Glime, J. M. 2021. Aquatic and Wet Marchantiophyta, Order Jungermanniales: Lophocoleineae, Part 2, Myliineae, Perssoniellineae. Chapt. 1-6. In: Glime, J. M. Bryophyte Ecology. Volume 4. Habitat and Role. Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 28 December 2021 and available at <http://digitalcommons.mtu.edu/bryophyte-ecology/>.

CHAPTER 1-6
AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES: LOPHOCOLEINEAE, PART 2, MYLIINEAE, PERSSONIELLINEAE

TABLE OF CONTENTS

CHAPTER 1-6
AQUATIC AND WET MARCHANTIOPHYTA, ORDER JUNGERMANNIALES – LOPHOCOLEINEAE, PART 2, MYLIINEAE, PERSSONIELLINEAE

Figure 1. ***Plagiochila porelloides*** by stream, where it is overgrowing a patch of ***Pellia***. Photo by Štěpán Koval, with permission.

Suborder Lophocoleineae, cont.

Plagiochilaceae

Pedinophyllum interruptum (Figure 2-Figure 4)

Distribution

Pedinophyllum interruptum (Figure 2-Figure 4) is a Northern Hemisphere species, best known from Europe, but also with scattered records in North American and Japan (GBIF 2020). De Miguel and Indurain (1984) considered it to be circumboreal. Martinez-Abaigar and Ederra (1992) reported it from Spain and Sotiaux and Vanderpoorten (2017) from nearby Andora. There are records from Belgium (Sotiaux *et al*. 2007), Albania, where it was removed from the red list (Marka *et al*. 2012), and Iran (Frey & Kürschner 1983). It is relatively abundant in Croatia (Pandža & Milović 2015).

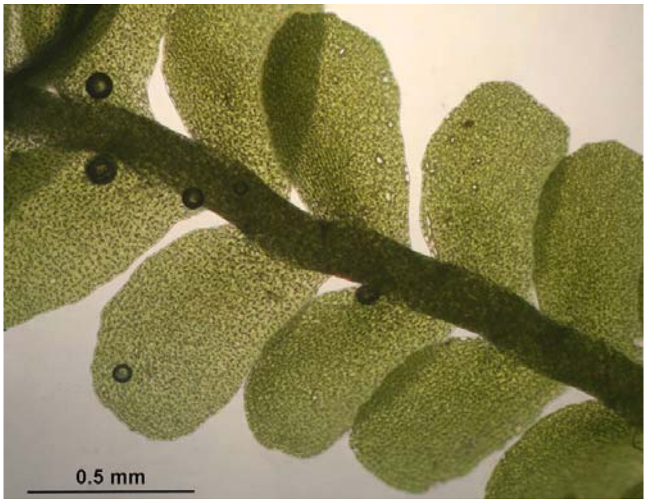

Figure 2. ***Pedinophyllum interruptum*** branch, a circumboreal species, occurring south into Europe, China, and Iran. Photo by Hermann Schachner, through Creative Commons.

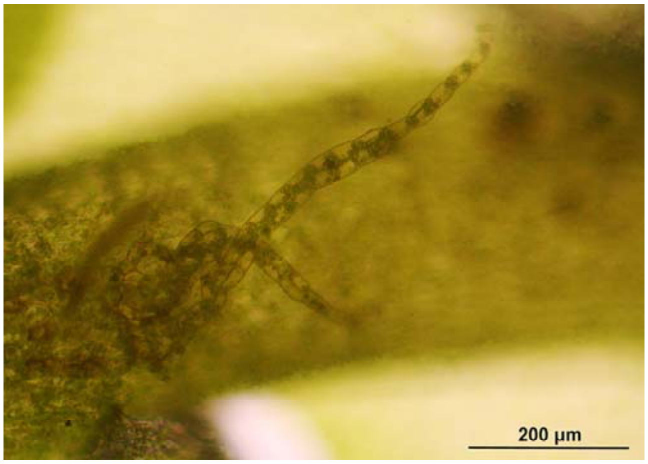

Figure 3. ***Pedinophyllum interruptum*** underleaf. Photo by Hermann Schachner, through Creative Commons.

Figure 4. ***Pedinophyllum interruptum*** forming mats. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Watson (1918) recognized the limestone association of ***Pedinophyllum interruptum*** (Figure 2-Figure 4) in East Somerset, UK. In the Tara River canyon, it occurs on limestone rock and at a spring in the Tara River canyon and the Durmitor area, Montenegro (Papp & Erzberger 2011). In the UK, it typically grows on or near Carboniferous or metamorphic limestone, occupying both rock and soil, or in wooded gorges or other very humid, sheltered upland sites (BBS 2020). It tolerates both open, bare limestone rock and deep shade. It likewise occupies shaded limestone in Croatia (Alegro *et al.* 2014), Macedonia (Papp *et al.* 2016), and Greece (Papp & Tsakiri 2017). Gerdol *et al.* (1991) found it to be frequent in moist carbonatic rocky habitats in the southern Italian Alps. De Miguel and Indurain (1984) considered it a saxicolous calcicole in La Foz de Arbayún, Spain.

Chytrý and Tichý (2003) termed the species **chasmophytic** (referring to plant growing in crevices of rocks) on shaded calcareous cliffs of the Czech Republic. In Bulgaria, Gecheva and Yurukova (2013) found it downstream from a karst spring. Veljié *et al.* (2001 similarly found it at well springs in a karst area of Serbia. Liu *et al.* (2019) found that it was rare outside karst sinkholes in Guizhou Province, Southwestern China, but could be found at the bottom of the sinkholes, a location they considered more suitable because of the greater presence of water and nutrition.

Pedinophyllum interruptum (Figure 2-Figure 4) occurs in Iskur River, Bulgaria, and its main tributaries (Papp *et al.* 2006). Choi *et al.* (2010) found it near streams or at the top of ridges on Mt. Deogyu in Korea. Tacchi *et al.* (2009) on rocks in ravines in the Apennines. In Thuringia, Germany, Marstaller (1987) found that ***Pedinophyllum interruptum*** occurs in streams with the ***Platyhypnidium*** (Figure 5) – ***Fontinalis antipyretica*** (Figure 6) association. But Frahm (1987) also found it in moist, shaded forests in Germany. In the UK, Preston *et al.* (2011) found that it is frequently associated with ***Scapania undulata*** (Figure 7).

Figure 5. ***Platyhypnidium riparioides***, often an indicator of suitable habit for ***Pedinophyllum interruptum***. Photo by Hermann Schachner, through Creative Commons.

Figure 6. ***Fontinalis antipyretica*** in Indian River, often an indicator of suitable habit for ***Pedinophyllum interruptum***. Photo by Matt Goff <www.sitkanature.org>, with permission.

Figure 7. ***Scapania undulata***, a species often associated with ***Pedinophyllum interruptum***. Photo by Hugues Tinguy, with permission.

In North America, ***Pedinophyllum interruptum*** (Figure 2-Figure 4) was found on dolomite rocks in a ravine in Brookfield, Connecticut, USA (Evans 1910). It is also known from Greenland, Labrador, a few additional locations in Canada, and Ohio, USA.

Reproduction

Pedinophyllum interruptum (Figure 2-Figure 4) is **monoicous** (Rycroft 2021).

Fungal Interactions

Bidartondo and Duckett (2010) examined 30 bryophyte species, represented by a total of 200 collections. Among these, only four species failed to present any fungal DNA sequences. One of these was ***Pedinophyllum interruptum*** (Figure 2-Figure 4). Perhaps ***Pedinophyllum interruptum*** is able to inhibit fungal growth through its extensive array of secondary compounds. Wang and Qiu (2006) likewise were unable to find any reference to a mycorrhizal relationship in this species.

But the species is not totally fungus free. Döbbeler (1998) reported ***Epibryon pedinophylli*** (see Figure 8) as a leaf-perforating ascomycete from ***Pedinophyllum interruptum*** (Figure 2-Figure 4). However, this fungus might not occur on aquatic populations (Peter Döbbeler, pers. comm. 8 September 2020).

Figure 8. ***Epibryon*** perithecia (arrows) on ***Sphagnum*** and surrounded by ***Botryococcus***. ***Epibryon pedinophylli*** is only known from ***Pedinophyllum interruptum***. Photo through Creative Commons.

Biochemistry

Pedinophyllum interruptum has oil bodies (Figure 9), where we might expect to find some of its secondary compounds. Feld *et al*. (2004) identified several secondary compounds in ***Pedinophyllum interruptum*** from Scotland. Liu *et al*. (2013) elucidated the structures of ten diterpenoids in Chinese populations of ***Pedinophyllum interruptum***. Seven of the pedinophyllols in this species inhibited seed germination and root growth of ***Arabidopsis thaliana*** (Figure 10) with a dose-dependent response (Wei *et al*. 2019). Do such compounds provide ***Pedinophyllum interruptum*** with a means to compete in its limestone habitats?

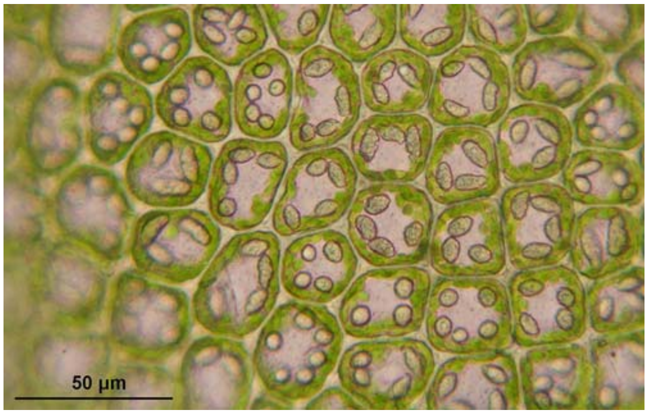

Figure 9. ***Pedinophyllum interruptum*** leaf cells showing oil bodies, a location of secondary compounds. Photo by Hermann Schachner, through Creative Commons.

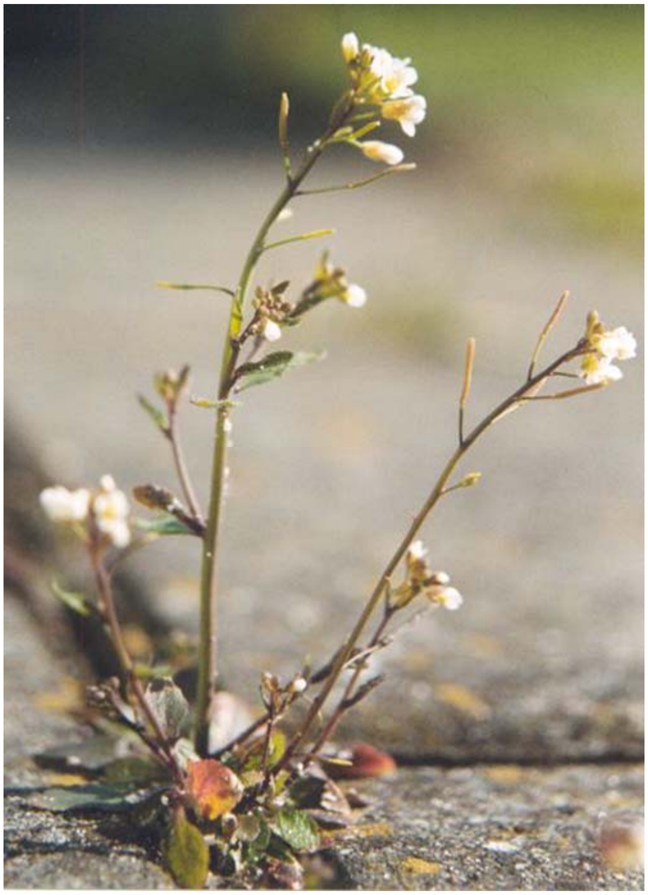

Figure 10. ***Arabidopsis thaliana***, a species for which root growth is inhibited by extracts from ***Pedinophyllum interruptum***. Photo through Creative Commons.

Plagiochila

The genus ***Plagiochila*** includes rheophytes in the wet tropics of SE Asia (Akiyama 1992) and west Africa (Shevock *et al*. 2017).

Other general characteristics of the genus include the documentation of surface wax in the family, including ***Plagiochilion mayebarae*** and five species of ***Plagiochila*** (Heinrichs *et al*. 2000). These waxes were previously unknown in the family and cannot be detected with a light microscope. I am aware of no evidence if these are present in aquatic populations, but it would be interesting to compare them in aquatic and terrestrial populations and through moisture gradients of streambank populations.

Plagiochila asplenioides (Figure 11, Figure 14)

(syn. = *Plagiochila maior*)

Plagiochila asplenioides (Figure 11, Figure 14) has been plagued by disagreements over the taxonomic level of ***Plagiochila porelloides*** (Figure 12). Schuster (1980) and Damsholt (2002) considered ***Plagiochila porelloides*** to be a subspecies of ***P. asplenioides***. Paton (1999) and Schumacker and Váňa (2000), however, consider them to be two separate species with different habitats. The species ***Plagiochila asplenioides*** *s.s.* is most common on herb-rich forest floors and moist depressions, whereas the closely related ***P. porelloides*** occurs at the bases of silicate boulders and in crevices. This taxonomic confusion creates difficulties in providing accurate descriptions of habitats. Some references attributed here to ***P. asplenioides*** might actually be for ***P. porelloides*** in areas where both species occur.

Figure 11. ***Plagiochila asplenioides*** ventral side. Photo by Ralf Wagner, with permission.

Figure 12. ***Plagiochila porelloides*** showing the succubous leaf arrangement. Photo by Hugues Tinguy, with permission.

Distribution

Using the two-species concept, in North America, ***Plagiochila asplenioides*** subsp. ***asplenioides*** (Figure 13) occurs only in western North America, on logs, rocks, and bases of trees (Hong 1992). It occurs in Europe (Schumacker & Váňa 2000). Marsh *et al*. (2010) reported it in Finland, Paton (1999) in the British Isles, Diekmann (1995) in Sweden, Pakalne and Čakare (2001) in Latvia, Grüll and Kvét (1976) in the Czech Republic. But in East and South Asia, So and Grolle (2000) specifically exclude this species from the flora based on their examination of herbarium material.

Figure 13. ***Plagiochila asplenioides*** subsp. ***asplenioides***, an endemic in western North America. Photo from Botany Website, UBC, with permission.

Aquatic and Wet Habitats

Typical of ***Plagiochila asplenioides*** (Figure 14), but not ***P. porelloides*** (Figure 12), the former occurs on decaying logs, leaf litter, and humus in Europe (Salachna 2007). Marsh *et al*. (2010) report ***Plagiochila asplenioides*** from herb-rich forest floors and moist depressions in Finland. It can tolerate slightly higher light levels than those in the forest, occurring among the tall turf (Gimingham & Birse 1957).

Figure 14. ***Plagiochila asplenioides***, a species of logs, litter and humus in Europe, but also near streams there. Photo by David T. Holyoak, with permission.

But other reports may represent what I am including as ***Plagiochila porelloides*** (Figure 12): ground, rock, spring, and water communities in or associated with streams near Lacko, Western Carpathians (Mamczarz 1970); not common in River Tweed, UK (Holmes & Whitton 1975a, b); in intermittent rivers (Dhien 1978); in the ***Platyhypnidium*** (Figure 5) – ***Fontinalis antipyretica*** (Figure 6) association, Thuringia, Germany (Marstaller 1987); at a spring in Tara River canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).

Marstaller (2012), in his studies on **epilithic** (rock-dwelling) species, considered ***Plagiochila asplenioides*** (Figure 13-Figure 18) to be **hygrophytic** (referring to plant living in location with high moisture level, but not submersed). Similarly, in Latvia, Pakalne and Čakare (2001) found ***P. asplenioides*** at the foot of river ravine slopes and in forest springs – very wet but not submersed. Baláži *et al*. (2010) termed it a **macrophyte** (easily visible aquatic plant) in the Slovak Republic. Farr *et al*. (2019) report this as a species that occurs on slightly acidic soil of vertical stream banks in the UK at tufa-forming sites. Kelly (1981) found it to be typical of stream banks, but also on limestone rocks in the forest in Killarney, Ireland.

Figure 15. ***Plagiochila asplenioides*** in a forest habitat. Photo by Hermann Schachner, through Creative Commons.

Figure 16. ***Plagiochila asplenioides***, dry, showing a typical growth form on stream banks. Photo from <www.aphotofauna.com>, with permission.

Figure 17. ***Plagiochila asplenioides***, wet, showing a typical growth form on stream banks. Photo from <www.aphotofauna.com>, with permission.

Sotiaux and Vanderpoorten (2017) again separated the two species by habitat, reporting ***Plagiochila asplenioides*** (Figure 15-Figure 17) at 1840 m asl in the montane fir woodland. By comparison, they reported ***Plagiochila porelloides*** (Figure 1, Figure 12, Figure 45) from the sub-Mediterranean to the sub-Alpine belt up to 2250 m asl on montane, base-rich siliceous rocks, shaded, humid montane siliceous rock outcrops, sub-Mediterranean to Alpine siliceous, sometimes base-rich shaded north-facing outcrops, sub-Mediterranean to sub-Alpine limestone outcrops, shaded siliceous boulders in woodlands, base-rich ground along streams, forest floor, and limestone outcrops.

Puczko *et al.* (2018) indicated that ***Plagiochila asplenioides*** (Figure 15-Figure 17) serves as an indicator of good water quality in lowland spring niches. Papastergiadou (1995) reported this species from Greek wetlands.

Cappers *et al.* (1997) reported that fragments of this species were found as part of the caulking material in shipwrecks excavated in The Netherlands, but it was not used in any abundance.

Adaptations

Proctor (1982) examined the water movement in several bryophytes. He found that bryophytes with central strands had a sustained movement of water upward and outward through transpiration, similar to the transpirational movement in tracheophytes. However, in ***Plagiochila asplenioides*** (Figure 15-Figure 17), there is no central strand and this transpirational movement does not occur.

Gupta (1977) described the effects of moisture stress on ***Plagiochila asplenioides*** (Figure 18). He found the highest solute leakage of dried plants to occur in the first two minutes of rewetting, then slowing down. He considered this rapid stoppage to be the result of reassemblage of the membrane structure or to a rapid decrease of the solutes in the injured and dead tissues. The leached solutes are resorbed by the viable cells. This is not different from that found for terrestrial mosses, but may indicate the tools they have to survive in habitats that can dry out for weeks at a time.

Figure 18. ***Plagiochila asplenioides*** dry, but retaining its green color. Photo by J. C. Schou, through Creative Commons.

Reproduction

Plagiochila asplenioides is **dioicous** (Watson 1965), but sporophytes can be found (Figure 19).

Figure 19. ***Plagiochila asplenioides*** with capsules. Photo by Hermann Schachner, through Creative Commons.

Fungal Interactions

Stenroos *et al.* (2010) found that four genera of bryophytes (out of 19 checked) exhibited the highest diversity of fungal associates: ***Plagiochila***, ***Polytrichum***, ***Ptilidium***, and ***Sphagnum***.

Döbbeler (1997) considered the ascomycete fungus ***Epibryon plagiochilae*** (Figure 20-Figure 21) to be specific on ***Plagiochila asplenioides*** (Figure 15-Figure 17) and ***P. porelloides*** (Figure 12). ***Pedinophyllum interruptum*** (Figure 2-Figure 4), in the same family **Plagiochilaceae**, does not get infected by this fungus.

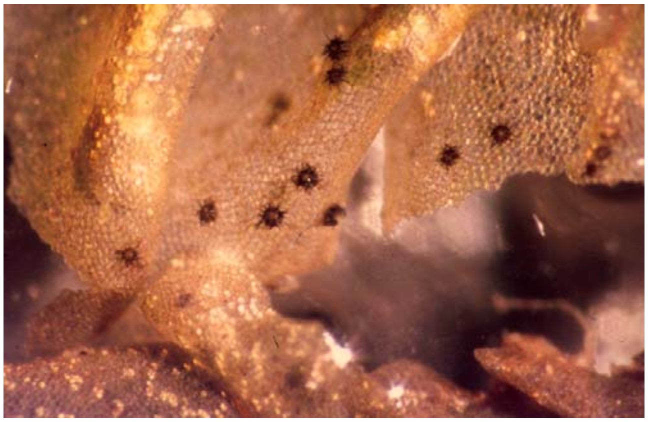

Figure 20. ***Epibryon plagiochilae*** (dark brown spots) on ***Plagiochila asplenioides*** leaves. Photo courtesy of Peter Döbbeler.

