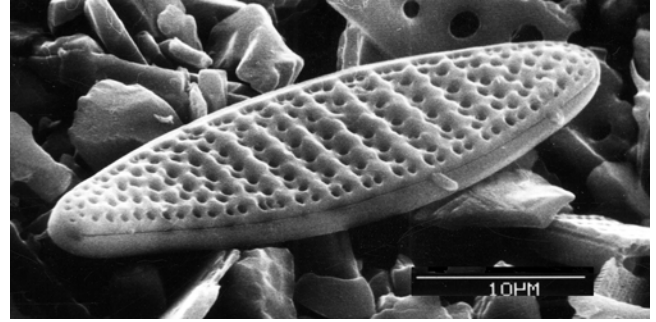


Figure 5. *Nitzschia kerguelensis*, in a genus of diatoms that often grows on species of *Cyathodium*. Photo by Hans Grobe, through Creative Commons.

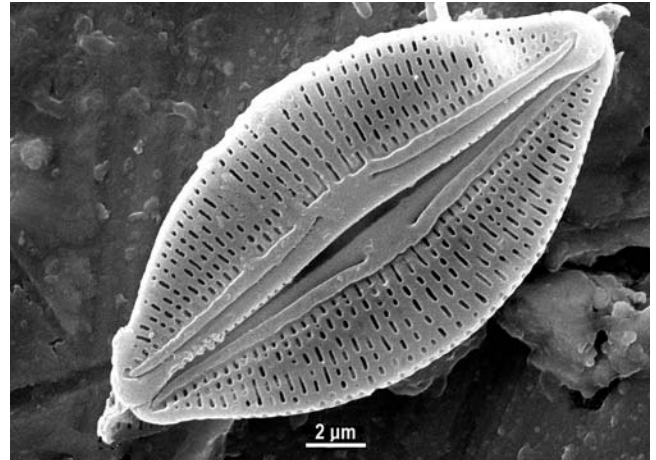


Figure 6. *Amphora* sp, in a genus of diatoms that often grows on species of *Cyathodium*. Photo by Berezovska, through Creative Commons.

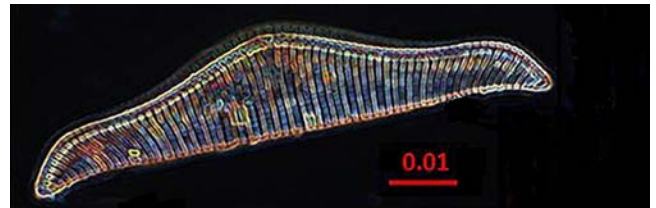


Figure 7. *Rhopalodia gibba*, in a genus of diatoms that often grows on species of *Cyathodium*. Photo by Leena Virta and Alf Norkko, through Creative Commons.



Figure 8. *Eunotia*, in a genus of diatoms that often grows on species of *Cyathodium*. Photo by National Museum of Natural History, through Creative Commons.

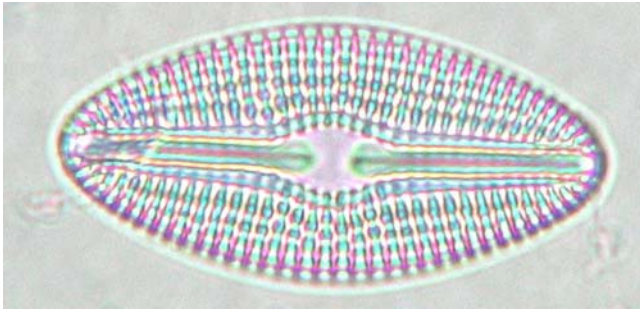


Figure 9. *Diploneis ovalis*, in a genus of diatoms that often grows on species of *Cyathodium*. Photo by Kristian Peters, through Creative Commons.

Members of *Cyathodium* prefer moist, shady habitats (Daniels 1998). Large communities of *Cyathodium* occur on unstable river banks in Costa Rica and Panama, and here they often experience submergence or become detached by floods. In other locations they are subject to drying on soil along cement road ditches in humid areas (Salazar Allen & Korpelainen 2006). The genus endures weak light intensities where it is able to grow on rock, soil, or in two species on bark. *Cyathodium* sp. (Figure 10) occurs over (overhanging?) water and in waterfalls in the tropics (Ruttner 1955). Although there are several semi-aquatic species in *Cyathodium*, Cavers (1910), citing Lang (1905) regarded it as a genus primarily adapted to shade, rather than as a hygrophyte.

Daniels (1998) noted that *Cyathodium* species lack the complex structure of many thallose liverworts, such as well-defined assimilatory and storage zones or scales.

Tiwari (1929a,b, 1935) studied the spore germination of *Cyathodium* spores. Crum (1976) noted that some of the species have spores that emit a yellowish luminescence. There are few spores in *Cyathodium* species, numbering 20-100 per capsule (Bischler-Causse *et al.* 2005).

Cyathodium bischlerianum (Figure 10)

Distribution

Cyathodium bischlerianum (Figure 10) is a Neotropical species known only from Panama (Salazar Allen 2001). Because of its small size and association with other *Cyathodium* species, it can easily be overlooked, and Salazar Allen suspects that it is more widely distributed in the Neotropics. For these reasons, information on it is also rather scant.



Figure 10. *Cyathodium bischlerianum* habit on tree near water. Photo by José Gudiño L., courtesy of Noris Salazar Allen.

Members of *Cyathodium* have a simple, slender, dichotomously branched thallus with no purple coloring (Figure 2-Figure 3). The pores are simple with a single ring of cells and no hyaline inner ring (Salazar Allen 2001; Bischler-Causse *et al.* 2005). The air chambers are empty. Most rhizoids are smooth, but some may be tuberculate. It has 2 rows of ventral scales, often restricted to the apex. Its asexual reproduction includes fragmentation of thallus segments and ventral tubers in some.

Aquatic and Wet Habitats

Cyathodium bischlerianum (Figure 10) is one of two species that can be corticolous (Salazar Allen & Korpelainen 2006). It typically grows mixed with other species of *Cyathodium* in very moist, shaded locations, particularly on rocks near or even in creeks, along eroding river banks, and in other locations subject to partial submergence during high water levels (Bischler-Causse *et al.* 2005). It is more mesic than *C. spruceanum* (Figure 2).

Cyathodium bischlerianum (Figure 10) occurs on stream and river banks, along with *C. cavernarum* (Figure 3), in the shaded, more moist habitats close to the rivers and seepage, whereas *C. spruceanum* (Figure 2) occurs on more upper slopes (Salazar Allen & Korpelainen 2006). *Cyathodium bischlerianum* also can occur on bark (Figure 11-Figure 12) near streams and rivers and in seepages and on moist rocks.



Figure 11. *Cyathodium bischlerianum* habit on bark. Photo by José Gudiño L., courtesy of Noris Salazar Allen.



Figure 12. *Cyathodium bischlerianum* on bark. Photo by José Gudiño L., courtesy of Noris Salazar Allen.

Reproduction

Cyathodium bischlerianum (Figure 10) is **monoicous** (Salazar Allen 2001; Bischler-Causse *et al.* 2005). The involucre can have 1 or 2 archegonia and sporophytes (Figure 13); male receptacles occur on the sides of the thallus. The species lacks any specialized asexual reproductive structures, with no tumors as found in dioicous members of the genus (Salazar Allen & Korpelainen 2006).



Figure 13. *Cyathodium bischleriana* thallus with sporangia. Photo by Noris Salazar Allen, with permission.

Cyathodium bischlerianum (Figure 10) is an **r-selected** species (Salazar Allen & Korpelainen 2006). This means that it has a high reproductive rate, its population size varies through time, and recolonization occurs every year, creating competition with itself and other species (Pianka 1970).

Biochemistry

Despite the newness of the species and its limited distribution, the biochemistry of *Cyathodium bischlerianum* (Figure 10) has been evaluated. It is unique among the *Cyathodium* species, containing mostly aromatic monoterpenes (Salazar Allen *et al.* 2017). It has less than 3% of the sesquiterpenes germacrene D and bicyclogermacrene.

Nerolidol is the main compound among these (Salazar Allen *et al.* 2017). This compound has a floral and woody fragrance (Padalia *et al.* 2015). Already known from other plants, it has been approved for use in fine fragrances, cosmetics, shampoo, soaps, detergents, and cleaning products (Padalia *et al.* 2015; Boskabady *et al.* 2014). The industry level consumption is 10-100 tons per year (Queiroga *et al.* 2014).

Cyathodium cavernarum (Figure 14-Figure 15)

syn. = *Cyathodium africanum*, *C. barodae*, *C. mexicanum*

Distribution

Cyathodium cavernarum (Figure 14-Figure 15) is a widespread pantropical species (Lye & Pócs 1997) and is the most widespread species in the genus (Bischler-Causse *et al.* 2005). It is known from China (Zhang *et al.* 2004a), Japan (Furuki *et al.* 2012), India, Java, Africa, Madagascar (Srivastava & Dixit 1996; Reeb *et al.* 2018), western Australia (Meagher 2002), and the American tropics in Colombia (Winkler 1976), Mexico, Costa Rica, Panama, Cuba, and Brazil (Srivastava & Dixit 1996; Salazar Allen 2005; Salazar Allen & Korpelainen 2006; Gradstein *et al.* 2016; Reeb *et al.* 2018). Shah and Gujar (2016) reported that *Cyathodium cavernarum* was the most widely distributed liverwort species in Gujarat, India.



Figure 14. *Cyathodium cavernarum* on roof of cave. Photo by Célio Moura Neto, through Creative Commons.



Figure 15. *Cyathodium cavernarum* showing young and old thalli. Photo by Eric Hough, through Creative Commons.

Aquatic and Wet Habitats

Lye and Pócs (1997) reported *Cyathodium cavernarum* (Figure 14-Figure 15) growing on overhanging, dripping, or sprayed rocks as well as temporarily inundated muddy forest floor low areas of Uganda. On river banks, it occupies lower positions than does *C. spruceanum* (Figure 2), preferring more shaded, damper sites or those with seepage (Bischler-Causse *et al.* 2005; Salazar Allen & Korpelainen 2006). In the Northern Western Ghats it is usually found in low altitudes where there is human habitation or shaded disturbed areas (Nair & Prajitha 2016). Glenny (2002) similarly reported it from stream and river banks in Australia.

Cyathodium cavernarum (Figure 14-Figure 15) usually occurs on calcareous substrata but it can also occupy slightly acidic substrates with underlying calcareous bedrock (Bischler-Causse *et al.* 2005). Its substrata include soil, wet rocks, walls, and termite mounds in moist deciduous, semi-evergreen, or evergreen forests (Nair & Prajitha 2016). In exposed habitats it is typically associated with members of the **Pottiaceae** (Figure 16); in ravines and river banks with species of *Philonotis* (Figure 17), *Fissidens* (Figure 18), *Notothylas* (Figure 19), *Racopilum tomentosum* (Figure 20), *Cyathodium spruceanum* (Figure 2), and **Lejeuneaceae** (Figure 21) (Bischler-Causse *et al.* 2005).



Figure 16. *Syntrichia ruralis*, a member of the **Pottiaceae**, a family that often occurs with *Cyathodium cavernarum*. Photo by Alexis Orion, through Creative Commons.



Figure 17. *Philonotis*, member of a genus that is often associated with *Cyathodium cavernarum*. Photo by A. Neuman, through Creative Commons.



Figure 18. *Fissidens fontanus*, member of a genus that is often associated with *Cyathodium cavernarum*. Photo by Bob Klips, with permission.



Figure 19. *Notothylas orbicularis*, member of a genus that is often associated with *Cyathodium cavernarum*. Photo by Christian , through Creative Commons.



Figure 20. *Racopilum tomentosum*, a species that is often associated with *Cyathodium cavernarum*. Photo by David Tng, with permission.



Figure 21. *Lejeunea flava*, member of a family that is often associated with *Cyathodium cavernarum*. Photo by Scott Zona, through Creative Commons.

Although caves are not aquatic habitats, they are often wet and at least damp, providing suitable habitat for *Cyathodium cavernarum* (Figure 22-Figure 25) including the Birds'-Nest Cave near Niah, Sarawak, Borneo (Holtum 1938). Reeb *et al.* (2018) likewise found this species at cave entrances in Madagascar, occupying naked, compact soils that were shady. And Furuki *et al.* (2012) found it on soil of a limestone cave in Japan and Zhang *et al.* (2004a,b) in karst caves of China.



Figure 22. *Cyathodium cavernarum* iridescence on wall of ruins in Bombay. Photo ©Patrick Blanc, with permission.



Figure 23. *Cyathodium cavernarum* on rock in cave. Photo by Cédric de Foucault, through Creative Commons.



Figure 24. *Cyathodium cavernarum* in cave. Photo by Cédric de Foucault, through Creative Commons.



Figure 25. *Cyathodium cavernarum* on cave ceiling. Photo by Célio Moura Neto, through Creative Commons.

Adaptations

Cyathodium cavernarum (Figure 14-Figure 15) exhibits a bright metallic-green color (Figure 26-Figure 27) (Bischler-Causse *et al.* 2005). Reeb *et al.* (2018) described it as iridescent, with colors that change when viewed from various angles. Zhang *et al.* (2004b) described it as luminous with a "peculiar light-reflecting power which produces a kind of starry effect, so that the plants seem to flood the dark caves where they grow with a luminous, golden-green light."



Figure 26. *Cyathodium cavernarum* iridescence in Bombay. Photo ©Patrick Blanc, with permission.



Figure 27. *Cyathodium cavernarum* showing iridescent colors. Photo by Jan-Peter Frahm, with permission.

But what does this peculiar light reflection mean for the liverwort? Does it increase the ability to capture light for photosynthesis? Does it attract some sort of invertebrate that henceforth carries sperm or fragments, thus aiding in dispersal? This is a mystery that needs to be investigated.

Water can collect on the thallus and remain there for some time (Figure 28), helping the plant to remain hydrated. This may be the mechanism that permits it to live in caves where it doesn't rain.



Figure 28. *Cyathodium cavernarum* with accumulated water droplets. Photo from Idleggraphics, through Creative Commons.

Cyathodium cavernarum has pores in the thallus that increase the loss of water (Figure 29). As with many liverworts, *C. cavernarum* (Figure 14-Figure 15) often benefits from the added water retention of living among mosses (Figure 30).

Reproduction

Cyathodium cavernarum (Figure 14-Figure 15) is **monoicous** (Srivastava & Dixit 1996; Bischler-Causse *et al.* 2005). Salazar Allen and Korpelainen (2006) demonstrated that *C. cavernarum* and *C. spruceanum* (Figure 2) have more similar genetics from nearby geographic areas than those from more distant areas, suggesting a role of sexual reproduction. Sporelings in culture develop initial filamentous growth followed by apical development into the thallus.

In addition to sexual reproduction, it can reproduce by fragments and spread by branching (Figure 31) (Bischler-Causse *et al.* 2005). Tubers are unknown in this and other monoicous species (Salazar Allen & Korpelainen 2006).

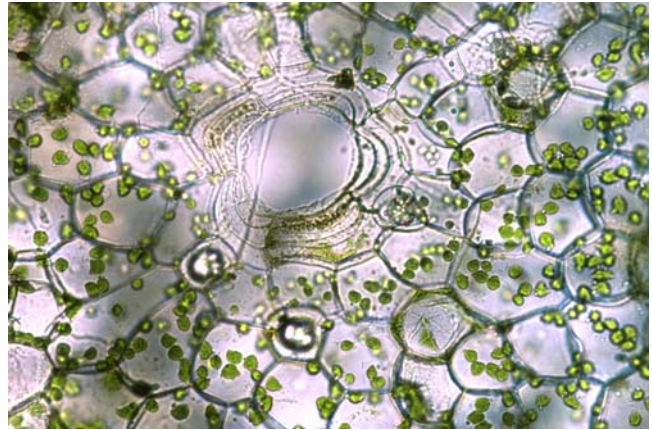


Figure 29. *Cyathodium cavernarum* pore showing layers of cells surrounding it. Photo courtesy of Noris Salazar Allen.



Figure 30. *Cyathodium cavernarum* growing among mosses. Photo by Célio Moura Neto, through Creative Commons.



Figure 31. *Cyathodium cavernarum* showing young thalli mixed with old ones. Some show branching. Others may be derived from fragments or spores. Photo by Eric Hough, through Creative Commons.

Interactions

Cyanobacteria (Figure 32) are common associates of *Cyathodium cavernarum* (Figure 14-Figure 15) (Bischler-Causse *et al.* 2005). Fungal endophytes are known from *Cyathodium cavernarum* in Panama (Salazar Allen & Korpelainen 2006).

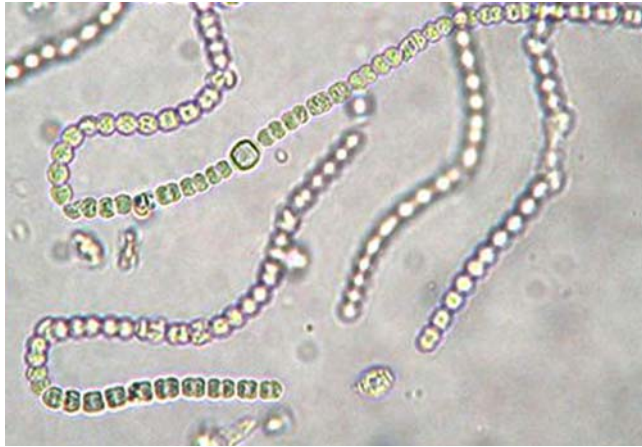


Figure 32. *Nostoc commune*, one of the **Cyanobacteria** often associated with bryophytes. Photo by Kristian Peters, through Creative Commons.

Biochemistry

Salazar Allen *et al.* (2017) found that *Cyathodium cavernarum* (Figure 14-Figure 15) has a distinct chemical composition with an octane derivative as its major compound, suggesting that this could be used as a chemical marker for the species. Nevertheless, Ulka and Karadge (2010) found little antimicrobial activity by extracts of *Cyathodium cavernarum*. Furthermore, Surendra Kumar *et al.* (2014-15) found that extracts of *C. cavernarum* were ineffective, compared to a standard drug, in causing paralysis or death in the Indian earthworm *Pheretima posthuma* (see Figure 33). It is interesting that this widespread species seems to lack the usual liverwort ability to inhibit potentially deadly organisms. Could it be that these other organisms seldom occur where it lives? Or does it have associated bacteria or fungi that accomplish this purpose?



Figure 33. *Pheretima praepinguis* from China; *P. posthuma* is unaffected by extracts of *Cyathodium cavernarum*. Photo by Panzer VI-II, through Creative Commons.

Cyathodium foetidissimum (Figure 34)

Cyathodium foetidissimum (Figure 34) is the largest of the *Cyathodium* species (Lang 1905).



Figure 34. *Cyathodium foetidissimum*. Photo by Philippe Birnbaum, with permission.

Distribution

Cyathodium foetidissimum (Figure 34) is Asiatic with limited records in the Neotropics (Salazar Allen *et al.* 2004). It is known from Java, Sumatra, Tahiti, Nukahiva (Srivastava & Dixit 1996), Cameroon (Wigginton 2002; Wigginton & Grolle 1996), Costa Rica (Salazar Allen *et al.* 2004), Ecuador (Bischler-Causse *et al.* 2005), and Colombia (Gradstein *et al.* 2016). The specimens from Ecuador might represent an error in identification. They have tubers (otherwise unknown in *C. foetidissimum*) and the uppermost thallus cells exceed the size of those found in specimens from Costa Rica (Bischler-Causse *et al.* 2005).

Duckett and Ligrone (2006a) reported the first record of *Cyathodium* in Europe. This they identified as *Cyathodium foetidissimum* (Figure 34). It was located in southern Italy, outside its normal tropical range. They suggested that it was probably a pre-glacial relic rather than a recent arrival from sub-Saharan Africa.

Aquatic and Wet Habitats

Lang (1905) described the habitat of *Cyathodium foetidissimum* (Figure 34) in Perak, Malaysia, as one on rocks in deep forest shade, especially on vertical faces of damp rocks. Salazar Allen and Korpelainen (2006) found that it is more mesic than is *C. spruceanum* (Figure 2). Lang (1905) considers it to be more adapted to shade conditions, rather than being a **hygrophyte** (plant that grows in wet conditions). Angeles *et al.* (2020) described the species as rupestrine, occurring as **chasmophytes** (plants growing in fissures and cracks of limestone) on rock.

In Costa Rica this species forms small patches in depressions in very shady conditions on sandy limestone rock (Bischler-Causse *et al.* 2005); it also occurred in a limestone valley in Italy (Duckett & Ligrone 2006a). Its common associates include *Dumortiera hirsuta* (Figure 35), *Marchantia* (Figure 36), *Fissidens flaccidus* (Figure

37), *Taxiphyllum taxirameum* (Figure 38), and *Lejeuneaceae* (Figure 21).



Figure 35. *Dumortiera hirsuta*, a common associate of *Cyathodium foetidissimum* in Costa Rica. Photo by David T. Holyoak, with permission.



Figure 36. *Marchantia polymorpha* ssp. *montivagans*, in a genus that is a common associate of *Cyathodium foetidissimum* in Costa Rica. Photo by Claire Halpin, with permission.



Figure 37. *Fissidens flaccidus* a common associate of *Cyathodium foetidissimum* in Costa Rica. Photo by Vinod Deora and Deora G.S., through Creative Commons.



Figure 38. *Taxiphyllum taxirameum*, a common associate of *Cyathodium foetidissimum* in Costa Rica. Photo by Bob Klips, with permission.

In Mali, Philippe found it in small caves on rocks (Figure 39-Figure 41).



Figure 39. *Cyathodium foetidissimum* in cave in Mali. Photo by Philippe Birnbaum, with permission.



Figure 40. *Cyathodium foetidissimum* in Mali. Photo by Philippe Birnbaum, with permission.



Figure 41. *Cyathodium foetidissimum* in small cave in Mali. Photo by Philippe Birnbaum, with permission.

Adaptations

Cyathodium foetidissimum (Figure 40) has a multistratose region of cells in the mid region of the thallus (Salazar Allen *et al.* 2004). These could give the thallus greater strength or act as a storage region, but the function needs to be explored. The oil cells have a single oil body. Unlike some species in the genus, this one has strongly dimorphic rhizoids (smooth and pegged) and large ventral scales, both adaptations that could facilitate water movement and uptake.

Srivastava and Dixit (1996) described the thalli as brownish-green and delicate, but usually larger than those of other species in *Cyathodium*. They likewise described large ventral scales, occurring just behind the involucre.

When Duckett and Ligrone (2006a) found this species in Italy, they discovered internal cells in the air chambers, the only report of such internal cells in the genus.

Cyathodium foetidissimum (Figure 40) has a phosphorescent appearance (Figure 42) – another mystery (Lang 1905; Salazar Allen *et al.* 2004). Duckett and Ligrone (2006a) suggested that this might enhance its light interception.

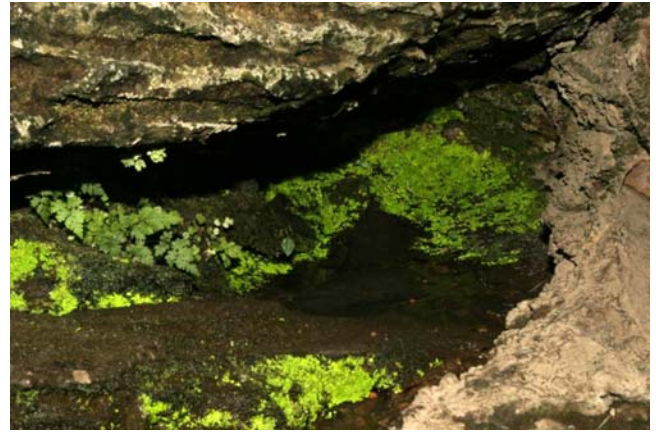


Figure 42. *Cyathodium foetidissimum* in cave in Mali. Photo by Philippe Birnbaum, with permission.

Reproduction

Cyathodium foetidissimum (Figure 40) is **monoicous**, but can also produce unisexual male plants in the same population (Salazar Allen *et al.* 2004). The male receptacle is apical with archegonia, wrapped in undulate laminar involucre, flanking it. It is **protandrous** (antheridia appear before archegonia).

The antheridia occur on short, disc-shaped antheridiophores (Srivastava & Dixit 1996). Archegonia are enclosed by an involucre that sits below the apex at the base of a sinus. Like those in *Targionia hypophylla* (Figure 43), antheridial receptacles occur not only on ventral shoots, but also on the main shoot along the midrib (Kashyap 1914).



Figure 43. *Targionia hypophylla*, a species that, like *Cyathodium foetidissimum*, has antheridial receptacles arising from both ventral shoots and main shoots. Photo by Ken-Ichi Ueda, through Creative Commons.

The capsule has an operculum of only 12 cells. Spores are verrucose (Salazar Allen *et al.* 2004). The spores initially germinate into a filamentous phase in culture (Salazar Allen & Korpelainen 2006). This is followed by apical development of thalli.

Cyathodium foetidissimum (Figure 40) grows in the rainy season, dying back when the dry season begins (Salazar Allen & Korpelainen 2006). Where the habitat is wetter and shaded on the banks of creeks and rivers, it is able to persist for more than one year.

Interactions

Cyanobacteria (Figure 32) are known associates of all species of *Cyathodium* (Salazar Allen & Korpelainen 2006).

Fungi are known to associate with *Cyathodium foetidissimum* (Figure 40) in the Malay Peninsula (Lang 1905) and in Italy (Duckett & Ligrone 2006a).

Biochemistry

Many liverworts have distinctive odors. As its name suggests, *Cyathodium foetidissimum* (Figure 40) is recognizable by its bad smell (Gradstein 2011). Sakurai *et al.* (2018) described it as the smell of an old person or old chest of drawers, but also called it a nostalgic odor. Collections from Tahiti were described as having a pleasant odor, whereas those in the Marquesas Islands smelled like urine and feces.

Ludwiczuk *et al.* (2009) found skatole, a well known compound produced by biodegradation of tryptophan and responsible for the fecal odor of *Cyathodium foetidissimum* (Figure 40). This species also biosynthesized izolepidozene (3.1%) and lunularin (2.4%). Izolepidozene is the main volatile component of *Conocephalum japonicum* (Figure 44) and *Marchantia emarginata* ssp. *tosana* (Figure 45). Among the six species of Polynesian liverworts tested, Ludwiczuk *et al.* (2010) found that each had a unique combination of volatile compounds.



Figure 44. *Conocephalum japonicum*, a species that, like *Cyathodium foetidissimum*, has the compound izolepidozene. Photo by David Long, with permission.



Figure 45. *Marchantia emarginata* ssp. *tosana*, a species that, like *Cyathodium foetidissimum*, has the compound izolepidozene. Photo by Lin Shanxiong, through Creative Commons.

Sakurai *et al.* (2018) identified three volatile components [4-methoxystyrene (24.4%), 3,4-dimethoxystyrene (28.7%), and skatole (15.9%)], as well as several aliphatic aldehydes [n-octanal, n-nonanal, and n-decanal] from Tahitian specimens. However, they did not find (E)-2-nonenal, a recognized compound causing an aged foul odor. Sakurai *et al.* (2018) found that a methanol extract ($100 \mu\text{g mL}^{-1}$) showed no activity against *Bacillus subtilis* (Figure 46), *Staphylococcus aureus* (Figure 47), *Escherichia coli* (Figure 48), or *Klebsiella pneumoniae* (Figure 49), although a number of bryophytes do show activity against these. Perhaps the volatile compounds have a role in antiherbivory?

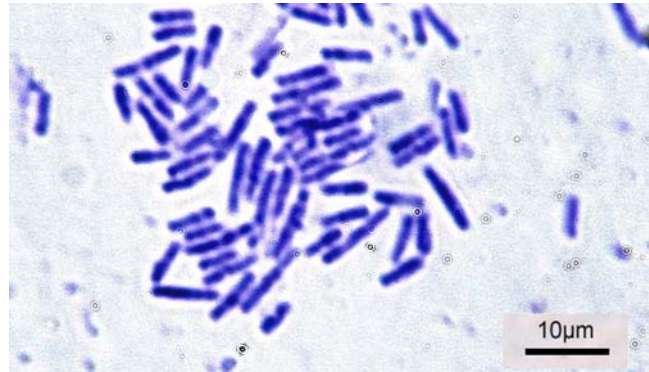


Figure 46. *Bacillus subtilis*, a bacterium that is not inhibited by methanol extracts of *Cyathodium spruceanum*. Photo by Graham Beards, through Creative Commons.

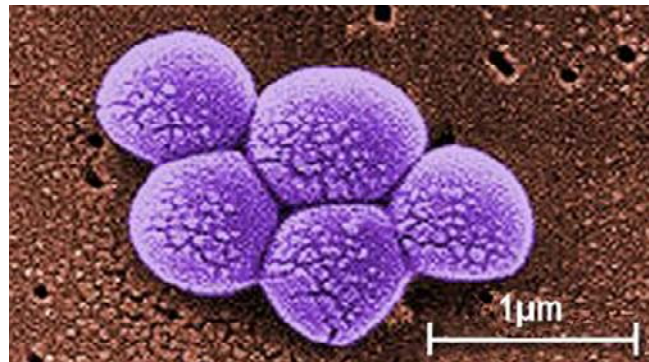


Figure 47. *Staphylococcus aureus*, a bacterium that is not inhibited by methanol extracts of *Cyathodium spruceanum*. Photo by Janice Haney Carr, through public domain.

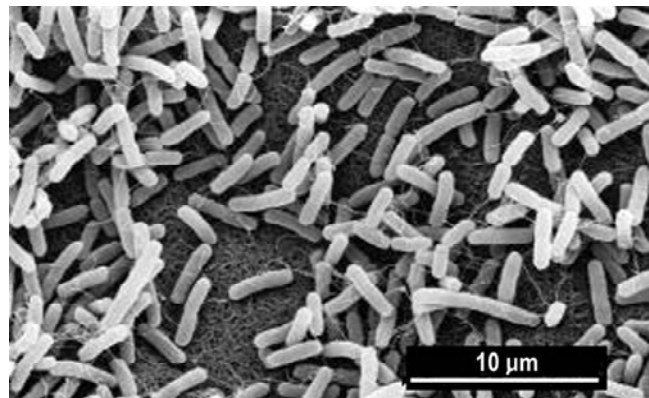


Figure 48. *Escherichia coli*, a bacterium that is not inhibited by methanol extracts of *Cyathodium spruceanum*. Photo by David Gregory & Debbie Marshall, through Creative Commons.



Figure 49. *Klebsiella pneumoniae*, a bacterium that is not inhibited by methanol extracts of *Cyathodium spruceanum*. Photo by NIAID, through Creative Commons.

Of four species of *Cyathodium*, Salazar Allen *et al.* (2017) found indole compounds only in *C. foetidissimum*. The researchers suggested that indole compounds could be used as species markers.

***Cyathodium spruceanum* (Figure 50)**

Among four Neotropical species they examined, Salazar Allen and Korpelainen (2006) found the greatest genetic differences between *Cyathodium foetidissimum* and *C. spruceanum* (Figure 50).



Figure 50. *Cyathodium spruceanum*. Photo by Jose De Gracia, through Creative Commons.

Distribution

Cyathodium spruceanum (Figure 50) is endemic to South America (Srivastava & Dixit 1996) in the Neotropics (Salazar Allen & Korpelainen 2006).

Aquatic and Wet Habitats

Cyathodium spruceanum (Figure 50) typically grows in homogeneous patches on exposed places (Salazar Allen & Korpelainen 2006). Proskauer (1951) reported the original *C. spruceanum* at the edge of a forest stream. The populations are usually rather large in years experiencing high rainfall. The species is less mesic than *C. cavernarum* (Figure 3) or *C. bischlerianum* (Figure 10), with *C. spruceanum* growing farther up the banks in less shaded, less damp habitats that are less mesic. At the Ratu Boko temple in Java, *Cyathodium spruceanum* occurs on limestone (Aryani 2014).

Adaptations

Cyathodium spruceanum (Figure 50) has a thallus that is light-green to whitish-green (Srivastava & Dixit 1996). However, Proskauer (1951) described it as iridescent with light-reflecting lens cells in the roofs of the air chambers. Other than the dark colors that protect against bright sun, little seems to be known about the adaptive values, if any, of some of the colors in bryophytes.

The thalli are overlapping (Srivastava & Dixit 1996), potentially helping to conserve water. Scales provide protection of the growing points (Proskauer 1951).

This species has numerous rhizoids, but the straight, smooth ones predominate (Proskauer 1951; Srivastava & Dixit 1996).

Reproduction

Cyathodium spruceanum (Figure 50) is **dioicous** (Srivastava & Dixit 1996). The female receptacles are ventral pouches. Male (Figure 51) and female plants can grow close to each other, permitting frequent fertilization success (Salazar Allen & Korpelainen 2006). Salazar Allen *et al.* (2017) found that the chemical composition of males and females was very similar, with three compounds found only in females [12-norcyercene-B, longifolenaldehyde and 1(5)-3-aromadenedraidene were found only in female plants].



Figure 51. *Cyathodium spruceanum* males. Photo by José Gudiño L., courtesy of Noris Salazar Allen.

Sporophytes are produced in abundance (Salazar Allen & Korpelainen 2006). Spores are numerous (>400 in a capsule). In culture, these can produce males and female gametophytes in the same year as produced, but there are no field observations to demonstrate germination in the same year as production. Salazar Allen and Korpelainen suggested that this delay in germination is due to soil dryness when the spores are released, a phenomenon that occurs because they are released at the onset of the dry season.



Figure 52. *Cyathodium spruceanum* with sporangia (S). Photo courtesy of Noris Salazar Allen.

The species of *Cyathodium* are **r-selected species** (Salazar Allen & Korpelainen 2006). **R-selected species** generally have high growth rates, produce many offspring, but have a low probability of survival to adulthood. The numerous offspring are able to exploit niches that are less crowded. The abundant sporophytes and spores permit *C. spruceanum* (Figure 50) to be among the better of the *Cyathodium* species at achieving high levels of reproduction. Long-term studies on individual populations are lacking.

The spores of *Cyathodium spruceanum* (Figure 50) are lamellate-reticulate (Salazar Allen *et al.* 2004). The sporeling initially produces a budlike protonema (Salazar Allen & Korpelainen 2006). From this structure, a thallus develops.

Cyathodium spruceanum (Figure 50) is one of the species in the genus to produce ventral tubers (Salazar Allen & Korpelainen 2006). These generally develop in the middle of the rainy season and remain attached to the parent thallus until the thallus decays. In culture, tubers are produced in abundance when nutrients are depleted. The tubers produce numerous rhizoids on their distal portion.

They germinate on agar, but germination in the field has thus far not been observed. Salazar Allen and Korpelainen suggest that when the tubers are covered by mud, they may remain dormant until the next season or become part of the diaspore bank to recolonize if the population is destroyed or if the growing season is extended with plentiful water.

Fungal Interactions

In Panama, fungal endophytes are known from *Cyathodium spruceanum* (Figure 50) (Salazar Allen & Korpelainen 2006). These interactions have barely been explored by bryologists, but mycological literature is not so scarce.

Biochemistry

As in *Cyathodium bischlerianum* (Figure 10), *C. spruceanum* (Figure 50) has less than 3% of the sesquiterpenes germacrene D and bicyclogermacrene (Salazar Allen *et al.* 2017). Oil bodies are present in all cells with the chloroplasts in this species, but the odor is not as offensive as that of *C. foetidissimum*. Nevertheless, the researchers identified far more volatile compounds in *C. spruceanum* than in the other four *Cyathodium* species assessed. Salazar Allen and coworkers identified 12-norcyercene B (70.2%), germacrene D (1.6%), and longifolinaldehyde (1.4%).

Dumortieraceae

Dumortiera hirsuta (Figure 53-Figure 55)

Most bryologists seem to recognize only one species of *Dumortiera* (Figure 53-Figure 55). However, Forrest *et al.* (2011) found two very distinct lineages, represented by ssp *hirsuta* (Figure 53-Figure 55) and ssp *nepalensis* (Figure 102-Figure 103). One (ssp. *hirsuta*) is restricted to Central America and the other (ssp. *nepalensis*) is more widely distributed throughout the range of the genus. See also the discussion of Taiwan populations (Akiyama *et al.* 2003). Forrest and coworkers concluded that there are at least two distinct species, a conclusion reached by O'Hanlon in 1934, but that the molecular basis for naming these is not known for much of the distribution. Therefore, in this chapter I will treat all as *Dumortiera hirsuta* (Figure 53-Figure 55) since most of the publications cited here do not distinguish these.



Figure 53. *Dumortiera hirsuta* mature colony. Photo through Creative Commons.



Figure 54. *Dumortiera hirsuta* s.l. Photo by Nicola van Berkel, through Creative Commons.



Figure 55. *Dumortiera hirsuta* on soil. Photo by Cheong Weei Gan, through Creative Commons.

More recently, the chloroplasts (Kwon *et al.* 2019a) and mitochondria (Kwon *et al.* 2019b) of Korean populations of this liverwort have been sequenced.

Distribution

Dumortiera hirsuta (Figure 53-Figure 55) is widely distributed in tropical and subtropical regions, extending into some temperate regions (O'Hanlon 1934; Forrest *et al.* 2011). It is rare in Europe (Aleffi *et al.* 1998), reaching its northernmost distribution in the UK (Callaghan 2020). In the same year Gaston (2020) found it in France.

This distribution includes more humid and warmer regions of the temperate zones of India, Nepal, Japan, Brazil, México, Jamaica, North and South America, Europe, British Isles, New Zealand, Hawaii, and Africa (O'Hanlon 1934; Nair *et al.* 2005). In the USA it is found in southeastern states, including Arkansas (Timme & Redfearn 1997).

Aquatic and Wet Habitats

Reeb *et al.* (2018) describe the habitat of *Dumortiera hirsuta* (Figure 53-Figure 55) as a shady, humid environment. Tosun *et al.* (2015) considered it to be a large thalloid on wet rocks. Gaston (2020) described it as a pantropical hydrophile.

Dumortiera hirsuta (Figure 53-Figure 55) occurs on dripping rocks (Watson 1919). Ruttner (1955) reported it in water spray, tuff wall, <40 cm above water level, and waterfalls (Figure 1) in the tropics. McAllister *et al.* (2019) found it to be common on rocks in deep canyons, in riparian habitats, on seepy hillsides, and abundant on shale near seepages. It could occur near tributaries, on slopes near or on the underside of sandstone ravines, and at springs (Figure 56-Figure 60).



Figure 56. *Dumortiera hirsuta* in a wet habitat in the UK. Photo by David T. Holyoak, with permission.

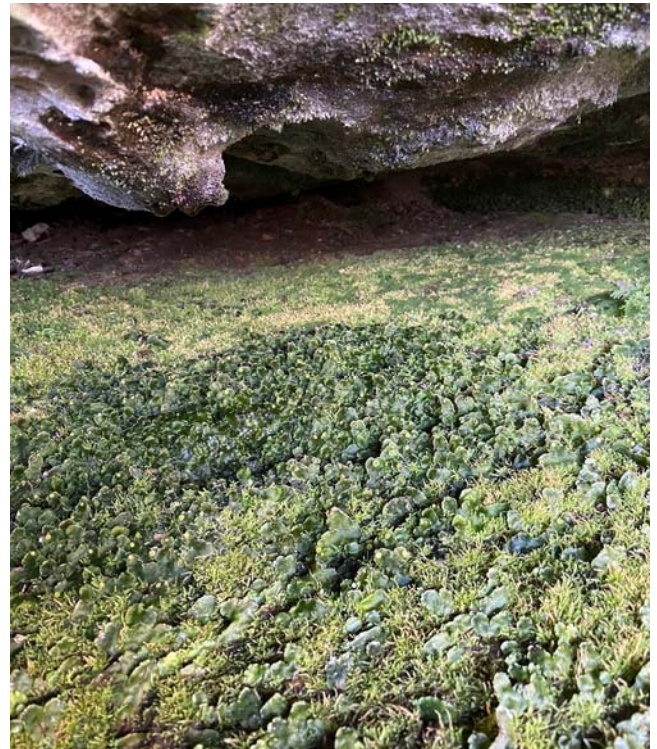


Figure 57. *Dumortiera hirsuta* habitat. Photo by Abel Kinser, through Creative Commons.



Figure 58. *Dumortiera hirsuta* on sandstone. Photo by Vitaly Charny, through Creative Commons.



Figure 61. *Plagiothecium nemorale*, an associate of *Dumortiera hirsuta* in Portugal. Photo by Hermann Schachner, through Creative Commons.



Figure 59. *Dumortiera hirsuta* where the liverwort can be found on the wet stream banks. Photo by Michael Lüth, with permission.



Figure 62. *Aneura pinguis*, an associate of *Dumortiera hirsuta* in Portugal. Photo by Proyecto Musgo, through Creative Commons.



Figure 60. *Dumortiera hirsuta* habitat on wet soil among rocks. Photo by Luis Funez, through Creative Commons.

Vieira *et al.* (2005) found that in Portugal it was not extensive but seemed stable in steep, water-dripping granite surfaces next to waterfalls. It was also found at the margin of fast flow in a streambed, where it was submerged for long periods and grew associated with *Plagiothecium nemorale* (Figure 61), *Aneura pinguis* (Figure 62), *Pellia epiphylla* (Figure 63), and *Riccardia multifida* (Figure 64), in mountain streams of northwest Portugal (Vieira *et al.* 2005).



Figure 63. *Pellia epiphylla*, an associate of *Dumortiera hirsuta* in Portugal. Photo by Bernd Haynold, through Creative Commons.

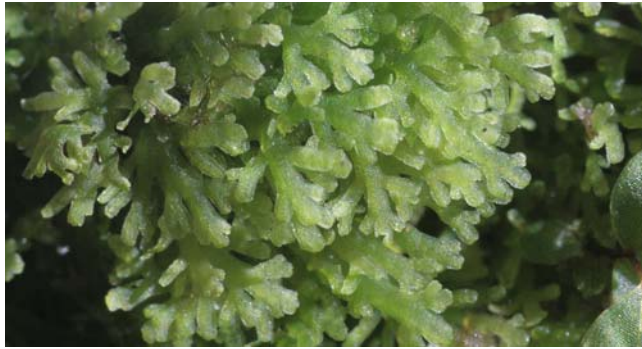


Figure 64. *Riccardia multifida*, an associate of *Dumortiera hirsuta* in Portugal. Photo by Hermann Schachner, through Creative Commons.

In the UK, Callaghan (2020) found all colonies in close association with flowing and moderately alkaline water, including springs, flushes and streams (Figure 56-Figure 60). It never occurred within the **spate zone** (zone suddenly flooded) of larger rivers. It occurs almost entirely on rocks (mudstone, sandstone, slate), predominantly in deciduous woodland and only in lowland sites. In these locations, it occurs with *Thamnobryum alopecurum* (most frequent associate; Figure 65), and *Conocephalum conicum* (Figure 66), as well as *Chrysosplenium oppositifolium* (flowering plant; Figure 67). Ottley (2014) reported a "strong colony" from dripping rocks at Rolvenden in the UK.



Figure 65. *Thamnobryum alopecurum*, the most frequent associate with *Dumortiera hirsuta* in the UK. Photo by Claire Halpin, with permission.



Figure 66. *Conocephalum conicum* on wet rock, a desiccation-intolerant liverwort and frequent associate of *Dumortiera hirsuta* in the UK. Photo by Samaritakis, through Creative Commons.



Figure 67. *Chrysosplenium oppositifolium*, a frequent associate of *Dumortiera hirsuta* in the UK. Photo by Richtid, through Creative Commons.

In the western Himalayas, Pant and Tewari (1984) found *Dumortiera hirsuta* (Figure 53-Figure 55) in tufaceous aquatic habitats, perennial springs, **Gadheras** (small river tributaries; active only during rainy season and stay wet and damp throughout year for growth of bryophytes), and the muddy banks of **Gadhs** (broad rivulets that never dry, resulting from joining of Gadheras). Srinivasan (1968) reported that in India it is often seen in very wet, shady situations where the flow is continuous or at least dripping.

In Java, Indonesia, Nadhifah *et al.* (2018) reported that in the Cibodas Botanical Garden this liverwort occurred on soil in wet areas such as rivers, waterfalls, and ponds. Gradstein (2006) reported that *Dumortiera* sp. was successfully cultivated in association with a small river and pond at the Cibodas Botanical Garden.

In China, *Dumortiera hirsuta* (Figure 53-Figure 55) occurs on brook sides, valleys, or slopes, in wet, mesic, or moist localities, usually in partial or full shade of forested habitats in **orotemperate** (temperate mountain climate) of deciduous and warm temperate evergreen primeval or secondary forests (Piippo & Koponen 2013).

Colon (2000) found it in limestone sinkholes in the karst zone of Puerto Rico, where it had the highest importance value among species in the Empalme Sink.

Not all of its habitats are aquatic. It occurs in oak-hickory forests with shale and sandstone, but still near streams (McAllister *et al.* 2019).

Physiology

Dumortiera hirsuta (Figure 53-Figure 55) is shade adapted (Callaghan 2020). The linear flow of electrons in photosystem II experiences a sharp decline when the photon flux density is greater than $200 \mu\text{mol m}^{-2} \text{s}^{-2}$. The chlorophyll *a:b* ratio was 1.61, contrasting with that of 2.04 in *Phaeoceros carolinianus* (Figure 68), a species of somewhat sunny habitats (Zhang *et al.* 2018). This means that the *D. hirsuta* has more chlorophyll *b*, an adaptation to low light. Duckett and Ligrone (1993, 2006b) reported massive grana and stromal crystals in the chloroplasts and considered it to be a species of extreme shade. The thylakoids in the grana often exceeded 100 (Duckett & Ligrone 2006b). All of these characteristics are consistent with adaptations to shade conditions.



Figure 68. *Phaeoceros carolinianus*, a somewhat sunny species with a higher Chlorophyll *a:b* ratio. Photo by Hermann Schachner, through Creative Commons.

Devi *et al.* (2015) found seasonal variation in the photosynthetic pigments of *Dumortiera hirsuta* (Figure 53-Figure 55). They found that chlorophyll *a* remained higher than chlorophyll *b* in *Dumortiera hirsuta* in all seasons. Chlorophyll *a* is at its lowest levels in winter, whereas there was no seasonal pattern for chlorophyll *b*. Total chlorophyll reaches its greatest levels at the end of the growing season. The carotenoid content was much lower in winter ($0.06 \pm 0.005 \text{ mg g}^{-1}$ fresh weight) than in the rainy season ($0.16 \pm 0.005 \text{ mg g}^{-1}$ fw) or the end of the growing season ($0.15 \pm 0.005 \text{ mg g}^{-1}$ fw).

Bold (1938) demonstrated that the sporophyte is strongly photosynthetic during development in *Dumortiera hirsuta* (Figure 53-Figure 55), exhibiting chloroplasts in the immature foot cells, seta cells, capsule wall cells, and elaters. This photosynthetic ability would provide greater energy for developing spores.

Beckett (1993) found that the turgor of *Dumortiera hirsuta* (Figure 53-Figure 55) correlates well with the other indicators of water stress damage, including photosynthesis, respiration, and potassium loss. The rate of respiration dropped to zero following desiccation and the plants did not recover. This was similar to results of other desiccation-intolerant liverworts such as *Conocephalum conicum* s.l. (Figure 66) (Slavik 1965). However, such measures of intolerance must be reviewed because we now know that the rate of desiccation can have a profound effect on the survival and recovery from desiccation. He developed a successful method, using a thermocouple psychrometer, to correct for apoplastic water. Nevertheless, he found that the error introduced by apoplastic water was negligible.

Loo (2005) noted the difficulties in studying the cytology of *Dumortiera hirsuta* (Figure 53-Figure 55). Nevertheless, Loo *et al.* (2005a) presented a cytological study on this species. In a separate publication (2005b), they reported that *Dumortiera hirsuta* survived at 47-1511 lux, 15-27°C, and relative humidity of 60-95% on Mt. Kinabalu. Frahm *et al.* (1996) considered the minimum light level for photosynthesis to be 400 lux. The numbers presented by Loo and coworkers suggest that this species has a good tolerance range of the physical parameters of the environment.

Proctor *et al.* (1998) found that the full-turgor water content reached 1400% in *Dumortiera hirsuta* (Figure 53-

Figure 55). In a different study it was 1636% (Proctor 1999). These are much higher figures than those in the mosses *Syntrichia ruralis* (Figure 16) or *Andreaea alpina* (Figure 69) (Proctor *et al.* 1998). Beckett (1993) found that *D. hirsuta* was very sensitive to desiccation. The cells lost potassium, and during drying the thallus continued respiration while shutting down photosynthesis, causing the thalli to lose weight. He used this species to show that turgor loss correlated with other indicators of stress-induced damage.



Figure 69. *Andreaea alpina*, a species with a much lower full-turgor water content than that of *Dumortiera hirsuta*. Photo by Stephen Moores, through Creative Commons.

Marschall and Beckett (2005) found that ABA and partial dehydration hardening can increase desiccation tolerance, with *Dumortiera hirsuta* (Figure 53-Figure 55) being much more responsive to ABA treatment than was *Atrichum androgynum* (Figure 70). Furthermore, unlike *A. androgynum*, *D. hirsuta* did not exhibit increased NPQ (non-photochemical quenching) or decreased PSII efficiency with dehydration hardening. It also had little change with partial dehydration hardening before the onset of stress, but following rehydration it displayed a 22% improvement in PSII activity within an hour.



Figure 70. *Atrichum androgynum*, a species that is more resistant to cadmium damage than is *Dumortiera hirsuta*. Photo by Niels Klazenga, through Creative Commons.

Many bryophytes are now known to produce superoxide during rehydration. *Dumortiera hirsuta* (Figure 53-Figure 55) is among those that produce extracellular superoxide rapidly, even when not stressed (Beckett *et al.* 2004). Nevertheless, the production of superoxide increases greatly in this species during rehydration even after a mild desiccation stress. There are indications that this production provides an important protection against invasion of bacteria and fungi during the period of membrane repair. (See Chapter 19 in Volume 2.)

Li *et al.* (2010) determined that cell wall peroxidases are responsible for the extracellular burst of superoxide in *Dumortiera hirsuta* (Figure 53-Figure 55). They also found that this oxidative burst may have roles in formation of protective substances such as suberin, melanin, and lignin, supporting the hypothesis that the burst of superoxide enhances protection against pathogens. These peroxidases might also have a role in signal transduction and protection against abiotic stress and Yadav *et al.* (2022) looked at seasonal changes in chemical constituents of *Dumortiera hirsuta* (Figure 53-Figure 55), particularly changes in oxidative stress responses. In the fruiting season, the plants had their highest level of malondialdehyde (MDA) and H_2O_2 , with the lowest levels occurring during the premonsoon and monsoon seasons. Protein content and pigment concentrations were maximal during the monsoon season and minimal during the fruiting season. On the other hand, the enzymatic activity and content of superoxide dismutase, catalase, and glutathione reductase and non-enzymatic antioxidants were higher during the fruiting season and low during the pre-monsoon and monsoon seasons. During the fruiting season, the temperature is very low and nutrient availability is diminished. Hence these activities provide a defense in neutralizing or suppressing the increased ROS (reactive oxygen species) during the fruiting season. The researchers suggested that the antioxidative defence system may have a role in the adaptation of the species against oxidative stress, mediated by seasonal changes.

Heavy metals are often a component in aquatic and semi-aquatic environments. These are often toxic to plants, including bryophytes, but the latter seem to have at least some coping mechanisms. Heavy metals can interact to provide varying responses in *Dumortiera hirsuta* (Figure 53-Figure 55). It exhibits both internal and external cadmium uptake (Mautsoe & Beckett 1996). The intracellular uptake is linear with time, displaying Michaelis-Menten kinetics, whereas the extracellular uptake exhibits saturation kinetics [K(m) and V(max) $149 \pm 19 \mu M$ & $11.0 \pm 0.8 \mu M g^{-1} h^{-1}$ respectively]. Both are temperature dependent and intracellular uptake is light stimulated, increasing by about 15. Incubation with Cd and equimolar concentrations of Ca, Mg, or Zn reduced both intracellular and extracellular uptake. Pretreating the thalli with KNO_3 stimulated Cd uptake, most likely due to the ability of the K to remove competing ions from the cell walls, a technique used to measure cation exchange. All of this suggests the involvement of cation exchange in the uptake of cadmium. The researchers suggested that such exchange sites might protect the liverworts by securing the heavy metal ions outside the cell.

When Mautsoe and Beckett (1996) explored the effects of Cd on *Dumortiera hirsuta* (Figure 53-Figure 55), they

found that intracellular Cd uptake was linear, but extracellular uptake exhibited saturation kinetics. These uptake processes were temperature dependent. Light also stimulated intracellular uptake, but storage for 20 days in the dark did not affect it. Uptake decreased when the plants were incubated with additional Mg, Zn, or Cd, whereas pretreatment with KNO increased uptake, indicating cation exchange with the KNO clearing the exchange sites of cations. Such exchange sites might protect the liverworts by securing the heavy metal ions outside the cell.

Mautsoe (1997) found that photosynthesis of *Dumortiera hirsuta* (Figure 53-Figure 55) was more sensitive to Cd than it was in *Atrichum androgynum* (Figure 70), with differences directly related to intracellular Cd concentrations. These concentrations were considerably higher in *D. hirsuta*. Furthermore, in *D. hirsuta* the Cd caused K loss, but this did not occur in *A. androgynum*. Intracellular uptake in *D. hirsuta* was affected by thallus age, K pretreatment, and site characteristics.

Loo *et al.* (2005b) described the tolerance range of *Dumortiera hirsuta* (Figure 53-Figure 55) to occur within the 480-1740 m asl on Mt. Kinabalu. Here it experienced ranges of 47-1511 lux, 15-27°C, and 60-95% humidity. Hence we should expect it to be adapted to stresses within these ranges.

Adaptations

Butt and Anima (2011) found that *Dumortiera hirsuta* (Figure 53-Figure 55) in Bhaderwah, northwest Himalayas, exhibits great diversity of habitat, pH, and altitude, with accompanying diversity of morpho-anatomical characters of both gametophyte and sporophyte. Piippo and Koponen (2013) noted that this species is likely to include many cryptic taxa.

Although *Dumortiera hirsuta* (Figure 53-Figure 55) occurs in moist habitats, those are not always moist (Figure 71). Thus, the plants need mechanisms to protect vulnerable life cycle stages that coincide with less favorable seasons. Perhaps one such adaptation is that the archegonial head is covered with hairlike appendages (O'Hanlon 1934), suggesting an adaptation that protects the critical archegonia and developing sporophytes from drying out. The adult thallus has no lacunae (unfilled space or interval; gap) and no definite demarcation between the chlorophyllous and colorless cells, the latter being mostly in the central part of the thallus. Does the lack of lacunae suggest faster drying, or does the absence of these air spaces slow it down? Based on movement of water through stomata of tracheophytes, we can hypothesize that the absence of lacunae would slow down water loss. Researchers have demonstrated that stomatal-derived water loss from plants is ~50% of the total terrestrial evaporation and 80-90% of the continental evaporation (Hetherington & Woodward 2003; Jasechko *et al.* 2013).

There are only vestigial ventral scales (Figure 72) (McAllister *et al.* 2019) – structures that usually help in water movement, uptake, and conservation, perhaps causing the restriction of *Dumortiera hirsuta* to moist habitats. Watson (1919) considered that having few or no ventral scales is an adaptation or characteristic of a species from an aquatic habitat.



Figure 71. *Dumortiera hirsuta* with thallus showing signs of drying. Photo by Blanka Aguero, with permission.



Figure 72. *Dumortiera hirsuta* ventral side showing absence of or vestigial scales. Photo by Nicola van Berkel, through Creative Commons.

Adaptations may differ between lineages. The Central American lineage has plants with a light green velvety appearance, caused by abundant papillae on the upper surface (Forrest *et al.* 2011). The role of papillae has been controversial and unproven, including movement of water into cells in some species, scattering light, and reducing water loss. The more widespread lineage is dark green and papillae range from absent to dense; marginal hairs are usually abundant. It appears that these two lineages might have different adaptations to surviving periods of drought and receding water.

Dumortiera hirsuta (Figure 53-Figure 55) is polyploid, with populations exhibiting monoploid or diploid gametophytes (Tatuno 1938, 1939). It is likely that the differences between monoploid and diploid gametophytes of *Dumortiera hirsuta* might confer some differences in adaptations. In some cases, some alleles of diploids were missing among monoploids, but both types shared the character of upright, short hairs scattered on the dorsal surface (Akiyama *et al.* 2003). In Taiwan populations, Akiyama and coworkers found that monoploids could grow on non-calcareous substrata, a single population could have different levels of ploidy, heterozygosity is fixed in diploids, and there are at least four monoploid lineages ("species" according to Akiyama *et al.*). The evidence suggests that these diploids are **allopolyploids** (two or more chromosome sets originating

as complete sets from different species or lineages). The presence of multiple chromosome sets and lineages would provide greater variation, thus permitting the species to survive a wider range of conditions.

Storage compounds can vary with seasons. Kapila *et al.* (2014) compared three liverworts and found that the more hydric *Dumortiera hirsuta* (Figure 53-Figure 55), with a habitat near streams or other hydric locations, exhibits higher carbohydrate and protein content with little seasonal change compared to *Marchantia emarginata* (Figure 73) and *M. paleacea* (Figure 74), both of mesic habitats. All three species experienced a decrease in α -amylase, β -amylase, and invertase near the end of the primary growth season due to carbohydrate accumulation in their tissues. There was an inverse relationship between protein and free amino acids. Protease activity, associated with protein metabolism, peaked in the rainy season.



Figure 73. *Marchantia emarginata*, a species with lower carbohydrate and protein content and more seasonal change compared with *Dumortiera hirsuta*. Photo by Li Zhang, with permission.



Figure 74. *Marchantia paleacea*, a species with lower carbohydrate and protein content and more seasonal change compared with *Dumortiera hirsuta*. Photo by Jan-Peter Frahm, with permission.

Reproduction

Mcallister *et al.* (2019) considered *Dumortiera hirsuta* (Figure 53-Figure 55) to be **monoicous**. But Bischler-Causse *et al.* (2005) considered it to be **monoicous** or **dioicous** (Figure 75-Figure 77). It has no known asexual propagules.



Figure 75. *Dumortiera hirsuta*, with emerging archegoniophores. Photo by Cheng-Tao Lin, through Creative Commons.



Figure 76. *Dumortiera hirsuta* with archegoniophores. Photo by Luis Funez, through Creative Commons.

Shimamura (2015) reported that the sperm possessed four flagella and experienced aerial dispersal. This species was the first to be documented with explosive sperm dispersal. Small droplets with sperm cells are expelled several centimeters into the air from the antheridial disk. Even in monoicous plants, this explosive dispersal facilitates the cross-fertilization between male and female reproductive structures on different individuals.

From South Carolina, USA, Patterson (1933) reported that male receptacles were initiated 11-19 August, with female receptacles (Figure 77) appearing 5-12 September. Fertilization occurred primarily 25 September to 5 October. Young embryos appeared 5 October to 15 October. Sporophytes developed in November and December, with meiosis occurring 26 January to 4 February. Meanwhile, the antheridial branches withered 20 December to 20 January. Spores matured in February. In March, the capsules blackened, fertile thalli were dying, and the receptacles elongated. In April the setae elongated and the spores were dispersed. Precipitation modified this schedule from year to year. Patterson detailed the development of the reproductive structures. One unusual character is that some receptacles have both male and female gametangia,

but these do not occur on the same radii, with radii of the same sex grouped together. These receptacles with both sexes were relatively common in populations from Jamaica, but were rare in the North Carolina populations.



Figure 77. *Dumortiera hirsuta* young archegoniophores. Photo by Lin Kyan, with permission.

All the archegonia within an involucre may experience fertilization, but only one will get beyond the 2-8 cell stage (Patterson 1933).

In the UK the production of sporophytes is rare (Callaghan 2020). Since the seasons there are quite different from those in the tropics, temperature, day length, and rainy season might modify the reproductive timing so that it is unlikely to be successful.

Patterson (1933) reported the species producing sporophytes (Figure 78-Figure 80) on the bank of a small stream near Columbia, South Carolina, USA. O'Hanlon (1934) found that only one or two sporophytes (Figure 81) in each of the typically eight groups of archegonia are able to reach maturity. In Florida, USA, O'Hanlon found ripe spores (Figure 82-Figure 83) in the middle of April. They remain viable for only a short time after dehiscence. In the lab they germinate within 6-7 days on a liquid medium.



Figure 78. *Dumortiera hirsuta* with archegoniophores. Photo by buggi, through Creative Commons.



Figure 79. *Dumortiera hirsuta* with mature sporangia. Photo by Chris Wagner, through Creative Commons.



Figure 82. *Dumortiera hirsuta* archegonial head with dehiscent sporangia, in this case with four sporangia. Photo courtesy of Zen Iwatsuki.



Figure 80. *Dumortiera hirsuta* with maturing sporangia. Photo by Chris Wagner, through Creative Commons.



Figure 83. *Dumortiera hirsuta* with sporangia and ripe spores. Photo by Luis Funez, through Creative Commons.



Figure 81. *Dumortiera hirsuta* with mature sporangia, showing only 1-3 mature sporangia per archegonial head. Photo by tigris 8, through Creative Commons.

The young sporocyte has a single large plastid, but the plastid divides before the nucleus divides, resulting in four plastids (Shimamura *et al.* 2000). These often continue to divide before nuclear division. The cytoplasm forms lobes around the four plastid domains, enclosing at least one plastid. This monoplastidic meiosis is rare among liverworts.

O'Hanlon (1934) found that *Dumortiera hirsuta* (Figure 53-Figure 55) produces 1-2 sporophytes (Figure 82) that reach maturity among the eight groups of archegonia. Spores reach maturity in mid April in Florida, USA. They remain viable only a short time after the capsule dehisces. These spores germinate within 6-7 days after culturing in a liquid medium. The spore first produces a rhizoid; then a bud forms from the spore.

The young sporocyte has a single large plastid, but the plastid divides before the nucleus divides, resulting in four plastids (Shimamura *et al.* 2000). These often continue to divide before nuclear division. The cytoplasm forms lobes around the four plastid domains, enclosing at least one plastid. This monoplastidic meiosis is rare among liverworts.

Miyoshi (1973) described the spore wall structure of *Dumortiera hirsuta* (Figure 53-Figure 55). Kamimura (1973) used the electron microscope to help describe the

fine structure of the spore walls. Pyramidal or rectangular planks or columnar protuberances have irregular patterns on the surfaces of the spore walls. Two-three of these protuberances frequently form lamellae. The foundation of the spore wall is nearly smooth.

Role

This species surely plays a greater role in housing invertebrates than the examples we know (Figure 84). And what might its role be in stabilizing the banks of streams during high water? The ecosystem role of *Dumortiera hirsuta* (Figure 53-Figure 55) remains mostly unexplored.



Figure 84. *Dumortiera hirsuta* with snail, a potential herbivore on this species. Photo by Chaturvedi, with permission.

Interactions

Iqbal *et al.* (2011) enumerated the wide array of organisms associated with *Dumortiera hirsuta* (Figure 85), including fungi, other bryophytes, pteridophytes, gymnosperms, angiosperms, and insects. In Bhaderway in the Doda district of Jammu, India, in the range of 1230-2600 asl *Conocephalum conicum* (Figure 66) formed the most frequent associations, but these researchers found 12 species of plants and one insect that were frequently associated with *D. hirsuta*.



Figure 85. *Dumortiera hirsuta* with the moss *Sematophyllum* sp. in India. Photo by Syamal L, through Creative Commons.

Fungal Interactions

The fungi associated with *Dumortiera hirsuta* (Figure 53-Figure 55) remain unexplored. The species has antifungal properties (Alam *et al.* 2011), but that is not usually enough to deter all fungi. And are those antifungal compounds produced by the liverwort, or by associated bacteria?

Alam *et al.* (2011) found that treatment of *Aspergillus niger* (Figure 86) by extracts from *Dumortiera hirsuta* (Figure 53-Figure 55) caused distinct morphological changes in the fungus. These included anomalies in the hyphae, flaccid cell wall, and cytoplasm leaking through cell wall and becoming granulated.

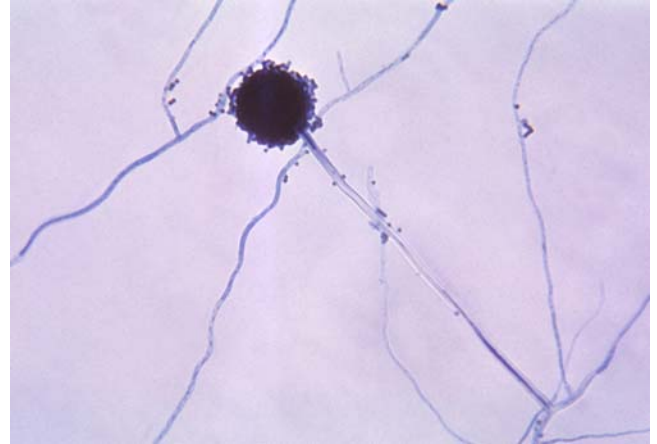


Figure 86. *Aspergillus niger*, a species that exhibits morphological aberrations after exposure to extracts of *Dumortiera hirsuta*. Photo from CDC, through public domain.

Egertová *et al.* (2018) described a new species of Ascomycetes growing on *Dumortiera hirsuta* (Figure 53-Figure 55). *Octosporopsis erinacea* (Figure 87) parasitizes the thallus, exhibiting tiny, light yellow, rimless apothecia. The hyphae develop both on and within the cells of the thallus, especially near a waterfall.



Figure 87. *Octosporopsis erinacea*, a species of Ascomycetes that parasitizes the thallus of *Dumortiera hirsuta*. Photo by Z. Egertová, through Creative Commons.

