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CHAPTER 1-11: AQUATIC AND WET MARCHANTIOPHYTA, ORDER METZGERIALES: ANEURACEAE

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Figure 1. ***Aneura pinguis*** growing in a zone that is just above and below the water surface, keeping it constantly wet. Photo by Michael Lüth, with permission.

As in the other chapters on liverworts in aquatic and wet habitats, nomenclature for this chapter is based primarily on Söderström *et al*. (2016). In addition, Lars Söderström has provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. Information on habitats of these unverifiable taxa has been included with the species.

Many of the species on this list are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study.

SUBCLASS METZGERIIDAE

Order Metzgeriales

Aneuraceae (Figure 1)

Aneura (Figure 2, Figure 3, Figure 7-Figure 10, Figure 18-Figure 26, Figure 29-Figure 32, Figure 52-Figure 57)

In a study of 48 streams on South Island, New Zealand, Suren and Duncan (1999) found that ***Aneura*** sp. was positively correlated with bankfull discharge. This genus has several species that are typically associated with water.

Bidartondo and Duckett (2010) found sebacinoid fungi in several species of ***Aneura***.

Aneura maxima (Figure 2, Figure 3, Figure 7-Figure 10; Figure 18-Figure 26)

The species ***Aneura maxima*** (Figure 2, Figure 3, Figure 7-Figure 10), ***A. pellioides*** (Figure 4), and ***A. pinguis*** (Figure 5-Figure 6) have created confusion in their identification (Frahm 2012). Frahm (2012) used water culture to determine if characters are modified by the culture conditions. This was done to understand the distinctions among several ***Aneura*** species. The unilayered thallus margin was retained in ***Aneura maxima*** (Figure 3) and the multilayered thallus margin was retained in ***Aneura pinguis*** in common garden culture of aquatic and terrestrial conditions.

Figure 2. ***Aneura maxima***, one of three species that have been confused with each other. Photo by Jan-Peter Frahm, with permission.

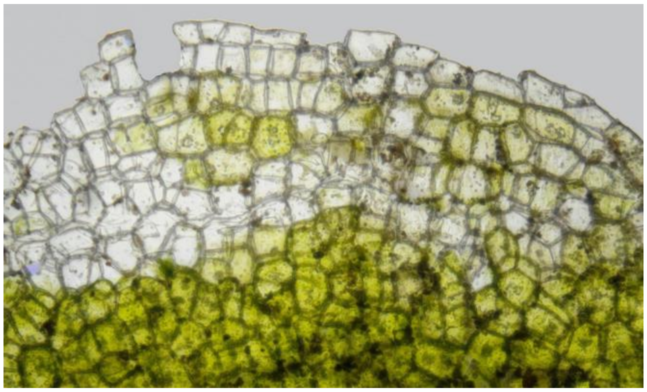

Figure 3 ***Aneura maxima*** showing 1-cell-thick thallus margin. Photo by Dick Haaksma, with permission.

Figure 4. ***Aneura** cf **pellioides***, one of three species that have been confused with each other. Photo by David Long, with permission.

Figure 5. ***Aneura pinguis***, one of three species that have been confused with each other. Photo by Hermann Schachner, through Creative Commons.

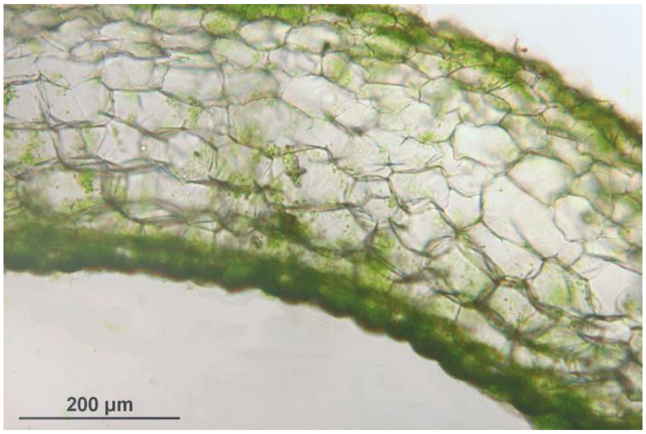

Figure 6. ***Aneura pinguis*** thallus cross section. Photo by Hermann Schachner, through Creative Commons.

Bączkiewicz *et al*. (2017) used DNA evidence to argue that ***Aneura pinguis*** (Figure 5-Figure 6) was comprised of many cryptic species, including ***Aneura maxima*** (Figure 2-Figure 3, Figure 7-Figure 10). I have treated the ones included here as separate species for two reasons. It is easy for the reader to combine the information to describe ***Aneura pinguis***, but once combined under one name it cannot be separated out without further research. Second, I have followed the nomenclature used by Söderström *et al*. (2016) throughout these wet habitat chapters, and they have listed it as a valid species. Furthermore, Buczkowska *et al*. (2016) demonstrated, using ISSR primers, that the ***Aneura maxima*** populations were genetically distinct from those of ***A. pinguis*** and these researchers maintained recognition of the species ***Aneura maxima***.

Distribution

Andriessen (1995) reported ***Aneura maxima*** (Figure 7-Figure 10) from Belgium in Europe, Asia (Indonesia, Japan, India), New Caledonia, and eastern North America. Miller (2002) noted its presence in Maine, and a number of other states in eastern USA. In 2006, Loskotová reported it from the Czech Republic and Slovakia. Later, Sérgio and Garcia (2009) reported it from the Iberian Peninsula, Frahm (2011) from Norway, Ştefănuţ (2012) from Romania, and Buczkowska and Byczkiewicz (2006) from Poland (see also Mierzeńska & Vončina 2010; Wawrzyniak *et al*.

2014). Frahm *et al*. (2009) reported it from Thailand. It is likely to have been collected elsewhere in Europe, hiding under a misidentified name.

Figure 7. ***Aneura maxima*** showing the wavy edge of the thallus. Photo by Hugues Tinguy, with permission.

Figure 8. ***Aneura maxima*** thallus. Photo by Dick Haaksma, with permission.

Figure 9. ***Aneura maxima*** showing new lobes. Photo by Jiří Kameníček, with permission.

Figure 10. ***Aneura maxima*** with upward-growing branching lobes. Photo by Jiří Kameníček, with permission.

Currently, neither TROPICOS nor Söderström *et al*. (2016) consider ***Aneura pellioides*** (Figure 4) a valid species, with the former listing it as a synonym of ***Aneura maxima*** (Figure 7-Figure 10).

Aquatic and Wet Habitats

Loskotová (2006) reported ***Aneura maxima*** (Figure 7-Figure 10) as most frequently occurring on wet mineral soil in spring habitats in Slovakia and the Czech Republic. The individual plants grow vertically upward (Figure 9-Figure 10) from the water, forming compact growths that resemble lettuce. It is a more robust species than common ***Aneura pinguis*** (Figure 5-Figure 6). It frequently occurs with ***Brachythecium rivulare*** (Figure 11), ***Chiloscyphus pallescens*** (Figure 12), ***Conocephalum conicum*** (Figure 13), ***Thuidium tamariscinum*** (Figure 14), and ***Trichocolea tomentella*** (Figure 15).

Figure 11. ***Brachythecium rivulare*** habitat, a species that sometimes accompanies ***Aneura maxima***. Photo by Michael Lüth, with permission.

Figure 12. ***Chiloscyphus pallescens***, a liverwort species that sometimes accompanies ***Aneura maxima***. Photo by Michael Lüth, with permission.

Figure 13. ***Conocephalum conicum*** by a stream from Poland where it can be associated with ***Aneura maxima***. Photo by Panek, through Creative Commons.

Figure 14. ***Thuidium tamariscinum***, a species that sometimes accompanies ***Aneura maxima***. Photo by David T. Holyoak, with permission.

In Poland, Buczkowska and Byczkiewicz (2006) found that ***Aneura maxima*** (Figure 7-Figure 10) was similarly associated with ***Conocephalum conicum*** (Figure 13) and ***Trichocolea tomentella*** (Figure 15). At other locations it occurred with ***Pellia epiphylla*** (Figure 16) or ***Pellia epiphylla*** subsp. ***borealis***. In all its locations, it was accompanied by cryptic species of ***A. pinguis*** (Figure 5-Figure 6). However, the substrata differed. ***Aneura maxima*** occurred on wet humus, peaty soil, a mire on river banks, and wet peaty soil of alder swamps. Jan-Peter Frahm photographed its habitat in a ravine near a lake (Figure 17)

Figure 15. ***Trichocolea tomentella***, a species that can be associated with ***Aneura maxima*** in Poland. Photo by Li Zhang, with permission.

Figure 16. ***Pellia epiphylla*** with developing sporophytes, a species that sometimes associates with ***Aneura maxima*** in Poland. Photo by Hermann Schachner, through public domain.

Figure 17. ***Aneura maxima*** habitat where a ravine enters a lake. Photo by Jan-Peter Frahm, with permission.

Schuster (1992) added habitats under waterfalls for some ***Aneura maxima*** (Figure 7-Figure 10) populations in North Carolina, USA. Furuki (2006) reported it from decaying logs in the mossy forest of the Philippines.

Vanderpoorten *et al*. (2006) developed a model to assess the rareness of ***Aneura maxima*** (Figure 7-Figure 10). They found that its localities in deep ravines on damp loamy soils (Figure 18-Figure 20) with light tree cover on the border between France and Belgium differed from conditions in other European localities. They considered this as evidence that it is not limited by a narrow ecological range. Rather, they considered it to be limited by poor dispersal ability. It is thus threatened by drainage of its preferred wet habitats.

Figure 18. ***Aneura maxima*** on a soil habitat. Photo by Dick Haaksma, with permission.

Figure 19. ***Aneura maxima*** in a habitat on soil. Photo by Dick Haaksma, with permission.

Figure 20. ***Aneura maxima*** in its habitat on soil. Photo by Dick Haaksma, with permission.

Adaptations

Aneura maxima has large, fleshy thalli that are deep green when fresh (Figure 21-Figure 22), pale brown when dry (Furuki 2006). These thalli sometimes grow upright (Figure 21), and they have pale margins that are one cell thick (Figure 23). The uppermost cells are lens-shaped and translucent (Figure 24-Figure 25), possibly focussing the light on the chloroplasts beneath.

Figure 21. ***Aneura maxima*** growing in upright clumps of fleshy thalli. Photo by Jiří Kameníček, with permission.

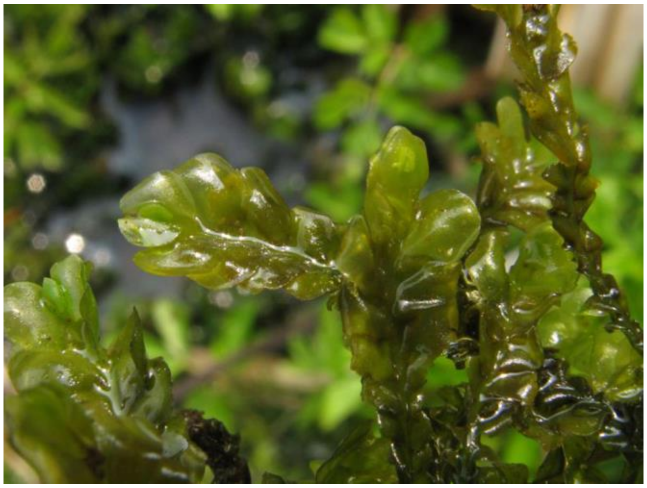

Figure 22. ***Aneura maxima*** showing its wavy margin and upright growth form. Photo by Jiří Kameníček, with permission.

Figure 23. ***Aneura maxima*** with translucent thallus wings. Photo by Jan-Peter Frahm, with permission.

Figure 24. ***Aneura maxima*** thallus showing lens-like upper cells. Photo by Dick Haaksma, with permission.

Figure 25. ***Aneura maxima*** showing lens-like upper cells that could focus light on the cells below. Photo by Dick Haaksma, with permission.

Reproduction

Aneura maxima (Figure 7-Figure 10) is **dioicous** and rarely fertile (Vanderpoorten *et al*. 2006). Gemmae are unknown (Preußing *et al*. 2010b). This combination seems to be responsible for its rarity. It is possible that the lobes (Figure 26) break off to form new plants and could even be dispersed short distances.

Figure 26. ***Aneura maxima*** with potentially reproductive branches. Photo by Jiří Kameníček, with permission.

Fungal Interactions

Duckett and Ligrone (2008) noted that whereas most species of ***Aneura*** have fungi, ***Aneura maxima*** (Figure 7-Figure 10) had never been investigated. Likewise, Bidartondo and Duckett (2010) were unable to find any associated with ***Aneura pellioides*** (Figure 4)/***maxima*** (Figure 7-Figure 10).

Biochemistry

Wawrzyniak *et al*. (2014) reported that volatile sesquiterpenoids, oxygenated sesquiterpenoids, and aliphatic hydrocarbons differed among the cryptic species within the ***Aneura pinguis*** (Figure 5-Figure 6) complex and ***Aneura maxima*** (Figure 7-Figure 10). They found that such compounds in all of the cryptic species within ***A. pinguis*** differed from those of ***A. maxima***.

Aneura mirabilis (Figure 29-Figure 32)

(syn. = *Cryptothallus mirabilis*)

This is perhaps the most unusual of all bryophytes because it is parasitic and totally lacking in chlorophyll.

Davis (2004) asserted that *Cryptothallus mirabilis* (Figure 27) was related to ***Aneura*** (Figure 7-Figure 10), a genus in the same family. Soon after that, Wickett *et al*. (2008a; Wickett & Goffinet 2008) used plastid genome sequencing to demonstrate the close relationships of the species to members of ***Aneura***. This **achlorophyllous** (lacking chlorophyll) species revealed loss of five chlororespiration (*ndh*) genes (Wickett *et al*. 2008a) compared to those of ***Marchantia polymorpha*** (Figure 28) (Wickett *et al*. 2008b), the only other liverwort with a completely sequenced chloroplast genome. Furthermore, six *ndh* genes that are subunits of PS I, PS II, and the cytochrome *b6f* complex were inferred to be **pseudogenes** (sections of chromosome that are imperfect copies of functional gene) (Wickett *et al*. 2008a). Bączkiewicz *et al*. (2017) used DNA barcoding to demonstrate the strong relationship between what was named *Cryptothallus mirabilis* and members of the genus ***Aneura***. Based on these studies, the species has been placed in ***Aneura*** as ***Aneura mirabilis*** (Figure 27, Figure 29-Figure 32).

Figure 27. ***Aneura mirabilis*** showing the many small branches typical of ***Aneura***, but totally lacking chlorophyll. Photo by Jan-Peter Frahm, with permission.

Figure 28. ***Marchantia polymorpha***, a thallose liverwort that has had its entire genome, including the chloroplast genome, sequenced. Photo by Holger Casselmann, through Creative Commons.