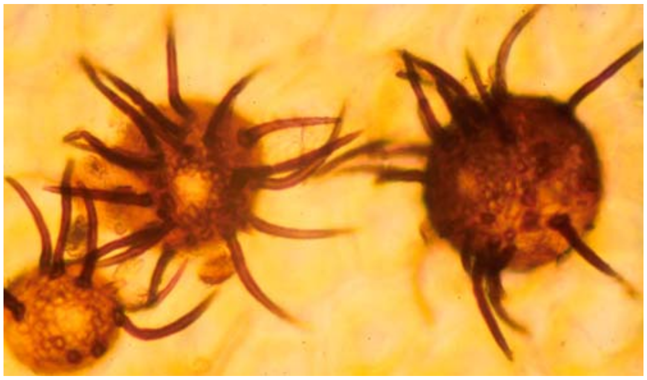

Figure 21. ***Epibryon plagiochilae*** on ***Plagiochila asplenioides*** showing the typical spider-like appearance. Photo courtesy of Peter Döbbeler.

Plagiochila asplenioides (Figure 15-Figure 17) serves as substrate for at least 7 genera and 13 species of fungi (Marsh *et al*. 2010). Out of more than 400 Finnish herbarium specimens of this species and ***P. porelloides*** (Figure 1, Figure 12, Figure 45), about 200 supported bryicolous species of fungi in the ascomycete genera ***Bryomyces*** (Figure 22-Figure 23), ***Dactylospora*** (Figure 24-Figure 25), ***Epibryon*** (Figure 8, Figure 20-Figure 21), ***Lichenopeltella*** (Figure 26), ***Octosporella*** (Figure 27-Figure 29), ***Pleostigma*** (Figure 30), and the **anamorphic** (unnatural grouping of fungi characterized by mitotic rather than meiotic production of spores – conidia) genus ***Epicoccum*** (Figure 31). ***Epibryon plagiochilae*** (Figure 20-Figure 21), a species that is apparently specific to ***P. asplenioides***, ***P. porelloides***, and ***P. britannica*** (Figure 32), shows a strong preference for the dorsal leaf border of its host liverwort, although ascomata can also occur on the stem or on female bracts and perianths. Bosanquet (2007) was delighted to discover ***E. plagiochilae*** on ***Plagiochila asplenioides*** and subsequently on ***P. porelloides*** and ***P. brittanica*** in Wales. In the next two months, he discovered this distinctive fungus on four of twelve colonies of ***P. asplenioides*** he examined and on two of three colonies of ***P. porelloides***. Many specimens of ***P. brittanica*** had the fungus, but the fungus was absent on all specimens of ***Pedinophyllum interruptum*** and all other species of ***Plagiochila***. Could it be that these species have the chemical ability to prevent the infection, or do the other **Plagiochilaceae** in Wales occur in habitats that are unsuitable for the fungus to become established?

Figure 22. ***Bryomyces velenovskyi***, in a genus known from ***Plagiochila asplenioides***, on moss leaves. Photo by George Greiff, with permission.

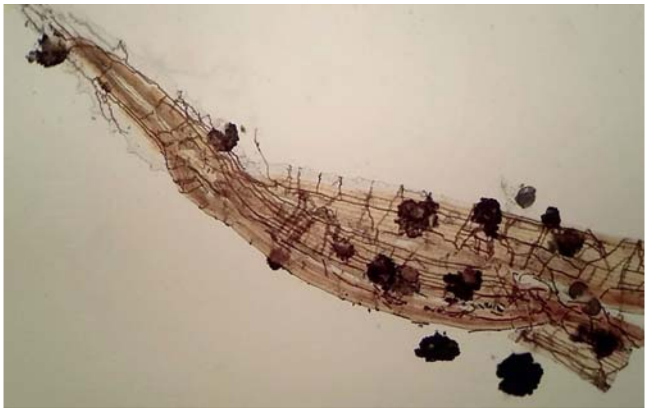

Figure 23. ***Bryomyces microcarpus*** var. ***rhacomitrii*** on moss leaf. Photo by George Greiff, with permission.

Figure 24. ***Dactylospora stygia*** on log; some members of the genus occur on ***Plagiochila asplenioides***. Photo by Milan Macalak, with permission.

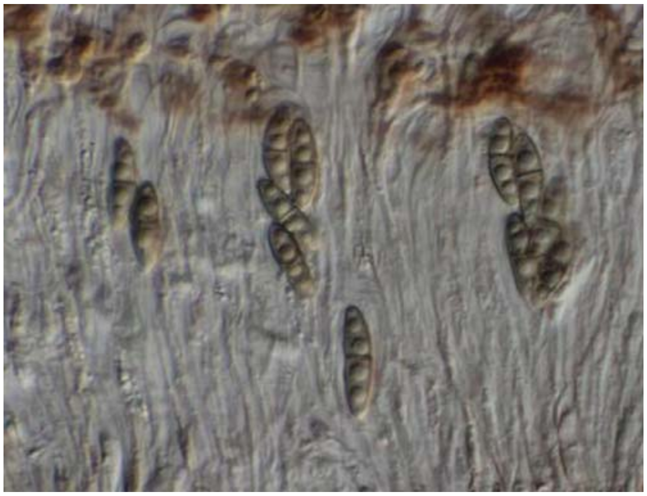

Figure 25. ***Dactylospora stygia*** asci. Photo through Creative Commons.

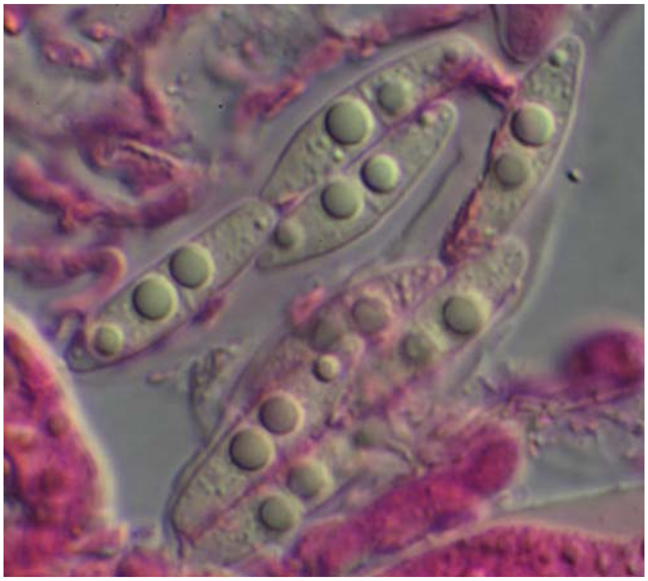

Figure 26. ***Lichenopeltella*** *santessonii* ascospores on dead *Peltigera membranacea*; some members of the genus ***Lichenopeltella*** occur on ***Plagiochila asplenioides*** leaves. Photo through Creative Commons.

Figure 27. ***Octosporella jungermanniarum*** probably, a species that occurs on ***Plagiochila asplenioides***, as shown here. Photo by Barry Stewart, with permission.

Figure 28. ***Octosporella jungermanniarum*** on ***Plagiochila asplenioides***. Photo courtesy of George Greiff.

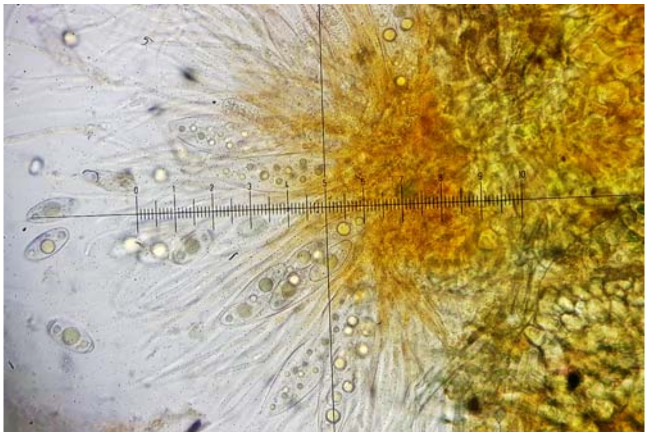

Figure 29. ***Octosporella jungermanniarum*** probably, showing ascospores. Photo by Barry Stewart, with permission.

Figure 30. ***Pleostigma jungermanniarum*** on ***Plagiochila porelloides***. Photo by courtesy of George Greiff.

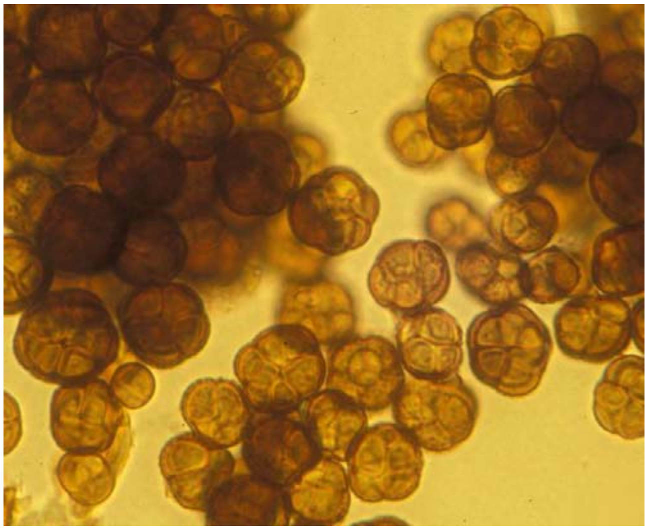

Figure 31. ***Epicoccum nigrum***; some members of this genus occur on ***Plagiochila asplenioides***. Photo by Gerald Holmes, through Creative Commons.

Figure 32. ***Plagiochila britannica***, a species that hosts the fungus ***Epibryon plagiochilae***. Photo by David S. Rycroft, with permission.

Epibryon endocarpum (see Figure 8) is another ascomycete that grows, and in this case fruits, within the cells of ***Plagiochila asplenioides*** (Döbbeler 1980). Among its adaptations is the small size of its ascomata (25-35 µm). In addition to these, George Greiff photographed ***Octosporella jungermanniarum*** (Figure 28), another ascomycete, on ***Plagiochila asplenioides***.

Biochemistry

When Suleiman and Lewis (1980) cultured ***Plagiochila asplenioides*** (Figure 15-Figure 17) in the dark for four months, the leafy plant rapidly lost starch, but little chlorophyll was lost. When revived, the tissues immediately became viable. The principal photosynthetic products were volemitol, sucrose, and starch, but the more abundant carbohydrates (fructans) were not among those most rapidly formed. Rather, conversion to fructans occurs in the prolonged four months of darkness. The starch turnover is rapid, but the volemitol and sucrose have a very slow turnover, even up to four months in the dark. This survival in the dark undoubtedly contributes to the plant's survival in the long winters in some of its more northerly locations.

Ultraviolet radiation can be a problem for bryophytes in exposed habitats. This can include wooded areas that lose the canopy leaves in winter. Whereas submersion in water reduces the effects of light, this species typically does not benefit from that habitat. Soriano *et al.* (2019) examined the role of phenolic compounds during these UV stress events. They found that the response of phenolic compounds was slow. They identified thirteen flavones in the methanol-soluble (mostly vacuolar) and two hydroxycinnamic acids in the insoluble (cell wall-bound) fractions. Only p-coumaric and ferulic acids, both from the insoluble fraction of ***Plagiochila asplenioides*** (Figure 15-Figure 17), exhibited a significant and rapid accumulation in response to UV radiation on the first day of exposure to elevated UV. This did not occur in the other leafy liverwort, the two thallose liverworts, or the two moss species. Six additional phenolic compounds accumulated during the 22 days of exposure, especially in the liverworts.

Plagiochila bifaria (Figure 33-Figure 35)

(syn. = *Plagiochila killarniensis*)

Distribution

Plagiochila bifaria (Figure 33-Figure 35) is widespread in the Neotropics, going by a variety of names (Grolle 1998; Gradstein 2015). Heinrichs *et al.* (1998a, b, 2004) argued for a broad species concept based on molecular, morphological, and phytochemical evidence. I have included here only the names I found in the aquatic literature. Heinrichs *et al.* (2004) reported it from the Western Hemisphere from Bolivia, Brazil, Costa Rica, Ecuador, Panama, and Mexico, as well as the British Isles and Tenerife on the eastern side of the Atlantic. Rycroft (2008) documented it from Venezuela and Peru. To these, Gradstein (2015) added Jamaica, Galapagos Islands, and the Barbados.

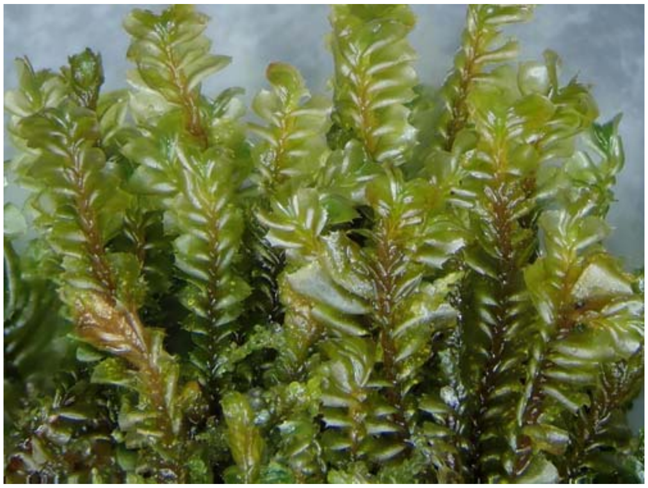

Figure 33. ***Plagiochila bifaria***, a Neotropical species, but extending into other hyperoceanic areas. Photo by Paul Bowyer, through Creative Commons.

Its range extends outside the tropics, including the Canary Islands (González M. *et al.* 2007), Madeira (Sim-Sim *et al.* 2005a), France (Hugonnot *et al.* 2013). Hugonnot *et al.* (2013) considered the species to be hyperoceanic.

Aquatic and Wet Habitats

Luis *et al.* (2015) described an aquatic habitat on Madeira Island, where it occurs at low altitudes in narrow streams and in mountainous streams with low flow. But Kürschner *et al.* (2007) found that the Madeira Island bryoflora was dominated by ***Plagiochila bifaria***, among others, that formed **tall turfs** (Figure 34-Figure 35).

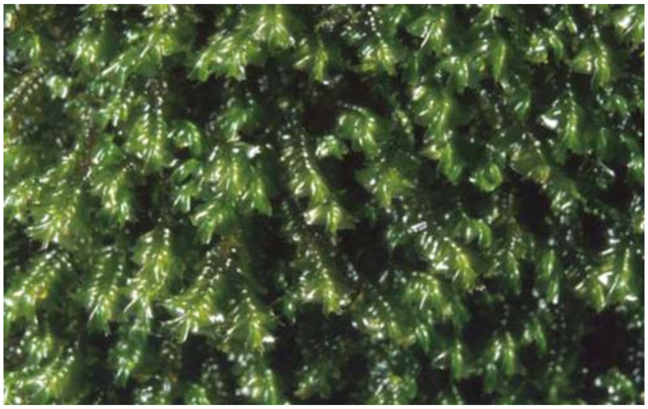

Figure 34. ***Plagiochila bifaria*** with green color, suggesting it grew in the shade. Photo by David S. Rycroft, with permission.

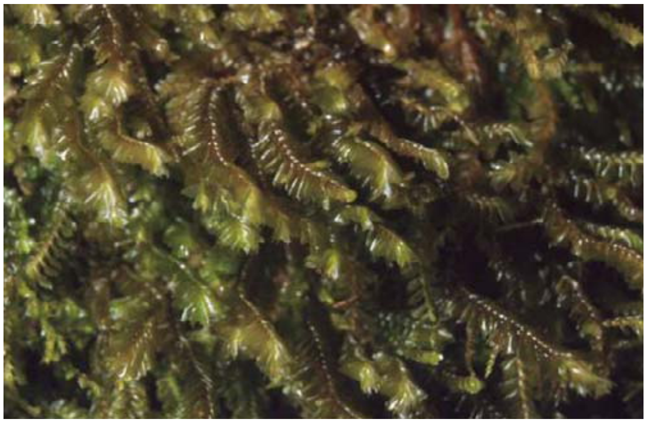

Figure 35. ***Plagiochila bifaria*** with olive-green color, suggesting sun exposure. Photo by David S. Rycroft, with permission.

In their studies on French populations, Hugonnot *et al.* (2013) reported ***Plagiochila bifaria*** (Figure 34-Figure 35) as a rock-dwelling forest species. Frahm (2013) reported it as relatively common in Italy, where it benefits from the high precipitation in the mountains. Holz *et al.* (2002) reported it as turfs on twigs and branches in Costa Rico in upper montane *Quercus* forests. On Madeira, it was the most frequent species in the Madeiran laurel forest. In the Azores, it was one of the ten most frequent species (Gabriel & Bates 2005). They found it in 88% of the bark samples and only 12% of the non-bark samples. At mid to high altitudes it is an indicator species of lower water availability and higher bark *p*H – not exactly what we would expect for an aquatic or wetland bryophyte.

Adaptations

Sim-Sim *et al.* (2005b) described the **rill-like** (upward folded, forming channel; Figure 36) leaf arrangement as an adaptation for condensing water vapor from fog and mist that is frequent at 1000-1299 m asl. This moisture permits it to maintain a moisture status that is almost as consistent as being submersed.

Figure 36. ***Plagiochila bifaria***, from a population originally identified as ***Plagiochila killarniensis***, showing rill-like leaf arrangement. Photo by Barry Stewart, with permission.

Reproduction

Heinrichs *et al*. (1998a) noted that the perianths of ***P. bifaria*** (Figure 34-Figure 35) became rarer toward the northern limits of distribution. Most of the fertilized archegonia appear to be confined to Macaronesia, whereas descriptions of younger perianths with no fertilization led to conflicting descriptions that supported spurious species separations, especially that of ***Plagiochila killarniensis*** (Figure 36), now considered a synonym (TROPICOS 2020). The Macaronesian perianths match those occurring in the Neotropics. This is consistent with the formation of sporophytes in the Neotropics and Macaronesia, but not in continental Europe (Heinrichs *et al*. 2004).

Biochemistry

Plagiochila bifaria has distinct oil bodies (Figure 37), suggesting the presence of secondary compounds that could be adaptive. Although the ecological information on this species is relatively sparse, it has undergone several biochemical studies. Hackl *et al*. (2006) isolated and identified three eudesmane type sesquiterpenes from ***Plagiochila bifaria***. Rycroft (2008) described what appears to be the first example of a monocyclic 4-pyrone that has a polyketide origin. Heinrichs *et al*. (2004) used the biochemical composition of the species to delineate clades within the species, with indications that the basal clade is represented in Costa Rica, Brazil, and Bolivia, concluding that the differences among clades did not support differences at the species level. Rycroft *et al*. (1999) determined that certain minor components were common to both the European ***Plagiochila killarniensis*** (Figure 36) and the Neotropical populations treated as ***Plagiochila bifaria*** (Figure 34-Figure 35). Like Heinrichs and coworkers, they considered the biochemical differences between Scottish populations and those of the Azores to be minor.

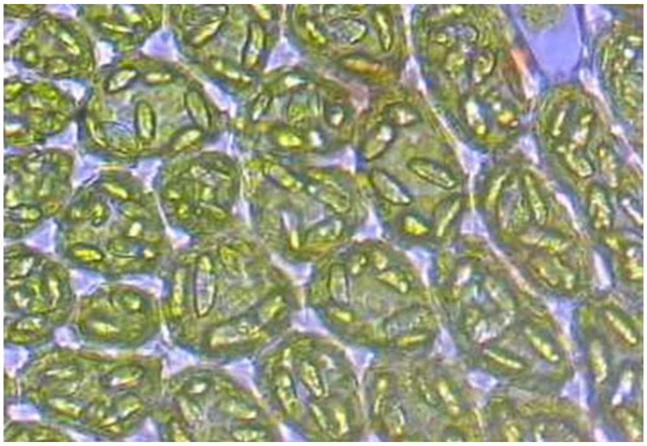

Figure 37. ***Plagiochila bifaria*** oil bodies (ovals in cells), a site of secondary compounds. Photo by David Rycroft, with permission.

Plagiochila porelloides (Figure 38-Figure 43)

(syn. = *Plagiochila asplenioides* var. *major*)

Distribution

In eastern North America, this species was for a long time interpreted as ***Plagiochila asplenioides***. Since it was later determined that these were instead ***Plagiochila porelloides***, I have herein included the eastern North American populations reported as ***P. asplenioides*** as ***P. porelloides***.