Animal Interactions

Among the inhabitants of *Dumortiera hirsuta* (Figure 53-Figure 55) is the odonate *Epiophlebia superstes* (Figure

88) (Asahina & Sugimura 1981). This odonate is intermediate between dragonflies and damselflies. It injects its eggs into the thallus of *D. hirsuta*. Later, Carle (2012) described the new species *Epiophlebia diana* from naiads in China. However, Büsse and Ware (2022) have considered it to be a synonym of *Epiophlebia laidlawi* (Figure 89), occurring in Nepal, India, Bhutan, and Vietnam. Members of this genus in China typically choose plants growing in wet and mostly shaded areas less than a meter from a stream.



Figure 88. *Epiophlebia superstes* on bryophytes. Photo by Tom Kompier, with online non-commercial permission.



Figure 89. *Epiophlebia laidlawi* naiad, an inhabitant of *Dumortiera hirsuta* in China. Photo modified from Robert John Tillyard, through public domain.

Lien (1989) suggested that species of biting midges (*Ceratopogonidae*: *Lasiohelea*) that rest on *Dumortiera hirsuta* (Figure 53-Figure 55) and other bryophytes are likely to be feeding on the *Cyanobacteria* (Figure 32) that are growing there. Lien found that *Anabaena* sp. (Figure 90) is especially beneficial for *Forcipomyia anabaenae* (see Figure 91), in a closely related genus.



Figure 90. *Anabaena circinalis*; the genus *Anabaena* is a beneficial food for some biting midges that visit bryophytes. Photo by B D Carl, through Creative Commons.



Figure 91. *Forcipomyia* sp., a genus wherein some members seem to benefit from eating *Anabaena* associated with bryophytes. Photo by XPDA, through Creative Commons.

The fly family *Agromyzidae* (Figure 92-Figure 94) occurs on liverworts throughout the world (Spencer 1990). It is a miner on *Dumortiera hirsuta* in Mexico.



Figure 92. *Phytoliriomyza dorsata* (*Agromyzidae*), in a family that mines thallose liverworts. Photo by Mardon Erbland, through Creative Commons.

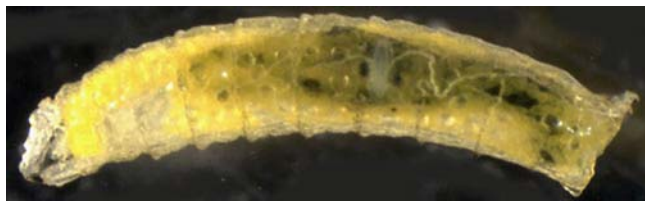


Figure 93. *Phytoliriomyza melampyga* larva (**Agromyzidae**), in a family that mines thallose liverworts. Photo by W. N. Ellis, through Creative Commons.



Figure 94. *Phytomyza* sp. leaf mining (**Agromyzidae**), in a family that mines thallose liverworts. Photo by Beatriz Moisset, through Creative Commons.

Biochemistry

Dumortiera hirsuta (Figure 53-Figure 55) has been the subject of a number of biochemical studies. Matsuo *et al.* (1976) reported 10 sesquiterpene hydrocarbons from *Dumortiera hirsuta*. Toyota *et al.* (1997a,b) reported on a new sesquiterpene compound and 13 additional known compounds from the species and described their structures. Saritas *et al.* (1998) added additional sesquiterpenes to this list, some of which were rare or unusual. To these, Lu *et al.* (2006) added more compounds (terpenoids and bisbibenzyls from Chinese populations, including riccardin D) and described their structure. Some of these were cytotoxic to the human HepG2 cells. One was also active against *Pseudomonas aeruginosa* (Figure 95).

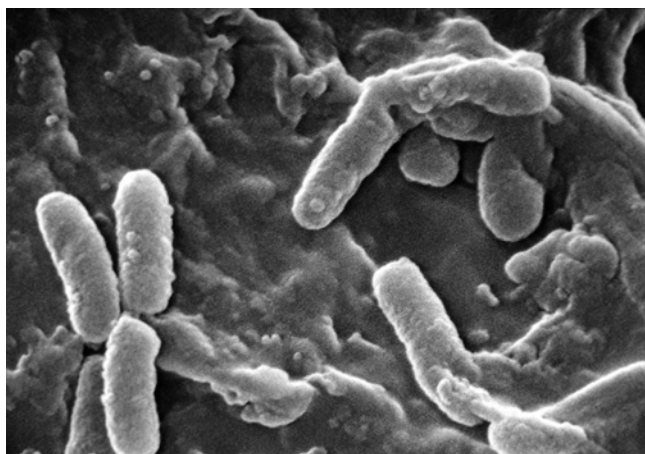


Figure 95. *Pseudomonas aeruginosa*, a species that experiences toxicity from one of the compounds produced by *Dumortiera hirsuta*. Photo by Janice Haney Carr, CDC, through public domain.

Liu *et al.* (2012) found that riccardin D (a macrocyclic bisbibenzyl compound), a product of *Dumortiera hirsuta* and other liverworts, was effective at inhibiting intestinal adenoma from forming in mice. Its effectiveness is through multiple mechanisms, including anti-proliferative, apoptotic, anti-angiogenic, and anti-inflammatory activity. Xue *et al.* (2012) found that the riccardin D also induces apoptosis of human leukemia cells.

Xie and Lou (2008) identified two calamenane-type sesquiterpenoids (5,7-dihydroxycalamenene and 7-hydroxycalamenene) from *Dumortiera hirsuta* (Figure 53-Figure 55). Bardón *et al.* (1999) isolated dumortane sesquiterpenes, four new, from Argentine populations of *Dumortiera hirsuta* (Figure 53-Figure 55). Linde *et al.* (2016) considered that the presence of dumortane-type sesquiterpenoids in *D. hirsuta* from South Africa indicated that this species is similar in chemistry to an Argentinean sample.

Xie *et al.* (2007) reported an unusual phenylethyl cyclohexadienone (dumhirone A) from Chinese populations of *Dumortiera hirsuta* (Figure 53-Figure 55).

Alam *et al.* (2011) found that aqueous extracts of *Dumortiera hirsuta* (Figure 53-Figure 55) were effective against seven plant pathogens. Six of seven plant pathogenic fungi were completely inhibited by the extract at 550-600 ppm. Joshi (1993) also found extracts to be effective against bacteria. Kumar *et al.* (2007) likewise found that extracts of this liverwort in Indian Himalayas were effective in enhancing wound healing due to its antibacterial properties.

Setyati *et al.* (2021) found that extracts from *Dumortiera hirsuta* (Figure 53-Figure 55) were able to prevent infection by pathogenic bacteria, including flavonoids, alkaloids, and steroids. These were able to inhibit the bacteria *Escherichia coli* (Figure 48), *Staphylococcus aureus* (Figure 47), and *Salmonella typhi* (Figure 96), causing weak to moderate responses (see also Luthfiah *et al.* 2021). Junairiah *et al.* (2015) similarly found that ethylacetate extracts of *D. hirsuta* from Indonesia contained flavonoids, alkaloids, and steroids that can inhibit the pathogenic bacteria *Staphylococcus aureus* and *Escherichia coli* and the yeast *Candida albicans* (Figure 97).



Figure 96. *Salmonella typhi*, a species that is inhibited by extracts from *Dumortiera hirsuta*. Photo by CDC, through public domain.

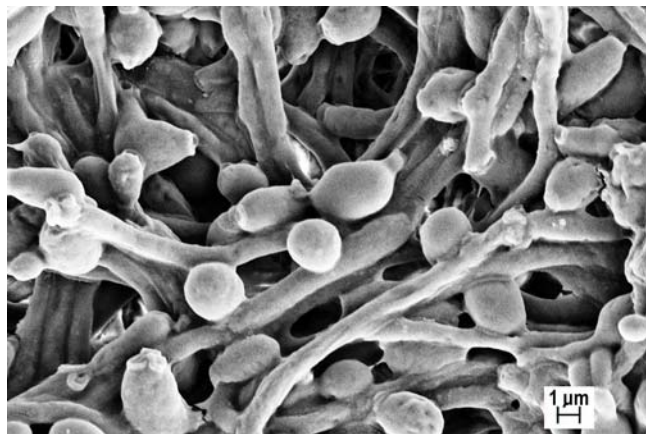


Figure 97. *Candida albicans* SEM, a yeast species that is inhibited by extracts from *Dumortiera hirsuta*. Photo by Vader1941, through Creative Commons.

An aqueous extract from *Dumortiera hirsuta* (Figure 53-Figure 55) exhibited fungitoxicity against seven plant pathogenic fungi, inhibiting their ability to produce germinable spores (Alam *et al.* 2011). Morphological aberrations were present in *Aspergillus niger* (Figure 86) treated with extracts of *Dumortiera hirsuta*.

Mukherjee *et al.* (2012) examined antibacterial activity of *Dumortiera hirsuta* (Figure 53-Figure 55) against *Serratia marcescens* (Figure 98) from various altitudes in the Himalayas. Those plants from higher altitudes exhibited slightly less antibacterial activity than those from lower altitudes. The reproductive thallus extracts exhibited less antibacterial activity than did the vegetative thallus.



Figure 98. *Serratia marcescens* on bread, a bacterial species that is inhibited less by populations of *Dumortiera hirsuta* from higher elevations than by those at lower elevations. Photo by DBM, through Creative Commons.

Noting that *Dumortiera hirsuta* contains the bioactive alkaloids, terpenoids, flavonoids, and saponin, Sari (2014) explored its usefulness in the treatment of malaria. It was effective in treating parasitemia caused by *Plasmodium berghei* (Figure 99) in mice, so its usefulness against *Plasmodium malariae* (Figure 100) was worth exploration. Unfortunately, in their further experiments against *P. berghei* in mice, they found that it damaged microanatomical structures in the liver and kidneys at levels of 300 mg kg⁻¹ BW and above.

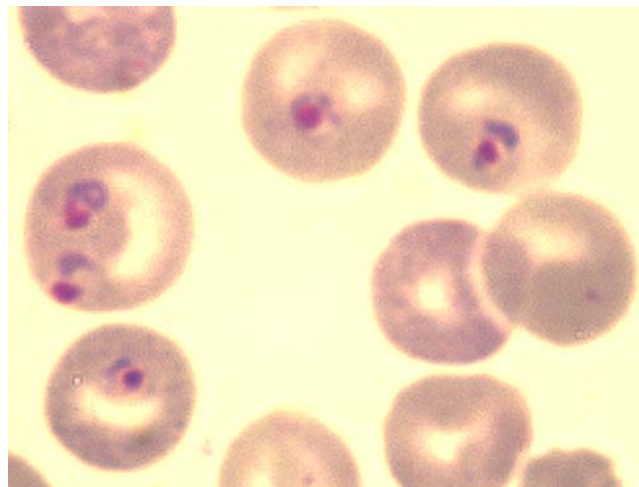


Figure 99. *Plasmodium berghei*, a species that can be inhibited successfully by extracts of *Dumortiera hirsuta*. Photo by C. J. Janse, through Creative Commons.

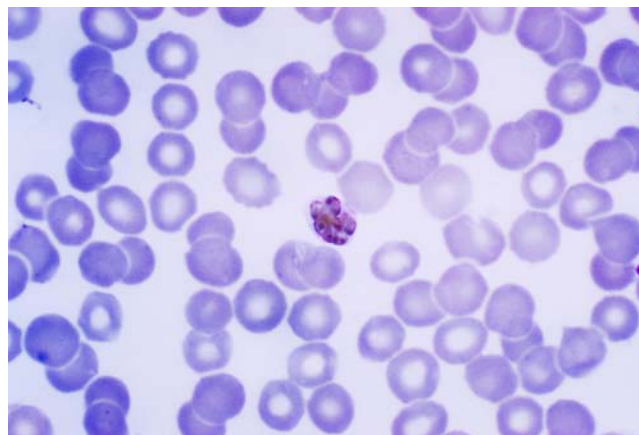


Figure 100. *Plasmodium malariae*, a species that might be inhibited by extracts of *Dumortiera hirsuta*. Photo by Mae Melvin, CDC, through public domain.

Shirzadian *et al.* (2009) found that ethanolic extracts of *Dumortiera hirsuta* (Figure 53-Figure 55) exhibited one of the broadest spectra of antifungal activities shown by the 23 bryophytes tested. Luthfiah *et al.* (2021) noted that this species can be used medically to prevent bacterial infection.

Asakawa (1982) used the terpenoids and aromatic compound differences to argue for separation of *Wiesnerella denudata* (Figure 101) and *Dumortiera hirsuta* (Figure 53-Figure 55) into different families. Those sesquiterpene lactones and monoterpenoids occurring in *W. denudata* appear to be absent in *D. hirsuta*. This supports the morphological differences also known between these two species. Kraut *et al.* (1996) reported several carboxylated α -pyrone derivatives and flavonoids from *Dumortiera hirsuta* and elucidated structures.

In their attempts to distinguish differences in secondary compounds between *D. hirsuta* ssp. *hirsuta* (Figure 53-Figure 55) and *D. hirsuta* ssp. *nepalensis* (Figure 102-Figure 103). Durant-Archibold *et al.* (2018) reported 34 compounds for the first time in the species *Dumortiera hirsuta*. They found that the two subspecies differed biochemically.



Figure 101. *Wiesnerella denudata* in Bhutan, a species wherein chemical differences separate it from *Dumortiera hirsuta*. Photo by David Long, with permission.

***Dumortiera hirsuta* ssp. *nepalensis* (Figure 102-Figure 103)**

(syn. = *Dumortiera trichocephala*)



Figure 102. *Dumortiera hirsuta* ssp. *nepalensis*. Photo courtesy of David Wagner.



Figure 103. *Dumortiera hirsuta* ssp. *nepalensis* from Bhutan. Photo courtesy of David Long.

In most cases, the subspecies *nepalensis* is considered as part of *Dumortiera hirsuta*, but it has been classified as a variety, a subspecies, and even a species. In the foregoing discussion I have considered *Dumortiera hirsuta sensu lato*. However, since I did find some separate information on it, I shall comment on that with the anticipation that it might be officially removed from *D. hirsuta* in the future.

Distribution

In 1919, Evans considered this to be the separate species *Dumortiera nepalensis* (Figure 102-Figure 103). He described its distribution as close to that of *D. hirsuta* (Figure 53-Figure 55), but absent in Europe and Africa. But it is rare in much of its range, especially the southern United States and West Indies, and David Long (pers. comm. 26 June 2022) considers these populations to belong to *Dumortiera hirsuta* ssp. *hirsuta* (Figure 53-Figure 55). *Dumortiera hirsuta* ssp. *nepalensis* (Figure 102-Figure 103) is most abundant in southeastern Asia.

Aquatic and Wet Habitats

Dumortiera hirsuta ssp. *nepalensis* (Figure 102-Figure 103) occurs submersed under water jets, above the water level, and in waterfalls in the tropics (Ruttner 1955). David Long (pers. comm. 26 June 2022) reports the subspecies from the slope of dry rocky side valley and under overhanging dripping rocks by roads in the Tashigang districts south of Tashi Yangtse, Bhutan.

Biochemistry

Durant-Archibold *et al.* (2018) found that the major volatile compounds in *Dumortiera hirsuta* ssp. *nepalensis* (Figure 102-Figure 103) from Panama were ledene, α -gurjunene, β -caryophyllene, and α -guaiene, differing from those of the subspecies *hirsuta*.

Summary

Cyathodium is **r-selected**. It has several species that occupy wet habitats in mostly tropical areas. Several species occur on stream and river banks, with *C. bischlerianum* and *C. cavernarum* typically closer to the water than is *C. spruceanum*. Species often have pungent odors, attesting to their unique secondary compounds. Others, such as *Cyathodium bischlerianum*, have pleasant odors suitable for cosmetics and soaps. Some species, such as *Cyathodium cavernarum*, have iridescent colors, but the function of those, if any, is unknown.

Dumortiera hirsuta has a similar distribution and occurs in splash zones of streams and waterfalls and on otherwise wet rocks. It is a shade-adapted species that otherwise occupies a wide range of habitat conditions, pH, and altitude. There are flies in **Agromyzidae** and **Ceratopogonidae** that are specialists on it. In some cases, the invertebrates occur there to consume associated **Cyanobacteria**. The secondary compounds of *D. hirsuta* possess antibiotic and medicinal properties.

Acknowledgments

Lars Söderström helped me find the current acceptable names for a number of older taxa.

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CHAPTER 1-23

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 1

TABLE OF CONTENTS

Marchantiaceae	1-23-3
<i>Marchantia</i>	1-23-3
<i>Marchantia berteroana</i>	1-23-4
Distribution	1-23-4
Aquatic and Wet Habitats	1-23-5
Physiology	1-23-6
Adaptations	1-23-7
Reproduction	1-23-7
Interactions	1-23-9
Fungal Interactions	1-23-9
Biochemistry	1-23-9
<i>Marchantia debilis</i>	1-23-10
Distribution	1-23-10
Aquatic and Wet Habitats	1-23-10
Adaptations	1-23-12
Reproduction	1-23-13
Biochemistry	1-23-13
<i>Marchantia emarginata</i>	1-23-13
Distribution	1-23-13
Aquatic and Wet Habitats	1-23-14
Adaptations	1-23-15
Reproduction	1-23-16
Fungal Interactions	1-23-17
Biochemistry	1-23-18
Culturing	1-23-19
<i>Marchantia inflexa</i>	1-23-19
Distribution	1-23-19
Aquatic and Wet Habitats	1-23-20
Physiology	1-23-21
Adaptations	1-23-22
Reproduction	1-23-23
Interactions	1-23-27
<i>Marchantia miqueliana</i>	1-23-27
Distribution	1-23-27
Aquatic and Wet Habitats	1-23-28
Adaptations	1-23-28
Biochemistry	1-23-28
<i>Marchantia paleacea</i>	1-23-28
Distribution	1-23-28
Aquatic and Wet Habitats	1-23-29
Physiology	1-23-31
Adaptations	1-23-33
Reproduction	1-23-34
Interactions	1-23-37
Biochemistry	1-23-39
Culturing	1-23-39
<i>Marchantia pappeana</i>	1-23-39
Distribution	1-23-39
Aquatic and Wet Habitats	1-23-40
Reproduction	1-23-41
Fungal Interactions	1-23-41

Biochemistry	1-23-42
Summary	1-23-42
Acknowledgments	1-23-42
Literature Cited	1-23-42

CHAPTER 1-23

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 1



Figure 1. *Marchantia debilis* on emergent rocks in Madagascar. Photo courtesy of Catherine Reeb.

Marchantiaceae

Marchantia

Marchantia is widespread in the world. In the western Cascade Mountains, Oregon, USA, it is a pioneer **riparian** (relating to wetlands adjacent to rivers and streams) genus (Campbell & Franklin 1979). Several species in this genus are associated with wet habitats, with some occasionally becoming submersed.

Like most of the older taxa, this genus has a history of species synonyms (Bischler-Causse 1993). For example, of the 28 species described in Africa, Bischler-Causse reduced them to only 6, although another 8 remained unresolved.

Zheng *et al.* (2020a) have suggested that the morphology of the gemmae can be used to help in separation of the taxa, and that molecular analyses support these separations.

Bischler-Causse (1993) suggested that dispersal of at least some of the species seems to be limited by temperature extremes, but the species also require water throughout the year, free space, and light, thus limiting their success in much of the dry parts of the African continent. This distribution is further limited by the low level of sexual reproduction, relying on vegetative multiplication – a means that is more limited in dispersal distance.

Although *Marchantia polymorpha* (Figure 2) is by far the liverwort of choice, other species have been important

in unravelling the genetic and evolutionary history of liverworts. Marks *et al.* (2019a,b) presented the genome assembly for *Marchantia inflexa* (Figure 3-Figure 4) and found evidence suggesting that dehydration tolerance may be related to sex-specific genes in *Marchantia*. They found that the genes on the sex chromosomes experience greater diversifying selection than do the autosomal and organellar genes.



Figure 2. *Marchantia polymorpha* at tree base on bank of small river in Pfälzer Wald, Germany. Photo courtesy of Michael Lüth.



Figure 3. *Marchantia inflexa* females, a species where dehydration tolerance may be related to sex-specific genes. Photo by Amelia Merced, with permission.



Figure 4. *Marchantia inflexa* with gemmae. Photo by Alan R. Franck, through Creative Commons.

Ahmad (1981) described the historical studies on spore germination and gametophyte development in *Marchantia*.

Marchantia berteriana (Figure 5-Figure 7)

(syn. = *Marchantia cephaloscypha*, *Marchantia tabularis*)

Campbell (1965) reviewed some of the history of the nomenclature for this species. Another species recorded for New Zealand and described by Stephani (1883), namely *M. cephaloscypha*, is considered by Evans after examination of an original specimen to correspond with *M. berteriana* (Evans 1917). In Columbia, Herzog (1934) described the variety *polylepida*, but that is now considered to be *M. berteriana* as well.

Distribution

Marchantia berteriana (Figure 5-Figure 7) is known in Australia, New Zealand (Campbell 1965; Wikipedia 2021), Southern Africa (Perold 1995; Lüth & Schafer-Verwimp 2004; Phephu 2012a,b), South America (Costa Rica to the Antarctic Peninsula) (Hassel de Menendez 1962; Campbell 1965; Lüth & Schafer-Verwimp 2004), Antarctica (Davey 1997), and non-continental locations such as Papua New Guinea, Java, New Caledonia, and various smaller islands (Driessen 2009; Wikipedia 2021). Phephu (2012a) noted that this species is prevalent in the winter-rainfall region of South Africa, but it also grows in regions that receive summer rain in KwaZulu-Natal, Mpumalanga and Limpopo provinces.



Figure 5. *Marchantia berteriana* thallus. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 6. *Marchantia berteriana* thallus. Photo by Sarah Lloyd, with permission.



Figure 7. *Marchantia berteriana* vegetative thallus with gemmae cups. Photo by Clive Shirley, Hidden Forest, with permission.

Aquatic and Wet Habitats

Marchantia berteriana (Figure 5-Figure 7) lives in constantly damp, shaded areas (Figure 8) (Wikipedia 2021), including fresh water, waterfall splash zones, forest floors, and streambanks (Phephu 2012a,b). The species is widespread in New Zealand, especially near hot springs, and in southern Africa in swampy areas, **kloofs** (steep-sided wooded ravine or valley in Africa), gorges, and burned areas (Campbell 1965; Perold 1995). Li Zhang (pers. comm. 4 August 2022) found it growing in peatlands in Chile (Figure 9). It also occurs in peatlands in Colombia (Campos 2014). On the Juan Fernández Islands, it grows in expansive colonies on the mountain tops (Figure 10-Figure 11) where clouds most likely maintain its needed moisture levels.



Figure 8. *Marchantia berteriana* thallus growing on a damp soil bank. Photo by Clive Shirley, Hidden Forest, with permission.

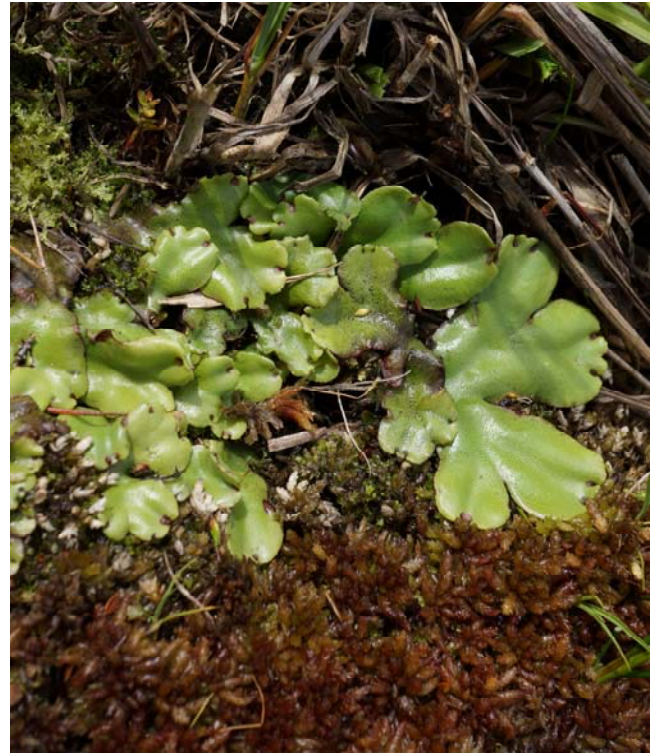


Figure 9. *Marchantia berteriana* in peatland in Puerto Williams, Chile. Photo courtesy of Li Zhang.



Figure 10. *Marchantia berteriana* soil habitat on Alejandro Selkirk Island, Juan Fernández Archipelago, Chile. Photo by Pato Novoa, through Creative Commons.



Figure 11. *Marchantia berteriana* habitat on Alejandro Selkirk Island, Juan Fernández Archipelago, Chile. Photo by Pato Novoa, through Creative Commons.

In geothermal areas in the Antarctic, *M. berteroa* (Figure 5-Figure 7) can occur at surface temperatures of 25-35°C and subsurface temperatures of 50-60°C, although these underground temperatures have no direct effect on the bryophytes (Convey & Lewis Smith 2006). Lewis Smith (2005a,b) found that on Deception Island in the South Shetland Islands, a geothermal gully included *Marchantia berteroa* (Figure 5-Figure 7) as one of the colonizers, forming a peripheral zone at the margin of the primary moss vegetation, living on fine moist compacted clay. He attributed its abundance to the "copiously produced and widely dispersed gemmae."

Halloy (1991) reported *Marchantia berteroa* (Figure 5-Figure 7) from heated areas (Figure 12) in the Andes, at 6000 m asl. These communities comprised the highest elevation of the known autotrophic communities on the planet.



Figure 12. Geothermal fissure and *Sphagnum*; heated areas in the Andes can be suitable habitats for *Marchantia berteroa*. Photo from a geothermal vent in Iceland, by Janice Glime.

Despite its seeming preference for wet habitats, it is a colonizer on soil following fire in Tasmanian mixed forests (Duncan & Dalton 1982) and also in southern Africa (Perold 1995). The rapid germination of the spores and rapid development of the gametophyte gives the species an advantage in this habitat. Brasell and Mattay (1984) found it as a colonizer in burned *Eucalyptus* forest (Figure 13) in Tasmania, where it accumulated a high concentration of potassium. In these forests, N, P, K, and Ca, but not Mg, all decreased with time following the fire. Brasell *et al.* (1986) found that *Marchantia berteroa* contributed significantly to nitrogen fixation in burned sites of southern Tasmania, greatly exceeding rates of bryophytes in unburned forests.



Figure 13. *Eucalyptus* forest at Sherbrooke, Victoria, Australia – fire-adapted forest where *Marchantia berteroa* often appears after fire. Photo by Patche99z, through public domain.

Duncan and Dalton (1982) showed that *Marchantia berteroa* spores germinated well on burned ground. The protonemal growth is more rapid than that of the non-colonizing species, giving the *M. berteroa* a chance to establish before other, more competitive species arrive.

Phephu (2012a) considers *Marchantia berteroa* to be important in nutrient cycles and erosion control, thus stabilizing the soil.

Physiology

Davey (1997) used measurements of respiration, photosynthesis, irradiance, and temperature to model the year-round net productivity of *Marchantia berteroa* (Figure 5-Figure 7), estimating a yearly net productivity of $823 \pm 75 \text{ mg C g}^{-1}$ ash-free dry weight. Desiccation was highly adverse to the thalli (Figure 14). Below a water content of 12 g g^{-1} ash-free dry weight the photosynthetic capacity was reduced. Recovery was only ca. 10% after dehydration and rehydration. Freezing also caused great photosynthetic reduction, although the model indicated that this species should be able to photosynthesize at sub-zero temperatures. Davey suggested that the photosynthetic capacity and freezing tolerance were likely to be seasonal.



Figure 14. *Marchantia berteroa* showing dying edges, suggesting drought damage. Note its low-lying habit on the mosses. Photo by Andrew Hodgson, with permission.

Despite that fact that the model indicates that freezing causes a great reduction in photosynthesis, the model suggests that photosynthesis at sub-zero temperatures is, nevertheless, likely (Davey 1997). It is suggested that seasonality in the photosynthetic capacity and the survival of these plants subjected to sub-zero temperatures might be important. However, their distribution is likely to be limited by available moisture.

Green and Lange (1995) found that the CO_2 compensation point is much lower for *Marchantia berteroa* (Figure 5-Figure 7) in 2% oxygen than for the other bryophytes they tested, and that the compensation points rise with a rise in temperature, resulting in inhibition (Figure 15). Photosynthesis at 21% oxygen [usual atmospheric oxygen concentration on Earth (National Geographic 2022)] is depressed compared to that at 2% oxygen (Figure 16), with the depression increasing at higher temperatures.

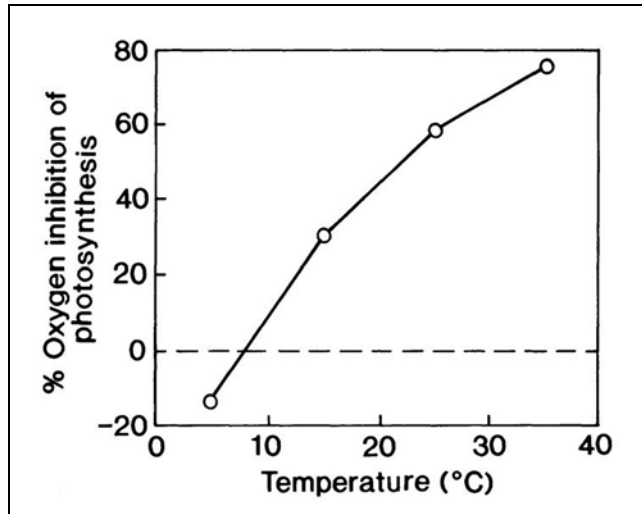


Figure 15. Temperature effect on oxygen inhibition in *Marchantia berteroana*. Modified from Green & Lange 1995.

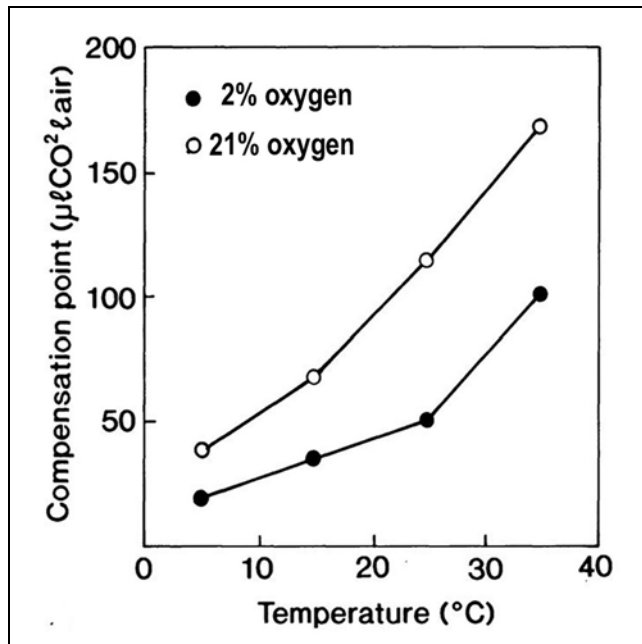


Figure 16. Temperature effect on CO₂ compensation point in *Marchantia berteroana*. Modified from Green & Lange 1995.

Adaptations

Marchantia berteroana (Figure 5-Figure 7) has scales on the lower surface, a common feature of the genus, but in this case they extend nearly to the margins (Phephu 2012a, b). These may be hyaline or colored reddish-brown (Campbell 1965). The thallus itself helps to maintain its moisture by its low-lying habit (Figure 14) that keeps it closer to the water in the soil and by reducing evaporation from the soil.

Like other members of *Marchantia*, the thalli have apical growing tips that are covered by scales (Figure 17). Presumably, these protect the important growing region from desiccation. When the older thallus dries out and dies, these apical areas can still retain living cells that can resume growth when favorable conditions return.



Figure 17. *Marchantia berteroana* thallus showing apical growing regions with apical scales covering them. Photo by Jan-Peter Frahm, with permission.

Reproduction

Marchantia berteroana (Figure 5-Figure 7) is **dioicous**, with a chromosome number of $n=9$ (Perold 1995; Phephu 2012a).

Males (Figure 18) are a bit larger than females (Figure 19-Figure 23) (Campbell 1965). In New Zealand, the antheridiophores (Figure 18) appear in August, followed in September by the archegoniophores (Figure 19-Figure 23).



Figure 18. *Marchantia berteroana* antheridiophore heads. Photo by Tom Thekathyl, with permission.



Figure 19. *Marchantia berteroana* with young archegoniophores. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 20. *Marchantia berteroana* with young archegoniophores before elongation. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 23. *Marchantia berteroana* with elongated archegoniophores, demonstrating how large a population can become. Photo by Pato Novoa, through Creative Commons.



Figure 21. *Marchantia berteroana* with developing archegoniophores. Photo by Pato Novoa, through Creative Commons.



Figure 22. *Marchantia berteroana* mature archegonial head before sporangia are mature. Photo by Andrew Hodgson, with permission.



Figure 24. *Marchantia berteroana* archegoniophore heads with emerging open sporangia. Photo by Tom Thekathyl, with permission.

Markham *et al.* (1978) found that there is a "dramatic" change in flavonoid pattern of *Marchantia berteroana* (Figure 5-Figure 7) that accompanies sexual reproduction. Is this a consequence or an adaptation? It would be interesting to know the role of the change in compounds in reproduction. Markham and Porter (1975, 1978) found that the aurone aureusidin 6-O-glucuronide occurs in antheridiophores (Figure 18) of at least two species of *Marchantia*, one of which is *M. berteroana*. It is unknown from any other organ of the liverworts. In flowering plants it gives brighter yellow colors to the flowers (Nakayama 2022). Markham and Porter suggested parallel evolution in bryophytes and flowering plants, although the compound is not common even in flowering plants.

The sporophyte begins development the following spring, continuing through the summer (Phephu 2012a). Once it matures, its stalk elongates by absorbing water, causing the cells to stretch. This causes the sporangia to protrude from the archegonial head (Figure 24-Figure 25). When the sporangium breaks open, it exposes the spores and elaters (Figure 25). Wiggling of the elaters in response to humidity changes helps to disperse the spores. Once the spores are dispersed, the fragile stalk disintegrates.



Figure 25. *Marchantia berteriana* mature sporangia with elaters protruding. Photo by Tom Thekathyl, with permission.

On the Falkland Islands, *Marchantia berteriana* (Figure 5-Figure 7) forms extensive patches several meters in diameter, from sea level to mountain tops (Duckett *et al.* 2012). Although it seems typical for females of this species to dominate elsewhere (Garcia-Ramos *et al.* 2007; Groen *et al.* 2010a), these populations produced males and females in about equal proportion. Perhaps this sex ratio is regulated by environmental/climatic conditions?

We know that gemmae (Figure 26-Figure 27) are produced when the sexual reproduction is inactive. High humidity suppresses the production of these gemmae cups, but high temperatures (ca. 15°C) promote greater production of the cups (Chopra & Kumra 1988). Gemmae, and probably at times spores, are dispersed by water (Phephu 2012a).



Figure 26. *Marchantia berteriana* thallus forming a rosette, with gemmae cups. Photo by Tom Thekathyl, with permission.

Scott (1963) observed that plants of *Marchantia berteriana* (Figure 5-Figure 7) failed to produce gemmae cups (Figure 26-Figure 27) in New Zealand when pots were covered with glass or polyethylene sheets. He experimented with plants growing in a saturated atmosphere and demonstrated that it was indeed moisture that inhibited the development of gemmae cups. This

behavior permits the liverwort to divert its resources to sexual reproduction at a time when conditions are most favorable for that type of reproduction.



Figure 27. *Marchantia berteriana* thallus showing distinct pores and gemma cups. Photo by Tom Thekathyl, with permission.

Interactions

Marchantia berteriana (Figure 5-Figure 7) has close associations with at least several other organisms. Meeks (2018) reported associations with **Cyanobacteria**. Brasell *et al.* (1986) found that *Marchantia berteriana* exhibited high rates of acetylene reduction, indicating a high rate of nitrogen fixation, in populations from burned sites in southern Tasmania. **Cyanobacteria** are important contributors to nitrogen fixation. Activity was considerably greater than that for the same species when they occurred in the adjacent undisturbed forest. There was no significant relationship with temperature, moisture, organic matter, nitrogen, or phosphorus in these associations. I found no studies regarding nitrogen fixation association in wet habitat populations, but I would expect it to occur there as well.

Fungal Interactions

Baylis (1970) found that *Marchantia berteriana* (Figure 5-Figure 7) formed mycorrhizal associations on unsteamed phosphorus-deficient soil. Baylis suggested that the fungi entered through the rhizoids. Johnson (1977) demonstrated that infection by members of the **Enogonaceae** in a New Zealand forest occurred in the lower part of the thallus and in rhizoids in *Marchantia berteriana*. These endophytes seemed to lack specificity, occurring in a variety of the tracheophytes tested. It is likely that many associations remain to be identified.

Biochemistry

This species does not have the large number of biochemical studies reported for some of the other *Marchantia* species. Markham and Porter (1975) provided early reports on the flavones isoscutellarein and hypolaetin 8-glucuronides in *Marchantia berteriana* (Figure 5-Figure 7). The composition and concentration of these change in response to seasonal changes and reproductive stage of the plant. Acacetin and its glycosides are absent when

gametangia are present (Markham *et al.* 1978). Instead, during the sexually active stage, the predominant flavonoids are 8-hydroxyapigenin and 8-hydroxyluteolin glycosiduronic acids. These latter flavonoids are absent during the stage of asexual reproduction when the acacetin and its glycosides achieve their most active concentrations.

Asakawa and Campbell (1982) found that the major components of terpenoids and bibenzyls in *M. berteriana* (Figure 5-Figure 7) are cuparene and (–)-2-hydroxycuparene. Cuvertino-Santoni *et al.* (2017) described a number of the volatile constituents.

***Marchantia debilis* (Figure 1, Figure 28-Figure 32)**

(syn. = *Marchantia chevalieri*)

Distribution

Marchantia debilis (Figure 28-Figure 32) is widespread in tropical Africa (Pócs & Lye 1999), where it is common north to south in the drier areas (Reeb *et al.* 2018).



Figure 28. *Marchantia debilis* on rock near water in Madagascar. Photo courtesy of Catherine Reeb.



Figure 29. *Marchantia debilis* in Madagascar, with archegoniophore. Photo courtesy of Catherine Reeb.



Figure 30. *Marchantia debilis* in Madagascar, showing dieback at the base of the thallus while the tips continue to grow. Photo courtesy of Catherine Reeb.



Figure 31. *Marchantia debilis* in Madagascar, showing numerous, overlapping thalli that help to conserve water. Photo courtesy of Catherine Reeb.



Figure 32. *Marchantia debilis* in Madagascar, growing on wet soil and rocks. Photo courtesy of Catherine Reeb.

Aquatic and Wet Habitats

Marchantia debilis (Figure 28-Figure 32) is more closely associated with water than some of the other species of *Marchantia* included here. It occurs on the edges of water in habitats like waterfalls, slow rivers (Figure 33-Figure 34), and ponds, on damp soil or rocks,

and sometimes experiences flooding, but it also occurs on terrestrial banks in both shaded and exposed areas (Reeb *et al.* 2018).



Figure 33. *Marchantia debilis* habitat on the riverbank in Madagascar. Photo courtesy of Catherine Reeb.



Figure 34. *Marchantia debilis* with *Riccia* on a riverbank in Madagascar. Photo courtesy of Catherine Reeb.

Hodgetts *et al.* (1999) similarly reported *Marchantia debilis* (Figure 28-Figure 32) from flushed rocks (Figure 35-Figure 36) in southern Africa. They are joined in this environment by the liverwort *Asterella bachmannii* (Figure 37), the mosses *Bryum alpinum* (Figure 38) and *Philonotis* spp. (Figure 39), and the hornworts *Anthoceros* spp. (Figure 40) and *Phaeoceros carolinianus* (Figure 41). *Marchantia debilis* also occurs on the soil and mud on river- and streambanks.



Figure 35. *Marchantia debilis* on rocks along riverbank in Madagascar. Photo courtesy of Catherine Reeb.



Figure 36. *Marchantia debilis* on rocks along riverbank in Madagascar. Photo courtesy of Catherine Reeb.



Figure 37. *Asterella bachmannii*, an associate of *Marchantia debilis* on flushed rocks in southern Africa. Photo by Ricky Taylor, through Creative Commons.



Figure 38. *Bryum alpinum*, an associate of *Marchantia debilis* on flushed rocks in southern Africa. Photo by Claire Halpin, with permission.



Figure 39. *Philonotis fontana*; several species of *Philonotis* associate with *Marchantia debilis* on flushed rocks in southern Africa. Photo by Claire Halpin, with permission.



Figure 40. *Anthoceros* sp., an associate of *Marchantia debilis* on flushed rocks in southern Africa. Photo by Bramadi Arya, through Creative Commons.



Figure 41. *Phaeoceros carolinianus*, an associate of *Marchantia debilis* on flushed rocks in southern Africa. Photo by Hermann Schachner, through Creative Commons.

Leonard (1994) found that *Marchantia debilis* (Figure 28-Figure 32) occurred on the periodically flooded parts of sandstone cliffs near Yanonge, Zaire, typically with *Garckea flexuosa* (Figure 42).



Figure 42. *Garckea flexuosa*, an associate of *Marchantia debilis* in the flooded parts of sandstone cliffs in Zaire. Photo by Manju C. Nair, through Creative Commons.

Adaptations

The adaptations of *Marchantia debilis* (Figure 28-Figure 32) involve the same structures as in other species of *Marchantia*. They have large air pores bordered with 5-8 rings of cells, with half projecting above the epidermis and half below into the photosynthetic air space (Reeb *et al.* 2018). The ventral scales occur in four rows and do not cover more than 30-50% of the thallus. These are purple, at least in the median portion of the thallus.

The thalli can grow over mosses (Figure 43), providing them with a water-retaining sponge that keeps them moist longer than just soil.



Figure 43. *Marchantia debilis* in Madagascar, growing with mosses that can help to retain moisture. Photo courtesy of Catherine Reeb.

Reproduction

As is typical for species of *Marchantia*, *Marchantia debilis* (Figure 28-Figure 32) is **dioicous** (Reeb *et al.* 2018). I have not found information on stimuli needed to produce archegoniophores (Figure 44-Figure 45) or antheridiophores or what their seasonal behavior is. Gemmae (Figure 46) serve as effective means of asexual reproduction.



Figure 44. *Marchantia debilis* with an archegoniophore, in Madagascar. Photo courtesy of Catherine Reeb.



Figure 45. *Marchantia debilis* archegoniophore in Madagascar, showing large pores. Photo courtesy of Catherine Reeb.



Figure 46. *Marchantia debilis* with gemmae cups, in Madagascar. Photo courtesy of Catherine Reeb.

Biochemistry

Anchang *et al.* (2016) reported a new methanol extract, marchantinquinone-l'-methyl ether, from *Marchantia debilis* (Figure 28-Figure 32). In addition it had three known bis-bibenzyls. Asakawa (2021) noted that *Marchantia debilis* produces large quantities of marchantin-type bis-bibenzyls. Anchang and Simonsen (2019) reported that extracts from both wet and dry liverworts were able to inhibit the bacteria *Staphylococcus aureus* and *Dermatophilus congolensis*, and the fungus *Aspergillus flavus*. On the other hand, the bacteria *Pseudomonas aeruginosa* and *Bacillus* spp. were inhibited by extracts from dry, but not wet, *Marchantia debilis*. This suggests that at least one of the inhibitory substances must be produced in response to desiccation.

Yongabi *et al.* (2016) reported that petroleum extracts from *Marchantia debilis* (Figure 28-Figure 32) could be used to treat at least some of the bacteria responsible for diabetic bacterial foot infections. This product has been marketed as BryoCreamTM. It had a 90% cure rate in three weeks.

Marchantia emarginata (Figure 47-Figure 53)

(syn. = *Marchantia palmata*, *Marchantia sumatrana*)

The taxonomic relationships of *Marchantia emarginata* (Figure 47-Figure 53) have recently been evaluated in India (Singh & Singh 2013) and Japan (Zheng & Shimamura 2021, 2022a).



Figure 47. *Marchantia emarginata* with enlarged terminal buds. Photo by Taiwan Mosses, through Creative Commons.

Distribution

Marchantia emarginata (Figure 47-Figure 53) is widespread, occurring in the Northern Hemisphere in Asiatic and Oceanic regions (Bischler-Causse 1989). Its distribution includes Borneo, China, Guam, Hong Kong, India, Indonesia Japan, Korea, Malaysia, Marianas, New Britain, New Caledonia, New Guinea, Philippines, Solomon Island, Sri Lanka, and Thailand (Bischler-Causse 1989; Siregar *et al.* 2020). In Malesia, it occurs from sea level to 1500 m asl, and Lu and Huang (2017) reported that it occurs below 1800 m asl, adding Taiwan to its distribution. Singh and Singh (2013) reported it for the first time in the Indian Himalayas. It is threatened in Singapore (Ho 2013).

Aquatic and Wet Habitats

Marchantia emarginata (Figure 47-Figure 53) occurs on walls of bays, in side brooks, on a large block in pouring water, in waterfalls, and in thermal acidic spray in the tropics (Ruttner 1955). In Sumatra, Siregar *et al.* (2020) found it on soil (Figure 48) and rocks (moist, damp or wet, shaded, semi-exposed places, riversides, creeks; Figure 49-Figure 50). Lu and Huang (2017) reported similar habitats in Taiwan, including damp soils up to 1800 m asl. As seen in the images, it occurs on the sides of drainage ditches (Figure 51-Figure 52) as well.



Figure 48. *Marchantia emarginata* male on soil. Photo by Ellen8355, through Creative Commons.



Figure 49. *Marchantia emarginata* on rocks in and beside stream. Photo courtesy of Tian-Xiong Zheng (NICH).

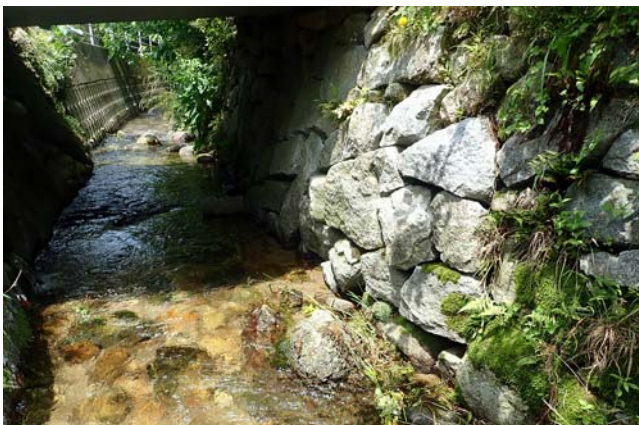


Figure 50. *Marchantia emarginata* on rocks along stream. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 51. *Marchantia emarginata* on rocks and concrete along ditch. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 52. *Marchantia emarginata* on rocks along ditch. Photo courtesy of Tian-Xiong Zheng (NICH).

But it can also occur on soil banks (Figure 53) if there is enough moisture. In southern China, this species is found frequently with *Dumortiera hirsuta* (Figure 54) on soil banks beside roads (Figure 55) (Li Zhang, pers. comm. 12 August 2022).



Figure 53. *Marchantia emarginata* ssp. *cuneiloba* on soil bank beside road. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 54. *Dumortiera hirsuta*, associate of *Marchantia emarginata* on roadside soil banks. Photo ©mutolisip, through Creative Commons.



Figure 55. *Marchantia emarginata* ssp. *tosana* with *Dumortiera hirsuta* (larger, hairy thalli). Photo courtesy of Li Zhang.

Tewari and Pant (1996) reported that *Marchantia emarginata* (Figure 47-Figure 53) grew along the borders of warm springs in hot spring areas of the Kumaon Himalaya, but was unable to grow in the hot, sulfurous springs.

Adaptations

This is not a truly aquatic bryophyte, but lives in habitats that can be wet part or most of the time, then experience drought when water levels recede. Hence we should expect adaptations that mediate these drier conditions.

Marchantia emarginata (Figure 47-Figure 53) has scales that are purple or pale-purple (see Figure 56) (Lu & Huang 2017). These contribute to water movement, absorption, and maintenance of hydration. One can only speculate about the advantages of the color. We have seen, in the chapter on light in Volume 1, that red pigments can be in higher concentrations in shade plants than in full sunlight (Melati *et al.* 2019). Furthermore, in the extreme shade of the rainforest, some forest floor tracheophytes have red or purple on the lower leaf surface, increasing the absorption of light at the upper end of the photosynthetic

action spectrum (Lee & Graham 1986). Hence, we can speculate that such a function might be operating in liverworts with purple scales. We need data to determine if the intensity of the color relates to the level of light in the habitat. I see no value to having this pigmentation on the ventral surface as a protection in high light. Do these scales somehow reflect light back to the photosynthetic tissue under low light conditions?



Figure 56. *Marchantia polymorpha* ssp. *ruderalis* scales showing purplish color of some *Marchantia* species. Photo by Des Callaghan, with permission.

Like other members of *Marchantia*, *M. emarginata* (Figure 47-Figure 53) has pores in the epidermis. These provide entry of CO₂ into the chamber beneath where photosynthetic filaments reside. And cuticular ridges around the pores are hydrophobic, preventing the entry of water that would greatly reduce the ability of CO₂ to enter the photosynthetic filaments.

Like many thallose liverworts, the thallus of *Marchantia emarginata* (Figure 47-Figure 53) often grows over mosses (Figure 57, Figure 61). These mosses provide a sponge-like base that helps to retain water longer than soil or pebbles alone, thus widening the habitat range of the liverwort.



Figure 57. *Marchantia emarginata* subsp. *tosana* growing on mosses. Photo from Taiwan Mosses, through Creative Commons.

Reproduction

Reproduction in *Marchantia emarginata* (Figure 47-Figure 53) follows that of other species in the genus. It is **dioicous** (Lu & Huang 2017). Cutting (1910) described the antheridial receptacles (Figure 58-Figure 59) of the species. A later description by Srinivasan (1939) suggests that it could actually be **protogynous** (female parts develop before male parts), with archegonial receptacles (Figure 60) developing first, then antheridial receptacles developing, a rather unusual order for bryophytes (see Vol. 1, Chapt. 3-2). Srinivasan describes the species as having receptacles that start as purely female, but soon one or more of the proliferations bear antheridia that grow out from the ventral surface. However, these proliferations once again become active lobes of the female receptacle. Srinivasan describes them as intermediate between an archegonium and an antheridium, later becoming typical antheridia. This observation leads him to the suggestion that the two reproductive structures are homologous. Nevertheless, the species is generally accepted as **dioicous**.



Figure 58. *Marchantia emarginata* males with antheridiophores. Photo by Ellen8355, through Creative Commons.



Figure 59. *Marchantia emarginata* males showing antheridial receptacles. Photo by Li Zhang, with permission.



Figure 60. *Marchantia emarginata* ssp. *tosana* females with archegonial heads. Photo courtesy of Li Zhang.

Asexual reproduction occurs by **gemmae** in cups (**cupules**) (Figure 61) (Ho 2013). In Singapore, these gemmae appear to be the primary means of reproduction, along with fragmentation and branching (see also Johnson 1958). On the other hand, Singh and Singh (2013) found no gemmae cups in the Himalayan material they studied, suggesting perhaps a climatic or photoperiod problem. We know that production of *Marchantia polymorpha* (Figure 2) gemmae are favored by short days (Carter & Romine 1969). If these conditions are coupled with the wrong temperatures, then the hormonal stimulus to produce gemmae might be absent.



Figure 61. *Marchantia emarginata* with gemmae. Photo by 楊玉鳳, through Creative Commons.

Kumra and Chopra (1989a,b) found that cytokinins (2iP, BAP, kinetin and zeatin) increased both growth and gemma cup formation in *Marchantia emarginata* (Figure 47-Figure 53) and were of decreasing effectiveness in that order. However, BAP is the most effective in increasing the number of gemmae. They also found (1989b) that vegetative growth and gemmae cup production were greatest in continuous light at 4500 lux, but were inhibited by applied auxins at most concentrations.

Li Zhang (pers. comm. 6 August 2022) sent me images of very unusual *Marchantia emarginata* ssp. *tosana* with

gemmae growing on the antheridiophore and archegoniophore (Figure 62-Figure 63). He concluded that the gemmae landed on these reproductive structures when the latter were young and the stalks had not yet elongated. These gemmae then were elevated as the antheridiophore and archegoniophore elongated. These two images represent two different populations in the same area. He considered that the high humidity in that location could make this unusual substrate possible. It also suggests that the inhibitor(s) to gemmae germination present in the thallus are absent in the archegoniophore and antheridiophore. But really, on the ends of the fingers of the antheridial head? It is interesting that the antheridial head does not have the typical shape seen in Figure 58.



Figure 62. *Marchantia emarginata* ssp. *tosana*, in Guangdong, S. China, with germinated gemmae and gemmae cups growing on male receptacle arms. Photo courtesy of Li Zhang.



Figure 63. *Marchantia emarginata* ssp. *tosana* with gemmaling on archegoniophore stalk, Guangdong, S. China. Photo courtesy of Li Zhang.

Fungal Interactions

Although I found little on fungal interactions for this species, Srinivasan (1939) reported fungal-forming **pycnidia** (flask-shaped fruiting body bearing conidiophores and conidia on interior and occurring in various imperfect fungi and Ascomycetes; Figure 64) in *Marchantia emarginata* (Figure 47-Figure 53). Srinivasan further suggested that the fungal attack might cause a change in the sex of the receptacle. This remains to be demonstrated experimentally, but with what we currently know about hormones from bacteria and fungi, and their influence on the development of bryophytes, this would be a worthwhile experiment.



Figure 64. *Phoma* (Coelomycetes) pycnidium. Some fungi have pycnidia that appear on *Marchantia emarginata*. Photo by Brawlings, through Creative Commons.

Iqbal *et al.* (1988) described vesicular-arbuscular mycorrhizal fungi from both rhizoids and the ventral thallus parenchyma of *Marchantia emarginata* (Figure 47-Figure 53).

Fatma (2018) determined an endophytic mold in *Marchantia emarginata* (Figure 47-Figure 53) to be *Daldinia eschscholtzii*. (Figure 65-Figure 66).



Figure 65. *Daldinia eschscholtzii*, an endophytic fungal species that can occur in *Marchantia emarginata*. Photo by Petra White, through Creative Commons.



Figure 66. *Daldinia eschscholzii* ventral view. Photo by Byrain, through Creative Commons.

Biochemistry

Many biochemical studies have described the biochemical properties and potential uses of secondary compounds in the genus *Marchantia*. See Jantwal *et al.* (2019) for a review. The species *Marchantia emarginata* (Figure 47-Figure 53) may be less well known than the widespread *M. polymorpha* (Figure 67), but its biochemical studies are nevertheless numerous. Only a sampling will be presented here to suggest their ecological importance.



Figure 67. *Marchantia polymorpha* female with archegoniophores; this species is the typical example used for teaching about liverworts. Image copyright Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Yuan *et al.* (2021) demonstrated the presence of uridine diphosphate-dependent glycosyl transferases (UGTs) in *Marchantia emarginata* (Figure 47-Figure 53), noting the importance of flavonoid glycosides for their pharmaceutical activities. The value of pharmaceutical

compounds to the liverworts needs much experimental study. Are they merely a consequence of some other function or pathway, or do they defend the bryophytes against pathogens or herbivores?

Huang *et al.* (2010) isolated marchantin A, a bibenzyl ether, from *Marchantia emarginata* subsp. *tosana* (Figure 68). This secondary compound is able to induce **apoptosis** (death of cells which occurs as normal and controlled part of organism's growth or development) in human MCF-7 breast cancer cells. It furthermore has good anti-oxidant activity. Fatma (2018) likewise demonstrated anti-oxidant activity in this species. Antioxidants can be important in rehydration of bryophytes, countering the oxidative burst that often occurs (see for example Minibayeva & Beckett 2001).



Figure 68. *Marchantia emarginata* ssp. *tosana* females, a source of marchantin A. Photo from Taiwan Mosses, through Creative Commons.

Kumar *et al.* (2007) found that *Marchantia emarginata* could be used against tumors.

Wang *et al.* (2017) described the chemistry of the cuticle of *Marchantia emarginata* (Figure 47-Figure 53). They isolated the fatty ω -hydroxyacid/fatty alcohol hydroxycinnamoyl transferase (HFT) from the species and, based on a species of tobacco, suggested that its occurrence in the cells indicate that the **feruloylation** (subclass of carboxylic acid esterases that hydrolyze ester bonds between hydroxycinnamic acids and sugars present in plant cell walls) of the cutin monomers takes place in the cytoplasm. Bryophytes are often described as lacking cuticle, but **cutin** (insoluble polyester of C₁₆ and C₁₈ hydroxy fatty acids and main component of cuticle) is becoming well known in bryophytes. It appears that in bryophytes the cuticle is simply thinner than in tracheophytes.

Toyota *et al.* (2004) described the **sesquiterpene** alcohol 1,6-Humuladien-10-ol from *Marchantia emarginata* subsp. *tosana* (Figure 68). These **sesquiterpenes** are C₁₅-terpenoids comprised of three isoprene units. They are especially common in tracheophytes, but also are becoming well known in bryophytes (Awouafack *et al.* 2013). We know that sesquiterpenes can include essential oils and aromatic constituents; others are antimicrobial or provide protection against oxidative damage.

Alcoholic and acetonc extracts of *Marchantia emarginata* (Figure 47-Figure 53) indicated the presence of

carbohydrates, proteins, diterpenes, phytosterols, and anthocyanin, whereas flavonoids were present only in the alcoholic extract and phenol only in the acetonic extract (James *et al.* 2020). Alcohol extracts exhibited activity against the bacterium *Escherichia coli* (Figure 69) and both alcohol and acetone extracts against *Klebsiella pneumoniae* (Figure 70). However, neither alcohol nor acetone extracts exhibited activity against *Staphylococcus aureus* (Figure 71). This is unfortunate because this hospital scourge has become methicillin-resistant (Solberg 2000) and a new treatment is needed.

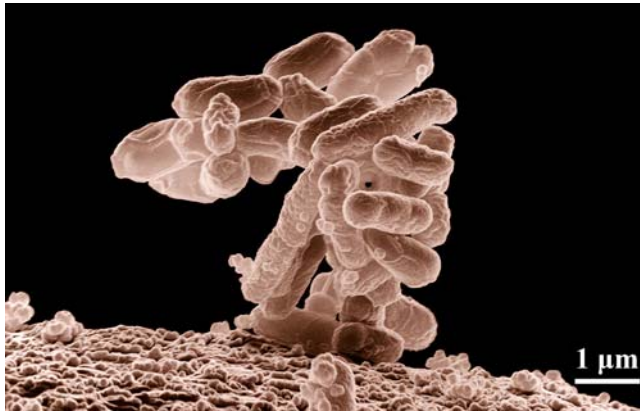


Figure 69. *Escherichia coli*, a bacterial species that is inhibited by alcohol extracts of *Marchantia emarginata*. Photo by USDA, through public domain.



Figure 70. *Klebsiella pneumoniae*, a bacterial species that is inhibited by both alcohol and acetone extracts of *Marchantia emarginata*. Photo from CDC, through public domain.

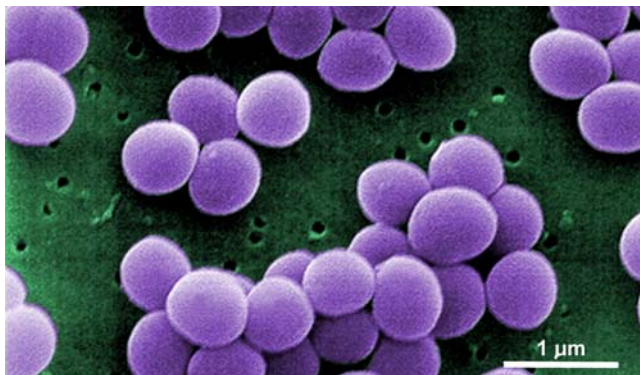


Figure 71. Colorized SEM of *Staphylococcus aureus*, a species that is not inhibited by alcohol or acetone extracts of *Marchantia emarginata*. Photo by Janice Haney Carr, CDC, through public domain.

Spermine is a polyamine in all **eukaryotic** (having nucleus with nuclear membrane) cells and is involved in cellular metabolism. The amino acid ornithine is its precursor. It is an essential growth factor in some bacteria as well.

Culturing

Chopra and Dhingra-Babbar (1986) studied the effects of various amino acids, complex organic substances, and active charcoal on the growth and development of *Marchantia emarginata* (Figure 47-Figure 53). The amino acid response was dependent on the concentration, with lower concentrations enhancing growth and higher ones inhibiting it. Glutamic acid, histidine, and methionine stimulated callus growth, whereas tryptophan induced thallus differentiation. Activated charcoal delayed callus formation and growth was extremely reduced. Coconut milk stimulated callus growth at 15% (v/v) and inhibited it at 25%.

Marchantia inflexa (Figure 72-Figure 74)

Despite its somewhat narrow tropical distribution, *Marchantia inflexa* (Figure 72-Figure 74) has received considerable attention regarding its sexual expression and the role of the environment in this expression. Marks *et al.* (2019a,b) revealed that those genes on sex chromosomes are subject to greater diversifying selection than those on autosomal (non-sexual) and organellar genes. This diversification occurs mostly among male-specific genes, whereas divergence of other sex-linked genes differs little from that of autosomal genes.

Distribution

Marchantia inflexa (Figure 72-Figure 74) is restricted to the Neotropics and bordering regions, from Central America and the Caribbean and from northern Venezuela to the southern United States (Marks *et al.* 2019a).



Figure 72. *Marchantia inflexa* thalli with brown scales covering apical growth regions. Photo by Scott Zona, with permission.



Figure 73. *Marchantia inflexa* with gemmae cups. Note brown scales covering the apical growth region. Photo by Alan R. Frank, through Creative Commons.



Figure 74. *Marchantia inflexa* showing large population of overlapping thalli. Photo by Alan R. Frank, through Creative Commons.

Aquatic and Wet Habitats

Marchantia inflexa (Figure 72-Figure 74) occurs mostly on streambank rocks (Figure 75-Figure 76) and soil (Figure 77-Figure 78) (Marks *et al.* 2019a).



Figure 75. *Marchantia inflexa* on rock. Note the meristematic tips on the branches, with brown scales covering them. Photo by Alan R. Frank, through Creative Commons.



Figure 76. *Marchantia inflexa* on streambank. Photo by Karen and Philip, through Creative Commons.



Figure 77. *Marchantia inflexa* on soil bank. Photo by Jeff Garner, through Creative Commons.



Figure 78. *Marchantia inflexa* on soil bank. Photo by Jeff Garner, through Creative Commons.

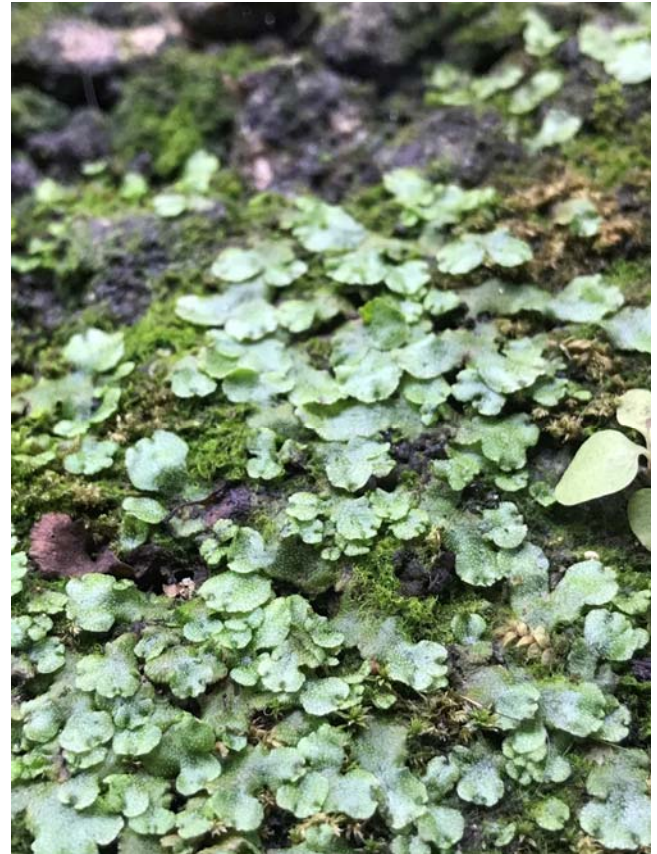


Figure 79. *Marchantia inflexa* population on soil bank where mosses can help it to maintain moisture. Photo by Alan R. Frank, through Creative Commons.

Physiology

water relations

Marks *et al.* (2019a,b) investigated dehydration tolerance, emphasizing differences between genetic lines, that allowed them to identify multiple dehydration-associated genes, two of which were sex-linked, suggesting that dehydration tolerance may be impacted by sex-specific genes. Identification of these genes permits the identification of gender when sexual expression is not present. Although the more common habitat for *Marchantia inflexa* (Figure 72-Figure 74) is on rock and soil surfaces along streambanks (Figure 79) in tropical forests, it can also colonize more exposed sites such as disturbed sites along roads.

Marks *et al.* (2019ab) explored the relationships to drought in five populations of *Marchantia inflexa* (Figure 72-Figure 74) in northern Trinidad and Tobago in the Republic of Trinidad. When grown in a common garden, the responses maintained the differences they had exhibited in their original habitats, indicating that they were genetically determined. They also found that males (Figure 86-Figure 87) had a lower desiccation tolerance than did females (Figure 88-Figure 89) in less exposed sites, but not in more exposed sites. The males furthermore exhibited more variation in morphology than did females, while females exhibited similar desiccation tolerance across the five sites.