Distribution

Aneura mirabilis (Figure 29-Figure 32) is primarily a north oceanic species, but it is known as far south as Portugal (Sérgio *et al*. 2005). Its European distribution includes England, Germany, France, Portugal, Russia, Sweden, Norway, Scandinavia, and Greenland (Bates & Hodgetts 1995; Merckx 2013; Merckx *et al.* 2013). Temperature, precipitation, and degree of continentality can define its distribution pattern (Sérgio *et al.* 2005).

Figure 29. ***Aneura mirabilis*** that has been exposed from among mosses in a peatland. Photo by Jan-Peter Frahm, with permission.

Figure 30. ***Aneura mirabilis*** exposed amid peat. Photo by Jeff Duckett and Silvia Pressel, with permission.

Figure 31. ***Aneura mirabilis*** thalli that have been exposed. Photo courtesy of Martin Bidartondo.

Figure 32. ***Aneura mirabilis*** revealed in a peat mire. Photo by Jeff Duckett and Silvia Pressel with permission.

Aquatic and Wet Habitats

Aneura mirabilis (Figure 29-Figure 32) is not a submersed species, but it does seem to prefer moist habitats (Figure 33-Figure 34). In Welsh Marches, it grows underground under birch trees, hiding under ***Hyocomium armoricum*** (Figure 35) and ***Sphagnum quinquefarium*** (Figure 36) near a stream (Lawley 2012). Hill (1988) characterizes its habitat in North Wales as acid boggy woodland (see also Hill 1969). Boudier *et al*. (1999) found it on "the fringes of Tardais pond" in France. It also occurs in a Lakeland (UK) habitat where it was found in a steep, wooded gully on the north bank of a stream, 70-100 cm above the stream, growing in several places in a patch of ***Pellia*** (Figure 37) (Hopkins 1953). Sérgio *et al.* (2005) found that it was not rare in Portugal, where it occurred mainly in wet forests with an oceanic influence. Richards (1959) noted that it often lives in surface litter (Figure 38) beneath ***Molinia*** (grass; Figure 39) or large mosses such as ***Hylocomium splendens*** (Figure 40). Its association with birch trees can be explained by its need for a fungal association with species that are also attached to birch roots (Read *et al*. 2000). Its subterranean habitat means that it is likely to be easily overlooked.

Figure 33. ***Aneura mirabilis*** habitat in Bretagne. Photo by Michael Lüth, with permission.

Figure 34. ***Aneura mirabilis*** revealed in a ***Sphagnum*** mire. Photo by Michael Lüth, with permission.

Figure 35. ***Hyocomium armoricum***, a species that contributes to the habitat of ***Aneura mirabilis***. Photo by David T. Holyoak, with permission.

Figure 36. ***Sphagnum quinquefarium***, a species that contributes to the habitat of ***Aneura mirabilis***. Photo by Michael Lüth, with permission.

Figure 37. ***Pellia epiphylla***, a species that was associated with ***Aneura mirabilis*** in a wooded gully in the UK. Photo by Hermann Schachner, through public domain.

Figure 38. ***Aneura mirabilis*** in a wet litter habitat. Photo by Michael Lüth, with permission.

Figure 39. ***Molinia caerulea***, a species that can occur in the same habitats as ***Aneura mirabilis***, where the liverwort hides beneath the surface. Photo by James K. Lindsey, with permission.

Figure 40. ***Hylocomium splendens***, a species that may have ***Aneura mirabilis*** growing beneath it in peatland habitats. Photo by Hermann Schachner, through Creative Commons.

Aneura mirabilis (Figure 29-Figure 32) is acidophilic and occurs in locations with high bryophyte cover (Sérgio *et al*. 2005). Williams (1950) found it near an ant's nest. Could it be that the ants helped in its dispersal?

Adaptations

Aneura mirabilis (Figure 29-Figure 32) typically lives in dark habitats – deep forest, ravines, or otherwise well-shaded areas. This makes it difficult for a plant to supply enough carbohydrate through photosynthesis (Merckx 2013). But ***A. mirabilis*** has evolved a novel means of gaining its carbohydrate, unique among liverworts – it gets it from birch trees by way of a fungus (Hawksworth 2003), as discussed below under fungal interactions. It succeeds in this relationship, completely lacking chlorophyll in either generation (Hill 1969; Mårtensson & Nilsson 1974). Even the spores lack green color (Hill 1969; Mårtensson & Nilsson 1974), and Hill (1969) found no development of chlorophyll in spores that were cultured in light. The young thallus shows some evidence of plastid structure, but this never develops chlorophyll (Sigee 1969). In fact, Sigee found that proplastids, similar to those of normal green plants, developed in the apical cell and the surrounding cells. However, in more mature cells there was no evidence of development of a chloroplast. The early development of protoplasts and their subsequent changes occurred before any evidence of fungal invasion, but rather is similar to early stages in other mutant plant albinos wherein a genetic change causes the albino development.

Mårtensson and Nilsson (1974) noted that we do not know the extent to which precursors of chlorophyll are present, and I am not aware of any more recent studies on the topic, although the genes of the chloroplasts have been sequenced (Wickett *et al*. 2008b). On the other hand, Wickett *et al*. (2008b) found little reduction in the genome size. In this case, all the losses of genes and pseudogenes are also seen in the parasitic flowering plant ***Epifagus virginiana***, a forest plant connected through a fungus to beech (***Fagus***) roots. These gene losses are typical of early "decay" stages of the genes in consort with the relaxation of selection pressures. This would seem to imply that evolutionarily, the genes were lost after the mycorrhizal relationship developed.

Although ***Aneura mirabilis*** (Figure 29-Figure 32) lives below the surface in wet peatlands, these plants can dry out. Duckett *et al*. (1990) discovered that when ***Aneura mirabilis*** dries out over a period of 420 days, it develops a covering of multicellular hairs on the dorsal (upper) surface. These could serve to deflect excessive light as the peat shrinks upon drying, reduce water loss, and provide capillary spaces for water uptake. But we have no data to determine if any of these properties actually help it in the field.

Reproduction

Aneura mirabilis is **dioicous** (Figure 41), and in Portugal Sérgio *et al.* (2005) found that it is usually fertile with both male and female plants present (Figure 41). Female plants have a greater longevity than do male plants in this species (Benson-Evans 1960). Lewis and Benson-Evans (1960) suggested that this longevity difference might account for the **female-biased** (more females than males) sex ratio.

Induction of antheridia in ***Aneura mirabilis*** (Figure 29-Figure 32) responds to temperature, but not to photoperiod or light intensity (Benson-Evans 1961). When collected from the field in winter, the plants formed sex organs after 5 weeks at 21ºC. If kept continuously at 18ºC, they remained vegetative through winter and the following year. Benson-Evans interpreted this to mean that they must need a period of low temperatures before developing gametangia.

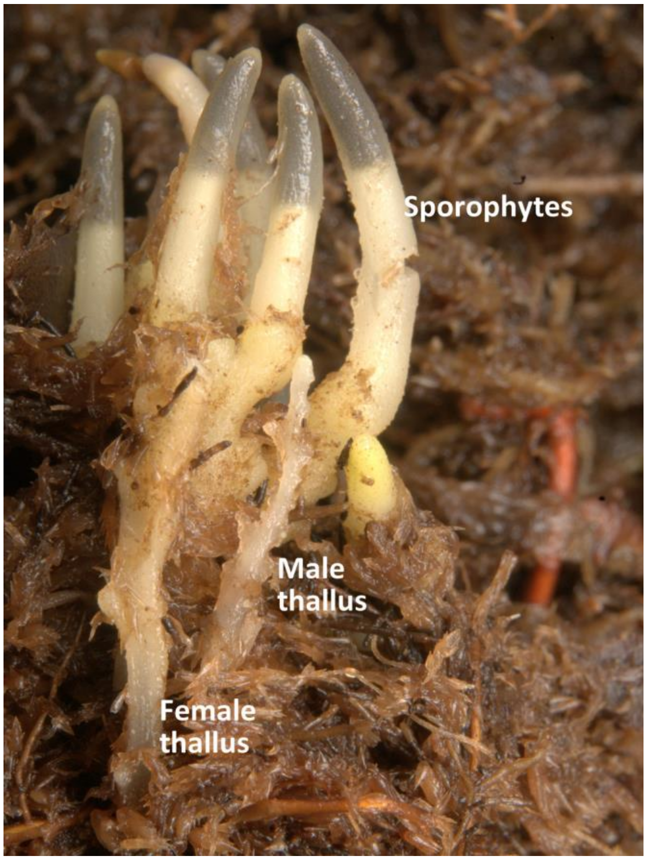

Figure 41. ***Aneura mirabilis***, showing male and female thalli and developing sporophytes *in situ* beneath ***Sphagnum*** among silver birch (***Betula pendula***). Photo by Brian Eversham, with permission.

Capsules of ***Aneura mirabilis*** (Figure 29-Figure 32) reach the surface of the moss layer through elongation of the seta (Figure 42-Figure 47) (Williams 1950), thus can be exposed to light at maturity (Benson-Evans 1960). Both Sjörs (1949) and Malmbörg (1933) found that at least some capsules reach the surface and dehisce there in the light. The large spores fall nearby and thus receive diffused light prior to germination.

Figure 42. ***Aneura mirabilis*** with developing sporophytes and exposed gametophyte thallus. Photo by David T. Holyoak, with permission.

Figure 43. ***Aneura mirabilis*** with peat and litter cleared away to expose the thallus and sporophytes protruding above the buried thallus. Photo by Hugues Tinguy, with permission.

Figure 44. ***Aneura mirabilis*** with sporophytes protruding. Photo by Hugues Tinguy, with permission.

Figure 45. ***Aneura mirabilis*** with sporophytes; exposed thallus is at the right, and evidence of the buried thallus is below the sporophytes in the image. Photo by David G. Long, through Creative Commons.

Figure 46. ***Anerua mirabilis*** under ***Hypnum cupressiforme***, showing mature capsules. Photo modified from Sérgio *et al.* 2005, with permission.

Figure 47. ***Anerua mirabilis*** dehiscing capsule. Photo modified from Sérgio *et al*. 2005, with permission.

In Portugal, the mature spores of ***Aneura mirabilis*** (Figure 29-Figure 32) are present in January to March, in France they are present in March, but farther north they appear in summer (Sérgio *et al.* 2005). The spores are large (30 µm) (Benson-Evans 1960). The spores remain in tetrads, even after dispersal. Upon germination, the tetrads separate and germination in culture occurs within a week. Keeping the tetrad intact until time for germination could explain the frequent presence of sporophytes – the male and female spores travel together and thus would germinate in proximity to each other.

Spores germinated on peat and peat extract agar, but not on Knop's agar or Voth's solutions (Benson-Evans 1960). Those cultured at -18ºC germinated within a few days. Germination was promoted by diffused daylight, but inhibited by strong light. In laboratory experiments, spores fail to germinate after 11-12 months, but they do remain viable throughout one season.

Young sporelings of ***Aneura mirabilis*** (Figure 29-Figure 32) may be washed to greater depths in the peat by rainwater (Benson-Evans 1960). Spores in culture never developed beyond the 20-30-cell stage, an indication that the developing gametophyte might be dependent on the fungus by that stage. The spores themselves seem to be free of fungal hyphae, so the fungal connection must be made at the site of germination for the ***Aneura mirabilis*** to succeed. It is therefore probably of little advantage for the species to have much long-distance dispersal as it has little chance of landing where it can find its partners. In the peatlands of the liverwort parents, the fungus is readily available nearby.

Hill (1969) notes that the achlorophyllous spores of ***Aneura mirabilis*** (Figure 29-Figure 32) nevertheless require light for germination, an accepted requirement for bryophyte spore germination (de Forest Heald 1898). But Benson-Evans (1960) found that reduced light was necessary even for germination of ***Aneura mirabilis*** spores.

Fungal Interactions

We are learning that most plant species are colonized by multiple species of mycorrhizal fungi, and in turn, the fungi are able to colonize many species of plants (Merckx 2013). Such is not the case for ***Aneura mirabilis*** (Figure 29-Figure 32) and associated fungi. In fact it seems that the **Metzgeriidae** often have specificity (Bidartondo & Duckett 2010). Thus far, only members of the **Aneuraceae** [***Cryptothallus*** (now in ***Aneura***), ***Aneura*** (Figure 7-Figure 10, Figure 18-Figure 26, Figure 29-Figure 32, Figure 52-Figure 57), and ***Riccardia*** (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133)] are known to host **Basidiomycete** endophytes (Pocock & Duckett 1984). These form extensive hyphal coils in the cells of the liverworts, similar to those in orchid **endomycorrhizae** (close relationship between plant and root fungi in which hyphae of fungus actually penetrate cells of root, rather than just colonizing on its surface). Pocock and Duckett suggested that these fungi in ***Aneura mirabilis*** might be the same as those living as an ectotroph (fungus living on root surface) of ***Betula*** roots.

The interaction between ***Aneura mirabilis*** (Figure 48) and the fungus ***Tulasnella*** (Figure 49) is unique among the liverworts (Bidartondo *et al.* 2003; Hawksworth 2003;

Wickett & Goffinet 2008; Wickett *et al*. 2008b; Oberwinkler *et al*. 2017). ***Aneura mirabilis*** is the only **mycoheterotrophic** (having symbiotic relationship between plant and fungus, in which plant gets all or part of its carbohydrate from parasitism upon fungi rather than from photosynthesis) liverwort (Merckx 2013). This relationship has been referred to as "cheating" (Bidartondo *et al*. 2003). The plant, in this case ***Aneura mirabilis***, is able to exploit the existing mycorrhizal relationship that already exists between the **Basidiomycete** fungus ***Tulasnella*** and a tree (Read *et al*. 2000; Wickett *et al*. 2008b). Bidartondo *et al*. (2003) demonstrated, using ^{14}C in CO_2, that the carbon was transferred from ***Betula pendula*** seedlings (Figure 50) through a species of ***Tulasnella*** to this achlorophyllous liverwort. It appears that ***Aneura mirabilis*** is able to share ***Tulasnella*** with both ***Betula*** and ***Pinus*** (Figure 51) (Bidartondo *et al*. 2003; Davis & Shaw 2008), depending on an otherwise suitable habitat.

Figure 48. ***Aneura mirabilis*** with the fungal partner ***Tulasnella***. Photo by Martin Bidartondo, with permission.

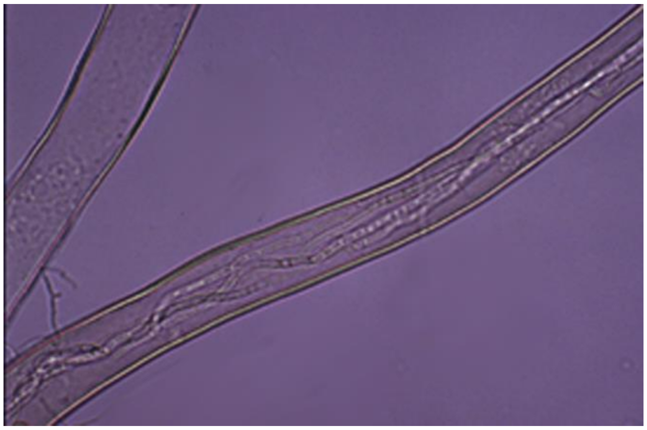

Figure 49. ***Aneura mirabilis*** rhizoid with ***Tulasnella*** inside. Photo by Martin Bidartondo, with permission.

