

CHAPTER 1-1

AQUATIC AND WETLAND: ANTHOCEROTOPHYTA

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CHAPTER 1-1

AQUATIC AND WETLAND: ANTHOCEROTOPHYTA



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 mountainous 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)

Anthoceros agrestis (Figure 2) (syn. = *Anthoceros punctatus* var. *cavernosus*) 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.

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 (Liverworts of New Brunswick 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).

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.

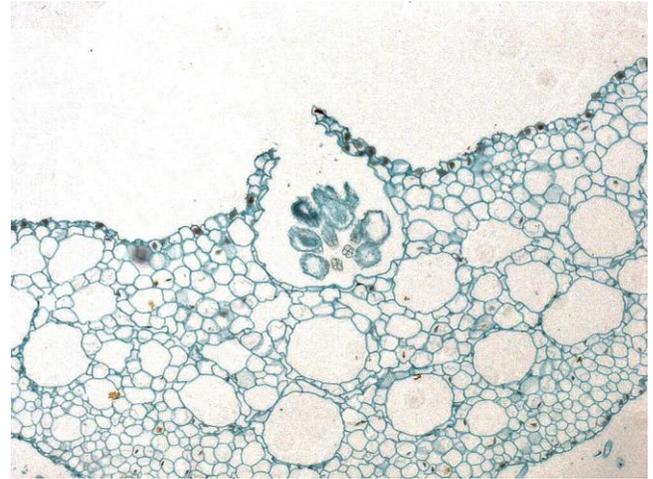


Figure 3. *Anthoceros* thallus cs showing large parenchyma cells and pore with *Nostoc*. Photo from Botany Website, UBC, with permission.

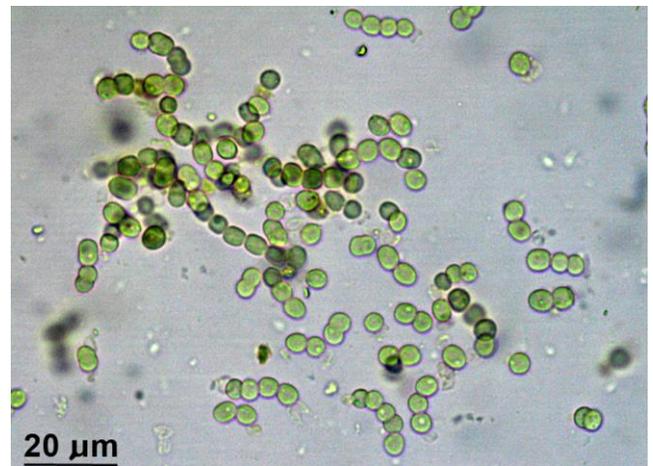


Figure 4. *Nostoc* from *Anthoceros agrestis*. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission

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)

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).

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)**

This species presents near absence in wetland studies, *Anthoceros punctatus* occurs in Europe, Asia, and North and South America (MBG 2020). 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.

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 8) 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.

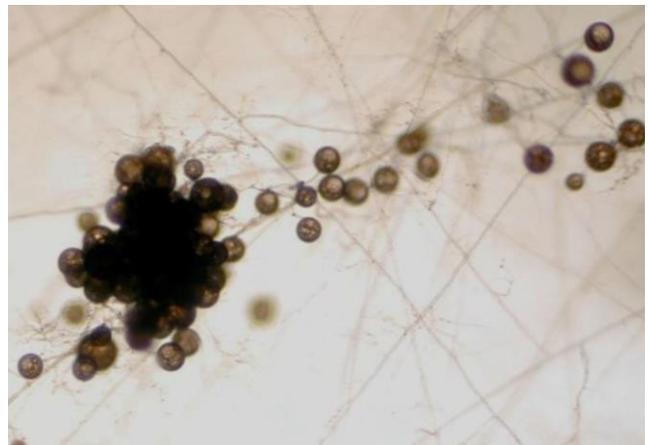


Figure 8. *Claroideoglomus claroideum*, an endophytic fungus that can occur within cells of *Anthoceros punctatus*. Photo by V. A. Silvani, M. Pégola, and S. Fracchia, through Creative Commons.

A much better-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 9) 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 9. *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 9) 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.

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 the spray of waterfalls 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)

Folioceros fuciformis (Figure 11) (syn. = *Aspiromitus falsinervius*) is often reported in checklists from various tropical locations and countries in Asia (TROPICOS

2020a), but its habitat is not included. Hence 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.



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.

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)

Folioceros glandulosus (Figure 12) (syn. = *Aspiromitus glandulosus*) 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)

Megaceros flagellaris (Figure 13) (syn. = *Megaceros salakensis*) 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.

Ruttner (1955) reported it 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.

The species is monoicous (Chantanaorrapint 2014). Desirò *et al.* (2013) did not find any colonization of this species by fungi, although a number of 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 publication 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)

Phymatoceros bulbiculosus (Figure 1, Figure 14) (syn. = *Phaeoceros bulbiculosus*) 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.



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

Proskauer (1957) reports this species as widespread in the Mediterranean region of Europe and Africa, and it is also present in North and South America. 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 agriculous in Slovakia, but protected (red-listed), suggesting that it might be under-recorded.

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 these 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.

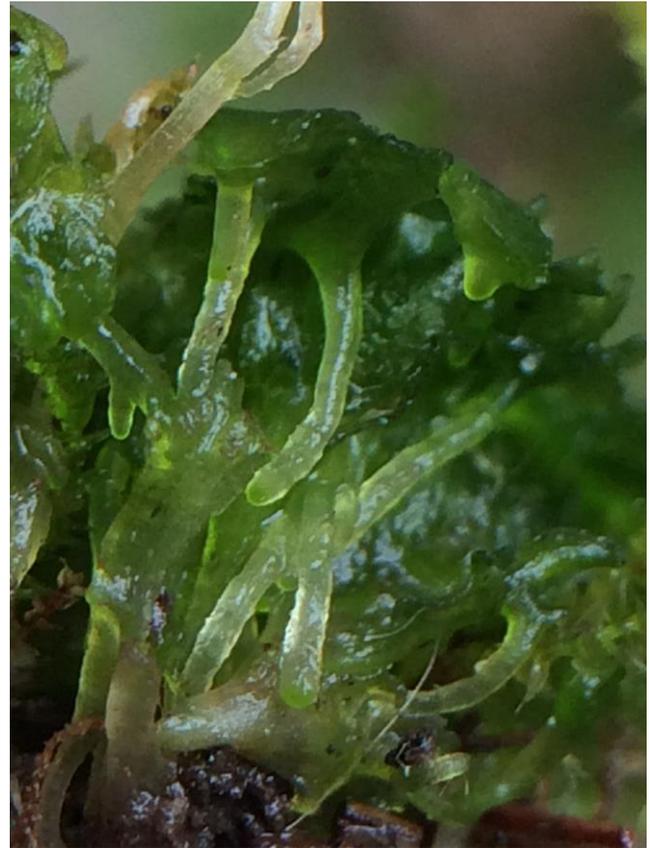


Figure 15. *Phymatoceros bulbiculosus* showing numerous ventral tubers. Photo by Donna Pomeroy, through Creative Commons.



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)**

Phaeoceros carolinianus (Figure 18) (syn. = *Anthoceros carolinianus*, *Anthoceros laevis* var. *carolinianus*, *Phaeoceros laevis* var. *carolinianus*) 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.

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.

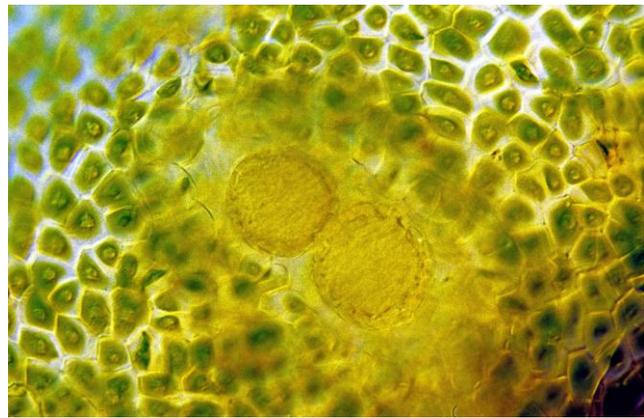


Figure 19. *Phaeoceros* antheridia in their yellow-orange mature stage. Photo by George Shepherd, through Creative Commons.

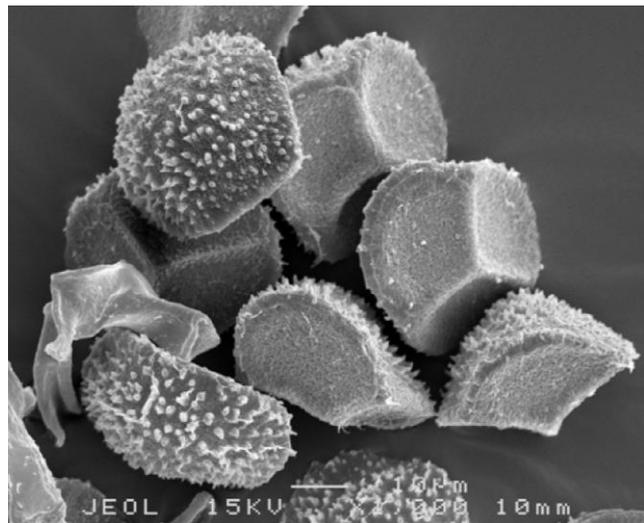


Figure 20. *Phaeoceros carolinianus* spores SEM. Photo by Christine Cargill, through Creative Commons.

***Phaeoceros laevis* (Figure 21)**

Phaeoceros laevis (Figure 21) (syn. = *Anthoceros laevis*) 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, it is 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 (Figure 21) can be found in rivers (Ferreira *et al.* 2008); and occurs in mountainous streams in Madeira Island, Portugal (Luis *et al.* 2015). The Southern Hemisphere records should be viewed with caution, as they are probably all misidentified *Phaeoceros carolinianus* (Figure 18) (Cargill & Fuhrer 2008).



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).

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).

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, the chloroplast loses starch and its **pyrenoid** (protein body in chloroplasts of algae and hornworts, involved in carbon

fixation and starch formation and storage), forming 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.

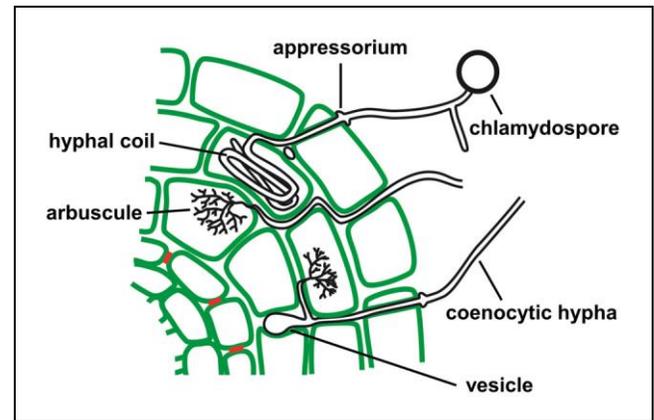


Figure 22. Diagram of arbuscular mycorrhiza, **Glomeromycota**, in a root. Diagram by M. Piepenbring, through Creative Commons.

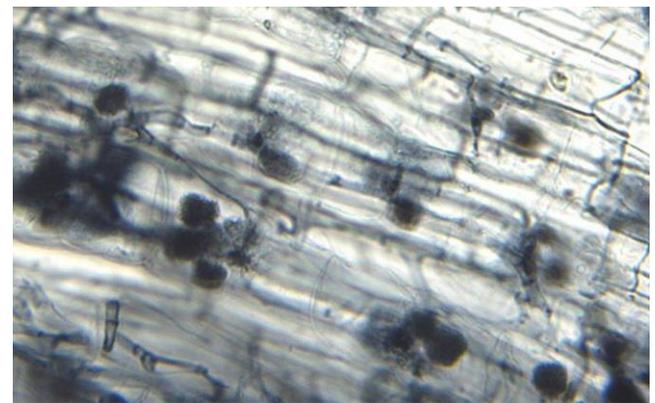


Figure 23. Arbuscular mycorrhiza in root cells. Photo by M. S. Turmel, through public domain.

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.

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CHAPTER 1-2

AQUATIC AND WETLAND: MARCHANTIOPHYTA, ORDER JUNGERMANNIALES – CEPHALOZIINEAE 1

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CHAPTER 1-2

AQUATIC AND WETLAND:

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 2)

Cuspidatula flexicaulis (syn. = *Jamesoniella balansae*, *Jamesoniella flexicaulis*, *Jamesoniella affinis* fo. *minor*; see Figure 2) is distributed in Malaysia, Indonesia, Papua New Guinea, and New Caledonia (GBIF 2020a). In New Zealand it is an abundant species in subalpine forests (Scott 1970). Ruttner (1955) reported it among the wetland and aquatic species in the tropics (Ruttner 1955).



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

Syzygiella sonderi (Figure 3)

Syzygiella sonderi (syn. = *Cryptochila grandiflora*; Figure 3) 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 3. *Syzygiella sonderi*, a Southern Hemisphere species that benefits from high water levels of mountain streams. Photo by Juan Larrain, through Creative Commons.

In the Andes, Gradstein *et al.* (2018) listed *Syzygiella sonderi* (Figure 3) 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* is restricted to mire drainage lines, where it is one of the dominant species.

Anastrophyllaceae

Anastrophyllum assimile (Figure 4)

Anastrophyllum assimile (Figure 4) 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 4. *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.

Anastrophyllum assimile (Figure 4) 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 5).



Figure 5. *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.

In higher altitudes in China and the Himalayas it 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.

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.

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 4) (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 6)

Anastrophyllum michauxii (syn. = *Sphenobolus michauxii*; Figure 6) 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 6. *Anastrophyllum michauxii*, a Holarctic species that prefers rotten logs, especially near streams and other wet areas. Photo by Michael Lüth, with permission.

On the Soyda River bank in the Russian Federation, Dulin and Philippov (2012) found *Anastrophyllum michauxii* (Figure 6) 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 7)**

Barbilophozia barbata (Figure 7) is widespread in the Northern Hemisphere, especially in the boreal and mountain regions (Düll 2004; Wagner 2009). 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, Mamczarz (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 8), *Lepidozia reptans* (Figure 8), and *Ptilidium ciliare* (Figure 9).



Figure 7. *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.



Figure 8. *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 9. *Ptilidium ciliare*, a species that may accompany *Barbilophozia barbata* on moist igneous cliffs. 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 7, Figure 10-Figure 11) 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 10. *Barbilophozia barbata* in a patch on a boulder (see arrow). Photo by Sture Hermansson, with online permission.

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

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 12) in association with *Barbilophozia barbata* (Figure 7, Figure 10-Figure 11) collected from Switzerland and the UK.



Figure 12. *Sebacina incrustans* on moss, a genus known to occur in association with *Barbilophozia barbata*. Photo through Creative Commons.

***Barbilophozia sudetica* (Figure 13-Figure 14)**

Barbilophozia sudetica (syn. = *Lophozia sudetica*; Figure 13-Figure 14). *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 (Bakalin 2004). In North America, Rahill (2018) found it among the tundra vegetation on Mount Washington, NH, USA.



Figure 13. *Barbilophozia sudetica*, an arctomontane species sometimes found on wet cliffs and stream banks. Photo by Hugues Tinguy, with permission.



Figure 14. *Barbilophozia sudetica* showing a color variant. Photo by Štěpán Koval, with permission.

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 74) 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 15), in an alpine fellfield, on an old pier, and on damp humus on a cliff shelf.



Figure 15. *Pohlia wahlenbergii* with water beads, in a habitat suitable for *Barbilophozia sudetica*. Photo by Michael Lüth, with permission.

Like *Barbilophozia barbata* (Figure 7, Figure 10-Figure 11), *B. sudetica* (Figure 13-Figure 14) is known to form symbiotic mycorrhizal fungal associations (Wang & Qiu 2006) with the *Sebacinaceae* (Figure 12) (Kottke *et al.* 2003).

***Gymnocolea inflata* (Figure 16-Figure 17, Figure 19, Figure 21)**

Gymnocolea inflata (Figure 16-Figure 17, Figure 19, Figure 21) is distributed in Africa, Europe, northern and southern Asia, and North America (Alaska, Canada, USA) (ITIS 2020a).



Figure 16. *Gymnocolea inflata*, a species with widespread distribution that can occur in or out of water. Photo by Hermann Schachner, through Creative Commons.

Gymnocolea inflata (Figure 16-Figure 17, Figure 19, Figure 21) is a **hydroamphibiont** (living in transition zone between water and land, depending on water level; compare to euhydrobiont and geoamphibiont) (Figure 17), occurring in acid water (pH 3.5-4.2) in streams of Gory Stolowe Mountains, Poland (Szweykowski 1951). In Europe it often occurs with *Carex goodenoughii*, but is uncommon with *Eleocharis quinqueflora* (Figure 72) and *Paludella squarrosa* (Figure 18) (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 17. *Gymnocolea inflata* growing in a wet habitat. Photo by Michael Lüth, with permission.



Figure 18. *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 19) 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 20) community where it covered the bottom of shallow depressions in heathland between bars.



Figure 19. *Gymnocolea inflata* showing one of its dark color forms. Photo by Michael Lüth, with permission.



Figure 20. *Rhynchospora fusca*, a community that often has *Gymnocolea inflata* in heathland low areas. Photo by Peter M. Dziuk, with online permission for educational use.

Watson (1919) reported *Gymnocolea inflata* (Figure 16-Figure 17, Figure 19, Figure 21) as form *laxa* on peaty sides of fast water streams, on banks with frequent submergence, and submerged in slow water with poor mineral salts.

In Westfalens, northwestern Germany, *Gymnocolea inflata* (Figure 16-Figure 17, Figure 19, Figure 21) occurs between *Sphagnum* (Figure 21) (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 21) include those

that are typically sterile, *i.e.*, not forming sexual reproductive structures. Frequently fertile species (*e.g.*, *Cephalozia* spp.; Figure 41-Figure 66) tend to occur on peat or litter, rather than on living *Sphagnum*.



Figure 21. *Gymnocolea inflata* in Perrault Fen, Houghton Co., MI, USA, with *Sphagnum*. Photo by Janice Glime.

Gough *et al.* (2006) found that *Gymnocolea inflata* (Figure 16-Figure 17, Figure 19, Figure 21) 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 16-Figure 17, Figure 19, Figure 21). 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 22-Figure 23)**

Isopaches bicrenatus (syn. = *Lophozia bicrenata*; Figure 22-Figure 23) 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 22. *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.

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).

Fulford (1955) described development of *Isopaches bicrenatus* (Figure 22-Figure 23). 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 23) in clusters. These, and leaf fragments that regenerate easily, make reproduction and spread easy for this species.

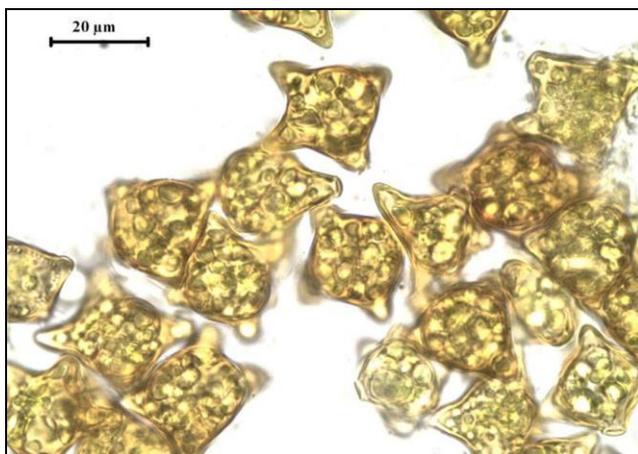


Figure 23. *Isopaches bicrenatus* gemmae; these become reddish at maturity. Photo by Hugues Tinguy, with permission.

Rivulariella gemmipara (Figure 24)

Rivulariella gemmipara (syn. = *Chiloscyphus gemmiparus*) 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 24. *Rivulariella gemmipara* leaves from upward-growing stem. Photo courtesy of David Wagner.

This species 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) place it in the **Anastrophyllaceae**, a family formerly included within the **Scapaniaceae**.

Rivulariella gemmipara grows in moderately fast water where there are small rocks (small pebbles to fist-sized cobbles) and gravel (Figure 25-Figure 27), 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 rapid. These 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.



Figure 25. *Rivulariella gemmipara* habitat in springfed stream. Photo courtesy of David Wagner.

The species has horizontal, flattened stems (Figure 26) 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 26, Figure 28). This method of gluing to the substrate seems to be a unique adaptation of this species.



Figure 26. *Rivulariella gemmipara* flat horizontal stems on rock that was overturned. Photo courtesy of David Wagner.



Figure 28. *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.

Reproduction seems to be primarily by fasciculate, multicellular gemmae (Figure 29), but sporophytes are known.



Figure 27. *Rivulariella gemmipara* on pebbles in springfed stream. Photo courtesy of David Wagner.



Figure 29. *Rivulariella gemmipara* leaf with gemmae. Photo courtesy of David Wagner.

***Schljakovia kunzeana* (Figure 30)**

Schljakovia kunzeana (syn. = *Lophozia kunzeana*, *Orthocaulis kunzeanus*; Figure 30) 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 30. *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.

Watson (1919) described *Schljakovia kunzeana* (Figure 30) 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 31, Figure 34-Figure 37)**

Sphenolobus minutus (syn. = *Anastrophyllum minutum*; Figure 31, Figure 34-Figure 37) 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).

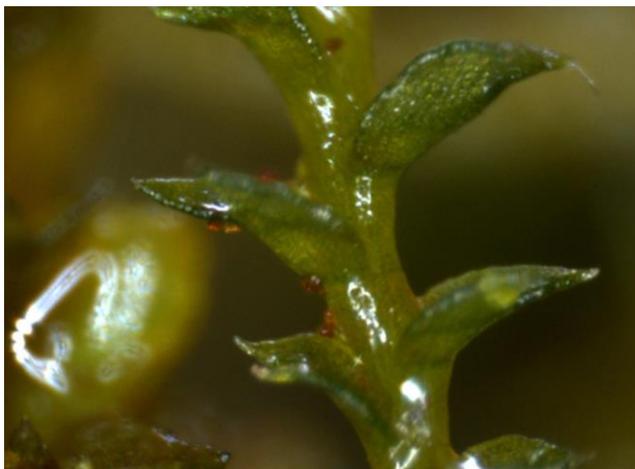


Figure 31. *Sphenolobus minutus*, a widely distributed Holarctic liverwort that is less common further south except on the mountains; it lives on peaty soil and areas of high moisture, but can become submerged in montane streams. Photo by Jouko Rikkinen, through Creative Commons.

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 32) at Franconia Notch, New Hampshire, USA it occurred on the flume wall (Glime 1982). In western Canada it occurs submerged as a hemicalciphilous species in montane streams and on stream banks (Figure 33) (Vitt *et al.* 1986; Glime & Vitt 1987). In these habitats, it forms mats (Figure 34).