Marks *et al.* (2021) identified stress responses to dehydration in *Marchantia inflexa* (Figure 72-Figure 74), including expression of LEA and ELIP genes and evidence of cell wall remodelling. They found, however, that there was little temporal synchronization of the responses across six genotypes. The researchers suggested that differences in timing of the transcriptional adjustments contribute to the variation seen among genotypes. Furthermore, developmental differences affect the relative tolerance of meristematic and differentiated tissues.

electrical responses

Measuring electrical responses in bryophytes is not a common activity, but such measures can be used to assess a plant's response to injury or environmental stimuli. Several studies have used *Marchantia inflexa* (Figure 72-Figure 74) as a subject. Cooper *et al.* (2022a) commented that the KCl-filled glass electrodes placed into plant tissues is subject to artifacts and is less reliable than the impedance method. Using the impedance method, one can detect plant injury and exposure to environmental compounds such as glutamate. This method was used successfully in *M. inflexa* by placing two impedance leads 2 cm apart into the thallus tissue, with a cut made to a third thallus between the two leads. Cooper *et al.* (2022b) found that the liverwort showed no electrical response to glutamate exposure, whereas *Arabidopsis thaliana* (Figure 80) and *Pisum sativum* (Figure 81) (both flowering plants) produced rapid depolarization upon exposure.



Figure 80. *Arabidopsis thaliana*, a species that, unlike *Marchantia inflexa*, experiences rapid depolarization upon exposure to glutamate. Photo by Stefan Lefnaer, through Creative Commons.



Figure 81. *Pisum sativum* var. *sativum*, a species that, unlike *Marchantia inflexa*, experiences rapid depolarization upon exposure to glutamate. Photo by Stefan Lefnaer, through Creative Commons.

Adaptations

Among the common adaptations is their ability to form dense mats that help to maintain moisture in the soil (Figure 82-Figure 83). But this ability to form mats brings its own problems of self-competition.



Figure 82. *Marchantia inflexa* with overlapping thalli that can help to conserve soil moisture. Photo by Scott Zona, with permission.



Figure 83. *Marchantia inflexa* with gemmae cups, showing closely contacting and overlapping thalli. Photo by Jamie Newman, through Creative Commons.

Crowley *et al.* (2005a) described three mechanisms for competition for space (Figure 82-Figure 83): **expansion** (spreading to unoccupied habitat), **lottery** (replacing dead competitors), and **overgrowth** (encroaching on competitors along zones of contact). For *Marchantia inflexa* (Figure 72-Figure 74), a local stable coexistence of the sexes requires the avoidance of this self-competition. This stable coexistence of the sexes seems to be possible in a narrow range of disturbance intensities, explaining ambiguous results in simulation studies (McLetchie *et al.*, 2002). Crowley *et al.* noted the importance of **contact inhibition** in this species. They considered that the improbability that a disturbance regime could maintain death rates within the high and restricted range is consistent with stable coexistence and that it indicates that long-term coexistence of the two genders may be dependent on processes operating at the scale of the metapopulation (Garcia-Ramos *et al.* 2002, 2007). Garcia-Ramos *et al.* (2002, 2007) indicated that single-sex populations were common and that males were rare. In the tropics the two sexes often coexisted in a single patch; in the USA only all-male or all-female populations were known. The spores were able to colonize disturbed sites, and large disturbed areas permitted

the colonization and coexistence by both sexes, with fertilization typically occurring between patches.

Reproduction

For a species that has few publications describing habitats, *Marchantia inflexa* (Figure 72-Figure 74) has an abundance of published reproductive studies, particularly related to the environmental conditions. Like the genus, the species is **dioicous**. Prominent among the studies are those related to environmental effects on sex ratio.

McLetchie and Puterbaugh (2000) noted that unisexual populations and female- or male-biased populations were common in this **dioicous** liverwort. Garcia-Ramos *et al.* (2002) found that whereas both sexes could coexist in a single patch in the tropics, in the USA only all-male or all-female populations are known. McLetchie and Puterbaugh (2000) found that sex-ratio patterns could be related to growth rates, number of meristematic regions (Figure 72-Figure 73), and asexual reproduction in the riverside populations they studied in Trinidad. Of the 209 patches they observed, 83% contained no sex-expressing thalli. Only 9% contained thalli of both sexes. The remainder were either entirely female-expressing (4%) or male-expressing (4%). Small patches were less likely to be expressing sexual reproductive structures. Shade (less canopy openness) also correlated with lower sexual expression. In those populations with expression of both sexes, the ratios of male (Figure 86-Figure 87) to female (Figure 88-Figure 89) ranged 0.22-0.80.

But what causes this variation? McLetchie and Puterbaugh (2000) found that females (Figure 88-Figure 89) of *Marchantia inflexa* (Figure 72-Figure 74) grew faster, produced more meristematic tips (Figure 73), and had lower levels of asexual reproduction (Figure 83-Figure 85) than did males (Figure 86-Figure 87). Furthermore, the number of meristematic tips exhibited a negative correlation with both asexual reproduction and growth rate. Hence, these factors could lead to female sex bias in reproductive colonies. A further factor in shifting toward female dominance is that populations that reproduce better asexually (*i.e.* males) are less likely to succeed under stressful conditions. These relationships position the species to produce more spores under stressful conditions and thus have a means to arrive at a different location where the stress might not be present.

McLetchie *et al.* (2002) followed with a study on the local sex-ratio dynamics using *Marchantia inflexa* (Figure 72-Figure 74) from rock surfaces and bark in Trinidad. These populations differed widely in their population sex ratios at the study site in the rainforest. They followed seven life history stages. In some stages the thalli became more abundant and extend over the substrate and each other in their quest for space (Figure 84-Figure 85). The sex ratio within a patch was not stable: at low to moderate disturbance levels, females gradually eliminated males. At high disturbance levels, males (Figure 86-Figure 87) eliminated females (Figure 88-Figure 89). This pattern was not dependent on whether sexual propagules (spores) could germinate within the patch, but germination of gemmae (Figure 84-Figure 85) within the patch had an important role. Hence, sexual reproduction, while unimportant within patches, is critical in spatial landscapes (Garcia-Ramos *et al.* 2002).



Figure 84. *Marchantia inflexa* with gemmae. Photo by Jeff Garner, through Creative Commons.



Figure 85. *Marchantia inflexa* with gemmae cups. Photo by Jamie Newman, through Creative Commons.

However, spores may be the primary means for recolonizing patches eliminated by large-scale disturbances (McLetchie *et al.* 2002). Once a patch became fully occupied, the production of the wind-dispersed spores was maximized. Once the colony became re-established, spore production declined and the sex ratio became increasingly more biased toward one or the other sex. Such scenarios support the concept that the sex ratio is determined at the **metapopulation** (group of spatially separated populations of same species which interact at some level; regional group of connected populations of species) level.

One question that arises is how does a species maintain sexually dimorphic pre-adult traits (Fuselier & McLetchie 2002). Fuselier and McLetchie noted that sexual dimorphism can influence the distribution of the sexes, the population sex ratios, the maintenance of the sex in populations, and the evolutionary potential of the species. Hence, in species like *Marchantia inflexa* (Figure 72-Figure 74), where sexual dimorphism results in greater growth and reproduction in females, the population could develop a female-biased sex ratio. Fuselier and McLetchie found that the sexes overlapped in habitat use. Furthermore, different populations exhibited differences in growth, asexual reproductive rates (Figure 84-Figure 85), degrees of sexual dimorphism, and the strength of their

among-trait correlations. The investment in growth and in asexual reproduction differed in single-sex and mixed-sex populations, but the degree of sexual dimorphism did not. The researchers concluded that the local environment may exert more influence than does the presence of the opposite sex in maintaining sexual dimorphism. Furthermore, between-sex correlations were not significant in the greenhouse common garden, but were significant in the field. Garcia-Ramos *et al.* (2002) found that males were able to persist longer in local populations due to minor disturbances such as drought.

Females (Figure 88-Figure 89) exhibited a cost for plasticity, whereas males (Figure 86-Figure 87) did not (Fuselier & McLetchie 2002). Among females, early sex-expressing individuals produced fewer gemmae cups than did late-expressing plants, supporting the concept that there is a tradeoff between the two modes of reproduction. These observations suggest that events during the life of the plant can influence its success at the local population level. These events can differ among the years of its life, making the success of a given population a somewhat random process dependent upon the changing conditions in the environment.



Figure 86. *Marchantia inflexa* males. Photo by Jeff Garner, through Creative Commons.

Fuselier and McLetchie (2004) explored several environmental parameters to determine if the two sexes exhibited different preferences. Using two populations in Trinidad and ten in the USA, they found no differences in preference for substrate, humidity, wind speed, or exposure among or within populations. However, in the USA, male populations (Figure 86-Figure 87) tended to occur under

more open canopies and in a wider light range than did females (Figure 88-Figure 89).



Figure 87. *Marchantia inflexa* males. Photo by Scott Zona, with permission.



Figure 88. *Marchantia inflexa* females. Photo by Jeff Garner, through Creative Commons.



Figure 89. *Marchantia inflexa* females. Photo by Jeff Garner, through Creative Commons.

Crowley *et al.* (2005b) postulated that the long-term coexistence of the sexes in *Marchantia inflexa* (Figure 72-

Figure 74) might be only temporary. They found that fragmentation is important in overgrowth competition. Stanley (2019) hypothesized that females (Figure 88-Figure 89) in bryophytes would show a greater competitive ability, thus at least in part accounting for the frequent female (Figure 88-Figure 89) bias in bryophyte sex ratio. In their greenhouse cultures of *M. inflexa*, they found that both sexes averaged 41% more growth if accompanied by the opposite sex than that of single-sex cultures. Their model predicted coexistence between the sexes, but that males (Figure 86-Figure 87), not females, would be in greater numbers, with a ratio of 3.2 males to 1 female.

Groen *et al.* (2010a) were surprised to find that males (Figure 86-Figure 87) of *Marchantia inflexa* (Figure 72-Figure 74), the gender that occurs in more tree-canopy openness, have lower chlorophyll *a:b* ratios than do females. Generally, a low chlorophyll *a:b* ratio, caused by more chlorophyll *b*, is an adaptation to shade. But both sexes had lower edge pore density in greater canopy openness; males had a weak positive correlation between edge pore density and light intensity (Groen *et al.* 2010b). Thus it appears that light intensity and canopy openness have opposing effects on edge pore density in males (Figure 86-Figure 87). The researchers suggest that males might be more responsive to water stress than are females (Figure 88-Figure 89). Females, on the other hand, have more support tissue, providing greater storage, and providing the resources needed for the female plants to support their sexual role.

Garcia-Ramos *et al.* (2007) noted that as a patch of *Marchantia inflexa* (Figure 72-Figure 74) persists through time, it is more likely to lose males (Figure 86-Figure 87) than females (Figure 88-Figure 89). This is due, at least in part, to the faster tissue growth of females. On the other hand, both sexes generally persist in the metapopulation, but with females predominating. Males had the advantage during patch filling, with their more abundant gemmae (Figure 84-Figure 85) providing an effective colonization strategy. Since males kept colonizing these available patches, they were maintained in the metapopulation. Similar maintenance of both sexes, particularly in small, highly disturbed populations where life-history traits and mortality differ between sexes, is likely to be a widespread phenomenon, particularly among dioicous bryophytes.

Using methods described by Chang *et al.* (2006), Fuselier (2008) found that geographically separated populations were significantly different. Single-sex populations of *M. inflexa* (Figure 72-Figure 74) in Oklahoma and Florida, USA form a distinct phenotypic group and it would be worthwhile to study physiological and developmental differences as well. Plants from single-sex and both-sex populations differed in their life history strategies. Those in single-sex populations invested more in growth than in asexual (gemmae; Figure 84-Figure 85) reproduction. While they produced as many sexual structures, they produced fewer gametangia per gametophore than did plants from both-sex populations, suggesting a possible chemical interaction among the plants. Characters of female plants (Figure 88-Figure 89) were positively correlated with geographic, nearest-neighbor distance. Characters of male plants (Figure 86-Figure 87) showed no relationship to geographic distance.

Dispersal is a logical choice for differences in population genders. Male plants produce more gemmae (Figure 84-Figure 85) and therefore should propagate more new plants near the parent colony. Female plants (Figure 88-Figure 89) produce spores and can therefore colonize areas at greater distances. But the gemmae, mostly falling within 1 m of the parent, have a greater chance of landing on a suitable substrate with suitable environmental conditions. To further complicate the picture, gemmae from males (Figure 86-Figure 87) (producing more males) have lower survivability than female gemmae due to desiccation (Stieha *et al.* (2014).

Brzyski *et al.* (2014) collected male and female plants from two strikingly different habitats within the same region: along natural sites (rivers) and along novel human-modified sites (roadsides). They used a common garden to demonstrate a strong sex by habitat interaction: male (Figure 86-Figure 87) and female (Figure 88-Figure 89) responses differed significantly by their source habitat. Road-collected females had higher growth and asexual reproduction compared to females from riverside habitats. In males, the pattern was not significant, but tended to be opposite to that of the females. The researchers found significant genetic differentiation between plants of the two habitats and found no evidence of individual differences in growth plasticity. However, there was a genotype effect for gemmae production. Although males and females did not differ genetically, river-collected plants with lower sexual potential were more diverse than roadside-collected plants. Could this be due to founder events, or are there selection pressures yet to be discovered? Nevertheless, these populations show that individual variation in reproduction is controlled by the interaction of genetics and environment.

Moore *et al.* (2016) questioned the selection for gamete dispersal and capture in clump water-holding capacity. In *Marchantia inflexa* (Figure 72-Figure 74), a dense tomentum-like mass of scales surrounds the archegonia (Figure 88-Figure 89), presumably retaining sperm-laden water. The male receptacle (Figure 86-Figure 87), on the other hand, has no scales and may serve as a dispersal splash platform (Figure 86).

Stieha *et al.* (2014) observed the productivity and dispersal of gemmae in *Marchantia inflexa* (Figure 72-Figure 74). Male plants produce more gemmae and more quickly than do female plants, but male plants have lower desiccation tolerance, leading to lower gemmae survival rates. They found that gemmae in this species can move up to 20 cm per minute in a light rain, permitting them to reach locations unoccupied by their parents. Models demonstrated that long-distance dispersal of gemmae is possible and they are likely to be successful if they stay moist. They warned that measurements of different stages to dispersal can be misleading about the survival of the sexes. Nevertheless, the gemmae are critical to the maintenance of both sexes.

Stieha *et al.* (2017) summarized the known mechanisms for maintaining both sexes to be "semi-independent dynamics of populations within a metapopulation. These semi-independent dynamics are influenced by dispersal and recolonization rates, which are affected by the spatial arrangement of populations." Using a mathematical model, Stieha and coworkers demonstrated

that at intermediate distances between populations, metapopulations maintained both sexes, and the spatial arrangement of populations changed the threshold at which one sex was lost. However, when populations were close to one another, one sex was eliminated and the single-sex metapopulation persisted through dispersal of asexual propagules. When populations were far apart, one sex was eliminated, and the metapopulation either went extinct due to lack of recolonization by asexual propagules or persisted because clumped populations facilitated recolonization. Hence, spatial arrangements are important in the maintenance or elimination of sexes in clonal organisms. This helps to explain the persistence of geographic parthenogenesis and the continuance of asexual species such as founder populations of dioicous species.

With so much known about the sexual behavior of *Marchantia inflexa* (Figure 72-Figure 74) populations, Walter (2015) set out to detect genetic evidence of sexual reproduction in sexual and asexual populations. She predicted that genetic variation would be higher in sexually reproducing populations when compared to asexually reproducing populations. In these haploid organisms, there is rapid selection for advantageous traits and rapid removal of deleterious ones. Sexual reproduction permits recombinations among the genes on different chromosomes, creating variability among offspring. Asexual reproduction such as gemmae produces a carbon copy of the parent. The results, using *Marchantia inflexa* (Figure 72-Figure 74), are fascinating. Bisexual populations are becoming more female biased (Figure 88-Figure 89), suggesting some mechanism of competition. The all-female populations have a low level of genetic diversity, implying that they have arisen mostly from asexual reproduction.

Brzyski *et al.* (2018) noted that sexual reproduction requires close proximity to potential mates. Clonal growth can increase this distance by carrying the reproductive structures farther from a neighboring plant of the opposite sex, thus reducing the probability of mating. The researchers calculated the spatial distributions as the likelihood that pairs of individuals were the same sex or genotype of *Marchantia inflexa* (Figure 72-Figure 74) and determined how the likelihood was affected by habitat patch size. In this species, asexual reproduction dominates within patches but could also occur between populations. Males (Figure 86-Figure 87) were more likely to occur near other males than the likelihood of females (Figure 88-Figure 89) being near other females, presumably reflecting the greater gemma production by males in *M. inflexa*. In small patches the likelihood of both sexes being near members of the same sex was greater than in large patches. In the large habitat patches, male genotypes were nearly 15% more likely to be near their own clone mates than were female plants. This difference is most likely due to differential survival or colonization. Thus, male plants were more likely to be aggregated clones than were females, particularly in large patches.

Based on earlier studies on differences in light preference, Lay *et al.* (2022) experimented with the effects of light intensity and quality on phytochromes in germination of gemmae of *Marchantia inflexa* (Figure 72-Figure 74). The germination responses of both sexual (spores) and asexual (gemmae) offspring were consistent

with a phytochrome-mediated event. This contrasts with germination in *M. polymorpha* (Figure 90) wherein photosynthesis mediates the event.



Figure 90. *Marchantia polymorpha* with gemmae in cups. Photo by Brenda Dobbs, through Creative Commons.

Stanley (2019) likewise found that in single-sex cultures, males had more asexual structures (gemmae) than in the mixed-sex cultures, with the reverse relationship for growth rate. Such an increase of asexual structures in single-sex cultures would increase the probability of encountering females. The reduction in growth is a tradeoff in resource allocation. The same pattern did not occur in the females.

These differences in behavior of males (Figure 86-Figure 87) in single- vs mixed-sex cultures suggest an interaction, perhaps hormonal, based on density of plants and presence of females (Figure 88-Figure 89). Stanley (2019) suggested that in this case there could be a change in sex ratio before the plants allocate their resources to sexual reproduction; this could also be caused by environmental conditions.

Such changes in sex ratio due to environmental conditions have been known in monoecious seed plants for some time. Freeman *et al.* (1981) found that in xeric conditions the males (Figure 86-Figure 87) were more prominent, whereas female (Figure 88-Figure 89) functions were more abundant on mesic sites. Similar results were found by Dawson and Elheringer (1993) for *Acer negundo* (box elder, Figure 91) in the Intermountain West, USA. In drought-prone habitats, the male:female ratio is 1.62:1, whereas in moist-streamside habitats (Figure 76) it is female (Figure 88-Figure 89) biased (0.65 male:1 female). By reviewing many publications, Golenberg and West (2013) indicated that environmental conditions could affect ethylene concentrations, which in turn affected other hormones in flowering plants, ultimately affecting the expression of sexual structures.

Blake-Mahmud and Struwe (2020) even found that sexual expression as male in the sexually plastic *Acer pensylvanicum* (striped maple, Figure 92-Figure 93) could be completely suppressed by wounding, with increasing likelihood of the sex changing to female as the severity of damage increased. Understanding such responses of bryophytes to environmental stresses is important to our

understanding of the changes we might expect as the climate becomes more stressful, particularly as drought increases and more severe weather events occur.



Figure 91. *Acer negundo* male flowers. Photo by Krzysztof Ziarnek, Kenraiz, through Creative Commons.



Figure 92. *Acer pensylvanicum* female flowers. Photo by Crosier, through Creative Commons.



Figure 93. *Acer pensylvanicum* male flowers. Photo by Ashley Bradford, through Creative Commons.

Interactions

Like many, probably most, other bryophytes, *Marchantia inflexa* (Figure 72-Figure 74) consorts with bacteria. The bacterial communities associated with bryophytes contribute to nutrient cycling, community interactions, and cost-benefit relationships of the individual organisms involved (Marks *et al.* 2018). There is evidence of nitrogen fixation by these associated bacteria from the early invasion of bryophytes on land (Knack *et al.* 2015).

Marks *et al.* (2018) compared the bacterial community between males (Figure 86-Figure 87) and females (Figure 88-Figure 89) of *Marchantia inflexa* (Figure 72-Figure 74) across habitats. They found an abundant and diverse community, even when grown in a common garden. Differences were present among habitats as well as between sexes. Marks and coworkers suggested that differences in communities between males and females may contribute to "subtle differences in both physiology and form," possibly contributing to their acclimation to the local environment. Females differed from males in having higher abundances of the bacterial order **Rhizobiales**, (Figure 142-Figure 143) an order known to have species that are able to fix nitrogen. At the same time, females had a lower abundance of nitrogen-fixing **Cyanobacteria** (Figure 94) compared to males.



Figure 94. *Cylandrospermum* sp., a nitrogen-fixing member of **Cyanobacteria**. Photo from CSIRO ScienceImage, through Creative Commons.

Graham *et al.* (2018) noted that some bacterial associations with *Marchantia inflexa* (Figure 72-Figure 74) growing on streambanks (Figure 75) appear to have methane oxidation capabilities. Since streams are known sources of methane, albeit heterogeneous within the stream (Crawford *et al.* 2017), the bryophytes might have an important role in reducing this greenhouse gas.

Marchantia miqueliana

(syn. = *Marchantia cataractarum*)

Distribution

Marchantia miqueliana appears to be endemic to Java. Because of this narrow distribution, little has been published about it. Siregar *et al.* (2013) were unable to relocate it in Sumatra, a location that had been reported by Bischler-Causse (1989). Instead they found what they

considered to be a new species on soil in a wet place around the Dwi Warna waterfall at 1100 m asl.

Aquatic and Wet Habitats

Marchantia miqueliana occurs on the walls of bays and in the spray of waterfalls in the tropics (Ruttner 1955). Campbell (1908) likewise reported it from near a waterfall in Java.

Adaptations

Biochemistry

Despite its rarity, Campbell *et al.* (1979) listed flavonoids from *Marchantia miqueliana*. These included apogenin and flavone.

Marchantia paleacea (Figure 97-Figure 99)

(syn. = *Marchantia nitida*, *Marchantia nepalensis*)

Bischler (1986) sank a number of species into this one, based on type material, but warned that other records of these species do not necessarily belong to *Marchantia paleacea* (Figure 98-Figure 100).

Marchantia paleacea (Figure 97-Figure 99) usually is considered to have two subspecies, ssp. *paleacea* and ssp. *diptera* (Figure 95-Figure 96) (Zheng & Shimamura 2019; Zheng *et al.* 2020b). In China and Japan, *Marchantia paleacea* subsp. *paleacea* tends to be distributed in higher altitudes and latitudes compared to subsp. *diptera* (Zheng & Shimamura 2019). Zheng and coworkers (2020b) found that the two subspecies overlap in western Japan and may be able to interbreed there.



Figure 95. *Marchantia paleacea* ssp. *diptera* in Japan. Photo by Janice Glime.



Figure 96. *Marchantia paleacea* ssp. *diptera* females with capsules, Arimma, Japan. Photo by Janice Glime.

Distribution

Marchantia paleacea (Figure 97-Figure 99) is a widely distributed tropical and subtropical species, ranging through the West Indies, Mexico, Guatemala, Asia, Europe, Azores, and Africa (Svihla 1940). Country records include Andaman Islands, China, India, Japan, New Guinea, Ryukyus, southeastern Asia, Sri Lanka, and Taiwan (Lu & Huang 2017; Bischler-Causse 1989). Borovichev and Bakalin (2014) added it to the known Russian flora, stating that it is poorly known there. It is considered vulnerable in Italy (Poponessi *et al.* 2020) and rare in southern Africa (Perold 1995). In the Americas, it is known from the southern states of the USA, Mexico, and Central America (Bischler 1988).



Figure 97. *Marchantia paleacea* thallus growing in Europe. Photo by Jan-Peter Frahm, with permission.



Figure 98. *Marchantia paleacea* in Europe, showing reddening of margins. Photo by Michael Lüth, with permission.



Figure 99. *Marchantia paleacea* with red bases and distinct dichotomous branching. Photo by Dmitry Ivanov, through Creative Commons.



Figure 101. *Marchantia paleacea* with gemmae on rock wall at edge of subtropical laurel forest, Madeira. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Marchantia paleacea (Figure 97-Figure 99) can occur submersed in small pools, on the walls of bays, and in waterfalls in the tropics (Ruttner 1955). Lu and Huang (2017) reported subspecies *paleacea* to occur on damp soil from 300 to 2500 m asl in Taiwan. It can occur on wet rocks beside rivers and streams (Figure 100). Des Callaghan photographed it on a rock wall at the edge of a subtropical laurel forest in Madeira (Figure 101). Zheng and Shimamura (2022b) described this subspecies in Japan as growing on boulders, soil, concrete, or limestone walls in wet or shaded places. They provided a similar but slightly different habitat description of *Marchantia paleacea* ssp. *diptera* (Figure 95-Figure 96) on stones or soil in shaded or semi-shaded areas, anthropogenic regions, or near streams.

Bischler (1986) reported that *Marchantia paleacea* (Figure 97-Figure 99) had a high environmental tolerance, *i.e.* a wide niche, for soil factors, but that its climate tolerance was narrower.

In Oklahoma, USA, *Marchantia paleacea* (Figure 97-Figure 99) occurs on constantly moist, shaded rock outcrops within a few feet of water, on travertine deposits along streams (Figure 102-Figure 106), and on moist, shaded bluffs (Figure 107) (Little 1936). Images provided by members of Bryonet indicate that in some parts of the world it can occur elsewhere on wet banks (Figure 108-Figure 109), on the sides of drainage ditches (Figure 109-Figure 110), and in the splash of spring water (Figure 111-Figure 112) used for drinking.



Figure 100. *Marchantia paleacea* wet by river. Photo by Rafael Medina, through Creative Commons.



Figure 102. *Marchantia paleacea* on emergent rocks in stream. Photo courtesy of Tian-Xiong Zheng (NICH).

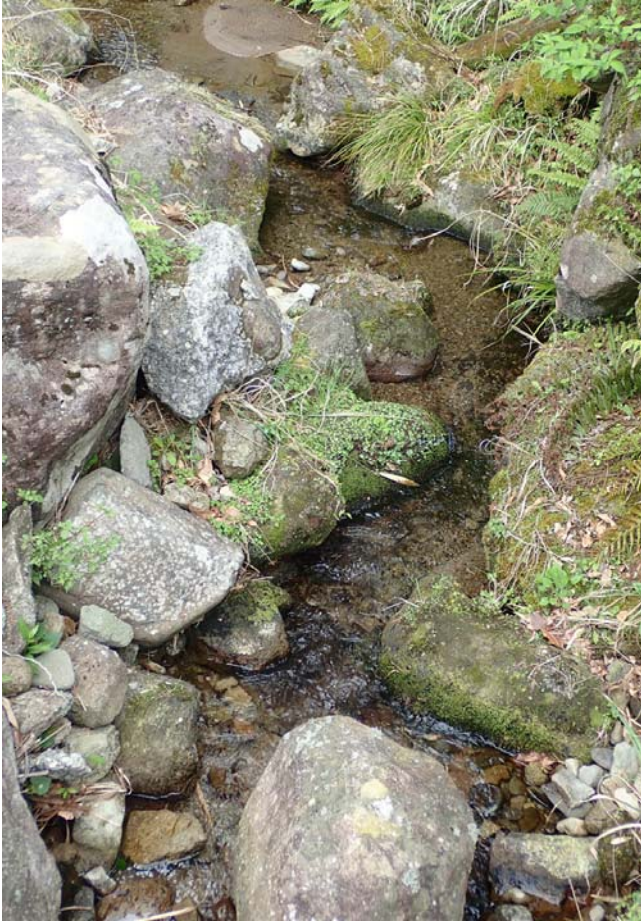


Figure 103. *Marchantia paleacea* on emergent rocks in stream. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 104. *Marchantia paleacea* on rocks at edge of stream. Photo courtesy of Tian-Xiong Zheng.



Figure 105. *Marchantia paleacea* on rocks in open stream. Photo courtesy of Tian-Xiong Zheng (NICH).

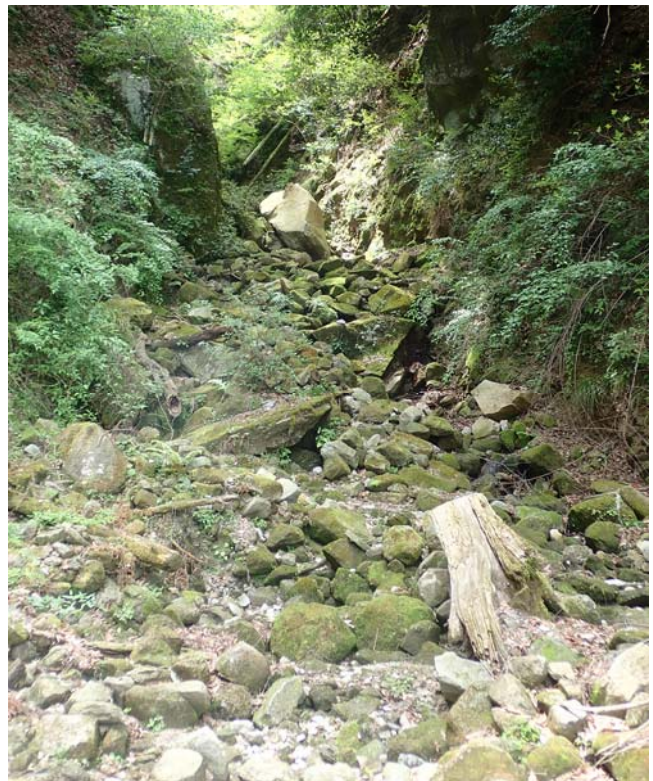


Figure 106. *Marchantia paleacea* on soil bank beside dry stream. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 107. *Marchantia paleacea* habitat on rocky bank in India. Michael Lüth, with permission.



Figure 108. *Marchantia paleacea* on a wet bank. Photo by Michael Lüth, with permission.



Figure 109. *Marchantia paleacea* on concrete wall of ditch. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 110. *Marchantia paleacea* on concrete wall of ditch. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 111. *Marchantia paleacea* on rocks near spring water pipe. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 112. *Marchantia paleacea* on rocks at spring. Photo courtesy of Tian-Xiong Zheng (NICH).

Physiology

Kaul *et al.* (1962) found that regenerating thalli of *Marchantia paleacea* (Figure 97-Figure 99) did not form protonemata, contrasting with regenerants of mosses. Liquid culture caused the production of more gemmae cups. Those gemmae germinated on solid media produced rhizoids, but those in liquid cultures did not, suggesting that these would not be able to attach if they germinated in water in nature. However, that might be remedied if the water level receded. Unlike observations for most *Marchantia*, gemmae frequently germinated within the cups.

Takio *et al.* (1988) demonstrated that *Marchantia paleacea* ssp. *diptera* (Figure 95-Figure 96) could synthesize chlorophyll in the dark as well as in the light in cell suspension culture. This ability continued for the one year of experiments. Doubling time (dry weight) required 1.2 days in the light, but 1.5 days in the dark. Could this behavior permit the species to survive and even grow while temporarily covered by litter or snow? Ngumi *et al.* (1990) further found that when the dark-grown cells were placed in the light, there was no lag phase before they were able to grow photoautotrophically. Their optimum light was 6 W m⁻² or higher in an atmosphere of 2.5% CO₂. Using *Marchantia paleacea* ssp. *diptera*, Taya *et al.* (1995) obtained "good growth" at 1% CO₂. They demonstrated both stimulatory and inhibitory light levels. At levels of 5.4-60 W m⁻² growth rate increased with light intensity; above 60 W m⁻² the rate decreased as the light intensity increased.

One has to ask what advantages a thallose liverwort has when it is able to grow heterotrophically in the dark. This would seem like a suitable trait for those in areas with snow, but this is a species (*Marchantia paleacea* ssp. *diptera*; Figure 95-Figure 96) that is mostly distributed in areas that do not see snow. Ngumi *et al.* (1990) grew it heterotrophically for two years, in the dark, then transferred it to light. The cells started to grow immediately, photoautotrophically, with no lag phase. Optimum growth occurred at 6 W m⁻² and above in an atmosphere of 25% (v/v) CO₂. The growth cycle exhibited high photosynthetic activity (7-88 mol O₂ per kg chlorophyll h⁻¹) with a high chlorophyll content of 17-25 g per kg dry weight. The cells once again returned to heterotrophic growth when placed in the dark.

Eguchi *et al.* (2002) investigated further and found that transfer of *Marchantia paleacea* var. *diptera* (Figure 95-Figure 96) to darkness resulted in a reversible repression in the gene coding for NADPH: protochloride oxidoreductase (EC 1.3.1.33). Further investigation suggested that the photosynthetic electron transport was involved in regulation of the stability of the por transcript involved in the reactions.

Nitrogen processing is also affected by light. Harada *et al.* (1993) found that when dark-grown cells were transferred to the light, the levels of activity of NaR and NiR activities decreased to about half those of cells remaining in the dark. When ammonium was the only nitrogen source supplied, activities of NiR, GS, and NADH-GOGAT were greatly reduced. Fd-GOGAT and GDH activities were not affected as greatly. But all this still begs the question how the dark production of chlorophyll is able to benefit the plant enough for the genes to remain in the population.

Many bryophytes are known for their ability to accumulate heavy metals. Concentrations of Pb, Cu, Ni, and Zn were higher in plant samples of *Marchantia paleacea* (Figure 97-Figure 99) from disturbed sites as compared to less disturbed sites in the Kumaon Hills, India (Sahu *et al.* 2014). Mn concentration, on the other hand, was higher in soil samples as compared to plant samples. Correlation analysis (r) was also performed to investigate the relationship between the soil samples and accumulation of metals in the plant. At the Bhowali taxi stand (Nainital),

Sahu and coworkers recorded significant accumulation ($P < 0.01$) of Pb, Cu, and Ni.

It appears that activation of enzymes might help to protect *Marchantia paleacea* ssp. *diptera* (Figure 95-Figure 96) from some heavy metals (Tanaka *et al.* 1995, 1996, 1998). The cytosolic Cu/Zn-superoxide dismutase is inactivated when the cells are copper deficient and reactivated when copper is added (Tanaka *et al.* 1995). The conversion from the active form to the inactive form of Cu/Zn-SOD by release of copper is the first step in the process of its degradation. Furthermore, a copper chelator causes transformation to the inactive form. Shiono *et al.* (2003) further found that the presence of copper decreases the accumulation of gene transcripts for Fe-SOD, but increases that for CuZn-SOD in a moss, whereas it produces little effect on the gene for Fe-SOD in the liverwort *Marchantia paleacea* ssp. *diptera*.

Shiono *et al.* (2003) found that whereas copper represses the expression of Fe-superoxide dismutase (Fe-SOD) in chloroplasts of the moss *Barbula unguiculata* (Figure 113), this is not the case in *Marchantia paleacea* ssp. *diptera* (Figure 95-Figure 96). Both are typical chloroplastic SODs, comparable to those in tracheophytes. The difference in *M. paleacea* var. *diptera* is that the copper has little effect on the gene for the Fe-SOD in the liverwort. Sakaguchi *et al.* (2004) found that instead the photosynthetic electron transport system differentially regulates the expression of the SOD genes in *M. paleacea* var. *diptera*.



Figure 113. *Barbula unguiculata*, a species in which copper represses the expression of Fe-superoxide dismutase (Fe-SOD) in chloroplasts. Photo by Michael Lüth, with permission.

Suzuki *et al.* (2001) explored the role of **phytochrome** (photoreceptor in plants; sensitive to light in red and far-red region of visible spectrum) and red/far-red reversibility in *Marchantia paleacea* ssp. *diptera* (Figure 95-Figure 96). Hata *et al.* (1997) found that the cell growth rate related so well to the light intensity that it could be used to calculate the light intensity. Chlorophyll content was inversely related to the light intensity.

Siregar *et al.* (2021) demonstrated strong antioxidant activity (LC50=25.25 µm mL⁻¹) for *Marchantia paleacea* (Figure 97-Figure 99). This is important during rehydration, when most bryophytes experience an oxidative

burst. It appears that the oxidative burst prevents bacteria from entering the cells, whereas the antioxidant prevents the high oxygen levels from harming the cells.

Marchantia paleacea (Figure 97-Figure 99) is one of the species that has been used as an indicator of heavy metals (Afroz & Srivastava 2009). Afroz and Srivastava found that it is a good accumulator, and therefore can be useful as an indicator species of heavy metals in the soil.

Sahu *et al.* (2014) similarly touted the use of *Marchantia paleacea* (Figure 97-Figure 99) as a bioindicator. Among their sites in the Kumaon Hills, they found that Pb, Cu, Ni, and Zn concentrations were higher from disturbed sites. Mn, on the other hand, was higher in soil samples than in the liverwort. Lead (Pb) exhibited a significantly higher concentration in the liverworts at a taxi stand.

Adaptations

Marchantia paleacea (Figure 97-Figure 99) requires a somewhat humid environment and can suffer from desiccation (Figure 114). Therefore, it survives with adaptations that permit it to live in places that are wet or sometimes submersed, but that also can become dry for days at a time.



Figure 114. *Marchantia paleacea* in a partially dry condition. Note that the terminal portions, where growth occurs, are still alive. Photo by Jan-Peter Frahm, with permission.

Marchantia paleacea (Figure 97-Figure 99), like other members of the genus, has pores (Figure 115) in the upper epidermis of the thallus, overlying air chambers that have photosynthetic filaments (Apostolakos *et al.* 1982). As noted earlier by Schönherr and Ziegler (1975), the cuticular ledges around the air pores prevent the entry of water into the thallus, thus permitting gas exchange without the interference of water within the thallus. The ledge has a surface of methyl and methylene groups and is covered by a layer of cutin. Schönherr and Ziegler considered these ridges to be "perfect" structures to protect against the entry of water.



Figure 115. *Marchantia paleacea* with gemmae cups, showing thallus pores. Photo by Efrain DeLuna, through Creative Commons.

Apostolakos and coworkers (Galatis *et al.* 1978b; Apostolakos *et al.* 1982; Apostolakos & Galatis 1985a,b,c) have provided us with a detailed study of the development of the air pores and air chambers in *Marchantia paleacea* (Figure 97-Figure 99).

Oil bodies can have multiple benefits to the liverwort plants. Oil bodies nearly fill the thallus cells they occupy in *Marchantia paleacea* (Figure 97-Figure 990) (Galatis *et al.* 1978c). The role of oil bodies was the subject of speculation for some time. Galatis *et al.* (1978a) provided an early assessment of the contents of oil bodies in *Marchantia paleacea*. They observed that the polysaccharidic material is first elaborated in the dictyosomes, then transferred into the oil bodies by their vesicles. Proteins appear to be absent in the oil bodies. However, phenolics and other aromatic compounds seem to be present, at least in the inner oil bodies. These observations suggest as the oil bodies serve as energy reserves and as sites of protective compounds such as phenolics.

One means of conserving water is to grow with overlapping thalli that reduce evaporation (Figure 116-Figure 118). Others grow on a mat of mosses (Figure 119). These mosses provide a sponge that keeps the water in proximity to the rhizoids and that further reduce evaporation from the soil.



Figure 116. *Marchantia paleacea* showing dense, overlapping thalli. Photo by Jan-Peter Frahm, with permission.



Figure 117. *Marchantia paleacea* with gemmae cup and overlapping thalli that reduce evaporation from the soil. Photo by Michael Lüth, with permission.



Figure 118. Overlapping thalli of *Marchantia paleacea* ssp. *diptera*. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 119. *Marchantia paleacea* growing over mosses in India. Photo by Michael Lüth, with permission.

Zheng and Shimamura (2019) suggested that the inward bent receptacle (Figure 120) of *Marchantia paleacea* ssp. *diptera* might help it to withstand the high temperatures and desiccation it experiences in its southern Japan distribution.



Figure 120. Females of *Marchantia paleacea* ssp. *diptera* showing inward bent margins of the female receptacle. Photo courtesy of Tian-Xiong Zheng (NICH).

Reproduction

Marchantia paleacea (Figure 97-Figure 99) is considered to be **dioicous** (Bischler 1986; Perold 1995; Lu & Huang 2017). Like other *Marchantia* species it develops antheridiophores (Figure 121-Figure 122) and archegoniophores (Figure 123-Figure 129). Other than these reproductive branches, the two sexes look the same (Bischler 1986). The life cycle is typical for species of *Marchantia*.



Figure 121. *Marchantia paleacea* male plants with antheridiophores. The two lower receptacles, at this stage looking like females, appear to be young male receptacles. Photo by Naufal Urfi Dhiya'ulhaq, through Creative Commons.



Figure 122. *Marchantia paleacea* males with antheridiophores. Note rows of antheridia on the fingers of the antheridial head. Photo by Naufal Urfi Dhiya'ulhaq, through Creative Commons.



Figure 125. Receptacles of *Marchantia paleacea* ssp. *diptera*, showing how dense these structures can be in the colony. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 123. *Marchantia paleacea* females showing archegonial heads. Photo by Jan-Peter Frahm, with permission.



Figure 126. *Marchantia paleacea* females with archegoniophores. Photo by Efrain DeLuna, through Creative Commons.



Figure 124. *Marchantia paleacea* females, Nichinan, Japan. Photo by Janice Glime.



Figure 127. *Marchantia paleacea* archegonial receptacle. Photo by Efrain DeLuna, through Creative Commons.



Figure 128. Receptacle of *Marchantia paleacea* ssp. *dipthera* with inward bent margins of the receptacle. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 129. *Marchantia paleacea* females with mature archegoniophores. Photo by 楊玉鳳, through Creative Commons.

Populations are usually small and do not increase in size rapidly (Bischler 1986). Growth seems to be limited by water availability. The lack of outcrossing may account for the limited variability of the species, the absence of ecotypes, and division into only two subspecies.

Male plants in nature are less frequent than female plants (Evans 1917; Bischler 1986). Near the borders of the range, males are almost completely absent (Bischler 1986).

Sporophytes can be found on the Azores islands and in the Caucasus mountains at fairly high elevations (Bischler 1986). Thus, male plants are present along with the females. Is it temperature that controls males, or do they have a dispersal limitation?

But even when both males and females are growing intermixed, only 25-42% of the females produce sporangia (Bischler 1986). Nevertheless, Bischler wondered why it was so high when both sperm and archegonia were elevated on stalked structures. But evidence presented in this chapter demonstrates that sperm, easily splashed, swim

directly to the archegoniophore and may even be carried upward by the same means that water moves upward.

With so few males, especially in some areas, *Marchantia paleacea* (Figure 97-Figure 99), relies to a great degree on gemmae (Figure 130-Figure 135) for local spread. As the gemmae age, the gemmae cups may disintegrate (Figure 136-Figure 138).



Figure 130. *Marchantia paleacea* with gemmae cups. Photo through Creative Commons.



Figure 131. *Marchantia paleacea* with gemmae cups in India. Note the conspicuous pores. Photo by Michael Lüth, with permission.



Figure 132. *Marchantia paleacea* with purple margins (suggesting stress) and gemmae cups. Photo by Maria Emília Martins, through Creative Commons



Figure 133. *Marchantia paleacea* with gemmae. Photo by Jan-Peter Frahm, with permission.



Figure 134. *Marchantia paleacea* with gemmae cups. Photo by Jan-Peter Frahm, with permission.



Figure 135. *Marchantia paleacea* gemmae cup. Photo by 楊玉鳳, through Creative Commons.



Figure 136. *Marchantia paleacea* with deteriorating and nearly empty gemmae cups in Europe. Photo by Michael Lüth, with permission.



Figure 137. *Marchantia paleacea* in Bhutan, with disintegrating gemmae cups. Photo by David Long, with permission.



Figure 138. *Marchantia paleacea* from India showing reddening of borders and disintegrating gemmae. Photo by Michael Lüth, with permission.

Interactions

Bacterial Interactions

Using cultures from gemmae of *Marchantia paleacea* (Figure 97-Figure 99), Alcaraz *et al.* (2018) isolated members of *Bryobacter*, *Lysobacter* (Figure 139),

Methylobacterium (Figure 140), *Paenibacillus* (Figure 141), *Pirellula*, *Rhizobium* (Figure 142-Figure 143), and *Steroidobacter* from the thalli. These bacteria are known to promote plant growth, degrade complex exudates, fix nitrogen, use and convert methylene, and suppress disease.

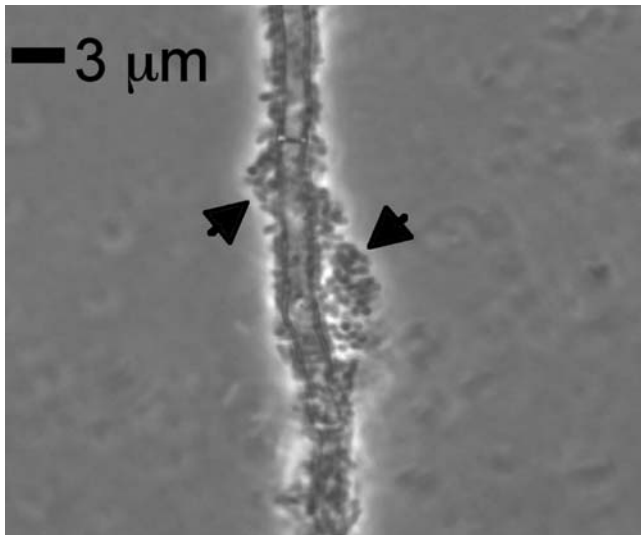


Figure 139. *Lysobacter* sp. hyphae, a genus associated with *Marchantia paleacea*. Photo by Don Kobayashi, through Creative Commons.

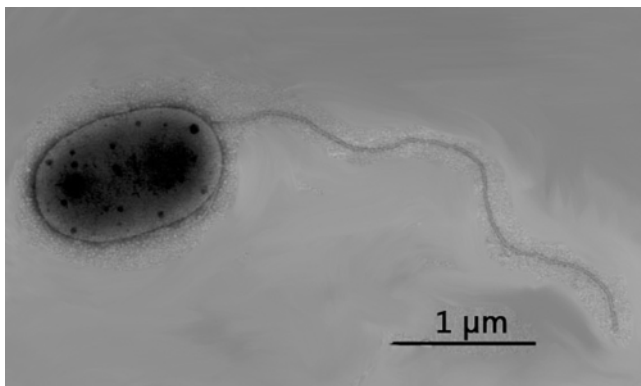


Figure 140. *Methylobacterium jeotgali*, member of a genus associated with *Marchantia paleacea*. Photo from Aslam *et al.* 2007, through Creative Commons.

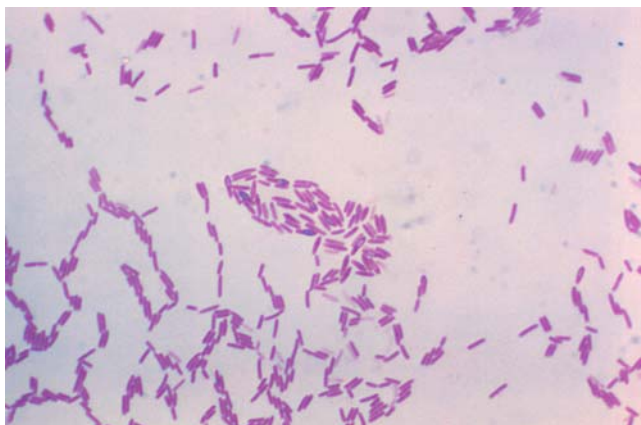


Figure 141. *Paenibacillus polymyxa*; some members of this genus are associated with *Marchantia paleacea*. Photo from CDC, through public domain.



Figure 142. *Rhizobium* root nodule on *Vicia faba* roots; *Rhizobium* is a known associate of *Marchantia paleacea*. Photo by Whitney Cranshaw, through Creative Commons.

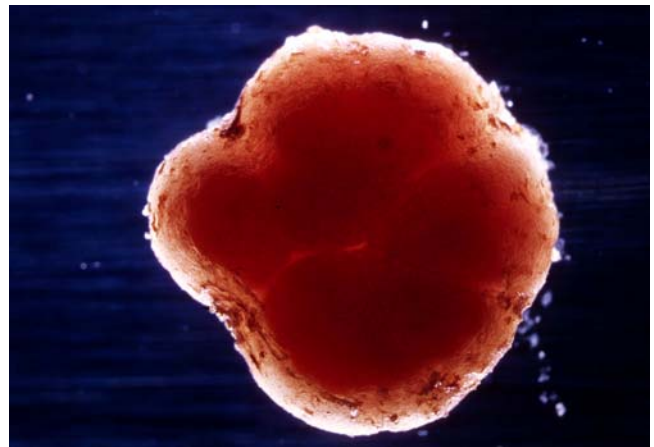


Figure 143. *Rhizobium* showing typical red color of nodules. Photo from CSIRO, through Creative Commons.

On the other hand, as in many liverworts, Pinfang *et al.* (2001) found that *Marchantia paleacea* (Figure 97-Figure 99) alcohol extracts were active against the Gram-positive bacterium *Bacillus subtilis* (Figure 144).

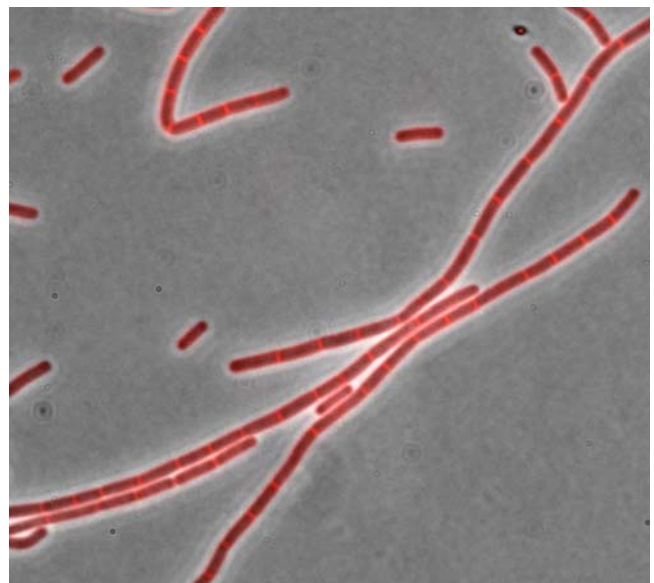


Figure 144. *Bacillus subtilis* stained with Nile Red, a species that is inhibited by alcohol extracts of *Marchantia paleacea*. Photo by EditorInTheRye, through Creative Commons.

In their study of 52 bryophyte species, Banerjee and Sen (1979) found that *Marchantia paleacea* (Figure 97-Figure 99) exhibited the broadest spectrum of antibiotic activity against the 12 microorganisms tested.

Fungal Interactions

Fungi have played a major role in the nutrition of land plants, and *Marchantia paleacea* (Figure 98-Figure 100) is no exception to these benefits. But they also contribute to this relationship. Rich *et al.* (2021) found that in the relationship between this species and its arbuscular mycorrhizal fungi, lipids are transferred from the liverwort to the fungus. Bouwmeester (2021) likewise found that liverwort lipids served to "entice" fungi into the mutualism and were essential to its establishment.

When gemmae (Figure 130-Figure 138) from this liverwort were cultured with tracheophyte roots, it took only 18 days for the liverwort to exhibit arbuscules, indicating fungal colonization (Kobae *et al.* 2019). These arbuscular mycorrhizal fungi entered through the rhizoids.

Field *et al.* (2019) identified the presence of both **Glomeromycotina** and **Mucoromycotina** fungal groups in *Marchantia paleacea* (Figure 97-Figure 99). They found that dual partnerships, hosting two different fungal species, provided complementarity both in greater nutrient pool use and greater allocation of photosynthate to the fungal partners. The partners seemed to provide different functions and the researchers argue for this complementarity as a reason for the success of multiple fungal partners in the plant kingdom. In this case, only the **Mucoromycotina** provided liverworts with substantial access to algal N, unrelated to atmospheric CO₂ concentration. Both fungal symbionts increased P uptake, but **Glomeromycotina** were often more effective.

Kodama *et al.* (2021) identified carotenoid-derived strigolactones in *Marchantia paleacea* (Figure 97-Figure 99). These compounds are known to both serve as hormones to regulate growth and development and to serve as rhizosphere-signalling molecules that induce a symbiotic relationship with arbuscular mycorrhizal fungi. However evidence suggests that in *Marchantia paleacea* the receptor needed for it to serve as a hormone is absent. It does, on the other hand, seem to serve as a mycorrhizal signalling device.

Other Interactions

It appears that *Marchantia paleacea* (Figure 97-Figure 99) might even have allelopathic effects on tracheophytes. Wang *et al.* (2013) found that secondary metabolites, in particular bibenzyls, from callus cultures of this species could inhibit seedling growth of the flowering plant *Arabidopsis thaliana* (Figure 80), with a dose-dependent response.

Biochemistry

Takio *et al.* (1998) found that expression of the cDNA that encodes the NADPH:protochlorophyllide oxidoreductase in *Marchantia paleacea* ssp. *diptera* (Figure 95-Figure 96) is light-dependent, whereas in most tracheophytes it is light-independent.

So *et al.* (2002) verified the presence of marchantin C, isoriccardin C, and the phenanthrene derivative, 2-hydroxy-3,7-dimethoxyphenanthrene in *Marchantia paleacea* (Figure 97-Figure 99). They also described the structures of two novel cyclic bis (bibenzyls), isoriccardinquinone A and B.

Yuan *et al.* (2021) characterized three genes for uridine diphosphate-dependent glycosyl transferases (DBRs) in this species. Wu *et al.* (2018) isolated and characterized two double bond reductases (DBRs). These enzymes are capable of catalyzing the NADPH-dependent reduction of the α,β -unsaturated double bond. The two reductases differed in their behavior and temperature optima. This was the first report of a microbial type of DBR in any plant. Both enzymes are important in protection against environmental stress in liverworts.

Mukhia *et al.* (2014) demonstrated that *Marchantia paleacea* (Figure 97-Figure 99) exhibited potential antioxidant activity and the existence of a variety of phytochemicals involved in scavenging activities.

Sakurai *et al.* (2016) identified the monocyclic monoterpene aldehyde, perillaldehyde, as the major component of volatiles, comprising about 50% of the volatiles in *Marchantia paleacea* subsp. *diptera* (Figure 95-Figure 96). This represents the first report of a perillaldehyde in a liverwort. Minor volatiles included α -selinene, β -selinene, β -caryophyllene, β -pinene, and limonene. But what do they do for the liverwort?

We have named a number of secondary compounds here, but in many cases their role for the liverwort is unclear. It is presumed that most of these serve in protection against pathogens and herbivores, but some might simply be intermediates in a pathway toward another needed compound. Others are apparently part of the ability to survive drought.

The antimicrobial properties (Xia *et al.* 2001) of many of these compounds may be of use to them. Examples include action against the Gram-positive bacterium *Bacillus subtilis* (Figure 144). Xia *et al.* (2001) isolated 2-hydroxy-3, 7-dimethoxyphenanthrene, marchantin C, and isoriccardin C from *Marchantia paleacea* (Figure 97-Figure 99).

Culturing

Awasthi *et al.* (2012) compared sterilization techniques in culturing *Marchantia paleacea* (Figure 97-Figure 99) and several other thallose liverworts. They found the best results with 1% sodium hypochlorite solution for 8-10 seconds. They used repeated sub-culturing to ultimately achieve aseptic cultures. All of these species grew well in half strength Knop's macronutrients + Nitsch's trace elements with 10 ppm freshly prepared ferric citrate under the continuous illumination of 4,500-5,000 lux at 20 \pm 2°C.

Marchantia pappeana (Figure 147)

Distribution

Marchantia pappeana (Figure 145) is widely distributed in tropical Africa. Bischler-Causse (1993) reported it from the Cape Verde Islands to Ethiopia and south to southern Africa, generally at an elevational range of 1000-2500 m. Its distribution in southern Africa

includes the Northern Province, Northern Transvaal, and Eastern Transvaal, Gauteng [PWV], Swaziland, KwaZulu-Natal, eastern [Orange] Free State, and Lesotho (Perold 1995). Müller (1995) recorded it for Zaire. Manyanga and Perold (2004) listed it for Zimbabwe. Enroth *et al.* (2019) recorded it from the Mwatate River in Kenya (see also Chuah-Petiot 2001). The World Flora Online (2022) simply describes the distribution as tropical Africa.



Figure 145. *Marchantia pappeana* along ditch in Ranomafana National Park, Madagascar. Photo courtesy of Catherine Reeb.

Aquatic and Wet Habitats

Marchantia pappeana (Figure 145) often grows in the same localities as *M. debilis* (Figure 28-Figure 36), including vertical soil banks of streams (Figure 146-Figure 148), at waterfalls, at sluice canals, rarely on rotting wood or on rocks, in open grassland, or in forests, sometimes in deep shade (Perold 1995; World Flora Online 2022).

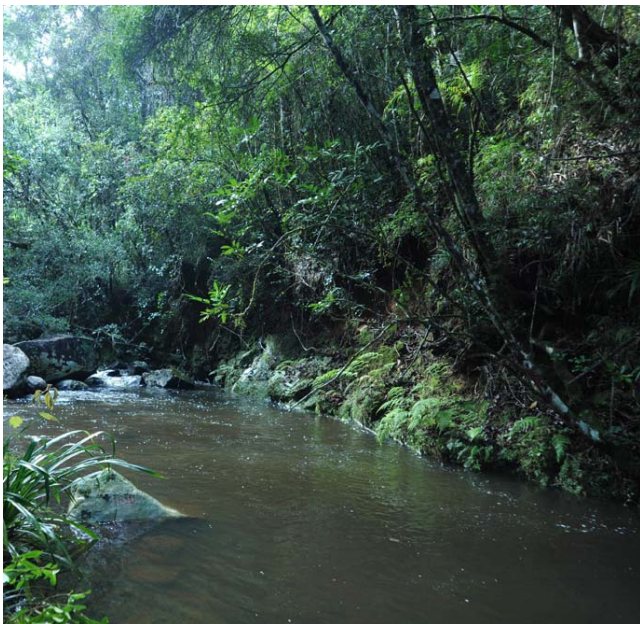


Figure 146. *Marchantia pappeana* habitat on Zahamean riverbanks, Madagascar. Photo courtesy of Catherine Reeb.



Figure 147. *Marchantia pappeana* habitat on Zahamean riverbanks, Madagascar. Photo courtesy of Catherine Reeb.



Figure 148. *Marchantia pappeana* habitat on Zahamean riverbanks, Madagascar. Photo courtesy of Catherine Reeb.

Wigginton (2013) considered *Marchantia pappeana* (Figure 145) on Ascension Island to be a plant that grows mostly on rocks and soil (Figure 146-Figure 149), rarely on tree roots. Catherine Reeb (pers. comm. August 2022) has found it on the walls of ditches (Figure 149).



Figure 149. *Marchantia pappeana* along ditch in Ranomafana National Park, Madagascar. Photo courtesy of Catherine Reeb.

Reproduction

Marchantia pappeana (Figure 145) is **dioicous** (Perold 1995). Male plants produce antheridiophores; females produce archegoniophores (Figure 150). But sometimes male branches appear on the female receptacle (World Flora Online 2022).



Figure 150. *Marchantia pappeana* with archegoniophores along ditch in Ranomafana National Park, Madagascar. Photo courtesy of Catherine Reeb.

Sporangia are elevated on the archegoniophore (Figure 151). These disperse spores that are aided by wiggling elaters (Figure 152) as moisture changes occur.



Figure 151. *Marchantia pappeana* habitat on Zahamena riverbanks, Madagascar. Photo courtesy of Catherine Reeb.



Figure 152. *Marchantia pappeana* with mature sporangia dispersing spores, along ditch in Ranomafana National Park, Madagascar. Photo courtesy of Catherine Reeb.

Like other species of *Marchantia*, gemmae (Figure 153-Figure 154) are important means of asexual reproduction. Their hormone system curtails production of gemmae cups when sexual development begins. Of the 50 specimens Perold (1995) examined, 62% had cupules, 20% had antheridiophores, and 34% had archegoniophores; only 6% had both cupules and sexual structures.



Figure 153. *Marchantia pappeana* with gemmae cups, in river in Zahamena, Madagascar. Photo courtesy of Catherine Reeb.



Figure 154. *Marchantia pappeana* with gemmae cups and distinct pores in river in Zahamena, Madagascar. Photo courtesy of Catherine Reeb.

Fungal Interactions

Strullu-Derrien *et al.* (2014) indicated that the fungal associations in *Horneophyton ligneri* from Rhynie Chert closely resemble the **Glomeromycota** symbionts in *Marchantia pappeana*. Field *et al.* (2015) found that the **Glomeromycota** found in *Marchantia pappeana* (Figure 155-Figure 156) were similar to the structures of the typical arbuscular mycorrhizae occurring in flowering plants. This species lacks studies on the benefits to *Marchantia pappeana* and its partner(s) in this association.

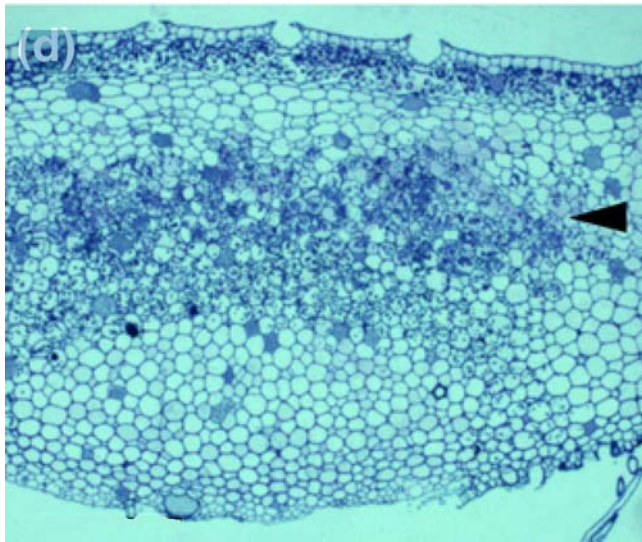


Figure 155. *Marchantia pappeana* mid thallus colonized by **Glomeromycota**. Modified from Strullu-Derrien *et al.* 2014, with permission from Jeff Duckett.

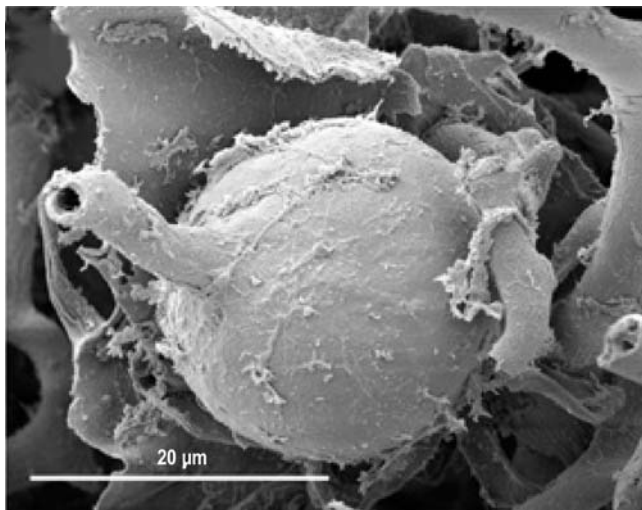


Figure 156. *Marchantia pappeana* colonized by **Glomeromycota** with detail of large vesicle. Modified from Strullu-Derrien *et al.* 2014, with permission from Jeff Duckett.

Biochemistry

Despite its somewhat narrow distribution, *Marchantia pappeana* (Figure 146) has experienced several biochemical studies. Linde *et al.* (2016) reported that sesquiterpene hydrocarbons are characteristic of this species (see also Combrinck *et al.* 2015). Linde *et al.* (2016) found that crude extracts of *M. pappeana* from South Africa (as well as *Pallavicinia lyellii*) had the highest level of antibacterial activity against *Escherichia coli* among the nine liverworts tested. Much remains for us to learn about the role of these sesquiterpenes for the liverwort.

Summary

The species of *Marchantia* covered in this subchapter are those of wet habitats. They may become

submersed occasionally during flooding events, but they do not normally live submersed. To survive in these habitats, they are protected by a thick thallus with air chambers to permit CO₂ entry. Oil bodies serve as a storage organ for polysaccharides and for secondary compounds that help prevent herbivory and protect the thallus from pathogens. A ridge of cutin around the pore prevents water entry. Scales on the lower surface help to move water to the thallus and to retain it in capillary spaces. Some rhizoids anchor the thallus while others help in directing water to the thallus on the lower surface.

They all have gemmae, which seem to be their primary means of reproduction. Yet some are able to colonize rapidly after a fire, suggesting that they are also dispersed by spores. The longevity of spores and gemmae has not been tested.

Secondary compounds, mostly sesquiterpenes and flavonoids, help to protect the plants from herbivory and pathogens.

Acknowledgments

Lars Söderström helped me with puzzling nomenclature. Masaki Shimamura alerted me to nomenclature problems in *Marchantia paleacea* vs. *M. polymorpha* in some important publications. Li Zhang sent me a variety of papers and reviewed my treatment of *Marchantia emarginata*. Catherine Reeb introduced me to *Marchantia debilis* and *M. pappeana* as species of wet habitats and provided me with many images and habitat information. Thank you to Tian-Xiong Zheng and for sending me much needed images. And thank you to the many photographers who have given me blanket permission to use their images or who have put them in Creative Commons.