When ***Aneura mirabilis*** (Figure 29-Figure 32) and ***A. pinguis*** (Figure 52-Figure 57) were collected from a variety of sites, the fungi were confined to specific regions of the gametophyte thallus in both liverwort species, and hyphal contact with the substratum occurred through the liverwort rhizoids (Ligrone *et al*. 1993). The colonization cycle presents a growth phase when the fungus forms large intracellular coils, host cytoplasm proliferates, and the starch content of the plastids decreases. This phase is followed by senescence in which the hyphae die back and aggregate into large masses. The fungus exhibits repeated colonization cycles. In ***Aneura mirabilis*** the young hyphae contain abundant glycogen and sometimes amyloid deposits. Despite these behavioral similarities, Ligrone *et al*. found that these two liverwort hosts did not share the same species of fungal partner. It seems that there is thus far no species name of the ***Tulasnella*** (Figure 48-Figure 49) species associated with ***Aneura mirabilis***.

Figure 50. ***Betula pendula*** seedling, a species that is able to share the fungus ***Tulasnella*** with ***Aneura mirabilis***. Photo by Krzysztof Ziarnek, through Creative Commons.

Figure 51. ***Pinus*** in peatlands, a habitat where the pines can share the fungus ***Tulasnella*** with ***Aneura mirabilis***. Photo by Runa S. Lindebjerg <Grida.no> with online permission.

Biochemistry

Although there have been a large number studies on the fungal partnership of ***Aneura mirabilis*** (Figure 29-Figure 32), the biochemical studies are relatively few. Rycroft (1998) reported that the new sesquiterpenoid 15-acetoxypinguisone was clearly the predominant compound in an extract of this species. But Rycroft and Cole (1998) noted that its relative abundance was much less in a second specimen. It would be interesting to determine to what degree the fungus alters the biochemical spectrum, and if the tree host plays any role in determining what secondary compounds are produced.

Aneura pinguis (Figure 52-Figure 57)

(syn. = *Riccardia pinguis*)

Wachowiak *et al*. (2007) used chloroplast DNA sequence variation and polymerase chain reaction-restriction fragment length polymorphism to demonstrate cryptic species in the ***Aneura pinguis*** (Figure 52-Figure 57) complex. (See also Myszczyński *et al*. 2017). Interestingly, they found that lowland and mountain populations exhibited different tRNALeu types, with two types in the mountains and a third in the lowlands. Later, Wawrzyniak *et al*. (2018) demonstrated a number of cryptic species within ***Aneura pinguis***, using mostly differences in sesquiterpene hydrocarbons. What is even more interesting in our ecological context, Bączkiewicz *et al*. (2017) found that the cryptic species, based on DNA differences, clearly differed in habitat preferences.

Figure 52. ***Aneura pinguis*** habit. Photo by Bernd Haynold, through Creative Commons.

Figure 53. ***Aneura pinguis*** in a slightly dry condition. Photo by Chris Wagner, with permission.

Figure 54. ***Aneura pinguis*** habit. Photo by Hermann Schachner, through Creative Commons.

Figure 55. ***Aneura pinguis*** habit. Photo by Hermann Schachner, through Creative Commons.

Figure 56. ***Aneura pinguis*** growing over mosses. Photo by Hermann Schachner, through Creative Commons.

Figure 57. ***Aneura pinguis*** terrestrial form among mosses. Photo by Jan-Peter Frahm, with permission.

But perhaps the cryptic species are not so cryptic. Buczkowska *et al*. (2006a) found that 13 quantitative traits differed significantly among the cryptic species of ***Aneura pinguis*** (Figure 52-Figure 57). These were mostly in the area of dorsal epidermal cells, thickness and number of cells in the thallus cross section, size of inner cells in the thallus cross section, and thallus width. Furthermore, there were differences in sizes of various aspects of males vs. females as well as male:female ratios.

Different forms have been identified in nature (Figure 58), so we must ask if these are due to genetic differences or to habitat modification. Frahm (2012) reported ***Aneura pinguis*** (Figure 52-Figure 57) fo. ***rivularis*** growing under water in a mill pond in the Vosges Mountains. However, when the form ***rivularis*** is grown in the same conditions as the typical form, the form ***rivularis*** retains the unistratose borders (Figure 59), whereas ***Aneura pinguis*** (Figure 5-Figure 6, Figure 52-Figure 57) retains the multistratose margins (Figure 60). Frahm implies that ***Aneura pinguis*** fo. ***rivularis*** is actually ***Aneura maxima*** (Figure 2-Figure 3, Figure 7-Figure 10, Figure 17-Figure 25). But Schuster (1992) seems certain that ***Aneura maxima*** from North America is really the same as ***Aneura pellioides*** (Figure 4) from Japan, but ***A. pellioides*** in Europe may not be synonymous with ***A. maxima***.

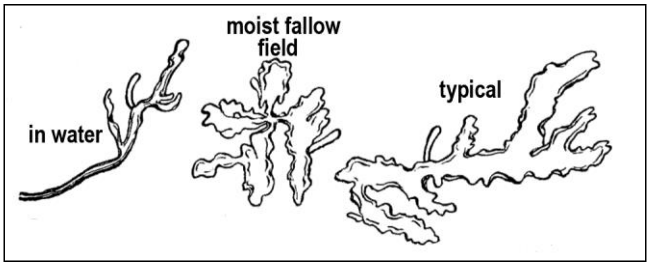

Figure 58. ***Aneura pinguis*** growing in water, in a moist fallow field, and in its typical growth form. Image modified from Watson 1915.

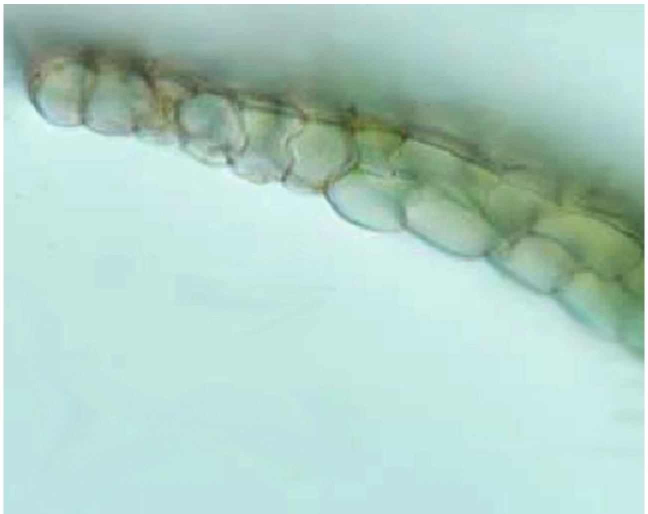

Figure 59. ***Aneura pinguis*** form ***rivularis*** thallus margin section after growing in water culture. Photo by Jan-Peter Frahm, with permission.

Figure 60. Typical form of ***Aneura pinguis*** thallus cultured in water for 4 months, showing its failure to develop thin margins. Photo by Jan-Peter Frahm, with permission.

Distribution

Aneura pinguis (Figure 52-Figure 57) is very cosmopolitan (Schuster 1992; Preußing *et al*. 2010a), extending from the High Arctic to the tropics (Schuster 1992). It occurs throughout most of Europe and North America, southward to the West Indies, South America, Africa, Asia, New Guinea, Australia, and New Zealand, south to Campbell Island (Schuster 1992), and in the Caribbean (Preußing *et al*. 2010b) and the Philippines (Furuki 2006).

Aquatic and Wet Habitats

Schuster (1992) refers to "enormous" habitat range for this species. Nevertheless, it seems to prefer basic conditions in moist habitats (Figure 61). Ceschin *et al*. (2012) considered the habitats of ***Aneura pinguis*** (Figure 52-Figure 57) to be so variable that it was an "invalid" indicator species.

Figure 61. ***Aneura pinguis*** on mud. Photo by Bas Kers, through Creative Commons.

Aneura pinguis (Figure 52-Figure 57) occurs on stream and river banks (Figure 62) with frequent submergence and slow water, often among wet rocks or soil, on rocks or soil in fast water, or submerged in slow water with poor mineral salts (Watson 1919). In Wales I found it near a stream and large waterfall (Figure 63). At Prudhoe Bay, Alaska, it is hydro-mesic or hydric (Rastorfer *et al*. 1973). It occurs in alpine streams (Figure 64) in the Swiss Alps (Geissler 1976). De Sloover and Goosens (1984) reported it from the travertine ***Cratoneuron*** (Figure 65) association of Lorraine River, Belgium. Geissler and Selldorf (1986) found that in their European studies it occurred with other wet habitat species (Figure 66), the moss ***Paludella squarrosa*** (Figure 67) and tracheophytes ***Eleocharis quinqueflora*** (Figure 68) and ***Trichophorum cespitosum*** (Figure 69), but was not common there. It occurs in streams in Belgium (Vanderpoorten & Tignon 2000), in mountain streams of northwest Portugal (Vieira *et al.* 2005), on European travertines (Pentecost & Zhang 2006), in rivers (Ferreira *et al*. 2008), and in poorly mineralized and basic waters in the Tiber River basin, Italy (Ceschin *et al*. 2012). On travertines, seepages and aspect are important and the liverworts are kept moist by capillarity (Pentecost & Zhang 2006).

Figure 62. ***Aneura pinguis*** in a streambank habitat at Cwm Idwal National Nature Reserve, Wales. Photo by Janice Glime.

Figure 63. ***Aneura pinguis*** at Cwm Idwal National Nature Reserve where it is kept moist by the nearby river and large waterfall. Photo by Janice Glime.

Figure 64. ***Aneura pinguis*** in water, where one can find it in alpine streams. Photo from Proyecto Musgo, through Creative Commons.

Figure 65. ***Cratoneuron filicinum***; ***Cratoneuron*** appears with ***Aneura pinguis*** on travertine rock in Belgium. Photo by Hugues Tinguy, with permission.

Figure 66. ***Aneura pinguis*** in wet habitat with other bryophytes. Photo by Kristian Peters, through Creative Commons.

Figure 67. ***Paludella squarrosa***, a species that occurs with ***Aneura pinguis*** in wet habitats. Photo by Hermann Schachner, through Creative Commons.

Figure 68. ***Eleocharis quinqueflora***, a species that occurs with ***Aneura pinguis*** in wet habitats. Photo by Ed Stikvoort, Saxifraga, through Creative Commons.

In western Canadian montane streams, ***Aneura pinguis*** (Figure 52-Figure 57) is submerged and hemicalciphilous (Vitt *et al.* 1986) in some, but can also occur on streambanks (Glime & Vitt 1987). Vitt and Horton (1990) reported it from fens in Missouri, USA. At Mountain Lake, Virginia, USA, Sharp (1944) reported ***Aneura pinguis*** from wet soil at the edge of a stream.

Figure 69. ***Trichophorum cespitosum***, a species that occurs with ***Aneura pinguis*** in wet habitats. Photo by Elke Freese, through Creative Commons.

In a Somerset, UK, heath, zonation depends on the supply of fresh water (Watson 1915). The streams have ***Potamogeton polygonifolius*** (Figure 70), and immediately above that constantly submersed zone of deeper water one can find ***Aneura pinguis*** (Figure 52-Figure 57) along with ***Pellia epiphylla*** (Figure 71). If the water is present continuously, these two species are present, including also living in furrows that may be too shallow for ***Potamogeton polygonifolius***. In these submerged locations, ***Aneura pinguis*** usually becomes long and narrow (Figure 72). Above that liverwort zone, where the water supply is intermittent and the zone remains above water for some time, ***Riccardia multifida*** (Figure 71) occurs instead. In shallow boggy pools, ***Aneura pinguis*** is usually absent and the pools are occupied instead by ***Scorpidium scorpioides*** (Figure 73), whether by competition or by a habitat that is otherwise unsuitable for ***Aneura pinguis***.

Figure 70. ***Potamogeton polygonifolius***, a species found in deeper water of heathland streams and wet areas, just below the ***Aneura pinguis*** zone. Photo by Bert Lanjouw, through Creative Commons.

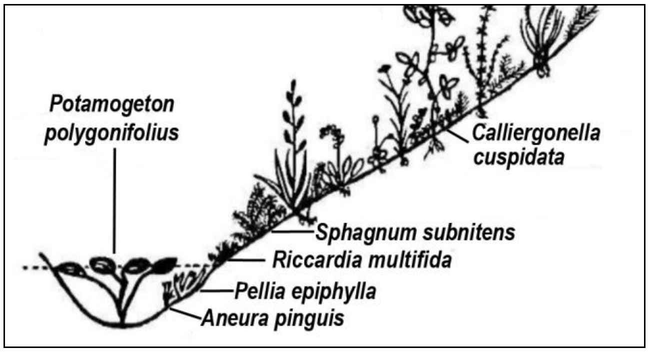

Figure 71. ***Aneura*** zonation in streams of wet heathland. Drawing modified from Watson 1915.

Figure 72. ***Aneura pinguis*** form ***rivularis*** thallus grown in water in a mill pond for 20 years. Photo by Jan-Peter Frahm, with permission.

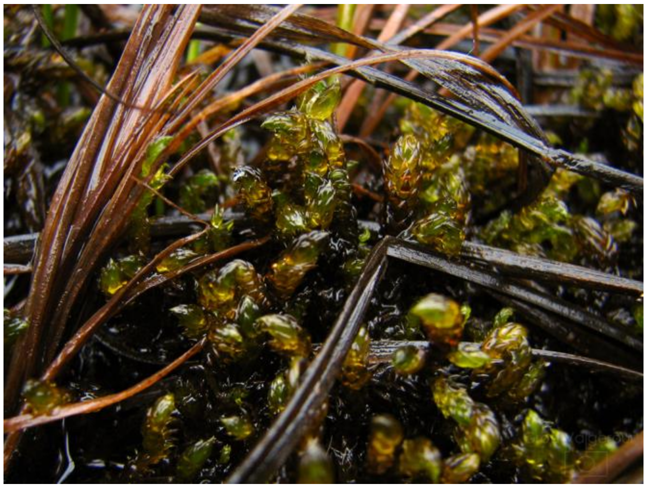

Figure 73. ***Scorpidium scorpioides***, a species that occurs in shallow pools that lack ***Aneura pinguis***. Photo by Gróa Valgerður Ingimunda, through Creative Commons.

Pentecost and Zhang (2006) examined effects of exposure and water availability on European travertine bryophytes, including ***Aneura pinguis*** (Figure 52-Figure 57). Only ***A. pinguis*** was significantly affected by aspect. It was also confined to seepages where moisture was ensured through capillarity.