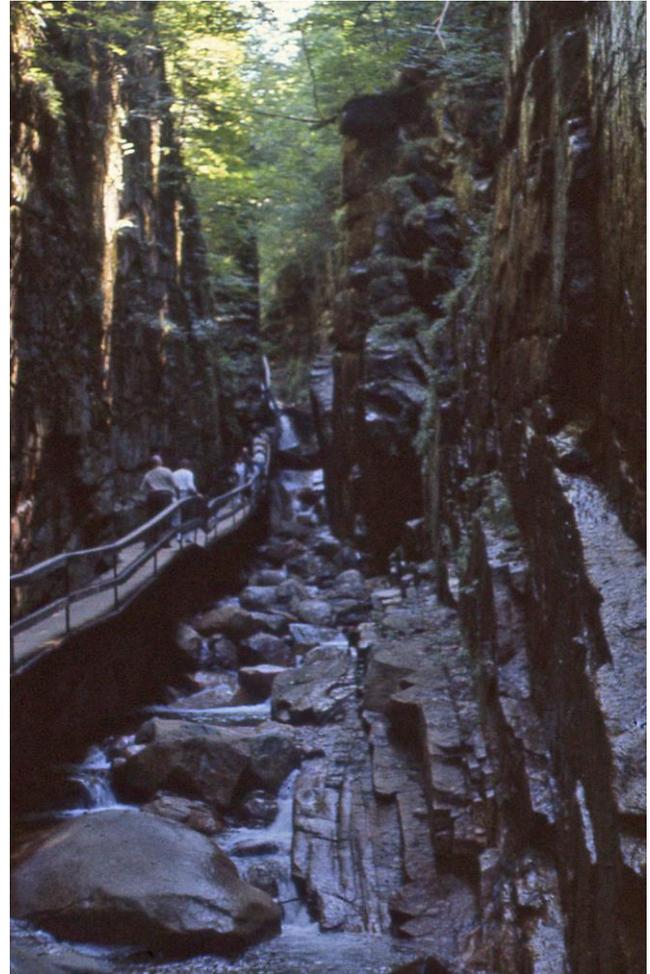


Figure 32. Flume, Franconia Notch, NH, site where one can find *Sphenolobus minutus* on the walls. Photo by Janice Glime.



Figure 33. Calcareous stream in BC, Canada, where one might find *Sphenolobus minutus*. Photo by Janice Glime.



Figure 34. *Sphenolobus minutus* forming a mat. Photo by Jouko Rikkinen, through Creative Commons.

Like most of the leafy liverworts, *Sphenolobus minutus* (Figure 34) produces gemmae (Figure 35-Figure 37). These provide a means of surviving unfavorable conditions as well as dispersal.



Figure 35. *Sphenolobus minutus* with gemmae. Photo by Jouko Rikkinen, through Creative Commons.

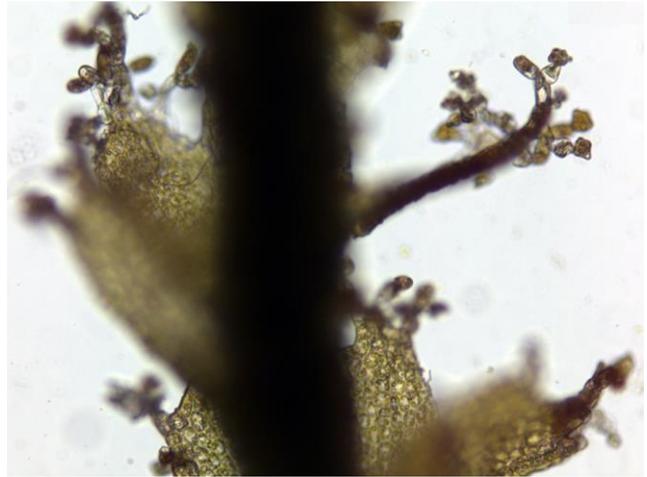


Figure 36. *Sphenolobus minutus* with gemmae on leaf tips. Photo by Jouko Rikkinen, through Creative Commons.

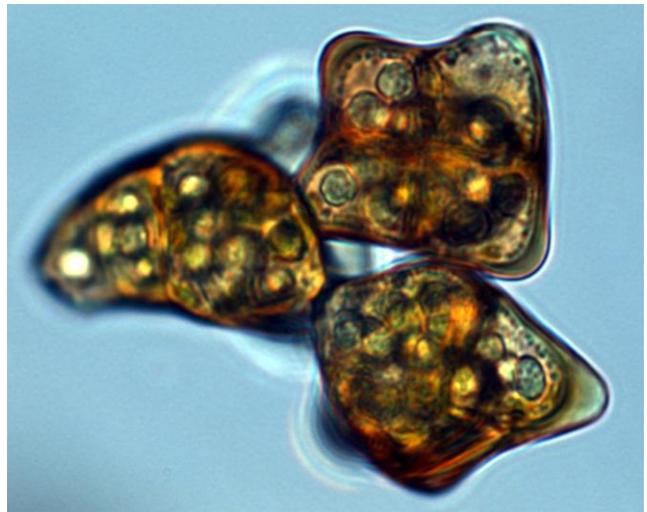


Figure 37. *Sphenolobus minutus* gemmae, showing their angular construction. Photo by Jouko Rikkinen, through Creative Commons.

Kitagawa (1974) reported nematode galls (Figure 39-Figure 38) on *Sphenolobus minutus* (Figure 31, Figure 34-Figure 37) 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 38. Nematode similar to the ones that can form galls on *Sphenolobus minutus*. Photo by courtesy of Andi Cairns.

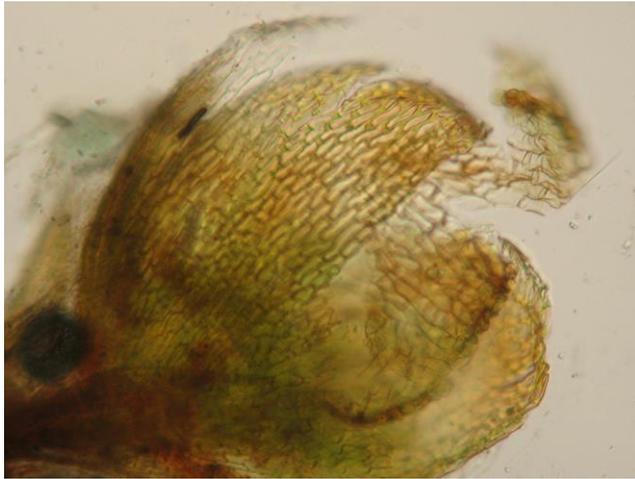


Figure 39. *Bryum argenteum* nematode galls, a parasitic attack that also occurs in *Sphenolobus minutus*. Photo courtesy of Claudio Delgado Moya.

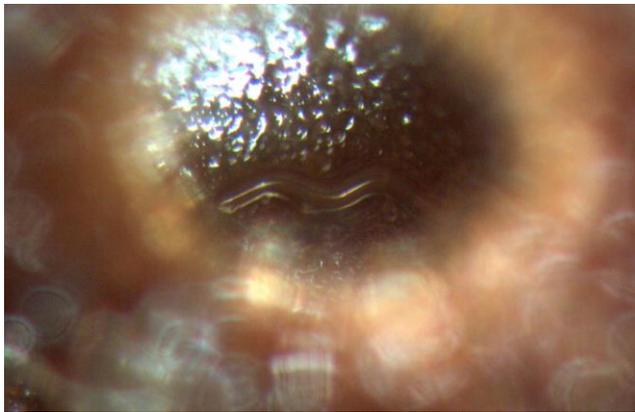


Figure 40. *Buxbaumia aphylla* nematode in gall showing nematode. Photo by Misha Ignatov, with permission.

Tetralophozia filiformis

Tetralophozia filiformis (syn. = *Chandonanthus filiformis*, *Chandonanthus pusillus*) 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). 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 41-Figure 55)

Cephalozia (Figure 41-Figure 55) 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 74) as a substrate, using an **avoidance strategy**.

Cephalozia ambigua (Figure 41-Figure 42)

Cephalozia ambigua (Figure 41-Figure 42) 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 41. *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.

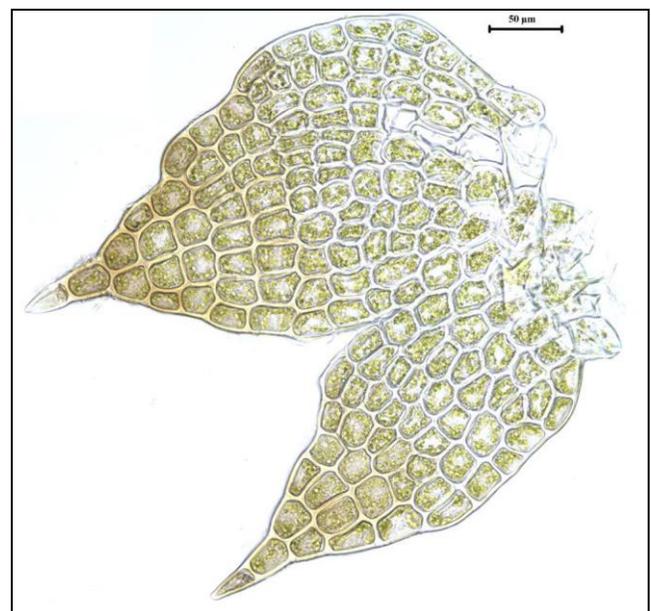


Figure 42. Leaf from *Cephalozia bicuspidata* complex. Note the thickened walls of the terminal cells compared to those at the base. Photo by Hugues Tinguy, with permission.

In the Swiss Alps, *Cephalozia ambigua* (Figure 41-Figure 42) 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).

Potemkin and Sofronova (2013) noted that most species of *Cephalozia* never develop any secondary pigmentation, thus always occurring as green or whitish green (Figure 41). However, members of the *Cephalozia bicuspidata* complex [*C. ambigua* (Figure 41-Figure 42), *C. bicuspidata* (Figure 43, Figure 49-Figure 51, Figure 55, Figure 66), *C. hamatiloba* (Figure 44)] from sunlit habitats are typically brown and/or purple. Furthermore, *C. catenulata* (Figure 45), *C. macrostachya* (Figure 46), *C. loitlesbergeri* (Figure 47) and *Nowellia curvifolia* (syn. = *Cephalozia curvifolia*; Figure 48) often develop brown pigmentation.



Figure 43. *Cephalozia bicuspidata* exhibiting reddish-brown color from exposure to direct sunlight. Photo by Hermann Schachner, through Creative Commons.

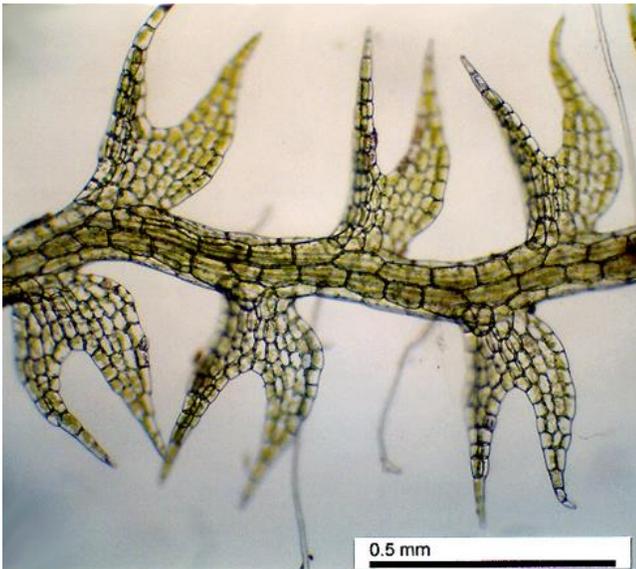


Figure 44. *Cephalozia hamatiloba*, from the *C. bicuspidata* complex, is usually brown or purple in sunlit habitats. Photo by David H. Wagner, with permission.



Figure 45. *Cephalozia catenulata*, a species that can develop brown pigmentation in direct sunlight. Photo by Michael Lüth, with permission.



Figure 46. *Cephalozia macrostachya*, a species that can develop brown pigmentation in direct sunlight. Photo by Michael Lüth, with permission.



Figure 47. *Cephalozia loitlesbergeri*, a species that can develop brown pigmentation in direct sunlight. Photo by Des Callaghan, with permission.

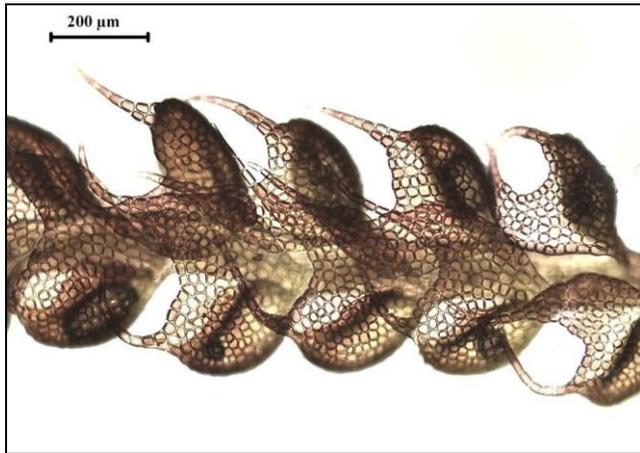


Figure 48. *Nowellia curvifolia*, formerly in the genus *Cephalozia*, red form from sunlit area. Photo by Hugues Tinguy, with permission.

Potemkin and Sofronova (2013) found that in *Cephalozia ambigua* (Figure 41-Figure 42) the extra thickenings of the apical wall of the terminal cells (Figure 42) is flexible, with the thickenings usually absent on soil, but present in populations growing on logs where humidity conditions are intermittent.

Cephalozia austrigena

The subspecies *Cephalozia bicuspidata* subsp. *austrigena* seems to be a separate species (*C. austrigena*) and is known only from New Zealand. Potemkin and Sofronova (2013) suggested that the other antipodal records of *C. bicuspidata* (Figure 49-Figure 51, Figure 55, Figure 66) need to be checked for *C. austrigena*.

Cephalozia austrigena occurs in North America over wet ledges or on wet talus as an initial invading species. It is very tolerant of direct sunlight as long as there is abundant water. By comparison, Potemkin and Sofronova (2013) reported *Cephalozia bicuspidata* (Figure 49-Figure 51, Figure 55, Figure 66) on acid and occasionally more or less neutral substrata – bare soil, rocks, rotten wood (Figure 50), among mosses and among *Sphagnum* (like Figure 74), particularly, at bases of trees. Schuster (1953, p. 507) considered the *C. bicuspidata* complex to have no tolerance for even tiny amounts of lime.

Cephalozia bicuspidata (Figure 43, Figure 49-Figure 51, Figure 55, Figure 66)

Cephalozia bicuspidata (Figure 43, Figure 49-Figure 51, Figure 55, Figure 66) 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, Chili, South Georgia, and Tasmania (Schuster 1974; Piippo 1990; Váňa 1993; Damsholt 2002).

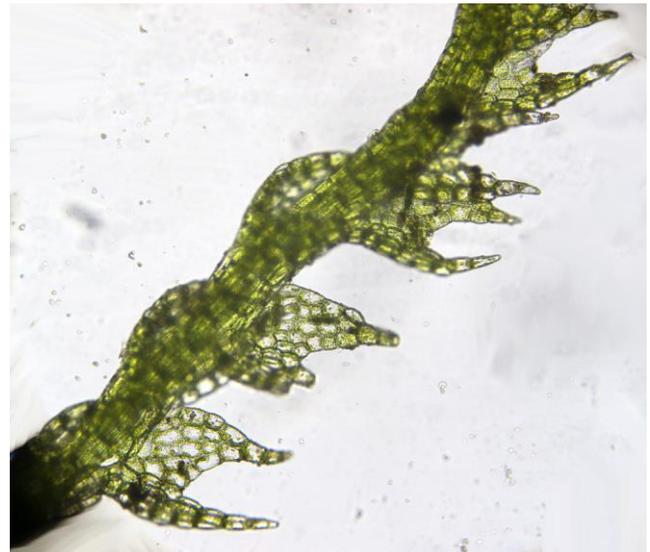


Figure 49. *Cephalozia bicuspidata*. Photo by Jay Avery, through Creative Commons.



Figure 50. *Cephalozia bicuspidata* on a wet log. Photo by Rambyro, through Creative Commons.

In his early summary of aquatic bryophytes, Watson (1919) described *Cephalozia bicuspidata* (Figure 49-Figure 51, Figure 55, Figure 66) 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; Glime & 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 52) 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 51. *Cephalozia bicuspidata*, showing its mat growth form. Photo by Malcolm Storey, DiscoverLife.com, with online permission.



Figure 52. *Fontinalis antipyretica*, a species that, along with *Platyhypnidium*, can be found in association with *Cephalozia bicuspidata*. Photo by Michael Lüth, with permission.

One of the more unusual occurrences of *Cephalozia bicuspidata* (Figure 49-Figure 51, Figure 55, Figure 66) is in the Kootenay Paint Pots (Figure 53), 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 54). The latter occurred only as protonemata.



Figure 53. 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 Ślusarczyk, through Creative Commons.



Figure 54. *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.

Potemkin and Sofronova (2013) observed that *C. bicuspidata* (Figure 49-Figure 51, Figure 55, Figure 66), like *C. ambigua* (Figure 41-Figure 42), has flexible cell wall thickenings (Figure 55) that seem to respond to intermittent humidity by developing stronger thickenings.

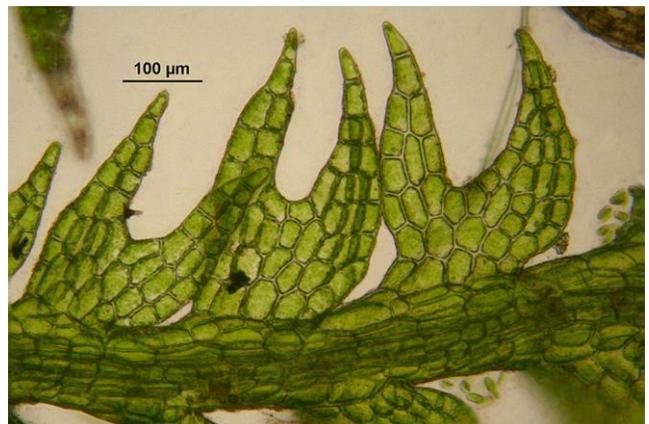


Figure 55. *Cephalozia bicuspidata* showing cell walls, in this case with no obvious thickening. Photo by Hermann Schachner through Creative Commons.

At Tuckerman Ravine on Mt. Washington, New Hampshire, USA (1300 m asl), Duckett and Slack (2013)

found *Cephalozia bicuspidata* (Figure 49-Figure 51, Figure 55) on wet vertical rocks where it was associated with *Scapania undulata* (Figure 56), *Solenostoma hyalinum* (Figure 57), *Blindia acuta* (Figure 58), *Philonotis fontana* (Figure 59), *Pohlia nutans* (Figure 60), *Racomitrium fasciculare* (Figure 61), and *R. heterosticum* (Figure 62). *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 56. *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 57. *Solenostoma hyalinum* with capsule, a species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by Michael Lüth, with permission.



Figure 58. *Blindia acuta*, a species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by David Holyoak, with permission.



Figure 59. *Philonotis fontana*, a species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by Janice Glime.



Figure 60. *Pohlia nutans* a species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by Michael Lüth, with permission.



Figure 61. *Racomitrium fasciculare*, a species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by Janice Glime.



Figure 62. *Racomitrium heterostichum*, a species often associated with *Cephalozia bicuspidata* on wet vertical rocks. Photo by Jan-Peter Frahm, with permission.

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 49-Figure 51, Figure 55, Figure 66) 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 74) 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.

Pressel and Duckett (2006) found that *Mniaecia jungermanniae* (Figure 63), a parasitic *Ascomycota*, associated with *Cephalozia bicuspidata* (Figure 49-Figure 51, Figure 55, Figure 66). 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.



Figure 63. *Mniaecia jungermanniae*, an *Ascomycota* fungus growing on *Cephalozia bicuspidata*. Photo courtesy of Jan Gaisler.

Mniaecia jungermanniae (Figure 63) is known from 17 species of liverworts, including *Cephalozia bicuspidata* (Figure 49-Figure 51, Figure 55, Figure 66) 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 63) 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*.

Liepina (2012) reported the occurrence of fungal structures in the cell walls of *Cephalozia bicuspidata* (Figure 55) 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 64), 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 64. *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 65) in the **Zygomycota** from nine liverwort species and successfully cultured it with *Gymnocolea inflata* (Figure 16-Figure 17, Figure 19, Figure 21), *Cephalozia bicuspidata* (Figure 49-Figure 51, Figure 55, Figure 66), *Cephaloziella* sp. (Figure 96-Figure 101), and *Lophozia ventricosa* (Figure 108-Figure 112). This association appears to be neither mycorrhizal nor parasitic, although when the liverworts become strongly infected the plants experience an unfavorable reaction.



Figure 65. *Mucor mucedo*; *Mucor rhizophilus* is known from nine liverwort species, including *Gymnocolea inflata*. Photo by Lena Wild, through Creative Commons.

Proctor (1982) determined that the photosynthetic activity of the sporophytes of *Cephalozia bicuspidata* (Figure 49-Figure 51, Figure 55, Figure 66) is very low when compared with that of the gametophyte structures [perianth (Figure 66), 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 66. *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).

***Fuscocephaloziopsis albescens* (Figure 67-Figure 68)**

Fuscocephaloziopsis albescens (syn. = *Pleurocladula albescens*; Figure 67-Figure 68) 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 67. *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.

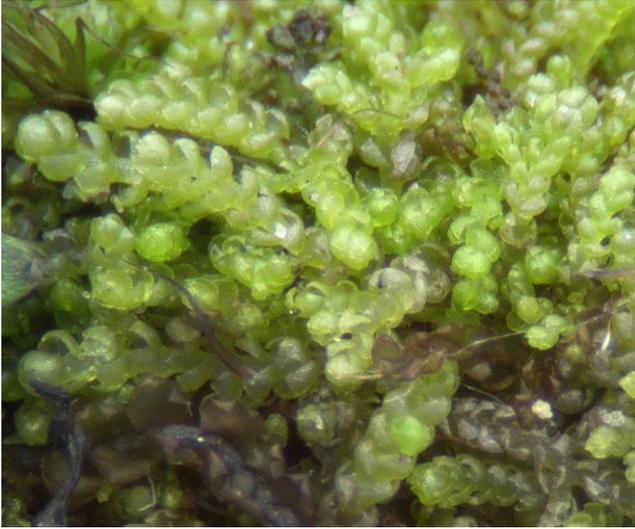


Figure 68. *Fuscocephaloziopsis albescens* forming a mat. Photo by Tomas Hallingbäck, with permission.

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 60) (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 69-Figure 74)**

Fuscocephaloziopsis connivens (syn. = *Cephalozia connivens*; Figure 69-Figure 74) 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).

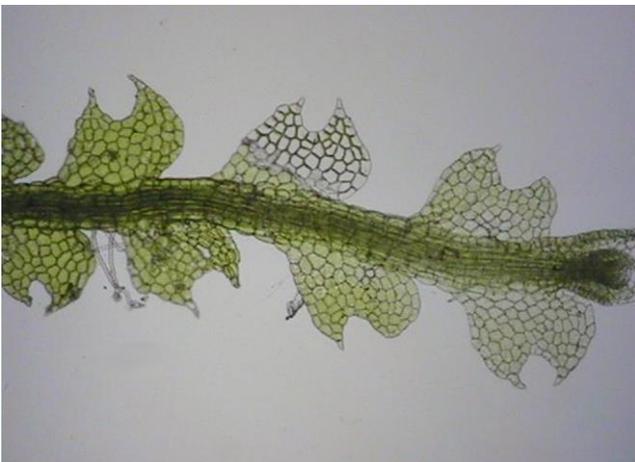


Figure 69. *Fuscocephaloziopsis connivens*, a holarctic species on streambanks and in wetlands. Photo by Paul Davison, with permission



Figure 70. *Fuscocephaloziopsis connivens*, the smaller liverwort mixed here with a larger liverwort. Photo by Jan-Peter Frahm, with permission.