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CHAPTER 1-24

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 2

TABLE OF CONTENTS

<i>Marchantia polymorpha</i>	1-24-2
A Liverwort Model	1-24-4
genetics and sequencing	1-24-4
teaching	1-24-7
Distribution	1-24-7
Aquatic and Wet Habitats	1-24-8
streams and rivers	1-24-9
stream and river banks	1-24-10
after fire	1-24-13
Physiology	1-24-13
Adaptations	1-24-31
Reproduction	1-24-35
Role	1-24-55
Interactions	1-24-56
Bacterial Interactions	1-24-56
Protozoa Interactions	1-24-59
Fungal Interactions	1-24-59
Invertebrate Interactions	1-24-65
Tracheophyte Interactions	1-24-65
Biochemistry	1-24-67
Culturing and Cultivating	1-24-72
Control	1-24-73
Summary	1-24-74
Acknowledgments	1-24-75
Literature Cited	1-24-75

CHAPTER 1-24

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 2



Figure 1. *Marchantia polymorpha* in a typical waterside habitat. Photo by Michael Lüth, with permission.

Marchantiaceae, cont.

Marchantia polymorpha (Figure 1-Figure 12)

(syn. = *Marchantia alpestris*; *Marchantia aquatica*; *Marchantia coarctata*) – see Long (1995) for a discussion of the history of older naming of the species and subspecies.

Boisselier-Dubayle *et al.* (1995) elaborated on the genetic variability in the three subspecies of *Marchantia polymorpha* (Figure 1-Figure 12). The three subspecies [*montivagans* (Figure 2-Figure 4), *polymorpha* (Figure 5), *ruderalis* (Figure 6-Figure 8)] had high genetic similarity within each subspecies over a wide geographic area, but the similarity was low between subspecies. These differences indicate that speciation included adaptation to different ecological niches, followed by reproductive isolation.



Figure 2. *Marchantia polymorpha* ssp. *montivagans* with antheridiophores. Photo by Jan-Peter Frahm, with permission.



Figure 3. *Marchantia polymorpha* ssp. *montivagans* with archegoniophores. Photo by Hugues Tinguy, with permission.



Figure 4. *Marchantia polymorpha* ssp. *montivagans* with gemmae cups. Photo by Hugues Tinguy, with permission.



Figure 5. *Marchantia polymorpha* ssp. *polymorpha*. Photo by Jan-Peter Frahm, with permission.



Figure 6. *Marchantia polymorpha* ssp. *ruderalis* with gemmae cups. Photo by Jiří Kameníček, with permission.



Figure 7. *Marchantia polymorpha* ssp. *ruderalis* antheridial receptacles. Photo by Malcolm Storey, DiscoverLife, with online permission.



Figure 8. *Marchantia polymorpha* ssp. *ruderalis* females with receptacles. Note smaller archegoniophores on the outer (younger) thalli. Photo by Malcolm Storey, DiscoverLife, with online permission.

The variety *aquatica* (Figure 9) (Campbell 1968; Hollensen & Taylor 1981; Kitagawa 1987) is not recognized by Söderström *et al.* (2016). Instead, it is considered within the species *Marchantia polymorpha* as ssp. *polymorpha*. Nevertheless, it appears that those thalli that develop underwater can be distinguished by a black

midrib (Michael Lüth, pers. comm.). Recognition of this distinction can give us an ecological history of plants we find and deserves some experimental attention.



Figure 9. *Marchantia polymorpha* ssp. *polymorpha* with distinct black midribs, typical of aquatic forms, in Europe. Photo by Michael Lüth, with permission.

Google Scholar found 20,500 references in a search for *Marchantia polymorpha* (Figure 1-Figure 12). *Marchantia polymorpha* has been a subject of intensive study for nearly 200 years (Shimamura 2016). The species offers many benefits for research, including its short life cycle, ease of propagation and crossing, high frequency of transformation, haploidy, and small genome size (approximately 280 Mb).



Figure 10. *Marchantia polymorpha* with overlapping thalli. Photo by Sanja through Wikimedia Commons.

Berrie and Webster (1982) elaborated on the ultrastructure of the plastids and mitochondria of the *Marchantia polymorpha* gemmae (Figure 4). They found that division among plastids and maturing vegetative cells differed from that of developing oil body cells and rhizoid initials. Bopp and Vicktor (1988) developed methods for following protoplast development, determining that cell wall formation requires light.



Figure 11. *Marchantia polymorpha* thallus. Photo from Botany Website, UBC, with permission.

A Liverwort Model

genetics and sequencing

The species has served as a model organism in many biological studies (Chiyoda *et al.* 2008), including the discovery of sex in cryptogams and more recently the elucidation of the V chromosome (term for male chromosome in haploid organism), understanding the plant life cycle, and origins of polarity in development. The use of *Marchantia polymorpha* s.l. (Figure 1-Figure 12) as a plant model system continues (Durand 1908; Alam & Pandey 2016; Shimamura 2016), with its dominant haploid generation being a benefit for genetic studies and gene expression as well as details of evolutionary and developmental biology.

Marchantia polymorpha (Figure 1-Figure 12) has been used to demonstrate the presence of "X" and "Y" chromosomes in bryophytes, now referred to as U and V chromosomes, respectively (Renner *et al.* 2017). I shall continue this discussion using the designation of U for female and V for male. This early discovery of sex chromosomes was followed by the sequencing of the male and female genomes (Ohya 2001). Ohya found that some of the genes on the V chromosome were unique, whereas those on the U chromosome were also on somatic chromosomes or even on the V chromosome. Since these are haploid organisms, the males have a very small V chromosome with no U chromosome and females have one U chromosome with no second U or any V (Lorbeer 1934; Tanurdzic & Banks 2004). Sporophytes are UV.

Yamato *et al.* (2007) reported that these V chromosomes differ from other chromosomes in lacking recombination. They reported the gene organization of the V chromosome of *Marchantia polymorpha* (Figure 1-Figure 12) and identified 64 genes on the V chromosome. Of these, 14 are found only in the male genome and are expressed only in male reproductive organs. Another 40 are expressed in thalli and reproductive organs. Interestingly, at least 6 of these have U-linked counterparts that are expressed in both thalli and sex organs of females. Yamato and coworkers suggested that these sex chromosomes share ancestral autosomal genes, and they predict that essential genes on sex chromosomes of haploid organisms are more likely to persist than those in diploid organisms.

As in many other studies, *Marchantia polymorpha* (Figure 1-Figure 12) was the choice for studying the divergence of land plant chloroplast (Figure 12) genes (Morton 1994). Bischler (1986) analyzed the karyotype. In *Marchantia polymorpha* the genes with the highest codon adaptation index correspond to the ones that are expressed at the highest levels (Morton 1994). This relationship is weaker in *Nicotiana tabacum* (Figure 13).



Figure 12. *Marchantia polymorpha* thallus section through pore, showing location of photosynthetic filaments with chloroplasts. Photo from Botany Website, UBC, with permission.



Figure 13. *Nicotiana tabacum*, a species that demonstrates the conservation of *Marchantia* genes in flowering plants. Photo through Creative Commons

One interesting finding is that chloroplast ribosomal protein rpl 21 in *Marchantia polymorpha* (Figure 1-Figure 12) is encoded by the plastid gene, but in tobacco and rice this is a nuclear gene (Smooker *et al.* 1990). Sone *et al.* (1999) reported for the first time a co-localization of repeat rDNA in land plants. These researchers suggested that the structural re-organization of rDNAs occurred after the evolutionary divergence of bryophytes from other plants.

Marchantia polymorpha (Figure 1-Figure 12) appeared to be one of the first organisms to have its chloroplast and mitochondrial DNA sequenced (Ohshima *et al.* 1986; Oda *et al.* 1992a; Kisiel *et al.* 2011; Lin *et al.* 2016). But unfortunately, the species used in early studies (Ohshima *et al.* 1986; Oda *et al.* 1992a,b,c,d) was a misidentified *Marchantia paleacea* (Figure 14) (Kijak *et al.* 2013, 2016; Masaki Shimamura, pers. comm. 10 July 2022). Hence, this first sequencing cannot be attributed to *Marchantia polymorpha*.



Figure 14. *Marchantia paleacea* with archegoniophores. Photo by Jan-Peter Frahm, with permission.

Posno *et al.* (1986) showed that there was "substantial" conservation in the chloroplast genome sequences between *Marchantia polymorpha* (Figure 1-Figure 12) and those of the aquatic flowering plant *Landoltia punctata* (Figure 15). Umesono and Ozeki (1987) found that the chloroplast genome sequence of *Marchantia polymorpha* differs little in gene makeup and function from that of flowering plants, despite flowering plants one that is 25%.



Figure 15. *Landoltia punctata*, a species with considerable conservation of the chloroplast genome sequences found in *Marchantia polymorpha*. Photo from US Dept. Interior, through Creative Commons.

Kohchi *et al.* (1988) characterized parts of the chloroplast DNA in presumably *Marchantia paleacea* (Figure 14), under the name of *M. polymorpha*. Raubeson and Jansen (1992) further explored what these DNA sequences had in common with later plants.

Takemura *et al.* (1992) elaborated on ribosomal proteins that are coded in the mitochondrial genome of *Marchantia polymorpha* (possibly *M. paleacea*), and these differ substantially in size from their counterparts in the bacterium *Escherichia coli* (Figure 16). In the same year, Oda *et al.* (1992a,b,c) found that the mitochondrial DNA of *Marchantia paleacea* (Figure 14; misidentified as *M. polymorpha*) is a single circular form that exhibits no incorporation of chloroplast DNA. Whichever species was actually used, Ohyama *et al.* (1982, 1983, 1986, 1988a,b,c; Ozeki *et al.* 1987; Los & Semenenko 1991) showed that many (most?) chloroplast genes in such liverworts as *Marchantia* have been conserved in tobacco, *Nicotiana tabacum* (Figure 13).

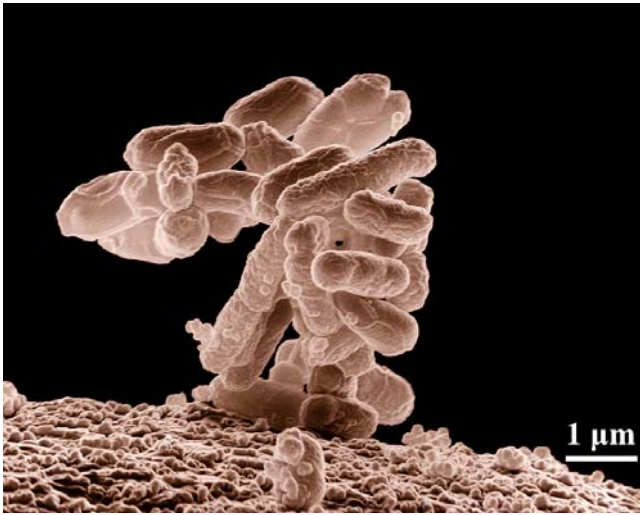


Figure 16. *Escherichia coli*, a bacterium that exhibits very different ribosomal proteins from those of *Marchantia polymorpha/paleacea*. Photo from USDA, through public domain.

Takemura *et al.* (1992) elaborated on ribosomal proteins that are coded in the mitochondrial genome of *Marchantia polymorpha* (possibly *M. paleacea*), and these differ substantially in size from their counterparts in the bacterium *Escherichia coli* (Figure 16).

Downie *et al.* (1991) and Sibbald (1988) subsequently compared chloroplast DNA of dicotyledonous flowering plants with those attributed to *Marchantia polymorpha*. Comparisons between mosses and liverworts with hornworts indicated that the two former groups were more closely related to each other than either was to hornworts (Katoh *et al.* 1983).

The entire gene sequence was not known until 2017, using *Marchantia polymorpha* ssp. *ruderalis* (Figure 17-Figure 19) (Bowman *et al.* 2017). Since then, the subspecies have been sequenced and their evolutionary relationships elucidated (Linde *et al.* 2020). The results supported the hypothesis that *M. polymorpha* ssp. *ruderalis* is not a hybrid of the other two subspecies, as some researchers had thought.



Figure 17. *Marchantia polymorpha* ssp. *ruderalis* gemmae cups. Photo by David T. Holyoak, with permission.



Figure 18. *Marchantia polymorpha* ssp. *ruderalis* with archegoniophore. Photo by Jiří Kameníček, with permission.



Figure 19. *Marchantia polymorpha* ssp. *ruderalis* with archegonial head showing numerous scales. Photo by Jiří Kameníček, with permission.

Marchantia polymorpha (Figure 1-Figure 12) has likewise been used as a model organism in understanding development in thallose liverworts (Suzuki *et al.* 2020).

But the scientific study of this species, especially regarding development, has been occurring for at least 200 years (Shimamura 2016). Suzuki and coworkers described merophyte lineages and elaborated on the derivation of growth from stem cells in the apical notch (Figure 20).



Figure 20. *Marchantia polymorpha* showing apical notch with brown covering scale. Photo by Li Zhang, with permission.

Linde *et al.* (2021) compared rates of mutations among the major plant groups and found that the gymnosperms had the fewest synonymous mutations, flowering plants the most, and bryophytes were located between those two. In this regard, the silent site substitution rate (neutral evolution) is lower for the liverwort compared to flowering plants, but not as low as that of gymnosperms. They found the same selective constraints on the haploid-specific genes as those on the diploid-specific genes. However, in the haploid generation the new mutations experience immediate and direct selection, hence quickly being lost if they are maladaptive. The nonsynonymous to synonymous substitution rate ratio (dN/dS) represents selective evolution. This silent site substitution rate is lower for liverworts as compared to flowering plants, but again not as low as for gymnosperms. The selection pressure, measured as dN/dS, is not remarkably lower for bryophytes when compared to diploid dominant plants as we might expect based on the **masking hypothesis** (predicts more efficient selection in haploids than in diploids, because dominant alleles can mask deleterious effects of recessive alleles in diploids; however, gene expression breadth and noise can potentially counteract the effect of masking on the rate at which genes evolve), indicating that other factors are more important than ploidy.

Liu *et al.* (2019) noted that the dN/dS for nuclear genes was more than three times higher for bryophytes when compared to seed plants. However, the sets of genes compared were not the same genes in both groups. Linde and coworkers (2021) compared the same 42 genes in both groups and found that the dN/dS rates were much more similar. This raises the question of why bryophytes, given their long history, are less diverse and appear to have less morphological diversity than tracheophytes, especially flowering plants. But as I have argued elsewhere, they are confined to being small due to their lack of lignin. They furthermore, because of this small size, are at greater risk of disappearance due to herbivory and pathogens. If one

considers their biochemical diversity, affording them protection from herbivores and pathogens, are they really less diverse?

Fang *et al.* (2014) reported for the first time the presence of oleosin genes in liverworts, using *Marchantia polymorpha* (Figure 1-Figure 12). The liverworts tested exhibited only M-oleosins, whereas three types are known from various plant lineages. This seems to be a precursor to the other two oleosins, suggesting another piece of the evolutionary story.

With all of our knowledge about molecular similarities and differences, molecular/genetic studies have become the driving force in plant systematics. Using the **Marchantiales**, Boisselier-Dubayle *et al.* (1997) were among the early researchers to point out that there can be an incongruence between morphological characters and molecular data, complicating our systematic efforts.

Understanding the genome, coupled with the greater ease of working with haploid organisms, has contributed to the use of *Marchantia polymorpha* (Figure 1-Figure 12) in transferring genes to determine their functions.

teaching

The genus *Marchantia* is notable in the pre-Renaissance literature, with illustrations of *M. polymorpha* (Figure 1-Figure 12) appearing as early as the mid-15th Century (Bowman 2016). Notable early treatments are those of Schmidel (1762) and Hedwig (1783). It has been used for centuries in nearly every textbook and classroom that teaches about bryophytes or life cycles (Cutting 1910; Inoue & Asakawa 1966; Register & West 1971; Une 1998; Bowman 2016).

Marchantia polymorpha (Figure 1-Figure 12) has also been used as a pedagogical model to teach the bioindicator concept to seventh graders (Pedroza-Manrique & Arévalo 2009). This was part of a study on comparison of learning strategies. Results demonstrated that "learning must be related to the environment of the students and must also represent a challenge for them, this allowed for significant learning."

Durand (1908), in preparing material for teaching a course in embryology, selected *Marchantia polymorpha* (Figure 1-Figure 12) to represent development in liverworts. He wrote that he "naturally selected *Marchantia polymorpha*" because of its accessibility and ease of study. And it is illustrated in practically every textbook that treats liverworts.

Distribution

Marchantia polymorpha (Figure 1-Figure 12) has a worldwide distribution (Figure 21), especially in the Northern Hemisphere (Bischler-Causse 1989; Lu & Huang 2017). It is known from Afghanistan, Bhutan, China, India, Indonesia (Java, Sumatra), Iran, Iraq, Israel, Japan, Korea, Lebanon, Malaysia, Nepal, New Guinea, New Zealand, Pakistan, Philippines, Russia, Sri Lanka, Syria, Tadjikistan, Taiwan, Tasmania, Thailand, Turkey, USSR, Uzbekistan, and Vietnam (Bischler-Causse 1989; Söderström *et al.* 2010; Ginting & Batubara 2019). As seen in Figure 21, it is also extensively reported throughout North America. *Marchantia polymorpha* has three subspecies. In South Africa, *M. polymorpha* ssp. *ruderalis* (Figure 6-Figure 8, Figure 17-Figure 19) only occurs in

nurseries (Figure 22-Figure 23), indicating that it has been introduced (Ginting & Batubara 2019).



Figure 21. *Marchantia polymorpha* distribution. Image from DiscoverLife, with online permission.



Figure 22. *Marchantia polymorpha* ssp. *ruderalis* in flower pot in nursery, the only place it occurs in South Africa. Photo courtesy of Javier Martínez-Abaigar.



Figure 23. *Marchantia polymorpha* ssp. *ruderalis* in flower pot intended for growing a tree. Photo courtesy of Javier Martínez-Abaigar.

Aquatic and Wet Habitats

Boisselier-Dubayle and Bischler (1989) described the electrophoretic biochemistry of *Marchantia polymorpha* (Figure 1-Figure 12) as having a good correlation with the habitats. They identified two ecotypes: domestic with a spread over a wide geographic area (possibly corresponding with *M. polymorpha* ssp. *ruderalis* – Figure 6-Figure 8, Figure 17-Figure 19), and a wet-habitat-restricted ecotype that exhibited two biotypes [corresponding with *M. polymorpha* ssp. *polymorpha* (Figure 5) and possibly *M. polymorpha* ssp. *montivagans* (Figure 2-Figure 4)].

In their recent publication on *Marchantia* in Japan, Zheng and Shimamura (2022) described the habitat of *Marchantia polymorpha* ssp. *polymorpha* (Figure 5) as growing on wet soil in marshland or stone near streams, seldom on wet concrete. They described *Marchantia polymorpha* ssp. *ruderalis* (Figure 6-Figure 8, Figure 17-Figure 19) as often on soil, stone, gravel, or walls of drainage channels in anthropogenic regions, supporting the conclusions of Long (1995). But Zheng and Shimamura (2022) also found that when the latter subspecies grows in dripping wet habitats, "plants often have an erect and robust thallus with a distinct and continuous blackish median band on the thallus and are sometimes difficult to distinguish from ssp. *polymorpha* based on these characters." However, they consider that the discontinuous blackish median band and prostrate thallus of ssp. *polymorpha* will distinguish them. I would like to see common garden experiments on the effects of wet vs drier habitats on the expression of the black median band (midrib) in each of the subspecies.

Subspecies *montivagans* (Figure 2-Figure 4) in Britain and Ireland is a species occurring in springs, marshes, and flushes, in somewhat calcareous areas, and occurs mostly in subalpine or montane habitats (Long 1995). It can also be found on damp calcareous mossy banks and rocks beside streams and ravines. However, in their studies Boisselier-Dubayle and Bischler (1989) found it in some locations together with *M. polymorpha* ssp. *polymorpha* (Figure 5).

Frye (1928) found that *Marchantia polymorpha* (Figure 1-Figure 12) was sometimes submersed in winter. This, presumably, was ssp. *polymorpha* (Figure 5).

Darigo (2004) reported the aquatic form of *Marchantia polymorpha* (as *Marchantia aquatica*; now *M. polymorpha* ssp. *polymorpha*; Figure 5) as new to Missouri, USA, noting its distinctive black midrib. He found it in dense mats on shaded moist soil and limestone bedrock at the base of a small waterfall. It was associated with *Fissidens grandifrons* (Figure 24), *Rhizomnium punctatum* (Figure 25), and *Leptodictyum riparium* var. *laxirete* (Figure 26).

Marchantia polymorpha s.l. (Figure 1-Figure 12) occurs in wet places around lakes, especially in shade, and in bog water in Scotland (West 1910). In Denmark it can be found on terrestrial soil or submerged (Sørensen 1948). It is uncommon with the graminoid *Eleocharis quinqueflora* (Figure 27) and the moss *Paludella squarrosa* (Figure 28) Geissler & Selldorf 1986).



Figure 24. *Fissidens grandifrons*, an associate of *Marchantia polymorpha* on limestone in wet habitats. Photo by Brad Von Blon, through Creative Commons.

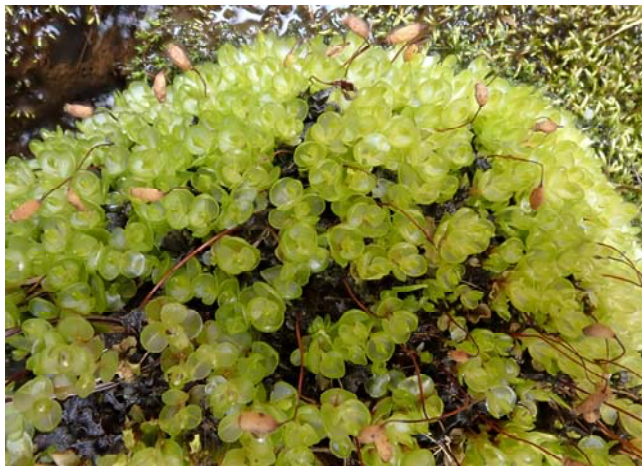


Figure 25. *Rhizomnium punctatum*, an associate of *Marchantia polymorpha* on limestone in wet habitats. Photo by Sharon Pilkington, with permission.

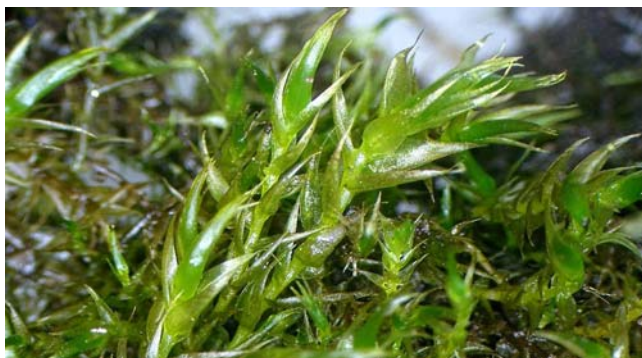


Figure 26. *Leptodictyum riparium*; var. *laxirete* is an associate of *Marchantia polymorpha* on limestone in wet habitats. Photo by William Lampa, through Creative Commons.



Figure 27. *Eleocharis quinqueflora*, an occasional associate of *Marchantia polymorpha* in Denmark. Photo by Kristian Peters, through Creative Commons.



Figure 28. *Paludella squarrosa*, an occasional associate of *Marchantia polymorpha* in Denmark. Photo by Hermann Schachner, through Creative Commons.

Marchantia polymorpha (Figure 1-Figure 12) occurs in shady areas with high humidity and exhibits a low tolerance to desiccation (Lagos-López 2008). In such areas it can develop extensive cover (Linares 1986; Churchill & Linares 1995; Uribe & Aguirre 1995; Lagos-López 2008). But perhaps one of the most extensive covers develops in burned over areas (Durand 1908; Janet Marr, pers. obs. 2022), usually not an aquatic habitat.

streams and rivers

Watson (1919) described the habitat of *Marchantia polymorpha* (Figure 1-Figure 12) as often on boulders in streams, on banks with frequent submergence and slow water. In the Western Carpathians it occurs in the rock community in streams near Lacko (Mamczarz 1970). It

occurs in streams in Greece (Papp 1998) and in streams in northeastern Finland (Heino & Virtanen 2006). It is among the most common species in the River Tweed, UK (Holmes & Whitton 1975) and is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006).

It can also be common in rivers (Ferreira *et al.* 2008), such as the Iskur River, Bulgaria, and its main tributaries (Papp *et al.* 2006), as a hygrophyte in Bulgarian rivers (Gecheva *et al.* 2010, 2013), and in the Iregua River of Spain (Martínez-Abaigar & Ederra 1992).

It is often a mountain species, occurring in alpine streams in the Swiss Alps (Geissler 1976) and in mountain streams of northwest Portugal (Vieira *et al.* 2005) as well as mountainous streams on Madeira Island (Luis *et al.* 2015). Frye (1928) reported it from western Washington, USA, in burned sites, but also in submersed sites. It is interesting that several *Marchantia* species occur in both aquatic habitats and as pioneers after fire.

stream and river banks

Perhaps the most common wet habitat for *Marchantia polymorpha* (Figure 1-Figure 12) is the damp banks of streams and rivers (Figure 29-Figure 32). In the Haute Ardenne rivers in Belgium, it occurs on earthy and gravelly substrates of river banks (Leclercq 1977) and in the UK it occurs on the riverbank of the River Tees (Holmes & Whitton 1977a). It can be found throughout the River Swale, Yorkshire, UK (Holmes & Whitton 1977b), and mostly in the mid to lower River Tyne, UK (Holmes & Whitton 1981b). It is similarly associated with the River Wear in England (Birch *et al.* 1988). In Germany it occurs in the middle and lower reaches in the Harz Mountains (Bley 1987). Ginting and Batubara (2019) similarly describe it from rocks of a creek wall in exposed places (Figure 33), at 1500 m altitude in Indonesia. In western Canada, it is restricted to terrestrial habitats of montane streambanks (Vitt *et al.* 1986; Glime & Vitt 1987).



Figure 29. *Marchantia polymorpha* ssp. *polymorpha* on the bank of a small stream, showing partially upright branches. Photo by Vladimir Bryukhov, through Creative Commons.



Figure 30. *Marchantia polymorpha* on steep stream bank. Photo by Olga Chernyagina, through Creative Commons.



Figure 31. *Marchantia polymorpha* ssp. *polymorpha* wet beside stream. Note the rhizoids hanging from the lower side of the thallus. Photo by Penny Anderson, with online permission.



Figure 32. *Marchantia polymorpha* with gemmae cups on moist soil by stream. Photo by Rudolf Macek, with permission.

In Denmark *Marchantia polymorpha* (Figure 1-Figure 12) can be found in ditches at pH 6.2-8.5 and in neutro-alkaline lakes, peat pits of spring bogs (Figure 34) at pH 6.2-8.0, on terrestrial soil or submerged (Sørensen 1948; Clausen 1952). Alfasane *et al.* (2013) recorded environmental conditions in Lake Rainkhyongkain, where it grew in masses in the shallow littoral zone of the lake. These included mean values ($n = 4$) of dissolved oxygen

content ($7.93 \pm 0.78 \text{ mg L}^{-1}$), alkalinity ($1.70 \pm 0.12 \text{ meq L}^{-1}$), soluble reactive phosphorus ($17.25 \pm 0.62 \text{ } \mu\text{g L}^{-1}$), soluble reactive silicate ($10.44 \pm 0.72 \text{ mg L}^{-1}$), and $\text{NO}_3\text{-N}$ ($34.00 \pm 4.00 \text{ } \mu\text{g L}^{-1}$). The mean temperature on the sampling date was 33.5°C and pH was 7.39.



Figure 33. *Marchantia polymorpha* with *Thuidium delicatulum* growing over flagstone at Mountain Moss Enterprise, demonstrating the breadth of its habitat. Photo by Annie Martin, with permission.

In the high moor transition areas of Denmark *Marchantia polymorpha* (Figure 1-Figure 12) can be found at pH 5.0-6.09 (Sørensen 1948). O'Toole and Synnott (1971) found that *Marchantia polymorpha*, along with *Funaria hygrometrica* (Figure 35), was an early indicator of increased calcium carbonate and phosphorus levels on blanket peat following fertilization of the peat. However, these two bryophytes are suited to other environmental conditions, with *M. polymorpha* preferring wet, unsheltered plots with no iron or copper, whereas *F. hygrometrica* prefers dry, sheltered locations with iron (Synnott 1987). Li Zhang (pers. comm. 4 August 2022) has found *Marchantia polymorpha* in peatlands (Figure 34) in China.



Figure 34. *Marchantia polymorpha* ssp. *montivagans* in a spring, Sierra Nevada near Merida, Venezuela. Photo courtesy of Javier Martínez-Abaigar.



Figure 35. *Funaria hygrometrica*, an indicator, along with *Marchantia polymorpha*, of increased calcium carbonate and phosphorus levels in blanket peat. Photo by Bonnie Nickel, through Creative Commons.

In Taiwan, Lu and Huang (2017) found *Marchantia polymorpha* (Figure 1-Figure 12) on damp soils from 300-2500 m asl, a habitat similar to that on Mt. Edith Cavell in Canada (Figure 36).

In high moors in Denmark it occurs in the transition areas at pH 5.0-6.0 (Sørensen 1948). In the Caucasus it is in watery and swampy lands (Alijev & Babajev 1976).



Figure 36. *Marchantia polymorpha* with gemmae, on damp soil with mosses on the mountainside of Mt. Edith Cavell, Jasper, Canada. Photo by Janice Glime.

Other damp soil habitats are also suitable, including open areas (Figure 37), moist slopes (Figure 38), marshy areas (Figure 39), and other wetlands (Figure 40). Thatcher (1949) found it in an artificially illuminated cave.



Figure 37. *Marchantia polymorpha* on soil, with gemmae cups, in Europe. Photo by Michael Lüth, with permission.



Figure 40. *Marchantia polymorpha* ssp. *montivagans* with *Calliergon cordifolium* in a wetland. Photo by Des Callaghan, through Creative Commons.



Figure 38. *Marchantia polymorpha* on a damp soil bank. Photo by Michael Lüth, with permission.



Figure 39. *Marchantia polymorpha* in a marshy habitat near a stream. Photo by Michael Lüth, with permission.

One of the more interesting habitats for *Marchantia polymorpha* (Figure 1-Figure 12) is on a **desalinating wadden-polder** (tract of low land reclaimed from the sea; Figure 41) (Joenje & During 1977). Although it was able to colonize, it was unable to compete after 2-3 years. It was especially common on mussel banks. Joenje and During suggested that its small spores contribute to its rapid arrival on newly available substrata.



Figure 41. Gradual transition from recently deposited salt marshes and the Wadden sea on a desalinating wadden-polder. This stage is too salty, due to manipulation, and the only bryophyte able to live here is *Hennediella heimii*. Photo courtesy of Bart van Tooren.

Another unusual habitat where *Marchantia polymorpha* (Figure 1-Figure 12) can thrive is in geothermal areas (Figure 42). These can have some similarities to saline areas because of sulfur and other salts. In the Antarctic, they provide a warm haven for species from warmer climes, including *M. polymorpha* (Kennedy 1996). Takaki (1967) found it on an active volcano in Japan. Takaoki and Mitani (1986) used *Marchantia polymorpha* in experiments to develop a method for measuring the effects of SO₂ on photosynthesis in bryophytes and lichens. They found that illumination during the exposure to SO₂ caused the SO₂ to have greater inhibition of photosynthesis in *M. polymorpha* than did SO₂ alone. In this species, the photosynthetic system was more sensitive than the respiratory system. In concentrations less than 4 ppm, the thalli were able to partially recover.



Figure 42. Geothermal fissure with *Sphagnum*, Geyser, Iceland, a potential habitat for *Marchantia polymorpha*. Photo by Janice Glime.



Figure 43. Mt. Hood Riverside, Oregon, USA, post-fire, at a stage where *Marchantia polymorpha* can be a pioneer. Photo from U.S. Department of Agriculture, through public domain.

after fire

It is interesting that several species of *Marchantia* are post-fire colonizers (Figure 43). This is true for *Marchantia polymorpha* (Figure 1-Figure 12) (Benson & Blackwell 1926; Torrey 1932; Bradbury 2006). Frye (1928) and Hoffman (1966) both reported it on burned sites in Washington, USA, and Graff (1936) similarly found that the species invaded after forest fires. Adámek *et al.* (2016) studied post-fire vegetation in central Europe and again found that *Marchantia polymorpha* was among the first invaders, but it typically disappeared after a few years. Froment (1975) found it to be among the pioneer dominants in a Belgian high fen post-fire site. Heras-Ibáñez *et al.* (1991) recorded it in post burn sites in SE Spain, where it had diminished numbers after 6 years. They noted that some of the species, including *M. polymorpha*, were known to fix nitrogen (through bacterial partners) on such sites. Duckett *et al.* (2008) noted that *M. polymorpha* is common after fires in Canada and explored post-fire invasion at Thursley Common, UK. Once again, *M. polymorpha* was a common invader. In fact, they noted that thalli had abundant reproductive structures in the first year following the fire. They attributed the rapid colonization to the tiny (10-16 µm) spores. Subspecies. *ruderalis* and ssp. *polymorpha* were present side by side. The species formed patches reaching up to 12 m in diameter, with individual colonies of 5-20 cm diameter (Duckett & Pressel 2009). Rather than naming tracheophyte competition, they attributed the later decline to nutrient leaching (Duckett *et al.* 2008). Its presence is so common after fire that Rees and Juday (2002), when reporting it from Alaskan burned sites, considered it to be a fire specialist.

The succession of species following fire is a fairly constant one, as noted already by Skutch (1929). Typically, the pioneer stage with *M. polymorpha* (Figure 1-Figure 12) is succeeded by *Polytrichum* (Figure 44).

These habitats would seem to be quite different from the wet ones already discussed. But one thing they have in common is reduced competition, giving the liverworts time to become established.



Figure 44. *Polytrichum juniperinum*, a post-fire species that succeeds *Marchantia polymorpha*. Photo by James K. Lindsey, with permission.

Having said that, how then do we explain that in East Anglia *Marchantia polymorpha* (Figure 1-Figure 12) is more common in town than in the countryside (Stevenson & Hill 2008)? Is the subspecies *ruderalis* more tolerant of competition, or do the spores manage to find spots with limited competition?

Physiology

It is not surprising that the anatomy and physiology of this well known species were among the early bryological studies (Mirbel 1835). Since that time, a long period of mostly taxonomic activity ignored the physiology of most bryophytes. However, *Marchantia polymorpha* (Figure 1-Figure 12) was frequently the subject of those studies that did address bryophyte physiology.

hormones - IAA

Among the many studies on *Marchantia polymorpha* (Figure 1-Figure 12), it often served as the model organism for understanding physiology of thallose liverworts, or bryophytes in general. Maravolo and Voth (1966) reported the actions of various concentrations of indoleacetic acid (IAA), naphthalene acetic acid (NAA), and maleic hydrazide on development of sterile gemmae (Figure 45) of *Marchantia polymorpha*. They found that the two auxins

(IAA and NAA) promoted similar responses, often resembling those of tracheophytes. In *M. polymorpha*, rhizoids elongated on the dorsal surface; the growing region became dormant, and cells became strongly elongated. When apical growth (Figure 20, Figure 46) was inhibited, the thallus became winged. The maleic hydrazide likewise elicited responses similar to those in tracheophytes, including inactivation of meristematic regions, deterioration of chloroplasts, inhibition of rhizoid production, and **hyperplasia** (enlargement of organ or tissue caused by increased reproduction rate of its cells).



Figure 45. *Marchantia polymorpha* with gemmae in gemmae cups. Photo by Holger Casselmann, through Creative Commons.

But at that time, the production of IAA by bryophytes was still unknown. Schneider *et al.* (1967) reported for the first time that IAA (indoleacetic acid) occurs in bryophytes, using *Marchantia polymorpha* (Figure 1-Figure 12) as one of the test organisms. Furthermore, Sheldrake (1971) reported auxin in the substrata of bryophytes, so its effect on them is relevant. However, concentrations of the IAA in substrata with no bryophytes were the same in those that had them. Hence, it is questionable whether these substrate sources were of importance to the development of the bryophytes. Nevertheless, they could play a role in the induction of rhizoids as they do for roots. And they might have more effect on some bryophytes not included in the tests.

Following up on the possible functions, Otto and Halbsguth (1976) examined the effects of light and the auxin IAA on the formation of the primary rhizoids of gemmae in *Marchantia polymorpha* (Figure 1-Figure 12). They found that the number of rhizoid-forming gemmae depends on the wavelength of irradiation. Following a 1-hour exposure to 10^{-4} M IAA, rhizoids developed as they would if exposed to red irradiation for one hour. They concluded that this relationship suggests a role of the phytochrome system in membrane permeability for IAA.

Transport of the auxin 11C-indoleacetic acid occurs basipetally in the thallus, where it is localized in the midrib (Figure 46-Figure 47) (Maravolo 1976; Gaal *et al.* 1982).

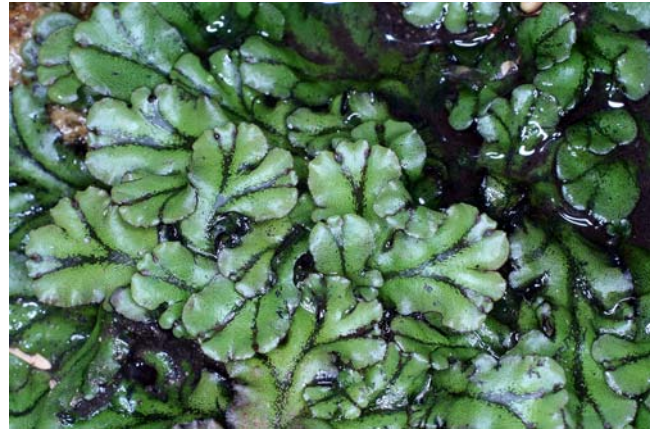


Figure 46. *Marchantia polymorpha* with strong midrib on older thalli; this character is common in aquatic forms. In several branches you can see apical dominance where a single branch is dominant and the other is shorter or has an unbranched midrib (e.g. center left). Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 47. *Marchantia polymorpha* with only hints of midrib on young thallus tissue, probably ssp. *ruderalis*. Photo by Janice Glime.

Reynolds and Maravolo (1973) determined that extracts of *Marchantia polymorpha* (Figure 1-Figure 12) contain substances that in the lab can enhance or inhibit IAA oxidation. These extracts contained four unknown phenolic compounds. Two of these enhanced the oxidase activity and two inhibited it. Although the inhibitors were present throughout the thallus, they were slightly more concentrated in basal and apical areas. In other words, there was an **acropetal** (movement of dissolved substances outward toward shoot and basal apices) gradient of increase in this cofactor concentration. In this case IAA moves away from the growing tips.

Gaal *et al.* (1982) used tracer experiments to determine that ^{14}C IAA transport is localized in the cells of the midrib of the thallus (Figure 46). It occurs both acropetally and basipetally, with a far greater intensity basipetally. In anaerobic conditions, basipetal transport was reduced by 40-50%. Centrifugation also disrupted it, reducing basipetal transport by 30-40%. Hence, in the parameters measured, transport of IAA in *Marchantia polymorpha* (Figure 1-Figure 12) is essentially the same as that in seed plants.

Davidonis and Munroe (1972) described apical dominance (Figure 46) in *Marchantia polymorpha* (Figure 1-Figure 12), a function known from tracheophytes. The species dichotomous branching and its apical dominance is exhibited by one of those branch lobes having greater growth than the other (Figure 46). They demonstrated that if the lobes are separated by a cut, the dominance is lost. IAA is needed to maintain this dominance. If it is applied to the smaller lobe after the cut, that lobe is again inhibited. It also exhibits greater inhibition of the smaller lobe when applied to the intact plant. Interestingly, the dominant lobe is neither inhibited nor enhanced by application of IAA to it. They suggested that this behavior indicates that the two lobes have a different sensitivity to the auxin. This is somewhat reminiscent of apical dominance in plants like snapdragons. IAA produced in the apex of the plant migrates downward and inhibits the development of side branches. If the apex is removed, a lower branch becomes dominant.

Hormones can both activate and suppress pathways in *Marchantia polymorpha* (Figure 1-Figure 12). Binns and Maravolo (1972) found that cytokinin suppressed the normal germination of gemmae (Figure 45), instead stimulating nodular, callus-like growths. Responses were time-dependent on the cytokinin-enriched medium. Auxin, on the other hand, had no effect on the regeneration of normal thallus growth. Auxin could, however, reverse the suppression caused by inhibiting compounds such as transcinnamic acid. Auxin exhibited a basipetal gradient and this gradient is essential to normal growth and regeneration. These two hormones interact, with high levels of cytokinin destroying the polarity by increasing the auxin-synthesizing capacity. Maintaining the right balance permits the liverwort to maintain its apical dominance (Figure 20, Figure 46).

Flores-Sandoval *et al.* (2015) characterized the functions of the auxin transcriptional response in *Marchantia polymorpha* (Figure 1-Figure 12). It acts to facilitate branching, differentiation, and growth, but it does not determine specific tissues.

Eklund *et al.* (2015) found that the auxin IAA regulates the dormancy of gemmae (Figure 48) on the *Marchantia polymorpha* (Figure 1-Figure 12) thallus. Kato *et al.* (2015) found that auxin repression could cause severe defects in the development of *Marchantia polymorpha*, including gemmaling development, dorsiventrality, organogenesis, and tropic responses, noting the interactions of hormones. Billhardt (2021) further discussed the interactions, and using these was able to explain the long-known observation that gemmae typically do not germinate while still on the parent thallus (Figure 48). This dormancy mechanism is controlled by high levels of abscisic acid (ABA) in the cup (see also Tougan *et al.* 2010). But gemmae are not attached to the thallus while they reside in the cup. Therefore, it appears that the actual signal is a gas. Billhardt found that when the regulators of the ethylene signalling pathway were mutated, it affected the dormancy, suggesting that ethylene regulates dormancy through ABA. Müller (2021) notes that ABA and ethylene commonly act antagonistically, possibly explaining these observations.

Ishizaki *et al.* (2012) used transgenic plants to monitor the effects of auxin-mediated transcriptional activation in

plants. This demonstrated that IAA had a role in the transcription of some genes. These genes were demonstrated at the bottom of the gemmae cups. Additional activity occurred at the gametophyte-sporophyte junction and in the developing sporophyte.



Figure 48. Gemmae cups with loose dormant gemmae on thallus of *Marchantia polymorpha*, demonstrating their continued dormancy while associated with the parent tissue. Photo by Hermann Schachner, through Creative Commons.

hormones - gibberellins

Melstrom *et al.* (1974) found that *Marchantia polymorpha* (Figure 1-Figure 12) exhibits gibberellin activity and was responsive to photoperiod. When they increased the photoperiod from 12 to 18 hours of light the activity of the gibberellins increased and thallus elongation and **orthogeotropic** (directly in line with gravitational pull; Figure 49) growth increased.



Figure 49. *Marchantia polymorpha* ssp. *polymorpha* growing upright in water. Photo by Oleg Kosterin, through Creative Commons.

Maravolo (1980) applied both auxins (IAA) and gibberellin to bryophytes, including *Marchantia polymorpha* (Figure 1-Figure 12). In this case, the applied auxin stimulated rhizoid growth, cell proliferation, and elongation. Gibberellin, on the other hand, promotes cell enlargement, chloroplast development, and starch degradation. Under the right photoperiod, it also influences the geotropic curvature and causes ultrastructural changes in starch granules and thylakoids.

Loomis and Maravolo (1985) found that exogenous gibberellin increases the amylolytic activity of two protein fractions from *Marchantia polymorpha* (Figure 1-Figure 12).

hormones - ethylene

Little information has been available on ethylene presence and physiology in bryophytes. Ethylene is a gaseous hormone and therefore can be used to communicate between plants. Katayose *et al.* (2021) noted that genes for ethylene have been conserved from the algae, but that the function and biosynthesis of this hormone remain unknown in the bryophytes. They found that *Marchantia polymorpha* (Figure 1-Figure 12) synthesizes ethylene. However, treatment with the precursor ACC only slightly promoted the production of ethylene. On the other hand, ACC "remarkably" suppressed thallus growth and rhizoids, contrasting with the slight promotion of thallus growth when external ethylene was applied. These experiments indicate that ethylene functions independently of ACC and that ACC is not essential to its production in *Marchantia polymorpha*.

Li *et al.* (2020) similarly found that ACC (ethylene precursor) and ethylene can induce different responses in *Marchantia polymorpha* (Figure 1-Figure 12). Ethylene causes larger gemmae, induces more gemmae cups, and promotes the dormancy of the gemmae. ACC, on the other hand, inhibits gemma growth and development by suppressing cell division. This suggests that the pathway might be different from that tracheophytes.

In *Marchantia polymorpha* (Figure 1-Figure 12), more ethylene is produced in the light than after prolonged darkness (Fredericq *et al.* 1977; Rethy *et al.* 1977). Veroustraete *et al.* (1982) further elaborated on ethylene physiology in the species. They found involvement of the low energy red:far-red reversible type of phytochrome action for both the light-induced ethylene production and the control of **epinasty** (nastic movement in which plant part such as flower petal or thallus branch is bent outward and often downward; Figure 50) in the species. They found that CO₂ had no effect on the production of ethylene when the thallus was irradiated with terminal far-red light, but in controls without the light treatment, there was a clear CO₂ dependency. This behavior suggests the involvement of phytochrome. De Greef *et al.* (1979) studied environmental effects on ethylene production in *M. polymorpha* and concluded that ethylene production requires energy and depends on either cyclic photophorylation or oxidative phosphorylation.



Figure 50. *Marchantia polymorpha* showing an unusual margin formation that exhibits **epinasty**. Photo by Steve Trynoski, with permission.

hormones - cytokinins

Binns and Maravolo (1972) found that cytokinin suppressed germination of gemmae (Figure 45) in *Marchantia polymorpha* (Figure 1-Figure 12). Externally applied auxins had no effect on regeneration from thallus discs.

Aki *et al.* (2019a,b) noted that cytokinins regulate a variety of physiological events in plants. They found that the cytokinin signalling pathway in *Marchantia polymorpha* (Figure 1-Figure 12) controls the formation of both gemmae cups (Figure 45, Figure 48) and rhizoids (Figure 53-Figure 54) during the development of the thallus. It is further implicated in the distribution of air pores (Figure 51) and the shape of the thallus margin (compare Figure 49 and Figure 50), suggesting that cytokinins regulate cell division or differentiation of precursor cells, thereby coordinating development.



Figure 51. *Marchantia polymorpha* epidermis with air pores, showing green layer beneath. Photo by Walter Obermayer, with permission.

hormones – ABA and lunularic acid

In 1979, Weiler used a radioimmunoassay in an attempt identify the presence of ABA in *Marchantia polymorpha* (Figure 1-Figure 12). At that time, using that sensitive technique, ABA appeared to be absent. Fortunately, that result was not accepted by everyone. Li *et al.* (1994) announced, for the first time, the presence of abscisic acid (ABA) in liverworts, using *Marchantia polymorpha* as the model organism. In fact, the concentrations were similar to those of tracheophytes.

Akter *et al.* (2014) found that pretreatment with ABA and sucrose increases the survival rate after both freezing and desiccation of gemmalings in *Marchantia polymorpha* (Figure 1-Figure 12). ABA also increases the accumulation of soluble sugars. Furthermore, ABA induces the accumulation of transcripts for proteins that are similar to late embryogenesis abundant (LEA) proteins, proteins that accumulate in maturing seeds as they acquire desiccation tolerance. ABA also causes the vacuoles to fragment, causing an increase in the cytosolic volume and increasing the volume and density of chloroplast distribution.

Eklund *et al.* (2018) also found that ABA delays the germination of gemmae (Figure 48) in *Marchantia polymorpha* (Figure 1-Figure 12).

Ghosh *et al.* (2016) was the first to report on the regulation of ABA in the liverwort *Marchantia polymorpha* (Figure 1-Figure 12). Previously, a hormone with similar functions, **lunularic acid**, was known from some liverworts. Ghosh and co-workers found that the expression of ABA-induced β -glucuronidase (GUS) reporter gene was less in older, mature thalli than in young gemmalings of this species. This change corresponded with reduction in the sensitivity to exogenous ABA. Lunularic acid, on the other hand, had no effect on GUS expression.

Nevertheless, it appears that *Marchantia polymorpha* (Figure 1-Figure 12) has **lunularic acid** (Gorham 1977; Abe & Ohta 1983), a hormone with functions similar to those of ABA. However, it appears that in *M. polymorpha*, the prelunularic acid greatly exceeds the lunularic acid (Abe & Ohta 1984). Gorham found it in all parts of *M. polymorpha*. In continuous light, both lunularic acid and fresh weight increased relative to that in interrupted light periods. It appears that the lunularic acid either was not inhibited by continuous light or that the photosynthetic products overrode the inhibition.

Imoto and Ohta (1985) found that lunularic acid compounds were equally distributed in vacuoles and cytoplasm, but they were absent in plastids, mitochondria, and peroxisomes.

hormones - brassinosteroids

Brassinosteroids occur in a wide range of organisms, including early land plants (Bajguz & Hayat 2009). These steroidal plant hormones affect the promotion of plant growth and development. Metabolism of these steroids is altered when plants respond to abiotic stresses as well as bacterial, fungal, and viral pathogens. Ko *et al.* (1995) characterized five 4-demethylsterols that seem to be potent biosynthetic precursors of brassinosteroids in suspension cell cultures of *Marchantia polymorpha* (Figure 1-Figure 12).

cell growth

Fries (1964) explored the effects of growth inhibitors on growth and elongation in *Marchantia polymorpha* (Figure 1-Figure 12).

Matsui *et al.* (1991) detected the activity of lipoxygenase in *Marchantia polymorpha* (Figure 1-Figure 12) in culture. Most of this activity occurred in the **cytosol** (aqueous component of cytoplasm of cell). The activity increases rapidly during the lag phase of cell growth (Matsui *et al.* 1996). This activity decreased in the logarithmic phase, then increased again in the stationary phase. This series of changes in lipogenase activity is caused by *de novo* synthesis and degradation of the same lipoxygenase. They also found enzyme activity that degrades fatty acid hydroperoxides – products of lipoxygenase.

circadian rhythm

Lagercrantz *et al.* (2020) examined the circadian clock in *Marchantia polymorpha* (Figure 1-Figure 12). They found that this clock coordinates the **nyctinastic** (periodic movement plant parts, especially flowers or leaves, caused by nightly changes in light intensity or temperature) thallus movement of the species and suggested it is controlled by auxin (IAA). The thalli "wave" up and down on a 24-hour cycle in 12 hours light: 12 hours dark. These movements

in gemmalings are maintained in continuous light. The auxin, produced in the apical region (Figure 20), travels basipetally through the midrib region, creating a gradient. The circadian rhythm regulates the IAA levels. At low doses (10-100 nM) the angle of growth is reduced, creating a more flattened thallus. These experiments support the observations of Went and Thimann (1937) that the response to auxin depends on the time of day.

Marchantia polymorpha (Figure 1-Figure 12) has often been a model for evolution in land plants. Linde *et al.* (2017) found homologues of core clock genes in *Arabidopsis* (Figure 52), bryophytes, and charophytes, with fewer copies in the latter. The data supported the hypothesis that adaptation to terrestrial life occurred earlier than that supposed by current theory, particularly occurring in the charophytes. The bryophytes exhibit not only duplication and acquisition of new genes, but also loss of genes in development of their circadian clock.



Figure 52. *Arabidopsis thaliana*, in a genus that has homolog genes with early land plants and is frequently used for evolutionary comparisons. Photo by Roepers, through Creative Commons.

Cuitun-Coronado *et al.* (2022) noted that photosynthesis is a circadian process in some flowering plants and Cyanobacteria. They reported the first record of circadian regulation of the photosynthetic pathway in a liverwort, *Marchantia polymorpha* (Figure 1-Figure 12). They determined that the light:dark cycle synchronized the 14-hour photosynthetic cycle, but that the phases of different thalli desynchronize under free-running

conditions. They suggested that chloroplast translation might be necessary for the clock to control the light-harvesting process in this plant.

Lagercrantz *et al.* (2021) used sequencing to identify the genes involved in circadian rhythms in *Marchantia polymorpha* (Figure 1-Figure 12). They identified a homolog of the *Arabidopsis* (Figure 52) gene *DE-ETIOLATE1* as having a high amplitude and morning phase. The circadian rhythm resulting from *MpDE1* expression is disrupted when core clock genes lose their function in mutants. In knock-down experiments with this gene, the circadian rhythm of nyctinastic thallus movement is altered. But the researchers were unable to detect any effect in response to light, leaving us with no explanation of the function of the *MpDE1* gene in *M. polymorpha*.

water relations

Ghosh *et al.* (2021) explored the drought tolerance in this model organism. They desiccated gemmae in various desiccating solutions and found that these led to extreme growth inhibition, disruption of membrane stability, and reduction in chlorophyll content. At the same time, the accumulation of hydrogen peroxide and malondialdehyde increased and electrolyte leaked from the gemmalings, creating oxidative stress. Activities of antioxidant enzymes, including superoxide dismutase, catalase, ascorbate peroxidase, dehydroascorbate reductase, and glutathione S-transferase increased, while total antioxidant activity also increased in response to increased oxidative stress. When they applied exogenous ABA, it reduced drought-induced tissue damage and improved the activities of antioxidant enzymes and accumulation of proline.

Godinez-Vidal *et al.* (2020) noted that both water deficit and ABA cause osmotic adjustment in *Marchantia polymorpha* (Figure 1-Figure 12). This species increases its ABA levels under water deficit. Like Ghosh and coworkers, they found decreased growth and morphological changes in response to water deficits. Cell organelles changed locations, largely due to the volume change of the central vacuole, a consequence of the change in osmotic potential.

Hatanaka and Sugawara (2010) found that after exposure to drying below $0.1 \text{ g H}_2\text{O g}^{-1}$ dry weight the desiccation tolerance level of *Marchantia polymorpha* (Figure 1-Figure 12) was very low, with a survival rate of less than 10%. When cells were pretreated in 0.5 M sucrose, the survival rate rose to 87%, even at lower water levels. This treatment caused cell alteration and the accumulation of a large amount of sucrose and newly made proteins.

Duckett and Ligrone (2003) found that rhizoids (Figure 53) in the bryophytes, particularly the **Marchantiales**, contribute to their water movement. They also contribute to movement of food. The smooth rhizoids (Figure 53-Figure 54) are living cells and often contain fungal hyphae. The pegged rhizoids (Figure 53-Figure 54) are dead, but they nevertheless contribute to the movement of water in the grooves of the archegoniophores. They also help to prevent the collapse when the thalli dry out and they facilitate recovery upon rehydration.



Figure 53. *Marchantia polymorpha* ventral surface of thallus showing pattern of horizontal pegged rhizoids that are close to the thallus and that facilitate water movement and uptake. The pinkish rhizoids toward the base are the perpendicular smooth rhizoids that adhere to the thallus. Photo by Larry Jensen, with permission.

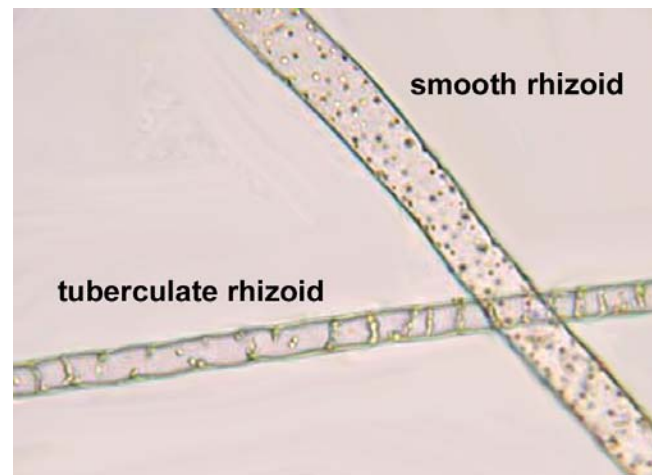


Figure 54. *Marchantia polymorpha* smooth and tuberculate (pegged) rhizoids. Photo from Botany Website, UBC, with permission.

Marchantia polymorpha ssp. *ruderalis* (Figure 6-Figure 8, Figure 17-Figure 19, Figure 56) was among the first plants to use extracellular ice formation (Figure 55) as a dehydrating agent, a mechanism to provide freezing avoidance (Schott *et al.* 2021). During exposure to freezing temperatures, ice crystals formed in the air chambers and grew out the pores. These hygroscopic crystals, along with other ice on the outside of the thallus, drew ice out of the cells and caused their dehydration. This ice removal can prevent the formation of crystals within the cells, where the crystals can cause membrane and structural damage. The thallose liverwort *Conocephalum salebrosum* (Figure 57) proved to be more resistant to frost than did *Marchantia polymorpha* ssp. *ruderalis* (Figure 56).



Figure 55. Extracellular ice crystals on *Marchantia polymorpha*, a mechanism for causing dehydration and preventing freezing damage to membranes. Photo by David Taylor, with permission.



Figure 56. *Marchantia polymorpha* ssp. *ruderalis* with gemmae. Photo by Malcolm Storey, DiscoverLife, with online permission.



Figure 57. *Conocephalum salebrosum*, a species that is more frost resistant than is *Marchantia polymorpha* ssp. *ruderalis*. Photo by Hermann Schachner, through Creative Commons.

translocation

Rota and Maravolo (1975) traced the translocation of ^{14}C sucrose in *Marchantia polymorpha* (Figure 1-Figure 12). They found that during regeneration, higher levels of ^{14}C -sucrose moved to the apical region than during normal growth. The auxin IAA inhibited the transport and thallus regeneration.

desiccation

Pence (1998) found that for successful cryopreservation, *Marchantia polymorpha* (Figure 1-Figure 12) required both ABA and encapsulation in alginate beads, differing from *Riccia fluitans* (Figure 58) and *Helicodontium capillare* (Figure 59) that only required one of these. Without ABA and encapsulation, *M. polymorpha* was killed upon drying in liquid nitrogen. I found that interesting because *R. fluitans* is more aquatic than is *M. polymorpha*, but perhaps it is because it is structurally smaller.



Figure 58. *Riccia fluitans*, a species requiring only one of the two cryopreservation treatments (ABA and encapsulation in alginate beads) required by *Marchantia polymorpha*. Photo by Kerry Wixted, through Creative Commons.



Figure 59. *Helicodontium capillare*, a species requiring only one of the two (ABA and encapsulation in alginate beads) cryopreservation treatments required by *Marchantia polymorpha*. Photo by D. Peralta, MNHN, through Creative Commons.

nutrients

Voth and Hamner (1940) described some of the symptoms of nutrient deficiency as expressed in *Marchantia polymorpha* (Figure 1-Figure 12). They found that cultures that lacked Ca ions but contained ions of K and Mg were able to regenerate new thalli, primarily from adventitious buds that arose from ventral cells in the midrib region. When NO₃ and PO₄ were absent, the ventral layers of cells developed a red-violet color in the walls, reminiscent of the phosphate deficiency in seed plants. Nevertheless, phosphate was needed in very small quantities in *Marchantia polymorpha*. Increasing levels of nitrate increased growth, provided all essential nutrients were present.

Rico-Reséndiz *et al.* (2020a) unravelled the responses to low phosphate in *Marchantia polymorpha* (Figure 1-Figure 12). They found that phosphate starvation elicited the induction of phosphatase activity, acidification of the media, reduction of the internal phosphate concentration, and developmental changes in the rhizoids. Lipid turnover enzymes led to the synthesis of **auronidins** (see below). Up-regulation of certain genes led to changes in organic acid biosynthesis and transport, favoring citric acid exudation. The genes involved in the synthesis of cytokinin are repressed and those involved in auxin and ethylene signalling are upregulated (Rico-Reséndiz *et al.* 2020b). Genes involved in jasmonate synthesis were highly upregulated, but those involved in jasmonate signalling did not change their expression. It appears that auxin and ethylene act as positive regulators in rhizoid development when phosphate is limited, possibly increasing surface area for potential phosphate absorption. Cytokinin, on the other hand, may act as a negative regulator. These observations revealed diverse strategies that contribute to the ability to cope with low phosphate levels.

Voth (1941, 1943) compared various nutrient solutions on *Marchantia polymorpha* (Figure 1-Figure 12) growth. It is interesting that vegetative growth was favored by different concentrations than were gemmae cups. Furthermore, gemmae cups are in greater number on male plants compared to female plants, with a ratio of 1.44 to 1.0. High salt concentrations caused the growing tips to die and the thalli to become translucent. In low salt concentrations, "anthocyanin" (probably auronidin; see Albert *et al.* 2018; Kubo *et al.* 2018) was produced, along with numerous rhizoids and a sturdy plant body with thicker cell walls. Presumably the assumption of anthocyanin was due to a red coloration.

Absence of K (potassium) in the medium causes development of tan-colored bases on the plants and narrower tips (Voth 1941). Absence of Ca causes nearly immediate death of the growing tips. Both nitrate and phosphate deficiency cause reddening of the scales (Figure 60-Figure 61), rhizoids, and lower epidermis.

Miller *et al.* (1962a) developed methods to obtain nutritionally deficient mutants of *Marchantia polymorpha* (Figure 1-Figure 12). At that time, even few mutants of tracheophytes had been created for that purpose. Nevertheless, little has been published on nutrient deficiency symptoms in bryophytes.

Takio (1987) reported nitrate reductase activities in extracts from cultured cells of *Marchantia polymorpha*

(Figure 1-Figure 12) growing in a medium with only nitrate as a nitrogen source. They found that the liverworts differed from the mosses in using NADPH as the electron donor, whereas the mosses used NADH. The coenzyme requirement also differed from that known for the other green plants.

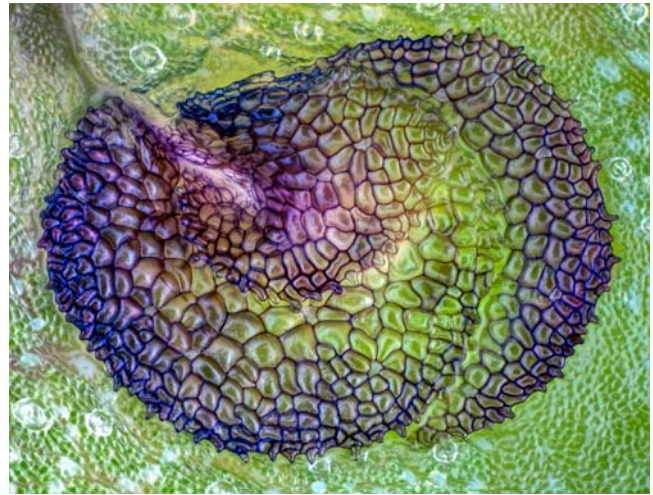


Figure 60. *Marchantia polymorpha* ssp. *ruderalis* scales showing purplish color that could develop as a deficiency symptom or possibly help to reflect the green light back to the chloroplasts. Photo by Des Callaghan, with permission.

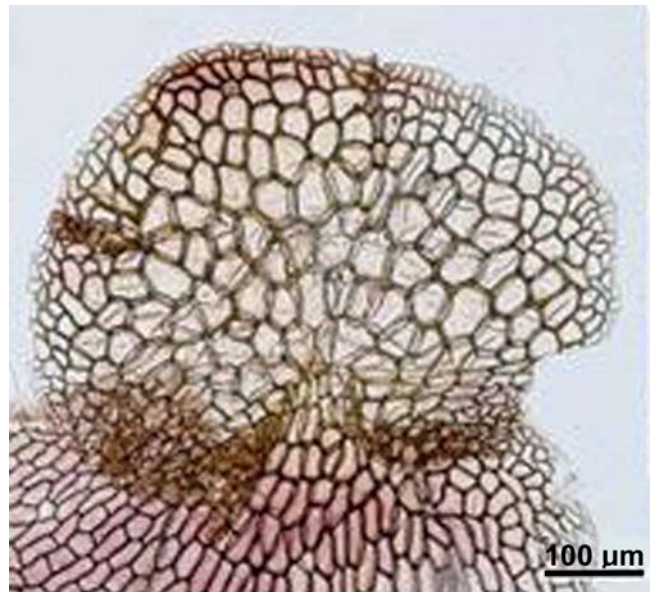


Figure 61. *Marchantia polymorpha* ventral scale and epidermis showing reddening that is typical of phosphate or nitrate deficiency. Photo by Masaki Shimamura, with permission.

Not all nutrients are inorganic compounds. Some of these are organic. Dunham and Bryan (1968) found that *Marchantia polymorpha* (Figure 1-Figure 12) is able to use a number of different nitrogenous compounds. They tested 24 compounds and found that nine of these had any effect on normal development. Among these, l-isoleucine, l-leucine, l-methionine, and l-threonine caused a disruption of the apical regions at concentrations of 10⁻³ M. At even lower concentrations, l-arginine, l-histidine, l-hydroxyproline, l-lysine, and l-tryptophan each caused morphological irregularities that were highly specific to the

amino acid. The modifications ranged from lack of development of the air chambers to complete thallus disorganization. The effects were dependent on the concentrations of the amino acids. This negative interaction raises questions about the role of compounds released by the decomposition of leaf litter in the environment in interfering with the growth of at least some bryophytes.

Effects of nutrients can differ between males and females of *Marchantia polymorpha* (Figure 1-Figure 12). Males with abundant nitrates produce many gemmae cups, narrower thalli, and incurved margins. Female plants in these conditions produce fewer cups, have broader thalli, and plant surfaces remain flat.

Bryophytes grow in strange places and on strange substrata. Walkinshaw *et al.* (1970) tested *Marchantia polymorpha* (Figure 1-Figure 12) among the plants used to see the effects of lunar rocks on plant growth. They found that this liverwort grew several times larger than normal and had enhanced pigmentation when grown on media enriched with lunar rocks. Hoffman (1974) tested the effects of finely ground ilmenite basalt and loam-textured C-horizon substrate that was rich in volcanic ash, mixtures that closely resemble lunar samples from the Apollo 11 mission, on the growth of *Marchantia polymorpha*. The moon rock was already known to stimulate the growth of *M. polymorpha*. Analyses of the two Earth volcanic soil types suggested that the growth stimulus resulted from additional nutrients present in the basalt or volcanic ash.

heavy metals and pollution

For most nutrients, high concentrations become lethal. This is particularly true for heavy metals (Wu & Bradshaw 1972; Ares *et al.* 2018). These are often needed in small quantities in enzymes, but soon become toxic at higher quantities.