The habitats of the various cryptic species of ***Aneura pinguis*** (Figure 52-Figure 57) differ. Gonera and Buczkowska (2016) reported that cryptic species A typically grows on humus over limestone rocks in the Western Carpathians, B is mainly on clay soil in Bieszczady Mts. and in clayish areas of lowlands, C grows both in lowlands and mountains and it occupies mostly wet sandy soils on the shores of oligotrophic lakes and river and mountain stream banks, E is associated with calcareous rocks in flowing water in mountains. Cryptic species A, B, and C differ somewhat in morphology, but the differences are subtle and relate mainly to thickness of the thallus and differences in thallus cells (Figure 74-Figure 76) (Buczkowska & Adamczak 2006).

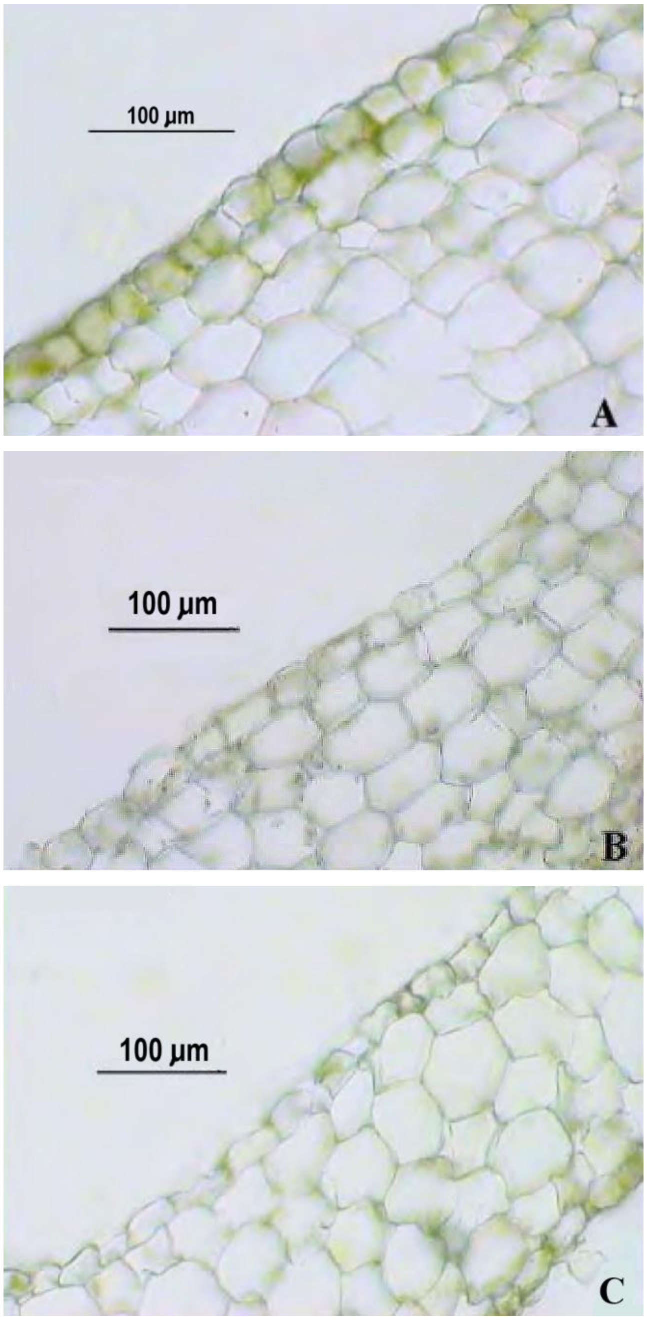

Figure 74. Cross sections of ***Aneura pinguis*** showing epidermis and median cells of cryptic species A, B, and C. Photo by Katarzyna Buczkowska, with permission.

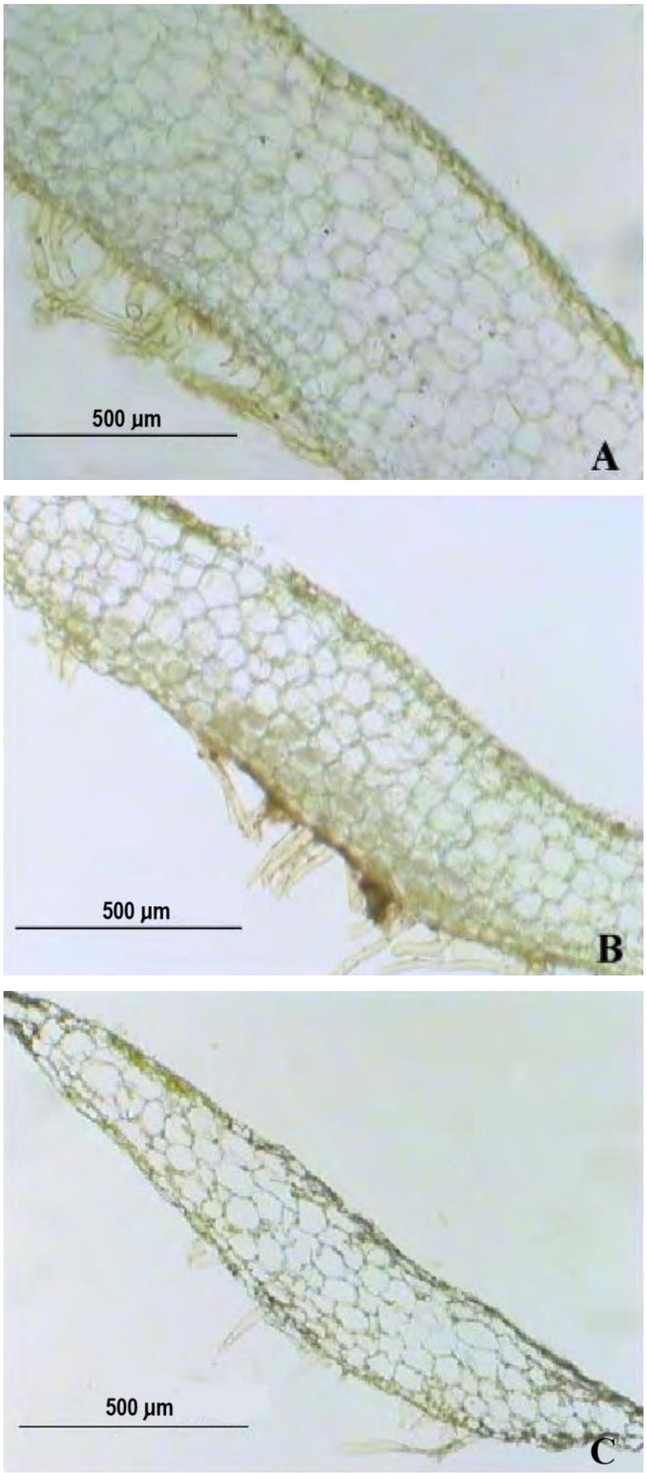

Figure 75. ***Aneura pinguis*** thallus cross section showing differences between cryptic species A, B, and C. Photo by Katarzyna Buczkowska, with permission.

Váňa and Ignatov (1995) reported that they found ***Aneura pinguis*** (Figure 52-Figure 57) in two types of habitats: wet sandy banks and bars of creeks and rivers; on rotten logs in conifer woods (Figure 77). While both of these are moist habitats, the substrata are quite different, as well as the former having the possibility of submersion. Could these be cryptic species differences?

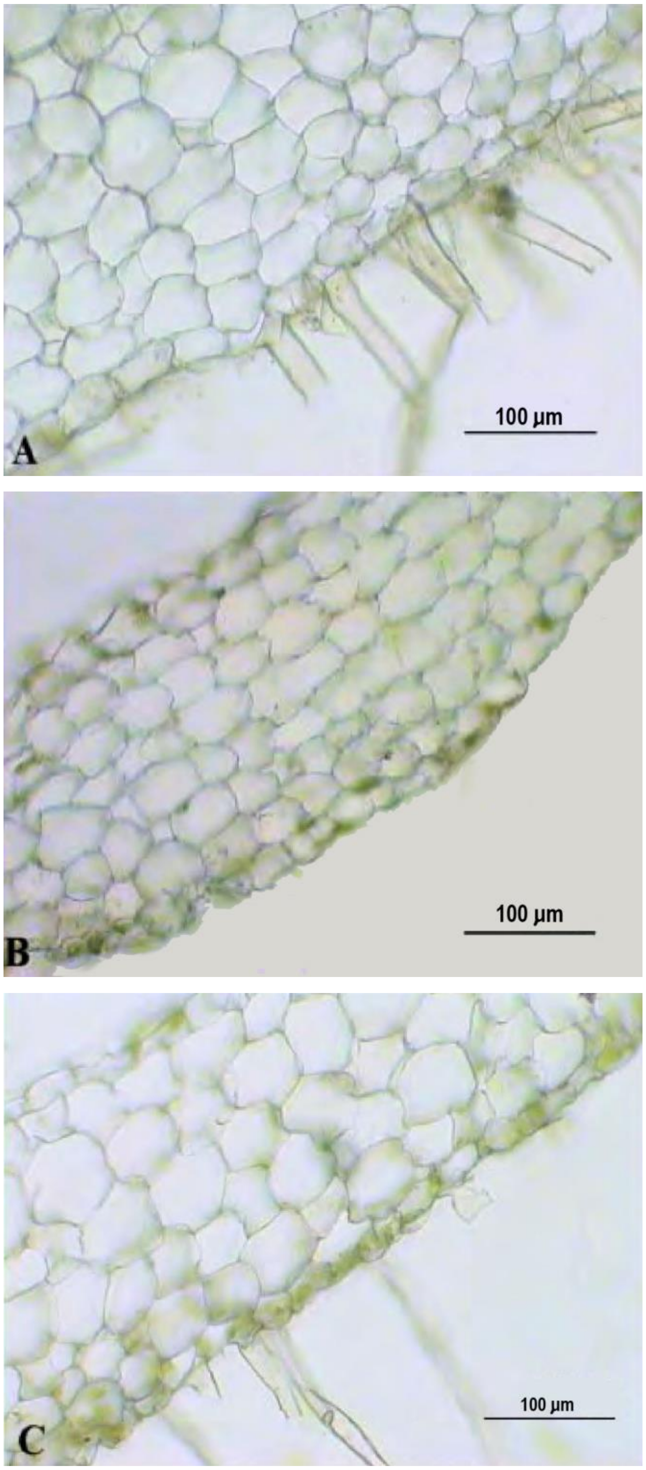

Figure 76. Cross section of ***Aneura pinguis*** showing ventral side of thallus in cryptic species A, B, and C. Photo by Katarzyna Buczkowska, with permission.

Foijt and Harding (1995) explored the effects of changes in Suffolk fens on the species composition of plants. Changes in the mires included lack of traditional management, changes in water regime, and increased fertility. In unmanaged areas, all of the fen associates and bryophytes were lost and replaced by non-fen species and ruderal tall herbs. When traditional management was maintained, small characteristic species of wet fens and semi-aquatic conditions still disappeared, but recruitment was not as evident. Those species that remained tended to be species that are either quite common in fens or non-fen recruits. When the fens remained wet, but were derelict, some species remained, with ***Aneura pinguis*** (Figure 52-Figure 57) and ***Riccardia multifida*** (Figure 140-Figure 149) among them. The researchers concluded that stable hydrology is more important than extensive management in conserving these sites.

Figure 77. ***Aneura pinguis*** on bark; it can be found on decaying logs. Photo by Li Zhang, with permission.

Despite the ability of ***Aneura pinguis*** (Figure 52-Figure 57) to occupy a wide range of habitats, and to survive changes to its fen habitats, Albinsson (1997) determined that liverworts, including ***Aneura pinguis***, have a narrow ecological amplitude in mires, whereas smaller liverworts tend to have wider amplitudes. Albinsson used the term **compromise strategy** to describe those species that rely on habitats created by other living bryophytes. These include species that are frequently sterile.

In Japan, ***Aneura pinguis*** (Figure 52-Figure 57) also occurs on decaying logs (Figure 77) in the mossy forest (Furuki 2006), but once again in a constantly moist environment. Logs that are in advanced stages of decay, especially missing bark, hold more water.

Adaptations

Aneura pinguis (Figure 52-Figure 57) has light green thalli when fresh, turning brown as they dry (Furuki 2006). Could this color change protect the species against bright light in the dry condition, helping to prevent photo damage?

Proctor *et al*. (1992) measured stable carbon isotope discrimination of $\delta^{13}C$ in relation to different sites and heights above water level in a North Carolina, USA, lake, and from two Marchantialean and two Metzgerialean liverworts from various habitats. Among these bryophytes, ***Aneura pinguis*** (Figure 52-Figure 57) had a slightly more negative reading. The researchers suggested that ***A. pinguis*** might have some uptake of recycled CO_2. But where is it stored? Buczkowska *et al*. (2006a) compared the thallus morphology among various cryptic species of ***Aneura pinguis***. This liverwort does not have internal air chambers (Figure 60, Figure 74-Figure 76) (Clapp 1912), but the thickness differs (Figure 75) among the cryptic species (Buczkowska *et al*. 2006a). Could the distance required for CO_2 to travel to exit the plant cause retention that would permit nearby cells to benefit from its attempt to escape? This raises interesting questions that require more exploration. Could greater thickness of the thallus facilitate recycling of CO_2? Could larger cell size cause a longer retention of respired CO_2? Does cell wall thickness play any role in recycling respired CO_2 in photosynthesis?

One growth form of ***Aneura piguis*** is upright (Figure 78). This form is an advantage in wet habitats where there is little danger of drying out because it exposes more surface to gas exchange and sunlight.

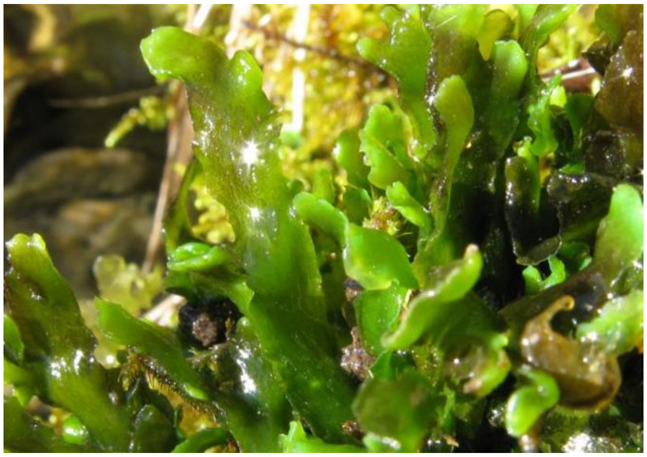

Figure 78. ***Aneura pinguis*** growing upright, a form that is possible in continuously wet habitats. Photo by Jiří Kameníček, with permission.

Reproduction

Aneura pinguis (Figure 52-Figure 57) is a thallose, **dioicous** species with sexual dimorphism (Buczkowska *et al*. 2006a). Male thalli are smaller and less branched than female thalli (Müller 1951-1958; Furuki 1991; Schuster 1992). d'Artenay and Renzaglia (2011) described the architecture of the spermatid in ***Aneura pinguis*** and provided high resolution images.