Watson (1919) included this species in his list of aquatic and wetland species. It occurs on banks with frequent submergence and slow water (Figure 71). Geissler and Selldorf (1986) considered it to be uncommon in association with *Eleocharis quinqueflora* (Figure 72). Henriques *et al.* (2017) considered *Fuscocephaloziopsis connivens* (Figure 69-Figure 74) to be a **humicolous** (thriving on humus) specialist.



Figure 71. *Fuscocephaloziopsis connivens* growing in a wetland habitat near water. Photo by Michael Lüth, with permission.



Figure 72. *Eleocharis quinqueflora*, sometimes an associate of *Fuscocephaloziopsis* in alpine regions. Photo by Max Licher, through Creative Commons.

Cores in peatlands demonstrate the regeneration capacity of *Fuscocephaloziopsis connivens* (Figure 73-Figure 74). 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 74), 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 74).



Figure 73. *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.



Figure 74. *Fuscocephaloziopsis connivens* growing with *Sphagnum* and other bog/poor fen vegetation. Photo by Michael Lüth, with permission.

***Fuscocephaloziopsis lunulifolia* (Figure 75, Figure 77-Figure 79)**

Fuscocephaloziopsis lunulifolia (syn. = *Cephalozia lunulifolia*, *Cephalozia media*; Figure 75, Figure 77-Figure 79) 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).

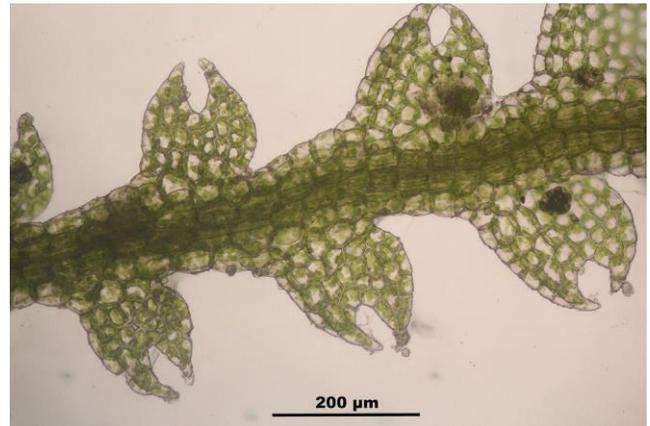


Figure 75. *Fuscocephaloziopsis lunulifolia*, a widespread species in the Northern Hemisphere, occurring on rotten wood, soil, rocks, or among other mosses. It is associated with lakes, stream banks, and bare peat in subalpine zones and the taiga. Photo by Hermann Schachner, through Creative Commons.

Potemkin and Sofronova (2013), from their experience in Russia, describe this species as one found among *Sphagnum* (like Figure 74), 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 75, Figure 77).

Nichols (1918) reported this species from moist hollows between *Sphagnum* hummocks (Figure 76) 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 75, Figure 77-Figure 79) from the riparian zone of the H. J. Andrews Experimental Forest in the western Cascades, Oregon, USA.



Figure 76. *Sphagnum* hummocks and hollows, similar to the ones where *Fuscocephaloziopsis lunulifolia* can occur. Photo by Nicholas A. Tonelli, through Creative Commons.



Figure 77. *Fuscocephaloziopsis lunulifolia* forming a mat on its substrate. Photo by Michael Lüth, with permission.

Fuscocephaloziopsis lunulifolia (Figure 75, Figure 77-Figure 79) 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.

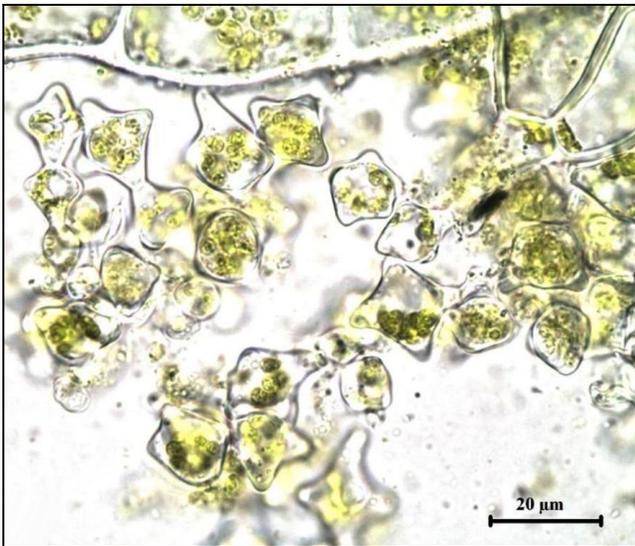


Figure 78. *Fuscocephaloziopsis lunulifolia* gemmae, potential members of the sporebank in upper layers of peat. Photo by Hugues Tinguy, with permission.

Fuscocephaloziopsis lunulifolia (Figure 75, Figure 77-Figure 79) presents evenly thickened leaf cell walls (Figure 79) 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 49-Figure 51, Figure 55, Figure 66) (Potemkin & Sofronova 2013).

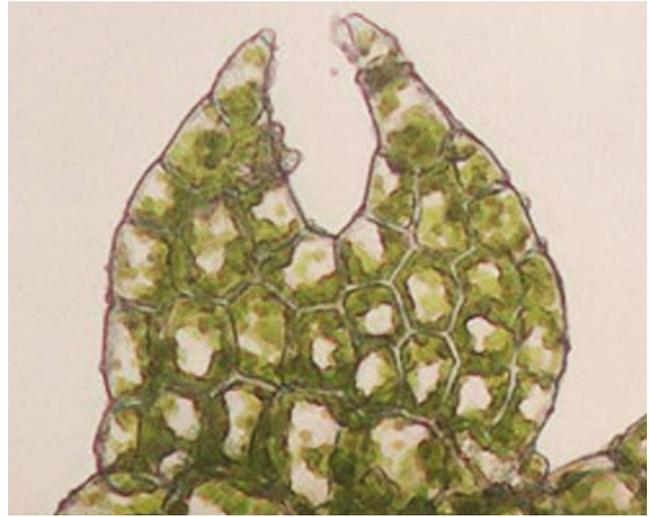


Figure 79. *Fuscocephaloziopsis lunulifolia* cells showing walls that are evenly thickened. Photo by Hermann Schachner, through Creative Commons.

Wang and Qiu (2006) reported mycorrhizal relationships with *Fuscocephaloziopsis lunulifolia* (Figure 75, Figure 77-Figure 79).

Odontoschisma elongatum (Figure 80, Figure 85-Figure 86)

Odontoschisma elongatum (syn. = *Odontoschisma denudatum* subsp. *elongatum*; Figure 80, Figure 85-Figure 86) presents a distribution in the Caribbean, Europe, Northern Asia, Alaska, Canada, and the continental USA (ITIS 2020c).

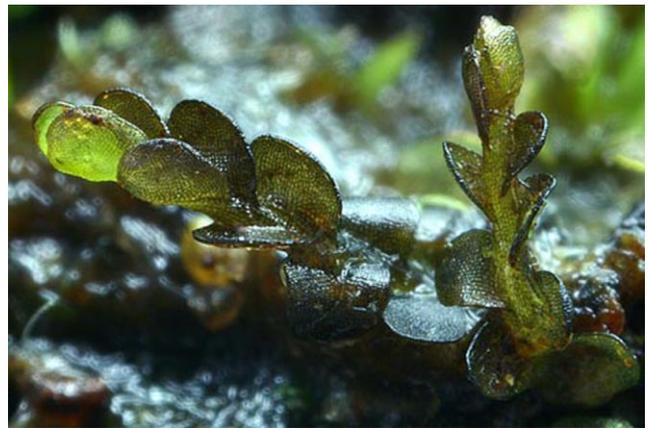


Figure 80. *Odontoschisma elongatum*, a Northern Hemisphere species that can occur in mires. Photo by Des Callaghan, with permission.

This species likewise is not a common member of wetland communities. Geissler and Selldorf (1986) found it with *Trichophorum cespitosum* (Figure 81) and *Carex chillanensis*, and uncommonly with *Eleocharis quinqueflora* (Figure 72) and *Paludella squarrosa* (Figure 18). Albinsson (1997) reported this species from *Sphagnum* associations (like Figure 74) in mires, noting that liverworts were encountered more often among species of *Sphagnum* in the subgenera *Sphagnum* (Figure 82) and *Acutifolia* (Figure 83) than in subgenus *Cuspidata* (Figure 84).



Figure 81. *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 84. *Sphagnum tenellum*, a member of the subgenus *Cuspidata*. Photo by David Holyoak, with permission.



Figure 82. *Sphagnum magellanicum*, a member of the subgenus *Sphagnum*. Photo by Michael Lüth, with permission.



Figure 83. *Sphagnum capillifolium*, a member of the subgenus *Acutifolia*. Photo by Blanka Shaw, with permission.

Odontoschisma elongatum (Figure 80, Figure 85- Figure 86) can be a bright green (Figure 85), but more commonly has a yellowish or brownish pigment (Figure 86) (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 85) and grow downward, holding the plant in place, especially in its *Sphagnum* habitat, and rhizoids are scarce.



Figure 85. *Odontoschisma elongatum* with flagelliform stolon (arrow) and green color. Photo by Norbert Schnyder, with permission.



Figure 86. *Odontoschisma elongatum* from a wetland community, exhibiting brownish and golden coloration. Photo by Andrew Hodgson, with permission.

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.

Pocock and Duckett (1985) found no mycorrhizal fungi in *Odontoschisma elongatum* (Figure 80, Figure 85-Figure 86) 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*.

Cyanobacteria (Figure 87) can also 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 80, Figure 85-Figure 86) 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 87. *Nostoc linckia*, a **Cyanobacterium**; some species of *Nostoc* are common on leafy liverworts as symbionts. Photo from Proyecto Agua, through Creative Commons.

***Odontoschisma fluitans* (Figure 88-Figure 89)**

Odontoschisma fluitans (syn. = *Cephalozia fluitans*, *Cladopodiella fluitans*; Figure 88-Figure 89) is distributed in temperate regions of the northern hemisphere and occurs in Europe and eastern North America (Gradstein & Ilkiu-Borges 2015).



Figure 88. *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.

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 89). 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 89. *Odontoschisma fluitans* forming mats. Photo by David T. Holyoak, with permission.

Unlike some members of the genus, *Odontoschisma fluitans* lacks gemmae (Figure 88-Figure 89) (Gradstein & Ilkiu-Borges 2015).

***Odontoschisma sphagni* (Figure 90-Figure 93, Figure 95)**

Odontoschisma sphagni (syn. = *Jungermannia sphagni*, *Odontoschisma prostratum*; Figure 90-Figure 93, Figure 95) 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).



Figure 90. *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 91. *Odontoschisma sphagni*. Photo by Michael Lüth, with permission.

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 90-Figure 93, Figure 95). *Odontoschisma sphagni* is exceptional in the genus in being autoicous; other members are dioicous (Gradstein & Ilkiu-Borges 2015).

Bley (1987) legitimizes *Odontoschisma sphagni* (Figure 90-Figure 93, Figure 95) as an aquatic species (Figure 92-Figure 93), 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 94) or among other mosses" (Figure 95).



Figure 92. *Odontoschisma sphagni* well hydrated, showing its (mostly) green form. Photo by Michael Lüth, with permission.



Figure 93. *Odontoschisma sphagni* in a dry state, showing its reddish color form. Photo by Michael Lüth, with permission.



Figure 94. *Leucobryum glaucum*; *Odontoschisma sphagni* will sometimes grow over members of this moss genus. Photo by Amadej Trnkoczy, through Creative Commons.



Figure 95. *Odontoschisma sphagni*, growing here with the moss *Polytrichum*. Photo by Michael Lüth, with permission.

Duckett and Clymo (1988) found that *Odontoschisma sphagni* (Figure 90-Figure 93, Figure 95) occurred in core samples from 12-23 cm depth, but was absent from the surface. Because this species does not produce gemmae, but exhibited 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 90).

Cephaloziellaceae

Cephaloziella (Figure 96-Figure 101)

Cephaloziella (Figure 96-Figure 101) 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 96-Figure 97)

Cephaloziella hampeana (Figure 96-Figure 97) 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.

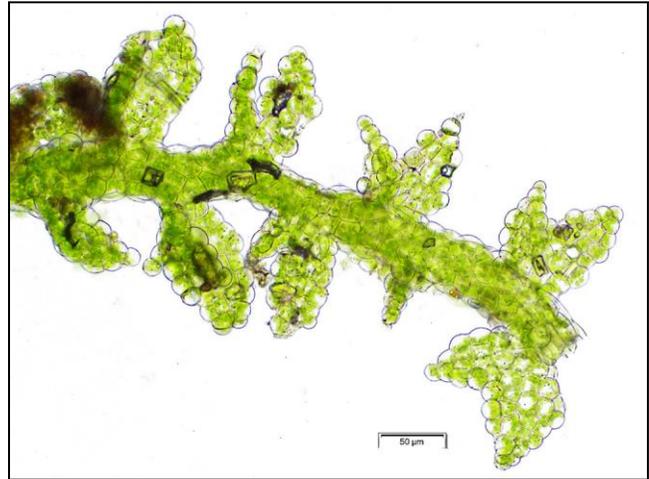


Figure 96. *Cephaloziella hampeana*, a species widely distributed in the Northern Hemisphere, but also at high elevations in the Southern Hemisphere, where it can be found in fens and mires and similar wetlands. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

Cephaloziella hampeana (Figure 96-Figure 97) 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 97. *Cephaloziella hampeana* with both gemmae and sporophytes. Photo by David T. Holyoak, with permission.

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 98-Figure 101)**

Cephaloziella rubella (Figure 98-Figure 101) occurs in the Northern Hemisphere, mostly in the Temperate Zone: Europe, Asia, North America (ITIS 2020d)



Figure 98. *Cephaloziella rubella*, a species of the temperate Northern Hemisphere that occurs occasionally on montane stream banks. Photo by Michael Lüth, with permission.

This species occurs as a submerged hemicalciphilous species in montane streams and on stream banks in western Canada (Figure 99) (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 87). In addition to its cyanobacterial symbiont, *Cephaloziella rubella* (Figure 98-Figure 101) has a fungal association (Wang & Qiu 2006).

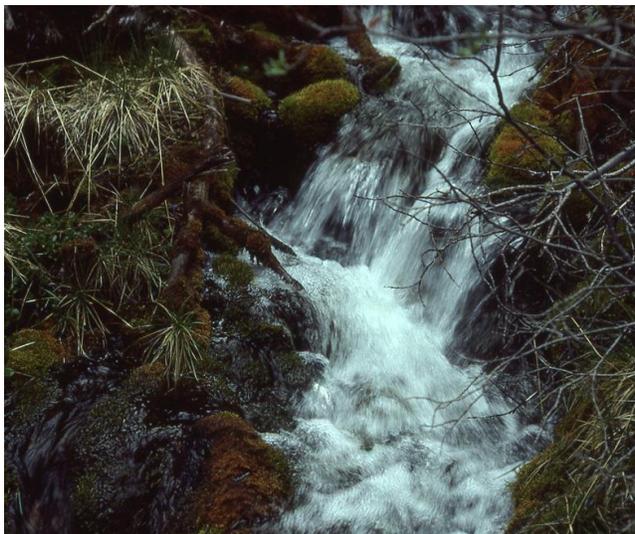


Figure 99. Glacial melt stream where *Cephaloziella rubella* grows in BC, Canada. Photo by Janice Glime.



Figure 100. *Cephaloziella rubella* showing its growth pattern in mats. Photo by Michael Lüth, with permission.

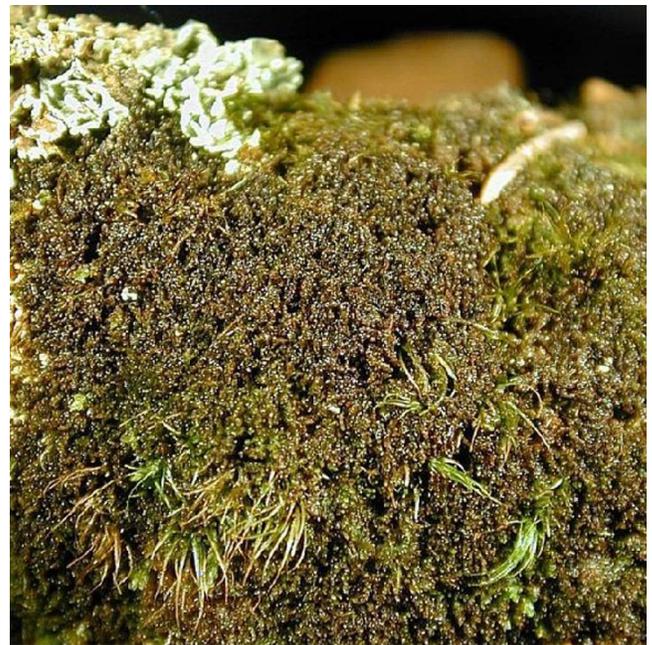


Figure 101. *Cephaloziella rubella* showing the large, dense mats it can form. Photo by Michael Lüth, with permission.

***Kymatocalyx* (Figure 102-Figure 107)**

Kymatocalyx (syn. = *Ruttnerella*, *Stenorrhypis*; Figure 102-Figure 107) 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 102)**

Kymatocalyx africanus (Figure 102) occurs in the Uluguru Mts. (1600-2350 m asl) of Tanzania, and Mt. Mulanje (1200-2220 m asl), Malawi.



Figure 102. *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.

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 & Váňa 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.

Kymatocalyx africanus (Figure 102) is **cladautoicous** (having male sexual organs on special branch separate from female organs) (Gradstein & Váňa 1999).

***Kymatocalyx cubensis* (Figure 103)**

In Madagascar, *Kymatocalyx cubensis* (Figure 103) 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 103. *Kymatocalyx cubensis*, a species that occurs within a meter of the tidal surface in Madagascar. Photo courtesy of Tamás Pócs.

***Kymatocalyx dominicensis* (Figure 104)**

Kymatocalyx dominicensis (Figure 104) 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 & Váňa 1999).

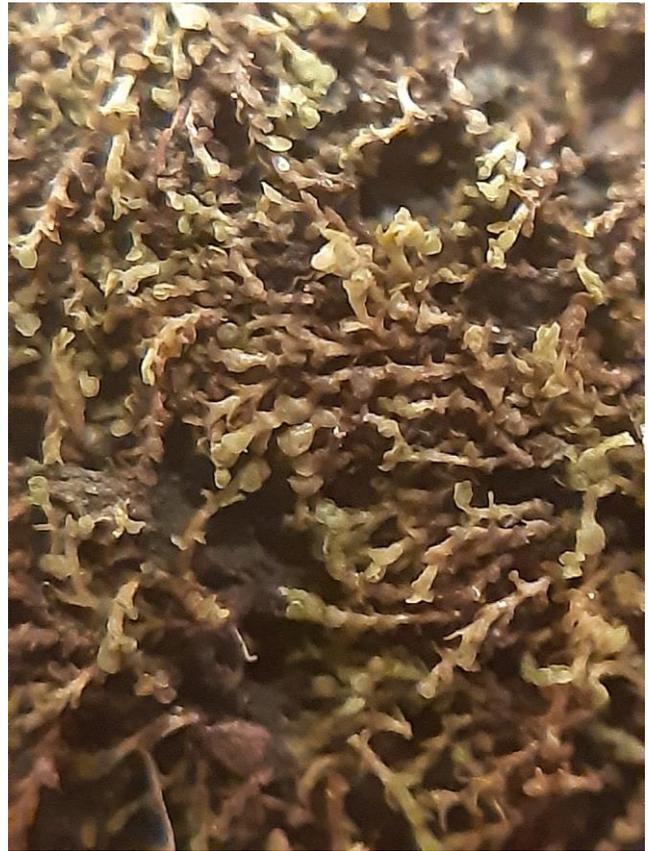


Figure 104. *Kymatocalyx dominicensis*, a species known from the Neotropics and Madagascar where it can occur on shaded rocks along rivers, in waterfalls, and at times be partly submerged. Photo courtesy of Tamás Pócs.

Like other taxa of the genus, *Kymatocalyx dominicensis* (Figure 104) 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 105-Figure 106)**

Kymatocalyx madagascariensis (Figure 105-Figure 106) 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 102) (Gradstein & Váňa 1999).



Figure 105. *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.

Kymatocalyx madagascariensis (Figure 105-Figure 106) 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). On Réunion Island it occurs in shady cracks in 5-20-year-old lava flows (Figure 106) (Tamás Pócs, pers. comm. 3 March 2020). In Madagascar, Comores, and the Mascarenes it occurs mostly on volcanic rocks of temporary water flows (see Figure 107), but also occurs on wet soil on roadsides.



Figure 106. *Kymatocalyx madagascariensis* in crevices of old lava flow, Reunion Island. Photo courtesy of Tamás Pócs.



Figure 107. *Kymatocalyx madagascariensis* temporary water flow habitat on old lava flow, Reunion Island. Photo courtesy of Tamás Pócs.

Kymatocalyx rhizomatica

Kymatocalyx rhizomatica (syn. = *Ruttnerella rhizocaula*) 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).

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 & Váňa 1999). It is cladautoicous and gemmae observations are rare.

Lophoziaceae

Lophozia (Figure 108-Figure 117)

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 108-Figure 112)

Records of *Lophozia ventricosa* (Figure 108-Figure 112) 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 108. *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.

Lophozia ventricosa (Figure 108-Figure 112) 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 109) in the Haute Ardenne rivers. Lenz (2011) reported this species from fens in the Bighorn National Forest, Wyoming, USA.

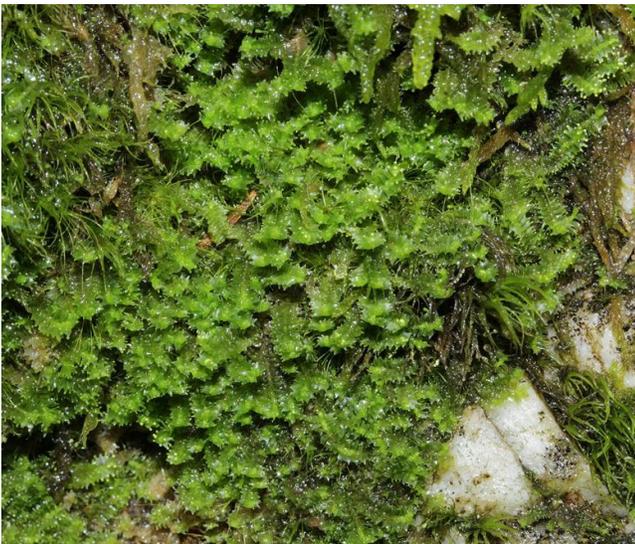


Figure 109. *Lophozia ventricosa*, appearing here with other bryophytes on a gravelly substrate. Photo by Hermann Schachner, through Creative Commons.

Lophozia ventricosa (Figure 108-Figure 112) produces gemmiferous shoots (Figure 110-Figure 112). Algar-Hedderon *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 110. *Lophozia ventricosa* with gemmiferous branches. Photo by Jan-Peter Frahm, with permission.