Plagiochila porelloides (Figure 38-Figure 43) is a circumboreal species (Sim-Sim *et al*. 2005a) distributed throughout Europe, including the Arctic, becoming submontane in the south (Hill *et al*. 1991). Ros *et al*. (2000) added it to Morocco in Africa. In Europe, it occurs in the Nordic countries (Schumacker & Váňa 2000; Damsholt 2002), in the British Isles (Paton 1999), in Greece and Poland (Cronberg 2000a, b), and in Germany in the forest (Marstaller 2007). Sim-Sim *et al*. (2005a) reported it as rare in the Madeiran laurel forests, but it occurred there in some sites that had high biodiversity and several rare species. In North America, it occurs from 82º32'N to the southeastern Coastal Plain in the east and California and Arizona in the west (Schuster 1980).

Figure 38. ***Plagiochila porelloides***, a species of stream banks in eastern and western North America and Europe. Photo by Hermann Schachner, through Creative Commons.

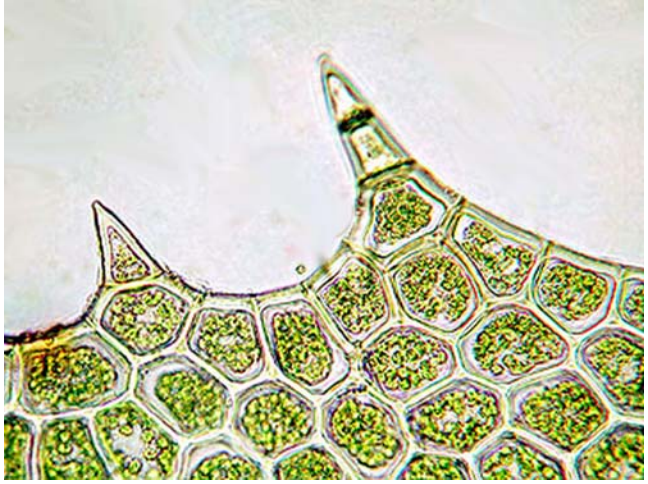

Figure 39. ***Plagiochila porelloides*** leaf teeth. Photo from Botany Website, UBC, with permission.

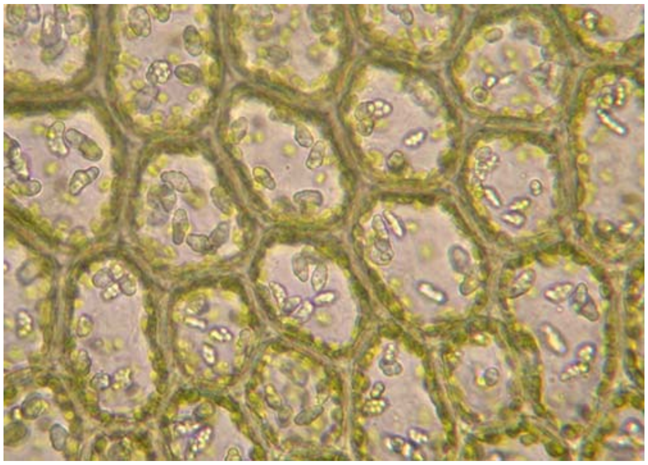

Figure 40. ***Plagiochila porelloides*** leaf cells showing oil bodies and peripheral chloroplasts. Photo from Botany Web Page, UBC, with permission.

Figure 41. ***Plagiochila porelloides*** in hydrated state. Photo by Štěpán Koval, with permission.

Figure 42. ***Plagiochila porelloides*** beginning to dry. Photo by Hermann Schachner, through Creative Commons.

Figure 43. ***Plagiochila porelloides*** showing leaves rolling as it dries out. Photo by Štěpán Koval, with permission.

Söderström *et al.* (1999) reported ***Plagiochila porelloides*** (Figure 38-Figure 43) from China in the Changbai Mountain, where it occurred on boulders, in the alpine heathland, and on decaying logs. Konstantinova, among others, (2011) documented it in the Eastern Caucasus of Russia, where it is often abundant.

Aquatic and Wet Habitats

Schuster (1980) comments that its wide variability in form is concurrent with a wide variability in habitat. It can, although rarely, be in xeric extremes at one end of its ecological spectrum to hydric, its most common form, at the other. It is very rarely submerged. Schuster considers it to be most common on moist rocks. And unlike most members of the genus, ***P. porelloides*** (Figure 38-Figure 43) tolerates high insolation when moisture is adequate. Because of its wide range of habitat conditions, it can be found with nearly half the species of liverworts found in eastern North America. Its occurrence over such a wide north-south geographic range coincides with its wide temperature tolerance, more than is known for any other member of the genus.

In North America, Nichols (1918) reported ***Plagiochila asplenioides*** (Figure 15-Figure 17) from streambanks and wet rock cliffs associated with streams, Cape Breton Island, Canada, but in this location it was most probably ***Plagiochila porelloides*** (Figure 38-Figure 43). Elsewhere in North America, ***P. porelloides*** occurs on wet or moist cliffs of ravines and on moist rock surfaces or springy banks of ravines in Connecticut, USA (Nichols 1916); in Appalachian Mountain, USA, streams (Glime 1968); just above the water surface most of the year in a headwater stream in New Hampshire, USA (Glime 1970); on the wall in the Flume at Franconia Notch, New Hampshire, USA (Glime 1982); in Adirondack Mountain streams (Slack & Glime 1985; Glime *et al.* 1987); but it is a restricted terrestrial of montane streams and streambanks in western Canada (Vitt *et al.* 1986; Glime & Vitt 1987), perhaps due to the strong flow and spring flooding there. In Minnesota, it occurs in mesophytic calcareous communities, on peat-covered banks, much disintegrated decaying wood, and over wet to saturated humus in ***Thuja***-spruce-fir forests (Figure 44).

Figure 44. ***Thuja***-spruce-fir swamp in Michigan, USA, a suitable habitat for ***Plagiochila porelloides***. Photo from National Park Service, through public domain.

On Cygnes Mountain, Québec, Canada, it occurs on moist granitic rock in mid stream (Kucyniak 1947). In Quaker Run, New York, Matthews (1932) likewise found it on rocks midstream in a stream with a gentle gradient and numerous small waterfalls. It is not uncommon to find ***Plagiochila porelloides*** (Figure 38-Figure 43) just above the water level (Figure 45) in streams in the Appalachian Mountains of the eastern USA, above but close to the water surface (Figure 45), occasionally becoming submersed (Glime 1970). This keeps it moist most of the time, dry occasionally, and submersed in high water. Similarly, in Cataracts Provincial Park, Newfoundland, Canada, Weber and Brassard (Weber 1976; Weber & Brassard 1976) found it in the inundation zone where it is periodically submerged and exposed as the water level rises and falls along the river. It also occurred in the next higher zone on the river bank.

Plagiochila porelloides subsp. ***porelloides*** occurs on cliffs, damp soil banks, decayed wood, and bark of trees (Figure 1) in western North America from Alaska southward to California, USA and in damp, calcareous high Arctic tundra (Hong 1992).

Figure 45. ***Plagiochila porelloides*** just above water level and ***Fontinalis novae-angliae*** just below the water level, in a stream in New Hampshire, USA. Photo by Janice Glime.

In Europe, ***Plagiochila porelloides*** (Figure 1) occurs on rocks or soil of fast streams (Watson 1919); in the arctic-alpine zone of the UK (Watson 1925); in the ***Platyhypnidium*** (Figure 5) **–** ***Fontinalis antipyretica*** (Figure 6) association, in Thuringia, Germany (Marstaller 1987); submersed in low-buffered water of streams (Tremp & Kohler 1991); on stream boulders above mean water level, with low cover and high frequency in Finland (Virtanen 1995); springs in Finland (Heino *et al*. 2005); common in flood valleys of Upper Bureya River (Russian Far East) (Konstantinova *et al*. 2002); emerged and vertical stony streambanks or in waterfall margins, pure patches usually not extensive, associated with ***Thamnobryum alopecurum*** (Figure 46) and ***Lejeunea cavifolia*** (Figure 47) in mountain streams of northwest Portugal (Vieira *et al.* 2005); in irrigation ditches in Spain (Beaucourt *et al.* 1987); on montane, base-rich siliceous rocks, shaded, humid montane siliceous rock outcrops, sub-Mediterranean to Alpine siliceous, sometimes base-rich shaded north-facing outcrops, sub-Mediterranean to sub-Mediterranean to Alpine siliceous, sometimes base-rich shaded north-facing outcrops, sub-Mediterranean to sub-Alpine limestone outcrops, shaded siliceous boulders in woodland from the sub-Mediterranean to the sub-Alpine belt at 2550 m asl, on base-rich ground along streams, forest floor, and limestone outcrops from the Mediterranean to the sub-Alpine belt in Andorra (Sotiaux & Vanderpoorten 2017).

Figure 46. ***Thamnobryum alopecurum***, an associate of ***Plagiochila porelloides*** in wet, vertical habitats in Europe. Photo by Hugues Tinguy, with permission.

Figure 47. ***Lejeunea cavifolia***, an associate of ***Plagiochila porelloides*** in wet, vertical habitats in Europe. Photo by Hermann Schachner, through Creative Commons.

Plagiochila porelloides (Figure 38-Figure 43, Figure 53-Figure 55) can be found in the Iskur River, Bulgaria, and its main tributaries (Papp *et al.* 2006) and as a mesophyte in Bulgarian rivers (Gecheva *et al*. 2010, 2013). It occurs on limestone rock and on bark of ***Pinus*** (Figure 48) at a stream in the Tara river canyon and Durmitor area, Montenegro (Papp & Erzberger 2011); in the upper course in Maritsa River, Bulgaria (Gecheva *et al*. 2011). In the Madeiran laurel forests, ***Plagiochila porelloides*** grows on moist, shady rocks, forming isolated, small mats near populations of other bryophytes such as ***Andoa berthelotiana*** (Figure 49), ***Fissidens luisieri*** (Figure 50), ***Thamnobryum maderense*** (Figure 51), ***Porella canariensis*** (Figure 52), and ***Plagiochila bifaria*** (Figure 33-Figure 35) (Sim-Sim *et al*. 2005a).

Figure 48. ***Pinus*** bark, a substrate where ***Plagiochila porelloides*** can occur in Montenegro. Photo by SusquehannahMan, through Creative Commons.

Figure 49. ***Andoa berthelotiana*** with capsules, a species that often occurs near small mats of ***Plagiochila porelloides***. Photo by Michael Lüth, with permission.

Figure 50. ***Fissidens luisieri***, a species that often occurs near small mats of ***Plagiochila porelloides***. Photo by Jan-Peter Frahm, with permission.

Figure 51. ***Thamnobryum maderense***, a species that often occurs near small mats of ***Plagiochila porelloides***. Photo by Michael Lüth, with permission.

Figure 52. ***Porella canariensis***, a species that often occurs near small mats of ***Plagiochila porelloides***. Photo by Paulo A. G. Borges, with permission through Azoresbioportal.

For Portuguese streams, Vieira *et al*. (2004) reported that ***Plagiochila porelloides*** (Figure 53-Figure 55) was threatened. It occurs there in seasonally emerged locations on vertical stony stream banks (Figure 53) or at waterfall margins, both habitats where it remains wet most of the time and could be occasionally submerged. Its patches were extensive, often pure, but typically not well developed. It was always found lacking sexual reproductive structures.

Figure 53. ***Plagiochila porelloides*** on a vertical substrate. Photo from Botany Web Page, UBC, with permission.

In Russia, ***Plagiochila porelloides*** (Figure 53-Figure 55) was recorded in some areas as ***P. asplenioides*** (Figure 13-Figure 18), but has since been determined to be ***P. porelloides*** (Konstantinova 2011). It occurs in a canyon with a rivulet, in deep ravines, on loamy and sandy soil on stream banks, but also on soil, rocks, decaying shaded wood, grasses and rocks in the mountain steppe, and in rock crevices, on ledges, and between boulders.

Adaptations

Color forms occur in response to solar radiation. In exposed sites, the plants are yellowish green (Figure 53-Figure 55); in the shade they can reach a deep green or dull olive green (Figure 41-Figure 43), but not brown (Schuster 1980).

Figure 54. ***Plagiochila porelloides***, showing a more yellowish green coloration of a species grown in an exposed site. Photo by Štěpán Koval, with permission.

Reproduction

The species is **dioicous**, with male plants slightly smaller than the females. Nevertheless, sporophytes (Figure 55) are present in at least part of the distribution, so some isozyme variability should be present in some areas.

Figure 55. ***Plagiochila porelloides*** with capsules. Štěpán Koval, with permission.

Cronberg (2000a,b) found a total absence of genetic variation in Greek and southern Scandinavian populations when comparing 16 isozyme loci. The study included areas that had been severely and mildly affected by the Pleistocene glaciations and supported an earlier study that found no variation among Polish populations. He suggested that the present-day populations may have passed through a severe bottleneck that reduced or eliminated the variability.

When Kowalczyk *et al.* (1997) cultured fragments of ten liverwort species, ***Plagiochila porelloides*** (Figure 54-Figure 55) was among them. The first problem in such studies is to obtain sterile material, which is difficult with wet and aquatic bryophytes where the surface is often replete with bacteria, algae, protozoa, and detritus, not to mention insects. They successfully sterilized this species with commercial bleach diluted 1:1 and 1:3 with distilled water with optimal time of 0.5-2.0 minutes. (I have found that longer exposures kill the bryophytes or at least destroy most of the chlorophyll.) The fragment should be no more than 3 mm long and should be obtained from a leafless branch or shoot tip.

Fungal Interactions

Marsh *et al.* (2010) compared the fungi on ***Plagiochila porelloides*** (Figure 54-Figure 55) and those (Figure 22-Figure 31) on ***P. asplenioides*** (Figure 13-Figure 18) in Finland. The former liverwort occurred on bases and crevices of shady silicate boulders, sometimes by brooks or on dead wood in shady forests, whereas the latter occurred mostly on herb-rich forest floors and in moist depressions. Thirteen species of bryicolous fungi are known to occur on one or both of these two species. Most of those found by Marsh and coworkers positioned their apothecia in leaf axils or perianths. The fungus ***Epibryon plagiochilae*** (Figure 20-Figure 21), however, strongly prefers the dorsal leaf border, although ascomata can occur on the stem or on female bracts and perianths. Although this fungus species has a strong preference for ***P. asplenioides***, it also occurs on ***P. porelloides***, but much less frequently. ***Pleostigma jungermannianum*** likewise occurs on both ***P. porelloides*** and ***P. asplenioides*** (Figure 30).

Biochemistry

One can easily see oil bodies (Figure 56) in fresh cells, indicating the presence of secondary compounds. Toyota *et al.* (1994) verified the presence and established the structure of three sesquiterpene esters in ***Plagiochila porelloides*** (Figure 54-Figure 55). Asakawa *et al.* (1980) identified sesquiterpenoids from fourteen species of ***Plagiochila***, including ***P. porelloides***, identifying some that caused the distinctive odors.

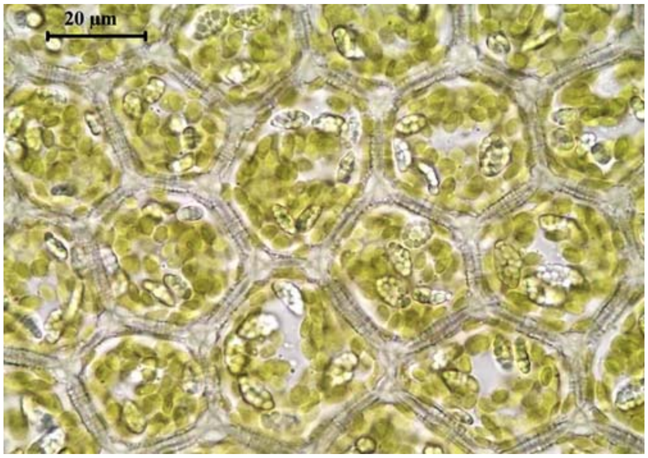

Figure 56. ***Plagiochila porelloides*** leaf cells showing oil bodies among the chloroplasts. Photo by Hugues Tinguy, with permission.

Plagiochila punctata (Figure 57-Figure 59)

(syn. = *Plagiochila stolonifera*, *Plagiochila choachina*, *Plagiochila patzschkei*, *Plagiochila subalpina*)

Distribution

Plagiochila punctata (Figure 57-Figure 59) is widespread in Neotropical mountains, but has, like so many tropical species, been known by a number of names now considered to be synonyms (Heinrichs *et al.* 2005). As a result of understanding its synonymy, it has been documented for Scotland, Spain, tropical Africa, Tanzania, Madagascar, Zaire, Karthala volcano (in Indian Ocean), Mexico, Venezuela, Ecuador, Colombia, Brazil, Bolivia, Costa Rica, and Dominican Republic. In 2006, Davison *et al.* added a record of ***Plagiochila punctata*** to the flora of Tennessee, USA.

Aquatic and Wet Habitats

Watson (1919) reported that ***Plagiochila punctata*** (Figure 58) is occasionally submerged. In the tropics, it is restricted to mountains, but it also occurs in Europe (Figure 58), where it occurs in the lowlands up to 1000 m asl. The feather-like habit is more common in the tropics than in Europe. But it is not always aquatic or in wetlands. It can also grow as an epiphyte (Figure 59).

Figure 57. ***Plagiochila punctata*** (larger plants with large teeth), a widespread and occasionally submerged species in Neotropical mountains. Photo by Paul Bowyer, through Creative Commons.

Figure 58. ***Plagiochila punctata*** growing on a vertical substrate. Photo by David Rycroft, with permission.

Figure 59. ***Plagiochila punctata*** growing as an epiphyte. Photo by Michael Lüth, with permission.

Reproduction

Plagiochila punctata (Figure 57-Figure 59) is **dioicous** (Gradstein *et al.* (2001).

Fungal Interactions

Plagiochila punctata (Figure 57-Figure 59) has several interesting interactions with other organisms. Döbbeler and Feuerer (2004) reported that ***Stenocybe***

nitida, an ascomycete, occurs on this liverwort species. Pilato *et al*. (2002) reported tardigrade specimens and eggs from ***Plagiochila punctata*** from the Otonga Forest in Ecuador and another two specimens from this liverwort in Alto Tambo, Ecuador.

Plagiochila renitens

Plagiochila renitens occurs in Australia and southern Asia (ITIS 2020). Its habitats are poorly reported. Ruttner (1955) reported it from acidic thermal spray in the tropics, but little else seems to connect it to aquatic or wetland habitats.

Plagiochila retrospectans (Figure 60) and *Plagiochila fuscella* (Figure 61)

Distribution

Engel and Merrill (2009) argued that ***Plagiochila retrospectans*** (Figure 60) does not occur in New Zealand, and specimens labelled with this name are actually ***Plagiochila fuscella*** (Figure 61), a New Zealand endemic. Nevertheless, ***Plagiochila retrospectans*** is known from Victorian rainforest streams in Australia (Carrigan & Gibson 2004; Fleisch & Engel 2006) and from the subAntarctic Macquarie Island (Hughes 1986), but the records of Suren (1988) from high alpine streams in New Zealand may actually be ***Plagiochila fuscella***, making that species one of the two dominant liverwort species in those streams.

Figure 60. ***Plagiochila retrospectans***, a Southern Hemisphere species that includes the subAntarctic. Photo by David Tng, with permission.

Figure 61. ***Plagiochila fuscella***, a segregate from ***Plagiochila retrospectans***, that occurs in New Zealand. Photo through Creative Commons.

Aquatic and Wet Habitats

In Cement Creek in Victoria, Australia, ***Plagiochila retrospectans*** (Figure 60) forms **cushions** on stream rocks (Carrigan and Gibson 2004). In New Zealand, ***P. fuscella*** (Figure 61) is especially common in chutes. On South Island, NZ, ***P. fuscella*** is in the group of species that prefer the highest number of days with low flow events, but also with the highest number of floods (Suren 1996). Wells *et al*. (1998) reported it from the 0-5 m sampling depth in a lake in New Zealand, but with low cover values.

Role

Plagiochila fuscella (Figure 61) is important for some aquatic invertebrates, especially insects. In the open headwater tributary of Otira River and shaded tributary of Bealy River, New Zealand, it occurred in 29% and 27% of the invertebrate guts, respectively (Suren & Winterbourn 1991). The liverworts provide habitat for the insects, substrate for periphyton, collector of detritus, and refuge from high flow (Suren 1991). This makes them ideal for oviposition and safe sites for small larvae and naiads while providing an abundant food source. Furthermore, ***P. fuscella*** contained the most CPOM, perhaps accounting for the greatest abundance of the stonefly ***Austroperla cyrene*** (Figure 62-Figure 63) and the mites **Oribatida** sp. B and ***Paratryssaturus*** sp. (Figure 64) occurring there compared to mosses.