In cryptic species A of ***Aneura pinguis*** (Figure 52-Figure 57) only 55% of the gametophytes were fertile, compared to 80% (Figure 79) in B and almost 70% in C (Buczkowska *et al*. 2006a). Most colonies consisted of only one sex. Sex ratios differed among the three cryptospecies. Furthermore, the cryptic species are partly intersterile, differing in time of gametangial maturity (Showalter 1926, 1928; Buczkowska *et al*. 2006a).

Figure 79. ***Aneura pinguis*** perianths and young sporophytes. Photo by Dick Haaksma, with permission.

Clapp (1912) described the development of the capsules of ***Aneura pinguis*** (Figure 80-Figure 85) from first embryo cell to splitting of the capsule into four valves. The capsules are "highly specialized" (Clapp 1912). Horner *et al*. (1966) described the development of the spores (Figure 86). Showalter (1925) described the early stages of spore germination.

Figure 80. ***Aneura pinguis*** with sporophytes emerging from the perianth. Photo by Bernd Haynold, through Creative Commons.

Figure 81. ***Aneura pinguis*** perianths with embryonic capsules inside. Photo by Dick Haaksma, with permission.

Figure 82. ***Aneura pinguis*** perianth with embryonic sporophyte inside. Photo by Dick Haaksma, with permission.

Figure 83. ***Aneura pinguis*** with maturing sporophytes. Photo by Štěpán Koval, with permission.

Figure 84. ***Aneura pinguis*** with maturing capsules and elongating setae. Photo by Jan-Peter Frahm, with permission.

Figure 85. ***Aneura pinguis*** with dehisced sporophyte and perianths. Photo by Li Zhang, with permission.

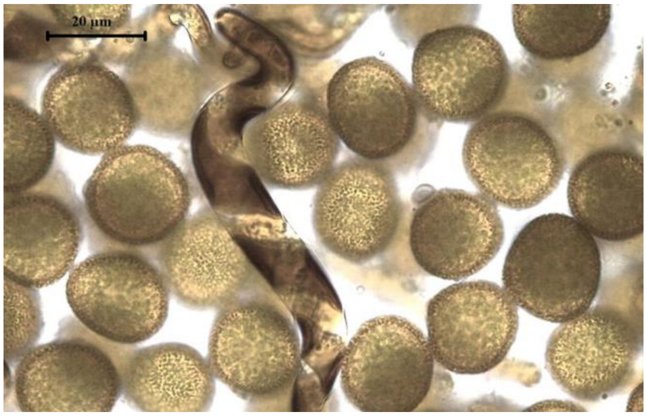

Figure 86. ***Aneura pinguis*** spores. Photo by Hugues Tinguy, with permission.

Gemmae are unknown in ***Aneura pinguis*** (Figure 52-Figure 57) (Clapp 1912; Preußing *et al*. 2010b). Vegetative reproduction occurs as older parts of the thallus die and apical portions become separated (Figure 87). This is facilitated by the production of lobes (Figure 88) that can break away. We do not know the degree to which these portions are dispersed, but we can assume that they are at least sometimes dispersed by flowing water. Waterfowl and insects might also contribute to dispersal.

Figure 87. ***Aneura pinguis*** showing older portions that are dying while tips are growing. Photo by Jouko Rikkinen, through Creative Commons.

Figure 88. ***Aneura pinguis*** showing vegetative lobes that can break off to form new plants. Photo by Hugues Tinguy, with permission.

Fungal Interactions

Aneura pinguis (Figure 52-Figure 57) is well known for its fungal interactions. In a study of symbiotic associations with liverworts, ***Aneura pinguis*** was associated with ***Tulasnella*** sp. (Figure 89; see also Figure 49), one of very few **Basidiomycetes** known to have a symbiotic relationship with liverworts (Kottke *et al*. 2003). These fungal interactions are typically highly species specific. Kottke *et al*. (2003) and Leake (2005) noted that the fungus in ***Aneura pinguis*** are closely related to those in ***Aneura mirabilis***. Liepiņa (2012) also demonstrated specificity between ***Fossombronia foveolata*** (Figure 90) and ***A. pinguis*** where thalli of the two species growing side-by-side housed different species of fungi.

Figure 89. ***Tulasnella violea*** on tree trunk, in a genus that is often associated with liverworts, including ***Aneura pinguis***. Photo by Esa Borén, through Creative Commons.

Figure 90. ***Fossombronia foveolata***, a species that can grow beside ***Aneura pinguis***, but that has different fungal associations. Photo by Hugues Tinguy, with permission.

Duckett *et al*. (2004) found different fungal endophytes in upland and lowland populations of ***Aneura pinguis*** (Figure 52-Figure 57) and likewise noted that the fungi had high host specificity. Bidartondo and Duckett (2010) considered the few overlaps of fungal species between ***Aneura pinguis*** and ***Aneura mirabilis*** (Figure 29-Figure 32) and the scattered occurrence of the fungus ***Sebacina*** (Figure 91-Figure 92) in ***Aneura pinguis*** may relate to the broad molecular diversity (cryptospecies) of this liverwort. Preußing *et al*. (2010a) determined that the composition of the communities of tulasnelloid fungi in ***A. pinguis*** differs between Ecuador and Europe, with a much higher diversity of tulasnelloid fungal partners at the Ecuadorian site, further supporting the hypothesis that the partnerships were related to cryptic species differences.

Figure 91. ***Sebacina sparassoidea*** with moss. Photo by Lloyd P. Roberts, through Creative Commons.

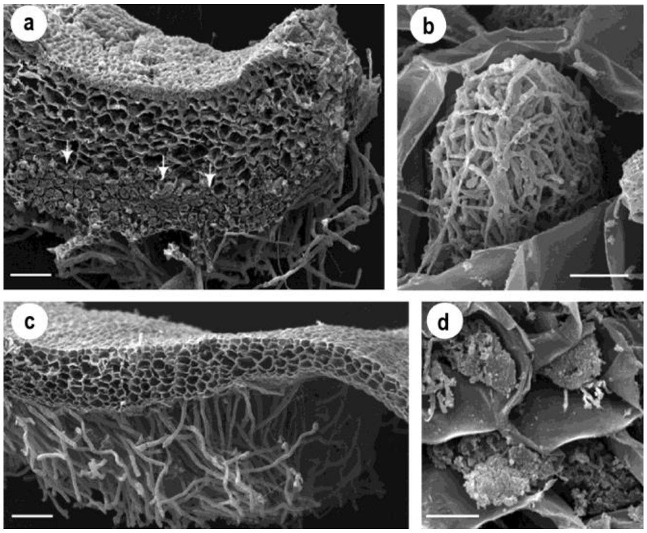

Figure 92. ***Sebacina*** infecting ***Aneura*** (a,b,d); ***Aneura pellioides*** hypha-free (c). Modified from Bidartondo and Duckett 2010, with permission.

Preußing *et al*. (2010b) consider the appearance of the mycothallus in the ***Aneura*** clade to be remarkably homogenous. Hyphae penetrate through living rhizoids; they colonize the parenchymal cells from the base of the rhizoid intracellularly by penetrating the cell walls, then forming dense coils of hyphae. Colonization of epidermal cells is rare (Brown & Braggins 1989) and intercellular infections are unknown (Preußing *et al*. 2010b).

Ligrone *et al*. (1993) learned through ultrastructural study that the interactions of endophytic Basidiomycetes were very similar in ***Aneura mirabilis*** (Figure 29-Figure 32) and ***Aneura pinguis*** (Figure 52-Figure 57). In both liverwort species, the fungus is confined to specific thallus regions. The fungus makes hyphal contact with its substrate through the rhizoids. Following the colonization phase, the fungus forms large intracellular coils. The liverwort cytoplasm then proliferates and starch content in the plastids diminishes. The fungal hyphae then senesce and die back, aggregating into large masses. A number of developmental characteristics of the ***A. mirabilis*** are identical to those of ***A. pinguis*** from alpine sites, but differ from those of ***A. pinguis*** from sand dunes and a chalk pit. These habitat differences further support the degree of differences among the cryptospecies. On the other hand, could the differences found among the cryptospecies be a result of different fungal epiphytes (see Damsholt 2002)?

Krause *et al*. (2011) followed the fungal colonization in ***Aneura pinguis*** (Figure 52-Figure 57) and a number of species of ***Riccardia*** (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133). They found that the mode of colonization of tulasnelloid mycobionts differs in the species of these genera, despite having identical fungal sequences. Thus they suggested that the mode of colonization may be host-dependent.

Culturing

For many, **axenic** (sterile; culture with no living organisms but intended one) culturing bryophytes has been a challenge. Buczkowska *et al*. (2006b) developed a protocol for axenic culturing of ***Aneura pinguis*** (Figure 52-Figure 57) that permitted them to regenerate. The two most successful media were hormone-free: the special liverwort medium of Lukavsky *et al.* (1991) and the MS medium of Murashige and Skoog (1992).

Biochemistry

Duckett and Renzaglia (1987) noted the difficulty of preserving the oil bodies for TEM studies, but confirmed their presence in ***Aneura***. As you can see in the image of ***Aneura pinguis*** below (Figure 93), they can be difficult to discern even in fresh material.

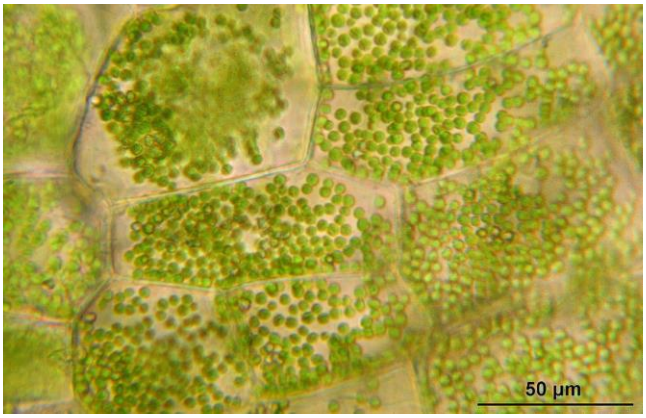

Figure 93. ***Aneura pinguis*** cells in which one cannot distinguish the oil bodies easily. Photo by Hermann Schachner, through Creative Commons.

In their study of cryptic species of ***Aneura pinguis*** (Figure 52-Figure 57), Wawrzyniak *et al*. (2018) found that the dominant compound among their samples was pinguisone, with deoxopinguisone being the second dominant. The differences among the samples were primarily due to genotype and little to habitat. Tazaki *et al*. (1995) reported that the concentrations of pinguisone were significantly high in the species. They were able to describe the structures of three new pinguisane-type sesquiterpenes (Tazaki *et al*. 1996).

Asakawa *et al*. (1981) demonstrated that the sesquiterpenes in ***Aneura pinguis*** (Figure 52-Figure 57) are chemically very different from those of two relatives that have been retained in ***Riccardia*** [***R. multifida*** (Figure 140-Figure 159), ***R. jackii***]. The pinguisones are not the dominant sesquiterpenes in the ***Riccardia*** (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133) species.

Lobatiriccardia (Figure 94-Figure 95)

Lobatiriccardia is a Southern Hemisphere genus, mostly in Australia and New Zealand, but more recently reported from Ecuador in South America (Preußing *et al*. 2010b). Preußing *et al*. (2010b) suggested that the positioning of female gametangia on the lobe margins of ***Lobatiriccardia***, rather than in a central position, permits the development of more sporophytes, thus increasing reproduction.

Symbiotic fungi occur in parenchymal cells in this genus, inhabiting 3-10 layers on the ventral side, never occurring in epidermal cells or intercellular locations (Duckett & Ligrone 2008).

Lobatiriccardia alterniloba (Figure 94-Figure 95)

(syn. = *Aneura alterniloba*; *Riccardia alterniloba*)

Several varieties have been described for ***Lobatiriccardia alterniloba*** (Figure 94) (Nebel *et al*. 2013).

Distribution

Lobatiriccardia alterniloba (Figure 94) is known from New Zealand, Australia, Tasmania, and Vanuatu (Hewson 1970; Furuki 2002; Preußing *et al*. 2010b).

Figure 94. ***Lobatiriccardia alterniloba*** on a soil bank. Photo by Marley Ford, through Creative Commons.

Aquatic and Wet Habitats

Lobatiriccardia alterniloba (Figure 94) occurs in Cool Temperate Victorian Rainforest streams (Carrigan & Gibson 2004; Carrigan 2008). In Cement Creek, Victoria, Australia, it occurs below the water line, but can also occur above (Carrigan & Gibson 2004). It does not occur on upstream sides of rocks that receive the full force of the current, but can occupy downstream, top, and base locations that do not receive the full force of the current. It was one of the two dominant species at the bases of rocks and achieved 8% cover in the study area.

Preußing *et al*. (2010b) described its habitat as occurring on rock, or soil in damp to wet conditions, often in the spray of waterfalls, or in running water. Nebel *et al*. (2013) similarly reported ***Lobatiriccardia alterniloba*** (Figure 94) **var. *robusta*** from Russell Falls, in Tasmania.

Not all of the habitats of ***Lobatiriccardia alterniloba*** (Figure 94) are so wet. Wilcox (2018) reported it from exposed roots of a pine tree in a shaded forest, near a small stream in Craigavon Park, Auckland, New Zealand.

Adaptations

Lobatiriccardia alterniloba (Figure 94) forms tight, thin **mats** that reduce the force of the current at the base of the mat (Carrigan & Gibson 2004; Carrigan 2008).

Preußing *et al*. (2010b) suggested that the reduction of lateral thallus branches to short, gametangia-bearing branches may save resources. The ventral position of gametangia under thallus lobes could result in better protection of the young sporophyte from injury and stronger anchoring and direct nutrient uptake by the dense rhizoid coverage at the capsule foot.

Reproduction

Lobatiriccardia alterniloba is **dioicous** but does at least sometimes reach successful fertilization (Figure 95); gemmae are unknown (Preußing *et al*. 2010b).

Figure 95. ***Lobatiriccardia alterniloba*** with young capsule. Photo by Marley Ford, through Creative Commons.

Fungal Interactions

Duckett and Ligrone (2008) described the **Basidiomycota** endophyte in ***Lobatiriccardia alterniloba*** (Figure 94) as limited to five cell layers, contrasting with colonization of the entire thallus in ***Aneura mirabilis***.

Biochemistry

Oil bodies of ***Lobatiriccardia alterniloba*** (Figure 94) are typically 2-5 per cell (Preußing *et al*. 2010b). I found no studies on the biochemistry of the species.

Lobatiriccardia athertonensis

Distribution

Thus far, ***Lobatiriccardia athertonensis*** is only known from Australia (Preußing *et al*. 2010b) and New Guinea (Hewson 1970).

Aquatic and Wet Habitats

In disturbed rainforests, ***Lobatiriccardia athertonensis*** occurs with other bryophytes on basalt rocks on creek banks (Preußing *et al*. 2010b).

Reproduction

Lobatiriccardia athertonensis is **dioicous**; gemmae are unknown (Preußing *et al*. 2010b).

Biochemistry

Oil bodies are few, 1-3(4) per cell (Preußing *et al*. 2010b). No biochemical studies seem to be available for this species.