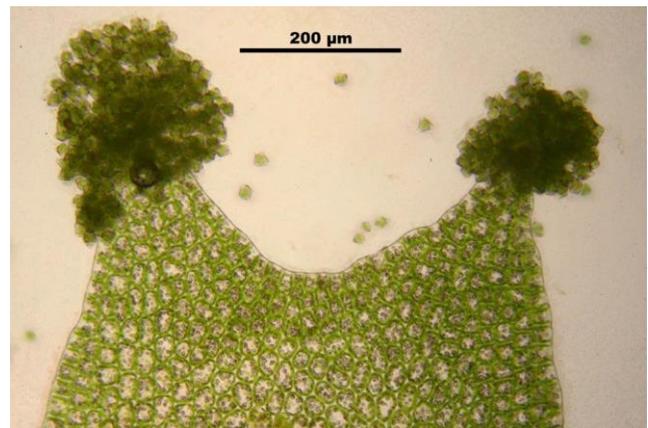


Figure 111. *Lophozia ventricosa* leaf showing gemmae at the tips of the leaf lobes. Photo by Hermann Schachner, through Creative Commons.

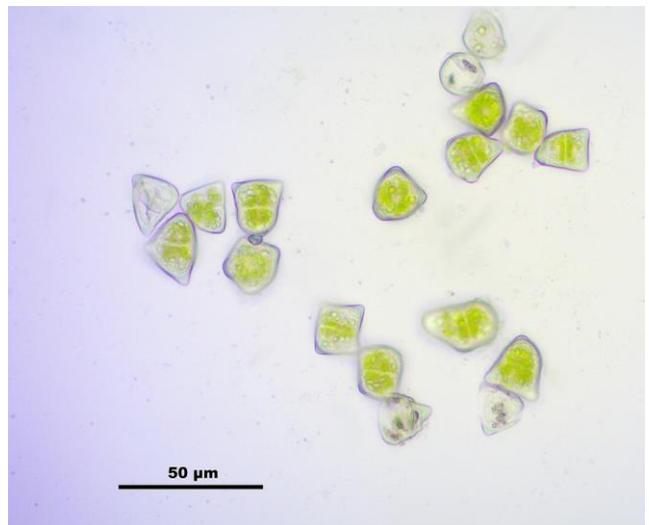


Figure 112. *Lophozia ventricosa* gemmae. Photo by Hermann Schachner, through Creative Commons.

Lophozia ventricosa (Figure 108-Figure 112) 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 113) was delayed in the growing

season when compared to the more common *Lophozia ventricosa* and *L. longiflora* (Figure 114). 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.



Figure 113. *Lophozia ascendens* with gemmae, a species that produces gemmae later than do *L. ventricosa* and *L. longifolia*. Photo by Michael Lüth, with permission.



Figure 114. *Lophozia longiflora*, a species that has earlier gemma production compared to *L. ventricosa*. Photo by Earth.com, with permission.

Like many liverworts, *Lophozia ventricosa* (Figure 108-Figure 112) associates with members of the **Ascomycota** fungus *Sebacina vermifera* (see Figure 12) species complex (Bidartondo & Duckett 2010). It is known to share identical *Sebacina vermifera* DNA with the fungus on the leafy liverwort *Nardia scalaris* (Figure 115).



Figure 115. *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 108-Figure 112) 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.

Lophozia ventricosa (Figure 108-Figure 112) 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 116-Figure 117)

Lophozia wenzelii (Figure 116-Figure 117) 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 116. *Lophozia wenzelii*, an arctomontane species that can occur in alpine streams, mountain bogs, and marshy areas. Photo by Des Callaghan, with permission.

Váňa (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 72) (Geissler & Selldorf 1986). In Russia at the Ushkovskii Volcano, Bakalin (2005) *Lophozia wenzelii* (Figure 116-Figure 117) 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 117. *Lophozia wenzelii* showing its growth habit. Photo by Štěpán Koval, with permission.

Bakalin (2005) reports that *Lophozia wenzelii* (Figure 116-Figure 117) 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 16-Figure 21), *Scapania* spp. (most frequently with *S. paludicola* – Figure 118), *Cephalozia* spp. (Figure 41-Figure 66), and *Odontoschisma fluitans* (Figure 88-Figure 89) (Bakalin 2004).



Figure 118. *Scapania paludicola*, a species that often accompanies *Lophozia wenzelii*. Photo by Michael Lüth, with permission.

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 116-Figure 117) is a critically endangered species in the Czech Republic (Číhal & 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.

In the Upper Puiva River in the Urals of Russia, Konstantinova and Lapshina (2017) found *Lophozia wenzelii* (Figure 116-Figure 117) 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.

***Lophozia excisa* (Figure 119-Figure 120)**

Lophozia excisa (syn. = *Lophozia excisa*; Figure 119-Figure 120) 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 119. *Lophozia 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 120. *Lophozia excisa* with gemmae. Photo by Jan-Peter Frahm, with permission.

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 121) 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 Timplon River Basin, South Yakutia, Russia, Sofronova (2017) found *Lophozia excisa* (Figure 119-Figure 120) mixed with other liverworts on soil of moist south-facing cliffs along the river bank as well as on fine soil in cliff cracks. 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 121. *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.

Newsham and Bridge (2010) noted the presence of fungi belonging to **Sebacinales** (Figure 12) clade B in *Lophozia excisa* (Figure 119-Figure 120) at Léonie Island in the southern maritime Antarctic. Newsham *et al.* (2014) reported the occurrence of *Cladophialophora* (Figure 122) 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.

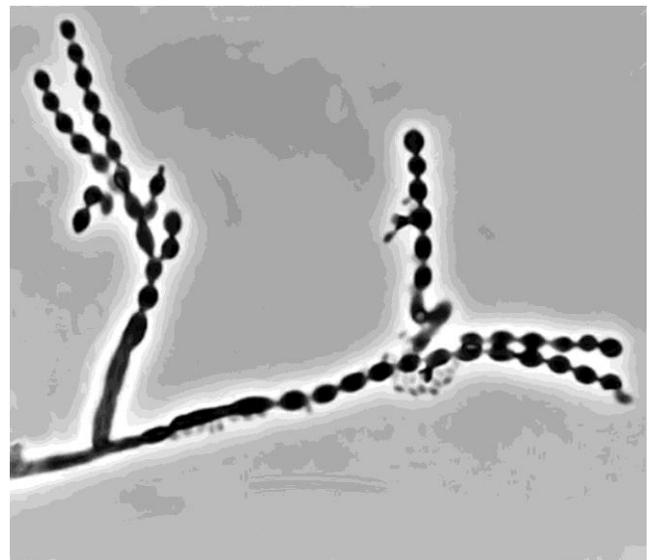


Figure 122. *Cladophialophora* sp.; some species of this fungal genus are found in tissues of *Lophozia excisa*. Photo by Medmyco, through Creative Commons.

Trilophozia quinquedentata (Figure 123-Figure 124)

Trilophozia quinquedentata (syn. = *Tritomaria quinquedentata*; Figure 123-Figure 124) 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 123. *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.

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 124) (Vieira *et al.* 2005). It is also typically associated with *Chiloscyphus polyanthos* (Figure 125) and *Aneura pinguis* (Figure 126) in mountain streams of northwest Portugal.



Figure 124. *Trilophozia quinquedentata* loosely attached to its substrate. Photo by Hugues Tinguy, with permission.

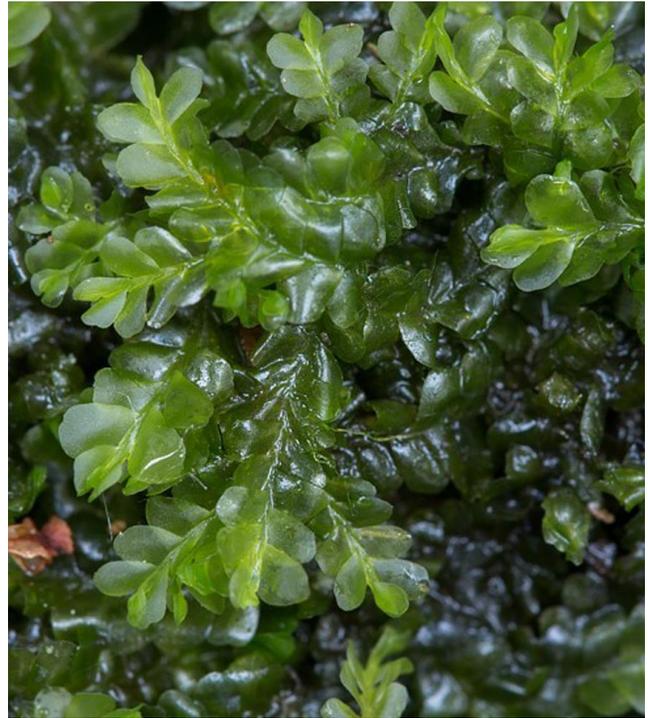


Figure 125. *Chiloscyphus polyanthos*, a common associate of *Trilophozia quinquedentata*. Photo by Štěpán Koval, with permission.



Figure 126. *Aneura pinguis*, a common associate of *Trilophozia quinquedentata*. Photo by Hermann Schachner, through Creative Commons.

Tritomaria exsecta (Figure 127-Figure 132)

Tritomaria exsecta (syn. = *Sphenolobus exsectus*; Figure 127-Figure 132) 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).



Figure 127. *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 130. *Tritomaria exsecta* with apical gemmae. Photo by Michael Lüth, with permission.



Figure 128. *Tritomaria exsecta*. Photo by Michael Lüth, with permission.

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 32) at Franconia Notch, New Hampshire, USA. It forms mats and can produce apical gemmae (Figure 129-Figure 132)



Figure 131. *Tritomaria exsecta* with gemmae. Photo by Michael Lüth, with permission.



Figure 129. *Tritomaria exsecta* in a mat with gemmae at the apex of shoots. Photo by Hermann Schachner, through Creative Commons.



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

***Tritomaria exsectiformis* (Figure 133, Figure 137-
Figure 139)**

Tritomaria exsectiformis (Figure 133, Figure 137-
Figure 139) 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 133. *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.

In Greenland, Hassel *et al.* (2014) found *Tritomaria
exsectiformis* (Figure 133, Figure 137-Figure 139) growing
on rocks in a heathland of *Vaccinium uliginosum* (Figure
134) with the mosses *Saelania glaucescens* (Figure 135),
Bartramia ithyphylla (Figure 136), and liverwort *Scapania*
sp. (e.g. Figure 118).



Figure 134. *Vaccinium uliginosum* with fruit, the dominant
species in heathland where one can find *Tritomaria exsectiformis*.
Photo by David Gaya, through Creative Commons.



Figure 135. *Saelania glaucescens*, a species growing with
Tritomaria exsectiformis on rocks in blueberry heathlands. Photo
by Michael Lüth, with permission.



Figure 136. *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 133, Figure 137-Figure
139) 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 137) in stage four decay and having
direct contact with water. It is never present where there is
high volume flow.



Figure 137. *Tritomaria exsectiformis* on wet, decaying
wood. Photo by Stan Phillips, through public domain.

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 138-Figure 139) and other vegetative means. The species is a restricted terrestrial associated with the montane streams and streambanks of western Canada (Figure 99) (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.

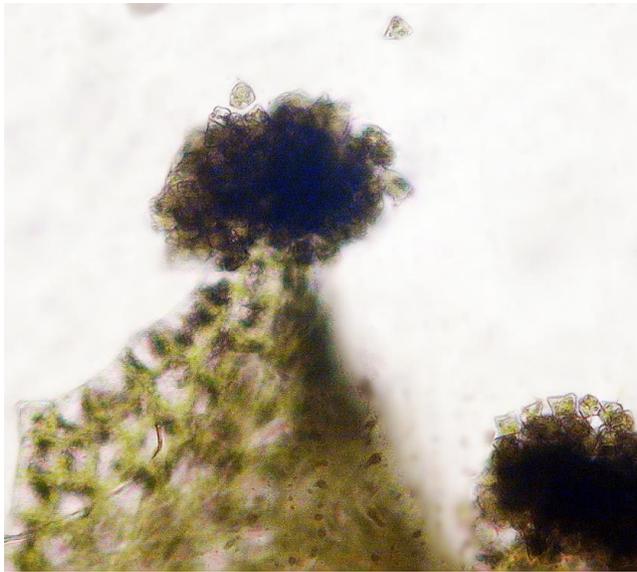


Figure 138. *Tritomaria exsectiformis* with clusters of gemmae on leaf tips. Photo by Michael Lüth, with permission.

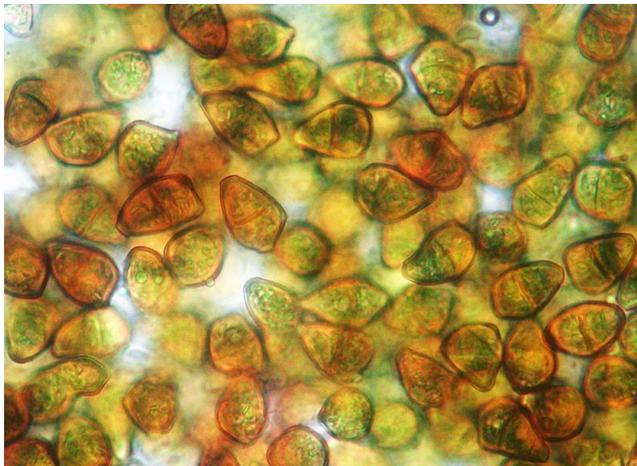


Figure 139. *Tritomaria exsectiformis* gemmae. Photo by Michael Lüth, with permission.

Tritomaria exsectiformis (Figure 133, Figure 137-Figure 139) 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 the 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.

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CHAPTER 1-3

AQUATIC AND WETLAND: MARCHANTIOPHYTA, ORDER JUNGERMANNIALES – CEPHALOZIINEAE 2

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CHAPTER 1-3

AQUATIC AND WETLAND: 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)

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.

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.

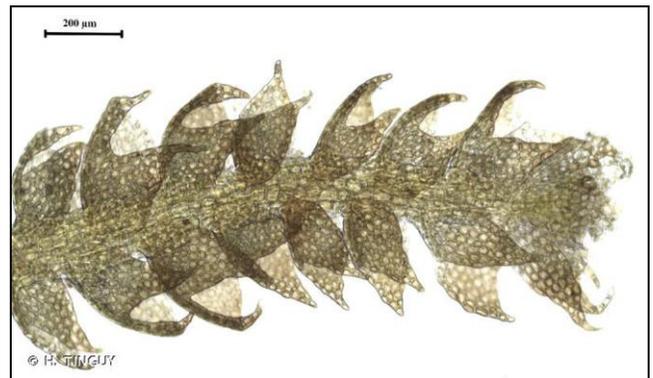


Figure 5. *Cephalozia ambigua*, a species that may accompany *Diplophyllum albicans* on wet cliffs and lake shore rocks. Photo by Hugues Tinguy, with permission.



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.

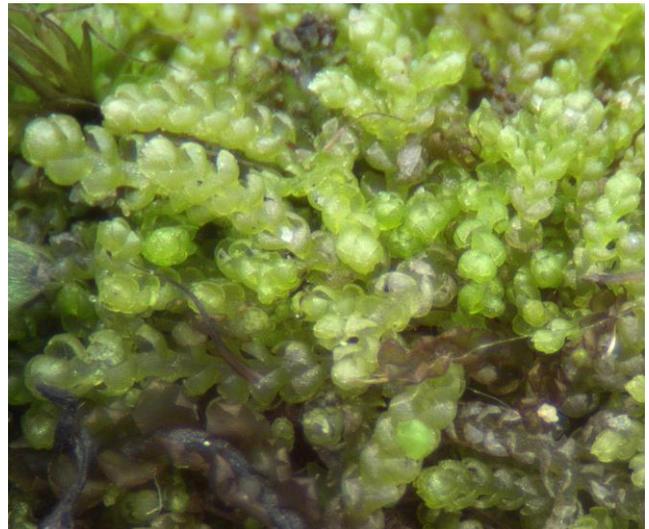


Figure 10. *Fuscocephaloziopsis albescens*, a species that may accompany *Diplophyllum albicans* on wet cliffs and lake shore rocks. Photo by Tomas Hallingbäck, with permission.

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.

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.

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

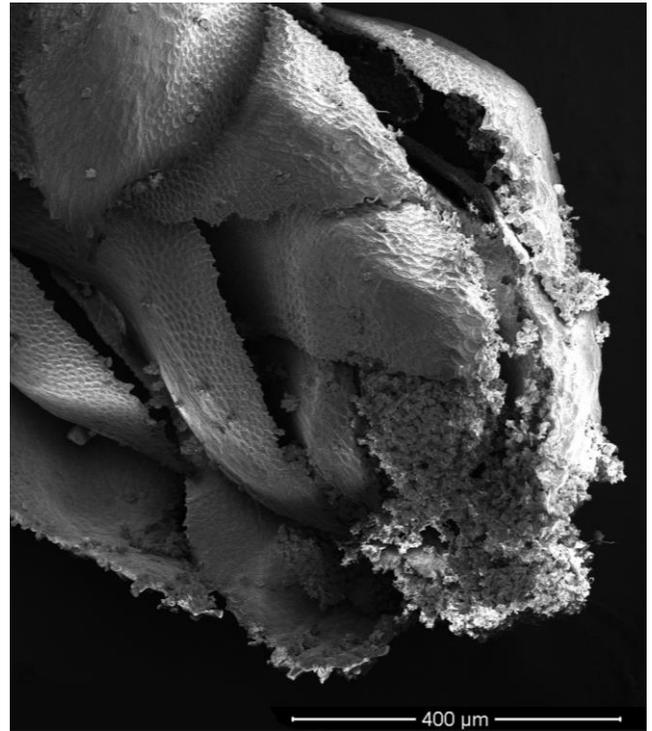


Figure 14. SEM of *Diplophyllum albicans* leaves with gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

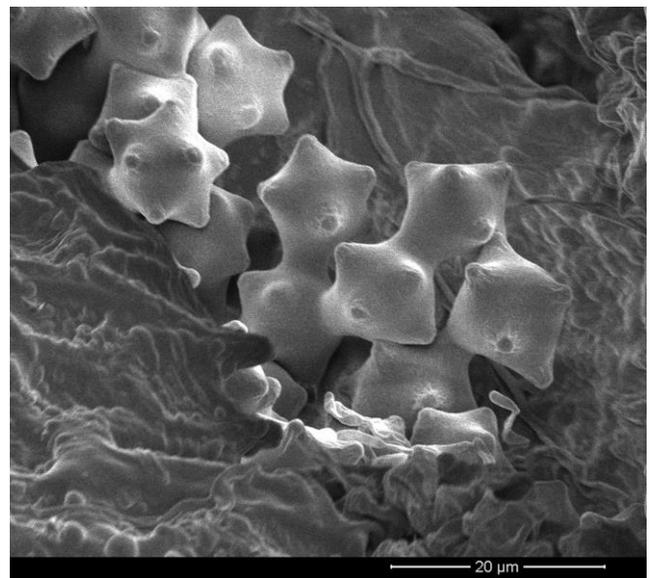


Figure 15. SEM of *Diplophyllum albicans* gemmae. Photo courtesy of Jeff Duckett and Silvia Pressel.

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.

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 nor-sesquiterpenoids 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.

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.

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.

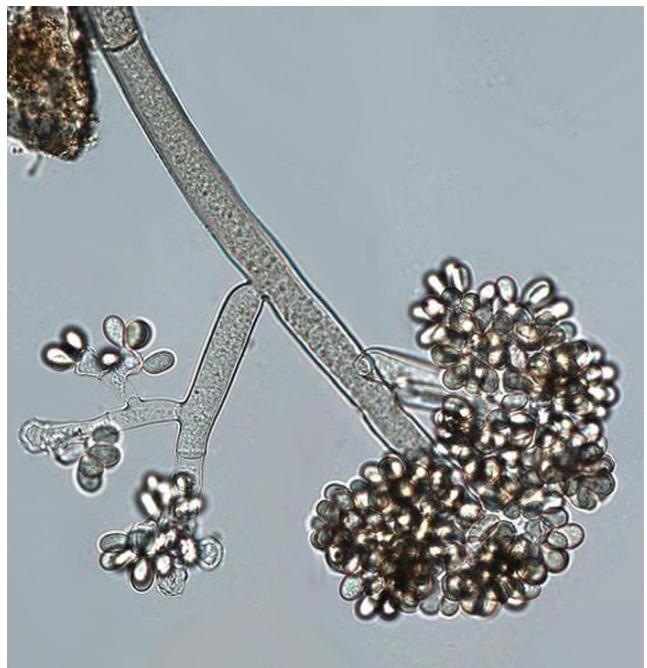


Figure 19. *Botrytis cinerea* a fungus that is inhibited by extracts of *Diplophyllum albicans*. Photo by Paul Bachi, USDA, through Creative Commons.



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 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.

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

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.

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.

But *Diplophyllum taxifolium* (Figure 22-Figure 23, Figure 29) does occur in habitats that one would expect to get dry (Figure 29). Růžička *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.

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.

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)**

Douinia ovata (syn. = *Harpalejeunea ovata*; Figure 30) is a subarctic species, distributed on the Pacific coast of North America from Alaska, USA, to British Columbia, Canada (Váña 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.

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.

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)**

Saccobasis polita (syn. = *Sphenolobus politus*; 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.

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 flotovianus*, 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.

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 156)

Scapania (Figure 34-Figure 156) 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)

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.

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

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.

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)

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

Vitt and Horton (1979) found *Scapania crassiretis* (Figure 36) on an east-facing shale cliff in the Olgivie 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)**

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.

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).

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.

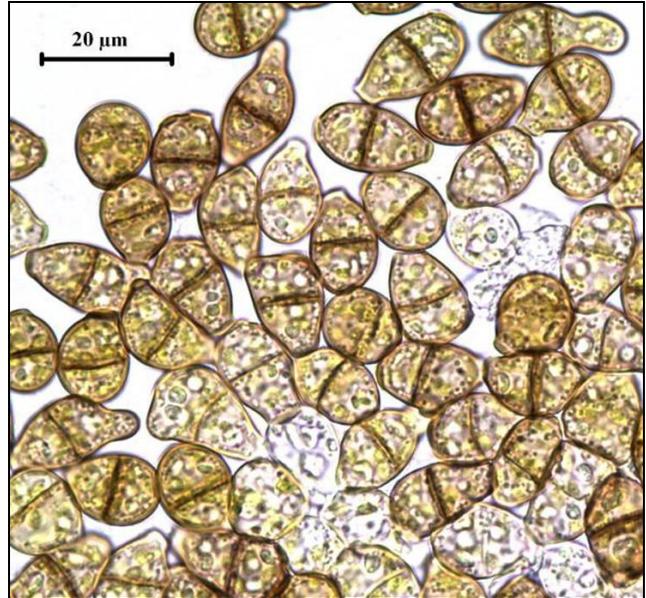


Figure 44. *Scapania cuspiduligera* gemmae showing their 2-celled structure. Photo by Hugues Tinguy, with permission.

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.



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

***Scapania hyperborea* (Figure 46, Figure 50)**

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.

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



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

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



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



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 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.

Scapania irrigua (Figure 55-Figure 56)

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.



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

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.