Figure 62. ***Austroperla cyrene*** naiad, a resident on ***Plagiochila fuscella*** in New Zealand. Photo by James Cooper, through Creative Commons.

Figure 63. ***Austroperla cyrene*** adult on bryophytes. Photo by Jacob Littlejohn, through Creative Commons.

Figure 64. ***Paratryssaturus cantermus***, a mite that inhabits ***Plagiochila fuscella*** in New Zealand. Photo modified from TePapa website, through Creative Commons.

Biochemistry

Nagashima *et al.* (1994) reported a new sesquiterpenoid from ***Plagiochila fuscella*** (Figure 61) in New Zealand.

Plagiochila spinulosa (Figure 65-Figure 69)

Distribution

Plagiochila spinulosa (Figure 65-Figure 69) is predominantly an eastern Holarctic species, but it also occurs in Lesotho in southern Africa and both North and South Islands of New Zealand (Renner *et al*. 2017; Renner 2018). González-Mancebo *et al.* (2009) reported that records of this species from the Canary Islands were actually other species, but that it does occur on the more temperate Madeira (Sim-Sim *et al*. 2005a).

Figure 65. ***Plagiochila spinulosa***, a species distributed mostly in the eastern Holarctic. Photo by Michael Lüth, with permission.

Figure 66. ***Plagiochila spinulosa***, a species distributed mostly in the eastern Holarctic. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Watson (1919) described ***Plagiochila spinulosa*** (Figure 65-Figure 69) as a species of waterfalls, occasionally becoming submerged. But in Scotland, it occurs in the Atlantic oakwood, forming large cushions or patches (Figure 67) on terrestrial rocks and tree trunks (Figure 68). Proctor (1980) found that this species in similar wooded habitats of the British Isles (Figure 69) received its peak irradiance in the spring before leaf expansion. On the Iberian Peninsula of northern Spain, Qlivan and Fuertes (2000) found it on wet acidic rocks and on quartzite rocks near the River Sobra. Renner (2018) reports that ***Plagiochila spinulosa*** occurs in a variety of habitats on South Island, New Zealand, including the low windswept broadleaf forest, tall ***Nothofagus***-dominated forest (Figure 70), waterfalls, cliff faces (Figure 71), and alpine herbfield. It also grows there as a lithophyte on cliff faces.

Figure 67. ***Plagiochila spinulosa*** habitat forming large cushion. Photo by Michael Lüth, with permission.

Figure 68. ***Plagiochila spinulosa*** on a birch log in Scotland. Photo by Michael Lüth, with permission.

Figure 69. ***Plagiochila spinulosa*** in a wooded habitat in England. Photo by Janice Glime.

Figure 70. ***Nothofagus*** forest, Western Ruahine Ranges, NZ. Photo courtesy of Marie-Claude Lariviere.

Figure 71. ***Plagiochila spinulosa*** on a vertical substrate. Photo by Barry Stewart, with permission.

One indication for the preference of ***Plagiochila spinulosa*** for moist sites is its sensitivity to desiccation. In their comparison of ten species of bryophytes regarding recovery from desiccation, Dilks and Proctor (1974) found that net assimilation and respiration of ***Plagiochila spinulosa*** and ***Hookeria lucens*** (Figure 72) showed the greatest sensitivity. Further details were added by Dilks and Proctor (1979), with indications of greater variability of water content in xeric species than in woodland species.

Figure 72. ***Hookeria lucens*** with capsules, a species that along with ***Plagiochila spinulosa*** showed the greatest sensitivity to drying. Photo by Michael Lüth, with permission.

Reproduction

Species in the group with ***Plagiochila spinulosa*** have **caducous** (easily detached; Figure 73-Figure 74) leaves that break at the base (Renner 2018) and permit them to reproduce asexually. These can account for both short- and long-distance dispersal.

Figure 73. ***Plagiochila spinulosa*** showing the portions of stems with lost leaves (caducous leaves). Photo by Paul Bowyer, through Creative Commons.

Figure 74. ***Plagiochila exiguua*** dispersing caducous leaves. Photo by Des Callaghan, with permission.

Fungal Interactions

Wang and Qiu (2006) found no references to document the presence of mycorrhizae in ***Plagiochila spinulosa*** (Figure 66-Figure 67, Figure 71-Figure 73).

Biochemistry

Rycroft *et al.* (2002) noted that one can distinguish between ***Plagiochila spinulosa*** (Figure 66-Figure 67, Figure 71-Figure 73) and ***P. stricta*** by the odors of the crushed plants. Hiroshi and Asakawa (1988) described oil body types and chemical constituents in ***P. spinulosa***, most of which are identical with those of ***P. exigua*** (Figure 75), a species that also has caducous leaves (Figure 74). Connolly *et al.* (1999) and Rycroft *et al.* (1999) identified some of the aromatic compounds in ***P. spinulosa***. Sim-Sim *et al.* (2005c) used the composition of the essential oils to verify the presence of ***P. spinulosa*** at elevations above the Madeira laurel forest where it is a hyper-humid zone.

Figure 75. ***Plagiochila exigua***, a species with secondary compounds like those of ***Plagiochila spinulosa***. Photo by Michael Lüth, with permission.

Plagiochila spinulosa (Figure 66-Figure 69, Figure 71-Figure 73) produces **volemitol** as one of its photosynthetic sugar products (Suleiman *et al*. 1980). It would be interesting to know if this product is in any way connected to its preference for moist habitats. In the intertidal brown alga *Pelvetia canaliculata*, concentrations of both mannitol and volemitol increased with increases in temperatures up to 27ºC (Pfetzing *et al*. 2000). Continuous emersion elicited no changes in concentrations of these two sugars at 10ºC for 7 days, but when the algae were emersed continuously for 8 or 12 days at 25ºC the volemitol concentrations exhibited significant decrease but mannitol concentrations did not change significantly. In its circumpolar distribution ***Plagiochila spinulosa*** is not likely to encounter such high temperatures in water, but above water it could encounter them for brief periods.

Rycroft (1990) identified two new bibenzyl-fusicoccane conjugates. Anton *et al*. (1997) identified hydroxy-4'-methoxy-bibenzyl in ***Plagiochila spinulosa*** (Figure 66-Figure 67, Figure 71-Figure 73).

One compound identified is **lunularic acid** (Rycroft *et al*. 1999), a hormone that has similar activity to that of abscisic acid and may help it to live in its wide range of habitats.

Plagiochilion oppositum (Figure 76)

Distribution

Plagiochilion oppositum (Figure 76) has a widespread distribution, including Australia, China, Fiji, India (West Bengal, southern Western Ghats, Eastern Himalaya, and Northeast India), Indonesia, Japan, Malaysia, Myanmar, New Caledonia, New Guinea, Philippines, Samoa, Solomon Islands, Sri Lanka, Taiwan, Thailand, Vanuatu, and Vietnam (Daniels & Kariyappa 2012). Renner *et al.* (2016) noted the variability of the species, but concluded that it "contains significant phylogenetic substructuring that is not necessarily the result of geographic isolation."

Figure 76. ***Plagiochilon oppositus***, Yunnan, China. Photo courtesy of Li Zhang.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Plagiochilion oppositum*** (Figure 76) from waterfalls in the tropics. But it appears that this species is more typical of montane forests (Gradstein *et al*. 2010; Daniels 2020). In West Java, it occurs on bark at higher elevations. It is typical in tropical montane evergreen forests and wet evergreen forests (Daniels 2020). In Sulawesi it occurs in both lowland and montane forests (Nunik & Gradstein 2007).

Trichocoleaceae

Trichocolea tomentella (Figure 77-Figure 86)

Distribution

Trichocolea tomentella (Figure 77-Figure 86) is distributed in the temperate regions in the Northern Hemisphere, where it is mostly oceanic and suboceanic (Korpelainen *et al*. 2004). It occurs in Africa, Oceania, Australia, the Caribbean islands, Europe, Asia, Central America, and North America (ITIS 2020), with the largest number of known locations in Europe and North America. In New Zealand, there are four species of ***Trichocolea***, but not ***T. tomentella*** (Hatcher 1958). These are forest species, on the ground or as epiphytes.

Figure 77. ***Trichocolea tomentella*** leaf, a highly dissected structure. Photo by Hermann Schachner, through Creative Commons.

Figure 78. ***Trichocolea tomentella*** microscopic view showing chloroplasts and the very different arrangement of cells when compared to most leafy liverworts. Photo through Creative Commons.

Figure 79. ***Trichocolea tomentella*** forming clumps like one can find in a wetland. Photo by Hugues Tinguy, with permission.

Figure 80. ***Trichocolea tomentella*** with red pigmentation, suggesting it has been exposed to bright sunlight. Photo by Rick Ballard, through Creative Commons.

Aquatic and Wet Habitats

Because of its moisture requirements, ***Trichocolea tomentella*** (Figure 81-Figure 84) is habitat limited, occurring in springs and mesic habitats in woodlands.

Figure 81. ***Trichocolea tomentella*** showing its branching pattern. Note the whitish color of the dry form. Photo by Almantas Kulbis, through Creative Commons.

Figure 82. ***Trichocolea tomentella*** wet. Note the change in color to green in the wet form. This results from water filling in the spaces and probably activates the chloroplasts. The reflection of light waves by dry cells might account for the color change when water fills in the spaces. Photo by Li Zhang, with permission.

Figure 83. ***Trichocolea tomentella*** dry, showing the tight spacing of the leaf dissections. Photo by Erika Mitchell, through Creative Commons.

Figure 84. ***Trichocolea tomentella***, showing water clinging in the many capillary spaces, permitting it to remain hydrated longer. Photo by Hermann Schachner, through Creative Commons.

Trichocolea tomentella (Figure 77-Figure 86) grows in shaded and humid habitats in seminatural or natural forests (Korpelainen *et al*. 2004). It is a vulnerable species in Finland and rare in Lithuania, while declining in southern England due to habitat loss (Korpelainen *et al*. 2004). Likewise, in southern Norway it is becoming extinct in many localities due to logging and draining near streams, springs, and gullies (Rydgren *et al*. 2012).

In Norway and Sweden, ***Trichocolea tomentella*** (Figure 77-Figure 86) occurs mostly in moist, well-shaded places, especially in deciduous forests (Figure 85) (Rydgren *et al*. 2012). It is common near springs, streams (Figure 86), and gullies. In earlier studies, Watson (1919) reported it from ground associated with fast water. Mamczarz (1970) reported it from a spring community in streams near Lacko, Western Carpathians. Marstaller (1987) reported it as occurring with the ***Platyhypnidium*** (Figure 5) **–** ***Fontinalis antipyretica*** (Figure 6) association in Thuringia, Germany. In northwest Portugal, Vieira *et al*. (2005) reported it in dripping and steep granite slabs in fresh environments, associated with ***Sphagnum subsecundum* var. *auriculatum*** (Figure 87), ***Fissidens polyphyllus*** (Figure 88), and ***Radula holtii***, in mountain streams, and similarly, Vieira *et al*. (2004) found it on dripping and steep granite slabs in Portugal. In Latvia, it not only occurs in the swampy spruce and mixed forests, but also on brook banks and springs (Bambe 2004).

Figure 85. ***Trichocolea tomentella*** on a tree base, with melting snow. Photo by Ekaterina Rozantseva, through Creative Commons.

Figure 86. ***Trichocolea tomentella*** on a stream bank. Photo Erika Mitchell, through Creative Commons.

Figure 87. ***Sphagnum subsecundum*** var. ***auriculatum***, a species that associates with ***Trichocolea tomentella*** on dripping, steep granite slabs in Portugal. Photo by Hugues Tinguy, with permission.

Figure 88. ***Fissidens polyphyllus***, a species that associates with ***Trichocolea tomentella*** on dripping, steep granite slabs in Portugal. Photo by Michael Lüth, with permission.

These records adequately describe most of its habitat in North America and other locations as well (Schuster 1953). Slack and Glime (1985) found it associated with Adirondack Mountain, USA, forest streams. In their study of 138 localities in the Polish Carpathians, Klama *et al.* (2019) concluded that ***Trichocolea tomentella*** (Figure 77-Figure 86) prefers wetland habitats, primarily in forests (Figure 89). These included areas in the vicinity of springs (34% stands), stream banks (32%; Figure 86), wet parts of the forest floor (20%), and mountain bogs (16%). The species is diminishing in frequency due to the loss of these habitats.

Figure 89. ***Trichocolea tomentella*** growing on a vertical bank. Photo by Bernd Haynold, through Creative Commons.

Vieira *et al.* (2004) reported that some populations of ***Trichocolea tomentella*** (Figure 77-Figure 86, Figure 89) in Portugal streams are threatened by human trampling in areas with easy access. They never found it fertile in the three years (2001-2004) that they studied it. It is a vulnerable species in Finland and rare in Lithuania, while declining in southern England due to habitat loss (Korpelainen *et al.* 2004). In Norway, this species has been lost from 23% of the localities where it occurred in 1950 (Rydgren *et al.* 2012). In southeastern Norway, losses are greater due to urbanization and logging and draining near streams, springs, and gullies.

Trichocolea tomentella (Figure 77-Figure 86, Figure 89) is a long-day plant, at least in southern Illinois (Zehr 1979). In southern Illinois it grows in restricted habitats, especially sandstone canyons with high moisture levels (Zehr 1977). It grows any time of the year that temperatures are above freezing (Zehr 1979). The finely divided leaves and paraphyllia seem to enable it to retain water. While it may cease growth during a drought, it resumes within 1-2 weeks upon rehydration. Zehr suggests that its lack of antheridia or sexual reproduction in southern Illinois may be due to the low irradiation in its habitats there. In more northern locations, more daylight reaches the plants in their habitats and sexual reproduction occurs at least occasionally. It is common for red light to be a stimulus for the production of gametangia.

Reproduction

Pohjamo *et al.* (2008) examined the genetic diversity, gene flow, and population structure in 18 populations of this species in Finland, Lithuania, UK, and Canada. This species is dioicous, so it is not surprising that gene flow between populations is limited. Spore production needed for longer dispersal distances requires sexual reproduction, a process that is difficult or impossible when only one sex is present in a population or the clones are disconnected. Rather, short-range dispersal of fragments is suggested by colonization within populations. Fortunately, this is promoted by the long life span of the species and its ramet productions that permit it to compete well in a suitable location with no disturbance. Nevertheless, the populations are small and becoming more and more fragmented, increasing the vulnerability of this dioicous species.

Although sporophytes (Figure 90) are rare in this **dioicous** species, most likely contributing to its increasing rarity, gametangia have been reported more frequently (Korpelainen *et al.* 2004). Nevertheless, the species exhibits a relatively high level of genetic diversity (Pohjamo *et al.* 2008), but gene flow between the disconnected populations is infrequent and suggests the occasional movement of fragments into new populations. The shoots have a long life span once they reach a suitable habitat. It expands its populations by efficient ramet production.

Figure 90. ***Trichocolea tomentella*** with capsule. Photo by Hermann Schachner, through Creative Commons.

Fungal Interactions

The fungus ***Penicillium chrysogenum*** (Figure 92) occurs on ***Trichocolea tomentella*** (Figure 77-Figure 86, Figure 89-Figure 90) (Rakotondraibe *et al.* 2015). Extracts from this fungus are known to be bioactive against the HT-29 colon cancer cell line. Ali (2017) and coworkers (Ali *et al.* 2017) found that ***Penicillium concentricum*** (see Figure 91-Figure 92) occurs as an endophyte in ***T. tomentella***. The interaction between the liverwort and its fungus induces the production of bioactive secondary metabolites by the fungus. Many of these are of medicinal value, including treatment for some types of cancer. Anaya-Eugenio *et al.* (2019) further elaborated on the medicinal compounds produced by endophytic ***P. concentricum***. Preziuso *et al.* (2018) explored the medicinal implications for the genus ***Trichocolea***.

Figure 91. ***Penicillium*** sp. on the moss ***Hylocomium splendens***. The genus ***Penicillium*** occurs on ***Trichocolea tomentella***. Photo courtesy of George Greiff.

Figure 92. ***Penicillium chrysogenum***, a species that is bioactive against the HT-29 colon cancer cell line, occurs on ***Trichocolea tomentella***. Photo by Crulina 98, through Creative Commons.

Biochemistry

Perry *et al*. (1996) identified structures of isoprenyl phenyl ethers and noted that these compounds were active as cytotoxic and antifungal agents. Nevertheless, fungi in the genus ***Penicillium*** (Figure 91-Figure 92) occur on and within ***Trichocolea tomentella*** (Figure 77-Figure 86, Figure 89). Barlow *et al*. (2001) described pathways of some of the isoprenyl phenyl ethers.

Asakawa *et al*. (1981) determined that isoprenyl benzoates serve as important chemical markers for ***Trichocolea tomentella*** (Figure 77-Figure 86, Figure 89) when compared to two other species in the **Jungermanniales**, supporting systematic classifications.

Suborder Myliineae

Myliaceae

Mylia anomala (Figure 93-Figure 102)

(syn. = *Leiomylia anomala*)

Distribution

Mylia anomala (Figure 93-Figure 102) occurs in the Northern Hemisphere, in Europe, Northern Asia, and North America. It has been recorded from Cape Breton Island, Canada (Nichols 1918), northern Alberta, Canada (Belland & Vitt 1995), Newfoundland, Canada (Weber 1976), New Hampshire, USA (Glime 1982), the Alps (Geissler & Selldorf 1986), Russia (Konstantinova *et al*. 2002; Shishkonakova *et al*. 2016), Finland (Pakarinen & Tolonen 1977; Pakarinen 1978; Väliranta *et al*. 2007), Sweden (Albinsson 1997), Spain (Reinoso & Rodríguez-Oubiña 1988), and UK (Duckett *et al*. 1991).

Figure 93. ***Mylia anomala***, a species that is widespread in the Northern Hemisphere. Photo by Hugues Tinguy, with permission.

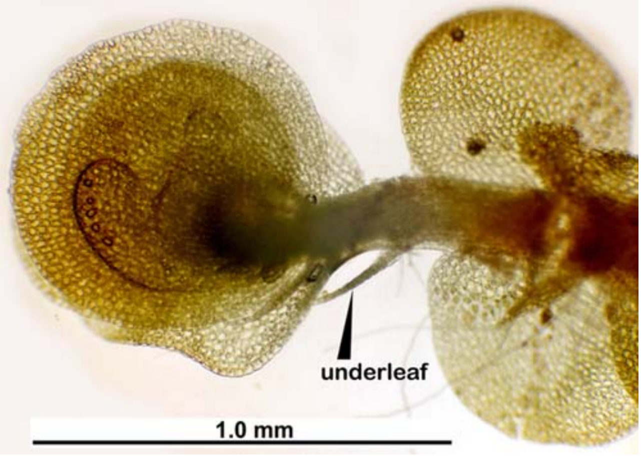

Figure 94. ***Mylia anomala*** branch. Photo modified from David H. Wagner, with permission.

Figure 95. ***Mylia anomala*** stem and leaf cross section. Photo by Kristian Peters, with permission.

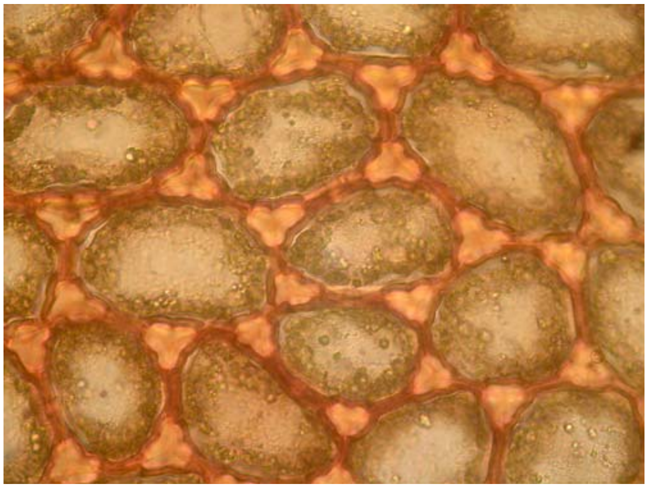

Figure 96. ***Mylia anomala*** cells showing trigones and wall pigmentation. Photo by Michael Lüth, with permission.