Lobatiriccardia coronopus

Distribution

Lobatiriccardia coronopus occurs in the Philippines, Malay Peninsula, Borneo, Sumatra, Java, Seram, and New Guinea (Furuki 1996, 2006)

Aquatic and Wet Habitats

Lobatiriccardia coronopus occurs on rocks and fallen logs at the waterside (Furuki 1996, 2006)

Lobatiriccardia oberwinkleri

Distribution

Lobatiriccardia oberwinkleri has a known distribution limited to South America, in Ecuador, at two locations in the same ravine (Preußing *et al*. 2010b). More recently, Schäfer-Verwimp and Nebel (2011) have added it to the flora of Brazil.

Aquatic and Wet Habitats

Lobatiriccardia oberwinkleri was found in a ravine in the upper mountain rainforest belt, where it occurs on steep, dripping rock faces beside two small cascades (Preußing *et al*. 2010b). It occurs there with ***Asterella macropoda***, ***Dumortiera hirsuta*** (Figure 96), and ***Riccardia*** (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133) species. In southern Ecuador it occurs on shady, humid soil and on dripping cliffs of the lower to upper montane rainforest from 1760 to 2880 m asl (Gradstein & Reeb 2018).

Figure 96. ***Dumortiera hirsuta***, a species that occurs with ***Lobatiriccardia oberwinkleri***. Photo by Luis Funez, through Creative Commons.

Reproduction

Lobatiriccardia oberwinkleri is **dioicous**, with male plants unknown (Preußing *et al*. 2010b). Gemmae are unknown.

Lobatiriccardia verdoornioides

Distribution

Lobatiriccardia verdoornioides is thus far known only from Cuenca, El Cajas, and Quito, Pichincha, in Ecuador (Preußing *et al*. 2010b).

Aquatic and Wet Habitats

Lobatiriccardia verdoornioides was described as a new species from wet páramo-vegetation, where it was found in a bog on the bank of a small lake, embedded in cushions of flowering plants, together with other bryophytes [***Riccardia*** (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133) and ***Campylopus*** (Figure 97) species], and in rivulets (Preußing *et al*. 2010b).

Figure 97. ***Campylopus atrovirens***; in the Páramo; ***Campylopus*** can occur with ***Lobatiriccardia verdoornioides***. Photo by Andrew Hodgson, with permission.

Schäfer-Verwimp *et al*. (2013) reported ***Lobatiriccardia verdoornioides*** from remnants of ***Polylepis***

(Figure 98) stands, where it occurred on very wet ground at 3995 m asl in Ecuador.

Figure 98. ***Polylepis rugulosa*** in Andes highland; ***Lobatiriccardia verdoornioides*** occurs in remnants of the ***Polylepis*** forest. Photo by Alexander Yates, through Creative Commons.

Adaptations

Thalli of ***Lobatiriccardia verdoornioides*** are very succulent and deeply embedded in the surrounding vegetation, which most likely protects them from the strong wind and sunlight (Preußing *et al*. 2010b).

Reproduction

Lobatiriccardia verdoornioides is **dioicous**; gemmae are unknown (Preußing *et al*. 2010b).

Lobatiriccardia yakusimensis

(syn. = *Riccardia lobata* var. *yakusimensis*)

Distribution

Lobatiriccardia yakusimensis is known only from the Ryukyu archipelago in southern Japan (Furuki 1991; Preußing *et al*. 2010b).

Aquatic and Wet Habitats

Lobatiriccardia yakusimensis occurs on wet rocks along streams, often submerged in running water (Preußing *et al*. 2010b).

Adaptations

The thallus of ***Lobatiriccardia yakusimensis*** is large and bluish-green when fresh (Preußing *et al*. 2010b). I don't know what this color indicates or if it is in any way adaptive.

Reproduction

Lobatiriccardia yakusimensis is **dioicous**; gemmae are unknown (Preußing *et al*. 2010b).

Biochemistry

Oil bodies occur in all epidermal and inner cells of ***Lobatiriccardia yakusimensis*** with 1-10 in each cell (Preußing *et al*. 2010b). Their biochemistry remains unknown.

Lobatiriccardia yunnanensis

Distribution

Lobatiriccardia yunnanensis is known only from Yunnan, China (Furuki & Long 2007; Preußing *et al*. 2010b). Unfortunately, a new road has been constructed, coming within a few meters of its only known location, accompanied with light deforestation, causing Furuki and Long (2007) to consider the species severely threatened.

Aquatic and Wet Habitats

Lobatiriccardia yunnanensis occurs on shady dripping cliffs of a river gorge in dense broadleaf evergreen forest in a humid subtropical valley at 1425 m asl (Furuki & Long 2007; Preußing *et al*. 2010b). In its single known location, it was associated with a number of other bryophytes (Furuki & Long 2007).

Adaptations

Plants of ***Lobatiriccardia yunnanensis*** form dense colonies with numerous rhizoids (Furuki & Long 2007), presumably facilitating their ability to persist on dripping cliffs. Is it possible that the translucent thallus permits light to penetrate to or focus on deeper layers in this low-light habitat?

Reproduction

Lobatiriccardia yunnanensis is **dioicous**, with its archegonia and sporophytes on the margins (Preußing *et al*. 2010b). As already suggested, this positioning permits more than one sporophyte to develop in a season on the same lobe, increasing the potential for reproduction. No gemmae are known.

Riccardia

Members of the genus ***Riccardia*** (Figure 99-Figure 111, Figure 128-Figure 131, Figure 134, Figure 140-Figure 159, Figure 132-Figure 133) are positively correlated with bankfull discharge in 48 streams in South Island, New Zealand (Suren & Duncan 1999). They are also among west African rheophytes (Shevock *et al*. 2017). Preußing *et al*. (2010b) suggested that the positioning of female gametangia on the lobe margins instead of the central position permits the development of more sporophytes, thus increasing reproduction. Furthermore, **endogenous** (formed within vegetative cells) gemmae are found regularly in ***Riccardia*** (Renzaglia, 1982), but are unknown in ***Aneura*** (Figure 7-Figure 10, Figure 18-Figure 26, Figure 29-Figure 32, Figure 52-Figure 57) or ***Lobatiriccardia*** (Figure 94-Figure 95).

Riccardia aequicellularis (Figure 99)

Distribution

Riccardia aequicellularis (Figure 99) occurs in Australia (English & Blyth 2000; Carrigan & Gibson 2004), Tasmania (Ratkowsky 1987; Jarman & Kantvilas 2001), and New Zealand (de Lange *et al*. 2020). Selkirk (2012) reported the species from the sub-Antarctic Macquarie Island.

Figure 99. ***Riccardia aequicellularis***, a species of the Eastern Southern Hemisphere. Photo by Tom Thekathyil, with permission.

Aquatic and Wet Habitats

Riccardia aequicellularis (Figure 99) occurs in Cool Temperate Victorian Rainforest streams (Carrigan & Gibson 2004; Carrigan 2008). In Cement Creek (Figure 100), Victoria, Australia, it occurs below the water line, but can also occur above. It is able to occupy upstream, downstream, and sides of rocks, but does not occupy the tops of rocks in the study stream. This is the only species in the studied area of Cement Creek that is able to withstand the force of the current on the upstream side of rocks. With these restrictions, it occupies less than 1% cover in the stream and occurs in only 2 of the 5 study locations.

Figure 100. Cement Creek, Yarra Ranges National Park, Victoria, Australia 1 98Octane, through Creative Commons.

Downes *et al.* (2003) listed ***Riccardia aequicellularis*** (Figure 99) as semi-aquatic. In two of the studied creeks in Australia it had a higher percentage cover on emergent than submerged rocks, but in another there was no difference; in a fourth the cover was greater on the submerged rocks. This is one of the species that seems to benefit from the additional habitats provided by splash zones above water.

Riccardia aequicellularis (Figure 99) occurs on peat mounds of tumulus springs (mound springs) in the Swan Coastal Plain of western Australia (English & Blyth 2000). Downing *et al.* (2007) found it in their study of a deep gully (Figure 101) in a closed canopy forest in the Blue Mountains of New South Wales, Australia.

Figure 101. Deep gully in Blue Mountains, Victoria, Australia, such as the ones where one might find ***Riccardia aequicellularis***. Photo by David Noble, with permission.

Adaptations

Riccardia aequicellularis (Figure 99) forms **threadlike mats** that permit it to reduce the rate of flow within the mat (Carrigan & Gibson 2004). At Deep Stream in New Zealand, it is a colonist (Michel *et al.* 2013).

Riccardia chamedryfolia **(Figure 102-Figure 108)**

(syn. = *Aneura sinuata*, *Aneura sinuata* fo. *submersa*, *Riccardia sinuata*)

Distribution

Riccardia chamedryfolia (Figure 102-Figure 108) is Holarctic, but is rare in the Arctic (Schuster 1992). It extends from Europe and the islands off the coast of Portugal, southward to northern Africa and eastward to China, Japan, Bonin, and Micronesia. In North America it extends along the western coastal states from Alaska to California and in some locations in the eastern USA states. Bakalin (2005) reported on its locations on the Kamchatka Peninsula, Russia.

Figure 102. ***Riccardia chamedryfolia*** (Jagged Germanderwort), a Holarctic species. Photo by Barry Stewart, with permission.

Figure 103. ***Riccardia chamedryfolia***. Photo by Des Callaghan, with permission.

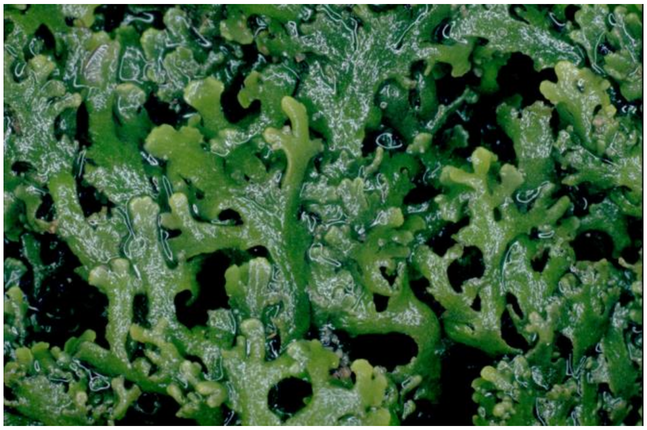

Figure 104. ***Riccardia chamedryfolia***. Photo by Jan-Peter Frahm, with permission.

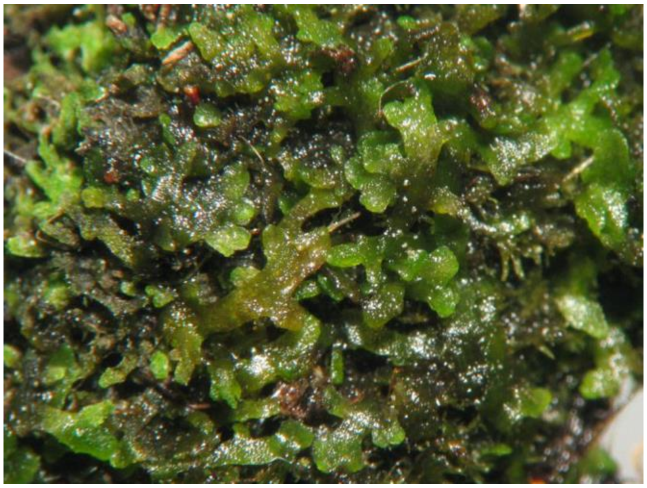

Figure 105. ***Riccardia chamedryfolia***. Photo by Kristian Peters, with permission.

Aquatic and Wet Habitats

Schuster (1992) described ***Riccardia chamedryfolia*** (Figure 102-Figure 108) as being typically associated with running water, but not always submersed. It is often kept wet by splash, or on damp to dripping rocks of ravines or gravelly bottoms of shallow springs.

Figure 106. ***Riccardia chamedryfolia***. Photo by Martin Hutten, with permission.

Figure 107. ***Riccardia chamedryfolia*** showing lush growth. Photo by Michael Lüth, with permission.

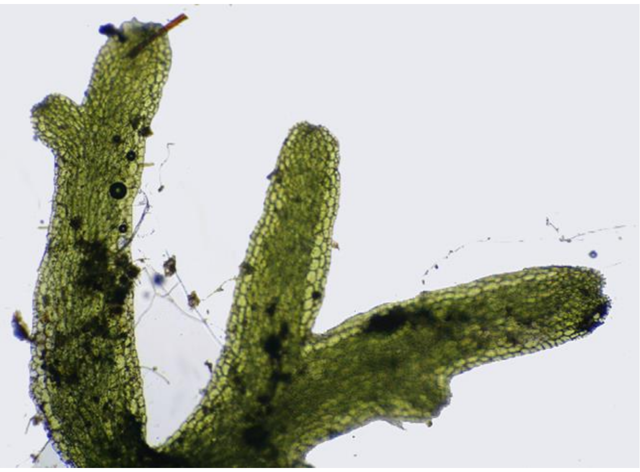

Figure 108. ***Riccardia chamedryfolia***. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Watson (1919) considered ***Riccardia chamedryfolia*** (Figure 102-Figure 108) to be the most hydrophilous of the "***Aneura***" species. It occurs on stony beds in fast water. It also occurs in rivers (Ferreira *et al*. 2008). In Westfalens, northwestern Germany, it occurs in water (Figure 109) and, less commonly, as a marsh plant (Koppe 1945). In Odenwald and southern Spessare, Philippi (1987) found it in spring areas in aquatic habitats; van Zanten and Colpa (2008) found it in seepage in North Gronigen, The

Netherlands. In southern Finland it occurs in small lakes (Toivonen & Huttunen 1995). It occurs in Portugal water courses (Vieira *et al.* 2012) and in northwest Portugal it can be found in mountain streams (Vieira *et al.* 2005). On Madeira Island, it occurs in upstream areas in mountainous streams (Luís *et al.* 2015). In the eastern USA, ***Riccardia chamedryfolia*** (Figure 102-Figure 108) occurs in Appalachian Mountain streams (Figure 110) (Glime 1968). Tremp (2003) considered the species to be oligo- to mesotrophic.

Figure 109. ***Riccardia chamedryfolia*** in water. Photo by Michael Lüth, with permission.

Figure 110. Appalachian Mountain stream, where some are inhabited by ***Riccardia chamedryfolia***. Photo by Janice Glime.

Barringer (2011) found ***Riccardia chamedryfolia*** (Figure 102-Figure 108) on dripping rocks near streams in New Jersey, USA. Vieira *et al*. (n.d.) found it at a mean of 8 cm above water that had velocities of 0-1.5 m s^{-1} in northwest Portugal. Daniel *et al*. (2006) found a negative correlation of depth with rheophilous bryophytes, including ***Riccardia chamedryfolia***, in the Scorff River and its tributaries, a salmon river system in southern Brittany of France. These studies support its description as living in habitats that stay wet (Figure 111), but not necessarily submerged.

Figure 111. ***Riccardia chamedryfolia*** above water, but wet on a wet rock. Photo by Bernd Haynold, through Creative Commons.