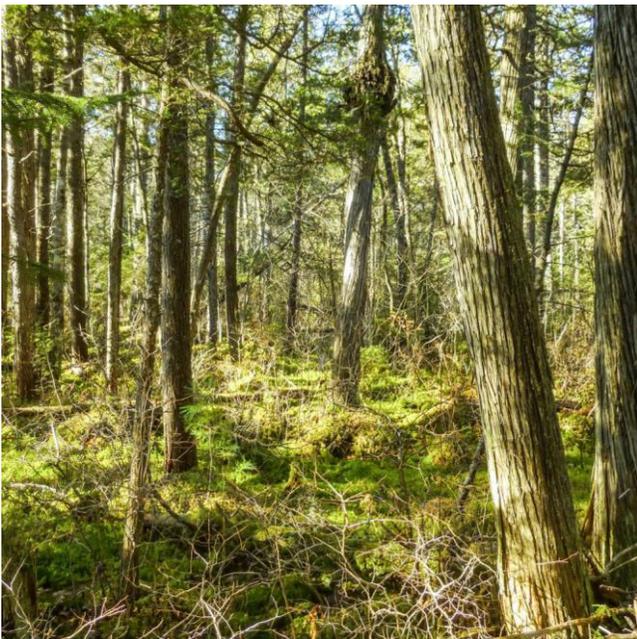


Figure 61. *Thuja* swamp habitat suitable for *Scapania irrigua*. Photo by Allen Norcross, with permission.

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 Algamma 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.

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.

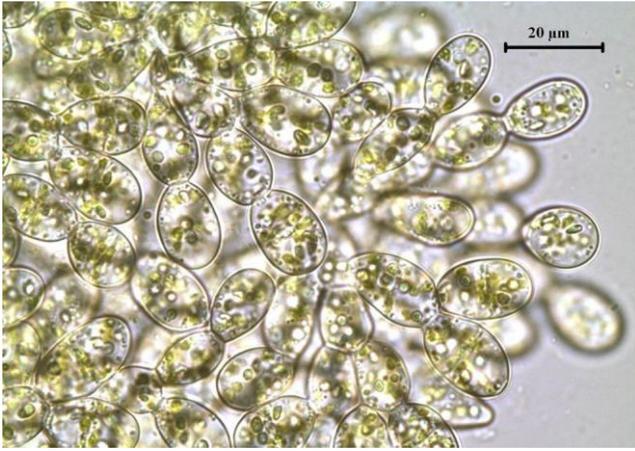


Figure 69. *Scapania irrigua* gemmae showing thin walls. Photo by Hugues Tinguy, with permission.

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)**

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

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 *Lophozia 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 quinqueidentata* (Figure 54).

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

Scapania nemorea (syn. = *Scapania nemorosa*, *Scapania nemorosa* var. *uliginosa*; 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 amphiatlantic 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 123-Figure 134). 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.

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 123-Figure 134), 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*, 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 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.

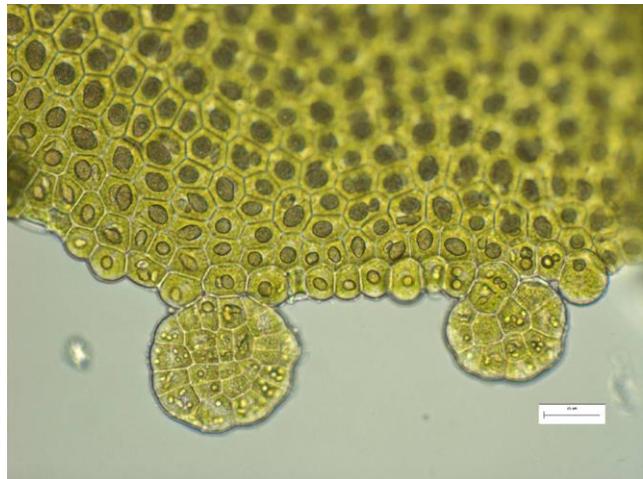


Figure 81. *Radula complanata* multicellular gemmae. Photo by Blanka Aguero, with permission.

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.

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.

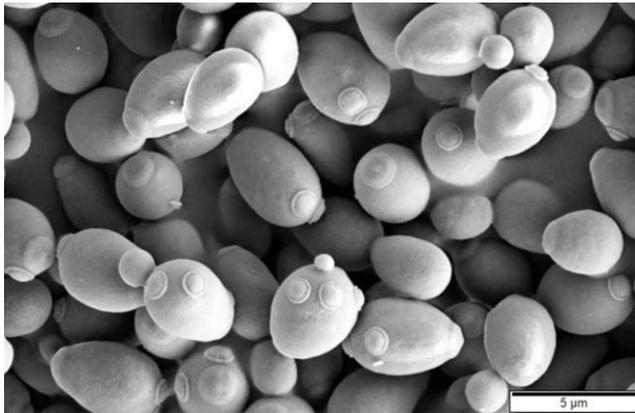


Figure 83. *Saccharomyces cerevisiae* (yeast) SEM. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

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.

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)**

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.

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)**

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.

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 101-Figure 107). Söderström *et al.* (2016) have not recognized this combination, so I shall maintain separate discussions for these two species.

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 93 shows the preferred temperatures, altitude, and water pH that make these alpine habitats suitable for the species.

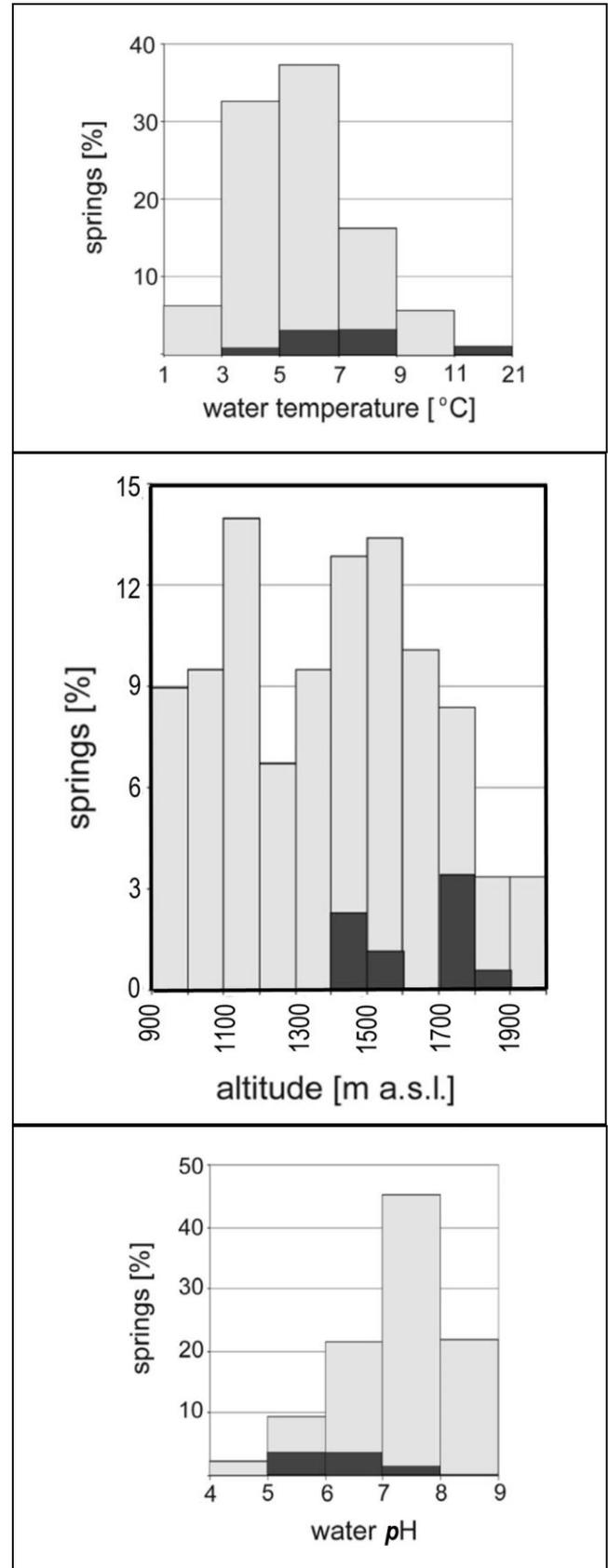


Figure 93. The distribution and habitat range of *Scapania paludosa* in the Tatra National Park springs, where it occurs in the upper montane zone. This liverwort is entirely restricted to bryophyte-dominated springs, where it forms extensive, swollen turfs. Black bars represent bryophytes; gray bars represent tracheophytes. Modified from Smieja 2014.

***Scapania rigida* (Figure 94-Figure 95)**

Scapania rigida (syn. = *Scapania rigida* fo. *minor*; Figure 94-Figure 95) seems to be a little-known species with almost no published information. The only information I have found is that of Ruttner (1955), who considered it to be among aquatic liverworts and reported it from the wall of a bay in the tropics.



Figure 94. *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.



Figure 95. *Scapania rigida* growing on a branch. Photo by Naufalurfi, through Creative Commons.

Scapania rufidula

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

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 quinquedentata* (Figure 54).

***Scapania subalpina* (Figure 96-Figure 100)**

Scapania subalpina (Figure 96-Figure 100) 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 96. *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 97. *Scapania subalpina* showing its growth habit. Photo by Andy Hodgson, with permission.

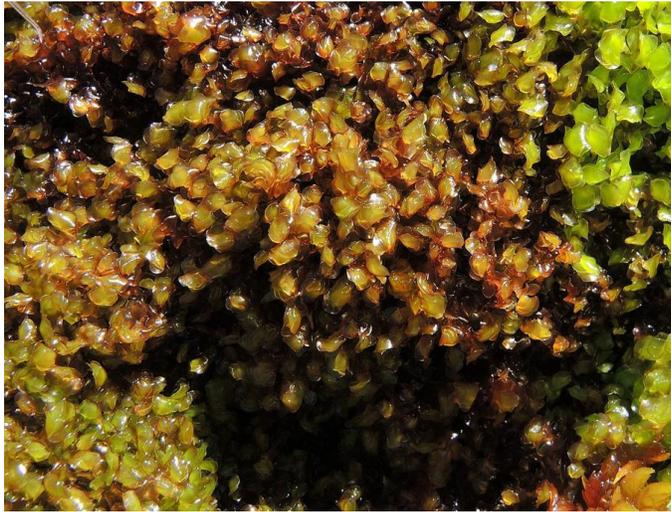


Figure 98. *Scapania subalpina* showing various color forms. Photo by Michael Lüth, with permission.

Koponen *et al.* (1995) reported *Scapania subalpina* (Figure 96-Figure 100) 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 99) 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 99. *Scapania subalpina* growing with a variety of other species. Photo by Michael Lüth, with permission.

The ecology of *Scapania subalpina* (Figure 96-Figure 100) is similar to that of *Scapania undulata* (Figure 123-Figure 134) (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 100), although it can occur on weakly basic rocks. Watson (1919) ascribed to it a habitat of gravelly detritus associated with fast water.



Figure 100. *Scapania subalpina* growing in a habitat that can dry out. Photo by Jean Faubert, with permission.

In experiments, *Scapania subalpina* (Figure 96-Figure 100) 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.

Schuster (1974) reports that *Scapania subalpina* (Figure 96-Figure 100) commonly produces gemmae but rarely produces capsules.

***Scapania uliginosa* (Figure 101-Figure 107)**

Scapania uliginosa (syn. = *Scapania obliqua*; Figure 101-Figure 107) 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 101. *Scapania uliginosa* is restricted to Arctic-alpine areas where it grows in streams and small lakes. Photo by Jan-Peter Frahm, with permission.



Figure 102. *Scapania uliginosa* showing its upright growth habit. Photo by Michael Lüth, with permission.



Figure 103. *Scapania uliginosa* showing a brown form with fist-like branch apices. Photo by Dick Haaksma, with permission.

Watson (1919) reported *Scapania uliginosa* (Figure 101-Figure 107) 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 101-Figure 107) is restricted to seepage-moistened rocks or cold springs and streams (Figure 104-Figure 106) (Schuster 1974). It sometimes occurs on stony, marshy ground in cold regions of high altitude or latitude (Figure 107). 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 123-

Figure 134), *S. paludosa* (Figure 89-Figure 92), *Marsupella aquatica* (Figure 108), and *M. sphacelata* (Figure 109). *Scapania uliginosa* (Figure 101-Figure 107) 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 104. *Scapania uliginosa* in an alpine seepage. Photo by Michael Lüth, with permission.



Figure 105. *Scapania uliginosa*, shown here in the middle, joins other bryophytes and a saxifrage in a seepage area. Photo by Michael Lüth, with permission.



Figure 106. *Scapania uliginosa* in a seepage area. Photo by Michael Lüth, with permission.



Figure 107. *Scapania uliginosa* in a marshy habitat. Photo by Michael Lüth, with permission.



Figure 108. *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 109. *Marsupella sphacelata*, a species that occurs on the sides of alpine rills similar to the ones to 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 101-Figure 107) on the stream bank in a *Larix* forest (Figure 110). Here it occurred with the leafy liverworts *Blepharostoma trichophyllum* subsp. *brevirete* (Figure 111), *Mesoptychia heterocolpos* (Figure 112), *Lophozopsis excisa* (Figure 51), *Scapania subalpina* (Figure 96-Figure 100), and *Trilophozia quinqueidentata* (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 110. *Larix* forest, a suitable habitat for *Scapania uliginosa* on a stream bank. Photo through public domain.



Figure 111. *Blepharostoma trichophyllum* subsp. *brevirete*, a species that occurs with *Scapania uliginosa* on stream banks. Photo by Hugues Tinguy, with permission.



Figure 112. *Mesoptychia heterocolpos*, a species that occurs with *Scapania uliginosa* on stream banks. Photo by Blanka Aguero, with permission.

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

Scapania uliginosa (Figure 101-Figure 107) 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.

Egorov (2007) examined the ability of associated **Cyanobacteria** (Figure 113) to fix nitrogen. The biological assimilation of atmospheric nitrogen by such microorganisms associated with *Scapania uliginosa* (Figure 101-Figure 107) during the growing period was 0, compared to 0.09 mg cm⁻² on a species of the moss *Bryum* (Figure 114). This is somewhat surprising to me due to the wet habitats where this liverwort is found.



Figure 113. *Nostoc*, one of the **Cyanobacteria** that occur on bryophytes and can fix nitrogen. Photo by Proyecto Agua, through Creative Commons.



Figure 114. *Bryum capillare*; some members of the genus *Bryum* support nitrogen-fixing **Cyanobacteria**. Photo by Michael Becker, through Creative Commons.

Scapania umbrosa (Figure 115-Figure 122)

Scapania umbrosa (Figure 115-Figure 122) 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 115. *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 116. *Scapania umbrosa* showing leaf folds. Photo by Hermann Schachner through Creative Commons.



Figure 117. *Scapania umbrosa* showing a moist, pale color form. Photo by Hermann Schachner, through Creative Commons.



Figure 118. *Scapania umbrosa* showing the upright habit and claw-like tips. Photo by Hugues Tinguy, with permission.



Figure 119. *Scapania umbrosa* showing a drier and darker appearance. Photo by Hermann Schachner, through Creative Commons.

Schuster (1974) considers *Scapania umbrosa* (Figure 115-Figure 122) to be restricted to locations where it is continually moist. These can include decaying, damp, shaded logs (Figure 120) or moist rocks. It is known from both igneous rock and calcareous or noncalcareous sandstone. Watson (1919) noted that it was occasionally submerged.



Figure 120. *Scapania umbrosa* on decaying wood. Photo by Hermann Schachner, through Creative Commons.

In Russia, Choi *et al.* (2012) reported *Scapania umbrosa* (Figure 115-Figure 120) 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).

Gemmae in this species are apical and 2-celled (Figure 121-Figure 122)



Figure 121. *Scapania umbrosa* with apical gemmae. Photo by Hermann Schachner, through Creative Commons.

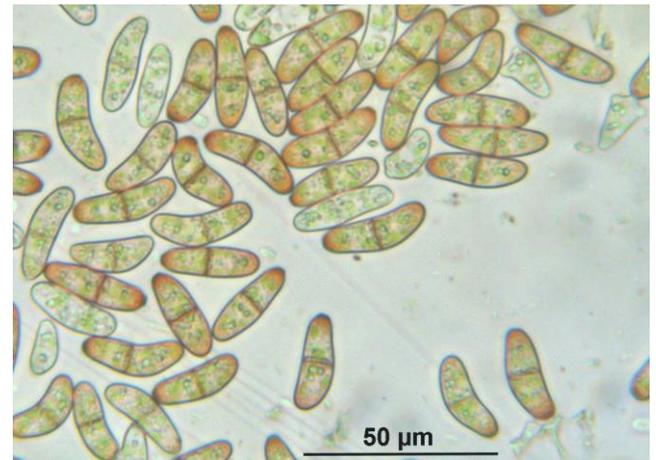


Figure 122. *Scapania umbrosa* gemmae. Photo by Hermann Schachner, through Creative Commons.

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

***Scapania undulata* (Figure 123-Figure 134)**

Scapania undulata (syn. = *Martinellius undulata*, *Plagiochila undulatum*, *Pleurozia cochleariformis*, *Scapania dentata*, *Scapania intermedia*; Figure 123-Figure 134) 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 123. *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 124. *Scapania undulata* showing its growth habit. Photo by Hermann Schachner, through Creative Commons.



Figure 125. *Scapania undulata* showing shoot apices. Photo by David T. Holyoak, with permission.



Figure 126. *Scapania undulata* with only the shoot apices emergent. Photo by Michael Lüth, with permission.

Of all the aquatic liverworts, *Scapania undulata* (Figure 123-Figure 134) 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 127-Figure 128) 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 127. *Scapania undulata* and habitat on rock just above the water. Photo by Jean Faubert, with permission.



Figure 128. *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 123-Figure 134) to be the most common bryophyte in small streams in Ireland, where it forms turfs (Figure 129). It is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006).



Figure 129. *Scapania undulata* in a dry montane stream bed, showing how abundant it can become. Photo by Michael Lüth, with permission.



Figure 130. *Scapania undulata* habitat on a dripping cliff. Photo by Dick Haaksma, with permission.

Scapania undulata (Figure 123-Figure 134) has been well-known from other parts of Europe as well. It occurs in European alpine streams (Figure 131), 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 131. 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 123-Figure 134) 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 132-Figure 134).



Figure 132. *Scapania undulata* on rock in stream. Photo by Michael Kesl, through Creative Commons.



Figure 133. *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 134. *Scapania undulata* partially submersed at Cranberry Lake, New York, USA. Photo by Janice Glime.

While *Scapania undulata* (Figure 123-Figure 134) is often the most common or abundant liverwort in streams, in upland Welsh streams it was surpassed by *Nardia compressa* (Figure 135) (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 135. *Nardia compressa* a species that can surpass *Scapania undulata* in upland Welsh streams. Photo by Barry Stewart, with permission.

Hall *et al.* (2001) used TWINSPLAN to assess the important parameters determining the suitable streams for plants, including bryophytes. For *Scapania undulata* (Figure 123-Figure 134), 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 123-Figure 134) is abundant in and out of water on rocks and stones at lake margins and on boggy shores (Figure 136) in Scotland (West 1910). Tremp (2003) reported it forming turfs in oligotrophic water.



Figure 136. *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 137)-*Fontinalis antipyretica* 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 138) occurred.



Figure 137. *Platyhypnidium riparioides*; *Scapania undulata* frequents streams with this species and *Fontinalis antipyretica*. Photo by David T. Holyoak, with permission.

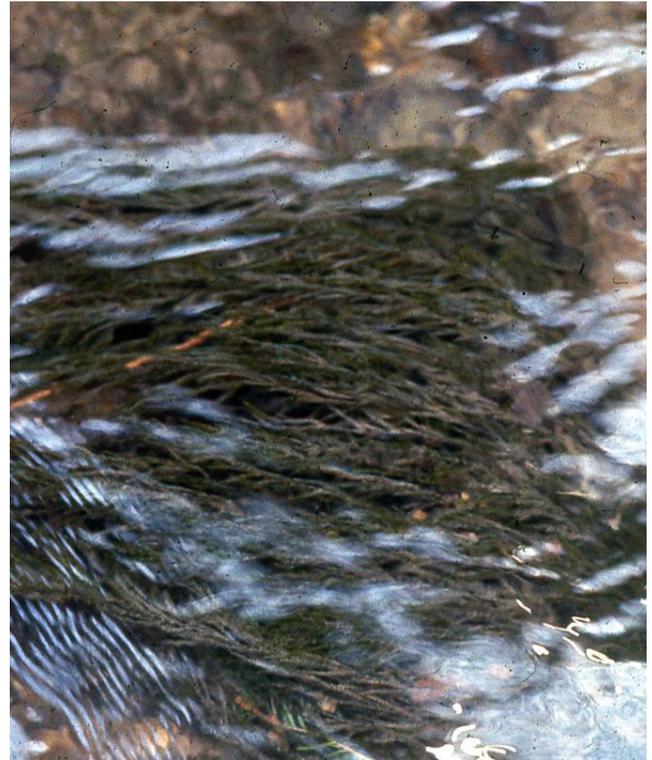


Figure 138. *Fontinalis dalecarlica*, a species characteristic of streams that also have *Scapania undulata*. Photo by Janice Glime.

Because of their ubiquity and ability to become relatively abundant, the plants of *Scapania undulata* (Figure 123-Figure 134) 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 139), *Fissidens polyphyllus* (Figure 140), and *Fontinalis* (Figure 138), 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 139. *Platyhypnidium lusitanicum*, one of the species used to assess fluvial status in Portuguese streams. Photo by Barry Stewart, with permission.



Figure 140. *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 141): *Sphagnum warnstorffii* (Figure 142) and *Scapania undulata* (Figure 123-Figure 134). 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 141. *Warnstorfia exannulata*, a species subjected to water level fluctuations. Photo by Michael Lüth, with permission.

pH

Scapania undulata (Figure 123-Figure 134) 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 submerged 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 142. *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 123-Figure 134) 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 143) and *Hyocomium armoricum* (Figure 144), all common in fast-flowing acidic streams.



Figure 143. *Racomitrium aciculare*, a species often associated with *Scapania undulata*. Photo by Michael Lüth, with permission.



Figure 144. *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 123-Figure 134) 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 123-Figure 134) 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 137), 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 123-Figure 134) 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 123-Figure 134) 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 123-Figure 134), 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 145) 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 146-Figure 147).



Figure 145. *Porella platyphylla*, an epiphytic species that has good drought resistance. Photo by Hugues Tinguy, with permission.



Figure 146. *Scapania undulata* habitat, in this case, emergent but wet. Photo by Dick Haaksma, with permission.



Figure 147. *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 123-Figure 134) occurs demonstrate its ability to tolerate cold temperatures, at least down to 0°C (Figure 148).



Figure 148. *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 123-Figure 134) 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 149).



Figure 149. *Scapania undulata* with capsules. Photo by Michael Lüth, with permission.

Scapania undulata (Figure 123-Figure 134) 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 150).



Figure 150. *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 151) (Potemkin 1998). Their walls are thin and they vary from green to red (Figure 152).

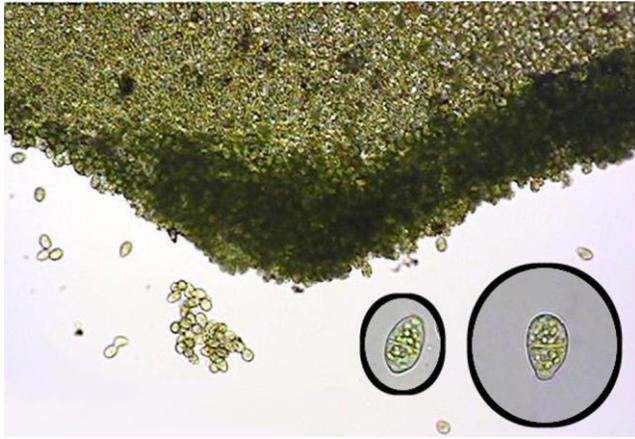


Figure 151. *Scapania undulata* gemmae on leaf. Photo by Paul Davison, with permission.