Figure 97. ***Mylia anomala*** forming a tight mat on ***Sphagnum***. Photo by Michael Lüth, with permission.

Figure 98. ***Mylia anomala*** developing pigments in response to exposure. Photo by Michael Lüth, with permission.

Figure 99. ***Mylia anomala*** forming a pigmented mat, indicative of exposure. Photo by Blanka Aguero, with permission.

Figure 100. ***Mylia anomala*** forming a green mat, indicative of shade. Photo by Jan-Peter Frahm, with permission.

Figure 101. ***Mylia anomala*** growing in an upright position. Photo by Des Callaghan, with permission.

Figure 102. ***Mylia anomala*** showing compact growth form. Photo by David Holyoak, with permission.

Aquatic and Wet Habitats

The habitats of this species typically are associated with ***Sphagnum*** (Figure 103). ***Mylia anomala*** (Figure 93-Figure 102) occurs in moist hollows between ***Sphagnum*** hummocks, Cape Breton Island, Canada (Nichols 1918). It occurs with ***Sphagnum*** at the edges of lakes (Figure 107) in New Hampshire (Lorenz 1908). Using macrofossil analysis, Väliranta *et al.* (2007) identified a wet lawn habitat in a southern Finnish boreal bog, based on the presence of ***Sphagnum rubellum*** (Figure 103) and ***Mylia anomala***.

Figure 103. ***Sphagnum rubellum***, species, along with ***Mylia anomala***, used to identify macrofossil wet lawn habitat in southern Finland. Photo by B. Gliwa, through Creative Commons.

Working in Finland, Pakarinen and Tolonen 1977) found that dead ***Sphagnum fuscum*** (Figure 104) could be covered by a thin layer of ***Mylia anomala*** (Figure 105). Pakarinen (1978) found that as the growth rate of ***Sphagnum fuscum*** decreases, liverworts, especially ***Mylia anomala*** (Figure 93-Figure 102), colonize the hummocks, increasing the volumetric density.

Figure 104. ***Sphagnum fuscum***; when this species dies, ***Mylia anomala*** can overgrow it. Photo by Hermann Schachner, through Creative Commons.

Figure 105. ***Mylia anomala*** overgrowing a hummock of ***Sphagnum fuscum***. Photo by Tuomo Kuitunen <luopioistenkasvisto.fi>, with permission.

In a study of peatland restoration Poulin *et al.* (2013) found that peatlands treatments differed in the responses they incurred after 8 years. Forest and ruderal species were more prominent in unrestored sites than in a reference site. Diversity and richness differed among sites. The peatland, forest, and wetland species were dominant in the restored sites. ***Mylia anomala*** (Figure 93-Figure 102), along with ***Sphagnum rubellum*** (Figure 103) and ***Pohlia nutans*** (Figure 106), were the main drivers of the revegetation.

Figure 106. ***Pohlia nutans*** with capsules, a species that, along with ***Mylia anomala*** and ***Sphagnum rubellum*** is a primary driver of revegetation in peatland restoration. Photo by Michael Lüth, with permission.

Shishkonakova *et al.* (2016) considered ***Mylia anomala*** (Figure 93-Figure 102), along with a number of lichen species, to be an indicator species for the soil subtype of destructive oligotrophic peat soils in the Russian classification of palso bogs. These are found in regressive bogs in the north taiga subzone of West Siberia. In Cataracts Provincial Park, Newfoundland, Canada, Weber (1976) considered ***Mylia anomala*** to be among the typical bog bryophytes. I should note here that at that time, North American botanists defined bogs as wetlands dominated by ***Sphagnum*** (Figure 103, Figure 104), thus not distinguishing them from poor fens.

In eastern Canadian bogs, the identification of early indicator species is a useful tool to indicate the need for intervention soon after restoration (González *et al.* 2013). Certain species are indicative when a site is not on a desired successional path. Important indicator species that signal a successful restoration are the bryophytes ***Sphagnum rubellum*** (Figure 103) and ***Mylia anomala*** (Figure 93-Figure 102), along with the black spruce tree ***Picea mariana*** (Figure 107-Figure 108).

Figure 107. ***Picea mariana*** "bog" forest in taiga (fen as described by Europeans), Quebec, Canada. Photo by Peupleloup, through Creative Commons.

Figure 108. ***Mylia anomala*** in a spruce fen. Photo by Michael Lüth, with permission.

In their study of boreal bog plants, Nordbakken *et al.* (2003) found that the lowest N percentages (0.8%) occurred in ***Mylia anomala*** (Figure 93-Figure 102). The N content increased in this species with experimental addition of N throughout the three years of the experiment. They suggested that the increases in the labelled N values in this species may represent an increasing importance of ammonium as the N source, or it could be due to its slow growth rate. Since this species grows between and over the top of the ***Sphagnum*** (Figure 103, Figure 104) shoots in the hummocks, the positive change in the N obtained may be due to its higher dependence on N in precipitation rather than that supplied by mycorrhizal relationships common in many tracheophytes of bogs. Prokaryotic endosymbionts are absent in these liverworts, so Duckett *et al.* (1991) considered the reports of nitrogen fixation by this and other liverworts to be due to associated **Cyanobacteria** (Figure 109).

Figure 109. ***Chroococcus*** sp. (**Cyanobacteria)** such as that one might find on ***Mylia anomala*** leaves. Photo by Jason Oyadomari, with permission.

Albinsson (1997) considered ***Mylia anomala*** (Figure 93-Figure 102) to have a narrow ecological amplitude in the mire habitat, particularly when compared to smaller species (Figure 110) like ***Cephalozia*** (Figure 111) or ***Kurzia*** (Figure 112) species. Gerdol (1995) determined that it likewise had a narrow nutrient niche. In the Swedish mires, it was among the most frequent of the 43 liverworts described by Albinsson (1997) and preferred poor mire conditions, occupying hummocks (Figure 113-Figure 116). The adaptations of ***Mylia anomala*** to this elevated habitat include increased desiccation resistance, ability to overgrow ***Sphagnum*** (Figure 103, Figure 104, Figure 113-Figure 116), penetration of leaves by liverwort rhizoids, and a high reproductive output (Økland 1990), including gemmae (Figure 117-Figure 119). Albinsson considered this to be a compromise strategy.

Figure 110. ***Mylia anomala*** in association with smaller liverworts. Photo by Michael Lüth, with permission.

Figure 111. ***Cephalozia bicuspidata***, in a genus that has a wider ecological amplitude than ***Mylia anomala***. Photo by Hugues Tinguy, with permission.

Figure 112. ***Kurzia trichoclados***, in a genus that has a wider ecological amplitude than ***Mylia anomala***. Photo by David T. Holyoak, with permission.

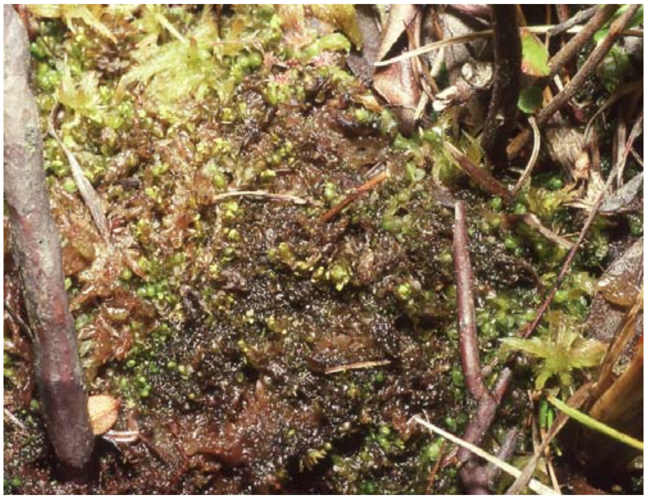

Figure 113. ***Mylia anomala*** overgrowing ***Sphagnum*** on a hummock in Perrault Fen, Upper Peninsula of Michigan, USA. Photo by Janice Glime.

Figure 114. ***Mylia anomala*** growing with cranberries on a hummock in a poor fen. Photo by Michael Lüth, with permission.

Figure 115. ***Mylia anomala*** growing with ***Sphagnum*** and ***Polytrichum***. Photo by Michael Lüth, with permission.

Figure 116. ***Mylia anomala*** with apical gemmae (yellow), growing with ***Sphagnum***. Photo by Michael Lüth, with permission.

Figure 117. ***Mylia anomala*** with gemmae on leaf tips. Photo by David Holyoak, with permission.

Figure 118. ***Mylia anomala*** with marginal and leaf-tip gemmae. Photo by Jan-Peter Frahm, with permission.

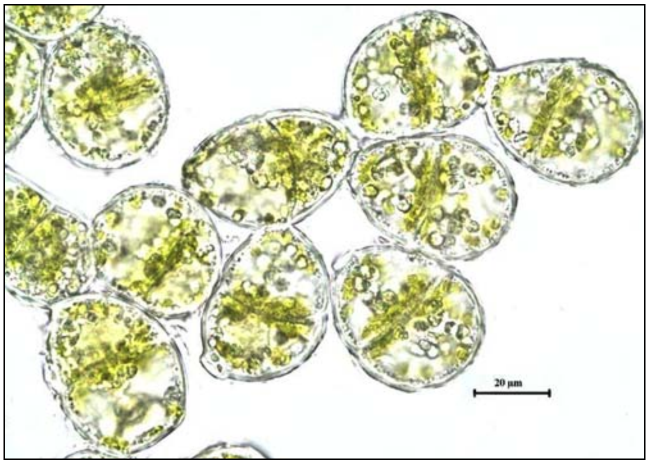

Figure 119. ***Mylia anomala*** gemmae. Photo by Hugues Tinguy, with permission.

But it is able to occupy other aquatic and wetland habitats as well; it appears on the walls in the flume (Figure 120) at Franconia Notch, New Hampshire, USA (Glime 1982). Some occur in moist moors (Figure 121). In the Alps, it is uncommon with ***Eleocharis quinqueflora*** (Figure 122) (Geissler & Selldorf 1986). In the Russian far east, it occurs on streambanks (Figure 123) at treeline of the Upper Bureya River (Konstantinova *et al*. 2002).

Figure 120. Flume at Franconia Notch, New Hampshire, USA, where one can find ***Mylia anomala*** on the walls. Photo by Janice Glime.

Figure 121. ***Mylia anomala*** with heather. Photo by Michael Lüth, with permission.

Figure 122. ***Eleocharis quinqueflora***, a wet habitat species in the Alps, but where ***Mylia anomala*** occurs uncommonly. Photo by Max Licher, through Creative Commons.

Figure 123. ***Mylia anomala*** habitat on streambank. Photo by Hermann Schachner, through Creative Commons.

Fungal Interactions

Duckett *et al*. (1991) found rhizoid-ascomycete fungi in ***Mylia anomala*** (Figure 93-Figure 102). In that liverwort, the fungi are restricted to the rhizoids (Figure 124) because this is one of the species that lacks flagelliform branches. They determined that the rhizoids swell in response to infection, with swelling being absent in sterile culture of the liverwort. It is in these swollen tips that most of the fungal hyphae reside.

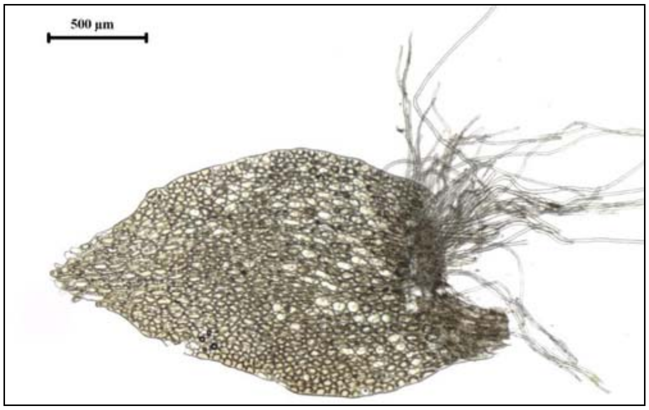

Figure 124. ***Mylia anomala*** underleaf with rhizoids, the site of ascomycete fungi. Photo by Hugues Tinguy, with permission.

Paul Davison has provided interesting images of the leaf cuticle of ***Mylia anomala*** (Figure 125). This cuticle may explain its ability to occupy habitats above water where it can become periodically dry. We know that the cuticle has a role in protecting tracheophytes from fungal invasions (Kolattukudy 1985). Could it serve any role in protection of these bryophytes against fungi?

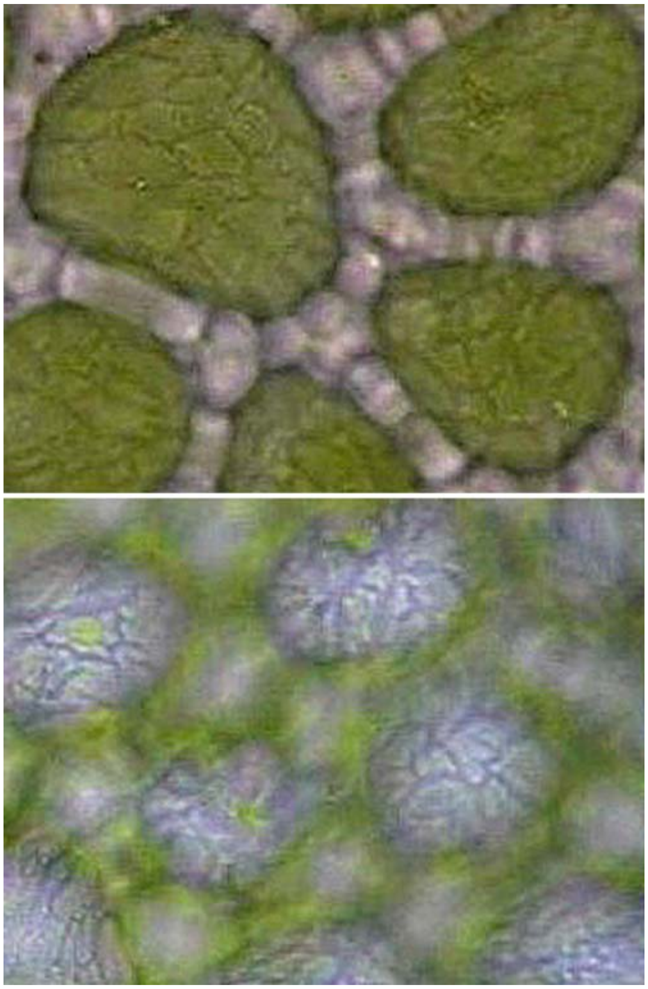

Figure 125. ***Mylia anomala*** showing cuticle. Photo by Paul G. Davison, with permission.

Biochemistry

Other potential protections against fungal presence are secondary compounds. Aromatic and other secondary compounds occur in oil bodies (Figure 126) of leaf cells. Ludwiczuk and Asakawa (2015) determined that ***Mylia anomala*** (Figure 93-Figure 102) produces mainly cyathane-type diterpenoids.

Figure 126. ***Mylia anomala*** cells with oil bodies, showing here mostly around the cell margins as oblong structures. Photo by Hermann Schachner, through Creative Commons.

Mylia taylorii (Figure 127-Figure 142)

Distribution

Mylia taylorii (Figure 127-Figure 142) is a circumboreal, mostly montane species with a suboceanic distribution (Engel & Braggins 2005). It occurs in mountainous districts of northern Europe, mountains of Continental Europe, Greenland, and eastern North America from Newfoundland to Tennessee (Wikipedia 2020). It is uncommon in western North America and eastern Asia, where it is known from Guizhou Province, China (Zhang & Chen 2006). It is best known from Great Britain and Scandinavia.

Figure 127. ***Mylia taylorii***, a circumboreal species. Photo by Tuomo Kuitunen <luopioistenkasvisto.fi.>, with permission.

Figure 128. ***Mylia taylorii*** with succubous leaves that help to conserve water. Photo by Martin Hutten, with permission.

Figure 129. ***Mylia taylorii*** showing the ability of the leaves to fold, reducing surface area for water loss. Photo by Kristian Peters, with permission.

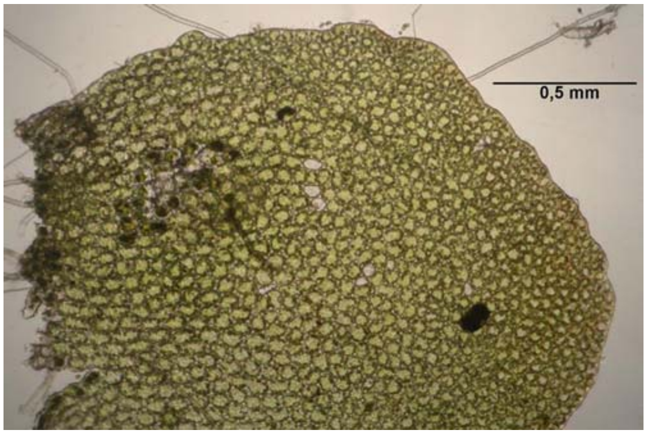

Figure 130. ***Mylia taylorii*** leaf. Photo by Snappy Goat, through public domain.

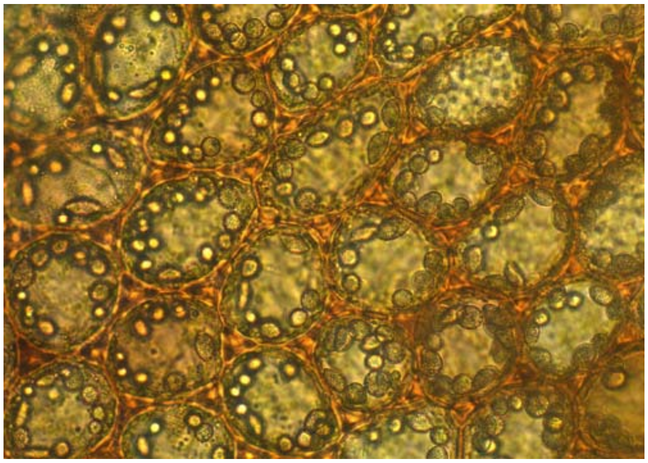

Figure 131. ***Mylia taylorii*** leaf cells showing trigones; the bright spots are oil bodies. Photo by Blanka Aguero, with permission.

Figure 132. ***Mylia taylorii*** forming a mat. Photo by Snappy Goat, through public domain.

Figure 133. ***Mylia taylorii*** green form that is typical of shade. Photo by Hermann Schachner, through Creative Commons.

Figure 134. ***Mylia taylorii*** red form that is typical of exposed sites. Photo by Hermann Schachner, through Creative Commons.

Figure 135. ***Mylia taylorii*** deep red form. Photo by Barry Stewart, with permission.

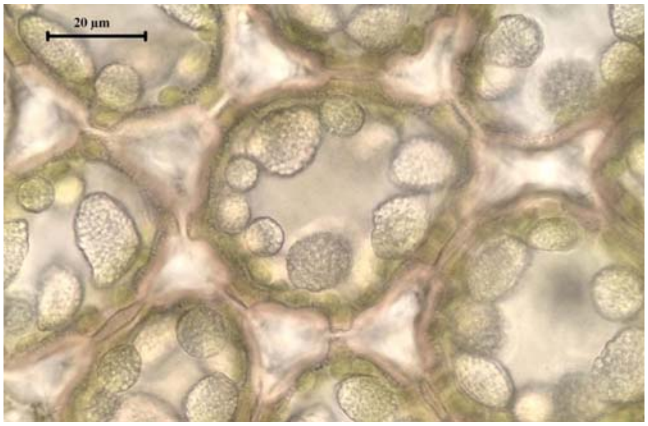

Figure 136. ***Mylia taylorii*** leaf cells showing oil bodies. Photo by Hugues Tinguy, with permission.

Aquatic and Wet Habitats

Mylia taylorii (Figure 127-Figure 142) occurs on wet shore rocks and wet sandy shores in Scotland (West 1910), on wet rock cliffs associated with streams, Cape Breton Island, Canada (Nichols 1918), and in upstream reaches in the Harz Mountains of Germany (Bley 1987).

On the very wet Queen Charlotte Islands, British Columbia, Canada, Hong (2007) found it on shaded, decayed wood and moist soil. In the Bavarian Alps, Lotto

(1987) also found it on logs, humus, and the acidic forest floor.

In Germany, ***Mylia taylorii*** (Figure 127-Figure 142) forms large tufts that are easy to recognize on moist non-calcareous rocks, including sandstone, granite, and gneiss (Schnittler *et al*. 2010). It occupies sheltered conditions with high humidity and a cool climate, but it is rarely found on decaying wood, humus, or ***Sphagnum*** peat (Figure 137) there.