Bakalin (2007) found ***Riccardia chamedryfolia*** (Figure 102-Figure 108) in wet hollows in the southern Kuril Islands. Callaghan and Ashton (2007) found it locally in younger dune slacks in England. In Japan, Bakalin *et al*. (2013) found it on moist and wet boulders and cliffs along streams, in spray zones of waterfalls, but also on clayish road cuts in mesic conditions and partial shade of secondary forests.

Hugonnot (2011) reported ***Riccardia chamedryfolia*** (Figure 102-Figure 108) from fens in Aubrac, France. Vellak *et al*. (2015) listed ***Riccardia chamedryfolia*** as sporadic in Estonia. Ingerpuu *et al*. (2014) found it to be rare in fens, transitional mires, and bogs in Estonia. It is likewise rare in the southeastern Carpathians of Romania (Jakab 1999). Similarly, Albinsson (1997) reported it from only one location out of 67 mire sites in southern Sweden, despite its being considered a characteristic mire species.

Philippi (1987) described the aquatic vegetation of streams in the eastern Odenwald and southern Spessart, Germany. He described the ***Riccardia chamedryfolia*** (Figure 102-Figure 108) community and the ***Fontinalis antipyretica*** (Figure 112) community as the characteristic communities of the spring area. Both are sensitive to high water velocity. ***Riccardia chamedryfolia*** is one of the few species that characterize the source. In these locations, it forms fresh, olive-green to yellow-green lawns that are under water most of the year.

Schuster (1992) found that ***Riccardia chamedryfolia*** (Figure 102-Figure 108) was mostly in acidic sites, but was not confined to them. Gabriel and Bates (2005) found that in the Azores, the mean *p*H for this species was 5.0 and water availability was not the highest among the groups of bryophytes. On Madeira, ***Riccardia chamedryfolia*** occurs where there are low nutrient concentrations, preferring reaches with low temperatures and little turbulence (Luís *et al*. 2012). It is acidophilic, indicating low *p*H in summer.

It is related to low dissolved oxygen, low magnesium, and low calcium ions in summer, and low concentrations of phosphates and high ammonium in winter. These latter relationships may explain its occasional appearance in non-acidic habitats.

Figure 112. ***Fontinalis antipyretica***, a characteristic community in springs where ***Aneura chamedryfolia*** also characterizes one of the communities. Photo by Bernd Haynold, through Creative Commons.

Riccardia chamedryfolia (Figure 102-Figure 108) occurred in rock crevices near water leakage (Ivanova 2009). In river gorges in Norway, ***Ctenidium molluscum*** (Figure 113), ***Hylocomiastrum umbratum*** (Figure 114), and ***Trichocolea tomentella*** (Figure 115) are characteristic companion species of ***Riccardia chamedryfolia*** (Rydgren *et al*. 2012). Frahm (2005) reported ***R. chamedryfolia*** from the wet lava rocks in the dark interior of a crater in the Azores. ***Riccardia chamedryfolia*** fo. ***major*** (syn. = *Aneura major*) occurs on banks with frequent submergence and slow water (Watson 1919).

Figure 113. ***Ctenidium molluscum***, a species that occurs with ***Riccardia chamedryfolia*** in Norwegian gorges. Photo by David T. Holyoak, with permission.

Figure 114. ***Hylocomiastrum umbratum***, a species that occurs with ***Riccardia chamedryfolia*** in Norwegian gorges. Photo by Hermann Schachner, through Creative Commons.

Figure 115. ***Trichocolea tomentella***, a species that occurs with ***Riccardia chamedryfolia*** in Norwegian gorges. Photo by Li Zhang, with permission.

Riccardia chamedryfolia (Figure 102-Figure 108) is not entirely a wet habitat species. It is also known from trunks of the tree fern ***Cyathea delgadoi*** (Figure 116) in Brazil (Vital & Prado 2006). In Estonia, Kannukene *et al*. (1997) found it on the bank of a bomb crater on sand.

Adaptations

In the Tottori Prefecture of Japan, ***Riccardia chamedryfolia*** (Figure 102-Figure 108) can occur in pure **mats** (Figure 117), but it is more commonly mixed with other liverworts, such as ***Aneura maxima*** (Figure 2, Figure 3, Figure 7-Figure 10; Figure 18-Figure 26), ***Conocephalum salebrosum*** (Figure 118), ***Heteroscyphus coalitus*** (Figure 119), ***Jubula hutchinsiae*** (Figure 120), ***Lejeunea aquatica***, ***Makinoa crispata*** (Figure 121), ***Megaceros pellucidus*** (see Figure 122), ***Pallavicinia subciliata*** (Figure 123), ***Pellia neesiana*** (Figure 124), and ***Wiesnerella denudata*** (Figure 125) (Bakalin *et al*. 2013). Both the **mat** life form and the accompanying liverworts can help ***Riccardia chamedryfolia*** maintain hydration.

Figure 116. ***Cyathea delgadoi***, a species that sometimes has ***Riccardia chamedryfolia*** growing on its trunks. Photo from <powo.science.kew.org>, through Creative Commons.

Figure 117. ***Riccardia chamedryfolia*** forming a mat. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Figure 118. ***Conocephalum salebrosum***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo by Paul Slichter, with permission.

Figure 119. ***Heteroscyphus coalitus***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo by Jia-Dong Yang, through Creative Commons.

Figure 120. ***Jubula hutchinsiae***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo by Michael Lüth, with permission.

Figure 121. ***Makinoa crispata***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo through Creative Commons.

Figure 122. ***Megaceros*** sp.; ***Megaceros pellucidus*** can occur mixed with ***Riccardia chamedryfolia***. Photo by Scott Zona, through Creative Commons.

Figure 123. ***Pallavicinia subciliata***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo by Li Zhang, with permission.

Reproduction

Riccardia chamedryfolia (Figure 102-Figure 111) is **autoicous** (Schuster 1992). Gemmae can be present on the tips of the ultimate branches.

Figure 124. ***Pellia neesiana***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo from Botany Website, UBC, with permission.

Figure 125. ***Wiesnerella denudata***, a species that can occur mixed with ***Riccardia chamedryfolia***. Photo by David Long, with permission.

Fungal Interactions

Vital *et al*. (2000) reported the fungus ***Phellinus wahlbergii*** (**Basidiomycota**; Figure 126) in association with ***Riccardia chamedryfolia*** (Figure 102-Figure 111) in undisturbed Atlantic forest in Brazil.

Figure 126. ***Phellinus wahlbergii***, a bracket fungus with moss on it; it can also associate with ***Riccardia chamedryfolia***. Photo by Clive Shirley, Hidden Forest, with permission.

Bidartondo and Duckett (2010) noted that **Aneuraceae** typically have basidiomycete fungi, in particular species of ***Tulasnella*** (Figure 89; see also Figure 49), giving them the potential to form **ectomycorrhizae** (form of symbiotic relationship between fungal symbiont, or mycobiont, and roots or rhizoids of various plant species; mycobiont is often from **Basidiomycota** or **Ascomycota**, and more rarely from **Zygomycota**). Using fungal DNA sequence data, they did not detect fungi in ***Riccardia chamedryfolia*** (Figure 102-Figure 111).

Biochemistry

Riccardia chamedryfolia (Figure 102-Figure 111) has 1-2 oil bodies per cell (Figure 127).

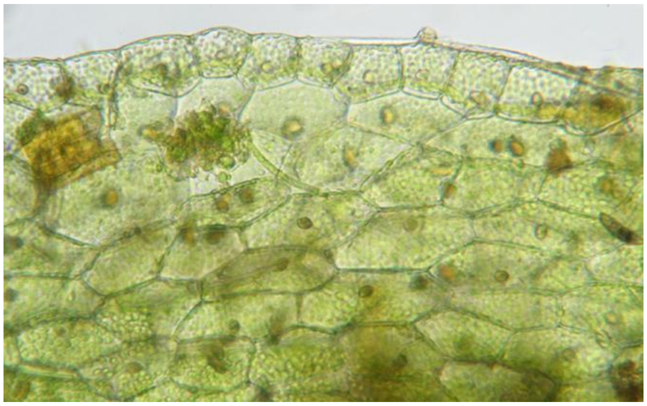

Figure 127. ***Riccardia chamedryfolia*** showing cells with 1-2 dark-colored oil bodies. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Some sesquiterpenoids have been isolated from ***Riccardia chamedryfolia*** (Figure 102-Figure 111) (Ge 2007).

Riccardia crassiretis

Distribution

Riccardia crassiretis is known from Sri Lanka, Philippines, Sumatra, Java, New Guinea, and New Caledonia (Furuki 2006).

Aquatic and Wet Habitats

In the Philippines, ***Riccardia crassiretis*** occurs on soil and rocks by water (Furuki 2006).

Adaptations

Although ***Riccardia crassiretis*** does not seem to live under water, its thick-walled thallus cells (Furuki 2006) could be of value if it is. On the other hand, they might be more important to prevent cell collapse when it dries out.

Reproduction

Riccardia crassiretis is **dioicous** (Furuki 2006). Capsules are described by Furuki (2001).

Riccardia crenulata

Distribution

Riccardia crenulata is known from Singapore, Philippines, Malaysia (Malay Peninsula and Borneo), and Indonesia (Java and Sumatra) (Furuki & Tan 2013). It is also reported from Taiwan (Buchanan *et al.* 1997; Lai & Wang-Yang 1976).

Aquatic and Wet Habitats

Riccardia crenulata (re-identified from *Riccardia tenuicostata*) occurs at <30 cm above water level in the tropics (Ruttner 1955). Furuki and Tan (2013) reported it from wet rocks in Singapore.

Reproduction

Riccardia crenulata is dioicous; its sporophytes are unknown (Furuki 2001).

Riccardia diminuta

Distribution

Furuki (2006) reported ***Riccardia diminuta*** from the Philippines, Sumatra, Java, and New Caledonia. Yin *et al.* (2016) listed it as one of the species on Hainan Island, China. Shu *et al.* (2016) added Vietnam and Horing (2017) added Malaysia.

Aquatic and Wet Habitats

Ruttner (1955) reported that ***Riccardia diminuta*** occurs in thermal acidic spray zones in the tropics (Ruttner 1955). Furuki (2006) reported that it occurs on soil and rocks by water in the Philippines.

Reproduction

Riccardia diminuta is **dioicous** (Furuki 2006).

Riccardia elata (Figure 128-Figure 131)

Distribution

Riccardia elata (Figure 128-Figure 131) is known from Singapore, Indonesia (Java, Sumatra). Malaysia (Malay Peninsula and Borneo) and the Philippines (Furuki & Tan 2013). Singh and Singh (2007) reported it from New Sikkim, India.

Figure 128. ***Riccardia elata*** showing its delicate branching. Photo by Li Zhang, with permission.

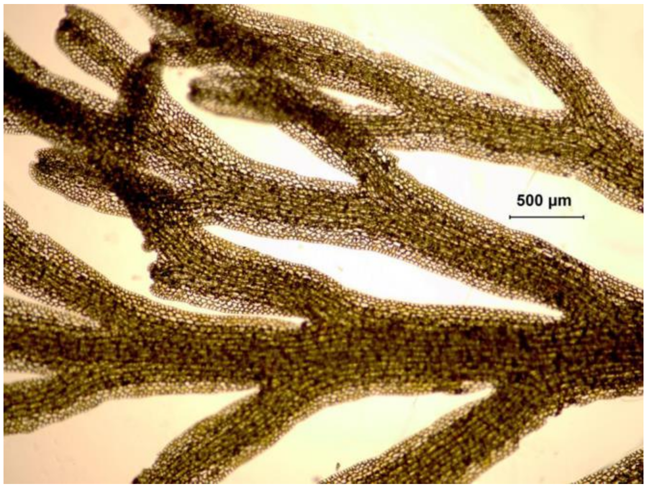

Figure 129. ***Riccardia elata*** showing the borders on the thalli. Photo by Li Zhang, with permission.

Aquatic and Wet Habitats

Ruttner (1955) included ***Riccardia elata*** (Figure 128-Figure 130) as an aquatic species in the tropics. In the Philippines, it is known from wet soil along a stream (Figure 130) (Furuki & Tan 2013). In Sikkim, India, it occurs in moist, shady locations under slowly dripping water (Singh & Singh 2007).

Figure 130. ***Riccardia elata*** in a wet habitat. Photo by Li Zhang, with permission.

Adaptations

Riccardia elata (Figure 128-Figure 130) is one of the larger (up to 10 cm) ***Riccardia*** species (Singh & Singh 2007). In the Philippines, ***Riccardia elata*** is deep green when fresh (Furuki & Tan 2013), but Singh and Singh (2007) described it as light green to yellowish green when fresh (Figure 130). This suggests that its color may depend on the environment, possibly light intensity or state of hydration, but also it could be a result of nutritional status.

Reproduction

Riccardia elata (Figure 128-Figure 130) is **dioicous**, with sporophytes mostly absent (Singh & Singh 2007; Furuki & Tan 2013). Finally, in 2017, Singh and Singh found and described capsules from the Himalayas in India. Furthermore, the 2-celled endogenous gemmae (Singh & Singh 2007) are rare, at least in the Philippines (Furuki & Tan 2013). Its chromosome number is n=9 m (Zheng & Zhu 2008).

Biochemistry

Biochemical studies on ***Riccardia elata*** (Figure 128-Figure 130) are rather limited. Figure 131 shows the cells with small oil bodies where one would expect secondary compounds to be stored.

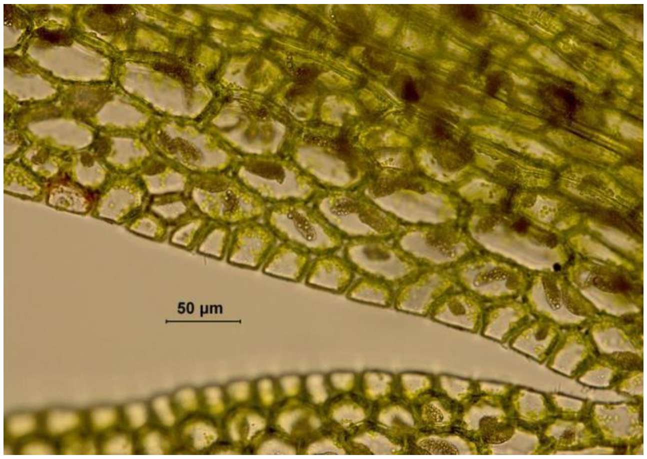

Figure 131. ***Riccardia elata*** showing cells with oil bodies (see cells near border) and a distinct border. Photo by Li Zhang, with permission.

From ***Riccardia elata*** (Figure 128-Figure 130) one stilbene and three flavonoids were isolated and their structures were determined (Ge 2007).