For this reason, bryophytes, including *Marchantia polymorpha* (Figure 1-Figure 12Figure 23), are suitable organisms to indicate heavy metal pollution (Maschke 1981). Coombes and Lepp (1974) examined the effects of zinc and copper on gemmalings of *Marchantia polymorpha*. Copper proved to be more toxic than zinc, inhibiting gemmaling growth at levels above 8 ppm. Zinc actually had little effect on the gemmalings.

Ares *et al.* (2018) examined the physiological responses of *Marchantia polymorpha* (Figure 1-Figure 12) to Cd, Cu, Pb, and Zn. Under high concentrations, there was a significant enrichment and translocation of Cu, Zn, and especially Cd, achieving a concentration of 1800 $\mu\text{g g}^{-1}$ in three weeks. On the other hand, Pb achieved the lowest concentration (50 $\mu\text{g g}^{-1}$), with 90% of the total concentration in the rhizoids. Ozkem *et al.* (2019) further found that when *Marchantia polymorpha* was exposed to elevated levels of CuCl_2 , ZnCl_2 , and $\text{Pb}(\text{NO}_3)_2$ it experienced a significant reduction in chlorophyll content.

Both zinc and copper are toxic to the gemmalings of *Marchantia polymorpha* (Figure 1-Figure 12), with copper being more effective (Coombes & Lepp 1974). At levels of copper above 8 ppm *M. polymorpha* gemmalings exhibited greatly reduced growth. Other morphological changes also occurred.

Lepp and Roberts (1977) found that cadmium at levels above 5 ppm had negative impacts on gemmaling growth

of *M. polymorpha* (Figure 1-Figure 12). Furthermore, respiration rates diminished with increasing Cd levels. Gekeler *et al.* (1989) found that *M. polymorpha* produces two phytochelatin when exposed to cadmium.

Samecka-Cymerman *et al.* (1997) summarized previous studies on heavy metals, noting that the concentrations of elements in the liverworts they studied, including *Marchantia polymorpha* (Figure 1-Figure 12), correlate positively with the concentrations of elements in the soil. Some, such as cobalt, surpass the background values found in most bryophytes, indicating the ability of the bryophytes to accumulate them. Some elements, such as Fe, Co, Pb, and Cu, caused an ionic imbalance in this liverwort and others.

Iron is sometimes considered a micronutrient and sometimes a macro nutrient. *Marchantia polymorpha* (Figure 1-Figure 12) uses reduction-based iron acquisition. Under deficiency conditions, growth of this species is reduced. Activity of ferric chelate reductase is increased and proton ATPase becomes active (Lo *et al.* 2016).

Manganese is needed in photosynthesis where it catalyzes the water-splitting reaction, but excess Mn creates metal stress. In *Marchantia polymorpha* (Figure 1-Figure 12) excess Mn causes a strong accumulation of N-methylalanine, a response differing from that of tracheophytes (Messant *et al.* 2022). When the concentrations of Mn were not optimal, the ratio of photosystem I to PSII changed and the organization of the thylakoid membranes was altered. This is important in photoprotection. The deficiency of Mn favors cyclic electron flow around PSI, thus protecting PSII against photoinhibition.

As demonstrated by the **bryometer** (air bags holding bryophytes), pollutants such as SO_2 , oxidants, NO, and NO_2 can cause severe toxicity to *Marchantia polymorpha* (Figure 1-Figure 12) on the leeward side of a pollution source, resulting in the lowest growth rate in the area (78%) (Yokobori 1978; Yokobori & Taoda 1980).

responses to abiotic stress

Fujita *et al.* (2006) pointed out that much of the research on molecular mechanisms that cope with stress in plants have been carried out independently. Hence, our understanding of the evolutionary relationships and convergence points between biotic and abiotic stress signaling pathways remains very incomplete. More recently, evidence is emerging that suggests that hormone signaling pathways regulated by abscisic acid, ethylene, jasmonic acid, and salicylic acid, in addition to ROS-signaling pathways, play important roles in the crosstalk between biotic and abiotic stress signaling.

Marchantia polymorpha (Figure 1-Figure 12) has a large repertoire of responses to environmental changes (Spinedi *et al.* 2021). In response to anthracene, they found an increase in the activity of main ROS-detoxifying enzymes of 34.09% of peroxidase and 692% of ascorbate peroxidase, supported at transcriptional level with the up-regulation of ROS-related detoxifying responses. The net result was the activation of antioxidant mechanisms and the accumulation of the anthracene pollutant within the plant tissues.

Hirata *et al.* (2000) used bornyl acetate as a chemical stressor of *Marchantia polymorpha* (Figure 1-Figure 12).

In response, the liverwort produced peroxidase. This is a glycoprotein that is stable at temperatures as high as 50°C for up to one hour, suggesting that the liverwort might have protection against the increasing temperatures of climate change. Its optimum pH is 6.5, which does not bode well for the dangers of acid rain. The peroxidase appears to be unlike any of those known from tracheophytes.

Hydrogen peroxide (H₂O₂) often has a protective role in plants. It forms in *Marchantia polymorpha* (Figure 1-Figure 12) in the presence of MnCl₂. Its production is also stimulated by phenols such as 2,4-dichlorophenol (a 2,4-D precursor) or *p*-coumarate, both processes similar to the last step in lignification, suggesting that while bryophytes apparently lack lignin, they already had a large part of the process required for its production. Phenols are important substances in antiherbivory in bryophytes.

Bryophytes are often resistant to stresses that can kill tracheophytes. Merwin (2003) found that herbicides designed for long-term use on tracheophytes actually promoted the growth of *Marchantia polymorpha* (Figure 1-Figure 12). They furthermore were resistant to the human traffic in the orchard.

Measurements of impedance can be a tool to determine health of small plants like *Marchantia polymorpha* (Figure 1-Figure 12). Bulanda (1980) Researchers have used this species to develop and test the efficacy of a method for measuring the resistance and capacity of the thallus, based on previous methods for measuring these in cell suspensions (Bulanda 1980; Paszewski *et al.* 1982).

radiation damage

A need to understand radiation damage arose as we began to explore space and to use radiation for energy. Typically, the effects on the nucleus were used to assess such damage (Miller & Sparrow 1964). One generalization that arose indicated that cells with smaller nuclei had more resistance to the radiation than did those with large nuclei. Using *Marchantia polymorpha* (Figure 1-Figure 12) Miller and Sparrow found that a more accurate indicator was the nuclear volume (at interphase) divided by the chromosome number. Miller *et al.* (1965) found that larger nuclei in gemmae exhibited inhibition at lower levels of radiation than did smaller nuclei.

Sarosiek and Wozakowska-Natkaniec (1967) demonstrated that chronic gamma radiation caused inhibition of the development of sex organs in *Marchantia polymorpha* (Figure 1-Figure 12).

One of the tools used in assessing effects of such things as X-rays is to use mutants (Miller *et al.* 1962a, b). Bryophytes, particularly *Marchantia polymorpha* (Figure 1-Figure 12), are particularly suitable for this because of their haploid condition. Miller and coworkers used the method to obtain nutritionally deficient mutants, a condition that could affect the response to radiation.

CO₂

The current atmosphere has a CO₂ concentration of about 0.0415% (415 ppm) (Climate.gov, accessed 21 September 2022). But it seems that most of the studies on CO₂ effects on the physiology of *Marchantia polymorpha* have been done at much higher levels.

Katoh *et al.* (1979) found that in 1% CO₂ *Marchantia polymorpha* (Figure 1-Figure 12) had a dry-weight doubling time of 1.76 days. The increase rate of chlorophyll was 1.6 times that of the growth rate. In the exponential phase of growth, the photosynthetic activity was at least 60 μmol mg⁻¹ chl h⁻¹. The highest chlorophyll content they recorded was 24 mg g⁻¹ dry weight.

Bockers *et al.* (1997) compared responses of *Marchantia polymorpha* (Figure 1-Figure 12) to two levels of CO₂. At the higher concentration (2.0%), the chloroplast shape seemed modified and there were 70% more chloroplasts per cell than at 0.4%. However, the chlorophyll content per cell indicated a reduction in chlorophyll per chloroplast. Furthermore, the cell size was about 37% lower in the higher CO₂ concentration. The net result was that the photosynthetic oxygen evolution was about the same under both conditions.

Marchantia polymorpha (Figure 1-Figure 12) has a C₃ pathway (Hanson *et al.* 2002), as do all bryophytes. Its growth form is a thallus, similar to that of hornworts. Its CO₂ compensation point (CO₂ concentration at which photosynthetic rate = respiration rate) was 64 ppm (Hanson *et al.* 2002), whereas the hornwort *Megaceros* (Figure 62), a genus lacking pyrenoids (Villarreal & Renner 2012), had a compensation point of 31 ppm (Hanson *et al.* 2002). On the other hand, *Notothylas* (Figure 63) and *Phaeoceros* (Figure 64), both with pyrenoids, had compensation points of 11-13 ppm CO₂. Those species lacking pyrenoids had more RuBisCo content, permitting them to increase their carboxylation catalytic rate (*Marchantia*, 2.6 s⁻¹; *Megaceros*, 3.3 s⁻¹; *Phaeoceros*, 4.2 s⁻¹; *Notothylas* 4.3 s⁻¹). *Marchantia polymorpha* had the highest percentage of RuBisCo per soluble protein (8%), *Megaceros* followed (4%), and the pyrenoid-containing species had only 3%.

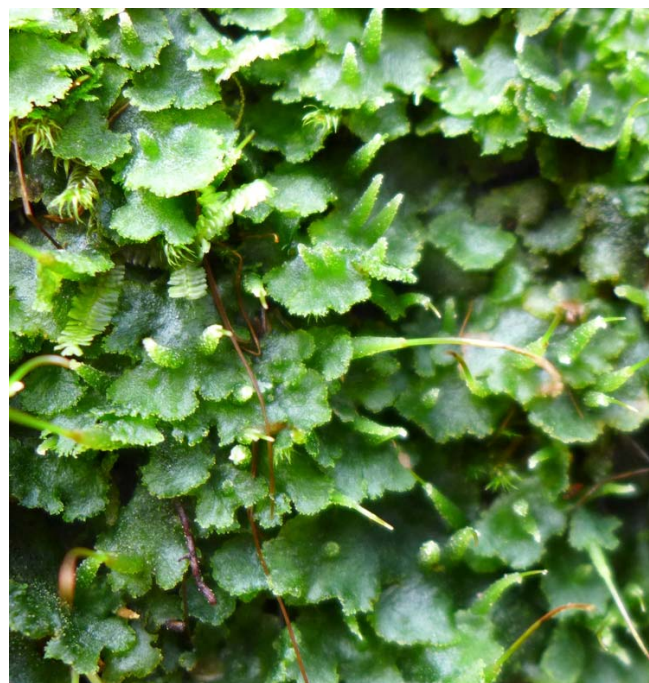


Figure 62. *Megaceros flagellaris*, a hornwort species that lacks pyrenoids and has a lower CO₂ compensation point than does *Marchantia polymorpha*. Photo by Scott Zona, through Creative Commons.



Figure 63. *Notothylas orbicularis*, a hornwort species that has pyrenoids and has a CO₂ compensation point that is lower than that of *Marchantia polymorpha* (liverwort) or *Megaceros* (hornwort with no pyrenoids). Photo from One Thousand Plant Transcriptomes Initiative, through Creative Commons.



Figure 64. *Phaeoceros carolinianus* with capsules, a species that has pyrenoids and has a CO₂ compensation point that is lower than that of *Marchantia polymorpha* or *Megaceros* (with no pyrenoids). Photo by Hermann Schachner, through Creative Commons.

photosynthesis

Katoh (1983a) grew a cell line of *Marchantia polymorpha* (Figure 1-Figure 12) in suspension culture, using 1% CO₂. He found a growth rate in the exponential phase of 0.171 and a doubling time of 1.76 days. The rate of chlorophyll increase was 1.6 times higher than the growth rate. The cells reached their highest chlorophyll content at 24 mg g⁻¹ dry weight in their exponential phase, with at least 60 μmol mg⁻¹ chlorophyll h⁻¹.

Katoh (1983b) considered the inability of cells of *Marchantia polymorpha* (Figure 1-Figure 12) in suspension culture to grow in the dark to be the result of low respiration. In the light, the respiration increased to four times that in the dark. The compensation ratio

(photosynthetic rate/respiration rate) was less than 1.0 during the growth period. Furthermore, these cells are unable to grow anaerobically in light in the absence of CO₂. Addition of 1% CO₂ permitted the liverwort to sustain growth. They found that at least one-third of the cellular carbon came from atmospheric CO₂.

light

Fredericq (1964) tested the influence of far-red light on thallus development in *Marchantia polymorpha* (Figure 1-Figure 12). Rethy *et al.* (1976) explored the effects of different light treatments on chlorophyll content in *Marchantia polymorpha*.

Courtoy (1965-1966) experimented with light regimes on the germination and development of gemmae of *Marchantia polymorpha* (Figure 1-Figure 12). In artificial light of 4000 lux and 16-hour photoperiod, there were two distinct phases of growth. In the **juvenile phase**, requiring at least 15 days, light quality was unimportant. Adding sucrose in the juvenile phase reduces the phase to 5 days. In the **inductive phase**, when primordia appear, incandescent light permits development, suggesting the importance of red wavelengths.

Mache and Loiseaux (1973) found that the maximum growth rate of *Marchantia polymorpha* (Figure 1-Figure 12) in low light was at 2-3 x 10³ lux, its saturation level. In optimal conditions, photosynthetic rates reach as high as 35 μM CO₂ h⁻¹ mg⁻¹. High light inhibited the photosynthetic rate, with small grana in the chloroplasts and fret membranes being replaced by continuous grana.

Carter and Nickell (1967) experimented with the effects of wavelengths of light on both thallus growth and gemmae cup production. Using 16-hr light:8 hr dark at 21°C day:13°C night, they incubated 4 gemmae per Petri dish. After 11 weeks the controls with no colored acetate had produced a mean of 32.7 cm² of thalli and 83.3 gemmae cups per dish. Dishes with single-wrapped red acetate produced only 16.11 cm² of thalli (Figure 65) and 19.83 gemmae cups per dish (Figure 66). On the other hand, double-wrapped red dishes produced 17.5 cm² of thalli and 8.25 gemmae cups, suggesting that the lower light inhibited production of gemmae cups, putting more of the available resources into thalli. Those in single-layered green dishes produced 14.8 cm² of thalli and 8.16 gemmae cups per dish, a response consistent with the greater activity of photosynthesis in the red range. The double green, single blue, and double blue produced a mean of 10.5, 11.5, and 1.2 cm² of thalli respectively, but produced no gemmae cups, again supporting the importance of red light.

Aro (1982) used *Marchantia polymorpha* (Figure 1-Figure 12) to show that bryophytes had more chlorophyll associated with their light-harvesting protein complexes and less with reaction center complexes than did tracheophytes. Furthermore, the tracheophytes had a chlorophyll *a:b* ratio of 3, whereas it was only 2 in the bryophytes. These figures indicate that the bryophytes are shade plants, having proportionally more chlorophyll *b* when compared to that of tracheophyte sun plants.

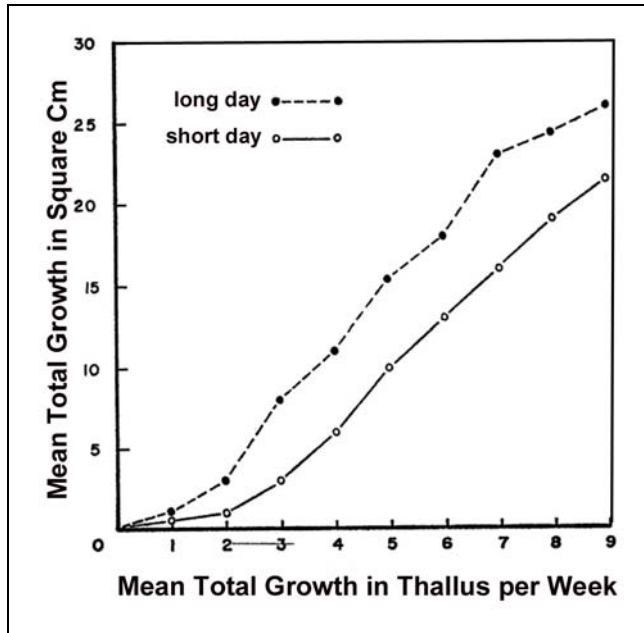


Figure 65. *Marchantia polymorpha* growth in long and short photoperiods. Image modified from Carter & Romine 1969.

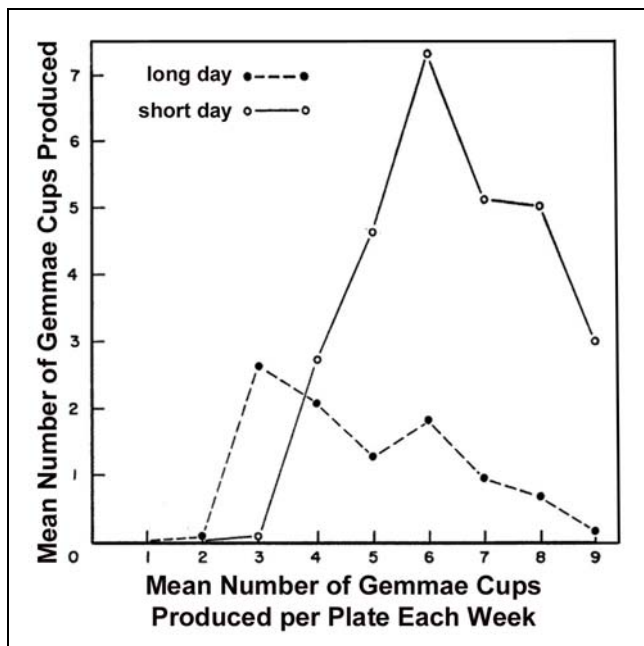


Figure 66. *Marchantia polymorpha* gemmae cups per week in long and short days. Modified from Carter & Romine 1969.

In further studies, Aro *et al.* (1981) determined that the plastid ultrastructure of the sun species *Ceratodon purpureus* (Figure 67) was characteristic of a sun plant, whereas in *Marchantia polymorpha* (Figure 1-Figure 12) it was characteristic of a shade plant. Nevertheless, both species exhibited photosynthetic kinetics typical of shade plants.



Figure 67. *Ceratodon purpureus* with young sporophytes, a sun species with plastid ultrastructure of a sun plant, but with photosynthetic kinetics of a shade plant. Photo by Claire Halpin, with permission.

Shinmen *et al.* (1991) determined that *Marchantia polymorpha* (Figure 1-Figure 12) produced arachidonic acid (ARA) and eicosapentaenoic acid (EPA) in cell culture. During high growth rate conditions the cells produced high quantities of both acids, with 98 mg L⁻¹ of arachidonic acid and 48 mg L⁻¹ of eicosapentaenoic acid. Kajikawa *et al.* (2004) isolated and characterized the genes behind the production of these acids in *Marchantia polymorpha*. The role of arachidonic acids in cold weather has already been discussed. Eicosapentaenoic acids are known for their antifungal effects against plant pathogens (Bajpai *et al.* 2008). Both of these compounds seem to be essential in the wounding response forming volatiles in *Marchantia polymorpha* (Kihara *et al.* 2014). Eight-carbon volatiles form rapidly (within 40 minutes) of wounding.

Kajikawa *et al.* (2008) reported that *Marchantia polymorpha* (Figure 1-Figure 12) synthesizes arachidonic acid and eicosapentaenoic acid. By causing the overexpression of the involved genes, they produced 3-fold and 2-fold accumulation of these two acids, respectively. They were able to transplant these genes to tobacco and soybean, a feat that suggests that *M. polymorpha* can provide genes for transplantation to tracheophytes and provide them with desirable traits.

Later, Takemura *et al.* (2011) elucidated some of the physiological mechanisms involved in the observed effects of light quality and intensity on these acids. They noted that *Marchantia polymorpha* (Figure 1-Figure 12) synthesized both arachidonic acid (AA) and eicosapentaenoic acid (EPA), polyunsaturated fatty acids that are not known in tracheophytes. They found that the relative content of EPA to total fatty acid was highest under blue light, but that of AA did not vary. EPA content also increased under higher intensity white light. They found that 80 photon flux density $\mu\text{mol m}^{-2} \text{s}^{-1}$ was the optimum intensity for both AA and EPA accumulation.

Harrer (2003) demonstrated that *Marchantia polymorpha* (Figure 1-Figure 12) has the same structure of the PS II-light-harvesting assembly as that of seed plants. They provided the first 3-d structure for such a large assembly by using this liverwort.

Marchantia polymorpha (Figure 1-Figure 12) was used in a study to describe the polyphasic rise of chlorophyll fluorescence at the onset of strong continuous light. Neubauer and Schreiber (1987) described the saturation characteristics and partial control by photosystem II.

In low light, bryophytes can exhibit etiolation. Ninnemann and Halbsguth (1965) elucidated the role of phytochrome in etiolation of ***Marchantia polymorpha*** (Figure 1-Figure 12). Ninnemann (1967) then described the growth substances, phytochrome, nucleic acid, and protein synthesis involved in the etiolation of the gemmae of ***Marchantia polymorpha***.

Rao *et al.* (1979) described the Hill reaction rates of three members of the Marchantiales, including ***Marchantia polymorpha*** (Figure 1-Figure 12). Using three different measures of the Hill reaction activity, they determined that the rate was lower in the three liverworts than in the seed plants tested. Furthermore, they also found lower total chlorophyll content and chlorophyll *a:b* ratio, all supporting the shade adaptation of these plants. They found that the greatest labelled ^{14}C occurred in the amino acids aspartate and alanine. ***Marchantia polymorpha*** exhibited higher photosynthetic rates than the other species in the test.

Maximum polyunsaturated fatty acids (PUFA) productivity is attained in ***Marchantia polymorpha*** (Figure 1-Figure 12) under low light intensity, with a photon flux density ca. $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Chiou *et al.* 2001). Optimal inoculum size and glucose concentration for PUFA production are 8-12% and 2030 g L^{-1} , respectively. Ferrous ions, necessary components of many enzymes, promote PUFA productivity by increasing the intracellular lipid content. The highest productivities measured for PUFA were 35.0 ± 2.1 , for arachidonic acid 6.7 ± 0.4 , and for eicosapentaenoic acid $6.6 \pm 0.4 \text{ mg L}^{-1} \text{ day}^{-1}$.

High light has different effects on ***Marchantia polymorpha*** (Figure 1-Figure 12) from those of low light (Volchenkova *et al.* 2001). It affects the area occupied by the lipid molecule. The digalactosyl diacylglycerol and phosphatidyl glycerol fractions increase significantly after high light stress, increasing from 0.50 to 0.80 nm^2 and from 0.47 to 0.63 nm^2 respectively.

red/far-red

Fredericq and de Greef (1966) examined the red:far-red control on growth and chlorophyll content in thalli of ***Marchantia polymorpha*** (Figure 1-Figure 12) grown in the light. Fredericq and de Greef (1968) followed up on these experiments by subjecting the plants to daily far-red (FR)-irradiations at the end of photoperiods of white fluorescent light. Following the first sequence, at the end of the night, the chlorophyll content of the tips of the thalli was significantly lower than that of the controls lacking the far-red treatment. Instead, upward growth (Figure 68) was beginning.

By the end of the night following the first FR-exposure, the chlorophyll content of the tips was already significantly lower than that of the controls, and there was a beginning of upward growth (Fredericq & de Greef 1968). After 8 hours in white light, those effects had become much more pronounced. After one week, a 5-minute far-red treatment at the end of the photoperiod cause a 20-30%

lower chlorophyll content in the tips after the 8-hour photoperiod in white light. Following a 16-hour photoperiod, the chlorophyll was decreased by $\pm 10\%$. Morphogenic effects also were less pronounced after 16 hours compared to 8 hours of white light. Basal parts of the thalli were less affected than the tips. On the other hand, a 1-hour photoperiod following far-red treatment caused much greater effects on the basal portions than on the tips. If the daily light period was diminished to 5 minutes, it caused drastic bleaching of 60-70% chlorophyll *a* loss compared to controls. Of relevance to the aquatic habitat, de Greef and Fredericq (1969) found that when the incandescent light was filtered through water for 10 minutes, it caused a somewhat weak effect. These responses are similar to those of tracheophytes and indicate that high levels of the PFR form of phytochrome are needed to maintain the horizontal growth and optimal chlorophyll content in these thalli.



Figure 68. ***Marchantia polymorpha*** exhibiting upward growth as it would occur under far-red light at the end of a period of white light. Photo by Vladimir Bryukhov, through Creative Commons.

Among the photoreceptors in ***Marchantia polymorpha*** (Figure 1-Figure 12) and other bryophytes are the phytochromes (Inoue *et al.* 2019). Phytochromes are the only known receptors for red light and far-red light and are therefore important in controlling various developmental processes. The phytochrome Mpphy regulates the formation of gametangioophores, similar to the far-red response of flowering plants. Inoue and coworkers identified the genes responsible for this regulation and demonstrated that the production of Mpphy increases when the gene is multiplied, while disappearing when the gene is deleted.

Another effect of far-red light is to accelerate senescence in ***Marchantia polymorpha*** (Figure 1-Figure 12) (de Greef & Fredericq 1972). Once again, the reversibility indicates the involvement of phytochrome. A daily exposure of only 5 minutes of red light will prevent this aging; photosynthesis plays no direct part in this response.

UV light

When photosynthetic organisms first invaded land, one of the new problems they had to deal with was their introduction to UV light (Jordan *et al.* 2016; Sancha 2017). The levels of UV reaching the Earth's surface at that time were higher than now due to the less-well developed ozone

layer. Therefore, it stands to reason that the surviving bryophytes, previously as early invaders of land, should have mechanisms to protect them from UV radiation. In seed plants, flavonoids are important in this role.

Khetwal (1985) demonstrated the presence of the flavonoid glucuronides apigenin, apigenin-7-O-glucuronide, luteolin, and luteolin-7-O-glucuronide in *Marchantia polymorpha* (Figure 1-Figure 12).

There has been much activity in recent years to determine the effects of increased UV light on bryophytes. Markham *et al.* (1998) found that as they increased UV-B levels, the growth rate of *Marchantia polymorpha* (Figure 1-Figure 12) decreased, the production of gemmae cups (Figure 69) decreased, and the proportion of dead thallus increased. Total flavonoid levels had no statistically significant change, but the ratio of luteolin to apigenin glycosides did increase (Figure 69-Figure 71). The researchers did not consider this to be a means of filtering and protecting the plants from the UV-B, but instead they experienced an improved level of antioxidant defense.



Figure 69. *Marchantia polymorpha* with red edges, perhaps in response to stress. Photo by Brenda Dobbs, through Creative Commons.



Figure 70. *Marchantia polymorpha* with red archegoniophores, perhaps responding to the stress of a cold climate in Laxarbakki, Myvatn, Iceland. Photo by Janice Glime.



Figure 71. *Marchantia polymorpha* with red archegoniophores, from Laxarbakki, Myvatn, Iceland, 26 July 1987. Photo by Janice Glime.

Clayton (2017) looked specifically at flavonoids in *Marchantia polymorpha* (Figure 1-Figure 12) exposed to UV-B radiation and determined that the flavonoids increased when UV-B radiation was enhanced. Flavones were the most predominant, with apigenin-based flavones in highest amounts and luteolin-based flavones second. The ratio shifted toward luteolin-based flavones at the higher UV-B levels. At these UV-B levels, reactive oxygen species (ROS) are produced, and the liverwort may require the luteolin flavones to scavenge these. Under low UV-B exposure, the flavone compounds accumulated in high concentrations in the epidermal layers, suggesting that they might participate in screening the UV-B. When flavone concentrations were lower, greater damage to the thallus occurred. Higher levels of flavones corresponded with greater protection and reduced thallus damage. When flavones were suppressed completely the plants became severely stunted under the UV-B treatment.

Sancha (2017) noted that bryophytes have "remarkable tolerance to UV radiation." Sancha subjected various bryophytes to enhanced UV radiation and found that all, including *Marchantia polymorpha* (Figure 1-Figure 12), showed increased levels of CARUVs (UV-radiation-absorbing compounds), with all being significant except for *Anthoceros agrestis* (Figure 72).



Figure 72. *Anthoceros agrestis*, a hornwort species with increasing, but not significant, UV-radiation-absorbing compounds with increasing of UV intensities. Photo by Hermann Schachner, through Creative Commons.

Soriano *et al.* (2019a) further examined UV damage in *Marchantia polymorpha* ssp. *ruderalis* (Figure 56, Figure 60, Figure 73). They found that liverworts subjected to low photosynthetically active radiation (PAR), low PAR+ UV-A, low PAR + UV-B, low PAR + UV-A + UV-B, and high PAR exhibited no significant difference in the maximum quantum yield of PSII after 35 days. There were no changes in the chl *a/b* ratio and only slight changes in growth. But both chlorophylls and carotenoids decreased in content in the UV radiation treatments and even more strongly in the high-PAR treatment. The xanthophyll index (antheraxanthin + zeaxanthin) / (violaxanthin + antheraxanthin + zeaxanthin) increased only in the high-PAR (Figure 73). On the other hand, the **sclerophylly index** (ratio between thallus dry mass and surface area) increased in the UV-B-exposed treatments, suggesting a UV-induced structural protection. Only the UV-B treated liverworts exhibited DNA damage.



Figure 73. *Marchantia polymorpha* ssp. *ruderalis* showing red bases, perhaps in response to high UV levels. Photo by Malcolm Storey <www.DiscoverLife.com>, with online permission.

In further studies, Soriano *et al.* (2021) found that the developmental stage was important in determining the accumulation of UV-absorbing compounds in *Marchantia polymorpha* ssp. *ruderalis* (Figure 56, Figure 60, Figure 73). They compared gemmae (Figure 69), one-month thalli, and two-month thalli after 38 days of exposure or non-exposure to UV radiation. They found that the UV responsiveness decreased with thallus age, with gemmae being the most responsive. Older thalli became progressively tougher in UV due to decreasing water content, possibly providing structural protection. Most phenolic compounds decreased with thallus age, but diglucuronide derivatives were highest in the 1-month thalli.

Close and McArthur (2002) contend that phenolics have the primary function of protecting plants from photodamage, not from herbivores as originally thought.

Kondou *et al.* (2019) reported that MpUVR8 provides physiological benefits in UV-B resistance in *Marchantia polymorpha* (Figure 1-Figure 12). It is highly expressed in

the apical notch (Figure 20) of the thalli and gametangiophores, including the antheridial and archegonial heads. In this species, citrine-fused MpUVR8 was translocated from the cytosol into the nucleus when exposed to increased UV-B radiation.

Ultraviolet light was a major stress to be overcome when plants first invaded land (Clayton *et al.* 2018). The *Marchantia polymorpha* (Figure 1-Figure 12) UVB response included many components already known from *Arabidopsis* (Figure 52), including production of UVB-absorbing flavonoids, the central activator role of ELONGATED HYPOCOTYL5 (HY5), and negative feedback regulation by REPRESSOR OF UV-B PHOTOMORPHOGENESIS1 (RUP1). Important differences included a greater importance for CHALCONE ISOMERASE-LIKE (CHIL). Mutants that disrupted the response pathway or flavonoid production were more easily damaged by UV-B than normal plants, whereas mutants that increased the flavonoid content exhibited increased UV-B tolerance.

Kondou *et al.* (2019) determined that UV-B resistance and the translocation of the UVR8 from the cytosol to the nucleus was operational in *Marchantia polymorpha* (Figure 1-Figure 12) in response to UV-B radiation. This series of events is highly expressed in the apical notch of the thalli and in the gametangiophores and receptacles.

fluorescence

It is widely known that chlorophyll fluoresces. The degree of fluorescence is a measure of the health of the plant. Shi *et al.* (1992) described two categories of fluorescence emission from bryophytes. *Marchantia polymorpha* (Figure 1-Figure 12) exhibits maximum emission around 725 nm. The fluorescence kinetics of primitive bryophyte photosynthesis, including *M. polymorpha*, exhibited lower PS II activity, lower efficiency of primary photoconversion in PS II, and lower photosynthetic C assimilation and efficiency than did the advanced bryophyte species.

photoperiod

Photoperiod is known to control various events in the life of a plant. Differences in response to photoperiod can keep closely related species from interbreeding by bringing reproductive parts to maturity at different times (see Reproduction section below), while taking advantage of the climatic conditions at the optimum time for the event.

Marchantia polymorpha (Figure 1-Figure 12) grown in a long photoperiod (18 hours daylight) are larger and have greater dry weight than those grown in a short photoperiod (9 hours daylight) (Voth & Hamner 1940; Carter & Romine 1969). Short photoperiods favor production of gemmae (Figure 69, Figure 153-Figure 170), whereas long photoperiods favor the production of gametangiophores.

Benson-Evans (1961) found that photoperiod influences the number of gametophores, and like Carter and Romine, found that longer days (16 hrs light) result in greater thallus size and fewer gemmae cups, but a faster production of the cups.

tropisms

A little-studied area of bryophyte physiology is tropisms. Yet the ability to grow in response to the

direction of light and gravity is of considerable adaptive importance to most bryophytes.

There is a long history of studies on rhizoid tropisms in *Marchantia polymorpha* (Figure 1-Figure 12). Haberlandt (1889) noted **positive gravitropism** (originally known as geotropism; growing toward the gravitational pull) in the apical rhizoids of *Marchantia polymorpha*. Weinert (1909) investigated rhizoid tropisms and growth in liverworts, including *Marchantia*. Rawitscher (1932) reviewed the tropisms in this species. Douin (1936) reported that the thallus exhibited photogravitropism. But Miller and Voth (1962) experimented with various orientations of the thalli and found that the rhizoids would securely anchor the thalli no matter what position the plant held, contrasting with the view held by Haberlandt (1889). Perhaps this is explained by the behavior I observed in *Fontinalis*. The rhizoids initially grow away from the plant and use a spiral growth pattern. However, once a rhizoid contacts a substrate, it branches and secures the plant to the substrate. I am not aware that this behavior has been observed in *Marchantia polymorpha*, but such behavior has not been disproved either.

So what does a gemma cup do when its parent plant is attached to a vertical surface? Miller and Voth (1962) observed that initially the cup exhibits no tropism, growing in a perpendicular alignment with its thallus. But when it develops the achlorophyllous scale-like rim of the cup, this is negatively gravitropic, permitting the cup to become upright with respect to gravity.

Rethy *et al.* (1990) described the role of far-red illumination in tropisms of *Marchantia polymorpha* (Figure 1-Figure 12). It causes greater cell elongation on the ventral side of the thallus just below the apical notch, causing upward growth, whereas red light reverses the reaction.

Komatsu *et al.* (2019) demonstrated that under low light both sporelings and thalli of *Marchantia polymorpha* (Figure 1-Figure 12) develop narrow shapes and their apices grow toward the light source. These responses are blue-light dependent and respond to **phototropin** (photoreceptor protein; flavoproteins).

temperature

Somehow, this fleshy liverwort manages to survive winter, even when covered by snow (Figure 74). Exact responses to temperature at the cellular level have been a puzzle. *Marchantia polymorpha* (Figure 1-Figure 12) serves as a model system to unravel these responses (Hirano *et al.* 2022). Chloroplasts respond to cold by changing positions, optimizing photosynthesis. This response is triggered by the blue-light photoreceptor phototropin, the cold-sensing molecule. This sensor is present in the plasma membrane, cytosol, Golgi apparatus, and periphery of the chloroplast. By using genetic variants, Hirano and coworkers demonstrated that the cold response originates with the phototropin in the plasma membrane, at least in this liverwort.

Antropova (1974) included *Marchantia* in studies on temperature adaptations in bryophytes. He incubated the bryophytes at 10 and 20°C for 72 hours. But this period of time does not influence either thermostability or cold resistance. A treatment of 3 hours at superoptimal temperatures does cause an increase in thermostability, but

no change in cold resistance. The behavior of the bryophytes was similar to that of flowering plants but differed from the temperature acclimation of algae.



Figure 74. *Marchantia polymorpha* in snow; note how dry the thallus appears, a condition that reduces damage from interior ice crystals. Photo by Vladimir Teplouhov, through Creative Commons.

But experiments by Weis *et al.* (1986) differed. Using *Marchantia polymorpha* (Figure 1-Figure 12) and other thallose liverworts, they found that high temperature treatment elicited a reversible depression of photosynthesis. The time required to achieve complete recovery depended on the extent of the heat damage. With severe heat treatment, PS II was damaged and inactivation of photosynthesis was irreversible. Unlike Antropova, Weis and coworkers found that exposure of these thallose liverworts to high sublethal temperatures did not result in the significant increase in heat stability of the photosynthetic apparatus as had been seen in seed plants. They interpreted this to mean that the heat hardening capacity of water-loving liverworts was extremely low.

Fletcher (1982) found no frost damage to *Marchantia polymorpha* (Figure 1-Figure 12) in cultivation in New Zealand populations. Some of the other species of thallose liverworts became severely bleached or blackened in greenhouse cultivation down to -5.5°C. The *M. polymorpha*, on the other hand, remained a healthy green all winter.

Response to heat appears to be more complicated. It involves several subcellular compartments as well as multi-level regulatory networks (Marchetti *et al.* 2021). Studies on *Marchantia polymorpha* (Figure 1-Figure 12) indicate that the core components of the response are conserved from bryophytes to flowering plants.

Temperature affects the relative production of fatty acids in *Marchantia polymorpha* (Figure 1-Figure 12) (Saruwatari *et al.* 1999). At 25°C this liverwort contained approximately 18% linolenic acid (18:3 ω 3), 11% arachidonic acid (20:4 ω 6) and 3% eicosapentaenoic acid (20:5 ω 3) as percentages of total fatty acids. At 15°C, the ratios of linolenic acid and arachidonic acid increased greatly, with less effect on the other acids. Arachidonic acid and eicosapentaenoic acid increased in the chloroplast but not elsewhere in the cell. Linolenic acid increased in

both fractions. Various galactolipids were present in one or the other or both compartments, but only monogalactosyldiacylglycerol and chloroplastic phosphatidylcholine increased in low temperatures. Gellerman *et al.* (1972) found that *Marchantia polymorpha* had arachidonic acid in all tissues, ranging 10-30% of the total fatty acids.

Takemura *et al.* (2012) likewise reported the production of arachidonic acid and eicosapentaenoic acid in *Marchantia polymorpha* (Figure 1-Figure 12), noting that neither is produced in tracheophytes. The accumulation of ω -3 polyunsaturated fatty acids increased significantly as the temperature decreased. At 5°C the concentration was approximately 3x that at 15°C. ω -6 polyunsaturated fatty acids, on the other hand, decreased at low temperatures.

Akter *et al.* (2011) acknowledged the role of ABA in both desiccation tolerance and freezing. This dual role is not surprising since one of the dangers of freezing is desiccation as ice crystals draw water out of the cell or make the water unavailable as ice. Akter and coworkers found that isolated gemmae (Figure 153-Figure 170) of *Marchantia polymorpha* (Figure 1-Figure 12) responded to increased ABA by increasing the sucrose concentration. These treated gemmae survived freezing, whereas most of the controls did not. The best survival occurred with 5% sucrose and 19 μ M ABA.

Takeuchi *et al.* (1980) even found a successful method for freezing *Marchantia polymorpha* (Figure 1-Figure 12) for cryopreservation.

The movement of organelles in response to stress is seldom discussed. In response to a cold treatment, *Marchantia polymorpha* (Figure 1-Figure 12) sporelings and gemmalings nuclei and peroxisomes relocated from the **periclinal cell wall** (wall parallel to surface of meristem or surface of organ; Figure 75) to the **anticlinal cell wall** (wall arranged perpendicular to surface of plant body; anticlinal division results in formation of anticlinal walls between daughter cells, enabling tissue to increase circumference, thus keeping pace with any increase in girth of organ; Figure 75) (Ogasawara *et al.* 2013). Mitochondria, on the other hand, did not relocate.

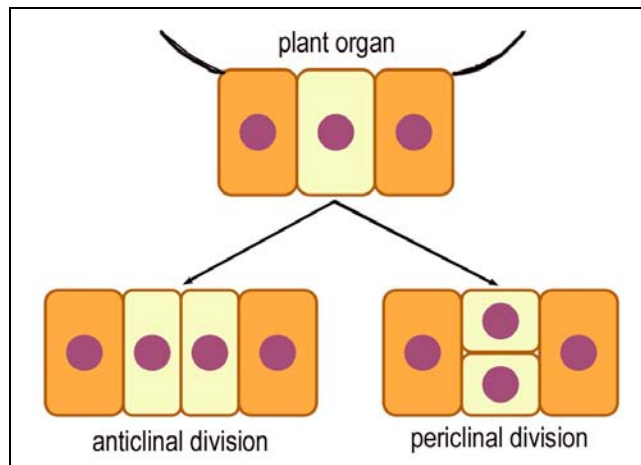


Figure 75. Comparison of anticlinal and periclinal divisions. Drawing modified from The Science of Plants, Meristem Morphology, Open Library <open.lib.umn.edu>.

senescence

Sometimes it seems like bryophytes never die. They just keep growing at the top while lower portions remain and may even decay. But **senescence** (process of aging) does indeed occur. Stanislaus and Maravolo (1994) examined cell factors that influenced senescence. They found light-induced senescence in young, middle-aged, and old tissues of *Marchantia polymorpha* (Figure 1-Figure 12) all exhibited suppressed senescence in treatments with spermine, spermidine, and putrescine. Not surprisingly, ethylene induced senescence in these tissue ages, an effect that could be retarded by putrescine, a compound they tentatively identified in *M. polymorpha* extracts.

LaBelle *et al.* (1997) identified two isophosphatases in senescing *Marchantia polymorpha* (Figure 1-Figure 12) thalli. They found that spermine reduced total phosphatase activity by 135-175%. Ethylene, on the other hand, reduced it by 133-155%. When ethylene and spermine were added together, they decreased the activity by 120-163% compared to the levels with the ethylene treatment alone. LaBelle and coworkers interpreted these findings to indicate that phosphatase and ethylene are associated with senescence. Spermine, on the other hand, functions in preventing senescence.

It may seem inconceivable to a bryologist, but *Marchantia polymorpha* (Figure 1-Figure 12) is not always a welcome visitor in a garden (Figure 76). Altland *et al.* (2008) found that quinclamine can serve as both a PRE and POST activity herbicide at 4-6 mg L⁻¹. It could inhibit PRE germination in gemmae (Figure 153-Figure 170), but its ability to stay on the substrate made it increase the efficacy of other kinds of treatments.

Aging brings a variety of responses in plants. Maravolo (1976) found that transport, a function especially of the midrib, was inhibited by aging, cinnamic acid, and ethylene in *Marchantia polymorpha* (Figure 1-Figure 12).

Seaman *et al.* (2005) examined the role of spermine in programmed cell death of *Marchantia polymorpha* (Figure 1-Figure 12). They found that PKC (protein kinase C) concentrations in untreated young thalli were higher than those of older tissues. PKC refers to a family of protein kinase enzymes involved in a variety of signal transduction pathways (Blumberg 1991). PKC enzymes play important roles in several signal transduction cascades. When Seaman and coworkers treated older tissues with spermine, they also had higher cytosolic putative PKC concentrations than even the young untreated thalli. The spermine also resulted in higher total protein levels than untreated tissues. Hence, it appears that the spermine causes both qualitative and quantitative decreases in senescence.

One of the consequences of spermine is to reduce DNA fragmentation, as demonstrated in *Marchantia polymorpha* (Figure 1-Figure 12) (Pagoria & Maravolo 2005). The fragmentation is localized near the lower epidermis of the apical meristem. From there it progresses into the mesophyll cells. However, when these plants were treated with 100 μ M spermine, they exhibited significantly lower ($p < 0.001$) levels of DNA fragmentation in aged (2-5 cm) tissues.



Figure 76. *Marchantia polymorpha* females in garden in Houghton, Michigan, USA. So far we have been unable to find any males. This illustrates the density it can reach. Fortunately, the owners find these plants fascinating, permitting their invasion. The yellow patches are *Brachythecium* cf. *salebrosum*. Photo courtesy of Craig Waddell.

genetics

Marchantia polymorpha (Figure 1-Figure 12) is typically considered a model for the early terrestrial colonizing plants. With this in mind, Bowman *et al.* (2017) characterized the genome of this species as having low genetic redundancy in most of its regulatory pathways. This species differs from its purported charophycean ancestors by encoding novel biochemical pathways, new phytohormone signalling pathways (especially auxin), expanded repertoires of signalling pathways, and increased diversity of transcription factor families. It sheds light on the evolution of haploid sex chromosomes as they occur in a dioicous plant. The haploid condition makes gene transfer and subsequent study easier than in the diploid tracheophytes (Chiyoda *et al.* 2008).

Ikeuchi and Inoue (1988) used a computer-assisted homology search to identify the D1-D2-cytochrome b-559 complex protein region in the chloroplast genome of *Marchantia polymorpha* (Figure 1-Figure 12).

Takenaka *et al.* (2000) found that *Marchantia polymorpha* (Figure 1-Figure 12) had at least 1-4 copies of the hpt gene, an example of gene redundancy in early land plants.

Chung *et al.* (2006a) compared two bryophytes and *Arabidopsis thaliana* (Figure 52) to determine the number of genes in common. They found 79% of the genes expressed by *Marchantia polymorpha* (Figure 1-Figure

12) were also expressed in the moss *Physcomitrium patens* (Figure 77). They found 763 genes expressed not only in both bryophytes, but also in *Arabidopsis thaliana*. Another 363 genes were found in the bryophytes, but not in *Arabidopsis*.



Figure 77. *Physcomitrium patens*, a species that expresses 79% of the same genes as in *Marchantia polymorpha*. Photo through public domain.

Chung *et al.* (2006b) contrasted gene expression in *Marchantia polymorpha* (Figure 1-Figure 12) with that of *Arabidopsis thaliana* (Figure 52). In the latter tracheophyte species, ~50% of the expressed genes exhibited cell-type-specific expression patterns. On the other hand, in *M. polymorpha* the expression in cultured cells did not differ from those of the thalli. Instead, 110 genes were expressed in cultured cells of *M. polymorpha*, but not in those of *A. thaliana*, whereas in the 10 *A. thaliana* genes checked, they were expressed in whole plants of both species, but not in cultured cells of *A. thaliana*. Thus, *Marchantia polymorpha* with transplanted genes can be used more easily to determine the expression of tracheophyte genes.

Lin and Bowman (2018) identified micro RNAs in *Marchantia polymorpha* (Figure 1-Figure 12). Tsuboyama *et al.* (2018) elaborated on methods of using the model liverwort *Marchantia polymorpha* in AgarTrap transformation for studying genetic transformation, achieving a 97% transformation efficiency.

Schmid *et al.* (2018) found that methylation pattern of DNA changes in cytosines varies significantly during the life cycle. These coincide with four major epigenetic states, corresponding to the states of vegetative gametophytes, antherozoids, archegonia, and sporophytes. They concluded that epigenetic reprogramming occurs in at least two events during the life cycle, once in each generation. These events occur in parallel with the differences in the gene expression involved in DNA methylation.

Ishizaki *et al.* (2008) used *Agrobacterium* (Figure 20)-mediated transformations on immature thalli of *Marchantia polymorpha* (Figure 1-Figure 12) that had developed from spores. Plants grown from gemmae (Figure 153-Figure 170) of these plants all expressed the introduced gene GUS. Because of the haploid state of the

thallus, these plants offer a very useful system for such transformations.

Marchantia polymorpha (Figure 1-Figure 12) has become a model organism for using promoters in overexpression studies to determine gene functions (Althoff *et al.* 2014). The protocol developed has the potential to screen large numbers of transgenic plants, including the use of knock-down mutants.

These studies have shown the usefulness of *Marchantia polymorpha* to test the function of genes.

One of the applications of our genetic knowledge of this species is to determine its susceptibility to radiation damage. Using Co⁶⁰ gamma rays, Miller and Sparrow (1965) determined that the ability of the two apical cells to reproduce was inhibited at doses less than the lethality dosage. The thallus exhibits different radiosensitivity from that of the gemmae (Figure 153-Figure 170) when based on energy absorption; the thallus is 4.3 times as sensitive as the gemmae.

Adaptations

Halbsohl (1953) explored the development of dorsiventrality in *Marchantia polymorpha* (Figure 1-Figure 12). We can assume that this body form has advantages, particularly in habitats that can at times be very wet and at other times can dry out. The overlapping thalli of the colony help to retain water in the soil (Figure 78). This same advantage can be accomplished by growing with mosses (Figure 79).



Figure 78. *Marchantia polymorpha* in Houghton, Michigan, showing overlapping thalli. Photo by Matt Tianen, with permission.

Bischler and Jovet-Ast (1981) commented that members of the **Marchantiales** seem to have some characters that are not essential for survival, reproduction, or dispersal. Others seem to be disadvantageous, but they have not prevented the continued existence of these traits. Instead, they concluded, the adaptations to their niches are linked primarily to biochemical and biophysical properties of the cell content rather than to morphological expressions.

Since wet habitat species typically experience dry seasons, among the most common adaptations are those that conserve water. McConaha (1941) described the

ventral structures that affect water uptake and conservation. In the Marchantiales, these include smooth and tuberculate rhizoids (Figure 80-Figure 84) and ventral scales (Figure 83-Figure 86). Using several members of the order, including *Marchantia polymorpha* (Figure 1-Figure 12), McConaha reported that the **smooth rhizoids** (Figure 80) emerge from the scales and can make contact with the substrate (Figure 81-Figure 82). **Tuberculate (pegged) rhizoids** (Figure 53, Figure 83) serve a different purpose. They originate beneath the scales, forming numerous connected capillary strands that lie parallel to the thallus (Figure 53, Figure 83). This arrangement provides a rapid capillary distribution of water to all the absorptive areas of the thallus. The efficiency in water balance depends on the form and imbrication of the scales (Figure 84-Figure 86), as well as with the length and number of these rhizoids.



Figure 79. *Marchantia polymorpha* with gemmae cups, overgrowing mosses that can help to retain moisture in the soil and the liverwort thallus. Photo by Janice Glime.



Figure 80. *Marchantia polymorpha* ventral side showing smooth rhizoids along midrib. Photo from Botany Website, UBC, with permission.



Figure 81. *Marchantia polymorpha* archegoniophores and thallus showing brown, perpendicular rhizoids. Photo by Janice Glime.

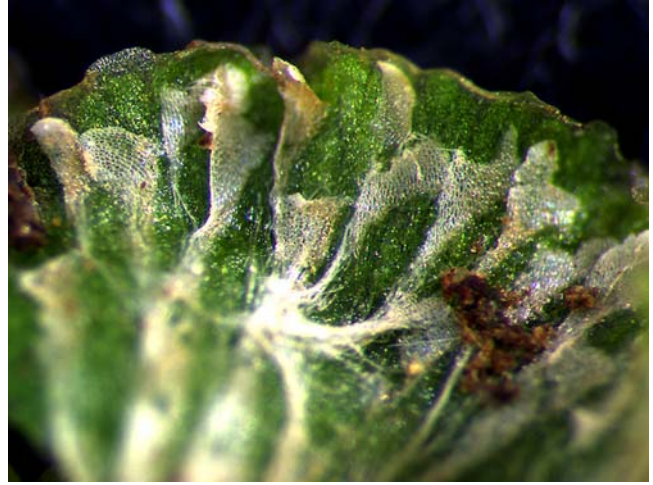


Figure 84. *Marchantia polymorpha* ventral growing tip of thallus with marginal scales. Photo by Larry Jensen, with permission.



Figure 82. *Marchantia polymorpha* ventral smooth rhizoids at midregion of thallus, along the midrib. Photo by Larry Jensen, with permission.

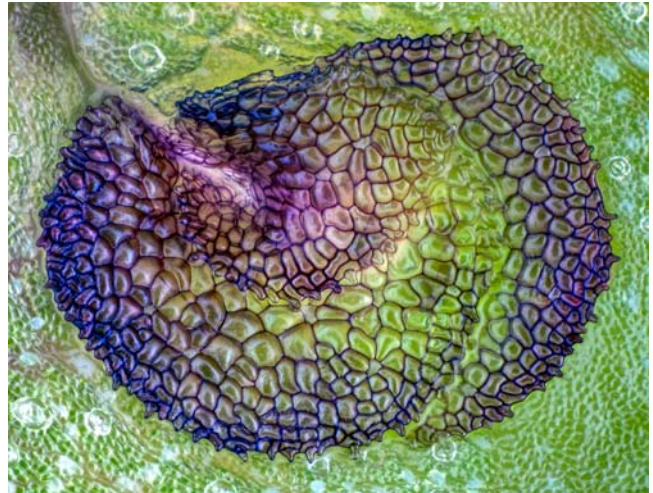


Figure 85. *Marchantia polymorpha* ssp. *ruderalis* scales showing purple coloring. Photo by Des Callaghan, with permission.



Figure 83. *Marchantia polymorpha* bundles of pegged rhizoids terminating in marginal scales. Photo by Larry Jensen, with permission.

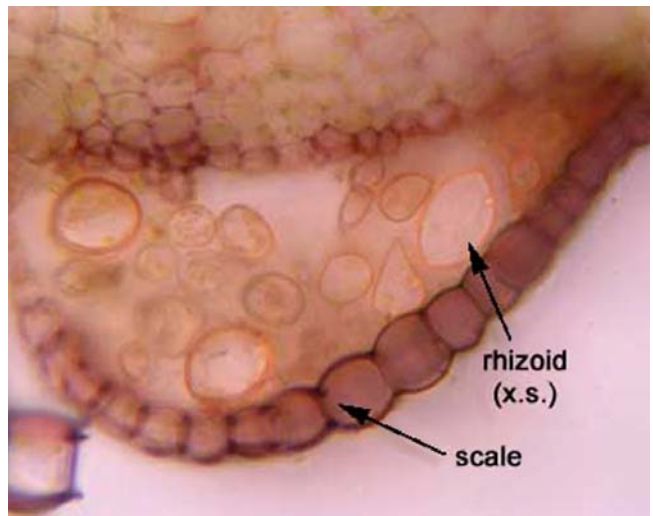


Figure 86. *Marchantia polymorpha* section showing scale and rhizoids on ventral surface. Photo from Botany Website, UBC, with permission.

Cao *et al.* (2014) further described the rhizoids (Figure 80-Figure 84) in *Marchantia polymorpha* (Figure 1-Figure 12). These researchers noted that the tuberculate (pegged) rhizoids converge toward the midrib (Figure 83-Figure 84). The smooth rhizoids occur in clusters in the free portions near the midrib at the thallus posterior (Figure 80, Figure 82). Unlike the tuberculate rhizoids, these lie perpendicular to the thallus, always growing toward the moist soil (Figure 81-Figure 82).

Many botany textbooks still claim that bryophytes lack cuticles. But we now know that this is not the case, at least for many bryophytes. Many species develop a thin cuticle that is not easily noticed. Brockington *et al.* (2013) and Xu *et al.* (2021) noted that even in flowering plants we lack understanding of the cuticle genetics and the role of the cuticle in evolution. Hence, these researchers have provided a detailed description of the cuticle and its genetic origins in *Marchantia polymorpha* (Figure 1-Figure 12). The cuticle is hydrophobic and is generally considered to be a barrier between the plant and the atmosphere wherein it helps to maintain internal moisture levels and to prevent entry of potentially pathogenic organisms. It is also a filter of UV radiation and barrier against mechanical damage. Because of these important roles in the terrestrial environment, it has been considered to be one of the key innovations needed for colonization of land (Corner 1964).

Xu *et al.* (2021) analyzed the role of the cuticle in preventing water loss in *M. polymorpha* (Figure 1-Figure 12). Using mutant plants, they found no change in morphology of the thallus for plants without a cuticle. However, they found more effects of desiccation in mutant plants with no cuticle. These plants frequently exhibited brownish tissues at the flank and tip of the thallus after five days with no cover and no added water. Most significantly, water content declined to about 70%, compared to 90% in non-mutant plants (Figure 87), the latter being only a 5% decrease in water content following the drying regime. Wu and coworkers were unable to detect any waxes in the cuticle of the lab-grown *M. polymorpha*. Rather, the cuticle of *M. polymorpha* in these experiments consisted only of cutin, except for the waxy cuticle surrounding the pores (Figure 88). We know that environmental conditions affect the manufacture of cuticle waxes in flowering plants and could have been a cause for suppression of these waxes in the lab populations of *M. polymorpha*.

While the plants with the addition of cuticles solved the problem of water loss, they had created another problem. An epidermis with a cuticle also interferes with gas exchange, impeding photosynthesis by the underlying photosynthetic tissue. In a thallose liverwort like *Marchantia polymorpha* (Figure 1-Figure 12) chloroplasts are buried (Figure 89, Figure 91-Figure 92) below the epidermis where light is reduced and it would be difficult to exchange CO₂ and O₂ if they did not have air pores (Figure 89-Figure 90). These openings permit the entry of air into the chambers (Figure 89, Figure 91-Figure 92) beneath them and the escape of the photosynthetic O₂. But these air pores present another problem. When the thallus becomes submersed or even when raindrops land in the pores, there is the danger that the water could enter the thallus and prevent the gas exchange. *Marchantia polymorpha* protects itself from this internal drowning by having cuticular ridges (Figure 90-Figure 94) around the

opening of the pores (Schönherr & Ziegler 1975). The hydrophobic waxes, helped by the cohesive properties of water, repel the water and prevent its entry. Schönherr and Ziegler considered them to be "perfect structures."

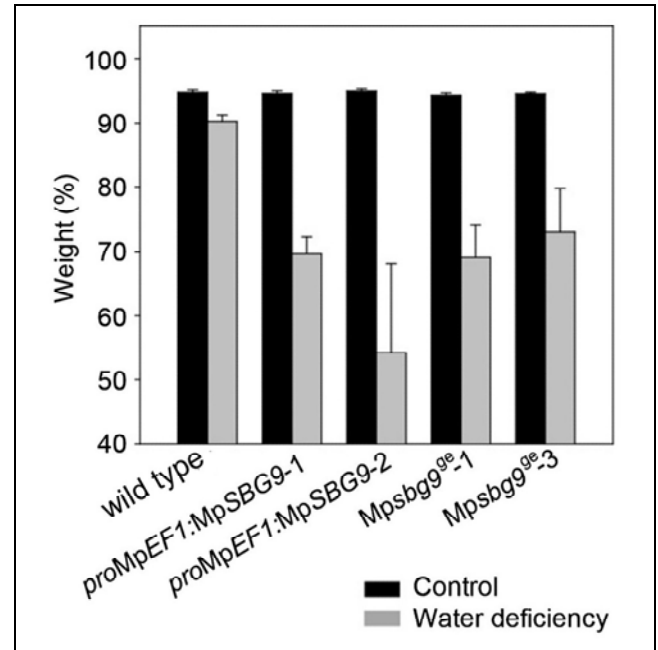


Figure 87. Cuticle water loss as percent weight in *Marchantia polymorpha* in wild type and four different mutants that reduce cuticle formation. Modified from Xu *et al.* 2021.

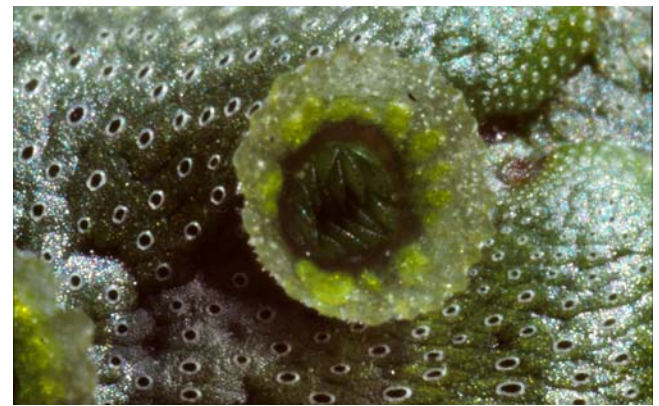


Figure 88. *Marchantia polymorpha* gemma cup and distinct air pores surrounded by white cuticle on thallus. Photo by John Forlonge, through Flickr.

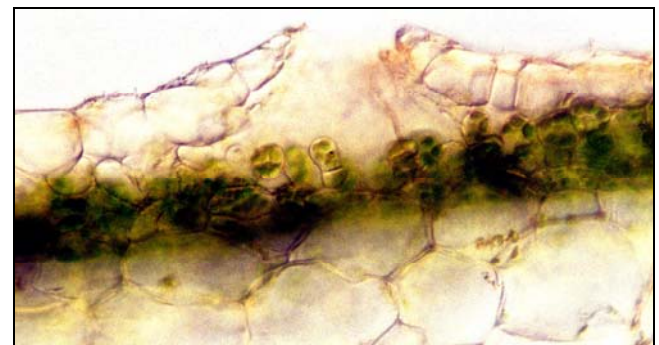


Figure 89. *Marchantia* thallus section showing pore opening and layer of chlorophyllous filaments. Photo by George Shepherd, with permission.

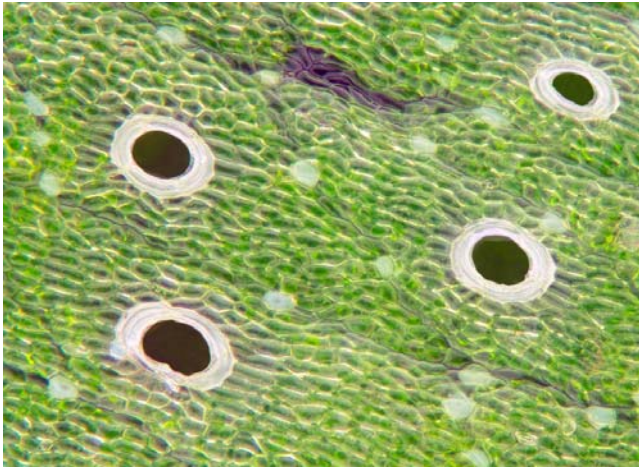


Figure 90. *Marchantia polymorpha* air pores and green layers showing through surface. Note the donut-shaped cuticular ridges. Photo by Des Callaghan, through Creative Commons.



Figure 93. *Marchantia polymorpha* pore opening as seen from thallus surface, showing cuticular ridge surrounding the opening. Photo by Wilhelm Barthlott, with permission.



Figure 91. *Marchantia polymorpha* section through pore opening. Note the photosynthetic cells beneath the pore. Photo by Walter Obermayer, with permission.

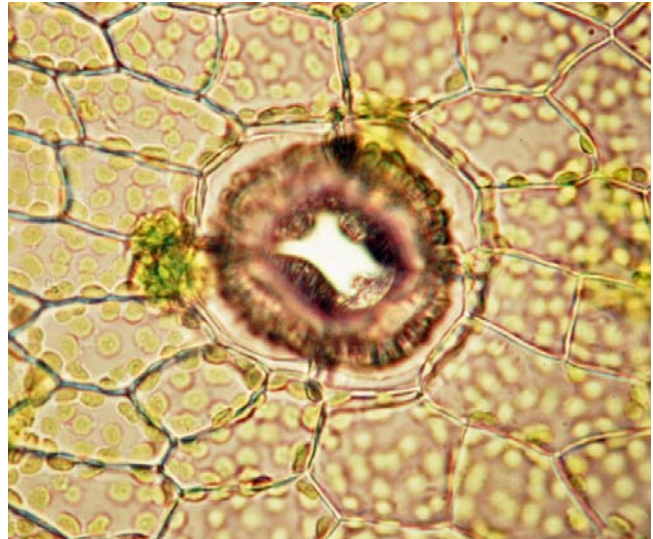


Figure 94. *Marchantia polymorpha* pore opening with cuticular ridge and small opening. Photo by Wilhelm Barthlott, with permission.

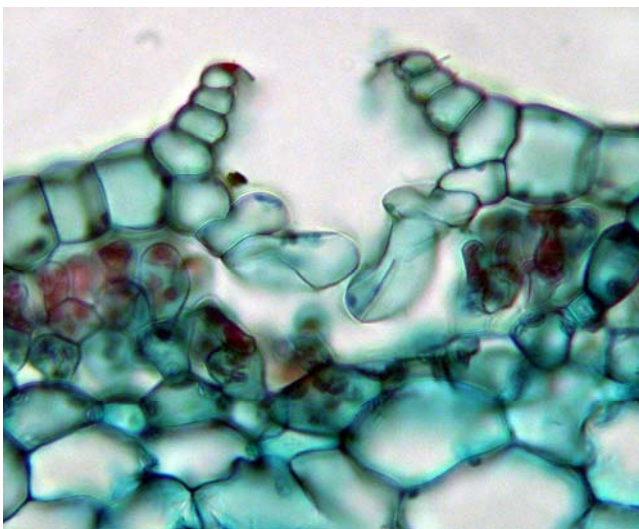


Figure 92. *Marchantia* thallus section showing pore opening. Photo by George Shepherd, with permission.

The adaptive value of oil bodies puzzled bryologists for a long time. Galatis and Apostolakis (1976) described the association of the microbodies with the cytoplasmic tubules of oil body cells in *Marchantia*. They found that the tubules increase in number at the stage when the cells are actively synthesizing oil.

One of the protections exhibited by liverworts is the ability to store sesquiterpenes and bisbibenzyls in oil bodies (Figure 95). Suire *et al.* (2000) isolated a number of isoprenoid biosynthetic enzymes from oil bodies (Figure 95-Figure 96) in *Marchantia polymorpha* (Figure 1-Figure 12). In *Marchantia polymorpha* these oil bodies are localized in oil body cells (Tanaka *et al.* 2016). Tanaka *et al.* (2016) reported that oil bodies served as sites of accumulation of sesquiterpenoids and marchantin A. They also observed that the number of oil body cells increased in thalli grown in low-mineral conditions.