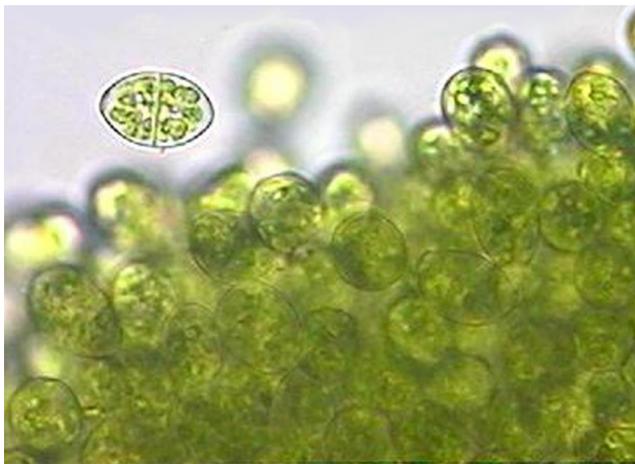


Figure 152. *Scapania undulata* gemmae. Photo by Paul Davison, with permission.

But this species may have another, possibly more successful, means of reproduction. Its detached leaves can germinate to produce new plants (Figure 153) (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.

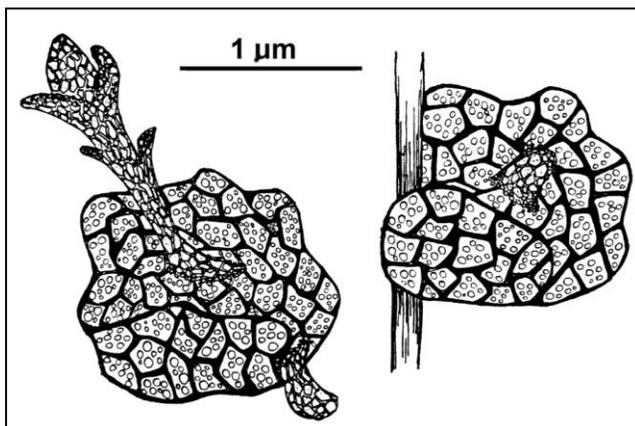


Figure 153. *Scapania undulata* plantlets on leaves from a stream in New Hampshire, USA. Drawings by Flora Mace.

Secondary Compounds

Like so many liverworts, *Scapania undulata* (Figure 123-Figure 134) 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 154) and DNA in high light environments. In direct sunlight, there is a dentate, pigmented form of *Scapania undulata* (Figure 155-Figure 156), 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 154. *Scapania undulata* showing non-red form. Photo by Michael Lüth, with permission.



Figure 155. *Scapania undulata* showing red pigments in a European population. Photo by Michael Lüth, with permission.



Figure 156. *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 123-Figure 134), 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 123-Figure 134), 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 123-Figure 134). 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 123-Figure 134), a pigment it shares with the floating liverwort *Ricciocarpos natans* (Figure 157) and the streambank liverwort *Marchantia polymorpha* (Figure 158).



Figure 157. *Ricciocarpos natans*, a species with the pigment riccionidin A. Photo by Murray Fagg, Australian National Botanic Gardens, with online permission.



Figure 158. *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 123-Figure 134) 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 123-Figure 134) 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 123-

Figure 134) 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 123-Figure 134), 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 123-Figure 134) is a species that has been used in a number of bioindicator studies (Samecka-Cymerman 1989).

When compared to *Fissidens polyphyllus* (Figure 140), *Fontinalis antipyretica* (Figure 159), *Platyhypnidium riparioides* (Figure 137), and *Brachythecium rivulare* (Figure 160), *Scapania undulata* (Figure 123-Figure 134) 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 123-Figure 134). 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 159. *Fontinalis antipyretica*, a species that has less capacity for heavy metal accumulation than *Scapania undulata*. Photo by Dick Haaksma, with permission.



Figure 160. *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 123-Figure 134). 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 123-Figure 134) 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 123-Figure 134) 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 123-Figure 134) 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 123-Figure 134) serves in a variety of roles in streams, lakes, and other wetlands. In streams, they are typically home to may 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 123-Figure 134) 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 161) 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 161. *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 162) uses *Scapania undulata* (Figure 123-Figure 134) (and *Chiloscyphus polyanthos* – Figure 161) to make its cases (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 162. 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 WETLAND: MARCHANTIOPHYTA ORDER JUNGERMANNIALES – JUNGERMANNINEAE

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CHAPTER 1-4

AQUATIC AND WETLAND: MARCHANTIOPHYTA, ORDER JUNGERMANNIALES – JUNGERMANNIINEAE

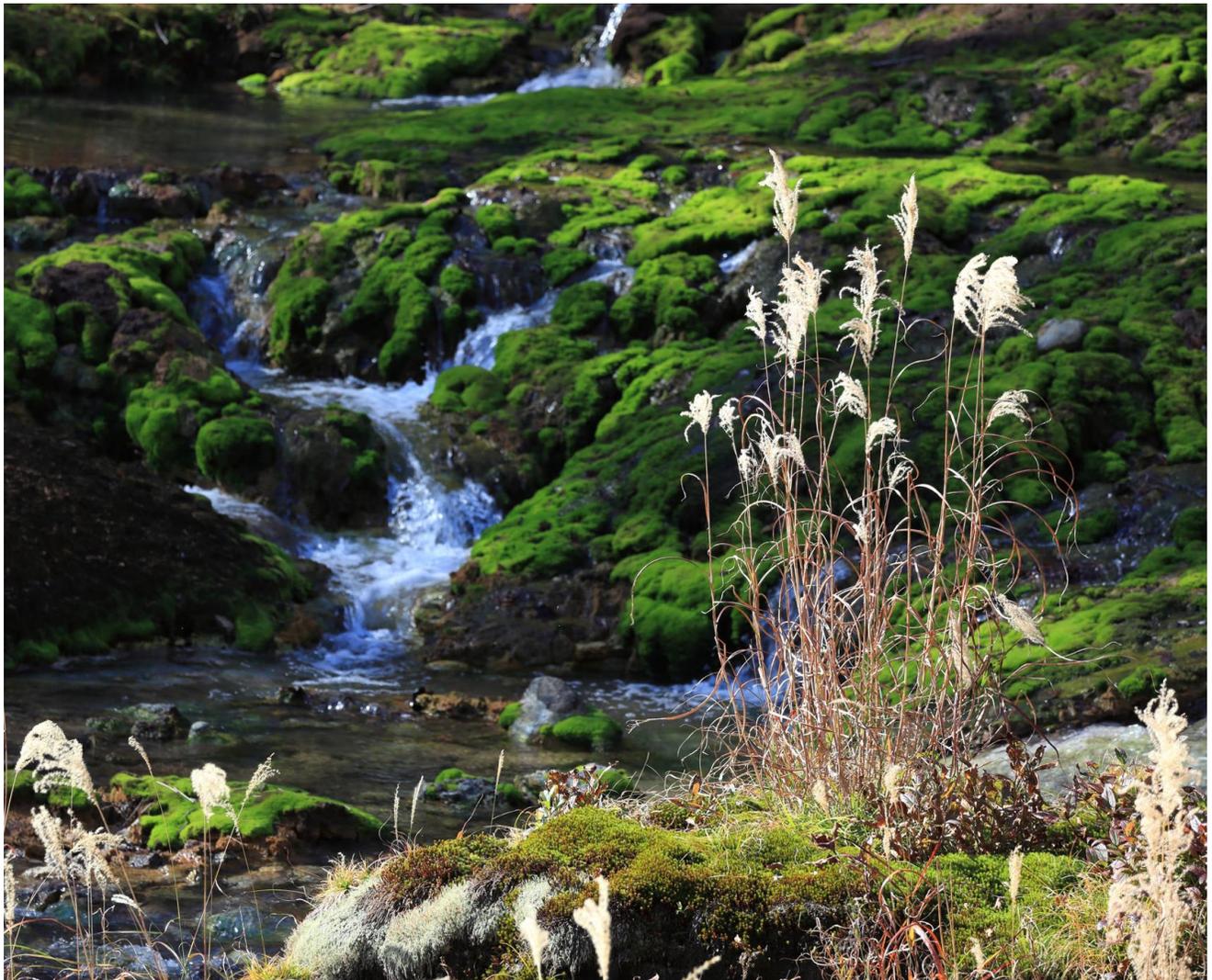


Figure 1. A sulfur stream in Japan where the dominant vegetation is *Solenostoma vulcanicola*. Photo by Juuyoh Tanaka, through Creative Commons.

Antheliaceae

Anthelia julacea (Figure 2-Figure 3)

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.

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



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



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

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. The species is dioicous, accounting for the fact it is usually lacking sporophytes.

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 .

Anthelia juratzkana (Figure 7-Figure 10)

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.

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 snowbank. Photo by Michael Lüth, with permission.

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.

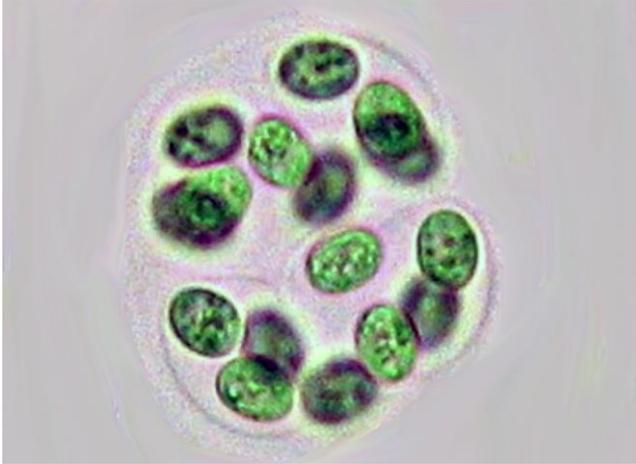


Figure 11. *Gloeocapsa* sp.; *Gloeocapsa montana* is a **Cyanobacterium** that associates with *Anthelia juratzkana*. Photo by John, through Creative Commons.

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, the 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 (the compensation point is the 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.



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)

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.



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.

Calypogeiaceae

Calypogeia (Figure 15-Figure 22, Figure 24-Figure 43)

Geissler (1976) reported *Calypogeia* (Figure 15-Figure 22, Figure 24-Figure 43) 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 22, Figure 24-Figure 43) species from West Virginia, USA, mountain streams. The preferred pH was around 5.95.

***Calypogeia arguta* (Figure 15-Figure 16)**

Calypogeia arguta (Figure 15-Figure 16) is widely distributed, from the Faroe 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.

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.

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 Faroe Islands when subjected to two days on ice at -10°C.

Nevertheless, Campisi *et al.* (2008) reported it from bark of *Quercus ilex* (Figure 20) in Calabria, S. Italy, where temperature fluctuations are wider than in water. Sukkharak *et al.* (2014) simply report it as saxicolous in Thailand. Bates *et al.* (2005) consider it to be a calcifuge and found it to be among the species with the strongest association with wet conditions at limestone grassland at Buxton in the southern Pennine Hills, UK. Norris (1967) reported it from shaded soil and rocks at Cumberland Falls State Park, Kentucky.



Figure 20. *Quercus ilex* bark, a suitable substrate for *Calypogeia arguta*. Photo by Christian R. Linder, through Creative Commons.

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

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.

Calypogeia arguta (Figure 15-Figure 16) is among the liverwort species that apparently inhibit the parasitic ascomycete *Mniaecia jungermanniae* (Figure 25-Figure 27) (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 21-Figure 22)**

Calypogeia azurea (Figure 21-Figure 22) is a widespread, subboreal-montane species (Buczowska *et al.* 2016), being widely distributed through the northern hemisphere, including North America (rare; in Pacific Northwest), Europe, and eastern Asia (Buczowska *et al.* 2018).



Figure 21. *Calypogeia azurea*, a species widely distributed in the Northern Hemisphere. Photo by Hermann Schachner, through Creative Commons.



Figure 22. *Calypogeia azurea* showing gemmae. Photo by Hermann Schachner, through Creative Commons.

It occurs on loamy soil, humus, peat, wet stones and rocks, to rotten logs (Buczowska *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 23) in European mountains.



Figure 23. *Eleocharis quinqueflora*, a sedge species that sometimes has *Calypogeia azurea* at its base. Photo by Max Licher, through Creative Commons.

Calypogeia azurea (Figure 21-Figure 22) is one of the few members of *Calypogeia* that has blue oil bodies (Figure 24) (Buczowska *et al.* 2016), giving it a bluish color and accounting for the epithet *azurea*. The species presents a variety of environmentally induced morphological differences.

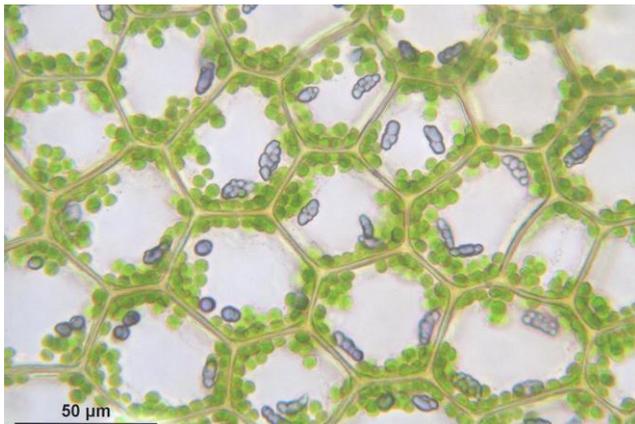


Figure 24. *Calypogeia azurea* leaf cells showing blue oil bodies. Photo by Hermann Schachner, through Creative Commons.

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 (Buczowska *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.

Calypogeia azurea (Figure 21-Figure 22) is a species where the fungal parasite *Mniaecia jungermanniae* (Figure 25-Figure 27) finds suitable habitat and host (Egertová *et al.* 2016). These occurrences include liverworts growing on wet soil.

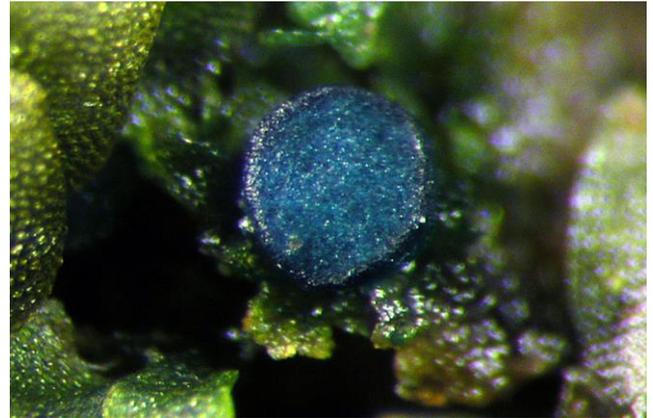


Figure 25. *Calypogeia azurea* with fungal parasite *Mniaecia jungermanniae*. Photo by Walter Obermayer, with permission.

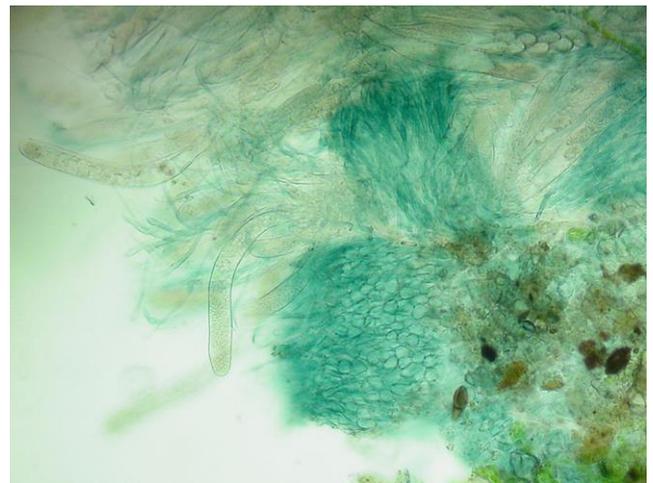


Figure 26. *Calypogeia azurea* with fungal parasite *Mniaecia jungermanniae* asci in the upper right corner of the image. Photo by Walter Obermayer, with permission.



Figure 27. *Calypogeia azurea* with asci of the fungal parasite *Mniaecia jungermanniae*. Photo by Walter Obermayer, with permission.

A number of studies have examined the secondary compounds in *Calypogeia azurea* (Figure 21-Figure 22). 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 28-Figure 30, Figure 32-Figure 33)**

Calypogeia fissa (Figure 28-Figure 30, Figure 32-Figure 33) has a suboceanic distribution pattern in North America, Europe, Asia, and North Africa (Potemkin 2018).



Figure 28. *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 29. *Calypogeia fissa*. Photo by Štěpán Koval, with permission.



Figure 30. *Calypogeia fissa* ventral side showing under leaves. Photo by Michael Lüth, with permission.

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 28-Figure 30, Figure 32-Figure 33) 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 31). *Calypogeia fissa* frequently forms rather extensive mats resulting from frequent production of gemmae (Figure 32) and probably regular spore production (Figure 33).



Figure 31. *Scapania nemorea*, a species that can occur in rock crevices with *Calypogeia fissa*. Photo by Michael Lüth, with permission.



Figure 32. *Calypogeia fissa* with gemmae. Photo by Štěpán Koval, with permission.



Figure 33. *Calypogeia fissa* with nearly mature capsule. Photo by Malcolm Storey, through Creative Commons.

Buczowska *et al.* (2011) identified two morphologically distinct groups of the *Calypogeia fissa* (Figure 28-Figure 30, Figure 32-Figure 33) 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* (Buczowska *et al.* 2012a): *Calypogeia fissa* subsp. *fissa* (Figure 34) in Europe and *C. fissa* subsp. *neogaea* (Figure 35) in North America (Buczowska *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.

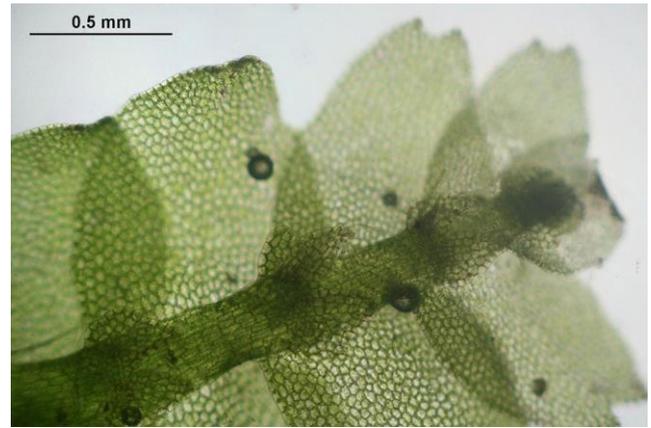


Figure 34. *Calypogeia fissa* subsp. *fissa*, the subspecies typical in Europe, showing underleaves. Photo by Hermann Schachner, through Creative Commons.

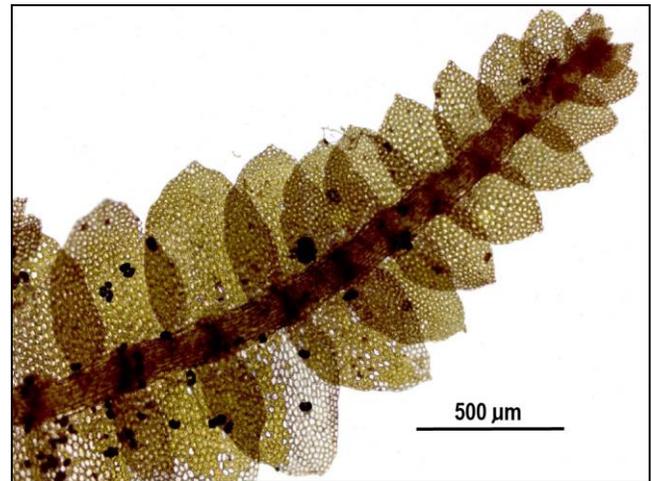


Figure 35. *Calypogeia fissa* subsp. *neogaea*, the subspecies typical in North America; ventral leaves in the photo are the darkened areas across the stem. Photo by Blanka Aguero, with permission.

Calypogeia fissa (Figure 28-Figure 30, Figure 32-Figure 33) is able to regenerate from peat slabs (Duckett & Clymo 1988). Unlike some leafy liverworts, this species lacks underground shoots (Figure 30). Therefore, it regenerates most abundantly at the surface, failing to have regenerative parts below 9 cm depth in the peat.

Wang and Qiu (2006) found a report of fungal association with this species.

Warmers and König (1999) found four new sesquiterpenes in *Calypogeia fissa* (Figure 28-Figure 30, Figure 32-Figure 33). Their role remains unknown, but they are likely to play a role in antiherbivory.

***Calypogeia goebelii* (Figure 36)**

Calypogeia goebelii (Figure 36) (syn. = *Kantia goebelii* fo. *thermarum*) 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 through Creative Commons.

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)**

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.

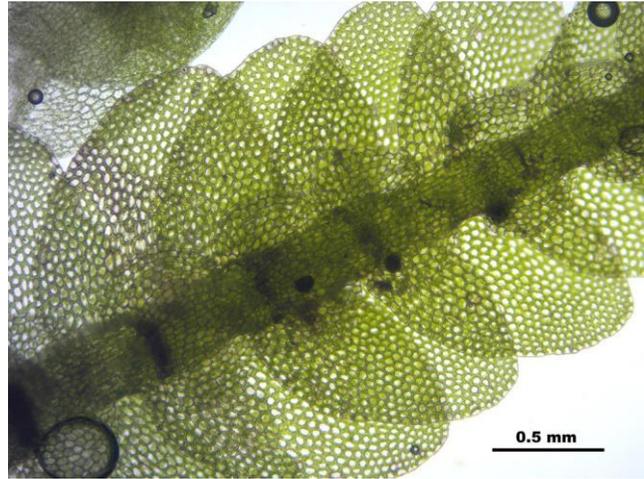


Figure 38. *Calypogeia muelleriana* ventral side with underleaves. Photo by Hermann Schachner, through Creative Commons.



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.

In the Pickle Springs, Missouri, USA, this species 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.

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* than it does *C. muelleriana* and this unnamed new species has also been identified in the USA (Buczkowska *et al.* 2013)

Some of its secondary compounds have been identified. Warmers *et al.* (1998) investigated the lipophilic constituents and reported three new sesquiterpene compounds.

***Calypogeia sphagnicola* (Figure 41-Figure 43)**

Calypogeia sphagnicola (Figure 41-Figure 43) (syn. = *Calypogeia muelleriana* fo. *sphagnicola*) 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.



Figure 41. *Calypogeia sphagnicola*, a species from sub-Arctic and alpine areas in the Northern Hemisphere. Photo by Erika Mitchell, through Creative Commons



Figure 42. *Calypogeia sphagnicola* showing underleaf. Photo by Scot Loring, through Creative Commons.

Of the many references I found documenting the presence of this species, all but one indicated it was associated with *Sphagnum* (Figure 43). 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 43. *Calypogeia sphagnicola* with *Sphagnum*. Photo by David T. Holyoak, with permission.