Figure 137. ***Mylia taylorii*** habitat in a seep with ***Sphagnum***. Photo by Michael Lüth, with permission.

Engel and Braggins (2005) consider ***Mylia taylorii*** (Figure 127-Figure 142) to be mostly restricted to acidic rocks never occurring on calcareous rocks. This makes moist siliceous rocks suitable, as well as vertical rock walls (Figure 138- Figure 141), but as just seen above, the species also finds suitable habitat on calcareous rocks and decaying logs.

Figure 138. ***Mylia taylorii*** habitat on rock. Photo by Richtid, with permission.

On the other hand, in Sakhalin, Russia, Bakalin *et al*. (2009) found ***Mylia taylorii*** (Figure 127-Figure 142) in wet moss mats on the seeping water in limestone cliff crevices. In these locations it can occur in pure mats (Figure 142) or with ***Sphenolobus minutus*** (Figure 143). It occurs on shady limestone cliffs and on decaying wood in ***Abies*** forests (Figure 144). In the tundra, it grows over moss mats on the seeping permafrost water and also in crevices of limestone cliffs. In addition to pure mats, it occurs with ***Bazzania denudata*** (Figure 145), ***Calypogeia integristipula*** (Figure 146), ***Eocalypogeia schusterana***, ***Douinia plicata*** (see Figure 147), ***Odontoschisma macounii*** (Figure 148), and ***Tritomaria exsecta*** (Figure 149).

Figure 139. ***Mylia taylorii*** habitat on rock. Photo by Richtid, with permission.

Figure 140. ***Mylia taylorii*** (red) habitat on rocks of an embankment. Photo by Michael Lüth, with permission.

Figure 141. ***Mylia taylorii*** showing growth form on a vertical substrate. Photo by Hugues Tinguy, with permission.

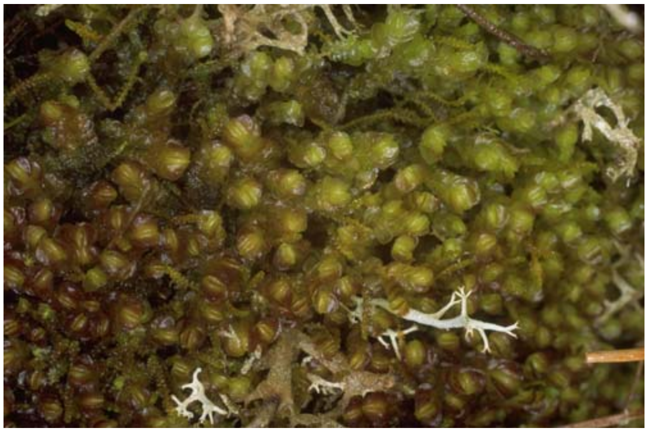

Figure 142. ***Mylia taylorii*** forming a pure wet mat (with occasional lichens), as one might find in seepage water of rock cliffs. Photo by Jan-Peter Frahm, with permission.

Figure 143. ***Sphenolobus minutus***, a species that occurs with ***Mylia taylorii*** in seeping water in limestone cliff crevices. Photo by Jan-Peter Frahm, with permission.

Figure 144. ***Abies sibirica*** forest, where ***Mylia taylorii*** can occur on shady limestone cliffs and decaying wood. Photo by Krasnoyarsk Territory, through Creative Commons.

Figure 145. ***Bazzania denudata***, a species that occurs with ***Mylia taylorii*** on limestone cliffs in the tundra. Photo from Botany Website, UBC, with permission.

Figure 146. ***Calypogeia integristipula***, a species that occurs with ***Mylia taylorii*** on limestone cliffs in the tundra. Photo by Hermann Schachner, through Creative Commons.

Figure 147. ***Douinia ovata***; ***Douinia plicata*** is a species that occurs with ***Mylia taylorii*** on limestone cliffs in the tundra. Photo by Des Callaghan, with permission.

Figure 148. ***Odontoschisma macounii***, a species that occurs with ***Mylia taylorii*** on limestone cliffs in the tundra. Photo from Earth.com, with permission.

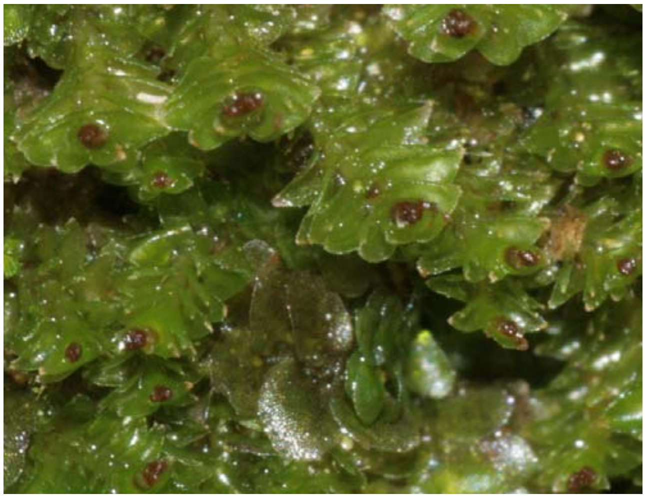

Figure 149. ***Tritomaria exsecta***, a species that occurs with ***Mylia taylorii*** on limestone cliffs in the tundra. Photo by Hermann Schachner, through Creative Commons.

Mylia taylorii (Figure 127-Figure 142) requires at least 120-140 wet days per year, a condition found in sessile oak (***Quercus petraea***; Figure 150) and downy birch (***Betula pubescens***; Figure 151) forests of the western UK (Ratcliffe 1968). It also occupies deep, wet bogs, but prefers sites where the ***Sphagnum*** (Figure 137) is unhealthy or has limited growth. It is interesting that Bakalin *et al*. (2009) found it in limestone habitats in Russia, whereas Ratcliffe and many other authors describe it as a calcifuge. Gaddy (2002) likewise reported ***Mylia taylorii*** from a montane acidic cliff, as well as on a spray cliff.

Figure 150. ***Quercus petraea*** forest, a habitat that typically provides the 120-140 wet days required by ***Mylia taylorii***. Photo by Gruban, through Creative Commons.

Figure 151. ***Betula pubescens*** forest, a habitat that typically provides the 120-140 wet days required by ***Mylia taylorii***. Photo by Dan Aamlid, through Creative Commons.

Juutinen *et al*. (2016) reported ***Mylia taylorii*** (Figure 127-Figure 142) from scree and stones at Kuusamo, Finland. Härtel *et al*. (2007) also considers this to be a liverwort of "rock cities."

Mylia taylorii (Figure 127-Figure 142) is a calcifuge, but it is able to live on rotten logs in calcareous areas (Olleck *et al*. 2020), finding there both acidic conditions and moisture. Perhaps there were mediating factors that provided acidic microhabitats with acidic conditions that could explain the report by Bakalin *et al*. (2009). Another possibility is that there are ecological races.

Its intolerance for desiccation explains the distribution of ***Mylia taylorii*** (Figure 127-Figure 142) in wet environments. At 85% relative humidity, about 75% of the cells remain alive (Clausen 1964). At 75% relative humidity, few cells remain alive. After 4-5 days at -10ºC in ice, only about 1/4 of the cells remain alive.

Adaptations

Many populations exhibit red coloration (Figure 152). Such coloration is usually an indication of stress, typically bright light or low temperatures or a combination of these. Nutrient stress could also be a factor. Research is needed to determine the stimulus for the coloration in this species.

Figure 152. ***Mylia taylorii*** exhibiting red coloration that typically is an indication of stress, including bright sunlight. Photo by Štěpán Koval, with permission.

Reproduction

In Finland where it grows on rock scree, ***Mylia taylorii*** (Figure 127-Figure 142) produces gemmae (Figure 153) on the margins of the upper leaves.

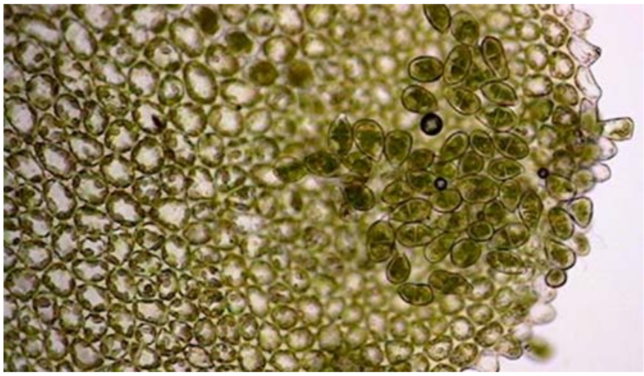

Figure 153. ***Mylia taylorii*** gemmae on leaf. Photo by Paul G. Davison, with permission.

Fungal Interactions

Mylia taylorii (Figure 127-Figure 142) is an indicator species for ravine myxomycetes, at least in parts of Germany (Schnittler *et al.* 2010). This liverwort was present in 64% of the myxomycete habitats in Saxonian Switzerland (Germany). And 96% of the records for the myxomycete ***Colloderma robustum*** (Figure 154) were associated with ***Mylia taylorii***. The liverwort turfs in this region are restricted to the deepest parts of the ravines where the climate is most uniform (Schnittler *et al.* 2010). The myxomycete plasmodium of ***Colloderma robustum*** lives in these turfs that are typically 2-5 cm thick. ***Colloderma robustum*** often has 500-1000 plasmodiocarps on a single ***Mylia taylorii*** turf of 10-20 cm diameter. The plasmodia are initially creamy-white, hiding within the turfs along with green algae. In about 2-3 weeks before fructification, these plasmodia emerge, later turning to a sulfur-yellow color. They then start to form their plasmodiocarps at the tips of the ***M. taylorii*** shoots and secrete a solid translucent slime sheath.

Figure 154. ***Colloderma robustum***, a common slime mold on ***Mylia taylorii*** in ravines. Photo by Sarah Lloyd, with permission.

Unlike ***Mylia anomala*** (Figure 93-Figure 102), ***Mylia taylorii*** (Figure 127-Figure 142) has normal rhizoids (Figure 155-Figure 156), indicating the absence of the ascomycete fungi that invade ***Mylia taylorii*** (Duckett *et al.* 1991).

Schnittler *et al.* (2010) observed that ***Mylia taylorii*** turfs (Figure 156) grow thicker each year. Eventually their weight causes them to drop from the rock and the growth cycle starts over. The result is that if a rock exceeds 60º inclination, it will not achieve more than 50% cover by this species due to this periodic loss.

Biochemistry

Matsuo *et al.* (1977) identified a new tetracyclic sesquiterpene ketone from ***Mylia taylorii*** (Figure 127-Figure 142). Later, the structure of another sesquiterpene ketone was described (Matsuo *et al.* 1979). Reuß *et al.* (2004) identified essential oils in this species.

Figure 155. ***Mylia taylorii*** rhizoids on ventral side of stem (**left**) and with underleaf (**right**). Photo by Paul G. Davison, with permission.

Figure 156. ***Mylia taylorii*** forming a turf, showing rhizoids along stem. Photo by Michael Lüth, with permission.

Suborder Perssoniellineae

Schistochilaceae

Schistochila aligera (Figure 157)

Distribution

Schistochila aligera (Figure 157) is distributed in Asia and Melanesia (So 2003a). It occurs in Indonesia, Java, Philippines, Fiji Islands, Samoa Islands, New Guinea, Tahiti, Cook Islands, New Caledonia, and Vanuatu (So 2003b). Daniels and Daniels (2008) have rediscovered it in India. More recently it has been reported from Thailand, where it is the most common species in the genus (Juengprayoon *et al*. 2015). Gao and Wu (2004) reported it from Taiwan and Hainan. But like so many tropical species, it is extremely variable and thus has been known by a number of names now considered synonyms.

Figure 157. ***Schistochila appendiculata***; ***Schistochila aligera*** occurs mostly in Asia and Ruttner (1955) listed it as aquatic in the tropics. Photo by Larry Jensen, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported this species as an aquatic species in the tropics. In Thailand it is epiphytic or lithophilic (Juengprayoon *et al*. 2015). Similarly, Gao and Wu (2004) described it from old trunks and decayed wood in Taiwan and Hainan. In Sulawesi, Indonesia, ***Schistochila aligera*** (Figure 157) forms one of three distinctive associations on bark (Gradstein & Culmsee 2010). We need to gather more information on its habitats and to determine just what sort of "aquatic" habitat it can occupy.

Reproduction

Schistochila aligera (Figure 157) can be **dioicous** or **autoicous** (Daniels & Daniels 2008), suggesting that it needs more biochemical and genetic studies to look for races and subspecies. Nagashima *et al*. (1991) identified diterpenoids in this species from Japan. Similarly Ludwiczuk and Asakawa (2008) reported pimarane-type diterpenoids from ***Schistochila aligera*** in Malaysia. Secondary compounds from ***Schistochila aligera*** from China and Mongolia have evidenced antibacterial activity against several species of bacteria (Zhu *et al*. 2006).

Fungal Interactions

An ***Octosporella***-like ascomycete (Figure 27-Figure 29) forms appressoria and haustoria on the leaves of ***Schistochila aligera*** (Figure 157) (Döbbeler 1978, 1997). However, there are no records of rhizoid infections on this liverwort (Pressel *et al*. 2008).

Summary

Members of the **Plagiochilaceae** and other families included here are mostly terrestrial, but some are restricted to or common in wet habitats, occupying stream banks, spray areas, and wetlands. The family is large, especially in the tropics, so the few presented here are only a small segment of the family.

Trichocolea tomentella occurs in fens, on streambanks, and in wet spots in forests.

Mylia anomala is predominantly a bog/poor fen species and other acidic habitats. ***Mylia taylorii*** seems to be restricted to non calcareous habitats in most of its range, but occupies limestone in Russia – a contrast that needs further study.

A number of the aquatic liverworts in these jungermannialian families have fungi on the surface or in the cells. The interactions of these fungi are not well known, but there is evidence that for some the bryophyte stimulates the fungus to produce antibiotic compounds that are active against some kinds of cancer cells.

Acknowledgments

Lars Söderström provided me with the current acceptable names for a number of older taxa. Peter Döbbeler and George Greiff provided me with needed images and references. Many images came from the internet, and I thank all who have put their images in Creative Commons or given me permission to use their images.

Literature Cited

Akiyama, H. 1992. Rheophytes of bryophytes in wet tropics of Southeastern Asia. Nat. Environ. Sci. Res 5: 43-55.

Albinsson, C. 1997. Niche relations and association analysis of southern Swedish mire hepatics. J. Bryol. 19: 409-424.

Alegro, A., Papp, B., Szurdoki, E., Šegota, V., and Šapić, I. 2014. Contributions to the bryophyte flora of Croatia III. Plitvička jezera National Park and adjacent areas. Stud. Bot. Hung. 45: 49-65.

Ali, T. A. H. 2017. New and bioactive compounds from *Penicillium concentricum*, an endophytic fungus of the liverwort *Trichocolea tomentella*. Doctoral dissertation, Ohio State University, Columbus, OH, USA, 303 pp.

Ali, T., Inagaki, M., Chai, H. B., Wieboldt, T., Rapplye, C., and Rakotondraibe, L. H. 2017. Halogenated compounds from directed fermentation of *Penicillium concentricum*, an endophytic fungus of the liverwort *Trichocolea tomentella*. J. Nat. Prod. 80: 1397-1403.

Anaya-Eugenio, G. D., Ali, T., Rakotondraibe, L. H., and Carcache de Blanco, E. 2019. Cytotoxic constituents from *Penicillium concentricum*, an endophytic fungus from *Trichocolea tomentella*. Anti-Cancer Drugs 30: 323-329.

Anton, H., Kraut, L., Mues, R., and Maria, I. M. 1997. Phenanthrenes and bibenzyls from a *Plagiochila* species. Phytochemistry 46: 1069-1075.

Asakawa, Y., Inoue, H., Toyota, M., and Takemoto, T. 1980. Sesquiterpenoids of fourteen *Plagiochila* species. Phytochemistry 19: 2623-2626.

Asakawa, Y., Toyota, M., Takemoto, T., and Mues, R. 1981. Aromatic esters and terpenoids of the liverworts in the genera *Trichocolea*, *Neotrichocolea* and *Trichocoleopsis*. Phytochemistry, 20(12), 2695-2699.

Bakalin, V. A., Ignatov, M. S., Ignatova, E. A., and Teleganova, V. V. 2009. Bryophytes of "Gora Vaida" State Nature Monument (Sakhalin, Russian Far East). Arctoa 18: 217-224.

Baláži, P., Mišíková, K., and Tóthová, L. 2010. Machorasty ako súčasť spoločenstva vodných makrofytov na vybraných monitorovaných lokalitách tečúcich vôd Slovenska. [Bryophytes as a part of the community of aquatic macrophytes in selected monitored locations of flowing waters of Slovakia.]. Acta Environ. Univ. Comenianae (Bratislava) 18: 2: 63-78.

Bambe, B. 2004. Spruce forest plant communities with *Trichocolea tomentella* (Ehrh.) Dum. Forest Sci. 1346: 119-128.

Barlow, A. J., Becker, H., and Adam, K. P. 2001. Biosynthesis of the hemi-and monoterpene moieties of isoprenyl phenyl ethers from the liverwort *Trichocolea tomentella*. Phytochemistry 57: 7-14.

BBS. 2020. <https://rbg-web2.rbge.org.uk/bbs/Activities/liverworts/Pedinophyllum%20interruptum.pdf>.

Beaucourt, N., Alvaro, A. G., Abaigary, J. M., and Olivera, E. N. 1987. Diversidad de briofitos en acequias de riego. Un avance. [Diversity of bryophytes in irrigation ditches. A step.]. Bol. Soc. Española Briol. 8: 6-11.

Belland, R. J. and Vitt, D. H. 1995. Bryophyte vegetation patterns along environmental gradients in continental bogs. Ecoscience 2: 395-407.

Bidartondo, M. I. and Duckett, J. G. 2010. Conservative ecological and evolutionary patterns in liverwort–fungal symbioses. Proc. Royal Soc. B Biol. Sci. 277: 485-492.

Bley, K. A. 1987. Moosfloristische und -oekologische Untersuchungen in Fliessgewaessern des Harzes. Herzogia 7: 623-647.

Bosanquet, S. D. S. 2007. *Epibryon plagiochilae* in south Wales: An overlooked British bryophilous fungus. Field Bryol. 91: 24-25.

Cappers, R. T. J., Mook-Kamps, E., Bottema, S., Zanten, B. O. van, and Vlierman, K. 1997. The analysis of caulking material in the study of shipbuilding technology. Palaeohistoria 39/40: 577-590.

Carrigan, C. and Gibson, M. 2004. Stream-rock bryophytes at Cement Creek Turntable, Victoria. Victorian Nat. 121(4): 153-157.

Choi, S. S., Bakalin, V. A., and Sun, B. Y. 2010. Unrecorded liverwort species from Mt. Deogyu, Korea. Korean J. Plant Tax. 40: 218-225.

Chytrý, M. and Tichý, L. 2003. Diagnostic, constant and dominant species of vegetation classes and alliances of the Czech Republic: A statistical revision. Vol. 108, pp. 1-231. Masaryk University, Brno.

Clausen, E. 1964. The tolerance of hepatics to desiccation and temperature. Bryologist 67: 411-417.

Connolly, J. D., Rycroft, D. S., Srivastava, D. L., Cole, W. J., Ifeadike, P., Kimbu, S. F., Singh, J., Hughes, M., Thom, C., Ute, G., Organ, A. J., Smith, R. J., and Harrison, L. J. 1999. Aromatic compounds from the liverwort *Plagiochila spinulosa*. Phytochemistry 50: 1159-1165.

Cronberg, N. 2000a. No difference in isozyme banding patterns between *Plagiochila porelloides* and *P. norvegica*. Lindbergia 25: 17-19.

Cronberg, N. 2000b. Absence of genetic variation in populations of the liverwort *Plagiochila porelloides* from northern Greece and southern Scandinavia. Lindbergia 25: 20-24.

Damsholt, K. 2002. Illustrated Flora of Nordic Liverworts and Hornworts. Nordic Bryological Society, Lund, 837 pp.

Daniels, A. D. 2020. Bryophytes as indicators of human disturbances in tropical rain forests. Contemp. Res. Bryo. 1: 95-102.

Daniels, A. D. and Daniels, P. 2008. The liverwort *Schistochila aligera* (Nees & Blume) J. B. Jack & Steph. (Schistochilaceae) rediscovered in India. Cryptog. Bryol. 29: 307-310.