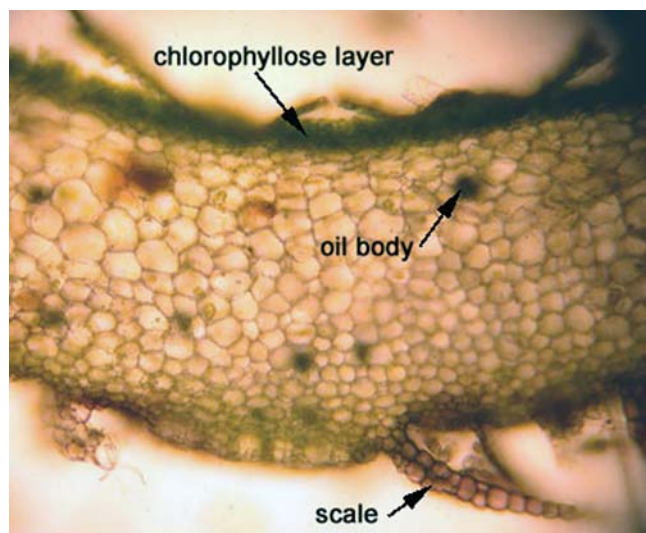


Figure 95. *Marchantia polymorpha* section showing scales and oil bodies. Photo from Botany Website, UBC, with permission.

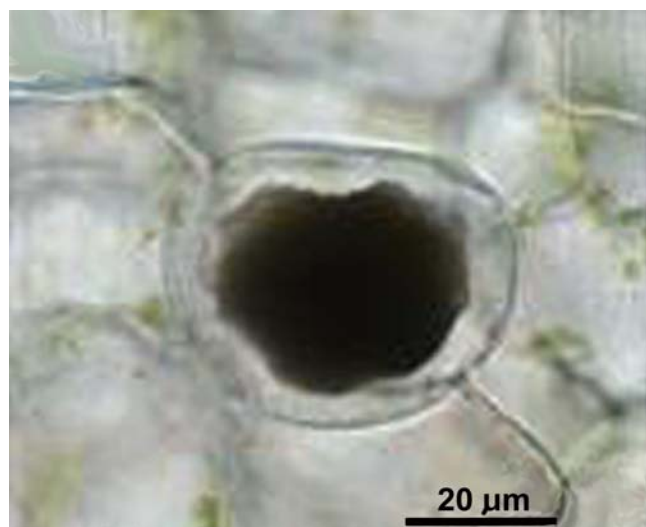


Figure 96. *Marchantia polymorpha* oil body in oil cell. Photo by Masaki Shimamura, with permission.

He *et al.* (2013) described the liverwort oil bodies (Figure 95-Figure 96) as "intracellular organelles bounded by a single unit membrane containing lipophilic globules suspended in a proteinaceous matrix." Oil bodies are unique to liverworts. In *Marchantia polymorpha* (Figure 1-Figure 12), we know that they contain protein complex that is immunologically related to the plastid and cytosolic enzymes of the isoprenoid synthesis. They are known as sites of essential oil accumulation and sequestration. Although they are known to contain compounds useful for medical purposes, their full function in liverworts remains unknown. What are the advantages of size and morphology – characters that differ sufficiently among species to be of taxonomic value?

By suppressing the genes controlling this sesquiterpenoid production, Romani *et al.* (2020) found that the terpenoid-rich oil bodies (Figure 95-Figure 96) are responsible for protecting *Marchantia polymorpha* (Figure 1-Figure 12) from arthropod herbivores, but that unlike those in tracheophytes, these oil bodies seem to have no

role in abiotic stress response, including desiccation. Takizawa *et al.* (2021) found that when *Marchantia polymorpha* was exposed to non-axenic conditions the number of oil bodies increased, as did the amounts of sesquiterpenes. They likewise demonstrated that the bacterium *Escherichia coli* (Figure 16) elicited the same response.

Kihara *et al.* (2014) found that *Marchantia polymorpha* (Figure 1-Figure 12) emitted C8 volatiles following mechanical wounding. Induction of these emissions occurred within 40 minutes of the wounding. When transgenic plants lacking arachidonic acid and eicosapentaenoic acid were wounded, only minimal C8 volatiles were detectable. Octan-3-one was produced only minimally when thalli were completely disrupted, but was the most abundant product in only partially disrupted thalli.

Yoshikawa *et al.* (2018) traced the wounding response in *Marchantia polymorpha* (Figure 1-Figure 12). Wounding of the thallus resulted in the synthesis of phenylpropanoids, including luteolin, apigenin, and isoriccardin C.

Watson (1919) suggests that reduced pores in *Marchantia* species might be an advantage in a wet habitat. Due to cohesion of the water molecules, water is unable to enter the smaller openings.

Among the advantages that bryophytes have are their plasticity and adaptability. Plasticity is exhibited by the various biochemical responses to different pathogens and environmental conditions. Adaptability is enhanced by the haploid condition. Selection on gametophyte plants is more rapid than in tracheophytes because there is only one set of chromosomes, permitting rapid removal of non-adapted genes in the population. This mechanism is evident in adaptations to heavy metals. Briggs (1972) demonstrated this in the response of *Marchantia polymorpha* (Figure 1-Figure 12) to lead contamination. When Briggs compared plants from areas with high levels of lead in the soil to those from an area with low levels of lead pollution, those from highly contaminated soil were highly tolerant of lead, whereas those from areas with less lead contamination are more sensitive. Krupinska (1976) found that lead tetraethyl causes distorted growth patterns in *Marchantia polymorpha*. The thalli become "profusely" branched, a reversible phenomenon. The chloroplasts degenerate and growth of the spores and gemmae is inhibited.

Reproduction

sexual

Marchantia polymorpha has been used in a number of studies on sexual expression in plants, particularly to demonstrate that expression in early plants. Nagai *et al.* (1999) generated 970 expressed sequence tag (EST) clones from an immature female sexual organ (Figure 112-Figure 128) of the liverwort *Marchantia polymorpha* (Figure 1-Figure 12). In 376 ESTs they found 123 redundant groups, reducing the unique sequences to 717.

Marchantia polymorpha (Figure 1-Figure 12) is a **dioicous** species with easily recognizable differences between **antheridiophores** (Figure 98-Figure 110) and **archegoniophores** (Figure 110-Figure 128). Durand (1908) described these as well as the sporangium. The

stages of the sexual life cycle can be seen in Figure 98-Figure 146.

As noted earlier, sex in *Marchantia* is determined by a **small V chromosome** in males and no U chromosome, whereas the female has a **single U chromosome** and no V chromosome (Lorbeer 1934). But the designation of the gender is not perfectly genetic. Naidu (1973) reported abnormal receptacles that bore both archegonia and antheridia, based on specimens from a population in India. The V chromosome (Figure 97) has several chromosome-specific sequence elements (Okada *et al.* 2001; Ishizaki *et al.* 2002). Okada *et al.* (2000) identified 70 male-specific PAC clones and verified that the V chromosome exhibits unique sequences that are not present on the U chromosome or any non-sex chromosomes. These repeat sequences contribute 2-3 Mb on the V chromosome. Okada and coworkers introduced us to the first active V chromosome-specific gene known in plants. Fujisawa *et al.* (2001) isolated two female-specific and six male-specific DNA fragments that originated from these U and V chromosomes. Okada *et al.* (2000) suggested that this liverwort was a suitable model for identifying roles of sex genes in sexual differentiation. Bisang *et al.* (2010) noted that molecular sex markers have thus far only been described for a few bryophytes, one of which is *Marchantia polymorpha*.

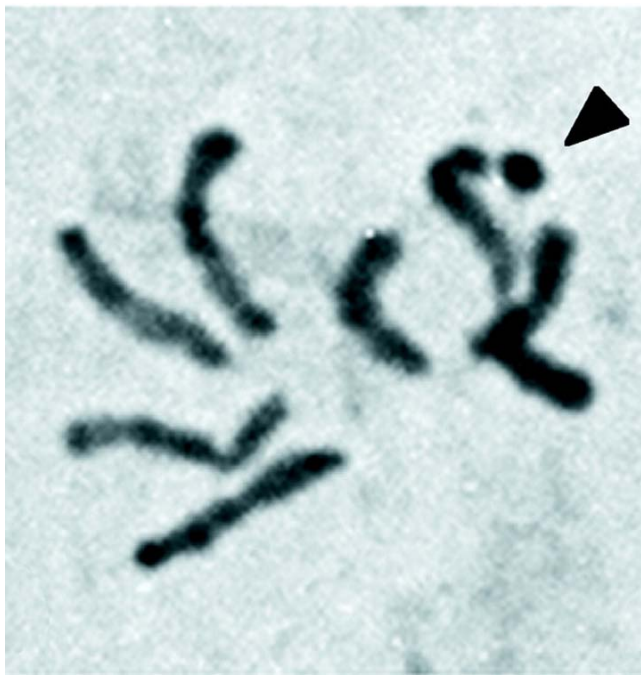


Figure 97. *Marchantia polymorpha* male chromosomes, with tiny V chromosome indicated by arrow. Photo from Okada *et al.* 2001, through Creative Commons.

Wann (1925) determined that photoperiod was important in initiating sexual branches in *Marchantia polymorpha* (Figure 1-Figure 12). In long days, males produce mature antheridiophores in 3-4 weeks. Females seem to respond to the same stimulus, but require 6-8 weeks for archegoniophores to reach maturity. The role of temperature remained unknown. High humidity hastens the sexual branches, but low humidity retards them and

may completely inhibit their production, particularly for archegoniophores. And as in some of the algae, low nitrogen relative to carbohydrate may initiate sexual branches. These nutrient relationships in algae signal the end of the growing season and the beginning of the unfavorable conditions of winter. The same could be likely for the bryophytes as the tracheophytes use up the nitrogen during the growing season. Hence, forming a sexual reproductive structure that can remain dormant until favorable conditions return is adaptive.

Lloyd and Steinmetz (1937) found that high temperatures (above 30°C) at least temporarily suppress development of archegoniophores and antheridiophores in *Marchantia polymorpha* (Figure 1-Figure 12). Low temperatures, on the other hand, promote development of these reproductive structures during short days. But during late autumn, plants moved to a warm greenhouse from the cool outdoors would also produce more archegoniophores and antheridiophores compared to plants that had remained in the greenhouse continuously. Furthermore, plants brought to the greenhouse in late autumn developed these sexual structures more quickly than those brought into the greenhouse earlier in the autumn. Greenhouse-grown plants could be induced to develop archegoniophores and antheridiophores during short days if they were exposed to natural autumn conditions found at Orono, Maine, USA. Nevertheless, a long photoperiod is important in inducing this sexual response.

Benson-Evans (1964) found that *Marchantia polymorpha* (Figure 1-Figure 12) produced gametangia at 21°C in long days (18 hours), but lowering the temperature to 10°C or the photoperiod to 6 hours resulted in no gametangia production.

Yamaoka *et al.* (2021) summarized that initiation of the development of gametangia depends on environmental factors such as light, but they considered that these factors are still elusive. They recognized recent studies that considered their development to use conserved regulatory modules that are involved in light signalling.

Maravolo *et al.* (1967) explored activity of 12 enzyme systems in various parts of *Marchantia polymorpha* (Figure 1-Figure 12). Of these, only phosphatases, esterases, and peroxidases were found in extracts of uninduced thalli, induced thalli, stalks, and antheridiophore and archegoniophore disks. They found an amplification of esterases in the antheridia (Figure 105-Figure 109). These esterases can hydrolyze particular esters into acids and alcohols or phenols. Gorska-Bryllass (1970) reported increased esterase activity in the early stages of spermatogenesis in *Marchantia polymorpha*, an activity that declines near the end of that cellular division. Could these be important in protecting the antheridia against stresses, especially desiccation?

Markham and Porter (1978) isolated an aurone (known for making flowers yellow) from *Marchantia polymorpha* (Figure 1-Figure 12) during its sexual phase. The aurone aureusidin 6-O-glucuronide is present only in the antheridiophores (Figure 98-Figure 110).



Figure 98. *Marchantia polymorpha* males with antheridial receptacles (antheridial heads). Photo by Li Zhang, with permission.



Figure 99. *Marchantia polymorpha* with expanding antheridiophores, showing development of the antheridial receptacle before elongation of the stalk. Photo by Des Callahan, with permission.



Figure 100. *Marchantia polymorpha* ssp. *polymorpha* male with antheridiophores that look healthy, despite the curling of the thallus. Photo by David Holyoak, with permission.



Figure 101. *Marchantia polymorpha* antheridiophores reaching full elongation. Photo by Walter Obermayer, with permission.



Figure 102. *Marchantia polymorpha* mature antheridial heads, showing how dense they can be. The presence of only one gender suggests that this is a clone. Photo by Steve Juntikka, with permission.



Figure 103. *Marchantia polymorpha* antheridial head in side view, with rhizoids and scales hanging from the head. Photo from Botany Website, UBC, with permission.



Figure 104. *Marchantia polymorpha* antheridial head that is not quite mature. Photo by Walter Obermayer, with permission.



Figure 105. *Marchantia polymorpha* mature antheridial receptacle showing yellow antheridia. Photo by Larry Jensen, with permission.



Figure 106. *Marchantia polymorpha* antheridial receptacle section showing arrangement of antheridia. Photo by Janice Glime.



Figure 107. *Marchantia polymorpha* antheridium section with developing sperm cells. Photo by Janice Glime.

Michelot-Gerne (1984) described the nuclear condensation during spermatogenesis in *Marchantia polymorpha* (Figure 1-Figure 12). Reynolds and Wolfe (1984) identified protamines in plant sperm, using *Marchantia polymorpha* as one of the representative organisms. These are small, arginine-rich proteins that replace histones near the end of the haploid phase of spermatogenesis; they are considered essential for sperm head condensation and DNA stabilization.

Carothers and Kreitner (1968) described the blepharoplast of the **spermatid** (developing spermatozoid) of *Marchantia polymorpha* (Figure 1-Figure 12). Bajon *et al.* (1995) described the nucleus of the **spermatozoid** (male gamete; sperm). They found that RNAs remain scattered in the spermatozoid throughout differentiation. They are closely associated with chromatin strands that fuse in the mature gamete. They found that mRNAs associated with the mature spermatozoid genome are stored mRNAs. They permit the transfer of paternal information to the zygote during fertilization. Using a high-speed video technique, Inouye and Hori (1991) described the movement of the sperm (spermatozoid) of *Marchantia polymorpha* as a breast stroke. Miyamura *et al.* (2002) further described the flagellar movement of the sperm, using high-speed video.

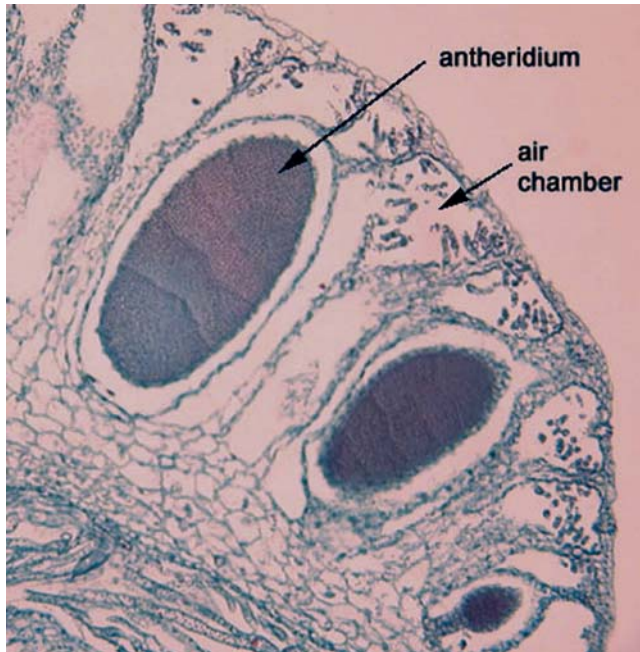


Figure 108. *Marchantia polymorpha* section of antheridial head. Photo from Botany website, UBC, with permission.

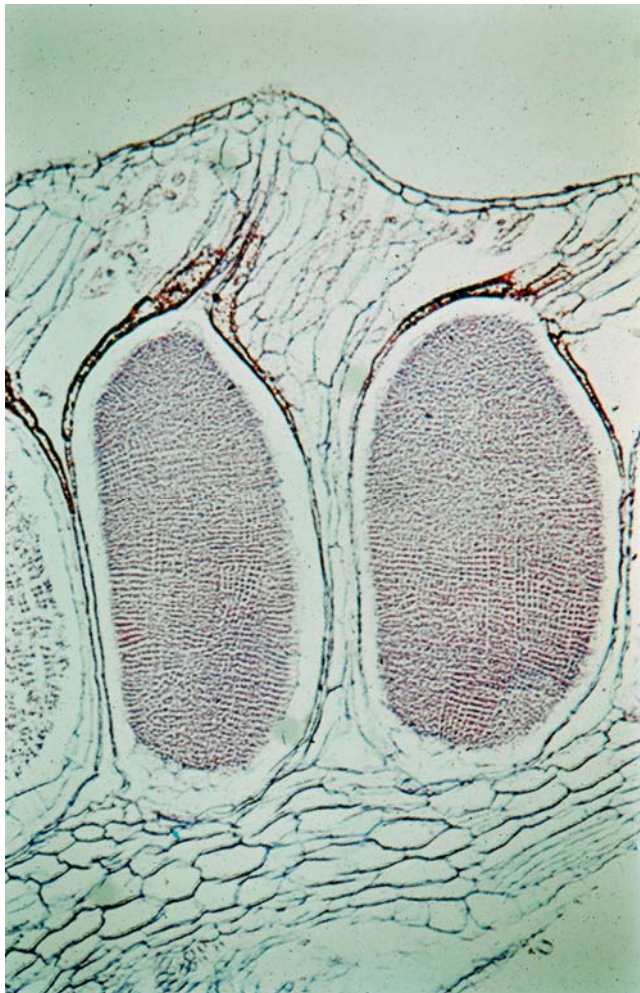


Figure 109. *Marchantia polymorpha* section of antheridia at maturity. Photo by Wilhelm Barthlott, with permission.



Figure 110. *Marchantia polymorpha* antheridiophores and archegoniophores, occurring on separate thalli. Photo by Robert Klips, with permission.

Une (1984) observed that female plants produce sexual branches more frequently than do male plants (Figure 111). Archegoniophores, in particular, may be inhibited by low humidity (Wann 1925). As in many algae, a low nitrogen:high carbohydrate ratio can stimulate the formation of sexual branches. This nutrient relationship often serves as a signal that growing conditions are declining and the formation of spores provides a mechanism for surviving until favorable conditions return or the spores land in a suitable habitat.



Figure 111. *Marchantia polymorpha* females in July 1982, in Rydhave, Denmark, showing how dense the population can become.

The archegoniophores (Figure 112-Figure 121) arise from a separate thallus from that of the antheridiophores. The archegoniophores are formed by an infolding and rolling of the thallus, trapping rhizoids and scales inside the stalk that is thus formed (Figure 118-Figure 121). The rhizoids, in particular, aid in the movement of water to the receptacle head at the top of the stalk.



Figure 112. *Marchantia polymorpha* archegonial heads before the elongation of the stalk. Photo by Rudolf Macek, with permission.



Figure 113. *Marchantia polymorpha* nearly mature archegoniophores before the arms of the receptacle spread. Photo from <www.aphotofauna.com>, with permission.



Figure 114. *Marchantia polymorpha* archegoniophores before the fingers spread. Photo from <www.aphotofauna.com>, with permission.



Figure 115. *Marchantia polymorpha* females before the fingers are uplifted. Photo by Craig Waddell, with permission.



Figure 116. *Marchantia polymorpha* archegoniophores with fully expanded fingers on the receptacle on 1 July 2009 in Michigan, USA. Photo by Janice Glime.



Figure 117. *Marchantia polymorpha* females in what appears to be a purely female clone in Houghton, Michigan, USA. Note the different stages of old and young archegoniophores. Photo courtesy of Craig Waddell.

The archegonial head, at maturity, is filled with scales that protrude from the fingers of the structure (Figure 118-Figure 122). These scales help to conserve water in the head and offer protection to the developing sporophyte.



Figure 118. Newly emerging and maturing archegoniophores of *Marchantia polymorpha*. Note the rhizoids along the stalk and the scales protruding from under the receptacle head. Photo copyright Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.



Figure 119. *Marchantia polymorpha* mature archegoniophores 1 July 2009 in Michigan, USA. Photo by Janice Glime.



Figure 120. *Marchantia polymorpha* archegoniophores showing numerous scales hanging from the receptacle and groove in stalk where the rolled edges meet. Photo by Janice Glime.



Figure 121. *Marchantia polymorpha* archegoniophores nearing maturity. Note the rhizoids at the left. Photo by Rudolf Macek, with permission.



Figure 122. *Marchantia polymorpha* archegoniophore showing rhizoids along stalk, from Tahquamenon Falls, MI. Photo by Janice Glime.

The archegonia form on the fingers with the oldest near the stalk (Figure 123-Figure 129). Maintenance of dormancy by the egg (Figure 124-Figure 125, Figure 130) can prolong the period of time in which fertilization is possible. In *Marchantia polymorpha* (Figure 1-Figure 12), MpRKD regulates gametophyte development and keeps the egg cell dormant until fertilization occurs (Rövekamp *et al.* 2016). By doing this, it also prevents **parthenogenesis** (development of a zygote without fertilization).

In 1974, Zinsmeister and Carothers (1974) elucidated details of the fine structure changes involved in egg (Figure 124-Figure 125, Figure 130) formation. An amorphous substance surrounds the egg, perhaps preventing desiccation and protecting the egg.



Figure 123. *Marchantia polymorpha* archegoniophore with developing archegonia; showing thallus nature of the receptacle. Photo by George Shepherd, through Creative Commons.

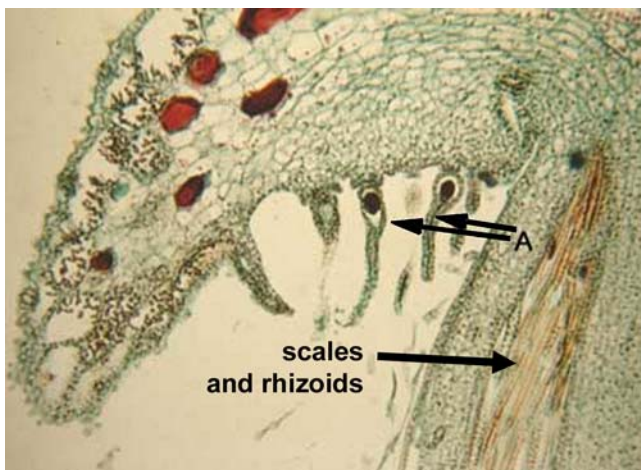


Figure 124. *Marchantia polymorpha* archegonial head longitudinal section showing archegonia (A) and scales and rhizoids in stalk. Image modified from Botany Website, UBC, with permission.



Figure 125. *Marchantia polymorpha* archegonia with what appear to be zygotes. Note the rhizoids within the stalk. Photo by Janice Glime.

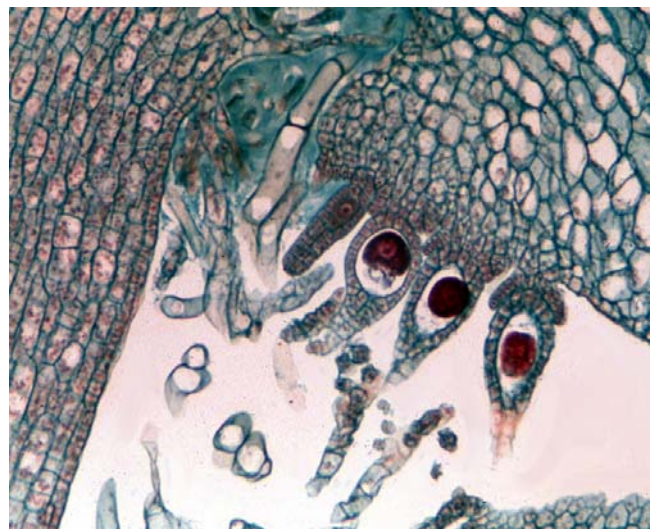


Figure 126. *Marchantia polymorpha* archegonia in various stages of development with least mature being closest to the stalk; the one furthest away has a zygote. Photo by Janice Glime.



Figure 127. *Marchantia polymorpha* with very young archegoniophores before stalk has expanded fully, mixed with mature archegoniophores showing yellow sporangia and elaters. Photo by Janice Glime.

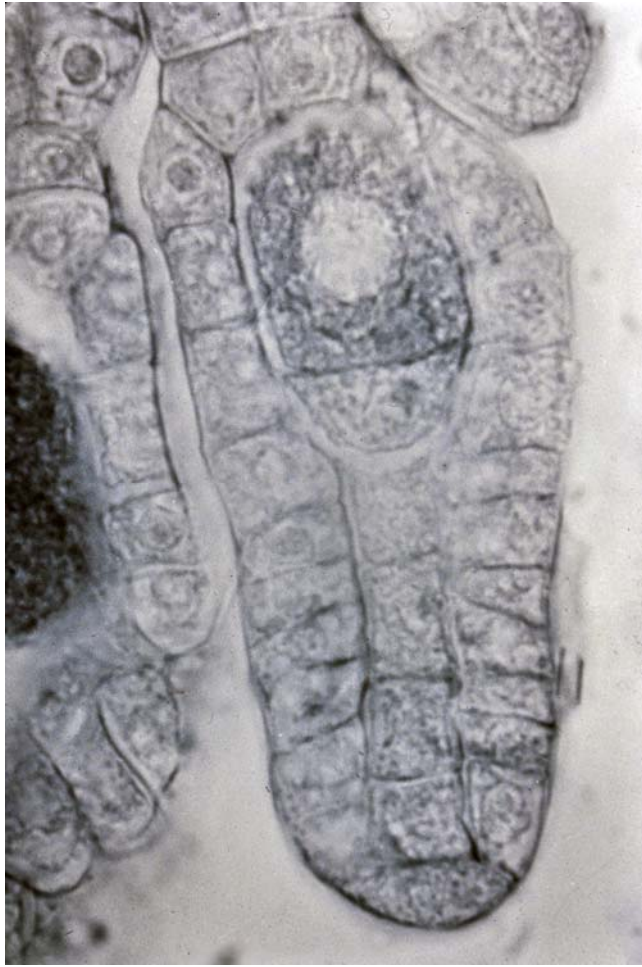


Figure 128. *Marchantia polymorpha* unfertilized archegonium before neck canal cells disintegrate. Photo by Wilhelm Barthlott, with permission.

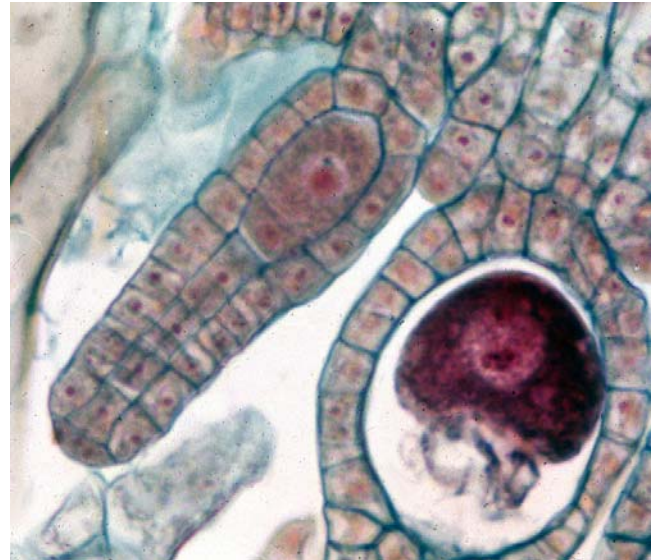


Figure 130. *Marchantia polymorpha* archegonia; one on left is immature with neck canal cells still in place; one on right has neck canal cells disintegrated (not shown) and the sperm is uniting with the egg. Photo by Janice Glime.

Strasburger (1869, in Parihar 1961) described the splashing of **sperm** (=male gamete, antherozoid, or spermatozoid; Figure 131-Figure 132) from the surface of the antheridial receptacle to the surface of the archegonial receptacle at a time when the antheridiophore was taller than the archegoniophore, thus permitting the water droplets to travel downward to the archegonial receptacles. He considered the splashing to extend to about 65 cm. By this time archegonia would have developed on the lower surface and the water would flow over the edge of the archegonial receptacle to reach them.



Figure 129. *Marchantia polymorpha* archegoniophores in a female clone on 6 July 2018 in Houghton, Michigan, USA; males were nearby in a separate clone. Photo by Janice Glime.

Part of this curiosity was to understand how the sperm could reach the egg in these dioicous plants. Kitagawa (1985) noted that due to the dioicous nature of *Marchantia polymorpha* (Figure 1-Figure 12), the male and female must be near each other (Figure 110) for fertilization to occur (Figure 130). But just how near is near?

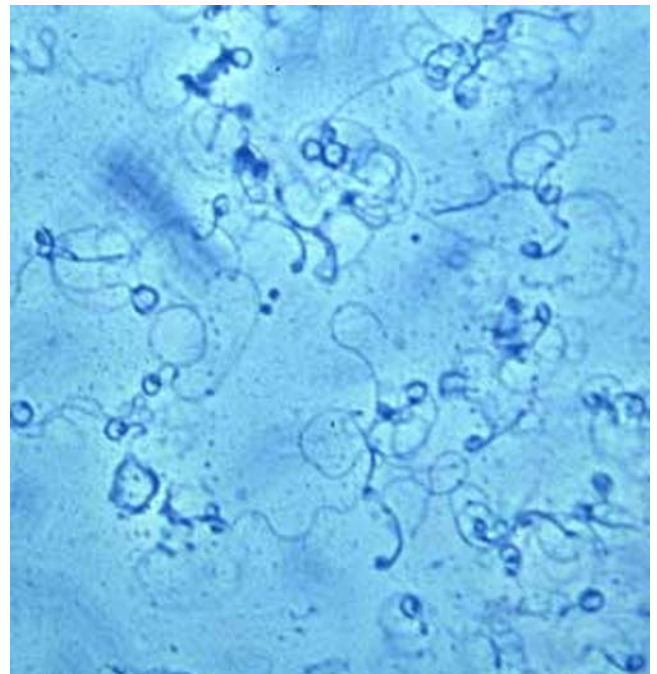


Figure 131. *Marchantia polymorpha* sperm. Photo from Botany Website, UBC, with permission.

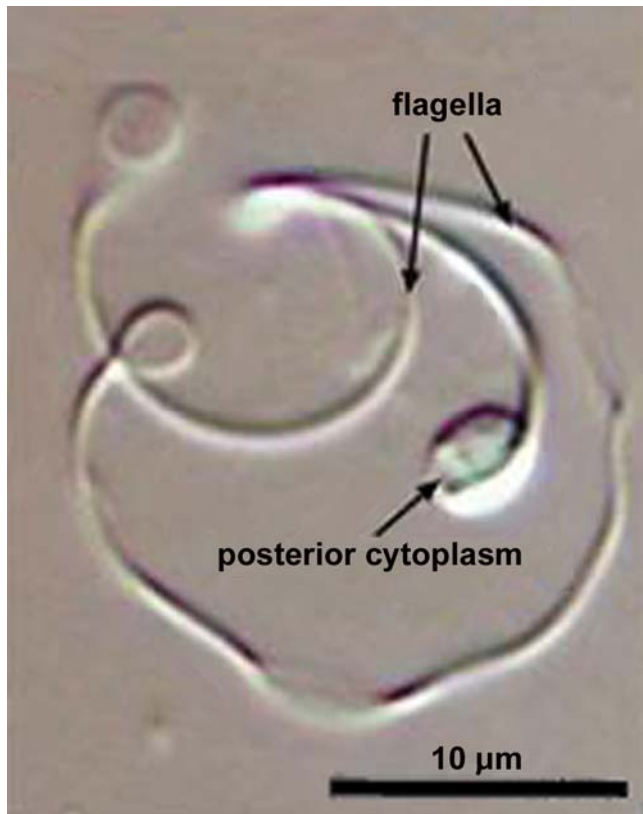


Figure 132. *Marchantia polymorpha* sperm. Photo by Masaki Shimamura, with permission.

One of the puzzles in fertilization of plants is how the sperm find the eggs, or at least the archegonium. Lidforss (1904) was among the early researchers on this question. Again using *Marchantia polymorpha* (Figure 1-Figure 12), Lidforss found the proteins albumin, hemoglobin, and diastase could each attract the sperm into the capillary tube that held them.

Åkerman (1910) experimented with various salts as attractants or repellants of sperm (Figure 131-Figure 132) in *Marchantia*, possibly *M. polymorpha* (Figure 1-Figure 12). Some salts had positive effects on chemotaxis, whereas others, especially heavy metals, had negative effects.

Furuichi and Matsuura (2016) found time-dependent changes in sperm motility (Figure 131-Figure 132) from high to low motility states in *Marchantia polymorpha* (Figure 1-Figure 12). Based on the average lifetime of the high motility state and the speed of movement, they estimated that these sperm would travel less than 3 cm. Hence, they concluded that other factors were needed to explain apparent travel distances greater than this, and that the motility of the sperm itself most likely only was important in the final fertilization step.

Alvarez (2017) described the movement of the sperm (Figure 131-Figure 132) in *Marchantia polymorpha* (Figure 1-Figure 12), based on the publication of Myamura *et al.* (2002). The movement caused by these biflagellated sperm is waveform and differs between the two flagella. This permits the sperm to adjust both steering and propulsion. The beat of the posterior flagellum is more 3-d than that of the anterior flagellum. When the sperm collides with an obstacle, it does not exhibit backward swimming.

Shimamura (2016) reported that water droplets could splash sperm cells (Figure 131-Figure 132) 30 cm or farther from the male plants of *Marchantia polymorpha* (Figure 1-Figure 12), as previously demonstrated experimentally (Burgeff 1943; Brodie 1951; Duckett & Pressel 2009). Drops of dye-containing water dropped onto the antheridia did limited splashing and most of the dye (>90%) was absorbed by the ventral side of the antheridial receptacles. But the dye also quickly moved to the ground level and managed to spread throughout the entire colony within an hour. This was facilitated by the bundles of rhizoids in the archegoniophore. When encountering a female plant, the dye moved up the archegoniophore stalk to the archegonial receptacle through the bundles of rhizoids enclosed by the stalk. This movement upward required 30-60 minutes. Furthermore, Duckett and Pressel (2009) observed that the youngest sporophytes are located near the stalk and the older ones are located near the periphery, indicating that fertilization continues after stalk elongation.

But Pressel and Duckett (2019) also measured the distances travelled by the sperm (Figure 131-Figure 132) of *Marchantia polymorpha* (Figure 1-Figure 12) to achieve fertilization. They followed more than 80,000 males and females for two years after a major fire and recorded the number of sporophytes. While these numbers seem high, they found the astounding number of more than 200,000 sperm in individual antheridia of *Marchantia polymorpha* (Figure 1-Figure 12). This is a greater number than in most bryophytes, but it is coupled with very effective sperm dispersal. They found that distances could exceed 20 m and that dispersal resulted in 100% fertilization of the female plants. The dehiscing antheridia release lipids that help to move the sperm in the surface water films both along the antheridiophores and across the surface water films to the archegoniophores. In a single flooding event, a male thallus with 10-12 antheridiophores can release more than 50 million sperm. This high fertilization success, coupled with the numerous tiny spores, can account for the ease with which the species seems to arrive after disturbances such as fire.

sporangia

Fertilization occurs in the archegonia, making possible a number of sporangia on the same archegonial head. The embryos (Figure 133-Figure 134) remain in the arms of the archegonial head where they are protected by many scales. The maturing embryo forms a foot, seta, and capsule inside the archegonium (Figure 135-Figure 136). The scales protrude more as the embryo matures (Figure 137-Figure 146), thus helping to maintain moisture.



Figure 133. *Marchantia polymorpha* archegonium with young sporophyte embryo. Photo by Janice Glime.



Figure 135. *Marchantia polymorpha* archegonium with young sporophyte showing foot, seta, and capsule (sporangium). Photo by Janice Glime.



Figure 134. *Marchantia polymorpha* archegonium with young embryo. Photo by Janice Glime.

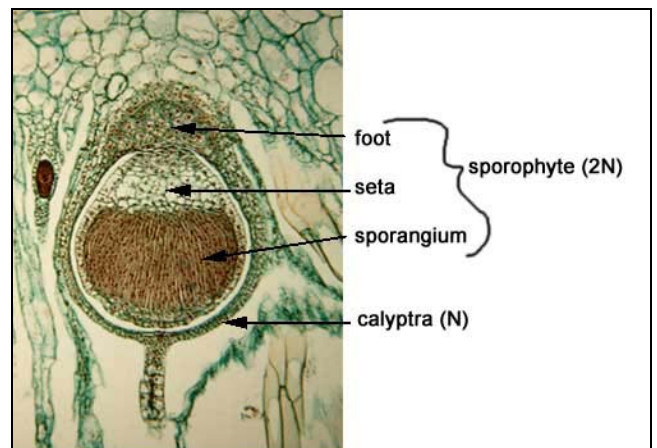


Figure 136. *Marchantia polymorpha* capsule longitudinal section. Image modified from Botany Website, UBC, with permission.



Figure 137. *Marchantia polymorpha* females with sporophytes, forming a female clone in Myvatn, Iceland, 8 August 1987. Photo by Janice Glime.



Figure 138. *Marchantia polymorpha* mature archegoniophores, Keweenaw Peninsula, Michigan, USA. Photo by Janice Glime.

Wann (1925) found that sporophytes (Figure 139-Figure 145) became mature in 10-12 weeks. This rate can be increased by high humidity and retarded by relatively low humidity.



Figure 139. *Marchantia polymorpha* archegonial heads showing a bluish green variant. Sporangia are just beginning to emerge from the scales. Photo by Felipe Osorio-Zúñiga, with permission.



Figure 140. *Marchantia polymorpha* archegoniophores showing population with bluish-green coloring and purple scales with capsules emerging. Photo from BlueRidgeKitties, through Creative Commons.



Figure 141. *Marchantia polymorpha* ripe, unopened sporangia. Photo by Felix Riegel, through Creative Commons.

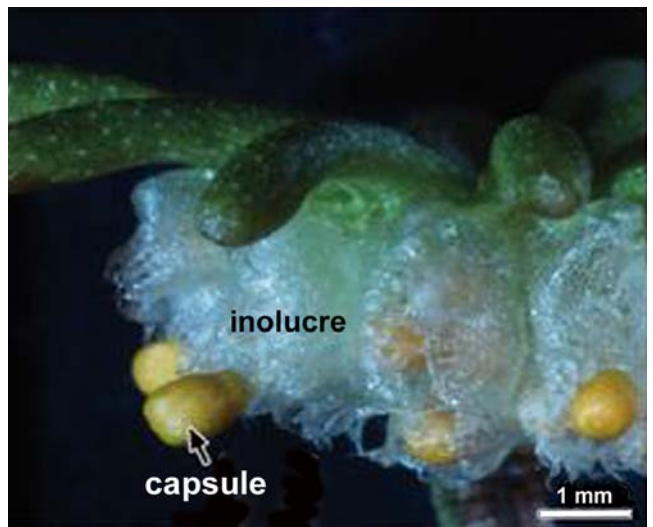


Figure 142. *Marchantia polymorpha* sporangia (capsules) emerging from the involucre. Photo by Masaki Shimamura, with permission.



Figure 143. *Marchantia polymorpha* archegonial head with elaters emerging on left, an empty capsule in center, and a capsule ready to open on right. Note the protective scales from which they are emerging. Photo by George Shepherd, through Creative Commons.



Figure 144. *Marchantia polymorpha* with mature sporangia dispersing spores, Laxarbakki, Myvatn, Iceland, 8 August 1987. Photo by Janice Glime.



Figure 145. *Marchantia polymorpha* archegoniophore with several unopened capsules on left and numerous elaters extended elsewhere. Note the purplish fringes on the scales of this specimen. Photo by Janice Glime.

Dörken (2012) described the sporophytes (Figure 139-Figure 145) of *Marchantia polymorpha* as short-lived, dying back after releasing the spores (Figure 146). A capsule typically contains several hundred thousand spores of similar size and shape, helping to account for the ability of this species to colonize newly disturbed areas such as those after fire.



Figure 146. *Marchantia polymorpha* archegonial head with empty sporangia among the scales and with sporangia beginning to die back. Photo by Janice Glime.

spores

O'Hanlon (1926) reported that in the Midwest of the USA, spores of *Marchantia polymorpha* (Figure 1-Figure 12) were "available" from early July to the middle of September. The sporophyte (Figure 147) produces an elater to spore (Figure 148-Figure 149) ratio of 1:128. A single capsule (Figure 141-Figure 142) of *Marchantia polymorpha* holds about 300,000 spores. Based on the typical number of capsules per archegonial head (~24), this would yield >7,000,000 spores per receptacle. But under favorable conditions, ~100 sporophytes are produced on one receptacle during a single growing season, suggesting that the total number of spores per individual archegonial receptacle is probably much greater (Duckett & Pressel 2009). The spores can be available for dispersal from early July to mid September, depending on latitude and altitude (O'Hanlon 1926). The spores remain viable for about one year.



Figure 147. *Marchantia polymorpha* archegonial head with dispersing sporangia having exserted elaters (yellow). Note the rhizoids on the rolled stalk. Photo by George Shepherd, through Creative Commons.

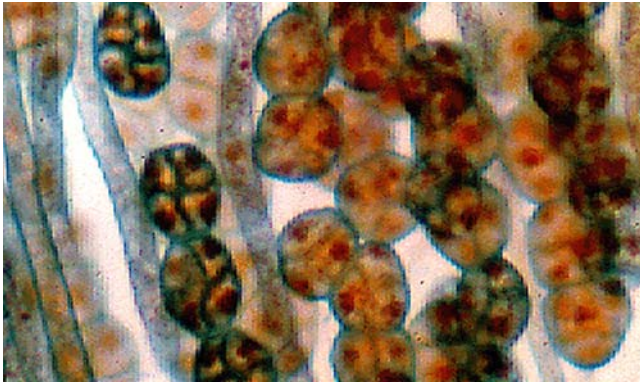


Figure 148. *Marchantia polymorpha* spore tetrads and immature elaters in capsule. Photo by Janice Glime.

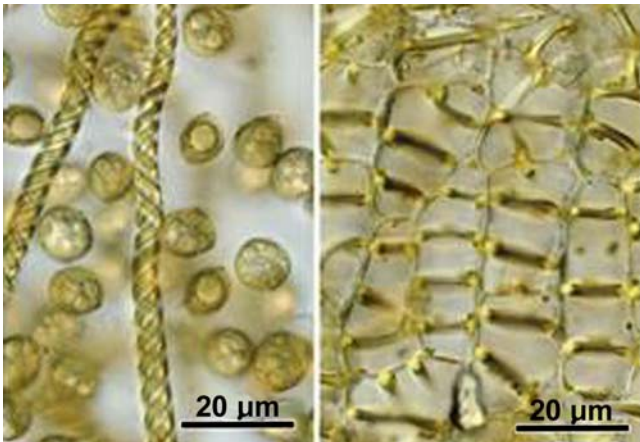


Figure 149. *Marchantia polymorpha* spores and elaters on left with closer view of thickenings of elaters on right. Photo by Masaki Shimamura, with permission.

Young and Kläy (1971) found *Marchantia polymorpha* (Figure 1-Figure 12) on the crater of a volcano on Deception Island, Antarctica, following the 1969 eruption. This rapid colonization of newly exposed substrata is itself remarkable, but the closest known source of propagules is 1,000 km away in South America! They assumed that numerous propagules must have arrived on just a small area to produce the colony pattern observed. Hence, the dispersal potential of this species is great, a factor that relates to the small size of its spores.

O'Hanlon (1925) detailed the germination of spores (Figure 150) and the early gametophyte stages in *Marchantia polymorpha* (Figure 1-Figure 12). Inoue (1960) studied the spore germination and early gametophyte development in the Marchantiales. Bischler (1984) examined spore morphology and germination in *Marchantia*.

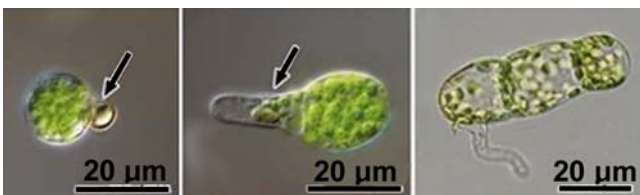


Figure 150. *Marchantia polymorpha* spore germination stages to a 3-celled protonema. Photo by Masaki Shimamura, with permission.

When the spore germinates (Figure 150), it typically produces a single primary rhizoid (Figure 151) after the spore has expanded and produced chlorophyll (O'Hanlon 1926). The spore first produces a very short filament. This is followed by division in a second cell, resulting in the thalroid structure that describes the mature protonema. Branching of the young thallus is common and can begin at an early stage. Rather than having a single apical cell dividing, it produces a marginal row of meristematic cells that continue to produce the mature thallus. At a stage of 30-40 cells, a notch develops in the apical region (Figure 151). Rhizoids develop behind this notch, anchoring the thallus and establishing its dorsiventrality. Mucilage cells arise on the lower side of the apex. In early stages, diminished light seems favorable, but by this stage 13-15 hours of light per day is optimum, with an optimum temperature of 18-22°C. However, the optimum for "fruiting" is lower at 10-15°C. They also germinate and grow better on a solid substrate than in a liquid medium.



Figure 151. *Marchantia polymorpha* protonema development. Apical notch is shown at arrow on right. Photo by Masaki Shimamura, with permission.

Nakazato *et al.* (1999) were able to induce spore germination in *Marchantia polymorpha* (Figure 1-Figure 12) with intermittent irradiation with 15-min red light pulses given every 1 or 2 h for 24 h. Germination could also be induced by the addition of glucose to spores in total darkness. Their experiments indicate that photosynthesis is involved in the photoinduction of spore germination in this species, supporting the conclusion of Inoue (1960).

In the right conditions, the spores swell and gain chlorophyll (Figure 150) (Shimamura 2016). Once swollen they shed the primary spore walls and germinate within a few days. This germination is light-dependent (Heald 1898), suggesting a need for additional energy resources. The light requirement is 10 hours or longer (Nakazato *et al.* 1999). It seems to require a brighter light for protonema and thallus development than that required by other liverworts (Inoue 1960).

Red and far-red light affect both cell division and elongation in *Marchantia polymorpha* (Figure 1-Figure 12) sporelings (Figure 150) (Nishihama *et al.* 2015). Thus, it is likely that phytochromes are involved in development of sporelings.

Gemmrich (1976) found that both Fe and $\text{Ca}(\text{NO}_3)_2$ induce germination of the spores (Figure 150) of *Marchantia polymorpha* (Figure 1-Figure 12). Optimal germination also requires KNO_3 and MgSO_4 . Gibberellic acid had no effect on induction of spore germination in dark cultures.

Initial spore germination (Figure 150) is dependent on light (Hartmann & Weber 1990). As shown in *Marchantia*

polymorpha (Figure 1-Figure 12), following the initial series of reactions that ultimately result in the swelling of the spore, polarity develops (Figure 150). This becomes obvious when the protonema protrudes from the spore as a filamentous germ tube (Figure 150).

Spore germination (Figure 150) of *Marchantia polymorpha* (Figure 1-Figure 12) requires 10 hours or longer (Nakazato *et al.* 1999). The entire light spectrum is effective for germination, but red light is the most effective. The effect of red light is not reversed by subsequent far-red light.

Shibaya *et al.* (2005) demonstrated that AGPs (arabinogalactan proteins) differed before and after protonema development, suggesting that they are involved in differentiation and development. Furthermore, binding of the AGPs inhibits protonema development in *Marchantia polymorpha* (Figure 1-Figure 12), causing disturbances at the cell surface and inhibiting cell-wall synthesis.

Upon germination, one primary rhizoid appears (Figure 150) following the growth of the spore and chlorophyll development (O'Hanlon 1926). At a stage of about 30-40 cells a notch appears in the apical region of the young gametophyte (Figure 151-Figure 152). Although germination seems to benefit from more moderate light, growth is best at 12-15 hours of "good intensity light," with the best temperatures in the range of 18°-22°C. However optimum temperatures for sporophyte development are 10°-15°C. It is interesting that chlorophyll can form in the spores as they imbibe water in the dark. Furthermore, with glucose in the medium spore germination can occur in the dark, further supporting the conclusion that photosynthesis, hence the production of sugar, is necessary for germination.

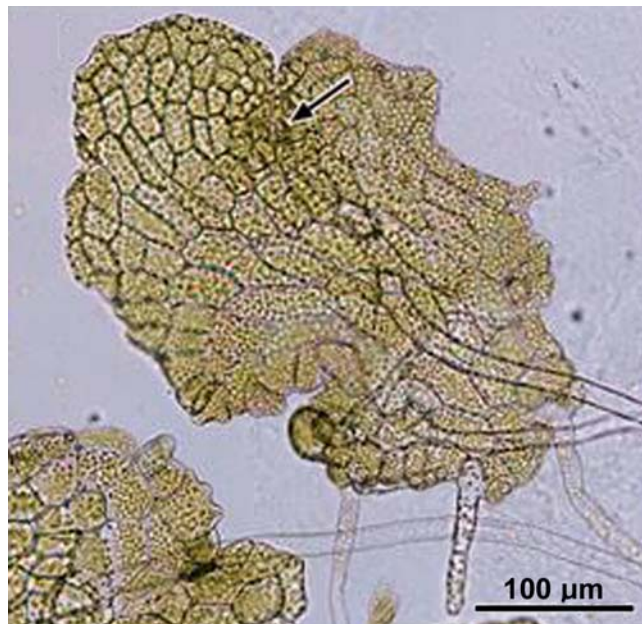


Figure 152. *Marchantia polymorpha* mature thalloid protonema with rhizoids. Arrow indicates apical notch. Photo by Masaki Shimamura, with permission.

gemmae (Figure 153-Figure 170)

Hallier (1966) experimented with germination of gemmae in *Marchantia polymorpha* (Figure 1-Figure 12).

He examined the effect of 2,4-mononitrophenol on respiration and induction of germination.

Terui (1981) reported that archegoniophore production in *Marchantia polymorpha* (Figure 1-Figure 12) occurs under long-day conditions, conditions that at the same time suppress the formation of gemmae cups. The gemmae cup suppression occurs about 20 days before the archegoniophore protrudes. High sucrose, on the other hand, induces gemmae cup development. When low light was provided for a prolonged time, it stimulated gemmae cup formation.

Une (1984) confirmed the negative correlation between gemmae cup (Figure 153-Figure 170) production and initiation of sexual structures. The gemmae cups occur more frequently on the margins of the colony, decreasing in number as sexual branches arise toward the inner part of that colony. This seems to relate to the age of the thalli and consequent change in the nutrient condition of the soil beneath the colony, with younger thalli occurring at the margins. Une also found that female plants produce sexual structures more frequently than do males.

Benson-Evans (1964) cultured *Marchantia polymorpha* (Figure 1-Figure 12) that produced gemmae (Figure 153-Figure 170) at 10°C in short days (6 hrs), the opposite conditions of those that resulted in archegoniophore production. On the other hand, Hedger *et al.* (1972) found that long days were needed to maintain the development of gemmalings of this species on an inorganic medium. Carbon additions did not affect the growth rate under long-day or short-day photoperiods.



Figure 153. *Marchantia polymorpha*; note the arrangement of the gemmae cups along the midrib in these older thalli. Photo by Jan-Peter Frahm, with permission.



Figure 154. *Marchantia polymorpha* gemmae cups arranged on midrib. Photo by Robert Klips, with permission.



Figure 155. *Marchantia polymorpha* showing gemmae cups along the midrib. Photo by Walter Obermayer, with permission.



Figure 158. *Marchantia polymorpha* gemmae cup. Photo by Bernard de Cuyper, with permission.



Figure 156. *Marchantia polymorpha* with red edges; note the rim within the gemmae cup, holding young gemmae within it. Photo by Brenda Dobbs, through Creative Commons.



Figure 159. *Marchantia polymorpha* gemmae in red cups that may indicate high light or other stress. Photo by Dick Haaksma, with permission.



Figure 157. *Marchantia polymorpha* gemmae cup with lenticular gemmae and thallus showing pores. Photo by Walter Obermayer, with permission.

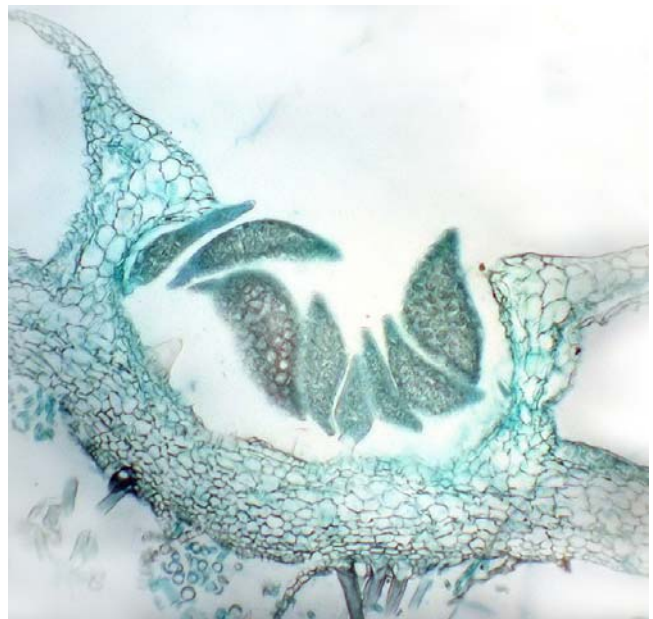


Figure 160. *Marchantia polymorpha* section of gemmae cup; note stalk on middle gemma. Photo by George Shepherd, with permission.



Figure 161. *Marchantia polymorpha* gemmae cup section. Note the inner rim that confines the young gemmae in the cup. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.



Figure 164. *Marchantia polymorpha* gemmae cups with a fringe; some gemmae are on the thallus, ungerminated. Photo from BlueRidgeKitties, through Creative Commons.



Figure 162. *Marchantia polymorpha* gemmae cups; note that some of the cups have disintegrated, permitting gemmae to escape easily, but mostly onto the thallus. Photo by Andrew Spink, with permission.



Figure 165. *Marchantia polymorpha* gemma. Photo by Des Callaghan, through Creative Commons.



Figure 163. *Marchantia polymorpha* gemmae cups as the mature gemmae begin to leave the cup. Photo by Walter Obermayer, with permission.



Figure 166. *Marchantia polymorpha* females showing gemmae cups on younger thalli and mature archegoniophores on older parts. Photo courtesy of Craig Waddell.

Tarén (1958) described the gemmae (Figure 165) as growing on stalks in the cup (Figure 160, Figure 167),

where they are surrounded by hairs that excrete slime (Figure 161). They have two growing regions and branches develop from both.



Figure 167. *Marchantia polymorpha* gemmae with arrows indicating stalks. Photo by Masaki Shimamura, with permission.

Hiwatashi *et al.* (2019) and Yasui *et al.* (2019) explored the genetic encoding for the genes that are involved in the regulation and formation of gemmae (Figure 153-Figure 165).

Gemmae cups (Figure 153-Figure 164) need nutrients to develop. Plants lacking nitrate become light green and have few gemmae cups and infrequent forking (Voth 1941). By contrast, those lacking phosphate become dark green and produce gemmae cups. They also have frequent dichotomies that cause the plants to form rosettes.

The mechanism of dispersal of the gemmae (Figure 153-Figure 165) has been a favorite example for textbooks. In fact, Laplaud *et al.* (2022) even presented their work at a meeting of the American Physical Society.

The splash cup (Figure 168) a dispersal mechanism served as the topic for an entire book (Brodie 1951). Brodie noted that splash cups commonly form 60-70° angles with their horizontal surface. These cups have a broad basal attachment and the propagules are **lenticular** (lens-shaped). He suggested that such cups could facilitate splashing of their contents for about 60 cm in *Marchantia polymorpha* (Figure 1-Figure 12). Equihua (1987) conducted further experiments, finding that raindrops could splash the gemmae up to 120 cm from the parent cup.



Figure 168. *Marchantia polymorpha* with gemmae cups. Note the bird's nest fungus (*Nidularia*) beside the thallus, a larger splash cup. Photo by Martin Hutten, with permission.

The ease of dispersal of the gemmae (Figure 153-Figure 165) has been a point of consternation for nursery growers, inspiring research on the mechanism. England and Jeger (2005) experimented with an overhead sprinkler system to determine various nozzle differences and their effects on dispersal. They demonstrated the effectiveness of the dispersal by using red dye in the cups in place of gemmae. At extreme water pressures of 1.5 and 3 bars, fewer gemmae were dispersed at all nozzle sizes. When the flow rate was adjusted to 160 L h⁻¹ dispersal number increased with height of the nozzle. At the other flow rates tested the nozzle height lacked any clear effect on number dispersed. The maximum distance travelled was 1.6 m.

The gemmae cup (Figure 153-Figure 164) has a decorated border and is cone-shaped (Figure 169). The cup-shaped container permits a raindrop to splash the gemmae to some distance from the cups (Laplaid *et al.* 2022). When a raindrop is non-centered when it lands, it creates a jet of water splash that carries a few gemmae with it. Laplaud and coworkers found that this propulsion can carry gemmae up to a meter from the cup. They are continuing their research to determine the effects of cone angle and the presence of decorations on its border (Figure 169).



Figure 169. *Marchantia polymorpha* gemma cup showing decorated border. Photo by John Forlonge through Flickr.

The climatic conditions can be right for germination, but the gemmae (Figure 153-Figure 164) could be in the wrong place. To determine if a substrate surface is present, ethylene is the most likely hormone to carry out this function. Because it is a gas, it is able to accumulate between a gemma and its substrate. Duarte (2020) used constant ethylene-signalling mutants to search for such a response. She found that the hormone ethylene could be part of the process of dormancy establishment, maintenance, and release of gemmae (Figure 153-Figure 165) in *Marchantia polymorpha* (Figure 1-Figure 12).

But experiments by Thullen (1965) suggest that the substrate is not important in the orientation of the rhizoids (Figure 82-Figure 54) of *Marchantia polymorpha* (Figure 1-Figure 12) gemmae (Figure 153-Figure 165). When the light source is above, surface gemmae produced 92% of their rhizoids on the side away from the light; those gemmae submersed in the agar produced only 85% on the side away from light. When the light source is beneath the gemmae, only 50 and 45% of the rhizoids, respectively,

appeared on the side opposite the light. When light was provided from beneath the gemmae it changed the percentage of rhizoids arising from the upper surface, but did not change the total number of rhizoids. Gemmae grown in total darkness produced rhizoids only on the lower side. Thullen concluded that both gravity and direction of light are important in rhizoid production. Light intensities seemed to have no effect. Temperature appears to be an important determinant in gemma germination of *Marchantia polymorpha* gemmae. Thullen found a sharp decrease in the number of rhizoids produced by gemmae at temperatures of 26°C and above.

Otto (1976) also demonstrated that the orientation of the gemma (Figure 153-Figure 165) determines where rhizoids form, with the gravitational force assuring their development on the lower side of the gemma. If that side is in contact with the substrate, more rhizoids are produced than if that surface is exposed to air. In the dark, only ~20% of the gemmae produce rhizoids. If the gravitational direction is alternated and no illumination is provided, no rhizoids form. The direction of light source influences the location of rhizoids only when the gravitational direction is not constant, with more rhizoids formed on the darker side.

As already noted, Otto and Halbsguth (1976) found that 350 nm light was the most effective wavelength to induce rhizoids in the gemmae of *Marchantia polymorpha* (Figure 1-Figure 12). Wavelengths below 550 or above 670 nm failed to stimulate rhizoid formation. The responses exhibited red far-red reversibility, suggesting that phytochrome was involved. IAA at 10^{-4} M causes the same effect as 1 hour of red radiation. They suggested that the wavelength of light might affect the influence of the phytochrome system on permeability of the membrane to IAA.

Rousseau (1952, 1953, 1954a) explored the influence of heteroauxins (IAA) on the growth of gemmae cups (Figure 169) in *Marchantia polymorpha* (Figure 1-Figure 12). Rousseau (1954b) further showed that coumarin inhibited the growth of the gemmae.

Prior and Brown (1970) attempted to identify the hormone(s) involved in initiation of rhizoids. They found no influence on germination or initial intercalary growth of gemmae (Figure 153-Figure 165) by 2,4-D, maleic acid hydrazide, gibberellic acid, or 2-furanacrylic acid (β -2-furylacrylic acid) in a range of concentrations. Gibberellic acid delayed development. But none of them caused a difference in number of rhizoids. They did, however, find that apical cell activity and cell elongation were suppressed. Both 2,4-D and maleic hydrazide suppressed internal differentiation. They did find that increasing age of the thallus caused greater sensitivity to both type and concentration of the regulator.

Dunham and Bryan (1968) explored the effects of amino acids on the development of the gemmalings in *Marchantia polymorpha* (Figure 1-Figure 12). At concentrations of 10^{-3} , l-isoleucine, l-leucine, l-methionine, or l-threonine resulted in a disruption of the apical regions. At lower concentrations, l-arginine, l-histidine, l-hydroxyproline, l-lysine, or l-tryptophan caused morphological irregularities. The irregularities were amino acid specific.

Gemmalings can reach reproductive maturity relatively quickly. Miller and Colaiaice (1969) found that within 3-6

weeks the gemmalings of *Marchantia polymorpha* (Figure 1-Figure 12) responded to a 1% agar medium in a 24-hour photoperiod at 23°C by producing antheridiophores and archegoniophores.

During (2001) hypothesized that the tradeoff between dispersability and longevity in soil diaspore banks could result in the scarcity of weedy species such as *Marchantia polymorpha* (Figure 1-Figure 12) in the soil bank. But in fact, the opposite appears to be the case. Species with large spores (i.e. limited dispersal distances) tend to be more persistent in the soil diaspore bank. Presumably, this larger diaspore would include the large gemmae of *M. polymorpha*. This is also in sharp contrast to seeds, wherein small seeds predominate in the diaspore bank. During suggests that there is more predation on larger seeds. Furthermore, bryophytes have much more representation of asexual diaspores than do seed plants. Such asexual diaspores as gemmae are generally produced through a greater part of the growing season than the very seasonal seeds or most kinds of bryophyte spores. The spores of *M. polymorpha* might be an exception to that spore seasonality, however. And certainly, its spores greatly exceed gemmae in number.

Miller and Alvarez (1965) emphasized that in gemmae both notches with apical cells are capable of growing. In their experiments with ^{60}Co they found that both cells had to be damaged to eliminate the survival of the gemma.

Miller (1966) described the gemmae of *Marchantia polymorpha* (Figure 1-Figure 12) as discoidal with two apical notches 180° from each other. Each notch has two apical cells. These apical cells, however, are not the only locations where growth, as cell proliferation, can occur. In irradiated gemmae, the nuclear volume is important in the cell survival, with larger nuclei having greater survival.

Nehira (1973, 1977) explored the development of the rhizoids of the gemmae of *Marchantia polymorpha* (Figure 1-Figure 12) and the adsorption of Ca on the rhizoids of the gemmae and its role in their differentiation.

One surprising effect on germination of the gemmae is that of nickel (Ni). Lepp and Hockenhull (1983) found that NiSO_4 served as a significant growth stimulus at 0.15 ppm Ni, but at concentrations above 0.25 ppm the gemmalings exhibited a toxic response. On the other hand, NiCl_2 stimulated growth of the gemmalings at 0.25 ppm Ni, and they could tolerate $\text{Ni}(\text{NO}_3)_2$ up to 0.5 ppm. Furthermore, they observed different toxicity depending on the environment of the gemmalings, with those from an urban area being more tolerant than those grown in the glasshouse.

regeneration and growth

Perhaps the earliest form of reproduction is **regeneration**. This ability to grow new plants from fragments is known from the *Cyanobacteria* and algae and permits them to survive from parts when most of the whole has died. It is particularly useful in aquatic organisms that can be moved rather easily to new locations by the water.

Vöchting (1885) noted the regeneration capability of the *Marchantiales* and in 1887 (Vöchting 1887) reported that that every living cell in *Marchantia polymorpha* (Figure 1-Figure 12) was capable of regenerating an entire plant. Frye (1928) determined the age of a population of *Marchantia polymorpha* in western Washington, USA, to

be four years old. Only three of these yearly growth segments was alive. The growth habit of *Marchantia polymorpha* to die at the postical end while growing at the bifurcating apical end permits the population to expand.

Giles (1971) discussed the mechanism that governed the stability of differentiation in *Marchantia*. These included a possible mechanism intrinsic to the cell, presumably in more highly differentiated species. However, in other bryophytes this control might be more affected by factors in the environment. But the factors affecting cellular dedifferentiation of an isolated fragment remained unknown. Giles suggested that these factors must be biochemical, probably involving RNA metabolism, and should be investigated.

Barner (1990) found that only the rhizoids from subcultured explants were able to regenerate thalli. The cultures required a directional light source.

Light is critical in regeneration of bryophytes (Nishihama *et al.* 2015). These researchers demonstrated that *Marchantia polymorpha* (Figure 1-Figure 12) has a single phytochrome gene and that phytochrome regulates re-entry into the cell cycle and control of cell shape in newly regenerating tissues. Nevertheless, light is not essential for regeneration, but it exhibits considerable control over the process. But, sugar can cause normal regeneration in the dark, suggesting the importance of photosynthesis to supply the energy.