Calypogeia sphagnicola (Figure 41-Figure 43) 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 Ōdake, 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 41-Figure 43) 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 44) and *Acutifolia* (Figure 45) than in subgenus *Cuspidatum* (Figure 46). 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 44), a moss in subgenus *Sphagnum*.



Figure 44. *Sphagnum magellanicum*, subgenus *Sphagnum*, showing a dense carpet that can serve as substrate for *Calypogeia sphagnicola*. Photo by Dale Vitt, with permission.



Figure 45. *Sphagnum girgensohnii*, subgenus *Acutifolia*, representing the more preferred substrate group for *Calypogeia sphagnicola*. Photo by Kari Pihlaviita, through Creative Commons.

Despite its relative rarity, *Calypogeia sphagnicola* (Figure 41-Figure 43) 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 43), whereas some leafy liverwort species avoid the *Sphagnum* competition by growing on bare peat as well as among *Sphagnum*.

In the Alaskan black spruce forest, *Calypogeia sphagnicola* (Figure 41-Figure 43) 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.



Figure 46. *Sphagnum cuspidatum* (subgenus *Cuspidatum*) submerged; 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.

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 47) on the upper part of north-facing slopes."



Figure 47. *Sphagnum capillifolium* and *Polytrichum commune* forming a hummock where *C. sphagnicola* fo. *paludosa* is able to grow. Photo by Sheila, through Creative Commons.

Wang and Qiu (2006) reported that *Calypogeia sphagnicola* (Figure 41-Figure 43) has fungi associated with it.

Calypogeia sullivantii (Figure 48)

Calypogeia sullivantii (Figure 48) 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 48. *Calypogeia sullivantii*, a species previously considered a variety of *C. arguta*, occurs around springs. Photo by Blanka Aguero, with permission.

Wittlake (1950) found that *Calypogeia sullivantii* (formerly placed in *C. arguta* as a variety; Figure 48) 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.

Geocalyceaceae

Geocalyx graveolens (Figure 49-Figure 51)

Geocalyx graveolens (Figure 49-Figure 51) is a widespread species in oceanic Holarctic regions (Szweykowski & Kozlicka 1974; Schäfer-Verwimp & Váňa 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 49. *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 50. *Geocalyx graveolens* ventral side showing underleaf at the red star. Photo by Michael Lüth, with permission.

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 49-Figure 51) is very rare, occurring in calcareous alder breaks with "brisk" water (Rätzel *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 51) (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 51. *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 49-Figure 51) seems to tolerate subcalcareous situations, but this is not the case in the British Isles (Paton 1999). Zobel (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).

Geocalyx graveolens (Figure 49-Figure 51) forms extensive creeping mats over *Sphagnum* species (Figure 44). Sharp (1944) described it as having a peculiar yellowish color (Figure 49). 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.

These mats can serve as home for the boreid beetle, *Caurinus dectes* (Figure 52), 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 dectes*.



Figure 52. *Caurinus dectes*, a boreid beetle that feeds on *Geocalyx graveolens*. Photo by CBG Photography Group, through Creative Commons.

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 53)

Gymnomitrium commutatum (syn. = *Marsupella commutata*; Figure 53) occurs in northern Europe, middle Europe, southwestern Europe, southeastern Europe, Siberia, Russian Far East, China, eastern Asia, Indian Subcontinent, Malesia, subarctic America, western Canada, northwestern USA (Váňa *et al.* 2010).



Figure 53. *Gymnomitrium commutatum*, a Northern Hemisphere wet habitat liverwort. Photo by Michael Lüth, with permission.

Konstantinova *et al.* (2002) found it on wet cliffs and cliff crevices associated with the Upper Bureya River in the Russian Far East. 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).

***Gymnomitrium crenulatum* (Figure 54-Figure 55)**

The distribution of *Gymnomitrium crenulatum* (Figure 54-Figure 55) 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 54. *Gymnomitrium crenulatum*, a Northern Hemisphere species with a poorly understood distribution; it seems to prefer emergent rocks of streams, but can get submerged. Photo by Andrew Hodgson, with permission.

This species seems to do best above the low flow water level in exposed streambed conditions, preferring moderately stable boulders (Figure 55) that are easily submerged (Vieira *et al.* 2005). They are tolerant of acid water, perhaps preferring it, especially in mountain streams of northwest Portugal.



Figure 55. *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.

***Marsupella* (Figure 56-Figure 57, Figure 60-Figure 64, Figure 67-Figure 75, Figure 77)**

Marsupella (Figure 56-Figure 57, Figure 60-Figure 64, Figure 67-Figure 75, Figure 77) 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 56-Figure 57)**

Marsupella aquatica (syn. = *Marsupella emarginata* var. *aquatica*; Figure 56-Figure 57) has an **arctomontane** (in Arctic and in montane regions at lower latitudes) semi-circumpolar distribution with oceanic affinities (Konstantinova 2000). More specifically, Váňa *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 56. *Marsupella aquatica*, an Arctic-montane semi-circumpolar species from wet and submerged rocks of streams and rivers. Photo by Štěpán Koval, with permission.



Figure 57. *Marsupella aquatica*, exhibiting a red form. Photo by Barry Stewart, with permission.

Nichols (1918) reported *Marsupella aquatica* (Figure 56-Figure 57) 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 62-Figure 63) 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 58) and *Fontinalis dalecarlica* (Figure 59). 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 Heggens 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 58. *Scapania undulata*, a species that associates with *Marsupella aquatica* on rocks in Maine, USA. Photo by Jan-Peter Frahm, with permission.



Figure 59. *Fontinalis dalecarlica*, a species that associates with *Marsupella aquatica* on rocks in Maine, USA. Photo by J. C. Schou, with permission.

This species has received less biochemical attention than some of the previously mentioned bryophytes. Nagashima *et al.* (1994) identified a new gymnomitrane-type sesquiterpenoid from it, as well as others that were previously known.

Marsupella boeckii (Figure 60)

Marsupella boeckii (Figure 60) 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 60. *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.

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 61) 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 62-Figure 64) in the same habitat in eastern Yakutia, Russia.



Figure 61. *Marsupella arctica* herbarium specimen, a species that forms mats at the edges of springs. Photo by CBG Photography Group, through Creative Commons.

***Marsupella emarginata* (Figure 62-Figure 64)**

Marsupella emarginata (syn. = *Nardia emarginata*; Figure 62-Figure 64) 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 62. *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.

Marsupella emarginata (Figure 62-Figure 64) 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 63. *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 64).



Figure 64. *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 62-Figure 64) 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 62-Figure 64) 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 58) in aquatic habitats of eastern Odenwald and southern Spessart (Philippi 1987) and in the *Platyhypnidium* (Figure 65)-*Fontinalis antipyretica* (Figure 66) association in Thuringia, Germany (Marstaller 1987).



Figure 65. *Platyhypnidium riparioides*, a species that can occur in association with *Marsupella emarginata*. Photo by Hermann Schachner, through Creative Commons.



Figure 66. *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 62-Figure 64) 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 62-Figure 64) on most rock surfaces, reaching about 3 m diameter, but only 20 cm in depth (*e.g.* Figure 64).

Wang and Qiu (2006) report *Marsupella emarginata* (Figure 62-Figure 64) as having associations with fungi, but with no mycorrhizal relationships known. Egertová *et al.* (2016) found *Mniaecia jungermanniae* (Figure 25-Figure 27) 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 67)**

Marsupella emarginata subsp. *tubulosa* (Figure 67) (syn. = *Marsupella tubulosa*) has been identified in several studies. It is a subspecies of the Northern Hemisphere, primarily in eastern Asia and nearby islands, but also occurring in fewer known locations in Europe and North America (GBIF 2020d).



Figure 67. *Marsupella emarginata* subsp. *tubulosa* forming mats. Photo from Taiwan Mosses, through Creative Commons.

The subspecies 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. Hakkō 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.

Despite the paucity of readily available ecological information, Matsuo *et al.* (1979) isolated three new sesquiterpenoids from this species.

***Marsupella sparsifolia* (Figure 68-Figure 70)**

Marsupella sparsifolia (Figure 68-Figure 70) 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 68. *Marsupella sparsifolia*, is a bipolar Arctic-alpine species that occurs on stream banks and other wet habitats. Photo by Kristian Peters (Korseby Online; Sagebud), with permission.



Figure 69. *Marsupella sparsifolia* in a wet habitat. Photo by Kristian Peters (Korseby Online; Sagebud), with permission.

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 62-Figure 64), it avoids calcareous sites but tolerates frequent inundation. Hong (1980) reported *Marsupella sparsifolia* (Figure 68-Figure 70) 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 70. *Marsupella sparsifolia* habitat. Photo by Kristian Peters (Korseby Online; Sagebud), with permission.

***Marsupella sphacelata* (Figure 71-Figure 75)**

Marsupella sphacelata (Figure 71-Figure 75) 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 71. *Marsupella sphacelata*, a boreal and low-Arctic species mostly of slow streams. Photo by Štěpán Koval, with permission.



Figure 72. *Marsupella sphacelata*. Photo by Giovanni Bergamo Decarli, through Creative Commons.



Figure 73. *Marsupella sphacelata* clone. Photo by Hermann Schachner, through Creative Commons.



Figure 74. *Marsupella sphacelata* showing its mat growth habit and dark pigments. Photo by Hermann Schachner, through Creative Commons.

Watson (1919) considered this 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 75) (Schuster 1974). It seems to be absent from calcareous rocks. It can form pure patches, but also grows with *Marsupella emarginata* (Figure 62-Figure 64), *Scapania undulata* (Figure 58), and *S. subalpina* (Figure 76). Its lax tufts are typically dull green and brownish-tinged above (Figure 73-Figure 75).



Figure 75. *Marsupella sphacelata* in submerged habitat. Photo by Hermann Schachner, through Creative Commons.



Figure 76. *Scapania subalpina*, a species that often grows with *Marsupella sphacelata* in mountain streams. Photo by Andy Hodgson, with permission.

The terrestrial forms of *Marsupella sphacelata* (Figure 71-Figure 75) are able to grow in direct sun, often with intermittent seepage (Figure 77) (Schuster 1974). They are able to endure long dry periods. These forms create blackish patches.



Figure 77. *Marsupella sphacelata* habitat on wet substrate, showing dark pigments that absorb UV radiation. Photo by Hermann Schachner, through Creative Commons.

Marsupella sphacelata (Figure 71-Figure 75, Figure 77) can produce UV-B-absorbing compounds (Figure 74, Figure 77) 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 programmed.

Nardia assamica

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.

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 78) and *Eleocharis* (Figure 23) in wet depression in wind-stressed community of *Sasa* (bamboo; Figure 79) and small herbs. It frequently occurs with other leafy liverworts.

Nardia compressa (Figure 80-Figure 83)

Nardia compressa (Figure 80-Figure 83) (syn. = *Alicularia compressa*) has a worldwide distribution, but avoids the hot tropics, occurring there only at high elevations (DiscoverLife.org 2020).



Figure 78. *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 79. *Sasa* ground cover in spruce forest at Bihora Pass Japan. *Nardia assamica* lives in association with *Sasa* in wet depression. Photo by Janice Glime.



Figure 80. *Nardia compressa*, a species with worldwide distribution outside the tropics, occurring in lakes and streams. Photo by Hermann Schachner, through Creative Commons.



Figure 81. *Nardia compressa* showing stoloniferous shoots. Photo by Hermann Schachner, through Creative Commons.

Based on early studies, West (1910) reported it to be abundant on wet and submersed rocks (Figure 82) 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 82. *Nardia compressa* habitat by a stream. Photo by Hugues Tinguy, with permission.

Watson (1919), on the other hand, reported it 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 65) and *Fontinalis antipyretica* (Figure 66).

Lepp (2012) reported *Nardia compressa* (Figure 80-Figure 83) 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 83), permitting tracheophytes to invade the mat.

Vieira *et al.* (2004, 2005) described *Nardia compressa* (Figure 80-Figure 83) 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 84), *Marsupella aquatica* (Figure 56-Figure 57), *Marsupella sphacelata* (Figure 73-Figure 75), *Platyhypnidium lusitanicum* (Figure 85), and *Scapania undulata* (Figure 58), in these mountain streams of northwest Portugal (Vieira *et al.* 2005).



Figure 83. *Nardia compressa* submersed. Photo by Hugues Tinguy, with permission.



Figure 84. *Fissidens polyphyllus*, a species that occurs with *Nardia compressa* in exposed peat bog areas. Photo by David T. Holyoak, with permission.



Figure 85. *Platyhypnidium lusitanicum*, an associate with *Nardia compressa*. Photo by Barry Stewart, with permission.

Geissler (1975) considered this 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 80-Figure 83) 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.

Nardia geoscyphus (Figure 86-Figure 87)

Nardia geoscyphus (Figure 86-Figure 87) 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 86. *Nardia geoscyphus*, a boreal Northern Hemisphere species from stream banks and constructed ditches. Photo by Štěpán Koval, with permission.



Figure 87. *Nardia geoscyphus* habitat on a stream bank. Photo by Martine Lapointe, with permission.

Beaucourt *et al.* (1987) reported *Nardia geoscyphus* (Figure 86) from irrigation ditches. It also grows on eroded soil beside roads and on stream banks (Figure 87) (Natcheva 2020).

Nardia geoscyphus (Figure 86-Figure 87) rarely occurs in dense mats and the shoots are usually prostrate and closely adhere to the soil (Evans 1912). The species is **paroicous** (having archegonia and antheridia on same branch), permitting it to frequently produce capsules.

Nardia scalaris (Figure 88-Figure 89, Figure 92)

Nardia scalaris (syn. = *Alicularia scalaris*, *Alicularia scalaris* var. *distans*, *Alicularia scalaris* var. *procerior*, *Alicularia scalaris* var. *rivularis*; Figure 88-Figure 89, Figure 92) 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 88. *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.

West (1910) reported *Nardia scalaris* (Figure 88-Figure 89, Figure 92) 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 58) 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 88-Figure 89, Figure 92) 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 88-Figure 89) can form continuous carpets (Figure 89) that seem to support the growth of *Saxifraga ferruginea* (Figure 90) (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 89. *Nardia scalaris* forming continuous carpet. Photo by Hermann Schachner, through Creative Commons.



Figure 90. *Saxifraga ferruginea*, a species that can grow on carpets of *Nardia scalaris* in Alaska. Photo by Paul Slichter, with permission.

The *Scapania* (Figure 58)-*Nardia* (Figure 88-Figure 89, Figure 92) community on Yakobi Island colonizes mountain rivulets, forming carpets that permit *Nephrophyllidium crista-galli* (syn. = *Fauria crista-galli*; Figure 91) to colonize and eventually succeed to a copperbush community (Shacklette 1965).

Nardia scalaris (Figure 88-Figure 89, Figure 92) is dioicous and rarely produces capsules (Figure 92), at least in North America (Evans 1912). It typically produces prostrate shoots that become suberect when growing in compact mats.

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.



Figure 91. *Nephrophyllidium crista-galli*, a species that colonizes the *Scapania-Nardia* community on Yakobi Island. Photo by Andy Tasler, through public domain.



Figure 92. *Nardia scalaris* with capsules. Photo by J. C. Schou, with permission.

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 88-Figure 89, Figure 92) its distinctive carrot-like odor (Beike *et al.* 2010).

Bidartondo and Duckett (2010) found that *Nardia scalaris* (Figure 88-Figure 89, Figure 92) predominantly and consistently associates with the *Sebacina vermifer* species complex (see Figure 147). An unusual find was that the DNA sequence of the fungus on this liverwort was identical to that on *Lophozia ventricosa* (Figure 93) at Ben Wyvis, Scotland. The only other shared DNA found in their study was for this fungus species on both *Nardia scalaris* and *Schizochilopsis 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?



Figure 93. *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 94-Figure 97)

Harpanthus flotovianus (Figure 94-Figure 97) occurs in Europe, Asia, and North America (ITIS 2020e), where it is widespread in boreal and montane regions.

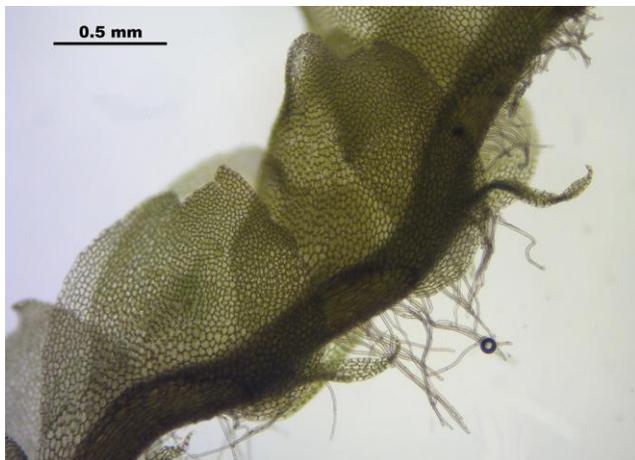


Figure 94. *Harpanthus flotovianus*, a widespread boreal-montane species, occurring in streams, springs, lakes, their banks, and other wet habitats. Photo by Hermann Schachner, through Creative Commons.



Figure 95. *Harpanthus flotovianus*. Photo by Hermann Schachner, through Creative Commons.



Figure 96. *Harpanthus flotovianus*. Photo by Štěpán Koval, with permission.



Figure 97. *Harpanthus flotovianus* showing its mat growth. Photo by Hermann Schachner, through Creative Commons.

In early records, *Harpanthus flotovianus* (Figure 94-Figure 97) 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 98) (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 98. *Harpanthus flotovianus* habitat in a wet spruce opening. Photo by Scot Loring, through Creative Commons.

In Estonia, *Harpanthus flotovianus* (Figure 94-Figure 97) occurs in fens, transitional mires, and bogs (Figure 99) (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 41-Figure 43), *Pohlia sphagnicola* (Figure 100), *Cephaloziella spinigera* (Figure 101), and *Kurzia makinoana* (Figure 102).



Figure 99. Peatland habitat suitable for *Harpanthus flotovianus* and associated *Pohlia sphagnicola*. Photo by Michael Lüth, with permission.



Figure 100. *Pohlia sphagnicola*, often an associate of *Harpanthus flotovianus* in bogs and poor fens. Photo by Michael Lüth, with permission.



Figure 101. *Cephaloziella spinigera* autoicous shoot, an associate of *Harpanthus flotovianus* in bogs and poor fens. Photo by David Wagner, with permission.



Figure 102. *Kurzia makinoana*, an associate of *Harpanthus flotovianus* in bogs and poor fens. Photo by Blanka Aguero, with permission.

Fertile plants are unknown in the Pacific Northwest (Schofield 2002) and are rare in the British Isles (Paton 1999). 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.

Wang and Qiu (2006) found no records of any associated mycorrhizal fungus with this species.

Hygrobiiellaceae

Hygrobiiella laxifolia (Figure 103)

Hygrobiiella laxifolia (Figure 103) 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 *Hygrobiiella intermedia* and *Hygrobiiella squamosa*. These two species and *Hygrobiiella 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.



Figure 103. *Hygrobiella laxifolia*, a Northern Hemisphere species of stream banks. Photo by Martine Lapointe, with permission.

Under the name of *Hygrobiella laxifolia* (Figure 103), 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 103). It grew on rocks in the spray zone of the stream margins where it was associated with other bryophytes.

Jungermanniaceae

Eremonotus myriocarpus (Figure 104-Figure 107)

Eremonotus myriocarpus (Figure 104-Figure 107) 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 104. *Eremonotus myriocarpus*, a rather rare Arctic-alpine species in the Northern Hemisphere, where it is occasionally submerged. Photo by Kristian Peters, with permission.



Figure 105. *Eremonotus myriocarpus* showing a green mat form. Photo by Kristian Peters, with permission.

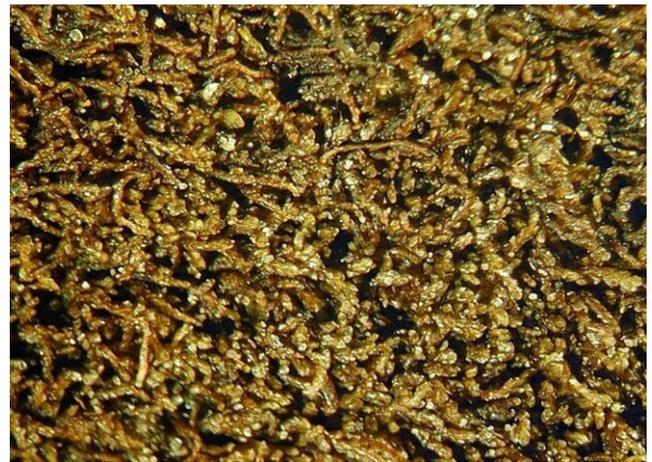


Figure 106. *Eremonotus myriocarpus* showing a color variant, perhaps in response to high light intensity. Photo by Michael Lüth, with permission.

Watson (1919) considered this to be a subalpine species that is occasionally submerged (Figure 107). Long (1982) reported it from a damp rock face.



Figure 107. *Eremonotus myriocarpus* habitat. Photo by Michael Lüth, with permission.

Fungi seem to find this to be a suitable habitat. However, Bidartondo and Duckett (2010) found only Ascomycetes in the usually basidiomycete-containing *Eremonotus myriocarpus* (Figure 104-Figure 107) from locations in Europe.

***Jungermannia* (Figure 108-Figure 109, Figure 111-Figure 114, Figure 116-Figure 118, Figure 121-Figure 124)**

Jungermannia (Figure 108-Figure 109, Figure 111-Figure 114, Figure 116-Figure 118, Figure 121-Figure 124) vs. *Solenostoma* (Figure 148-Figure 151, Figure 155-Figure 160, Figure 164-Figure 167) – 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 108-Figure 109, Figure 111)**

Jungermannia atrovirens (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*; Figure 108-Figure 109, Figure 111) is listed by ITIS (2020g) for Europe, Asia, Africa, and North America.



Figure 108. *Jungermannia atrovirens*, a relatively widespread, predominantly Northern Hemisphere species submerged in streams and lakes. Photo by Hermann Schachner, through Creative Commons.

Jungermannia atrovirens (Figure 108-Figure 109, Figure 111) 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 109) 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 65)-*Fontinalis antipyretica* (Figure 66) 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 109. *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 58) or *Chiloscyphus polyanthus* (Figure 110).



Figure 110. *Chiloscyphus polyanthus*, a frequent species in siliceous mountain brooks where *Jungermannia atrovirens* is able to grow. Photo by Hermann Schachner, through Creative Commons.

Although the species is dioicous, males and females (Figure 111) are typically both abundant (BBS 2020), reducing the disadvantage of separate sexes.



Figure 111. *Jungermannia atrovirens* with abundant perigynia. Photo by Hugues Tinguy, with permission.

Jungermannia borealis (Figure 112)

The distribution of *Jungermannia borealis* (Figure 112) 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 112. *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.

Jungermannia borealis (Figure 112) 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.

Like most leafy liverworts, this species is dioicous (Figure 112) (Damsholt & Vána 1977).

Wang and Qiu (2006) found no records of fungi associated with this species.

Jungermannia callithrix (Figure 113)

Jungermannia callithrix (Figure 113) (syn. = *Solenostoma callithrix*) is primarily Neotropical (Schumaker & Vána 1999), but is known off the coast of Africa (Luis *et al.* 2015).



Figure 113. *Jungermannia callithrix*, a mostly Neotropical species from narrow mountain streams. Photo by Tomas Hallingbäck, with permission.