Daniels, A. E. D. and Kariyappa, K. C. 2012. The liverworts *Mastigophora diclados* and *Plagiochilion oppositum* – New to the hepatic flora of Peninsular India. Nelumbo 54: 207-212.

Davison, P. G., Smith, D. K., Feldberg, K., Lindner, M., and Heinrichs, J. 2006. *Plagiochila punctata* (Plagiochilaceae) in Tennessee, new to North America. Bryologist 109: 242-246.

Diekmann, M. 1995. Delimitation of syntaxa in northern Europe – a case study. Ann. Bot. 53: 65-79.

Dilks, T. J. K. and Proctor, M. C. F. 1974. The pattern of recovery of bryophytes after desiccation. J. Bryol. 8: 97-115.

Dilks, T. J. K. and Proctor, M. C. F. 1979. Photosynthesis, respiration and water content in bryophytes. New Phytol. 82: 97-114.

Döbbeler, P. 1978. Moosbewohnende Ascomyceten. I. Die pyrenocarpen, den Gametophyten besiedelnden. Mitteil. Bot. Staats. München 14: 1-360.

Döbbeler, P. 1980. *Epibryon endocarpum sp. nov.* (Dothideales), ein hepaticoler Ascomycet mit intrazellulären Fruchtkörpern. Zeit. Mykol. 46: 209-216.

Döbbeler, P. 1997. Biodiversity of bryophilous Ascomycetes. Biodiv. Conserv. 6: 721-738.

Döbbeler, P. 1998. *Epibryon pedinophylli* – a new leaf-perforating ascomycete on *Pedinophyllum interruptum* (Hepaticae). Sendtnera 5: 19-25.

Döbbeler, P. and Feuerer, T. 2004. *Stenocybe nitida* (Mycocaliciales), an unusual ascomycete on *Plagiochila punctata*. Biblio. Lichenol. 88: 91-102.

Duckett, J. G., Renzaglia, K. S., and Pell, K. 1991. A light and electron microscope study of rhizoid–ascomycete associations and flagelliform axes in British hepatics with observations on the effects of the fungi on host morphology. New Phytol. 118: 233-257.

Engel, J. J. and Braggins, J. E. 2005. Are *Mylia* and *Trabacellula* (Hepaticae) related? Unsuspected links revealed by cell wall morphology, with the transfer of *Mylia anomala* to a new genus (*Leiomylia* J J Engel & Braggins) of Jungermanniaceae. Taxon 54: 665-680.

Engel, J. J. and Merrill, G. L. 2009. Austral Hepaticae 46. The identity of *Plagiochila retrospectans* (Nees ex Spreng.) Lindenb. and *P. fuscella* (Hook. f. & Taylor) Gottsche, Lindenb. & Nees, two misunderstood Australasian species. Nova Hedw. 89: 287-301.

Evans, A. W. 1910. Notes on New England Hepaticae VIII. Rhodora 12: 193-204.

Farr, G., Graham, J., Marriott, A., and Hamilton, E. 2019. Survey of selected tufa forming sites in Staffordshire, UK. British Geological Survey Internal Report, OR/19/054, 35 pp.

Feld, H., Rycroft, D. S., and Zapp, J. 2004. Chromenes and prenylated benzoic acid derivatives from the liverwort *Pedinophyllum interruptum*. Zeit. Nat. B 59: 825-828.

Fleisch, M. and Engel, J. J. 2006. Stream bryophytes in Victorian rainforest streams. Victorian Nat. 123: 279-281.

Frahm, J.-P. (ed.). 1987. A Guide to bryologically interesting regions in Germany. prepared for a bryological fieldtrip during the XIV Botanical Congress, Berlin.

Frahm, J. P. 2013. A guide to bryological hot spots of the world: The Apuanian Alps (Tuscany, Italy). Univ.-Bibliothek. Arch. Bryol. 188: 7 pp.

Frey, W. and Kürschner, H. 1983. Contributions towards a bryophyte flora of Iran, new records from Iran. Iranian J. Bot. 2(1): 13-19.

Gabriel, R. and Bates, J. W. 2005. Bryophyte community composition and habitat specificity in the natural forests of Terceira, Azores. Plant Ecol. 177: 125-144.

Gaddy, L. L. 2002. Macon, Jackson, and Swain Counties. A Biological Survey for Plant Communities, Wetlands, and Rare Plants Associated with the Duke Power–Nantahala Area Relicensing Project Area. Prepared For Duke Power Company Nantahala Area Charlotte, NC 28201-1224, 35 pp.

Gao, C. and Wu, Y. H. 2004. On seven species of the Schistochilaceae (Hepaticae) in China, including one new species and one new combination. J. Hattori Bot. Lab. 95: 263-270.

GBIF. 2020. Global Biodiversity Information Facility. <https://www.gbif.org/species/search>

Gecheva, G. and Yurukova, L. 2013. Reference aquatic macrophyte communities at rivers in southwestern Bulgaria. Comptes Rendus Acad. Bulgare Sci. Sci. Math. Nat. 66: 223-230.

Gecheva, G., Yurukova, L., Cheshmedjiev, S., and Ganeva, A. 2010. Distribution and bioindication role of aquatic bryophytes in Bulgarian rivers. Biotech. Biotech. Equip. 24(suppl.): 164-170.

Gecheva, G., Yurukova, L., and Ganeva, A. 2011. Assessment of pollution with aquatic bryophytes in Maritsa River (Bulgaria). Bull. Environ. Contam. Toxicol. 87: 6 pp.

Gecheva, G., Yurukova, L., and Cheshmedjiev, S. 2013. Patterns of aquatic macrophyte species composition and distribution in Bulgarian rivers. Turkish J. Bot. 37: 99-110.

Geissler, P. and Selldorf, P. 1986. Vegetationskartierung und Transektenanalyse im subalpinen Moor von Cadagno di Fuori (val Piora, Ticino). [Vegetation mapping and transect analysis in the subalpine bog of Cadagno di Fuori (val Piora, Ticino).]. Saussurea 17: 35-70.

Gerdol, R. 1995. Community and species-performance patterns along an alpine poor-rich mire gradient. J. Veg. Sci. 6: 175-182.

Gerdol, R., Tomaselli, M., and Boiti, I. 1991. Bryophyte flora and vegetation of the glaciokarst plains in the Dolomites (S. Alps, Italy). J. Bryol. 16: 413-427.

Gimingham, C. H. and Birse, E. M. 1957. Ecological studies on growth-form in bryophytes. 1. Correlations between growth-form and habitat. J. Ecol. 45: 533-545.

Glime, J. M. 1968. Ecological observations on some bryophytes in Appalachian Mountain streams. Castanea 33: 300-325.

Glime, J. M. 1970. Zonation of bryophytes in the headwaters of a New Hampshire stream. Rhodora 72: 276-279.

Glime, J. M. 1982. Bryophytes of the flume, Franconia Notch State Park, N. H. Rhodora 84: 149-152.

Glime, J. M. and Vitt, D. H. 1987. A comparison of bryophyte species diversity and niche structure of montane streams and stream banks. Can. J. Bot. 65: 1824-1837.

Glime, J. M., Slack, N. G., and Meston, C. L. 1987. A comparison of the Levins' and Freeman-Tukey niche width measures for the bryophytes in an Adirondack stream. Symp. Biol. Hung. 35: 457-466.

González M., J. M., Albertos, B., Barrón, A., Cezón, K., Cros i Matas, R. M., Draper, I., Estébanez, B., Gariletti, R., Hallingbäck, T., Hernández M., R, Lara G., F., Lima, A. L., Mateo, R. G., Mazimpaka N., V., Muñoz F., J., Medina, R., Medina, N. G., Patiño L., J., Puche, F., Rams, S., Ros E., R. M., and Ruiz, E. 2007. Bryophytes collected by the Spanish Bryological Society during a field trip at La Gomera (Canary Islands). Bol. Soc. Española Briol. 30: 43-52.

González-Mancebo, J. M., Draper, I., Lara, F., Marrero, J. D., Munoz, J., Patino, J., Romaguera, F., and Vanderpoorten, A. 2009. Amendments to the bryophyte flora of the Cape Verde and Canary Islands. Cryptogamie 30: 433-441.

González, E., Rochefort, L., Boudreau, S., Hugron, S., and Poulin, M. 2013. Can indicator species predict restoration outcomes early in the monitoring process? A case study with peatlands. Ecol. Indic. 32: 232-238.

Gradstein, S. R. 2015. New synonyms and new lectotypifications in Neotropical *Plagiochila* (Marchantiophyta). Cryptog. Bryol. 36: 369-379.

Gradstein, R. and Culmsee, H. 2010. Bryophyte diversity on tree trunks in montane forests of Central Sulawesi, Indonesia. Trop. Bryol. 31: 95-105.

Gradstein, S. R., Churchill, S. P., and Salazar-Allen, N. 2001. Guide to the Bryophytes of Tropical America. Mem. N. Y. Bot. Gard. 86: 577 pp.

Gradstein, R., Kien–Thai, Y., Suleiman, M., Putrika, A., Apriani, D., Yuniati, E., Kanak, F. A., Ulum, F. B., Wahyuni, I., Wongkuna, K., Lubos, L. C., Tam, L. T., Puspaningrum, M. R., Serudin, M. R. P. H., Zuhri, M., Min, N. A., Junita, N., Pasaribu, N., and Kornochalert, S. 2010. Bryophytes of Mount Patuha, West Java, Indonesia. Reinwardtia 13(2): 107-123.

Grolle, R. 1998. The gender of *Mnioloma* Herzog and *Plagiochilion* S. Hatt. (Hepaticae). J. Bryol. 20: 497-500.

Grüll, F. and Kvét, J. 1976. Charakteristik der Bodentemperaturen in natürlichen Pflanzengesell-schaften des Mährischen Karstes mit Anwendung der Invertzuckermethode. [Characteristics of the soil temperatures in natural plant communities of the Moravian Karst using the invert sugar method.]. Preslia 48: 247-258.

Gupta, R. K. 1977. A study of photosynthesis and leakage of solutes in relation to the desiccation effects in bryophytes. Can. J. Bot. 55: 1186-1194.

Hackl, T., König, W. A., and Muhle, H. 2006. Three ent-eudesmenones from the liverwort *Plagiochila bifaria*. Phytochemistry 67: 778-783.

Härtel, H., Sádlo, J., Swierkosz, K., and Marková, I. 2007. Phytogeography of the sandstone areas in the Bohemian Cretaceous Basin (Czech Republic/Germany/Poland). Sandstone Landscapes, pp. 177-189.

Hatcher, R. E. 1958. The genus *Trichocolea* in New Zealand. Trans. Royal Soc. N. Z. 85: 237-246.

Heino, J., Virtanen, R., Vuori, K. M., Saastamoinen, J., Ohtonen, A., and Muotka, T. 2005. Spring bryophytes in forested landscapes: Land use effects on bryophyte species richness, community structure and persistence. Biol. Conserv. 124: 539-545.

Heinrichs, J., Grolle, R., and Drehwald, U. 1998a. The conspecificity of *Plagiochila killarniensis* Pearson and *P. bifaria* (Sw.) Lindenb. (Hepaticae). J. Bryol. 20: 495-497.

Heinrichs, J., Gradstein, S. R., and Grolle, R. 1998b. A revision of the Neotropical species of *Plagiochila* (Dumort.) Dumort. (Hepaticae) described by Olof Swartz. J. Hattori Bot. Lab. 85: 1-32.

Heinrichs, J., Anton, H., Gradstein, S. R., Mues, R., and Holz, I. 2000. Surface wax, a new taxonomic feature in Plagiochilaceae. Plant Syst. Evol. 225: 225-233.

Heinrichs, J., Groth, H., Lindner, M., Feldberg, K., and Rycroft, D. S. 2004. Molecular, morphological, and phytochemical evidence for a broad species concept of *Plagiochila bifaria* (Hepaticae). Bryologist 107: 28-40.

Heinrichs, J., Lindner, M., Groth, H., and Renker, C. 2005. Distribution and synonymy of *Plagiochila punctata* (Taylor) Taylor, with hypotheses on the evolutionary history of *Plagiochila* sect. Arrectae (Plagiochilaceae, Hepaticae). Plant Syst. Evol. 250: 105-117.

Hill, M. O., Preston, C. D., and Smith, A. J. E. 1991. Atlas of the Bryophytes of Britain and Ireland, Vol. 1. Liverworts (Hepaticae and Anthocerotae). Brill, Leiden, The Netherlands, 352 pp.

Hiroshi, I. and Asakawa, Y. 1988. Phytochemical Studies on *Plagiochila spinulosa* (Dicks.) Dum. Bull. Nat. Sci. Mus. Ser. B Bot. 14(4): 143-147.

Holmes, N. T. H. and Whitton, B. A. 1975. Submerged bryophytes and angiosperms of the River Tweed and its tributaries. Trans. Bot. Soc. Edinburgh 42: 383-395.

Holz, I., Gradstein, S. R., Heinrichs, J., and Kappelle, M. 2002. Bryophyte diversity, microhabitat differentiation, and distribution of life forms in Costa Rican upper montane *Quercus* forest. Bryologist 105: 334-348.

Hong, W. S. 1992. *Plagiochila* in western North America. Bryologist 95: 142-147.

Hong, W. S. 2007. The hepatic flora and floristic affinity of hepatics around Takakia Lake, Queen Charlotte Islands, British Columbia. Can. Field-Nat. 121: 24-28.

Hughes, J. M. 1986. The relations between aquatic plant communities and lake characteristics on Macquarie Island. N. Z. J. Bot. 24: 271-278.

Hugonnot, V., Celle, J., and Vergne, T. 2013. Bryophytes hyperocéaniques dans les vallons du sud-ouest du Massif Central (France). Cryptog. Bryol. 34: 325-339.

ITIS. 2020. Integrated Taxonomic Information System. Accessed in 2020 at <http://www.itis.gov>.

Juengprayoon, W., Sukkharak, P., and Chantanaorrapint, S. 2015. Genus *Schistochila* Dumort. (Schistochilaceae, Marchantiophyta) in Thailand. Songklanakarin J. Sci. Technol. 37: 409-415.

Juutinen, R., Åkesson, R., Syrjänen, K., and Virtanen, R. 2016. The annual excursion of the Nordic Bryological Society (NBS) and the Finnish Bryophyte Expert Group to Kuusamo (Finland) in 2014. Lindbergia 39: 20-23.

Kelly, D. L. 1981. The native forest vegetation of Killarney, south-west Ireland: An ecological account. J. Ecol. 69: 437-472.

Klama, H., Stebel, A., Salachna, A., and Zubel, R. 2019. Occurrence of *Trichocolea tomentella* (Ehrh.) Dumort. (Marchantiophyta, Trichocoleaceae) in the Polish Carpathians: Distribution, habitat preferences, current threats, and recommendations. Acta Soc. Bot. Polon. 88(3): 6 pp.

Kolattukudy, P. E. 1985. Enzymatic penetration of the plant cuticle by fungal pathogens. Ann. Rev. Phytopath. 23: 223-250.

Konstantinova, N. A. 2011. Contribution to the hepatic flora of the Republic of Dagestan (Eastern Caucasus, Russia). Arctoa 20: 175-182.

Konstantinova, N. A., Bakalin, V. A., Potemkin, A. D., and Ignatov, M. S. 2002. Hepatic flora of the Upper Bureya River (Russian Far East). Arctoa 11: 393-398.

Korpelainen, H., Laitinen, R., and Pohjamo, M. 2004. Lack of intraspecific variation in cpDNA in *Trichocolea tomentella*.nnJ. Bryol. 26: 221-223.

Kowalczyk, A., Przywara, L., and Kuta, E. 1997. *In vitro* culture of liverworts. Acta Biol. Cracoviensia Ser. Bot. 39: 27-33.

Kucyniak, J. 1947. A bryophyte flora of interest on Lac des Cygnes mountain, Québec. Bryologist 50: 327-340.

Kürschner, H., Stech, M., Sim-Sim, M., Fontinha, S., and Frey, W. 2007. Life form and life strategy analyses of the epiphytic bryophyte communities of Madeira's laurel and ericaceous forests. Bot. Jahrb. 127: 151-164.

Liu, N., Li, R.-J., Wang, X.-N., Zhu, R.-X., Wang, L., Lin, Z.-M., Zhao, Y., and Lou, H.-X. 2013. Highly oxygenated ent-pimarane-type diterpenoids from the Chinese liverwort *Pedinophyllum interruptum* and their allelopathic activities. J. Nat. Prod. 76: 1647-1653.

Liu, R., Zhang, Z., Shen, J., and Wang, Z. 2019. Bryophyte diversity in karst sinkholes affected by different degrees of human disturbance. Acta Soc. Bot. Polon. 88(2): 12 pp.

Lorenz, A. 1908. Report on the Hepaticae of Franconia Mountains, NH. Bryologist 11: 112-114.

Lotto, R. 1987. The Wettersteingebirge (Bavarian Alps) by Reinhard Lotto. In: Frahm, J.-P. (ed.). A guide to bryologically interesting regions in Germany. Prepared for a bryological fieldtrip during the XIV Botanical Congress, Berlin 1987.

Ludwiczuk, A. and Asakawa, Y. 2008. Chapter Five: Distribution of terpenoids and aromatic compounds in selected southern hemispheric liverworts. Field. Bot. 47: 37-58.

Ludwiczuk, A. and Asakawa, Y. 2015. Chemotaxonomic value of essential oil components in liverwort species. A review. Flav. Frag. J. 30: 189-196.

Luis, L., Bergamin, A., and Sim-Sim, M. 2015. Which environmental factors best explain variation of species richness and composition of stream bryophytes? A case study from mountainous streams in Madeira Island. Aquat. Bot. 123: 37-46.

Mamczarz, H. 1970. The bryophyte communities in streams near Lacko in the Sadecki Beskid. Ann. Univ. Mariae Curie-Sklodowska, Sec. C Biol. 3. Biol. 25: 105-136.

Marka, J., Papp, B., Erzberger, P., Colacino, C., and Sabovljević, M. 2012. Towards a red list of the Albanian bryophytes. Stud. Bot. Hung. 43: 13-25.

Marsh, T., Döbbeler, P., Huhtinen, S., and Stenroos, S. 2010. Ascomycetes and anamorphic fungi growing on *Plagiochila* (Hepaticae) in Finland. Karstenia 50: 59-72.

Marstaller, R. 1987. Die Moosgesellschaften der Klasse *Platyhypnidio-Fontinalietea antipyreticae* Philippi 1956. 30. Beitrag zur Moosvegetation Thueringens [The moss communities of the class *Platyhypnidio-Fontinalietea antipyreticae* Philippi 1956. 30. Contribution to the Thuringian moss vegetation]. Phytocoenologia 15: 85-138.

Marstaller, R. 2007. Die Moosgesellschaften des Schlossberges zu Lichtenberg (Landkreis Hof, Oberfranken). [The moss societies of Schlossberg to Lichtenberg (Hof district, Upper Franconia).]. Ber. Bayer. Bot. Gesell. 77: 71-92.

Marstaller, R. 2012. Epilithische Moosgesellschaften auf Buntsandstein im Tal der Fränkischen Saale bei Bad Kissingen (Unterfranken). Ber. Bayer. Bot. Gesell. 82: 33-66.

Martinez-Abaigar, J. and Ederra, A. 1992. Brioflora del río Iregua (La Rioja, España). Cryptog. Bryol. Lichenol. 13: 47-69..

Matsuo, A., Nozaki, H., Shigemori, M., Nakayama, M., and Hayashi, S. 1977. (-)-Dihydromylione A, a novel tetracyclic sesquiterpene ketone containing two conjugated cyclopropane rings, from *Mylia taylorii* (liverwort). Experientia 33: 991-992.

Matsuo, A., Sato, S., Nakayama, M., and Hayashi, S. 1979. Structure and absolute configuration of (–)-taylorione, a novel carbon skeletal sesquiterpene ketone of ent-1, 10-seco-aromadendrane form, from *Mylia taylorii* (liverwort). J. Chem. Soc. Perkin Trans. 1: 2652-2656.

Matthews, V. D. 1932. The aquatic vegetation of Quaker Run. J. Elisha Mitchell Sci. Soc. 47: 74-84.

McKnight, B. N. 1985. Notes on the bryophytes of Indiana: I. Additions to the flora. Proc. Indiana Acad. Sci. 95: 101-106.

Miguel, A. de and Indurain, A. E. 1984. Ensayo briosociológico y ecológico de La Foz de Arbayún (Navarra). An. Biol. 2: 257-264.