Li (1990) described the difficulties of culturing gemmae and gametophytes of *Marchantia polymorpha* (Figure 1-Figure 12). They found that in their cultures it required dedifferentiation and redifferentiation, with rather specific cultural conditions and media. They used 2,4D and 3% sucrose to encourage the tissue development. This process could require as long as 10 months. Nevertheless, they found the process to be easier than in tracheophytes.

Bryophytes are known for their "extraordinary competency of regeneration" (Nishihama *et al.* 2015). This is possible due to their high level of developmental plasticity, permitting them to regenerate from cells, tissue fragments, branches, and even reproductive organs. Gardeners in Japan and elsewhere take advantage of this ability to propagate many plants from just a few by drying and fragmenting them (see Horticulture chapter in Volume 5).

Yoshikawa *et al.* (2018) found that the stress caused by wounding (Figure 170) induces phenylalanine ammonia lyases. These lyases initiate the accumulation of phenylpropanoids in *Marchantia polymorpha* (Figure 1-Figure 12). Wounding induces the biosynthesis of luteolin, apigenin, and isoriccardin C, all of which are biosynthesized through the phenylpropanoid pathway.

Ishida *et al.* (2022) found that diminished auxin signalling triggers the cellular reprogramming needed for regeneration in *Marchantia polymorpha* (Figure 1-Figure 12). Auxin is produced in apical cells, and removal of the apex enhances regeneration. Addition of auxin inhibits regeneration. They were able to identify the gene responsible for the cell proliferation needed for regeneration.

Mechanisms that control regeneration are also at play in controlling apical dominance (Figure 20) in *Marchantia polymorpha* (Figure 1-Figure 12). Davidonis and Munroe (1972) found that the larger lobe in this dichotomously

branching plant is always the one closest to the midrib. If these two lobes are separated by a cut while still in an early stage of lobe growth, the smaller lobe is no longer inhibited and is able to grow to equal size. Adding the auxin IAA to the smaller lobe after cutting will re-establish the dominance of the other lobe. The researchers suggested "that the type of neighbor lobe dominance in *Marchantia* resulting in its typical fan-shaped growth habit is maintained by auxin through a differential sensitivity of the two neighbors to auxin inhibition."



Figure 170. *Marchantia polymorpha* gemmae cups and antheridiophores in Europe; note the dead thalli and the red gemmae cups that indicate stress. At the same time, the apical portions continue to grow. Photo by Michael Lüth, with permission.

Maravolo *et al.* (1975) traced the transport of labelled IAA in the thallus of *Marchantia polymorpha* (Figure 1-Figure 12). There was a marked dominance of the hormone in the primary lobe. Movement to the secondary lobe could be enhanced by disruption of the conductive tissue or by removing the primary apex. Gibberellin and cytokinin also increased the activity of the IAA in the subdominant lobe, indicating that gradients of these three hormones might serve as growth regulators and these could be established independently at each apex.

Bhargava and Chauhan (1978) reported a dichotomously branched vegetative thallus at the tip of a gametophore stalk. I have to wonder if this is a germinated gemma, such as that observed by Li Zhang for *Marchantia emarginata* (Figure 171) rather than a branch.



Figure 171. *Marchantia emarginata* ssp. *tosana*, in Guangdong, S. China, with germinated gemmae and young thalli with gemmae cups growing on male receptacle arms. Photo courtesy of Li Zhang.

Kubota *et al.* (2013) were successful in achieving *Agrobacterium*-mediated (Figure 172) transformation in regenerating thalli of *Marchantia polymorpha* (Figure 1-Figure 12). Developmental timing is important to the success of this transformation. Previously, efficient *Agrobacterium*-mediated transformation had only been accomplished with sporelings. Iwakawa *et al.* (2021) further described a protocol useful for using this method in *M. polymorpha*. GUS (β -glucuronidase) activity was detected 2 days after infection and became saturated after 3 days.

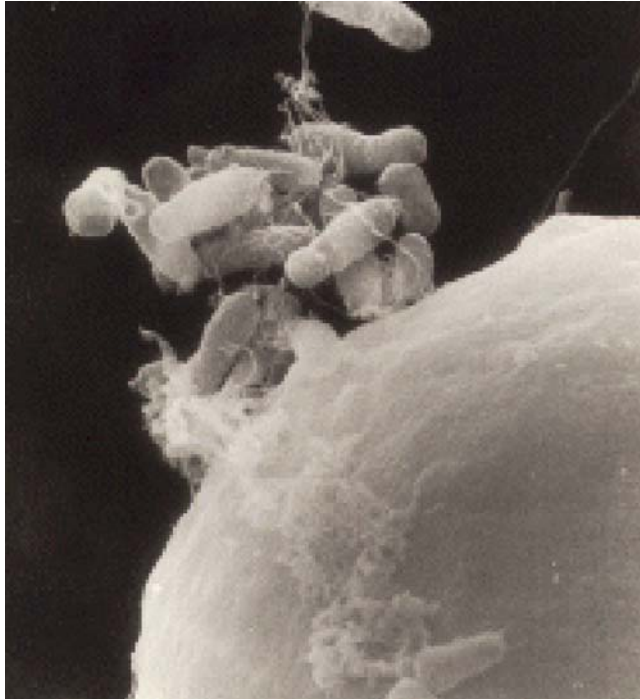


Figure 172. SEM of *Agrobacterium tumefaciens*; the genus *Agrobacterium* is used for genetic transformation and has been developed as a tool in *Marchantia polymorpha*. Photo from CDC, through public domain.

Shibaya and Sugawara (2007) found that the protoplasts of *Marchantia polymorpha* (Figure 1-Figure 12) could regenerate new cell walls in the initial culture, but the survival rate then decreased rapidly. β -glucosyl Yariv reagent (β glcY) could suppress this reduction in the survival rate. This substance binds to arabinogalactan proteins (AGPs) and does not increase survival except when added during the incipient cell wall regeneration. The researchers suggested that AGPs were involved in cell wall regeneration. Adding activated charcoal to the medium also permitted the cells to divide vigorously. It appears that AGPs and β -1,3-glucan are important in the survival and subsequent cell division of regenerated cells of *M. polymorpha* protoplast cultures.

Harashima and Ono (1991) tested the long-term culturing of *Marchantia polymorpha* (Figure 1-Figure 12). They found that after years of suspended culture they regained regeneration potential. The loss of morphogenetic potential in some was correlated with chromosome aberrations. They were able to maintain gemmae cultures for 213 months and spore cultures for 64 months.

Takenaka *et al.* (2000) used *Marchantia polymorpha* (Figure 1-Figure 12) for direct particle bombardment with

plasmid pMT. They produced hygromycin-resistant cell masses that developed into hygromycin-resistant thalli. These modified thalli transmitted the genetic modification to their gemmae for three generations. Hence, this could be a valuable tool for molecular analysis of this species and others.

Role

The role of aquatic bryophytes in accumulating pollutants is well known. Even *Marchantia polymorpha* (Figure 1-Figure 12) has been tested for its ability to purify water (Baltazar Pereda & Rebaza 2021). The researchers were concerned that there is no treatment for the wastewater for a sewage system in La Libertad. The water is used to irrigate stem crops, but it causes bad odors and endangers the health of those living around the canal. Both the water hyacinth (*Eichhornia crassipes* – Figure 173) and duckweed (*Lemna minor* – Figure 174) showed an excellent removal efficiency, improving oxygen and diminishing coliforms. However, the *Marchantia polymorpha* failed to make significant changes in water quality.



Figure 173. *Eichhornia crassipes* (water hyacinth), a species that is much more efficient at removing pollutants than is *Marchantia polymorpha*. Photo by Wouter Hagens, through public domain.



Figure 174. *Lemna minor* (duckweed), a species that is much more efficient at removing pollutants than is *Marchantia polymorpha*. Photo by Barbarossa, through Creative Commons.

Briggs (1972) reported that this species contains higher levels of lead than bryophytes that had been used in previous studies. Large quantities of plants could be grown quickly from gemmae, then exposed in a lead-polluted atmosphere to determine levels in the plants, and by extrapolation, the environment.

Accumulation of heavy metals characterizes many bryophytes (Cahuana & Aduvire 2019). Sharma (2007) placed *Marchantia polymorpha* (Figure 1-Figure 12) in moss bags to monitor pollution in several areas to compare pollutants. Plants accumulated the highest levels (2276 $\mu\text{g g}^{-1}$ dry weight) of lead in summer. But *Marchantia* lacks the high level of surface area seen in most mosses, making Sharma conclude that it a less useful accumulator than we might find in mosses and leafy liverworts.

Perhaps the most useful role of *Marchantia polymorpha* (Figure 1-Figure 12) is its use in the laboratory. The gemmae (Figure 153-Figure 165) of liverworts such as *M. polymorpha* represent isogenic progeny that can be used to experiment with gene expression (Kubota *et al.* 2013). The most common system used is to supply *Agrobacterium* (Figure 20) to regenerating thalli produced from these gemmae. These bacteria are able to transfer genes into the liverwort.

Interactions

Seed plants have an array of structural defenses as well as biochemical defenses against herbivores. Bryophytes, on the other hand, generally lack structural defenses, at least the elaborate ones such as spines, thick cuticle, and dense, lignified tissues. But the bryophytes, instead, are endowed with an extremely varied array of biochemical defenses.

Despite knowing about the wide diversity of secondary compounds in bryophytes, especially in liverworts, the research on their functions in the ecosystem and their sources, particularly in cooperation with microorganisms, has been rather neglected until recently (Stelmasiewicz *et al.* (2021). Noting that bryophytes produce many compounds unique to bryophytes, Stelmasiewicz and coworkers used a volatile extract to isolate the volatile compounds produced by the *Marchantia polymorpha* (Figure 1-Figure 12)-microorganism symbiosis. They isolated cuparane-, chamigrane-, acorane-, and thujopsane-type sesquiterpenoids from *Marchantia polymorpha*. These compounds proved to be active against some types of human cancer. But what do they do for the liverwort?

Poveda (2020a) touted the use of *Marchantia polymorpha* (Figure 1-Figure 12) as a model organism in studies of plant-microorganism interactions. He reviewed the published literature on these interactions.

Bacterial Interactions

As new studies are emerging, we are learning of the great dependence of bryophytes on other organisms. Bacteria are among these partners. Kutschera and Koopmann (2005) found that epiphytic methylobacteria promote the growth of *Marchantia polymorpha* (Figure 1-Figure 12). While living on the surfaces of plants these bacteria secrete cytokinins. The bacterial extracts had no effect on seeds of maize or sunflower, but did promote the growth of isolated *M. polymorpha* gemmae (Figure 153-Figure 165) on agar plates.

Alcaraz *et al.* (2018) identified *Bryobacter*, *Lysobacter* (Figure 175), *Methylobacterium* (Figure 176), *Paenibacillus* (Figure 177), *Pirellula*, *Rhizobium* (Figure 178-Figure 179), and *Steroidobacter* from *Marchantia polymorpha* (Figure 1-Figure 12) as well as from *M. paleacea* (Figure 14; see part 1 of this chapter). These plant symbionts are known for plant-growth promotion, complex exudate degradation, nitrogen fixation, methylophiles, are disease-suppressive bacteria, and are hosted within the plant thallus.

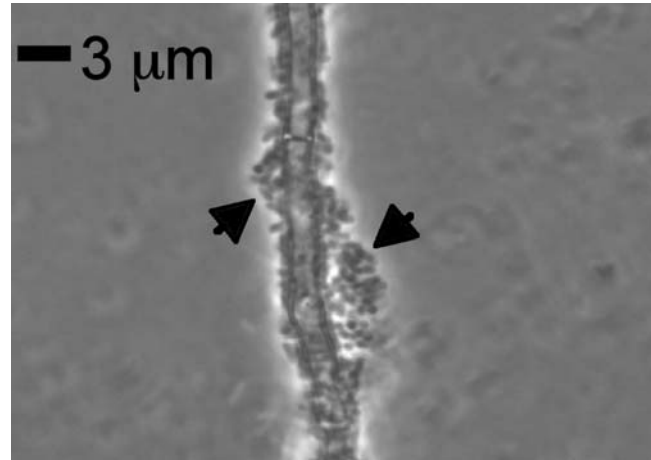


Figure 175. *Lysobacter* hyphae, a genus that is sometimes associated with *Marchantia polymorpha*. Photo by Don Kobayashi, through Creative Commons.

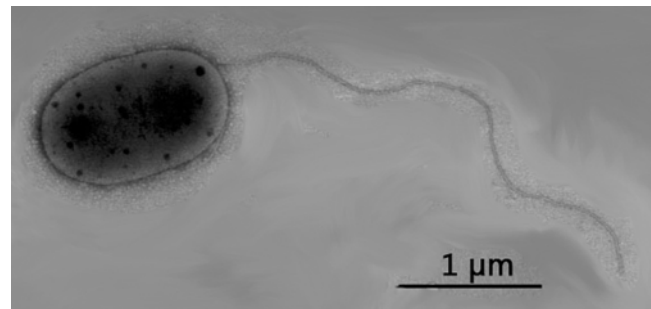


Figure 176. *Methylobacterium jeotgali*; *Methylobacterium* is a genus that is sometimes associated with *Marchantia polymorpha*. Photo from Aslam *et al.* 2007, through Creative Commons.

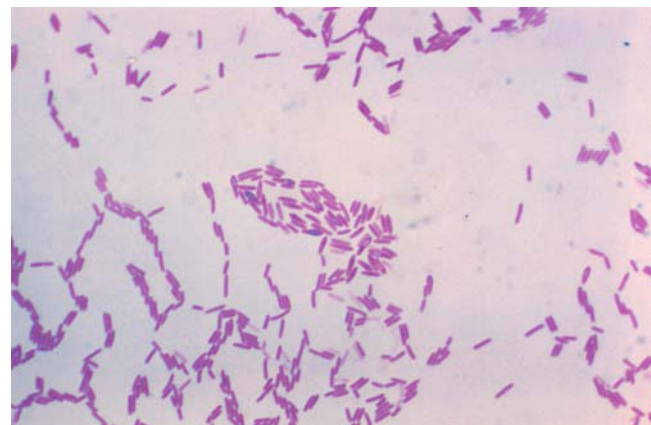


Figure 177. *Paenibacillus polymyxa*; *Paenibacillus* is a genus that is sometimes associated with *Marchantia polymorpha*. Photo from CDC, through public domain.



Figure 178. *Rhizobium* root nodule on *Vicia faba* (broad bean) roots; *Rhizobium* is a nitrogen fixer and known associate of *Marchantia polymorpha*. Photo by Whitney Cranshaw, through Creative Commons.



Figure 179. *Rhizobium* nodule, showing typical red color. Photo from CSIRO, through Creative Commons.

Bryophytes are used in some cultures as medicinal plants. Some groups of Indonesian people use *Marchantia polymorpha* (Figure 1-Figure 12) as a traditional medicine to treat skin infections (Ramadhan & Agustien 2019). The species has flavones and flavone glycosides as well as simple terpenoids that are able to inhibit the multiplication of bacteria. These researchers chose to isolate endophytic bacteria from *Marchantia polymorpha*. Six species of endophytic bacteria that have the potential to produce antibiotics were successfully isolated from the thallus; these bacteria were successful against *Staphylococcus aureus* (Figure 180).

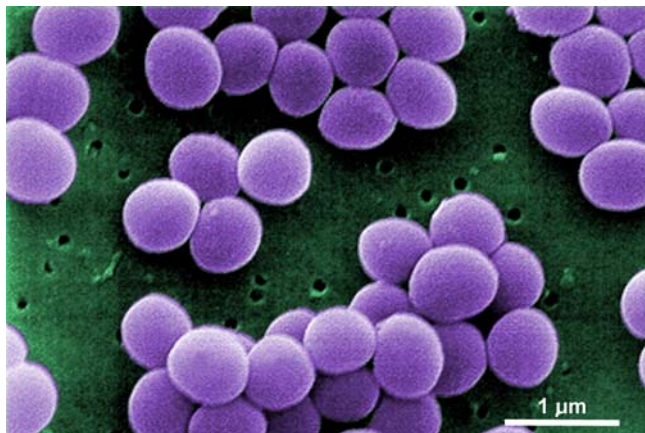


Figure 180. Colorized SEM of bacterium *Staphylococcus aureus*, a species that is inhibited by antibiotics produced by other bacteria endophytic in *Marchantia polymorpha*. Photo by Janice Haney Carr, CDC, through public domain.

Himanshu *et al.* (2007) found that acetone-soluble extracts of *Marchantia polymorpha* (Figure 1-Figure 12) had antibiotic activity against the Gram negative bacteria *Escherichia coli* (Figure 16) and *Salmonella typhi* (Figure 181) and two fungi *Aspergillus niger* (Figure 182) and *Candida albicans* (Figure 183-Figure 184), all human pathogens. Such antibiotic activity makes this species of interest for finding applications to replace the ever-growing number of antibiotics that are helping to create "super bugs" with antibiotic resistance. But do they help the bryophyte? One indication that they might not, at least as antibacterial agents, is that the water soluble extracts did not show any inhibitory effects on the pathogens tested.

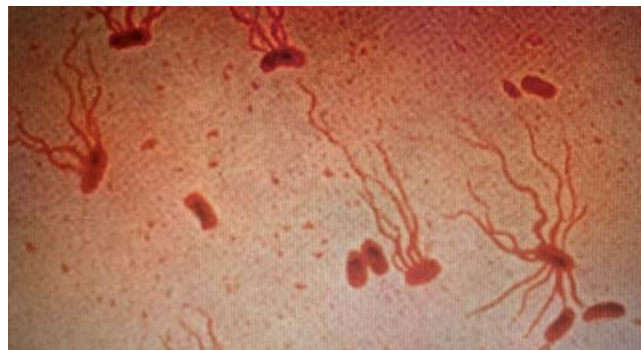


Figure 181. *Salmonella typhi* with flagellar stain, a species of bacteria that experiences antibiotic activity from acetone-soluble extracts of *Marchantia polymorpha*. Photo by Microbewriter, through Creative Commons.

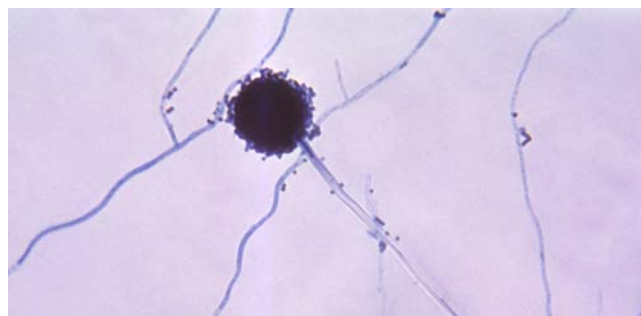


Figure 182. *Aspergillus niger*, a species of fungus that experiences antibiotic activity from acetone-soluble extracts of *Marchantia polymorpha*. Photo from CDC, through Creative Commons.



Figure 183. *Candida albicans*, fungus that experiences antibiotic activity from acetone-soluble extracts of *Marchantia polymorpha*. Photo by Graham Colm, through Creative Commons.

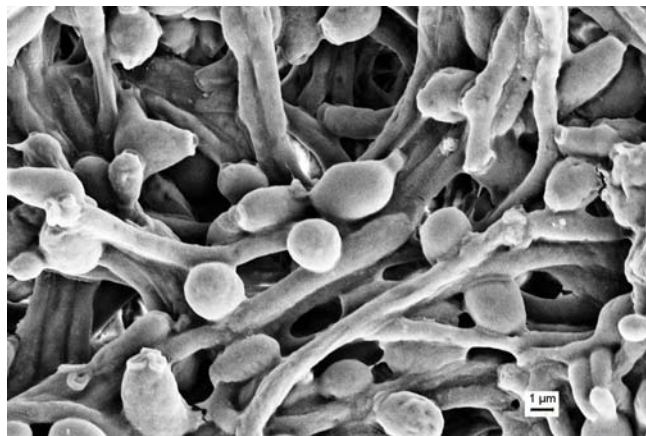


Figure 184. SEM of *Candida albicans*. Photo by Vader1941, through Creative Commons.

Using specimens from Vietnam, Son *et al.* (2020) isolated lunularin, marchantin A, isoriccardin C, luteolin, and apigenin from *Marchantia polymorpha* (Figure 1-Figure 12). Isoriccardin C had "remarkable" antibacterial activity against *Staphylococcus epidermidis* (Figure 185). Several extracts exhibited anticancer activity.

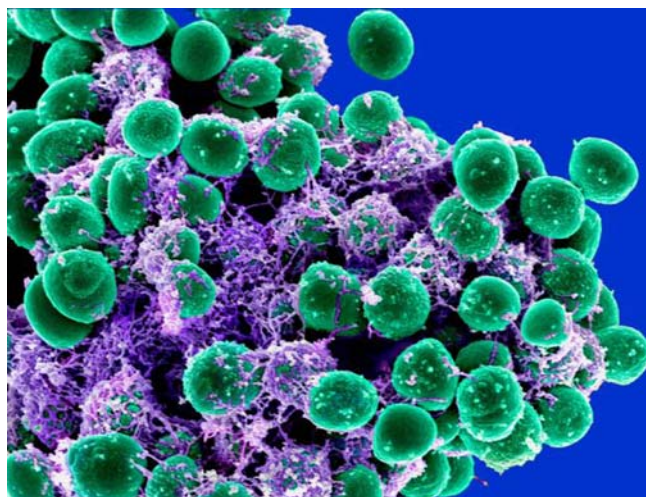


Figure 185. *Staphylococcus epidermidis*, a species that experiences strong negative effects from isoriccardin C from *Marchantia polymorpha*. Photo from NIAID, through Creative Commons.

Ivković *et al.* (2021) identified terpenes, oils, sugars, and bis-benzyls in methanol extracts of *Marchantia polymorpha* (Figure 1-Figure 12). These extracts were effective in inhibiting Gram-positive bacteria but had no effect on Gram-negative bacteria.

Mewari and Kumar (2008) tested antibacterial activity using crude methanol and flavonoid extracts of *Marchantia polymorpha* (Figure 1-Figure 12) against three strains of bacteria [*Escherichia coli* (Figure 16), *Proteus mirabilis* (Gram negative; Figure 186), and *Staphylococcus aureus* (Figure 180) (Gram positive)] and four of fungi [*Aspergillus flavus* (Figure 187), *A. niger* (Figure 182), *Candida albicans* (Figure 183-Figure 184), and *Trichophyton mentagrophytes* (Figure 188)]. All the microorganisms proved to be sensitive to all of the extracts, suggesting that *M. polymorpha* had a good potential as a source of antimicrobial drugs.

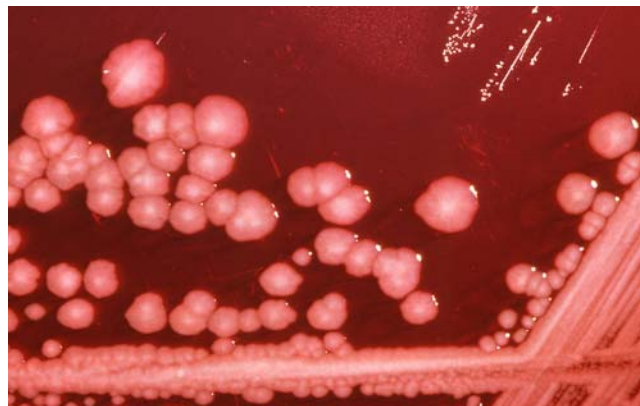


Figure 186. *Proteus mirabilis*, a bacterial species that is sensitive to crude methanol and flavonoid extracts of *Marchantia polymorpha*. Photo from CDC, through public domain.



Figure 187. *Aspergillus flavus*, fungal species that is sensitive to crude methanol and flavonoid extracts of *Marchantia polymorpha*. Photo from Medmyco, through Creative Commons.



Figure 188. *Trichophyton mentagrophytes*, fungal species that is sensitive to crude methanol and flavonoid extracts of *Marchantia polymorpha*. Photo by Dr. Libero Ajello, CDC, through public domain.

Wang *et al.* (2016) found that the total flavonoid content of the archegoniophore was ten times that of the thallose gametophyte. This correlated with greater bioactivity in the archegoniophore, potentially protecting the reproductive structure from bacteria, fungi, and perhaps even herbivory.

Most of the work on antibacterial activity by secondary compounds in bryophytes has been done on human pathogens. The question remains, what can they do for bryophytes? De *et al.* (2015) noted that bryophytes lack the mechanical protections available to tracheophytes and that instead use secondary metabolites as protectants. If such is the case, then we should see greater selection for higher concentrations in bryophytes from habitats where there are more herbivores or pathogens present. However, few studies have attempted to address this hypothesis. De and coworkers compared secondary compounds from *Marchantia polymorpha* (Figure 1-Figure 12) from five different altitudes in Darjeeling Himalayas. To my surprise, they found higher antibacterial activity at higher altitudes. This suggests to me that their antibacterial activity is not the most important factor operating in selection for these secondary compounds.

Protozoa Interactions

Protozoa are also inhibited by extracts from *Marchantia polymorpha* (Figure 1-Figure 12). Jensen *et al.* (2012) found that marchantin A extracted from this liverwort inhibited the proliferation of the protozoan *Plasmodium falciparum* (Figure 189). *Trypanosoma brucei rhodesiense* (Figure 190), *T. cruzi* (Figure 191), and *Leishmania donovani* (Figure 192), all human pathogens, likewise experienced inhibition by marchantin A.

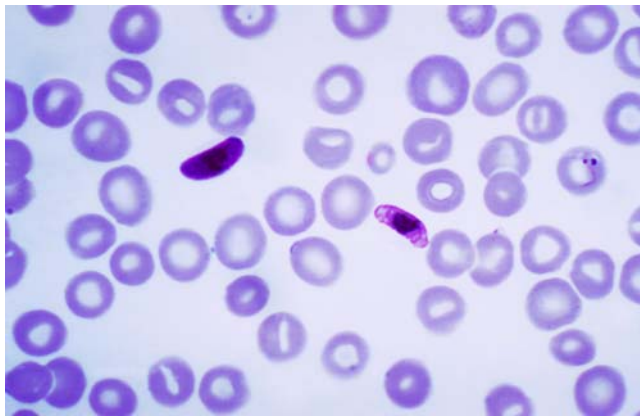


Figure 189. *Plasmodium falciparum*, protozoan inhibited by marchantin A extracted from *Marchantia polymorpha*. Photo from CDC, through public domain.

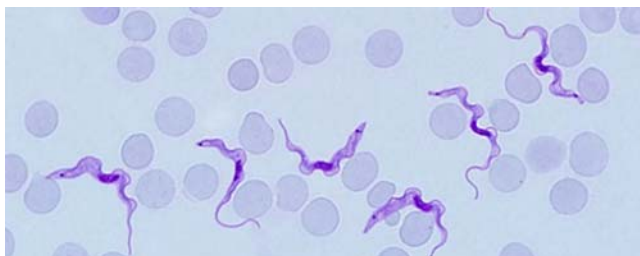


Figure 190. *Trypanosoma brucei*, protozoan inhibited by marchantin A extracted from *Marchantia polymorpha*. Photo from CDC, through public domain.

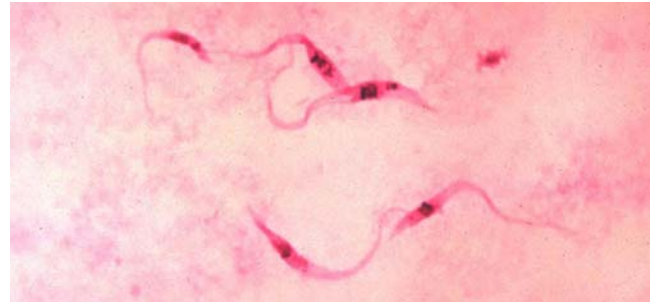


Figure 191. *Trypanosoma cruzi*, protozoan inhibited by marchantin A extracted from *Marchantia polymorpha*. Photo by Dr. Myron G. Schultz, CDC, through public domain.

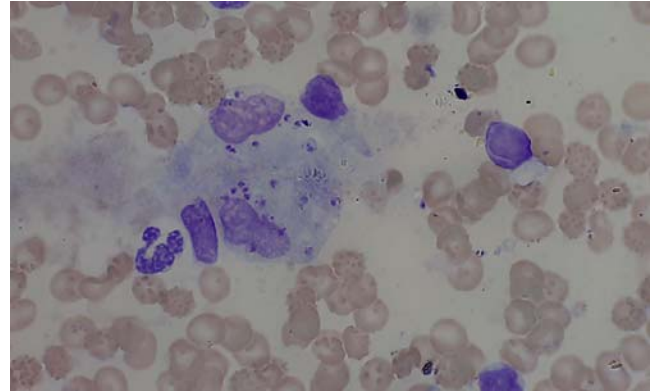


Figure 192. *Leishmania donovani*, protozoan inhibited by marchantin A extracted from *Marchantia polymorpha*. Photo by Ajay Kumar Chaurasiya, through Creative Commons.

Fungal Interactions

The associations of fungi with bryophytes was a long-neglected topic in bryology. In fact, many seemed to assume that fungi could not live with bryophytes, or that the bryophytes had too low a nutrient concentration to be of value to the fungi. But this view has now been disproved.

endophytes

Döbbeler (1979) found fungal infections in the rhizoids of *Marchantia polymorpha* (Figure 1-Figure 12). Duckett and Ligrone (2003) further reported that the living smooth rhizoids of **Marchantiales** contained the hyphae of fungal endophytes (Figure 193). Benkert (1998) reported a fungus (*Octospora inthacaensis*) growing on *M. polymorpha*. But what does this relationship mean for the bryophyte?

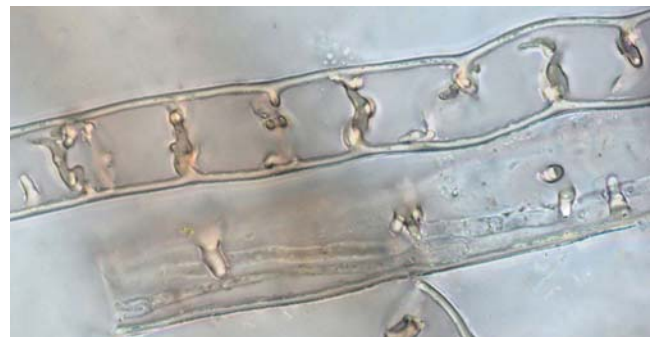


Figure 193. Rhizoids of *Marchantia polymorpha* with fungus in lower rhizoid. Photo by Walter Obermayer, with permission.

Döbbeler (2002) reported that the Ascomycetes (fungi) growing on the gametophytes of bryophytes typically did not form ascomata on general locations on their bryophyte hosts, but instead occupied distinct locations that were specific for the host species. These microsites usually offered protection against rapid water loss by the fungus and permitted enough exposure to permit unhindered spore dispersal of the fungus by air currents. Among the thallose liverworts, the ascomata were typically immersed in the spongy thalli. But what do they do to or for the liverwort?

Fungal actions may be subtle, and certainly fungi can inhabit *Marchantia polymorpha* (Figure 1-Figure 12). Guminska and Mierzenska (1992) reported that the fungus *Loreleia marchantiae* (= *Gerronema marchantiae*; Figure 194) was associated with this species and with *Nostoc* sp. (Cyanobacteria).



Figure 194. *Loreleia marchantiae* growing with *Marchantia polymorpha*. Photo by Alexey Sergeev, with permission.

Nelson and Shaw (2019) found a very diverse fungal community that was distinct between patches of *Marchantia polymorpha* (Figure 1-Figure 12). Only a few core fungi were the same across widely separated populations across the USA. However, they found that the two methods used detected different species.

symbiosis?

Trees are usually dependent on fungal partners in their roots as a means of scavenging nutrients from a much larger soil volume than that available to roots. Hanke and Rensing (2010) considered that *Marchantia polymorpha* (Figure 1-Figure 12), with what is now a sequenced genome, provided many genetic tools by which to establish the association of fungi such as *Glomus intraradices* with gametophyte plants, including culturing, infection strategies, and staining procedures.

Marchantia species, including *M. polymorpha* ssp. *montivagans* (Figure 34) (Ligrone *et al.* 2007), often form mycorrhizal associations (Bowman *et al.* 2016). However, such associations are not known in *M. polymorpha* ssp. *polymorpha* or ssp. *ruderalis* (Figure 6-Figure 8, Figure 17-Figure 19). Bowman and coworkers (Bowman *et al.* 2017) attribute this independence to increased transport capacity in the subspecies, permitting them to be weedy colonizers of newly disturbed habitats.

pathogens

Certainly not all fungi have a friendly relationship with the bryophytes. Verkley *et al.* (1997) reported the ascomycete *Bryoscyphus atromarginatus* (Figure 195) as a new species parasitizing the thallus of *Marchantia polymorpha* (Figure 1-Figure 12) in the Netherlands. The type specimen of the species named as *Bryoscyphus marchantiae* (Figure 196) was actually collected from *Reboulia haemisphaerica* (Figure 197). The description given by Naumov (1964) of the collection he reported as *Hymenoscyphus marchantiae* (Figure 198) on *M. polymorpha* agrees well with the new species described by Verkley *et al.* Naumov commented that it appeared that this could be a new species.



Figure 195. *Bryoscyphus atromarginatus* growing on thallus of *Marchantia*. Photo ©Michel Hairaud, through Creative Commons.



Figure 196. *Bryoscyphus marchantiae* on *Marchantia*. Photo ©Iain Munro, through Creative Commons.



Figure 197. *Reboulia hemisphaerica*, apparently also another host substrate for *Bryoscyphus atromarginatus*. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 198. *Hymenoscyphus kathiae* on submerged twig of *Alnus glutinosa*; *Hymenoscyphus marchantiae* can inhabit *Marchantia polymorpha*. Photo ©Nick Aplin, through Creative Commons.

Fraiture and Ertz (2007) reported that the fungus *Didymosphaeria marchantiae* (Figure 199) was a parasite on *Marchantia polymorpha* (Figure 1-Figure 12).



Figure 199. *Didymosphaeria marchantiae* infecting leafy liverwort, but also known to be a parasite on *Marchantia polymorpha*. Photo by Dragiša Savić, with permission.

Nelson (2017; Nelson *et al.* 2018) noted the lack of studies on fungal endophyte interactions with bryophytes while at the same time realizing that the reactions of the plants to these organisms is quite varied. They found that such fungi in *Marchantia polymorpha* (Figure 1-Figure 12) ranged from "aggressively pathogenic to strongly growth-promoting." Nevertheless, most of them seemed to cause no change in host growth. Furthermore, those that promoted growth were dependent on nutrient concentrations and their effects on growth were inhibited by inoculation of the liverwort with multiple fungi. Some of the fungi that are known as pathogens in tracheophytes were actually beneficial to the liverworts.

With the large arsenal of secondary compounds, we should consider it to be likely that some of these are effective against fungal pathogens. Takikawa *et al.* (2014) inoculated several powdery mildews on the thallus and gemmae (Figure 153-Figure 165) of *Marchantia polymorpha* (Figure 1-Figure 12). The conidia and germ tubes of *Erysiphe trifoliorum* (Figure 200) were destroyed. The germ tube tip was destroyed in four hours when it reached the gemma leaf surface. After six hours the conidial bodies were destroyed as well. On the other hand, *Oidium neolycopersici* (see Figure 201) continued growth with no destruction of conidia and produced normal appressoria on the surface of the gemmae.



Figure 200. *Erysiphe trifoliorum* on *Trifolium pratense* leaves; this fungus is destroyed when inoculated on thallus or gemmae of *Marchantia polymorpha*. Photo by John Plischke, through Creative Commons.

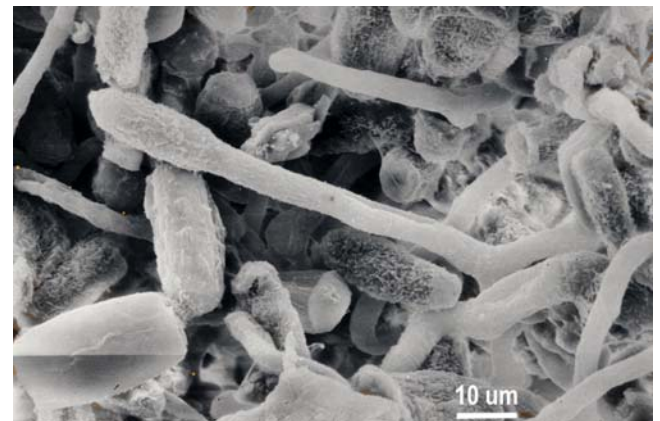


Figure 201. SEM of *Oidium* sp; *Oidium neolycopersici* continued growth with no destruction of conidia and produced normal appressoria on surface of gemmae of *Marchantia polymorpha*. Photo by Gerald Holmes, through Creative Commons.

Peumans *et al.* (2007) found the surprising result that a **lectin** (protein that binds to carbohydrates – features that lectins use to defend plants in nature may cause problems during human digestion; lectins resist being broken down in gut and are stable in acidic environments, features that protect lectin-containing plants in nature) identified in *Marchantia polymorpha* (Figure 1-Figure 12) had never been found in any plant, but that instead it closely resembles one from the common edible mushroom *Agaricus bisporus* (Figure 202), *i.e.*, it is a lectin that was hitherto considered to be exclusive to fungi. It was also confirmed in the moss *Syntrichia ruralis* (Figure 203).



Figure 202. *Agaricus bisporus*, common edible mushroom that has lectin similar to one found in *Marchantia polymorpha*. Photo by Мышь Денис, through Creative Commons.



Figure 203. *Syntrichia ruralis*, species that shares same lectin as that found in *Marchantia polymorpha*. Photo by Alexis Orion, through Creative Commons.

Carella *et al.* (2019) explored the molecular response of *Marchantia polymorpha* (Figure 1-Figure 12) to oomycete infection. These early land plants necessarily had to defend against pathogens with their new exposure to land. We know of many pathogens and defenses in tracheophytes, but we know little about the plant-pathogen interactions in these early land plants. Whereas we have explored their medical use and even uses as fungicides for

tracheophytes, we know relatively little about their functions in the bryophytes that produce them. Carella and coworkers traced the response of this liverwort to the oomycete pathogen *Phytophthora palmivora* (Figure 204). They found that the liverwort shared a set of orthologous microbe-responsive genes with tracheophytes. These include members of the phenylpropanoid metabolic pathway. Using both knockout and induction techniques, they determined that MpMyb14 leads to the accumulation of anthocyanin-like pigments (**auronidin**) while greatly enhancing the resistance of *Marchantia polymorpha* to *Phytophthora palmivora* infection. The auronidin prevented the penetration of the fungal hyphae into the pigmented portions of the liverwort.



Figure 204. *Phytophthora palmivora* infecting papaya; *Marchantia polymorpha* was used to identify the mechanism of resistance to this plant pathogen. Photo by Scot Nelson, through Creative Commons.

Gahtori and Chaturvedi (2011) used methanol and chloroform extracts to test the activity of *Marchantia polymorpha* (Figure 1-Figure 12) against three bacterial and four fungal species. The extracts exhibited antimicrobial activity with potency that differed among organisms that were pathogenic to both plants and animals. Some were inhibitory toward multiple organisms, and others showed potential.

In other experiments, Mewari and Kumar (2011) made similar tests and found that *Marchantia polymorpha* (Figure 1-Figure 12) completely inhibited the mycelial growth of the fungal pathogen *Rhizoctonia solani* (Figure 205). Furthermore, most extracts also caused 100% inhibition of spore germination of fungal pathogens *Alternaria solani* (Figure 206) and *Fusarium oxysporum* (Figure 207).



Figure 205. *Rhizoctonia solani*, fungal species that is completely inhibited by extracts of *Marchantia polymorpha*. Photo by Gerald Holmes, through Creative Commons.



Figure 206. *Alternaria solani* on tomato leaf. Extracts of *Marchantia polymorpha* completely inhibit spore germination of this fungal pathogen. Photo from USDA Cooperative Extension, through Creative Commons.



Figure 207. *Fusarium oxysporum* on *Cucumis sativa*; extracts of *Marchantia polymorpha* completely inhibit spore germination of this fungal pathogen. Photo by Jerzy Opiola, through Creative Commons.

In China, Niu *et al.* (2006) isolated seven bis[bibenzyl]-type macrocycles, including three new ones. They assessed their antifungal activities against *Candida albicans* (Figure 183-Figure 184), using TLC bioautography. This fungal species is an opportunistic pathogenic yeast that is the most prevalent cause of fungal infections in humans. Several of the compounds proved to be active against this fungus.

Purkon *et al.* (2022) reported the medicinal use of *Marchantia* in China, North America, Ancient Greece, and Indonesia for treatment of open wounds, burns, hepatotoxicity (damage to liver caused by medicine, chemical, or herbal or dietary supplement), and infection prevention.

Matsui *et al.* (2020) found antagonism between salicylic acid and jasmonate in the fungal pathogen interaction with *Marchantia polymorpha* (Figure 1-Figure 12). They isolated *Bjerkandera adusta* (Figure 208), *Irpex lacteus* (Figure 209), and *Phaeophlebiopsis peniophoroides* (Figure 210) from diseased *M. polymorpha*. They found that salicylic acid promotes infection by *I. lacteus*, but this action is suppressed when jasmonate is treated at the same time.



Figure 208. *Bjerkandera adusta*, species that has been isolated from diseased *Marchantia polymorpha*. Photo by James K. Lindsey, with permission.



Figure 209. *Irpex lacteus*, species that has been isolated from diseased *Marchantia polymorpha*. Jasmonate can stop the infection. Photo by Otto Miettinen, through Creative Commons.



Figure 210. *Phaeophlebiopsis ravenelii*; *Phaeophlebiopsis peniophoroides* is a species that has been isolated from diseased *Marchantia polymorpha*. Photo by James K. Lindsey, with permission.

Hipol and Broñola-Hipol (2016) screened 22 fungal associates of *Marchantia polymorpha* (Figure 1-Figure 12) for their carboxyl esterase activity. Half were endophytes and half were epiphytes on the liverwort. All of the isolates produced this enzyme, with the fungus *Colletotrichum boninense* (see Figure 211) producing the lowest levels of the enzyme and *Nodulisporium* sp. (Figure 212) produced the highest levels.



Figure 211. *Colletotrichum lindemuthianum*; *Colletotrichum boninense* produced lowest levels of carboxyl esterase activity among 22 fungi isolated from association with *Marchantia polymorpha*. Photo by David B. Langston, through Creative Commons.



Figure 212. *Nodulisporium cecidiogenes* on rotten wood; species of *Nodulisporium* produced highest levels of carboxyl esterase activity among 22 fungi isolated from association with *Marchantia polymorpha*. Photo by Alexey Sergeev, with permission.

Poveda (2020b) asked if the arbuscular-mycorrhizal fungal (AMF) association with *Marchantia polymorpha* ssp. *ruderalis* (Figure 6-Figure 8) was beneficial or harmful. Despite all the studies on this species, this is one of the many questions remaining unanswered. They found that *in vitro*, the interaction is detrimental, causing reduced growth and tissue viability, with only those elements involved in plant defenses increasing in nutritional content. These changes were coupled with increases in reactive oxygen species (ROS) content. One such fungus is *Rhizophagus fasciculatus* (Figure 213) – a species present only when there is evidence of thallus damage. Hence, this fungus appears to be a pathogen to *Marchantia polymorpha* ssp. *ruderalis*. Further examination of fungi with bryophytes could reveal interesting symbiotic relationships, modes of infection, and defenses against fungi. *Marchantia polymorpha* (Figure 1-Figure 12) is large enough, cultures easily, and is known to respond in a variety of ways to fungal invaders. Hence, it would be a good initial test organism to help us understand these relationships and their effects in their ecosystem.

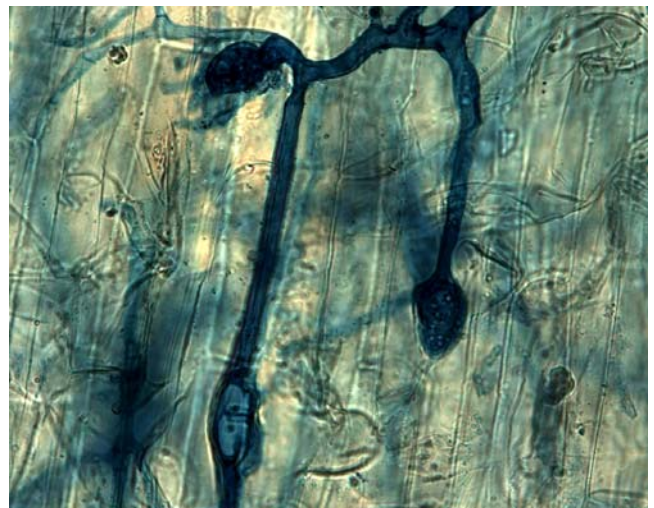


Figure 213. *Rhizophagus irregularis*; *Rhizophagus fasciculatus* is fungal pathogen on *Marchantia polymorpha* ssp. *ruderalis*. Photo by Mylène Durant, through Creative Commons.

Invertebrate Interactions

Herbivory (Figure 214) on liverworts seemed to be a blind spot in older bryological studies, but recent reports tell us it is real. Sawangproh *et al.* (2016) reported the feeding of *Scatopsciara cunicularius* (Diptera: Sciaridae) larvae on *Marchantia polymorpha* (Figure 1-Figure 12). They found that larvae fed at 12°C fed more slowly than those at 22°C, but those at the lower temperature fed over a longer period of time, ultimately causing more damage to the liverwort. The researchers suggested using these larvae to control the invasion of the liverwort in plant nurseries and greenhouses. I wonder what other plants they eat?



Figure 214. *Marchantia polymorpha* female eaten on one of the receptacle fingers. Photo by Li Zhang, with permission.

Koeduka *et al.* (2022) found that allene oxide synthase (AOS) from *Marchantia polymorpha* (Figure 1-Figure 12) is important in inhibiting the survival rate and oviposition of the spider mite *Tetranychus urticae* (see Figure 215). When mutants lacking the AOS gene were subjected to these spider mites, survival of the mites was greater than in the wild type. Their research indicated that defense system signalling pathways respond to spider mite presence.



Figure 215. *Marchantia polymorpha* gemmae cups with mite, possibly spider mite. Photo By Bernard de Cuyper, with permission.

Some invertebrates commonly live among bryophytes, *Marchantia polymorpha* (Figure 1-Figure 12) included. A common bryophyte inhabitant is the isopod (Figure 216). In some cases these might actually eat the bryophytes. In other cases, there is no evidence of herbivory. Spiders also build webs (Figure 217), perhaps catching some of the other inhabitants of the thallus community.



Figure 216. *Marchantia polymorpha* and isopod; there does not seem to be any evidence of herbivory – yet. Photo by Walter Obermayer, with permission.



Figure 217. *Marchantia polymorpha* males with gemmae cups and spider web. Photo by Nancy Leonard, with permission.

The importance of bryophyte herbivory in the ecosystem is virtually unknown. This seems to be particularly true for *Marchantia polymorpha* (Figure 1-Figure 12). As the climate shifts and herbaceous plant communities change, it is possible some herbivores could shift to consumption of bryophytes. Few studies have addressed the effects of temperature or precipitation patterns on the interaction of invertebrates with bryophytes.

Tracheophyte Interactions

Little has been written about the interaction between bryophytes and tracheophytes. Bryophytes are not good competitors with tracheophytes because of the small size of

the bryophytes. How, then, do the tiny bryophytes survive in habitats dominated by tracheophytes?

Whittemore (1991) suggested that bryophytes such as those in the **Marchantiales** might be toxic not only to herbivores and pathogens, but also to competing plants such as tracheophytes. On the other hand, Asakawa *et al.* (1982) found that compounds from the tracheophyte family Apiaceae could inhibit the growth of *Marchantia polymorpha* (Figure 1-Figure 12).

Nakayama *et al.* (1996) tested the inhibitory effects of lunularic acid and its analogs on the growth of *Marchantia polymorpha* (Figure 1-Figure 12), *Rorippa nasturtium-aquaticum* (watercress; Figure 218), and *Phleum pratense* (timothy grass; Figure 219). The analogs proved to be more inhibitory than lunularic acid, suggesting that the liverworts that produce this hormone might have less growth inhibitory activity than tracheophytes, or they are somehow protected from its inhibitory effects.



Figure 218. *Rorippa nasturtium-aquaticum*, plant that has less inhibition by lunularic acid than more advanced analogs. Photo by Matt Lavin, through Creative Commons.



Figure 219. *Phleum pratense*, species that has less inhibition by lunularic acid than more advanced analogs. Photo through Creative Commons.

Sharma *et al.* (2009) used *Marchantia polymorpha* (Figure 1-Figure 12) water extracts as one of the bryophyte species they tested for allelopathic effects on the flowering plant *Bidens biternata* (Figure 220). Although there was 100% inhibition of seed germination in the lipophilic extract, germination was not delayed significantly in water extracts. Sharma and coworkers reasoned that hydrophilic allelochemicals would be released more easily into the environment, but that these would also leach from the soil more quickly, thus favoring hydrophobic allelopathic compounds as a better defense.



Figure 220. *Bidens biternata*, species for which seed germination is 100% inhibited by lipophilic extracts of *Marchantia polymorpha*, but not by water extracts. Photo by J. M. Barg, through Creative Commons.

Kaihara and Takimoto (1990) found that a water extract of *Marchantia polymorpha* (Figure 1-Figure 12) could inhibit the flower-inducing activity of L-pipecolic acid. This L-pipecolic behaved synergistically with water extracts of *Lemna aequinoctialis* (duckweed; Figure 221) and *Ipomoea hederacea* (ivy-leaved morning glory; Figure 222) to enhance flowering, but all other tested plants suppressed it. This flowering inhibition is a sneaky way for the liverwort to compete with tracheophytes, but we have no field assessment of its effectiveness.



Figure 221. *Lemna aequinoctialis*, plant for which its water extracts work synergistically with L-pipecolic to enhance flowering. Photo by Kevin Thiele, through Creative Commons.



Figure 222. *Ipomoea hederacea*, plant for which its water extracts work synergistically with L-pipecolic to enhance flowering. Photo by Bobby Hattaway <www.discoverlife.org>, with online permission.

Marchantia polymorpha (Figure 1-Figure 12) can even become a pest in domestic gardens. The need to control weeds can provide new spaces where this liverwort can easily invade through gemmae or spores brought to the surface by the disturbance or as companions when new plants are introduced. Callaghan (2009) assessed domestic gardens in Britain and found that more than 80% of them included six moss species, but that *Marchantia polymorpha* was present in only 30% of the gardens. Nevertheless, Caron (1972) emphasized the need to fight such bryophytes as *Marchantia polymorpha* in arboriculture.

At least some herbicides tend to have different effects on different groups of plants. Bryophytes are no exception. Balcerkiewicz and Rusinska (1987) found that *Marchantia* actually expanded its populations in areas treated with herbicides. This may be due to the elimination of the competing tracheophytes, but the possibility existed that the herbicides could actually promote the growth of the liverworts. Iwata *et al.* (1992) subsequently suggested that *Marchantia polymorpha* (Figure 1-Figure 12) suspension cultures would be an excellent system for herbicide assays because of the rich chlorophyll content of the liverwort and its ability to grow in both **mixotrophic** (deriving nourishment from both autotrophic and heterotrophic mechanisms) and **autotrophic** (producing complex organic compounds using carbon from simple substances such as carbon dioxide) conditions.

Biochemistry

In a species that has been fundamental in so many studies to represent bryophytes, it is not surprising that there have been many biochemical studies as well. Those included here are only representative of the many publications.

Konno *et al.* (1987) isolated three classes of pectic polysaccharides from *Marchantia polymorpha* (Figure 1-Figure 12): rhamnogalacturonan polymer class, glucose rich polymer class, and galacturonan core. The cell walls are low in arabinosyl residues, unlike those of flowering plants.

Boisselier-Dubayle and Bishler (1989) reported on the presence of esterases, peroxidases, acid phosphatases, and glutamate-oxaloacetate transaminase as revealed by their

electrophoretic studies on *Marchantia polymorpha*. Izumi *et al.* (1995) identified esterase secreted from suspension cell culture of *Marchantia polymorpha*.

flavonoids

Singh *et al.* (1987) confirmed the presence of saponins, tannins, and flavonoids in *Marchantia polymorpha* (Figure 1-Figure 12). However all tests for alkaloids were negative, thus eliminating one of the chemical groups used in antiherbivory in some tracheophytes.

Markham and Porter (1974) identified major flavonoids of *Marchantia polymorpha* ssp. *polymorpha*. Flavonoids exhibit properties of antiherbivory and UV filters (Johnson 1983; Treutter 2006). Treutter (2006) reviewed the literature on their roles in plants and found that they act as stress protecting agents, attractants, or feeding deterrents, and have a significant role in plant resistance.

Flavonoids are important compounds that enabled the first land plants to interact with their environment (Davies *et al.* 2020). Hence, it is hypothesized that the flavonoid pathway must have evolved during the colonization of land by early plants, about 450 million years ago, providing essential protection against abiotic stress (Albert *et al.* 2018). The flavonoids are important reactants that permitted early plants to tolerate both abiotic and biotic stresses. Their production in plants can be induced by cold, UV-B light, strong white light, nutrient deficiency, desiccation, salinity, metal toxicity, senescence, and attack by pests and pathogens (Agati & Tattini 2010; Cheynier *et al.* 2013; Landi *et al.* 2015; Davies *et al.* 2018, 2020). They provide signals to microbes, serve as **allelochemicals** (chemical produced by living organism, exerting detrimental physiological effect on individuals of another species when released into environment), and can be important **nutraceuticals** (any food substance that provides medical or health benefits, including prevention and treatment of disease) in the animal diet (Taylor & Grotewold 2005).

Kubo *et al.* (2018) demonstrated that the regulation of gene expression as a stress response was already present in *Marchantia polymorpha* (Figure 1-Figure 12). They found that overexpression of one regulatory gene greatly increased the amount of rickionidins, a flavonoid. The gene was up-regulated by UV-B irradiation, nitrogen deficiency, and NaCl treatment.

Clayton *et al.* (2018) monitored the biosynthesis of flavonoids in *Marchantia polymorpha* (Figure 1-Figure 12), using three different UV-B regimes and mutant cultures. They found that the **chalcone** isomerase-like compound was one of greater importance. Mutants with a disrupted pathway for this enzyme were more easily damaged by UV-B. Those mutants with increased flavonoid content demonstrated greater UV-B tolerance.

The flavonoid pathway starts with **chalcones** as the first flavonoids (Davies *et al.* 2020). Since their origin, more than 8,000 different flavonoid structures have been reported (Andersen & Markham 2006). The major flavonoid classes are the flavones, flavonols, isoflavonoids, aurones, 3-deoxyanthocyanins, anthocyanins, proanthocyanidins (condensed tannins), and auronidins (Davies *et al.* 2020). Most flavonoids go to the vacuoles as water-soluble glycosides, but in some species they are

transported to the cell wall or are released to the environment.

Many flavonoids can absorb UV light, but the colored anthocyanins and auronidins can screen visible light (Lee & Gould 2002; Landi *et al.* 2015; Berland *et al.* 2019). Thus far, flavonoids have not been found in hornworts. They seem to have no role in development in bryophytes; a mutant of *Marchantia polymorpha* (Figure 1-Figure 12) lacking flavonoids has normal developmental patterns (Clayton *et al.* 2018).

In *Marchantia polymorpha* (Figure 1-Figure 12), nitrogen deprivation and increased white light exposure both induce the accumulation of auronidin (Albert *et al.* 2018; Kubo *et al.* 2018), a phenomenon similar to that of seed plants for anthocyanin accumulation in *Arabidopsis* and apples (Rubin *et al.* 2009; Wang *et al.* 2018). But in *M. polymorpha* auronidin also greatly increases the resistance of the plants to infections by *Phytophthora palmivora* (Figure 204), with hyphae apparently unable to penetrate into highly pigmented regions of the plant (Carella *et al.* 2019). Thus their roles are widespread.

Berland *et al.* (2019) reported **auronidins** for the first time. These flavonoid pigments seem to be important in protecting the plants from such environmental stresses as high light, drought, and nutrient deprivation. We initially thought that the red pigments bound in the cell walls of the early land plants were anthocyanins, but recent studies have revealed that they are in fact a group of phenylpropanoids that Berland and coworkers named **auronidins**. Their colors are similar to those of anthocyanins, but they are synthesized differently and have different optical properties. It appears that they contribute to the ability of *Marchantia polymorpha* (Figure 1-Figure 12) to survive extreme environments.

Excess light of any quality enhances the biosynthesis of flavonoids in plants, performing multiple functions at the expense of the antioxidant flavonoids and hydroxycinnamates (Agati & Tattini 2010). Several research groups have provided indications that common oxidative signal components may up-regulate flavonoid biosynthesis, regardless of their origins (Taylor & Grotewold 2005; Fujita *et al.* 2006; Quattrocchio *et al.* 2006) and may link the REDOX potential of the cell to the control of flavonoid accumulation (Taylor & Grotewold 2005). It appears that the main purpose of the flavonols is their involvement in responses to abiotic and biotic stresses (Roberts & Paul 2006; Kilian *et al.* 2007; Mellway *et al.* 2009). More research is needed on their involvement in reducing oxidative stress.

Using knockout genes, Albert *et al.* (2018) determined that all pigmentation was lost from the flavonoid riccionidin A in *Marchantia polymorpha* (Figure 1-Figure 12), but when overexpression was used these plants produced large amounts of flavones and riccionidin A and exhibited red pigmentation. Light- and nutrient-deprivation stress induced flavonoid pigmentation in the thallus, as these stresses do for the anthocyanins in flowering plants.

In evolutionary theory, red leaves represent a signal of the health status of a tree, providing a signal to insects to migrate when trees change color in autumn (Cheynier *et al.* 2013). Could similar signals be active in bryophytes, with red plants signalling nutrient deficiency or other poor

health condition? Red can also signal toxicity and is known as **warning coloration**.

phenolics

From the beginning of my interest in antiherbivory, I understood that phenolics were the important antiherbivore compounds in plants. But Close and McArthur (2002) challenged that thinking. They contend that it is not antiherbivory, but photoprotection, that makes these compounds so important for plants. They suggest that phenolics accomplish this role by acting as antioxidants and that their levels may vary with environmental conditions to provide this protection. Thus, their level of phenolics in the plants is dependent on the risk of photodamage and not on resources in the environment.

Cheynier *et al.* (2013) noted that for the successful colonization of land plants needed UV light screens. These were apparently achieved by phenolic compounds. These compounds play no role in the developmental and growth processes, but they are vital for survival in the interaction of the plants with their environment, for their reproductive strategy, and reputedly, for their defense. These survival mechanisms are controlled by plant phenolics that respond to potentially overlapping regulatory signals. Some of these effects are likewise associated with the growth hormone auxin.

Soriano *et al.* (2019b) found that bryophytes rarely exhibited a quick response to UV radiation in their production of UV-absorbing compounds. They experimented with *Marchantia polymorpha* (Figure 1-Figure 12) and measured the phenolic content under three realistic UV levels on day 1 and day 22 (Figure 223). The levels of UV-absorbing compounds mostly responded with linear or hyperbolic relationships with the UV level (Figure 224). They identified thirteen flavones (apigenin and luteolin derivatives) and two hydroxycinnamic acids (p-coumaric and ferulic acids) in the soluble and insoluble fractions, respectively. The speed of response depended on the compound, but those identified in *M. polymorpha* were slow responders.

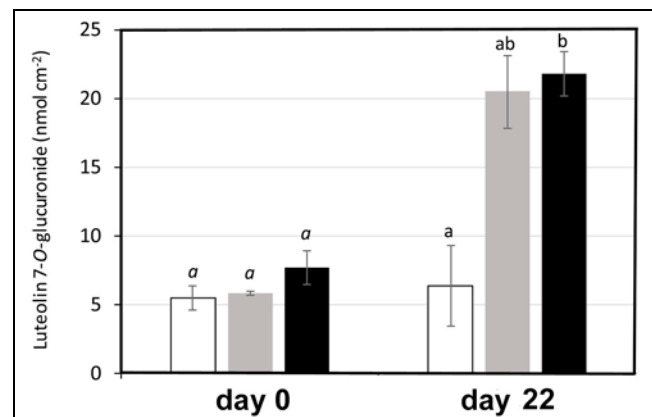


Figure 223. UV-absorbing compounds and time. White bars = UVBE low; grey bars = medium; black bars = high. Letters that are same represent means that are not significantly different from each other. Image modified from Soriano *et al.* 2019b.

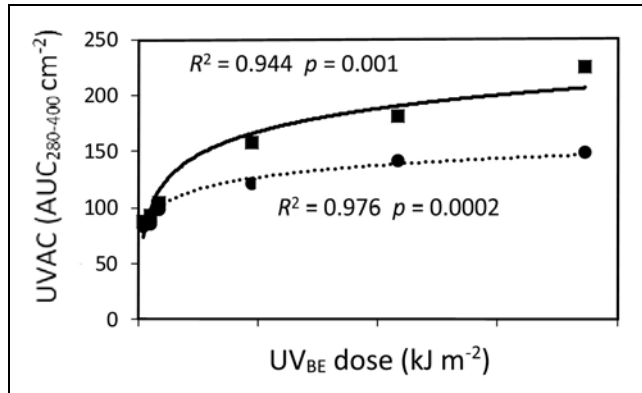


Figure 224. *Marchantia polymorpha* phenolics produced with increasing levels of UV-B. Photo modified from Soriano *et al.* 2019b.

light effects

Roberts and Paul (2006) introduced the concept that light serves to modulate plant defenses, in some cases being essential for the development of that resistance. They suggest that this interaction is multifaceted, extending across both temporal and biological scales. This needs further exploration in bryophytes and might explain our (false?) assumption that phenolic compounds have antiherbivore properties. Perhaps they accomplish both light protection and antiherbivory.

phenolics - phenanthrenes

Adam and Becker (1993a) reported phenanthrenes and other phenolics from cultured *Marchantia polymorpha* (Figure 1-Figure 12). Phenolics are secondary compounds that were widely considered to be antiherbivory compounds, but now their importance in antiherbivory is questionable. Phenanthrenes, on the other hand, have been used in traditional medicine, including usefulness in cytotoxicity, antimicrobial, spasmolytic, anti-inflammatory, antiplatelet aggregation, antiallergic activities, and phytotoxicity (Kovács *et al.* 2008), suggesting that they could serve as antiherbivore compounds as well as antibiotics. But perhaps their role in allelopathy toward tracheophytes is also feasible.

Anton *et al.* (1997) also found phenanthrene in the leafy liverwort *Plagiochila* (Figure 225), suggesting that it might be somewhat widespread in liverworts. Phenanthrene seems to have an interesting relationship with plants. It is one of the PAHs – phenols that occur naturally in coal, crude oil, and gasoline. PAHs are released from burning coal, oil, gas, wood, garbage, and tobacco and are toxic to both plants and animals (Wei *et al.* 2014). For example, phenanthrene inhibits seed germination and affects growth and chlorophyll levels of wheat seedlings. They also decrease the effects of antioxidants. Dupuy *et al.* (2016) also found that phenanthrene exposure causes developmental perturbation in maize roots. In the environment, they are degraded by bacteria (Anton *et al.* 1997). Corgié *et al.* (2003) demonstrated that root exudates are able to stimulate the degradation of PAHs in soil. In fact, it appears that the presence of the phenanthrene stimulates the release of more of these exudates, thus increasing the bacterial populations that accomplish the breakdown of the phenanthrene (Muratova *et al.* 2009).

Thomas *et al.* (2019) also noted that plants can stimulate microbial degradation of PAHs, using phenanthrene as the test compound. The soil bacteria **Proteobacteria** (*Pseudomonadota*; Figure 16), **Actinobacteria** (Figure 226), and **Firmicutes** (bacterial groups that are also common on bryophytes; Figure 227) are phenanthrene degraders. Plant root exudates enhanced the development of these phenanthrene-degrading bacteria.



Figure 225. *Plagiochila strombifolia*; phenanthrene occurs in at least some members of this genus. Photo by John Walter, through Creative Commons.



Figure 226. *Actinomyces israelii*, member of **Actinobacteria**, group often associated with bryophytes and soil; some are phenanthrene degraders. Photo by Graham Beards, through Creative Commons.



Figure 227. A member of **Firmicutes**, group often associated with bryophytes and soil; some are phenanthrene degraders. Photo by Argonne National Laboratories, through Creative Commons.

This raises the question of the presence of phenanthrenes in liverworts. Does it help, harm, or have a neutral action on them? Or like many of these compounds, might it have multiple roles? Perhaps the work with grassland plants might suggest a possible interaction. Chiapusio *et al.* (2007) found that in grasslands the phenanthrene did not generally affect plant biomass. In fact, red clover biomass was enhanced by it. This apparently resulted by a stimulation of its *Rhizobium* partner, a nitrogen-fixing bacterium. On the other hand, phenanthrene had a drastic negative effect on the mycorrhizal colonization of both ryegrass and red clover. As in other studies, the phenanthrene stimulated the PAH degraders in the soil.

This raises a possibility for *Marchantia polymorpha* (Figure 1-Figure 12) and its production of phenanthrene. It could stimulate the bacterial partners that are so common among the bryophytes (see Volume 2 chapter on bacterial interactions). In this role, it could play a critical role in their development. This won't be discovered in a sterile lab culture.

sesquiterpenoids and terpenes

Matsuo *et al.* (1985) isolated a series of ent-sesquiterpenoids that were stereoisomers of those compounds known in the tracheophytes, supporting the ancient origin of many of the defense compounds.

In 1990, Asakawa *et al.* described three new ent-sesquiterpenoids from German populations of *Marchantia polymorpha* (Figure 1-Figure 12). The chemistry of this species, including other isolates in this study, suggest that the German populations are close to the Japanese *M. polymorpha* and *M. paleacea* ssp. *diptera* (Figure 228).



Figure 228. *Marchantia paleacea* ssp. *diptera* females with capsules, Arima, Japan, 7 August 1988 – subspecies that has chemistry similar to that of *M. polymorpha* from Germany. Photo by Janice Glime.