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 114)

Jungermannia exsertifolia (Figure 114) 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 116-Figure 121), 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 108-Figure 109, Figure 111) as well as failure to recognize it as a subspecies in some European records (Zubel 2008).



Figure 114. *Jungermannia exsertifolia* is a widely distributed Holarctic species, primarily in cold-water streams. Photo by Paul Bowyer, through Creative Commons.

Koponen *et al.* (1995) considered *Jungermannia exsertifolia* (Figure 114) 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).

Jensen *et al.* (2008) found that *Jungermannia exsertifolia* (Figure 114) was among the first liverworts that showed good dose-dependent activity against the malaria parasite *Plasmodium falciparum* (Figure 115). It is interesting that these liverworts were collected from Iceland where malaria is unknown.

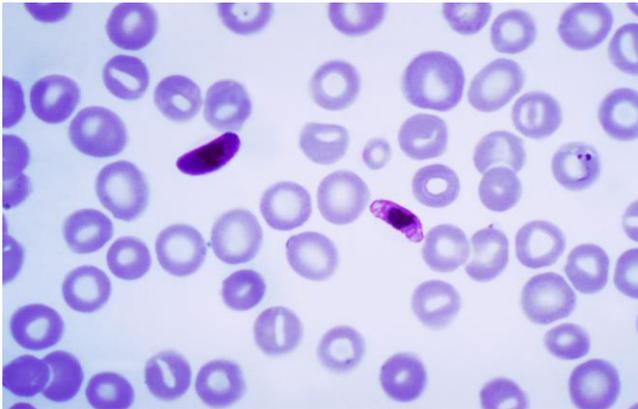


Figure 115. *Plasmodium falciparum* macro and microgametocyte. Photo from CDC - Dr. Mae Melvin Transwiki, through public domain.

Jungermannia exsertifolia subsp. *cordifolia* (Figure 116-Figure 118, Figure 121)

Jungermannia exsertifolia subsp. *cordifolia* (Figure 116-Figure 118, Figure 121) (syn. = *Aplozia cordifolia*; *Jungermannia cordifolia*; *Jungermannia eucordifolia*; *Solenostoma cordifolia*) occurs in Europe, Asia, and North America (ITIS 2020i) where it is sub-Arctic-boreal-subalpine in its distribution (Zubel 2008).



Figure 116. *Jungermannia exsertifolia* subsp. *cordifolia*, a sub-Arctic-boreal-subalpine species of fast water. Photo by Des Callaghan, with permission.



Figure 117. *Jungermannia exsertifolia* subsp. *cordifolia* from a wet habitat. Photo by Des Callaghan, with permission.

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 118). 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, Marstaller (1987) found it in the *Platyhypnidium* (Figure 65)-*Fontinalis antipyretica* (Figure 66) association – a stream association.



Figure 118. *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 116-Figure 118, Figure 121) proved to be very sensitive to pollution events; *Fontinalis antipyretica* (Figure 66) was more tolerant. This research team (Martínez-Abaigar *et al.* 2002) also found that this subspecies accumulated P and 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.

Jungermannia exsertifolia subsp. *cordifolia* (Figure 116-Figure 118, Figure 121) 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 116-Figure 118, Figure 121) 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 116-Figure 118, Figure 121). 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 116-Figure 118, Figure 121) and *Fontinalis antipyretica* (Figure 66) 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 116-Figure 118, Figure 121) acclimates to UV radiation intensity. Its response differences between sun and shade plants were moderate compared to those of *Marchantia polymorpha* (Figure 119-Figure 120), but greater than those of *Fontinalis antipyretica* (Figure 66).



Figure 119. *Marchantia polymorpha* gemmae cups on a wet population. Photo by Rudolf Macek, with permission.



Figure 120. *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 116-Figure 118, Figure 121) 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 116-Figure 118, Figure 121). However, some pigments were affected negatively. UV-B protective compounds rarely increased (Figure 121). They attributed these muted responses to acclimation at their field altitudes of 1850-2000 m asl.



Figure 121. *Jungermannia exsertifolia* subsp. *cordifolia* on rock at edge of stream, emergent and underwater. Photo by Dick Haaksmas, 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 116-Figure 118, Figure 121). 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 116-Figure 118, Figure 121) 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 116-Figure 118, Figure 121). 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 116-Figure 118, Figure 121) 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 116-Figure 118, Figure 121) 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 116-Figure 118, Figure 121). 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 116-Figure 118, Figure 121). 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-ferulic 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 116-Figure 118, Figure 121). 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.

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 116-Figure 118, Figure 121). 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 122-Figure 124)**

Jungermannia pumila (syn. = *Aplozia pumila*, *Jamesoniella ruttneri*, *Solenostoma pumila*; Figure 122-Figure 124) is distributed in Europe, Asia, and North America (ITIS 2020j).



Figure 122. *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 123. *Jungermannia pumila*. Photo by Rambryo, through Creative Commons.



Figure 124. *Jungermannia pumila* forming a mat. Photo by Rambryo, through Creative Commons.

Watson (1919) attributed *Jungermannia pumila* (Figure 122-Figure 124) 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 65)-*Fontinalis antipyretica* (Figure 66) 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 122-Figure 124) 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).

Jungermannia quadridigitata

Jungermannia quadridigitata (syn. = *Lepidozia setacea*, *Microlepidozia setacea*) 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.

The species is not a true aquatic, but occurs in moist hollows between *Sphagnum* hummocks (Figure 125) 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 125. 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 126-Figure 128, Figure 130)

Mesoptychia badensis (syn. = *Lophozia badensis*; Figure 126-Figure 128, Figure 130) 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 126. *Mesoptychia badensis*, a species widely distributed in the Northern Hemisphere in calcareous habitats, including streams and rivers. Photo by Hugues Tinguy, with permission.



Figure 127. *Mesoptychia badensis*. Photo by Štěpán Koval, with permission.

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 129) association (de Sloover & Goossens 1984). Bakalin *et al.* (2019) 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 128. *Mesoptychia badensis*. Photo by Štěpán Koval, with permission.



Figure 129. *Cratoneuron filicinum*; *Mesoptychia badensis* occurs in association with *Cratoneuron* in the travertine. Photo by Barry Stewart, with permission.

The species is dioicous, but at least sometimes produces capsules (Figure 130). 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 130. *Mesoptychia badensis* with capsules, despite being dioicous. Photo by Štěpán Koval, with permission.

Mesoptychia bantriensis (Figure 131-Figure 133)

Mesoptychia bantriensis (Figure 131-Figure 133) (syn. = *Leiocolea bantriensis*) occurs in Europe, Asia, and North America (Bakalin 2018). Hodgetts (2015) listed it specifically from Norway, Sweden, United Kingdom, and Italy in Europe.

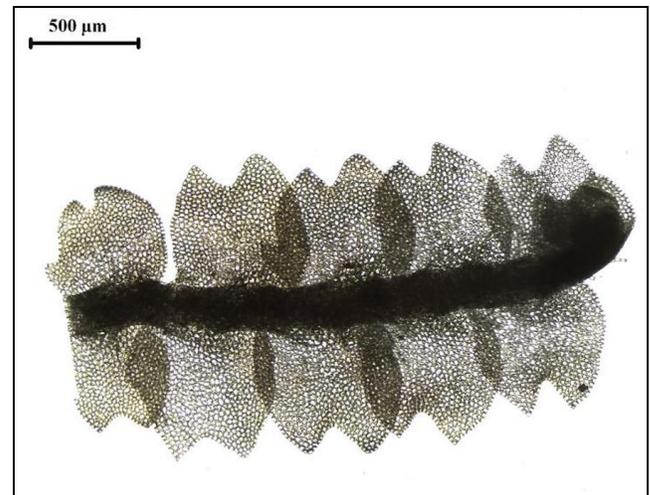


Figure 131. *Mesoptychia bantriensis*, a Northern Hemisphere liverwort of streams, rivers, lakes, and their banks, as well as mires and moist tundra. Photo by Hugues Tinguy, with permission.



Figure 132. *Mesoptychia bantriensis* showing growth habit. Photo by Štěpán Koval, with permission.

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 133).



Figure 133. *Mesoptychia bantriensis* showing mat formation. Photo by Barry Stewart, with permission.

Mesoptychia collaris (Figure 134)

Mesoptychia collaris (Figure 134) (syn. = *Leiocolea collaris*, *Lophozia muelleri*) occurs in Europe, Asia, Africa, and North America (ITIS 2019).



Figure 134. *Mesoptychia collaris*, a Northern Hemisphere species that is hemicalciphilous in cold streams and seepage areas. Photo by Hermann Schachner, through Creative Commons.

This species 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 65)-*Fontinalis antipyretica* (Figure 66) 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.

Mesoptychia gillmanii (Figure 135)

Mesoptychia gillmanii (syn. = *Leiocolea gillmanii*; Figure 135) is widespread around the northern hemisphere in boreal and montane regions, although it is considered vulnerable in Europe (Hodgetts *et al.*).

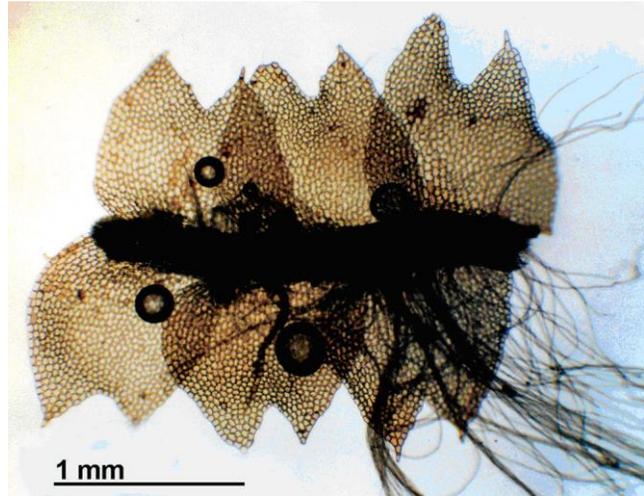


Figure 135. *Mesoptychia gillmanii*, a species from boreal and montane regions of the northern hemisphere. It is a calciphile in streams, on peaty soil, and on cliffs and ledges. Photo by David Wagner, with permission.

In Finland, *Mesoptychia gillmanii* (Figure 135) 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.

Mesoptychia gillmanii (Figure 135) 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).

Mesoptychia turbinata (Figure 136-Figure 137)

Mesoptychia turbinata (syn. = *Lophozia turbinata*; Figure 136-Figure 137) is apparently restricted to the Mediterranean area of Europe and North Africa (Schuster 1969).

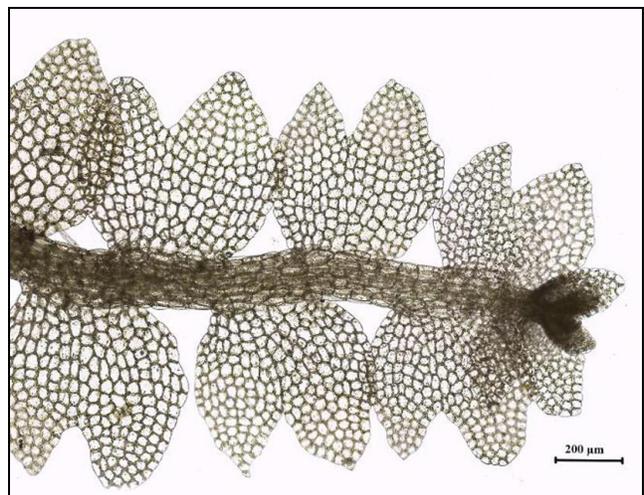


Figure 136. *Mesoptychia turbinata*. Photo by Hugues Tinguy, with permission.



Figure 137. *Mesoptychia turbinata* showing the extensive mats that are possible. Photo by Hugues Tinguy, with permission.

Watson (1919) considered *Mesoptychia turbinata* (Figure 136-Figure 137) 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.

Notoscyphaceae

Notoscyphus lutescens (Figure 138)

Notoscyphus lutescens (syn. = *Notoscyphus paroicus*; Figure 138) 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 138. *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.

Ruttner (1955) reported this 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>.

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* and two strains of *Staphylococcus aureus*. 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.

Saccogynaceae

Saccogyna viticulosa (Figure 139-Figure 141)

Saccogyna viticulosa (Figure 139-Figure 141) 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 139. *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 140. *Saccogyna viticulosa* with branches in a semi-upright position. Photo by Dick Haaksma, with permission.



Figure 141. *Saccogyna viticulosa* forming a mat. Photo by Dick Haaksma, with permission.

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 139-Figure 141) 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 142), *Fissidens polyphyllus* (Figure 84), *Hyocomium armoricum* (Figure 143-Figure 144), *Plagiothecium nemorale* (Figure 145), and *Riccardia multifida* (Figure 146) 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 142. *Pellia epiphylla* showing an associated leafy liverwort. Photo by Jan-Peter Frahm, with permission.



Figure 143. *Hyocomium armoricum* habitat such as those where we might find *Saccogyna viticulosa* in association. Photo by Dick Haaksma, with permission.



Figure 144. *Hyocomium armoricum*, sometimes an associate of *Saccogyna viticulosa*. Photo by Michael Lüth, with permission.



Figure 145. *Plagiothecium nemorale*, sometimes an associate of *Saccogyna viticulosa*. Photo by Hermann Schachner, through Creative Commons.



Figure 146. *Riccardia multifida* showing its habitat with a leafy liverwort on the right. Photo by Rick Ballard, through Creative Commons.

One reason for the scarcity of this species 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).

In northwestern Portugal, *Saccogyna viticulosa* (Figure 139-Figure 141) 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 139-Figure 141) lives in niches with the lowest irradiance and least severe desiccation, especially avoiding direct summer sun.

Wang and Qiu (2006) reported fungal associations with this species. *Saccogyna viticulosa* (Figure 139-Figure 141) is known to host the fungus *Sebacina* (Figure 147) (Bidartondo & Duckett 2010). It produces numerous hyphae associated with the branched rhizoid apex. Döbbeler (2011) found that the **Ascomycete** fungus *Octospora fortunata* 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 147. *Sebacina incrustans*, in a genus that is known from *Saccogyna viticulosa*, shown here on a moss. Photo through Creative Commons.

Several biochemical studies have revealed the array of secondary compounds in *Saccogyna viticulosa* (Figure 139-Figure 141). 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 148-Figure 151, Figure 155-Figure 160, Figure 164-Figure 167)

Solenostoma (Figure 148-Figure 151, Figure 155-Figure 160, Figure 164-Figure 167) has **psychrorithral** (cold upper stream reaches) species in European alpine streams (Geissler 1975).

Solenostoma ariadne

Solenostoma ariadne (syn. = *Nardia ariadne*) is known from India and China. Ruttner (1955) reported it as a wetland/aquatic species from the tropics.

Solenostoma gracillimum (Figure 148-Figure 151)

Solenostoma gracillimum (syn. = *Jungermannia gracillima* fo. *crenulata*, *Solenostoma crenulatum*; Figure 148-Figure 151) is known from Europe, Asia, Africa, North America, and South America (ITIS 2020I).



Figure 148. *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 149. *Solenostoma gracillimum* showing its growth habit. Photo by David T. Holyoak, with permission.

Most of the wet habitat reports are relatively recent. Bley (1987) reported *Solenostoma gracillimum* (Figure 148-Figure 151) 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 150) when exposed to the sun (Breil 1970).



Figure 150. *Solenostoma gracillimum* showing red coloration often seen with sun exposure. Photo by Barry Stewart, with permission.

The species is dioicous (Figure 151) (Breil 1970), but has a widespread distribution that suggests that at least some spores have dispersed. It does not produce gemmae (Bakalin 2012).



Figure 151. *Solenostoma gracillimum* with numerous perianths. Photo by David T. Holyoak, with permission.

This 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 148-Figure 151) 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 152), along with *Pohlia cruda* (Figure 153) and *Schizothrix* sp. (Figure 154) (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 152. Anglesite, a rock type that can precipitate onto bryophytes. Photo by Parent Géry, through Creative Commons.



Figure 153. *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.

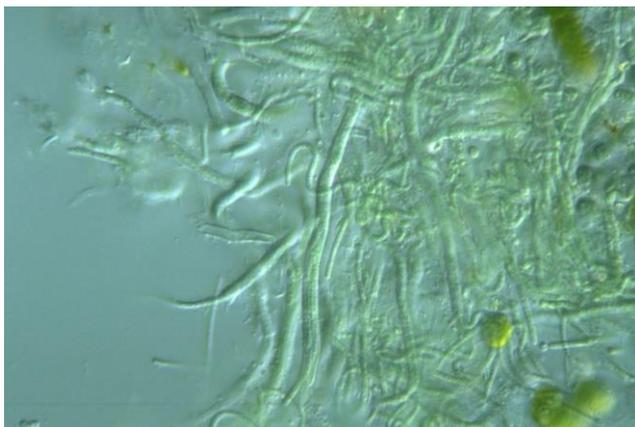


Figure 154. *Schizothrix* sp., member of a genus that occurs with *Solenostoma gracillimum* in areas with high levels of zinc. Photo by Yuuki Tsukii, with permission.

This species is one of the hosts of the fungus *Mniaecia jungermanniae* (Figure 25-Figure 27) (Egertová *et al.* 2016). Pressel and Duckett (2006) found that it infected some liverwort species, but not others.

***Solenostoma hyalinum* (Figure 155-Figure 157)**

Solenostoma hyalinum (syn. = *Eucalyx hyalina*, *Jungermannia hyalina*; Figure 155-Figure 157) 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.

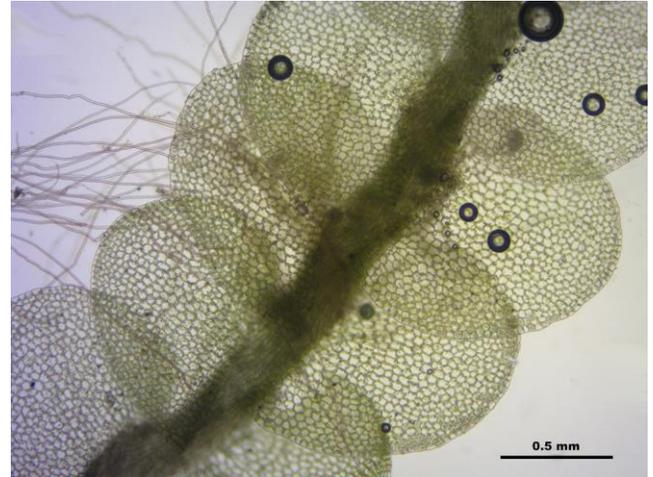


Figure 155. *Solenostoma hyalinum*, a Northern Hemisphere species that lives where it is constantly wet or submerged. Photo by Hermann Schachner, through Creative Commons.



Figure 156. *Solenostoma hyalinum*, a Northern Hemisphere species that lives where it is constantly wet or submerged. Photo by Hermann Schachner, through Creative Commons.

This species 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 it 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 58), *Hyocomium armoricum* (Figure 143-Figure 144), *Fissidens polyphyllus* (Figure 84), and *Platyhypnidium lusitanicum* (Figure 85), 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.

In northwest Portugal, it has only been found sterile in pure or mixed well-developed patches (Vieira *et al.* 2004). Nevertheless, it can produce capsules (Figure 157) when both genders are present.



Figure 157. *Solenostoma hyalinum* with a capsule, indicating that some populations can successfully reproduce sexually. Photo by Michael Lüth, with permission.

This species is one of the known hosts for the Ascomycete fungus *Mniaecia jungermanniae* (Figure 25-Figure 27) (Egertová *et al.* 2016). The exact relationship needs to be explored.

Solenostoma javanicum

Solenostoma javanicum (syn. = *Aplozia javanica*) 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 158)

Solenostoma obovatum (syn. = *Eucalyx obovata*, *Eucalyx obovata* fo. *elegatus*, *Eucalyx obovata* fo. *laxus*, *Eucalyx obovata* var. *rivularis*, *Jungermannia obovata*, *Nardia obovata*, *Plectocolea obovata*; Figure 158) occurs sparingly in the Arctic, then southward in the mountains of Europe and North America (Schuster 1969).



Figure 158. *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.

An early report by Nichols (1918) attributed *Solenostoma obovatum* (Figure 158) 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 65)-*Fontinalis antipyretica* (Figure 66) 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.

Solenostoma sphaerocarpum (Figure 159-Figure 160, Figure 164)

Solenostoma sphaerocarpum (syn. = *Aplozia sphaerocarpa*, *Haplozia sphaerocarpa*, *Jungermannia sphaerocarpa*; Figure 159-Figure 160, Figure 164) occurs across Siberia and is known from Japan (Váňa *et al.* 2013). ITIS (2020n) lists Europe, Asia, Africa, Oceania, Australia, North America from Alaska to Mexico, and South America.



Figure 159. *Solenostoma sphaerocarpum*, a worldwide species from streams and rivers and their banks. Photo by Hugues Tinguy, with permission.



Figure 160. *Solenostoma sphaerocarpum* showing its matted growth habit. Photo by Hugues Tinguy, with permission.

Szweykowski (1951) reported *Solenostoma sphaerocarpum* (Figure 159-Figure 160, Figure 164) 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 161), *Mesoptychia heterocolpos* (Figure 162), *Tritomaria scitula*, and *Lophozipsis excisa* (Figure 163) 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 65)-*Fontinalis antipyretica* (Figure 66) 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 161. *Blepharostoma trichophyllum*, an associate of *Solenostoma sphaerocarpum* on stream banks. Photo by Jan-Peter Frahm, with permission.



Figure 162. *Mesoptychia heterocolpos*, an associate of *Solenostoma sphaerocarpum* on stream banks. Photo by Jan-Peter Frahm, with permission.



Figure 163. *Lophozipsis excisa*, an associate of *Solenostoma sphaerocarpum* on stream banks. Photo by Štěpán Koval, with permission.

Solenostoma sphaerocarpum (Figure 159-Figure 160, Figure 164) is very **polymorphous** (expressing multiple forms). It becomes red-colored in exposed situations (Váňa *et al.* 2013). It is **heteroicous** (male & female organs on same plant; Figure 164), 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 164. *Solenostoma sphaerocarpum* with perigynia visible. Photo by Hugues Tinguy, with permission.

Solenostoma stephanii

Solenostoma stephanii (syn. = *Aplozia stephanii*) occurs in Australia, Oceania, and southern Asia (ITIS 2020o).

Ruttner (1955) reported it as submersed in the littoral zone in the tropics.

Solenostoma tetragonum

Solenostoma tetragonum (syn. = *Nardia tetragona*) is known from Australia, Oceania, and southern Asia (ITIS 2020p).

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 165)**

Solenostoma truncatum (Figure 165) (syn. = *Nardia truncata*) 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 165. *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.

Ruttner (1955) reported *Solenostoma truncatum* (Figure 165) 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 166-Figure 167)**

Solenostoma vulcanicola (syn. = *Jungermannia vulcanicola*, *Nardia vulcanica*; Figure 166-Figure 167) has a relatively small distribution in Indonesia, Japan, and India (Singh & Singh 2015).



Figure 166. *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 167. *Solenostoma vulcanicola* showing dense clumps from an acid spring in Japan. Photo by Juuyoh Tanaka, through Creative Commons.

In 1955, Ruttner listed this species 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 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 166) 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 166-Figure 167), 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 166-Figure 167) 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 166-Figure 167) from a stream (Figure 1) at *pH* 4.2-4.6. Satake *et al.* (1983; 1984) found the highest mercury content (12,100 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 166) 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.

Summary

The **Jungermanniineae** 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 **Jungermanniineae** 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.

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