Matthews, V. D. 1932. The aquatic vegetation of Quaker Run. J. Elisha Mitchell Sci. Soc. 47: 74-84.

Nagashima, F., Tori, M., and Asakawa, Y. 1991. Diterpenoids from the east Malaysian liverwort *Schistochila aligera*. Phytochemistry 30: 849-851.

Nagashima, F., Tanaka, H., Toyota, M., Hashimoto, T., Kan, Y., Takaoka, S., Tori, M., and Asakawa, Y. 1994. Sesqui- and diterpenoids from *Plagiochila* species. Phytochemistry 36: 1425-1430.

Nichols, G. E. 1916. The vegetation of Connecticut. V. Plant societies along rivers and streams. Bull. Torrey Bot. Club 43: 235-264.

Nichols, G. E. 1918. The vegetation of northern Cape Breton Island, Nova Scotia. Trans. Conn. Acad. Arts Sci. 22: 249-467.

Nordbakken, J. F., Ohlson, M., and Högberg, P. 2003. Boreal bog plants: Nitrogen sources and uptake of recently deposited nitrogen. Environ. Pollut. 126: 191-200.

Nunik, S. A. and Gradstein, S. R. 2007. Wallace's line and the distribution of the liverworts of Sulawesi. Cryptog. Bryol. 28: 3-14.

Økland, R. H. 1990. A phytogeographical study of the mire Northern Kisselbergmosen, SE Norway. III. Nordic J. Bot. 10: 191-220.

Olleck, M., Reger, B., and Ewald, J. 2020. Plant indicators for folic histosols in mountain forests of the calcareous Alps. Appl. Veg. Sci. 23: 285-296.

Pakalne, M. and Čakare, I. 2001. Spring vegetation in the Gauja National Park. Latvijas Veģ. 4: 16-33.

Pakarinen, P. 1978. Production and nutrient ecology of three *Sphagnum* species in southern Finnish raised bogs. Ann. Bot. Fenn. 15: 15-26.

Pakarinen, P. and Tolonen, K. 1977. Distribution of lead in *Sphagnum fuscum* profiles in Finland. Oikos 28: 69-73.

Pandža, M. and Milović, M. 2015. Floristic researches of the island of Pašman, Croatia. In: Book of Abstracts. 36th Meeting of Eastern Alpine and Dinaric Society for Vegetation Ecology. Osijek (Croatia), 17-20 June 2015, p. 13.

Papastergiadou, E. 1995. Aquatic vegetation of the Greek wetlands. Ann. Bot. 53: 81-86.

Papp, B. and Erzberger, P. 2011. Additions to the bryophyte flora of the Tara river canyon and the Durmitor area, Montenegro. Stud. Bot. Hung. 42: 31-39.

Papp, B. and Tsakiri, E. 2017. Contributions to the bryophyte flora of the Paiko, Tzena and Pinovo Mts in Greece. Stud. Bot. Hung. 48(1): 33-49.

Papp, B., Ganeva, A., and Natcheva, R. 2006. Bryophyte vegetation of Iskur River and its main tributaries. Phytol. Balcan. 12: 181-189.

Papp, B., Szurdoki, E., Pantović, J., and Sabovljević, M. 2016. Contributions to the bryophyte flora of the Mavrovo National Park (Republic of Macedonia). Stud. Bot. Hung. 47: 279-296.

Paton, J. 1999. The Liverwort Flora of the British Isles. Harley Books, Colchester, 626 pp.

Perry, N. B., Foster, L. M., Lorimer, S. D., May, B. C., Weavers, R. T., Toyota, M., Nakaishi, E., and Asakawa, Y. 1996. Isoprenyl phenyl ethers from liverworts of the genus Trichocolea: Cytotoxic activity, structural corrections, and synthesis. J. Nat. Prod. 59: 729-733.

Pfetzing, J., Stengel, D. B., Cuffe, M. M., Savage, A. V., and Guiry, M. D. 2000. Effects of temperature and prolonged emersion on photosynthesis, carbohydrate content and growth of the brown intertidal alga *Pelvetia canaliculata*. Bot. Marina 43: 399-407.

Pilato, G., Binda, M. G., Napolitano, A., and Moncada, E. 2002. Tardigrades from Ecuador, with the description of two new species: *Mixibius ornatus* n. sp. and *Diphascon* (*Adropion*) *onorei* n. sp. (Eutardigrada, Hypsibiidae). Studies Neotrop. Fauna Environ. 37: 175-179.

Pohjamo, M., Korpelainen, H., and Kalinauskaitė, N. 2008. Restricted gene flow in the clonal hepatic *Trichocolea tomentella* in fragmented landscapes. Biol. Conserv. 141: 1204-1217.

Poulin, M., Andersen, R., and Rochefort, L. 2013. A new approach for tracking vegetation change after restoration: A case study with peatlands. Restor. Ecol. 21: 363-371.

Pressel, S., Ligrone, R., Duckett, J. G., and Davis, E. C. 2008. A novel ascomycetous endophytic association in the rhizoids of the leafy liverwort family, Schistochilaceae (Jungermanniidae, Hepaticopsida). Amer. J. Bot. 95: 531-541.

Preston, C. D., Harrower, C. A., and Hill, M. O. 2011. Distribution patterns in British and Irish liverworts and hornworts. J. Bryol. 33: 3-17.

Preziuso, F., Taddeo, V. A., Genovese, S., Epifano, F., and Fiorito, S. 2018. Phytochemistry of the genus *Trichocolea*. Nat. Prod. Comm. 13: 1205-1207.

Proctor, M. C. F. 1980. Estimates from hemispherical photographs of the radiation climates of some bryophyte habitats. in the British Isles. J. Bryol. 11: 351-366.

Proctor, M. C. F. 1982. Physiological ecology: Water relations, light and temperature responses, carbon balance. In: Smith, A. J. E. Bryophyte Ecology. Springer, Dordrecht, pp. 333-381.

Puczko, K., Zieliński, P., Jusik, S., Kołakowska, A., and Jekatierynczuk-Rudczyk, E. 2018. Vascular plant and bryophyte species richness in response to water quality in lowland spring niches with different anthropogenic impacts. Environ Monit Assess 190: 338.

Qlivan, G. and Fuertes, E. 2000. *Plagiochila spinulosa* new for the Iberian Peninsula and other interesting liverworts for Cantabria (northen Spain). J. Bryol. 22: 149-150.

Rakotondraibe, L. H., Nichols, K., Park, H. Y., Ali, T., Chai, H. B., and Rappleye, C. 2015. Antiproliferative compounds from *Penicillium chrysogenum*, a fungal associate of the liverwort *Trichocolea tomentella*. Planta Med. 81(11), PL3.

Ratcliffe, D. A. 1968. An ecological account of Atlantic bryophytes in the British Isles. New Phytol 67: 365-439.

Reinoso, J. and Rodríguez-Oubiña, J. 1988. *Mylia anomala* (Hook.) Gray y *Kurzia pauciflora* (Dicks.) Grolle en España. Orsis: organismes sistemes 3: 15-19.

Renner, M. A. 2018. A revision of Australian *Plagiochila* (Lophocoleinae: Jungermanniopsida). Telopea 21: 187-380.

Renner, M. A., Heslewood, M. M., Patzak, S. D., Schäfer-Verwimp, A., and Heinrichs, J. 2016. The genera *Chiastocaulon*, *Cryptoplagiochila* and *Pedinophyllum* (Plagiochilaceae) in Australia. *Austral. Syst. Bot. 29:* 358-402.

Renner, M. A., Heslewood, M. M., Patzak, S. D. F., Feldberg, K., Schäfer-Verwimp, A., Rycroft, D. S., and Heinrichs, J. 2017. The New Zealand endemic *Plagiochila caducifolia* is a disjunct population of *Plagiochila spinulosa* (Plagiochilaceae: Jungermanniopsida). N. Z. J. Bot. 55: 276-292.

Reuß, S. H. von, Wu, C.-H., Muhle, H., and König, W. A. 2004. Sesquiterpene constituents from the essential oils of the liverworts *Mylia taylorii* and *Mylia nuda*. Phytochemistry 65: 2277-2291.

Ros, R. M., Cano, M. J., Muñoz, J., and Guerra, J. 2000. Contribution to the bryophyte flora of Morocco: The Jbel Toubkal. J. Bryol. 22: 283-289.

Ruttner, F. 1955. Zur Okologie tropischer Wassermoose. [On the ecology of tropical water moss.]. Arch. Hydrobiol. (Suppl.) 21: 343-381.

Rycroft, D. S. 1990. Some recent NMR studies of diterpenoids from the Hepaticae. In: Zinsmeister, H. D. and Mues, R. (eds.). Bryophytes: Their Chemistry and Chemical Taxonomy. Series: Proceedings of the Phytochemical Society of Europe (29). Oxford University Press, Oxford, pp. 109-119.

Rycroft, D. S. 2008. Structure determination of a 4-pyrone from the liverwort *Plagiochila bifaria* (Sw.) Lindenb. (Plagiochilaceae). In: Mohamed, H., Baki, B. B., Nasrulhaq-Boyce, A., and Lee, P. K. Y. (eds.). Bryology in the New Millennium. University of Malaya, Kuala Lumpur, pp. 395-403.

Rycroft, David. 2021. Pedinophyllum interruptum. Accessed 12 January 2021 at <https://websites.rbge.org.uk/bbs/Activities/liverworts/Pedinophyllum%20interruptum.pdf>.

Rycroft, D. S., Srivastava, D. L., Cole, W. J., Ifeadike, P., Kimbu, S. F., Singh, J., Connolly, J. D., Thom, C., Gerhard, U., Orga, A. J., Smith, R. J., Hughes, M., and Harrison, L. J. 1999. Aromatic compounds from the liverwort *Plagiochila spinulosa*. Phytochemistry 50: 1159-1165.

Rycroft, D. S., Cole, W. J., Heinrichs, J., Groth, H., Renker, C., and Pröschold, T. 2002. Phytochemical, morphological, and molecular evidence for the occurrence of the Neotropical liverwort *Plagiochila stricta* in the Canary Islands, new to Macaronesia. Bryologist 105: 363-372.

Rydgren, K., Stabbetorp, O. E., and Blom, H. H. 2012. Distribution and ecology of *Trichocolea tomentella* in Norway. Lindbergia 35: 1-6.

Salachna, A. 2007. Abstract. A review of main morphological features in European taxa of the genus *Chiloscyphus* Corda (Marchantiophyta, Geocalycaceae). Special issue International Bryological Meeting 2007.

Schnittler, M., Unterseher, M., Pfeiffer, T., Novozhilov, Y. K., and Fiore-Donno, A. M. 2010. Ecology of sandstone ravine myxomycetes from Saxonian Switzerland (Germany). Nova Hedw. 90: 277-302.

Schumacker, R. and Váňa, J. 2000. Identification keys to the liverworts and hornworts of Europe and Macaronesia (distribution and status). Documents de la Station Scientifique des Hautes–Fagnes 31: 1-160.

Schuster, R. M. 1953. Boreal Hepaticae. A Manual of the Liverworts of Minnesota and Adjacent Regions. Amer. Midl. Nat. 49: 257-683.

Schuster, R. M. 1980. The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian. Vol. IV. Columbia University press, New York and London, 1334 pp.

Shevock, J. R., Ma, W. Z., and Akiyama, H. 2017. Diversity of the rheophytic condition in bryophytes: Field observations from multiple continents. Bryol. Divers. Evol. 39: 75-93.

Shishkonakova, E. A., Avetov, N. A., and Tolpysheva, T. Y. 2016. Peat soils of boreal regressive bogs in West Siberia: Problems of biological diagnostics and systematics. Dokuchaev Soil Bull. 84: 61-74.

Sim-Sim, M., Esquível, M. D. G., Fontinha, S., and Stech, M. 2005a. The genus *Plagiochila* (Dumort.) Dumort. (Plagiochilaceae, Hepaticophytina) in Madeira Archipelago – Molecular relationships, ecology, and biogeographic affinities. Nova Hedw. 81: 449-462.

Sim-Sim, M., Carvalho, S., Fontinha, S., Lobo, C., Esquível, M. G., and Figueiredo, A. C. 2005b. Diversity of Bryophytes – Useful indicators of Madeira Laurel forest conservation. Monitoring and Indicators of Forest Biodiversity in Europe– From Ideas to Operationality, pp. 247-257.

Sim-Sim, M., Stech, M., Esquivel, M. G., Figueiredo, A. C., Costa, M. M., Barroso, J. G., Pedro, L. G., Fontinha, S., and Lobo, C. 2005c. *Plagiochila spinulosa* (Dicks.) Dumort. (Plagiochilaceae, Hepaticophytina) in Madeira Island – Morphological, phytochemical, and molecular evidence. J. Hattori Bot. Lab. 98: 131-147.

Slack, N. G. and Glime, J. M. 1985. Niche relationships of mountain stream bryophytes. Bryologist 88: 7-18.

So, M. L. 2003a. The genus *Schistochila* in Asia. J. Hattori Bot. Lab. 93: 79-100.

So, M. L. 2003b. *Schistochila* (Hepaticae) in Oceania. N. Z. J. Bot. 41: 255-275.

So, M. L. and Grolle, R. 2000. Studies on *Plagiochila* sect. *Plagiochila* (Hepaticae) in East and South Asia. J. Bryol. 22: 17-28.

Söderström, L., Rycroft, D. S., Cole, W. J., and Wei, S. 1999. *Plagiochila porelloides* (Plagiochilaceae, Hepaticae) from Changbai Mountain, new to China, with chemical characterization and chromosome measurements. Bryobrothera 5: 195-201.

Soriano, G., Del-Castillo-Alonso, M. Á., Monforte, L., Núñez-Olivera, E., and Martínez-Abaigar, J. 2019. Phenolic compounds from different bryophyte species and cell compartments respond specifically to ultraviolet radiation, but not particularly quickly. Plant Physiol. Biochem. 134: 137-144.

Sotiaux, A. and Vanderpoorten, A. 2017. A checklist of the bryophytes of Andorra. J. Bryol. 39: 353-367.

Sotiaux, A., Stieperaere, H., and Vanderpoorten, A. 2007. Bryophyte checklist and European red list of the Brussels-Capital region, Flanders and Wallonia (Belgium). Belg. J. Bot. 140: 174-196.

Stenroos, S., Laukka, T., Huhtinen, S., Döbbeler, P., Myllys, L., Syrjänen, K., and Hyvönen, J. 2010. Multiple origins of symbioses between Ascomycetes and bryophytes suggested by a five-gene phylogeny. Cladistics 26: 281-300.

Suleiman, A. A. A. and Lewis, D. H. 1980. Carbohydrate metabolism in the leafy liverwort, *Plagiochila asplenioides* (L.) Dum. var. *major* Nees. New Phytol. 84: 45-58.

Suleiman, A. A. A., Gadsden, M., Sutcliffe, T. P., and Lewis, D. H. 1980. Photosynthetic products in leafy liverworts and their taxonomic significance. J. Bryol. 11: 161-168.

Suren, A. M. 1988. The ecological role of bryophytes in high alpine streams of New Zealand. Internat. Verein. Theoret. Ange. Limnol. Verh. 23: 1412-1416.

Suren, A. M. 1991. Bryophytes as invertebrate habitat in two New Zealand alpine streams. Freshwat. Biol. 26: 399-418.

Suren, A. M. 1996. Bryophyte distribution patterns in relation to macro-, meso-, and micro-scale variables in South Island, New Zealand streams. N. Z. J. Marine Freshwat. Res. 30: 501-523.

Suren, A. M. and Winterbourn, M. J. 1991. Consumption of aquatic bryophytes by alpine stream invertebrates in New Zealand. N. Z. J. Marine Freshwat. Res. 25: 331-343.

Tacchi, R., Miserere, L., and Aleffi, M. 2009. Ecological aspects of the bryoflora of some ravines of the Umbro-Marchegian Apennines. Plant Biosyst. 143(suppl): 88-96.

Toyota, M., Nakamura, I., Huneck, S., and Asakawa, Y. 1994. Sesquiterpene esters from the liverwort *Plagiochila porelloides*. Phytochemistry 37: 1091-1093.

Tremp, H. and Kohler, A. 1991. Passives Monitoring mit Wassermoosen zur Überwachung der Versauerungsdynamik in pufferschwachen Fließgewässern Erste Ergebnisse. [Passive monitoring with water mosses to monitor acidification dynamics in low-buffer waters. First results.]. Verh. Gesell. Ökol. 20: 529-535.

TROPICOS. 2020. Missouri Botanical Garden. 27 Aug 2020 <http://www.tropicos.org>

Väliranta, M., Korhola, A., Seppä, H., Tuittila, E. S., Sarmaja-Korjonen, K., Laine, J., and Alm, J. 2007. High-resolution reconstruction of wetness dynamics in a southern boreal raised bog, Finland, during the late Holocene: A quantitative approach. Holocene 17: 1093-1107.

Veljié, M., Marin, P. D., Boza, P., and Petkovié, B. 2001. Bryoflora of some well-springs of the Dinaric Alps and Carpathian Karst in Serbia. Bocconea 13: 343-351.

Vieira, C., Sérgio, C., and Séneca, A. 2004. Threatened bryophytes occurrence in Portuguese stream habitat. Accessed 29 February 2020 at <https://www.researchgate.net/publication/28145237_Threatened_bryophytes_occurrence_in_Portuguese_stream_habitat>.

Vieira, C., Sérgio, C., and Séneca, A. 2005. Threatened bryophytes occurrence in Portuguese stream habitat. Bol. Soc. Esp. Briol. 26-27: 103-118.

Virtanen, V. 1995. Floristic composition and habitat ecology of stream bryophytes in Lohja parish, southern Finland. Ann. Bot. Fenn. 32: 179-192.

Vitt, D. H., Glime, J. M., and LaFarge-England, C. 1986. Bryophyte vegetation and habitat gradients of montane streams in western Canada. Hikobia 9: 367-385.

Wang, B. and Qiu, Y. L. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16: 299-363.

Watson, W. 1918. The bryophytes and lichens of calcareous soil. J. Ecol. 6: 189-198.

Watson, W. 1919. The bryophytes and lichens of fresh water. J. Ecol. 7: 71-83.

Watson, W. 1925. The bryophytes and lichens of arctic-alpine vegetation. J. Ecol. 13: 1-26.

Watson, E. V. 1965. British Mosses and Liverworts. Cambridge University Press, Cambridge, 419 pp.

Weber, D. P. 1976. The Bryophytes of Cataracts Provincial Park, Newfoundland. M.S. thesis, Department of Biology, Memorial University of Newfoundland, 85 pp.

Weber, D. P. and Brassard, G. R. 1976. Bryophytes of Cataracts Provincial Park, Newfoundland: ecology and phytogeography. Can. J. Bot. 54: 1697-1708.

Wei, W., Li, Y., Li, H., Ma, K., Wang, L., and Gao, K. 2019. Phytotoxic diterpenoids from plants and microorganisms. Chem. Biodiv. 16(10), e1900398.

Wells, R. D., Clayton, J. S., and Winton, M. D. de. 1998. Submerged vegetation of Lakes Te Anau, Manapouri, Monowai, Hauroko, and Poteriteri, Fiordland, New Zealand. N. Z. J. Marine Freshwat. Res. 32: 621-638.

West, G. 1910. An epitome of a comparative study of the dominant phanerogamic and higher cryptogamic flora of aquatic habit, in seven lake areas of Scotland. In: Murray, J. Bathymetrical Survey of the Scottish Fresh-water Locks, Conducted Under the Direction of Sir John Murray… and Laurence Pullar… During the Years 1897 to 1909. Report on the Scientific Results. Edinburgh, Challenger Office, pp. 156-260.

Wikipedia. 2020. *Mylia taylorii*. Last updateded 15 July 2020. Accessed 10 September 2020 at <https://en.wikipedia.org/wiki/Mylia_taylorii>.

Zehr, D. R. 1977. An autecological investigation of selected bryophytes in three sandstone canyons in southern Illinois. Bryologist 80: 571-583.

Zehr, D. R. 1979. Phenology of selected bryophytes in southern Illinois. Bryologist 82: 29-36.

Zhang, Z. H. and Chen, J. K. 2006. Marchantiophyta and Anthocerophyta in Guizhou province, PR China. J. Bryol. 28: 170-176.

Zhu, R. L., Wang, D., Xu, L., Shi, R. P., Wang, J., and Zheng, M. 2006. Antibacterial activity in extracts of some bryophytes from China and Mongolia. J. Hattori Bot. Lab. 100: 603-615.