Terpenes are volatile unsaturated hydrocarbons that constitute the essential oils and are aromatic compounds found in plants. Kumar *et al.* (2016) noted that despite their ability to accumulate structurally diverse terpenes that are "believed" to serve in deterring disease and herbivory, the genes and enzymes responsible for this chemical diversity of terpenes in *Marchantia polymorpha* have never been described. They were able to identify four diterpene synthase genes by function that were related phylogenetically to those in diverged plants. However,

there were also nine "rather unusual" monoterpene and sesquiterpene synthase-like genes.

lectins

Adam and Becker (1993b) tested *Marchantia polymorpha* (Figure 1-Figure 12) for **lectins**. **Lectins** are proteins that bind to carbohydrates. They are defense compounds in plants, but can cause problems in human digestion because they are able to resist being broken down in the gut and remain stable in acidic environments. In some cases they interfere with the absorption of other nutrients. These capabilities make them good antiherbivore compounds. They are in many human foods, especially dried beans, and those extracted from *Marchantia polymorpha* agglutinate the erythrocytes of various mammals and exhibit carbohydrate specificity against complex carbohydrate structures. This was the first report of lectins in liverworts. On the other hand, they are important in attracting specific *Rhizobium* species toward roots of host plants, suggesting they could possibly have a similar role in bryophytes.

bibenzyls

Asakawa *et al.* (1987) isolated two new cyclic bis[bibenzyls] from Indian populations of *Marchantia polymorpha* (Figure 1-Figure 12). Bis[bibenzyls] are rare products of plants, but more than 125 types have been discovered among liverworts (Asakawa *et al.* 2021). They are biosynthesized from lunularic acid, perhaps explaining why this compound has remained in even those liverworts such as *Marchantia* that also have ABA. The known biological activities of cyclic bis[bibenzyls] include antimicrobial, antifungal, cytotoxic, muscle relaxation, antioxidant, tubulin polymerization inhibitory, and antitrypanosomal activities.

Niu *et al.* (2006) isolated and identified seven bis[bibenzyl]-type macrocycles from Chinese populations of *Marchantia polymorpha* (Figure 1-Figure 12). Several of these compounds exhibited antifungal activities against *Candida albicans* (Figure 183).

The **marchantins** are bis[bibenzyls]. As far as we know, these are unique to bryophytes and are cytotoxic, having cancer treatment applications (Kodama *et al.* 1988). Kámory *et al.* (1995) isolated marchantin A from *Marchantia polymorpha* (Figure 1-Figure 12). This was followed later by isolation of a number of different marchantins. At least some of these have proven antibacterial activity.

Fang *et al.* (2007) described three new bibenzyl (=1,1'-(ethane-1,2-diyl)bisbenzene) derivatives from Chinese populations of *Marchantia polymorpha* (Figure 1-Figure 12). Its polymorphin A was a new type of bis[bibenzyl] and one compound was described as the first discovery of a bibenzyl that is oxidatively coupled to a phenylmethanol.

Friederich *et al.* (1999) elaborated on the pathway from lunularic acid to formation of marchantin C and CO₂ and the hydroxylation of marchantin C to marchantin A. Both of these reactions depend on the presence of O₂ and NADPH. Both are also inhibited by CO in the dark.

Marchantins are another example in which Kubo *et al.* (2018) demonstrated that the regulation of gene expression as a stress response was already present in *Marchantia polymorpha*. They found that overexpression of one

regulatory gene greatly increased the amount of several marchantins. The gene was down-regulated by NaCl.

antibacterial

Zehr (1990) found that ether extracts of *Marchantia polymorpha* (Figure 1-Figure 12) inhibited bacteria at 84.4%, whereas the ethanol extract lacks inhibitory ability. Those most affected were *Bacillus subtilis* (Figure 229) and *Escherichia coli* (Figure 16), whereas *Enterococcus faecalis* (Figure 230) was least inhibited. Zhu *et al.* (2006) noted that the antibacterial activity of *Marchantia* was "particularly prominent." As in many antibacterial studies with bryophytes *Staphylococcus aureus* (Figure 180) was the most resistant of the seven bacterial species tested. *Bacillus subtilis* was the most sensitive species to liverwort extracts.

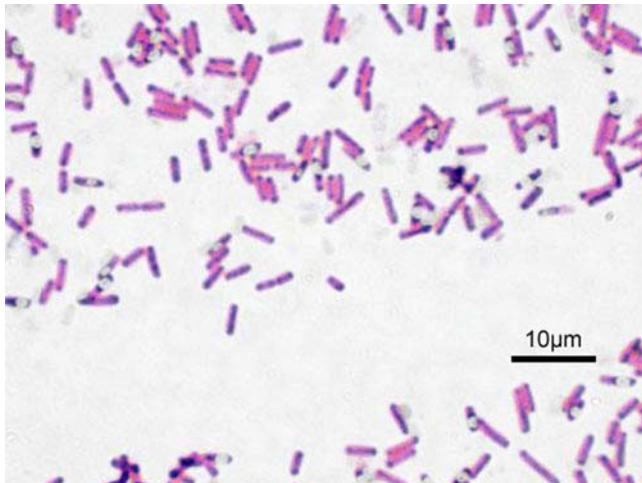


Figure 229. *Bacillus subtilis* Gram stained, one of bacteria most affected by extracts of *Marchantia polymorpha*. Photo by Y. Tambe, through Creative Commons.

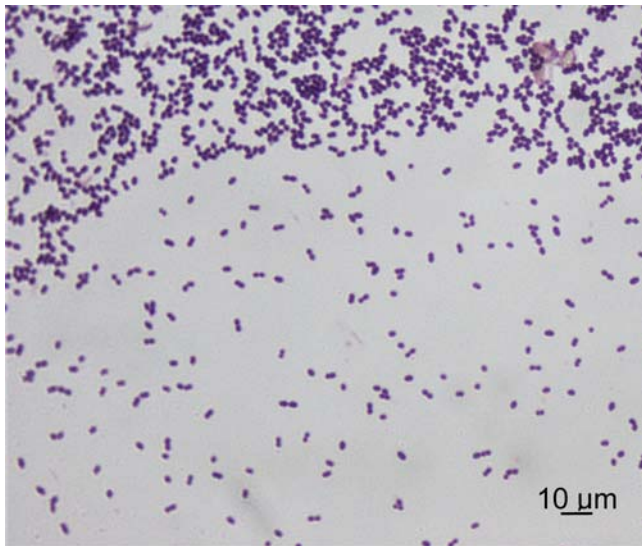


Figure 230. *Enterococcus faecalis*, one of bacteria least affected by extracts of *Marchantia polymorpha*. Photo by Dr. Sahay, through Creative Commons.

Gahtori and Chaturvedi (2011) likewise touted the usefulness of extracts of *Marchantia polymorpha* (Figure 1-Figure 12) as antimicrobial agents, some killing the

organisms and others simply arresting growth. Among those affected were the Gram-negative bacterial strains *Pasteurella multocida* (Figure 231), *Salmonella enterica* (Figure 232), and *Xanthomonas oryzae* pv. *oryzae* (Figure 233), and the four fungal strains *Fusarium oxysporum* f. sp. *lini* (Figure 207), *Rhizoctonia solani* (Figure 205), *Sclerotium rolfsii* (Figure 234), and *Tilletia indica* (Figure 235). They found a unique activity against *X. oryzae* and *P. multocida*. They also acted against the fungi *S. rolfsii* and *F. oxysporum*. *Marchantia polymorpha* showed different potencies against micro-organisms that are pathogenic to both plants and animals.

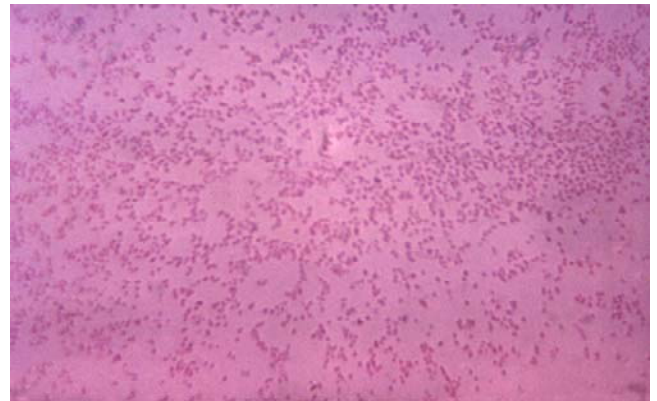


Figure 231. *Pasteurella multocida* bacteria, causative agent of fowl cholera, and species that is negatively affected by extracts of *Marchantia polymorpha*. Photo by Dr. R. Weaver, CDC, through public domain.



Figure 232. *Salmonella* in human tissue, and species that is negatively affected by extracts of *Marchantia polymorpha*. Photo by NIH, HHS, through public domain.



Figure 233. *Xanthomonas oryzae*, species that is negatively affected by extracts of *Marchantia polymorpha*. Photo by Rui map Zheng at <Bugwood.org>, through Creative Commons.



Figure 234. *Sclerotium rolfsii*, fungal species that is negatively affected by extracts of *Marchantia polymorpha*. Photo by Bridget Lassiter, NCDA&CS <Bugwood.org>, with online permission.

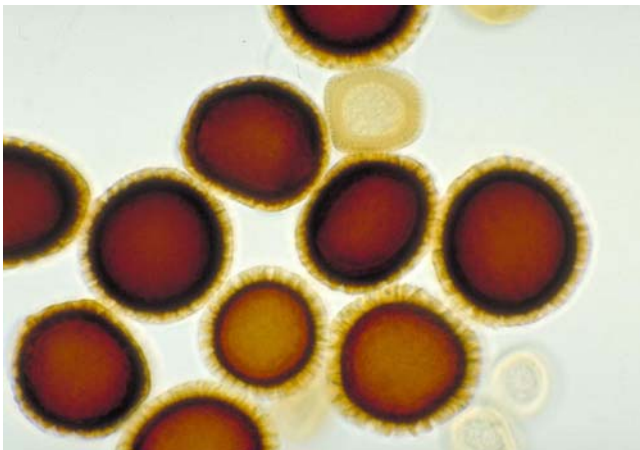


Figure 235. *Tilletia indica*, fungal species that is negatively affected by extracts of *Marchantia polymorpha*. Photo by Ruben Durán, through public domain.

antifungal

Hamashima *et al.* (2019) noted the development of many techniques using *Marchantia polymorpha* (Figure 1-Figure 12). They used S-Agar Trap to genetically transform the species, using spores. They were able to insert a T-DNA mutant and isolate and characterize a gain-of-function mutant. This mutant hyper-accumulates the flavonoid riccionidin A, verifying that this technique is a powerful tool in the genetic tool library, including production of antibiotics.

In a comprehensive study on published antifungal activities of bryophytes, Miranda *et al.* (2022) found that in the period of 2000 to 2019 *Marchantia polymorpha* (Figure 1-Figure 12) was included in the most publications.

glycosides

Qu *et al.* (2007) isolated four new glycosides and three known aromatic glycosides from *Marchantia polymorpha* (Figure 1-Figure 12) and described their structures. Many drugs and poisons derived from plants are glycosides, such as the several cyanogenic glucosides used by the Heliconius butterfly that incorporate these plant compounds in their tissues as a defense against predators

(Nahrstedt & Davis 1983). I wonder if anything eats bryophytes to gain their secondary compounds for their own defense.

medicinal uses

Dioscorides (De Materia Medica, 50-70 AD) extolled the value of *Marchantia polymorpha* (Figure 1-Figure 12) for treating liver ailments, based on its liver form (Doctrine of Signatures; in Schuster 1966). In Yunnan and Sichuan this liverwort is available in street markets (Wu & Yu 2003). It is used to cover the skin for curing jaundice and as an antipyretic. Asakawa (1981, 1982) reported that this species contains sesquiterpenoids that have anti-tumor activity. Hartwell (1982) referred to its use against cancer, referring to Pliny the Elder.

Fischer *et al.* (1995) verified the presence of chalcone synthase activity in *Marchantia polymorpha* (Figure 1-Figure 12), and the subsequent presence of naringenin. Chalcones are used medicinally in treatment of viral disorders, cardiovascular diseases, parasitic infections, pain, gastritis, and stomach cancer. **Naringenin** has strong anti-inflammatory and antioxidant activities and seems to be beneficial in treating obesity, diabetes, hypertension, and metabolic syndrome in humans.

Kumar *et al.* (2007) reported that *Marchantia polymorpha* (Figure 1-Figure 12) was among those liverworts useful for treating tumors and that it was among the traditional herbal medicines in India.

Culturing and Cultivating

With so many studies being performed on the species *Marchantia polymorpha* (Figure 1-Figure 12), the methods of culturing have been worked out well (Figure 236). Voth and Hamner (1940) grew *Marchantia polymorpha* on glass cloth in an open moist chamber. They tested 56 nutrient solutions to develop suitable conditions for culturing the species in the lab. Voth (1941) indicated that the omission of K, Ca, NO₃, or PO₄ ions caused differences in the gross appearance of the species. Mg and SO₄ are not indicated by any characteristic symptoms. Effects of calcium appear to be dose dependent. Almost immediate death occurs in its absence, whereas in 0.3 mM of calcium per liter of solution the thallus apices die and degenerate.



Figure 236. *Marchantia polymorpha* ssp. *ruderalis* in peat disc culture. Photo courtesy of Javier Martínez-Abaigar.

Molar concentrations that are adequate for good growth, based on Voth (1941) are:

K 0.0012 M L⁻¹
 Ca 0.0007 M L⁻¹
 Mg 0.0014 M L⁻¹
 NO₃ 0.0034 M L⁻¹
 PO₄ 0.0004 M L⁻¹
 SO₄ 0.0008 M L⁻¹

These can be provided in a 1 L, 0.5 M solution of the following forms:

KNO₃ 1.6 cc
 Ca(NO₃)₂ 1.4 cc
 Mg(NO₃)₂ 1.2 cc
 KH₂PO₄ 0.8 cc
 MgSO₄ 1.6 cc

Minor variations of the concentrations do not cause growth problems.

Voth (1943) contributed additional experiments on nutrient concentrations, finding that some were better for production of gemmae cups than others. High salt concentrations often killed the growing tips and thalli became translucent.

Schneider *et al.* (1967) further developed culture methods that attempted to standardize them and address some of the inconveniences of past methods. They found that five substrates worked well, including vermiculite, perlite, glass cloth, nutrient agar, and nutrient solution. These are compared for their maintenance, yields, and usefulness for particular experimentation.

Miller (1964) contributed to the culturing protocol by defining procedures for harvesting, surface sterilizing, and culturing of gemmae. He also described conditions for a high production of gemmae and large numbers of gemmae cups in stock plants. He described methods for culturing the gemmae axenically, noting that they did not fare well at temperatures above 25°C, but that they were tolerant of high light. Miller *et al.* (1962b) used five different photoperiods to determine the best photoperiod for developing gemmalings. The greatest size and weight were achieved in an 18-hour photoperiod. They experimented with X-rays, light intensity, various nutrients, amino acids, vitamins, and other supplements to determine their effects and ability to prevent damage to the plants.

Miller and Colaiace (1969) cultured gemmae to ultimately produce antheridiophores and archegoniophores, structures that developed after 3-6 weeks on 1% agar medium in 24-hour photoperiods at 23°C.

In his attempts to grow gemmae of *Marchantia polymorpha* (Figure 1-Figure 12), Gemmrich (1976) found that Fe and Ca(NO₃)₂ induced germination, but optimal germination occurred on Ca(NO₃)₂, KNO₃, and MgSO₄. Gibberellic acid failed to induce germination in the dark.

Sugawara *et al.* (1983) found that activated charcoal in the culture medium increases cell wall regeneration and subsequent cell division, suggesting that something in the medium is too strong for the plant, or that the plant's own by-product(s) become inhibitory. Charcoal is usually used to bid things, thus removing them from availability to plants.

Pedroza-Manrique and Caballero Arévalo (2009) recognized that bryophytes typically require lower nutrients than do tracheophytes and algae. They successfully grew

Marchantia polymorpha (Figure 1-Figure 12) propagules in 25% Murashige and Skoog (1962) mineral salt concentration, incubated at 25°C ± 1°C. They warned that when transplanting such cultures to their natural environment or other conditions, one should provide gradual adjustment to new humidity, temperature, and substrate conditions.

Katoh *et al.* (1980) used a modified Murashige and Skoog's medium to culture *Marchantia polymorpha* (Figure 1-Figure 12). They improved the medium for use with the liverwort, including only eight of the 24 original micro-organic constituents. This new medium resulted in richer chlorophyll and a higher growth rate in the exponential phase.

Xu *et al.* (2021) found that they could induce reproductive organs in *Marchantia polymorpha* (Figure 1-Figure 12) on agar plates. Cultures from gemmae were transplanted after 10 days onto soil at 22°C with a 16h:8h photoperiod using white light. After 14 days, they supplemented the cultures with far red light.

Gradstein (2006) reported the successful cultivation of *Marchantia* in the bryophyte garden of the Cibodas Botanical Garden, Java, Indonesia. Supplementary spray is needed during the dry season.

Control

Marchantia polymorpha (Figure 1-Figure 12) can be a serious weed in some types of gardens, especially in nurseries, and in greenhouses. Jin and Pyon (2007) noted the need to control it in ginseng gardens. Uva *et al.* (1997) even listed it in their publication on the weeds of the northeastern USA. Schofield (1997) listed the species as one obviously spread by human activity in British Columbia, Canada.

Sato *et al.* (1991), working in Japan, used Cyclohexanedione derivatives on *Marchantia*, causing photosynthetic inhibition in cultured cells. They suggest that indicated the usefulness of the liverwort in herbicide assays.

Fausey (2003) considered *Marchantia polymorpha* (Figure 1-Figure 12) to be highly invasive and difficult to control, becoming a concerning pest in ornamental containers. They compared pre-emergence and postemergence herbicides, using chlorothalonil, captan, ammonium chlorides, hydrogen dioxide, flumioxazin, oxyfluorfen, pelargonic acid, acetic acid (vinegar), Cu sulfate, cinnamaldehyde, prodiamine, and oxadiazon. Of these, only flumioxazin, oxyfluorfen, pelargonic acid, acetic acid, and oxadiazon elicited acceptable control. Sprayable preparations were more effective than were granular ones.

Newby *et al.* (2007) experimented with various herbicides as a means of controlling *Marchantia polymorpha* (Figure 1-Figure 12) in nursery containers. The effectiveness differed by location, with flumioxazin and oxadiazon being the most effective for control in Alabama, whereas flumioxazin and oxyfluorfen + oryzalin were the most effective for control in Oregon.

Since *Marchantia polymorpha* (Figure 1-Figure 12) benefits from the same high humidity and shading as that needed in most nurseries for growing native tree seedlings, it quickly becomes a pest species there (Navas *et al.* 2014). Navas and coworkers used a variety of treatments,

including sterilizing the soil, using three concentrations of acetic acid, using two concentrations of oxygenated water, and using the herbicides glyphosate and fomesafen. They also used pre-emergence application of diuron and trifluralina. Only the two pre-emergence applications caused a 100% control of *Marchantia polymorpha*.

Särkkä and Tahvonon (2020) suggested several means of control of *Marchantia polymorpha* (Figure 1-Figure 12) in nurseries where it appeared as a weed. In pots with growing horticultural plants it can reduce access to water and nutrients (Figure 237). Growth of the liverwort can be minimized with mulches. Särkkä and Tahvonon used *Sphagnum* (Figure 238) and 1-cm blackcurrant stem pieces. Highbush blueberry and blackcurrant controlled the liverwort for two years, whereas rhododendron controlled it for only one year. Blueberry and rhododendron require an acid medium that is beneficial for the liverwort. Blackcurrant mulch was nearly 100% effective, whereas other treatments ranged 78-99%.



Figure 237. *Marchantia polymorpha* with splash cups, in nursery flower pot. Photo by Janice Glime.



Figure 238. *Sphagnum capillifolium*; *Sphagnum* can be used in layers to discourage growth of *Marchantia polymorpha* in pots. Photo by Bernd Haynold, through Creative Commons.

Khamarea *et al.* (2021) used a method of substrate stratification and fertilizer to control *Marchantia*

polymorpha (Figure 1-Figure 12) growth. They used pine bark and other layers with different physical properties to manipulate the soil moisture dynamics and improve irrigation and fertilizer efficiency. This proved to also work as a tool of weed management. Each of the stratified techniques reduced the liverwort coverage by nearly 100%.

Summary

Marchantia polymorpha is perhaps the most studied bryophyte on the planet. It is a teaching model for liverworts, has had its genome sequenced, and is common in both wet habitats and as an invader after fires. It has been the subject of many physiological studies, including hormone effects and capillary movement of water among rhizoids. Growth hormones such as IAA elicit responses like those in tracheophytes. The thalli exhibit circadian rhythms that regulate the IAA levels. Lipxygenase also contributes to control of cell growth. Gibberellins respond to photoperiod. Ethylene causes larger gemmae, induces more gemmae cups, and promotes the dormancy of the gemmae, whereas the precursor ACC inhibits gemma growth and development by suppressing cell division. Cytokinins control formation of both gemmae cups and rhizoids during thallus development and seem to influence distribution of air pores and shape of thallus margin, implicating control of cell division. Desiccation causes oxidative stress. *Marchantia polymorpha* has both lunularic acid and ABA, important hormones in desiccation tolerance. Light affects senescence, but spermine, spermidine, and putrescine reduce it. Ethylene induces senescence. Nitrate and phosphate deficiency cause the ventral layers of cells to develop a red-violet color. Thalli can grow on vertical surfaces, but gemmae cups exhibit gravitropisms.

Adaptations are a coordinated set of resistance to effects of drying. These include rhizoids, scales, thick thallus, thin cuticle, air pores with a waxy ring, and oil bodies, as well as a suite of biochemical adaptations.

It is dioicous and prolifically produces sexual structures. However, gemmae are usually the most important means of reproduction and enable it to colonize rapidly after a disturbance. Short photoperiods favor production of gemmae, whereas long photoperiods favor the production of gametangiophores and greater growth. Developmental stage is important in determining the accumulation of UV-absorbing compounds in *Marchantia polymorpha* ssp. *ruderalis*. High temperatures can change the ratios of fatty acids and cause a reversible depression of photosynthesis; there seems to be limited thermostability. They are much more cold tolerant and don't suffer frost damage. The ω -3 polyunsaturated fatty acids increase as the temperature decreases and ABA seems to play a role in cold survival.

Marchantia polymorpha produces sesquiterpenoids that are active against some fungi and bacteria. Some methylobacteria promote the growth of gemmae. Other bacteria promote thallus growth, fix nitrogen, and inhibit pathogens. Extracts of the liverwort have antibiotic properties. The

archegoniophore is particularly well protected, with a flavonoid content ten times that of the thallose gametophyte. Antibacterial properties increase with altitude. The antibacterial compounds also inhibit protozoa. Fungi can occur as endophytes and pathogens, but others might contribute to symbiosis. The subspecies *montivagans* develops mycorrhizal associations with some fungi, but this relationship is not known in subspecies *polymorpha*. The liverwort protects the fungi from water loss and can have a number of species living in association with it.

We have a meager understanding of the invertebrates that depend on *Marchantia polymorpha*. At least one fly (*Scatopsciara cunicularius*) feeds on it as larvae. Extracts of allene oxide synthase inhibits oviposition and survival rate of the spider mite *Tetranychus urticae*. Spiders and isopods inhabit them, but herbivory needs to be studied.

Some members of the **Apiaceae** can inhibit growth of *Marchantia polymorpha*, whereas the liverwort can inhibit seed germination in *Bidens biternata*.

It appears that the species has evolved numerous biochemical adaptations. Anthocyanins and auronidins can screen visible light, protecting it from strong sunlight. Auronidins seem to be important in protecting the liverwort in the extremes of its environmental conditions. Flavonoids protect against UV light and herbivory. They may provide antibiotics benefitting animals in nature. Their phenolic compounds are important in UV protection and might not have the importance in antiherbivory we once thought.

Large increases in CO₂ cause a number of changes in the *Marchantia polymorpha* photosynthetic system, but the net result is that there is little change in photosynthetic rate. High light intensity inhibits photosynthesis. Light quality can affect growth and gemma production. The red:far red ratio affects chlorophyll concentration and senescence and is mediated by phytochromes.

The species accumulates heavy metals, but not in large quantities like mosses do, due to lower surface area. Its best role seems to be in the laboratory. It is easy to culture, so easy that in greenhouses it is necessary to find ways to discourage its growth in pots for trees and other plants. Chronic gamma radiation causes inhibition of the development of sex organs in *Marchantia polymorpha* and its responses can be used to monitor radiation effects. Rapid and easy growth and haploid condition make the species useful to test the function of plant genes.

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CHAPTER 1-25

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 3

TABLE OF CONTENTS

Marchantiaceae, cont.	1-25-2
<i>Marchantia quadrata</i>	1-25-2
Distribution	1-25-3
Aquatic and Wet Habitats	1-25-3
Physiology.....	1-25-7
Adaptations	1-25-8
Reproduction.....	1-25-11
Fungal Interactions.....	1-25-15
Biochemistry	1-25-15
<i>Marchantia treubii</i>	1-25-15
Distribution	1-25-15
Aquatic and Wet Habitats	1-25-15
Adaptations	1-25-15
Reproduction.....	1-25-15
Summary.....	1-25-15
Acknowledgments	1-25-16
Literature Cited.....	1-25-16

CHAPTER 1-25

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 3



Figure 1. *Marchantia quadrata* on dripping cliff, a wet habitat with a more constant set of conditions than open areas. Photo courtesy of Keir Wefferling.

Marchantiaceae, cont.

Marchantia quadrata (Figure 1-Figure 5)

(= *Preissia quadrata*)

Most readers may be more familiar with the synonym *Preissia quadrata*. However, Stotler and Crandall-Stotler (2017) have moved it to the genus *Marchantia* and this seems to be the name the bryological community has accepted. But Zheng & Shimamura (2022) just published a paper that once again offers support for the separation of this species into the genus *Preissia*. And they have added another species to that genus, *Preissia platycarpa*. This conclusion on their part is based on several differences in morphology, including the absence of gemmae cups and the presence of only one archegonium and sporophyte per arm in the female receptacle. This genus argument among bryologists seems to depend on the degree of difference accepted, both morphological and genetic, to define a different genus.



Figure 2. *Marchantia quadrata* showing frequent character of purple edges. Photo by Andy Hodgson, with permission.



Figure 3. *Marchantia quadrata* with young archegonial heads and distinct red-purple margins. Photo by Hermann Schachner, through Creative Commons.



Figure 4. *Marchantia quadrata* with expanded archegoniophores. Photo by Janice Glime.



Figure 5. *Marchantia quadrata* thallus. Photo from Snappy Goat, through public domain.

Boisselier-Dubayle *et al.* (1997) reported that there was an incongruence between molecular data and morphological characters in the **Marchantiales**. They recommended a weighting of the morphological character data and were able to resolve the contradictions by so doing. They suggested that this might mean that the molecular sampling is too limited.

Distribution

Marchantia quadrata (Figure 1-Figure 5) is known from Australia, Europe, Northern and Southern Asia, Central America, North America, Oceania, and South America (ITIS 2022). It was recently reported as new to Turkey (Şimşek *et al.* 2014).

Aquatic and Wet Habitats

In North America, *Marchantia quadrata* (Figure 1-Figure 5) occurs along calcareous rivers in Connecticut, USA (Nichols 1916). I have seen it at the top of a waterfall in shallow water on bedrock (Figure 6) in the Keweenaw Peninsula, Michigan, USA. Forrest (2018) found it at the edge of a stream at the top of Snowbird Mountain in Utah, USA. McNeilus and Sharp (1975) reported it from limestone bluffs with dripping water in Tennessee, USA. Nichols (1918) reported it along a rock ravine streambank, Cape Breton Island, Canada. In western Canada, it occurs submerged, in hemicalciphilous montane streams (Vitt *et al.* 1986) and also on streambanks (Figure 7) (Glime & Vitt 1987).



Figure 6. *Marchantia quadrata* habitat in river gorge at top of falls, Keweenaw County, Michigan, USA. Photo by Janice Glime.



Figure 7. *Marchantia quadrata* growing with mosses beside water. Photo by Claire Halpin, with permission.

Watson (1919), in his discussion of aquatic bryophytes, reported that *Marchantia quadrata* (Figure 1-Figure 5) usually occurs on rocks (Figure 8-Figure 9) (Watson 1919). Near Lacko in the Western Carpathians, it is part of the ground community in streams (Figure 10) (Mamczarz 1970). In the River Tweed, UK, it is not common (Holmes & Whitton 1975), but occurs on the river bank of River Tees, UK (Holmes & Whitton 1977a) and occurs in the upper upstream of River Swale, Yorkshire, UK (Holmes & Whitton 1977b). It is again infrequent in River Tyne, UK (Holmes & Whitton 1981).



Figure 8. *Marchantia quadrata* on wet rock at edge of stream. Photo by Andy Hodgson, with permission.

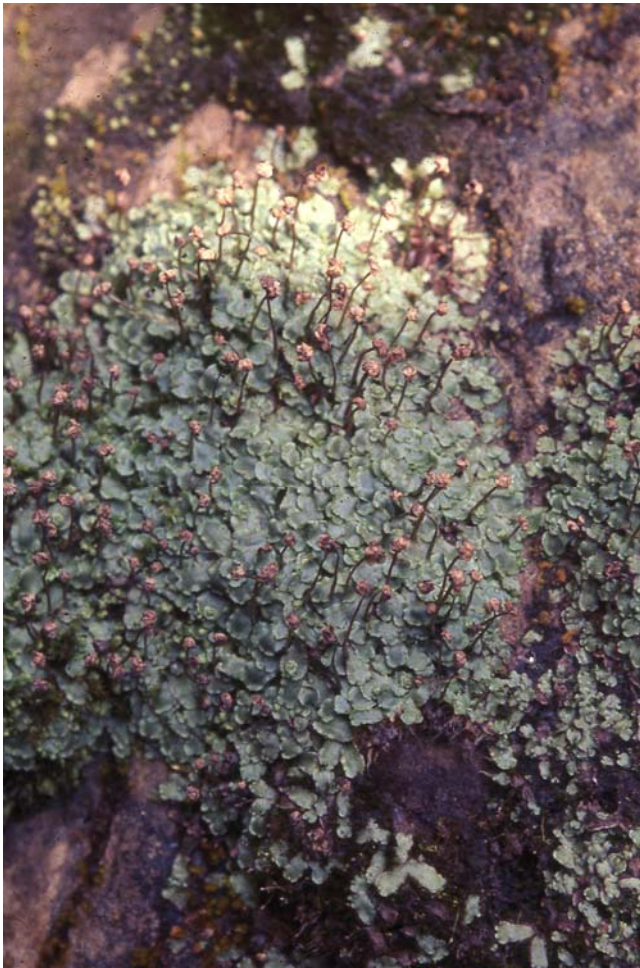


Figure 9. *Marchantia quadrata* on rock at waterfall, Michigan, USA. Photo by Janice Glime.



Figure 10. *Marchantia quadrata* with archegoniophores, growing on soil. Photo by Hermann Schachner, through Creative Commons.

Lee and Greenwood (1976) reported that *Marchantia quadrata* (Figure 1-Figure 5) was able to occupy calcareous waste deposits in the UK in areas where there were no natural calcareous substrata.

Marchantia quadrata (Figure 1-Figure 5) occurs in the travertine *Cratoneuron* (Figure 11) association in the Lorraine River, Belgium, (de Sloover & Goossens 1984), in streams in Greece (Papp 1998), and at springs in the Tara river canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).



Figure 11. *Cratoneuron filicinum*, a species associated with *Marchantia quadrata* on travertine rock. Photo by Hermann Schachner, through Creative Commons.

Contrasting with these limestone habitats, Haupt (1926) reported *Marchantia quadrata* (Figure 1-Figure 5) on thin soil (Figure 10) over granitic rocks, particularly along stream banks. It tends to occur in drier situations than *Marchantia polymorpha* (Figure 12) or *Conocephalum* (Figure 13-Figure 14), but they can occur intermixed. Nevertheless, it can occur close to the water (Figure 15-Figure 17).



Figure 12. *Marchantia polymorpha* gemmae cups in Europe; *Marchantia quadrata* prefers drier conditions than does *M. polymorpha*. Photo by Michael Lüth, with permission.



Figure 15. *Marchantia quadrata* on stream bank. Photo by Scot Loring, through Creative Commons.



Figure 13. *Marchantia quadrata* with archegoniophores on wet canyon wall by stream at Hocking Hills, Ohio, USA. Note the *Conocephalum* cf. *salebrosum* at the bottom of the view, illustrating the presence of *Marchantia quadrata* in a higher zone above the water. Photo by Janice Glime.



Figure 16. *Marchantia quadrata* on wet rock. Photo by Andy Hodgson, with permission.



Figure 14. *Marchantia quadrata* with archegoniophores stacked on canyon wall at Hocking Hills, Ohio, USA, growing next to *Conocephalum salebrosum*. Photo by Janice Glime.



Figure 17. Wet *Marchantia quadrata* near falls at Tahquamenon Falls, Michigan, USA. Photo by Janice Glime.

In the Netherlands, *Marchantia quadrata* (Figure 1- Figure 5) occurs on the **trilveen** (Kooijman & During 1989). The **trilveen** (Figure 18) is a bog that is a rare, with thin, extremely soft "soil" and vegetation type with sedges

and grass roots. It floats on water or soft mud and occurs in low moor areas such as peat meadows.



Figure 18. Trilveens in The Netherlands. Note the person pushing one across the water surface. Photo from Wikiwand, through Creative Commons.

Keir Wefferling found it growing on dripping sandstone cliffs in Wisconsin, USA (Figure 1-Figure 5, Figure 19).



Figure 19. *Marchantia quadrata* (bottom) forming a zone above the base of a dripping cliff in Wisconsin, USA. Photo courtesy of Keir Wefferling.

In Turkey *Marchantia quadrata* (Figure 1-Figure 5) occurs on moist calcareous rocks (Figure 20) of the subalpine zone (Şimşek *et al.* 2014).



Figure 20. *Marchantia quadrata* growing among calcareous rocks. Photo by Michael Lüth, with permission.

I have also seen the species on a rock ledge of a cliff in New York, USA (Figure 21). It can occur on rock and cavern walls (Figure 22-Figure 26).

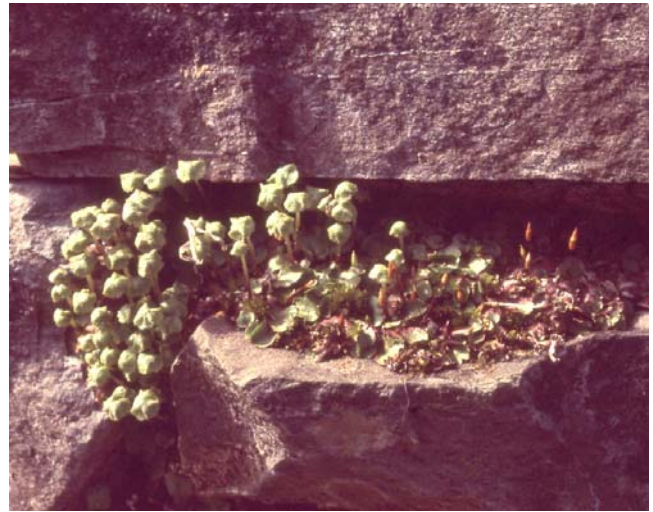


Figure 21. *Marchantia quadrata* on ledge in New York, USA. Photo by Janice Glime.

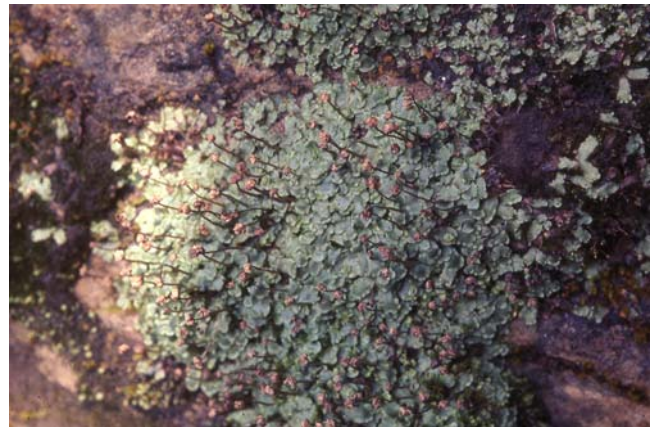


Figure 22. *Marchantia quadrata* on rocky bank at Tahquamenon Falls, Michigan, USA. Photo by Janice Glime.



Figure 23. *Marchantia quadrata* on calcareous rock. Photo by Michael Lüth, with permission.



Figure 24. *Marchantia quadrata* on rock in NW Iowa, USA. Associated mosses can help it to retain moisture. Photo by Janice Glime.



Figure 25. *Marchantia quadrata* with archegoniophores on rock. Photo by Michael Lüth, with permission.



Figure 26. *Marchantia quadrata* on a rock depression – a common habitat for the species. Photo by Oskar Gran, through Creative Commons.

Others have found it in open areas on soil, as seen in these pictures by Michael Lüth (Figure 27-Figure 28).



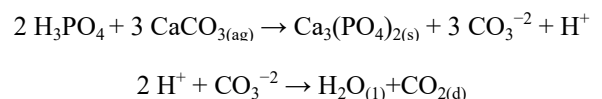
Figure 27. *Marchantia quadrata* with archegoniophores, growing on open soil. Photo by Michael Lüth, with permission.



Figure 28. *Marchantia quadrata* with archegoniophores, growing on soil in the location shown above. Photo by Michael Lüth, with permission.

Physiology

Tyler *et al.* (1995) found that soluble phosphate was important to the occurrence of *Marchantia quadrata* (Figure 1-Figure 5) on limestone soil. It produced 7 times as much biomass when phosphate was added to the soil. Perhaps this is due to the ability of the calcium carbonate of the limestone to be an effective binder of phosphate (Yanamadala 2005). Furthermore, the liverwort is likely to be phosphate limited without the high levels of phosphate. The mix of CaCO_3 and phosphate could also encourage certain bacteria, particularly nitrogen-fixing bacteria, that are beneficial to the liverwort. The reaction with limestone further releases water and CO_2 , the latter being a limiting factor in submersed plants:



Fletcher (1982) reported that *Marchantia quadrata* (Figure 1-Figure 5) was among the *Marchantia* species from several areas that sustained no frost damage when other bryophytes suffered blackening, bleaching, or growth cessation in cultivation down to -5.5°C . In nature, it can survive winter under the snow and ice in the 5-6 months of snow cover in the Keweenaw Peninsula, Michigan, USA (Figure 29).



Figure 29. Snow covering *Marchantia quadrata* habitat at top of Manganese Falls, Keweenaw County, Michigan, USA. Photo by Janice Glime.

Heat is less kind, but it can have reversible damage effects on *Marchantia quadrata* (Figure 1-Figure 5) (Weis *et al.* 1986). Mild heat treatment suppresses photosynthesis. More severe heat causes irreversible damage of PSII similar to that known in tracheophytes. Exposure to high but sublethal temperatures does not increase the heat stability of these liverworts, indicating an extremely low heat-hardening capacity.

Adaptations

Marchantia quadrata (Figure 1-Figure 5) has a thallus that is multiple cells in thickness (Figure 30-Figure 31). The upper layer and the epidermis cells (Figure 32) contain chloroplasts, but these are absent in the cells surrounding the pores (Walker & Pennington 1939). The thickness is likely to aid in moisture retention during drought periods.



Figure 30. *Marchantia quadrata* thallus section showing photosynthetic cells on top and scales hanging from the ventral side. Photo by Hermann Schachner, through Creative Commons.

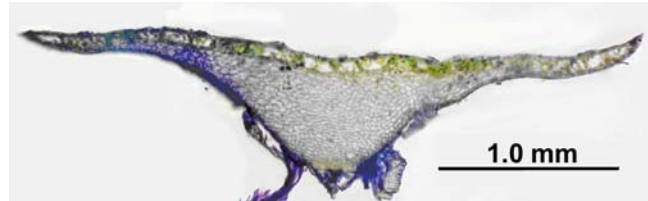


Figure 31. *Marchantia quadrata* section showing distinctive photosynthetic layer on top. Rhizoids hang from the ventral surface. Photo by David Wagner, with permission.



Figure 32. *Marchantia quadrata* thallus showing epidermis with pores. Photo from Bioimages, through Creative Commons.

Rhizoids (Figure 33) are known to create capillary spaces that conduct water in the **Marchantiales**. McConaha (1941) suggests that the more numerous rhizoids present in *Marchantia quadrata* (Figure 1-Figure 5) compensate for its less compact arrangement of the capillary system. It also does not have its capillary system over the wings of the thallus to the extent seen in *Marchantia* s.s. Thallus areolation in *M. quadrata* exposes a greater surface to water loss despite having pores that are able to achieve partial closure; there is little regulation of the transpiration.

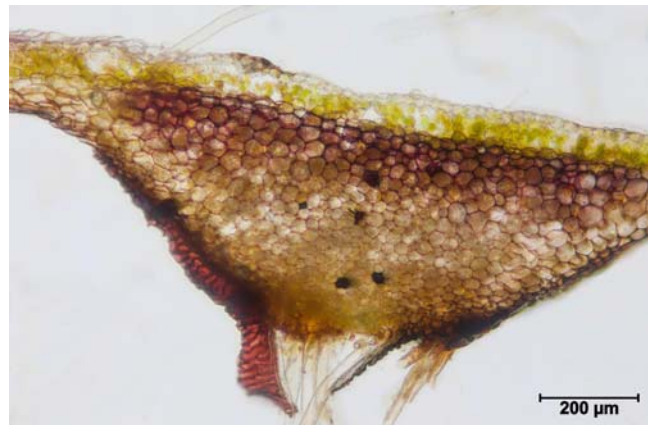


Figure 33. *Marchantia quadrata* thallus cross section with scales and rhizoids projecting from the lower surface. Photo by Kristian Peters, with permission.

Like other *Marchantia* species, *M. quadrata* (Figure 1-Figure 5) has both smooth and pegged rhizoids (Figure 33) as well as appendaged scales (Figure 33-Figure 34) on the lower surface (Cavers 1904). Presumably, these serve the same functions in conduction as those of *M. polymorpha* (Figure 12).

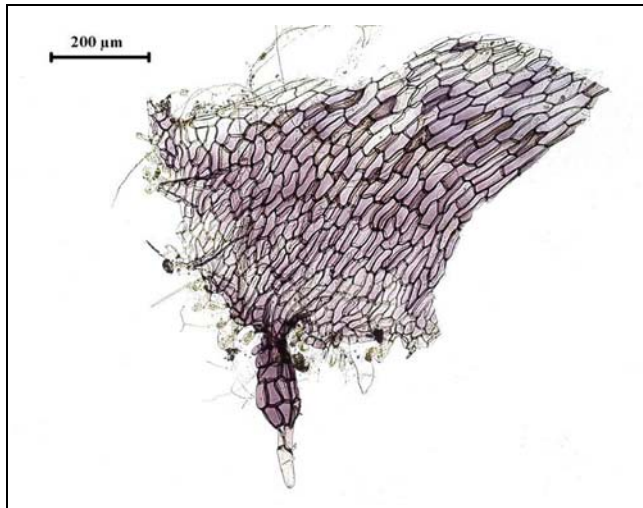


Figure 34. *Marchantia quadrata* ventral scale. Photo by Hugues Tinguy, with permission.

Like other species of *Marchantia*, *M. quadrata* (Figure 1-Figure 5) has air pores (Figure 35-Figure 43) in the thallus that permit more rapid gas exchange than the thallus epidermis does (Haupt 1926). In this species, the pore is barrel-shaped with cells in four or five tiers (Figure 38, Figure 40, Figure 43) (Walker & Pennington 1939). The upper opening is always wide open (Figure 40, Figure 41, Figure 43), but the inner part is narrower and can be closed (Figure 41-Figure 43). Each cell of the basal tier, referred to by Walker and Pennington as **motor cells**, has a papilla which projects freely inward. The papilla has a thinner wall than the remainder of the motor cell. Movements of the papillae are responsible for changes in the size of the opening.



Figure 35. *Marchantia quadrata* showing epidermis with pores. Photo by Jan-Peter Frahm, with permission.



Figure 36. *Marchantia quadrata* thallus portion showing pores. Photo by Kristian Peters.

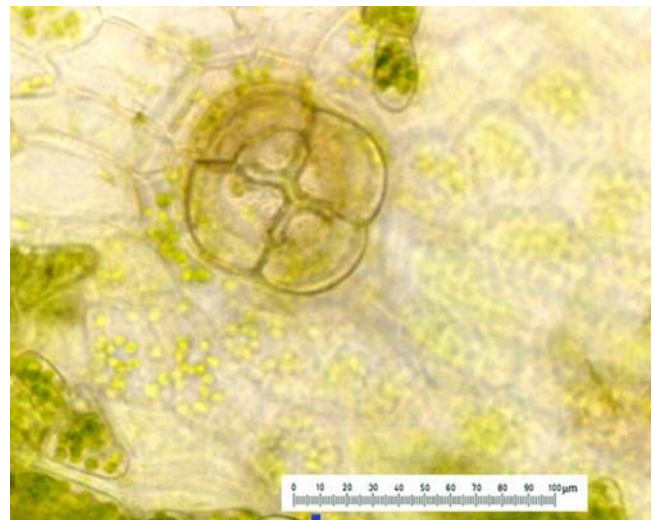


Figure 37. *Marchantia quadrata* thallus showing pore viewed from ventral surface. Photo by David Wagner, with permission.

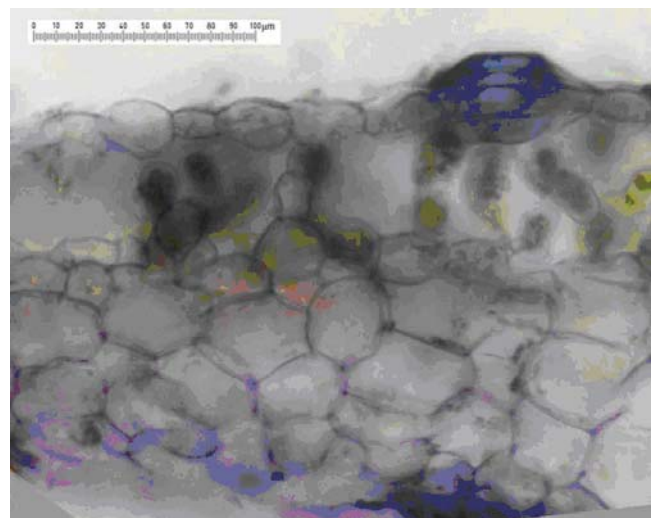


Figure 38. *Marchantia quadrata* thallus section showing air spaces, photosynthetic cells, and pore. Photo by David Wagner, with permission.

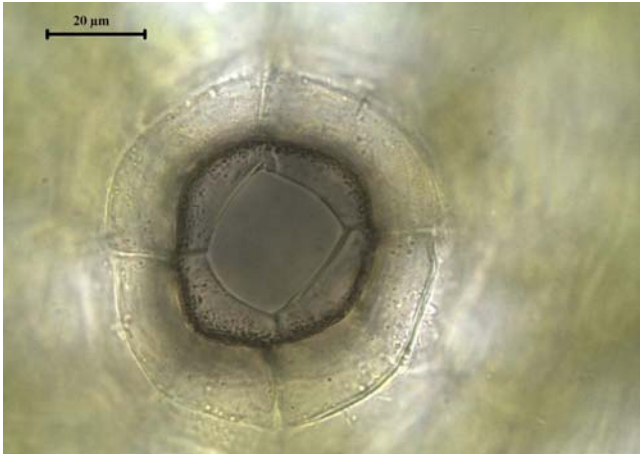


Figure 39. *Marchantia quadrata* pore showing cuticular ridge (grey). Photo by Hugues Tinguy, with permission.

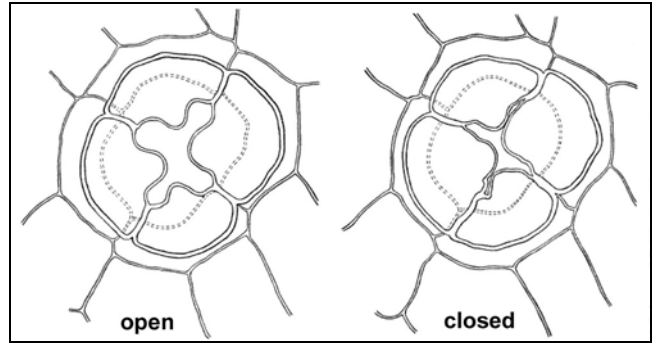


Figure 42. *Marchantia quadrata* pore closing. Image modified from Walker & Pennington 1939.

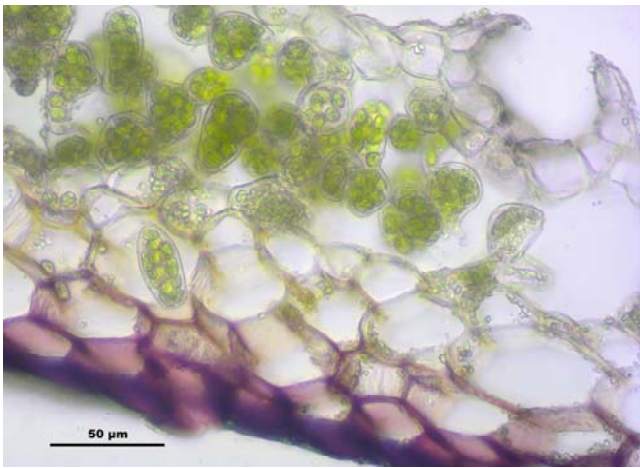


Figure 40. *Marchantia quadrata* thallus section showing closed pore, photosynthetic layer, and purple ventral side. Photo by Hermann Schachner, through Creative Commons.

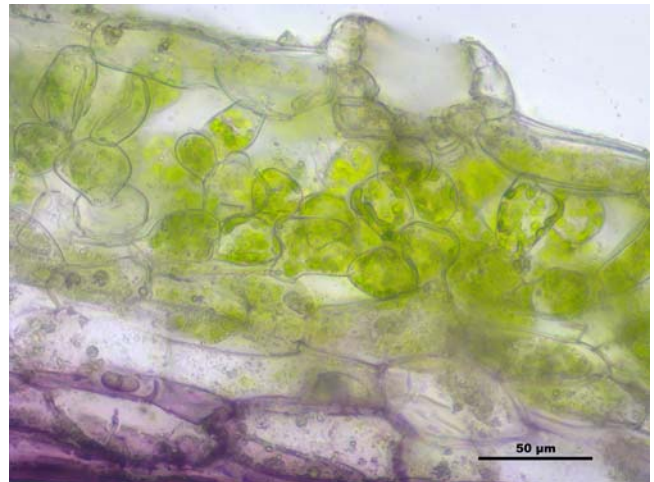


Figure 43. *Marchantia quadrata* thallus section showing pore and chamber beneath it with photosynthetic filaments. Photo by Hermann Schachner, through Creative Commons.

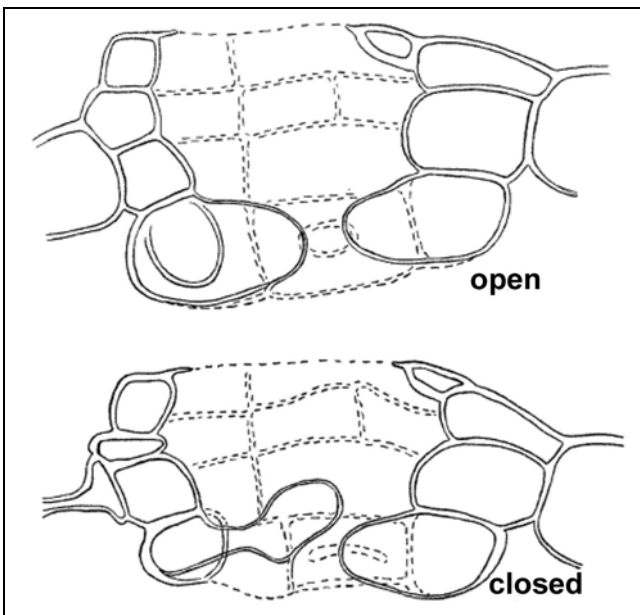


Figure 41. *Marchantia quadrata* pore closing. Note that the motor cell on the right is not functioning, presumably due to injury. Image modified from Walker & Pennington 1939.

Growth occurs at the apical notch, which is covered by a small scale that is usually purplish (Figure 44-Figure 45). The thallus can dry out or senesce while the reproductive branches continue to grow (Figure 46). Red coloration on the thallus margins (Figure 47) is common in this species and could indicate that it has experienced stress.



Figure 44. *Marchantia quadrata* in Europe, showing purple covers of the apical growing region. Photo by Michael Lüth, with permission.



Figure 45. *Marchantia quadrata* in Europe, showing purple covers of the apical growing region. Photo by Michael Lüth, with permission.



Figure 46. *Marchantia quadrata* archegoniophores and dying thallus, showing the ability of archegoniophores to persist even when the thallus is senescing or dying. Photo by Jiří Kameníček (BioLib, Obázek), with permission.



Figure 47. *Marchantia quadrata* with red margins, indicating stress. Photo by Allen Norcross, with permission.

One feature that seems to lack documentation for liverworts, but present in *Marchantia quadrata* (Figure 1-Figure 5), is the presence of scattered sclerotic cells in the ventral part of the thallus (Haupt 1926). These are elongated, thick-walled, dark brown, fiber-like cells with pointed ends. Their significance is not clear. Cavers (1904) suggests that their primary function is conduction and storage of water. These fibers are absent in the plants that grow in a moist atmosphere (Haupt 1926).

Isolated mucilage cells can be found in all parts of the thallus, but mucilage canals are absent (Haupt 1926). Starch grains seem only to accumulate in the older female receptacles where they presumably are available to the growing sporophytes. Oil globules occur in the apical region, particularly in the epidermal cells, and in the epidermis of the receptacles.

Reproduction

Marchantia quadrata (Figure 1-Figure 5) is usually considered to be **dioicous** (Haupt 1926). However, Haupt (1926) also found a few **monoicous** plants, comprising about 1% of the material studied. Zheng and Shimamura (2022) furthermore noted that dioicous plants are known to be widely distributed in the temperate boreal region and monoicous plants are usually found in the Arctic (Schuster 1972, 1985, 1992; Long & Crandall-Stotler 2020). Are these different races, or different expression of genes in the cold Arctic with its long summer days?

However, all the Japanese *M. quadrata* plants that Zheng and Shimamura (2022) examined and found during fieldwork were **monoicous**. Because the growing season of archegoniophores and antheridiophores is different and the archegoniophores do not grow unless fertilization is successful (Haupt 1926) it is easy to falsely conclude that one sex is absent in the population.

In spring in Japan, thalli with young antheridiophores arise from the apex of the ventral side of previous thalli with a well-stalked female receptacle bearing sporophytes (Zheng and Shimamura (2022)). In summer, a new thallus with a new archegoniophore occurs in the same way from the underside of the apex of the previous thalli with a well-stalked male receptacle and the oldest archegoniophore withers after spore dispersal. That is, each time a new branch is formed, the sexuality alternates. Only by following the same population throughout the year can the true sexuality condition be determined.

Usually the antheridia are produced on a separate stalk, the **antheridiophore** (Figure 48-Figure 50), and archegonia are produced on **archegoniophores** (Figure 51-Figure 58). When the plants are **monoicous**, antheridia occur on the upper surface of the anterior portion of the receptacle and the archegonia occur on the under side of the posterior portion (Haupt 1926). Haupt, presumably in North America, found that antheridia begin to appear in late spring, with archegonia developing somewhat later in early summer.



Figure 48. *Marchantia quadrata* antheridiophores. Photo from Bioimages, through Creative Commons.



Figure 49. *Marchantia quadrata* antheridiophores. Photo from Bioimages, through Creative Commons.



Figure 50. *Marchantia quadrata* antheridiophores. Photo from Bioimages, through Creative Commons.

Benson-Evans (1964) reported that in the UK *Marchantia quadrata* (Figure 1-Figure 5) is a long-day plant for sexual reproduction. In 16 hours of light, 66% of

the plants expressed sexual structures; in 18 hours of light this increased to 80%. Light of 16.1-87.6 lux was suitable for gametangia development. However, when the temperature was dropped to 10°C in 18 hours light, the plants exhibited few sexual structures and had slow growth. These were even more limited at both 10°C and 21°C in 6 hours light. This species is, however, mostly influenced by photoperiod, operative within a somewhat broad temperature range (Longton 1990).

Both sexual organs continue to form during the entire growing season, with young archegonial receptacles in northern New York, USA, appearing as late as the end of September (Haupt 1926). On 24 September, Haupt observed that nearly all of the plants had the same sexual condition. The male nucleus was within the egg and in contact with the egg nucleus, but not yet fused. These archegonial receptacles overwinter with sporogenous tissue that has just differentiated. In the spring, growth of the sporophytes continues and the female receptacle stalk continues growth. In this location, the spores mature in June.



Figure 51. *Marchantia quadrata* with developing archegoniophores. Photo by Hermann Schachner, through Creative Commons.



Figure 52. *Marchantia quadrata* with developing archegoniophores. Photo by Claire Halpin, with permission.



Figure 53. *Marchantia quadrata* with developing archegoniophore. Photo by Hermann Schachner, through Creative Commons.



Figure 54. *Marchantia quadrata* with expanding archegoniophores. Photo by Jan-Peter Frahm, with permission.



Figure 55. *Marchantia quadrata*, showing numerous fertile plants at Pictured Rocks, Michigan, USA. Photo by Janice Glime.



Figure 56. *Marchantia quadrata* young (at tip) and older archegoniophores in Europe. Photo by Michael Lüth, with permission.



Figure 57, *Marchantia quadrata* with extended archegoniophores. Note white scales showing at the margins. Photo by Hermann Schachner, through Creative Commons.



Figure 58. *Marchantia quadrata* with mature archegoniophores, showing how numerous they can be. Photo by Michael Lüth, with permission.

When the sporangia mature, they protrude from the archegonial head (Figure 59-Figure 63). They burst and elaters wiggle among the spores (Figure 64-Figure 65) in response to moisture changes, in some cases helping the spores to exit the capsule, but in others entangling them in clusters of tangled elaters.



Figure 59. *Marchantia quadrata* with mature archegoniophores. Photo by Michael Lüth, with permission.



Figure 60. *Marchantia quadrata* mature archegoniophores with green thalli in Europe. Photo by Michael Lüth, with permission.



Figure 61. *Marchantia quadrata* archegoniophores with emerging sporangia. Photo by Michael Lüth, with permission.



Figure 62. *Marchantia quadrata* mature archegonial head with sporangia. Photo by Des Callaghan, with permission.



Figure 63. *Marchantia quadrata* archegoniophore with emerging sporangia and elaters. Photo by Bob Klips, with permission.

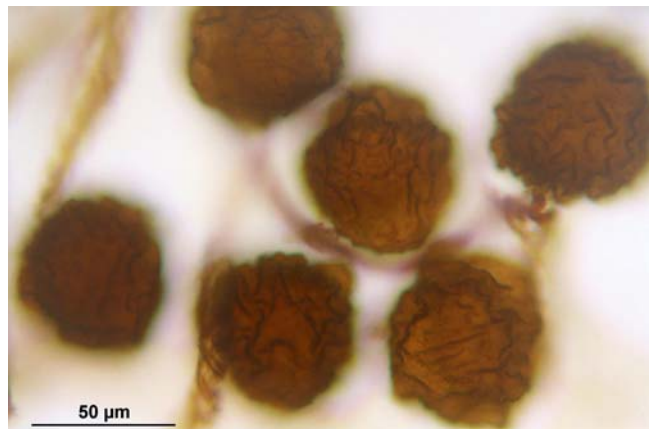


Figure 64. *Marchantia quadrata* spores and elaters. Photo by Hermann Schachner, through Creative Commons.

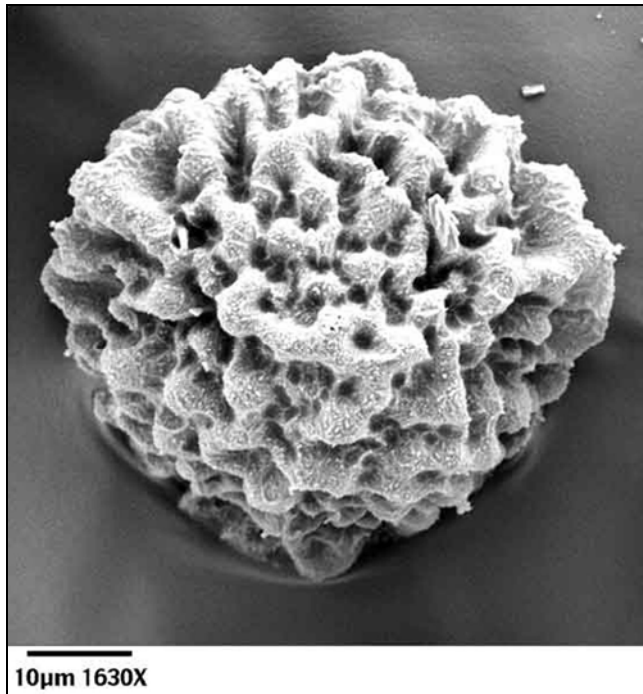


Figure 65. SEM of *Marchantia quadrata* distal spore wall. Photo by William T. Doyle, with permission.

Unlike other members of the **Marchantiaceae**, *M. quadrata* (Figure 1-Figure 5) has no gemmae (Boisselier-Dubayle & Bischler 1997; Zheng *et al.* 2020). Nevertheless, members of an individual colony were genetically identical, suggesting vegetative reproduction was important, achieved by growth and division of the thalli. There was little indication of any genetic exchange between colonies growing in proximity.

Fungal Interactions

Haupt (1926) reported intracellular fungi in the lower part of the *Marchantia quadrata* (Figure 1-Figure 5) thallus (see also Golenkin 1902). These occur mostly along the median line and are more abundant in older tissues. This fungal zone frequently occupies one-half to two-thirds the thickness of the thallus, sometimes reaching the air chambers. In the ventral region, the hyphae form parallel strands that extend longitudinally. Above this area they form compact tangled masses inside the shorter thallus cells.

Biochemistry

Gorham (1977) reported the presence of lunularic acid in all parts of *Marchantia quadrata* (Figure 1-Figure 5). This presence was greatest in continuous light. Gorham suggested that either the lunularic acid was not inhibited in continuous light or the inhibition was overcome by products of photosynthesis.

König *et al.* (1996) reported that the main constituent of a southern German chemotype of *Marchantia quadrata* (Figure 1-Figure 5) is the labile sesquiterpene hydrocarbon germacrene C. These researchers also observed several rare ent-sesquiterpenes as major constituents.

Asakawa *et al.* (1997) reported a number of sesquiterpenes and the cyclic bis(bibenzyls) riccardin B and

neomarchantin A from *Marchantia quadrata* (Figure 1-Figure 5).

Marchantia treubii

(syn. = *Marchantia sciaphila*)

Distribution

Siregar *et al.* (2013) reported on *Marchantia treubii* from Sumatra. This species is among the most common *Marchantia* species on Mount Sibayak, found from lowland to high altitude. It is relatively widespread in Indonesia (Sumatra, Java, Lesser Sunda Island), Borneo, and Malaysia (Bischler-Causse 1989; Chuah-Petiot 2011).

Aquatic and Wet Habitats

Marchantia treubii occurs in the spray of waterfalls in the tropics (Ruttner 1955). *Marchantia treubii* occurs on soil and rocks in open places and semi-shaded places in Indonesia (Siregar *et al.* 2013; Haerida 2017). Raihan *et al.* (2018) reported that this liverwort occurs almost everywhere on rocks at their study area at Peucari Bueng Jantho Waterfall in the Aceh Besar District of Indonesia.

Azwir *et al.* (2022) reported its environmental parameters from Mesjid Raya in Indonesia. The site was humid, with pH ranging 4.9-7.3 (mean 6.3) and a low light intensity of 0.07-0.09 lux, mean of 0.08 lux. Since the light intensity also affects the temperature and humidity, this indicates lower temperatures and higher humidity in its habitat.

Adaptations

Most of the adaptations described for other species of *Marchantia* apply here. *Marchantia treubii* from Indonesia had purplish lines on the thallus and fine hair at the edge (Raihan *et al.* 2018). I was unable to find much specific information on this species.

Reproduction

Fritsch (1991) reported a chromosome count of $n=9$ for *Marchantia treubii*. It is **dioicous** (Siregar *et al.* 2013). Raihan *et al.* (2018) found *Marchantia treubii* with gemmae cups as well as sporophytes in Indonesia, exhibiting female receptacles with 3-5 lobes.

Summary

Marchantia quadrata was classified in the genus *Preissia* and might return there. It lacks gemmae, but occurs in similar habitats to some of the *Marchantia* species. Its distribution is similar (Australia, Europe, Northern and Southern Asia, Central America, North America, Oceania, and South America). It occurs on wet rocks and soil of stream banks, waterfalls, and dripping cliffs, including limestone. It benefits from phosphates, especially on limestone. It survives winter under the snow, but does not do well in high temperatures. Its adaptations are similar to those of other *Marchantia* species, with thick thallus, pores, photosynthetic chambers, rhizoids that either anchor or provide capillary spaces for conduction, and scales that help move and conserve water.

Marchantia treubii occurs in a small, tropical portion of Asia. It is best known from waterfalls, but in some areas of Indonesia it is the most common liverwort on the mountain. It is dioicous and has gemmae.

Acknowledgments

I appreciate the email discussions with T. Zheng and M. Shimamura on the classification of *Marchantia quadrata*.

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