Riccardia graeffii (Figure 132-Figure 133)

(syn. = *Riccardia androgyna*, *Riccardia platyclada*)

In recent years, this species has gone by both *Riccardia platyclada* (Söderström *et al.* 2016) and ***Riccardia graeffei*** (Figure 132-Figure 133) (Furuki 1991; TROPICOS 2021). TROPICOS considers *Riccardia platyclada* to be a synonym of ***Riccardia graeffei***; The Plant List considers *Riccardia platyclada* an unresolved name, while accepting ***Riccardia graeffei***. In these chapters I am following the nomenclature used by Söderström *et al.* (2016) which recognizes ***Riccardia graeffei*** and not *Riccardia platyclada*. In any case, they are apparently accepted as the same species and I have treated them as such here.

Distribution

Riccardia graeffei (Figure 132-Figure 133) is widely distributed in tropical Asia, Australasia, and the Pacific (Furuki & Tan 2013). Its known records include India (Srivastava 1972; Sharma & Alam 2011; Gupta & Asthana 2016), Vietnam, Japan, Philippines, Malay Peninsula, Singapore, Borneo, Sumatra, Java, New Guinea, Caroline, New Caledonia, Vanuatu, Samoa, Fiji, Tonga, Tahiti, and Australia (del Rosario 1967; Furuki 2006). Singh and Singh (2015) recently reported it as new to Andaman and Nicobar Islands in the Bay of Bengal. To this list, Singh and Singh (2015) noted records from China, Indonesia, Malaysia, Taiwan, and Thailand.

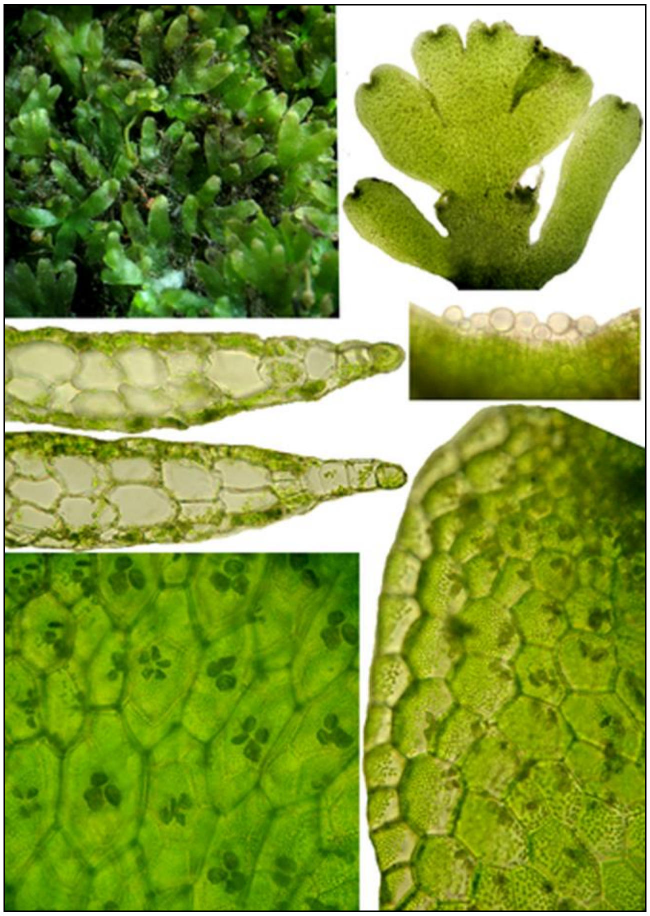

Figure 132. ***Riccardia graeffei*** showing growth form, cs with multi-layered ells, and oil bodies in cells. Photos from MySpecies.info, through Creative Commons.

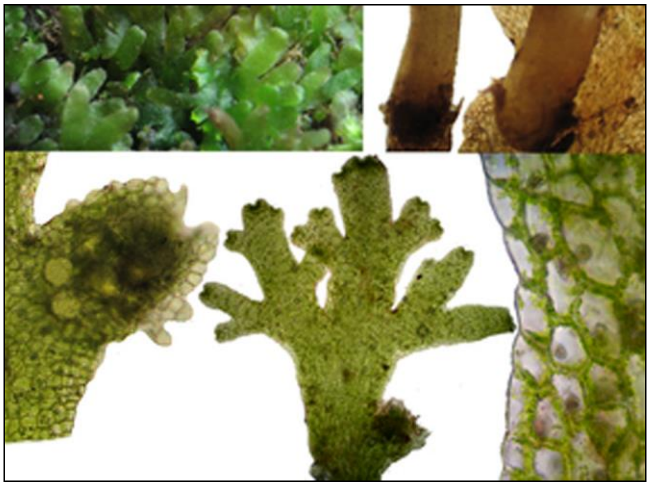

Figure 133. ***Riccardia graeffei***. Photos from MySpecies.info, through Creative Commons.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Riccardia graeffei*** (Figure 132-Figure 133) from the wall of a bay, source of pond inflow, **tuff** (light, porous rock formed by consolidation of volcanic ash) wall, <30 cm above water level, on submerged tree trunk, and overhanging water in the tropics. Ruttner also listed ***Riccardia graeffei***) as an aquatic inhabitant in the tropics. Furuki reported it from wet rocks, fallen logs, and soil by water in lowland (Furuki 2006; Furuki & Tan 2013). Singh and Singh (2015) described it as terrestrial, lithophytic, or corticolous, growing in very moist places along a sheltered stream in dense tropical rainforest on the Andaman and Nicobar Islands, India. In India, Gupta and Asthana (2016) reported it from wet rocks and soil-overed rocks.

By contrast, Yamaguchi *et al*. (2005) identified ***Riccardia graeffei***; Figure 132-Figure 133) in plots that had been heavily burned in tropical lowland forest of East Kalimantan, Indonesia.

Adaptations

Riccardia graeffei (Figure 132-Figure 133) has yellowish green to green thalli when fresh (Furuki & Tan 2013). It lacks rhizoids, but possesses a smooth to granulose cuticle (Singh & Singh 2015). Its color suggests an adaptation to low light.

Reproduction

Riccardia graeffei exhibits the **heteroicous** condition with male, female, and paroicous branches (Furuki 2006; Furuki & Tan 2013; Singh & Singh 2015). The capsules are blackish brown (Singh & Singh 2015). Singh and Singh (2015) reported it with 2-celled endogenous gemmae. Its chromosome number is *n*=9 m (Zheng & Zhu 2008).

Biochemistry

Riccardia graeffei has numerous botryoidal oil bodies (bottom of Figure 132) in all cells of the thallus (Furuki & Tan 2013). Ge (2007) reported riccardiphenol C and two benzoic acids from ***Riccardia graeffei***.

Riccardia jackii

(syn. = *Riccardia jackii* fo. *submersa*)

Distribution

Riccardia jackii occurs in the Philippines and Java (Furuki 2006).

Aquatic and Wet Habitats

In the tropics ***Riccardia jackii*** is known from water spray and on volcanic tuff walls, in thermal acidic spray, and submersed in ponds (Ruttner 1955). But in the Philippines, Furuki (2006) found it on soil and humus.

Reproduction

Riccardia jackii is **dioicous** (Furuki 2006). Ono (1978) described the gemmalings of this species.

Biochemistry

Matsuo *et al*. (1982) isolated enantiomeric type sesquiterpenoids from ***Riccardia jackii***. It produces ent-selinane-, ent-aromadendrane and ent-bicyclogermacrane-type sesquiterpenes together with (R)-cuparene and α-barbatene (Asakawa *et al*. 1981; Ge 2007). In addition, 3,4-dimethoxy-5-hydroxy-9,1-dihydrophenanthrene is a rare dihydrophenanthrene derivative among liverworts and was first described in ***Riccardia jackii*** (Salamani 1978).

Riccardia marginata

(syn. = *Aneura marginata***,** *Riccardia muscoides*)

Distribution

Riccardia marginata (Figure 134) occurs in New Zealand and the north coast of Australia (DiscoverLife 2008). To these locations, Furuki and Tamura (2015) have added Japan with ***Riccardia marginata*** var. ***pacifica***.

Figure 134. ***Riccardia marginata***, a species mostly of New Zealand and Australia. Photo by Shirley Kerr, with permission.

Aquatic and Wet Habitats

The liverwort ***Riccardia marginata*** (Figure 134) occurs on the wet banks of running water and grows on moist soil among rushes and introduced herbs in New Zealand reserves (Macmillan 1976). Tangney (1988) reported it from permanently wet open sites in New Zealand where ***Sphagnum cristatum*** (Figure 135) was one of the characteristic species.

Figure 135. ***Sphagnum cristatum***, a species that characterizes wet, open sites where ***Riccardia marginata*** occurs in New Zealand. Photo by Clive Shirley, The Hidden Forest, with permission.

Adaptations

Riccardia marginata (Figure 134) is small and brown (Pearson 1922). This coloration suggests protection against the damaging effects of high light intensity.

Reproduction

Riccardia marginata (Figure 134) is **dioicous** (Pearson 1922). Its spores are tiny, making them easily dispersed by wind, but providing it with limited resources with which to germinate and establish.

Fungal Interactions

I have seen no reports of fungi growing on or within ***Riccardia marginata*** (Figure 134). However, this may be a real absence based on its antibiotic activity, as discussed below, or a lack of study.

Biochemistry

It is interesting that this tiny species, ***Riccardia marginata*** (Figure 134), with so little ecological information has had a number of biochemical studies. Baek *et al*. (2004) isolated three new chlorinated bibenzyls from this species, the first time any simple chlorinated bibenzyl was reported from a natural source. These three compounds exhibited antimicrobial activity against ***Bacillus subtilis*** (bacterium; Figure 136), ***Candida albicans*** (yeast; Figure 137), and ***Trichophyton mentagrophytes*** (**Ascomycota**; Figure 138-Figure 139).

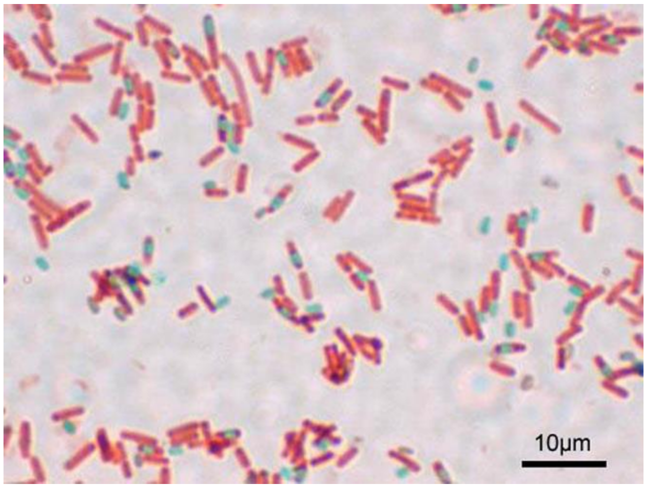

Figure 136. ***Bacillus subtilis*** spores, a species that is inhibited by extracts of ***Riccardia marginata***. Photo by Y. Tambe, through Creative Commons.

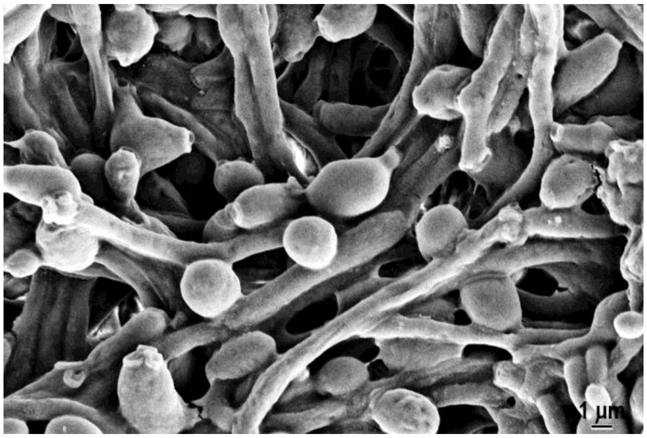

Figure 137. SEM of ***Candida albicans***, a species that is inhibited by extracts of ***Riccardia marginata***. Photo by Vader 1941, through Creative Commons.

Figure 138. ***Trichophyton mentagrophytes*** ringworm on arm, a species that is inhibited by extracts of ***Riccardia marginata***. Photo through Creative Commons.

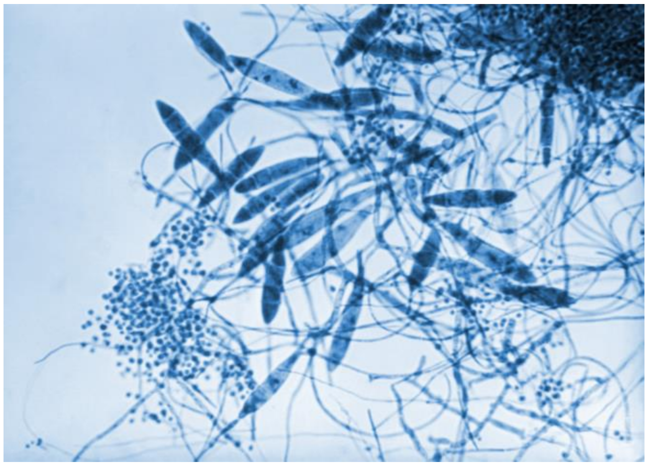

Figure 139. ***Trichophyton mentagrophytes*** as it appears stained under the microscope. Photo by Lucille K. Georg, through Creative Commons.

Unsinn *et al*. (2013) prepared an antimicrobial product (2,6-dichloro-3-phenethylphenol) from ***Riccardia marginata*** (Figure 134). Na *et al*. (2005a, b) likewise found that extracts of this species inhibited the Gram positive bacterium ***Bacillus subtilis*** (Figure 136), yeast (***Candida albicans***; Figure 137), and has strong action against the skin fungus ***Trichophyton mentagrophytes*** (Figure 138-Figure 139). It was ineffective against P388 murine leukemia cells.

Riccardia multifida (Figure 140-Figure 149)

Distribution

Riccardia multifida (Figure 140-Figure 149) has a wide distribution, known from India [Western Himalaya (Uttarakhand), Eastern Himalaya (Arunachal Pradesh, Assam, Sikkim, West Bengal), Western Ghats (Kerala, Maharashtra, Tamil Nadu), Central India (Madhya Pradesh)], China, Hawaii, Micronesia, Nepal, Russia, Sri Lanka, Taiwan, Turkey, Africa, Europe, and North America (Singh & Singh 2017). Damsholt (2017) listed it as known from the Faeroe Isles. Frey and Kurschner (1983) reported it from Iran.

In North America, it occurs in the northwestern part of the continent and in the east from Newfoundland southward (Perold 2001). Kruse and Davison (2012) reported it from Texas, USA. In Europe it is reported from Greenland, Iceland, and the British Isles. It occurs in both north and south Africa, Madagascar, and west Java. Furuki (1991) reported the subspecies ***R. multifida*** (Figure 140-Figure 149) subsp. ***decrescens*** from Japan. It is likely that many more records of this species exist in the USA and elsewhere.

Figure 140. ***Riccardia multifida***, a widespread species, forming a dense cushion. Photo by David T. Holyoak, with permission.

Figure 141. ***Riccardia multifida*** showing the branching pattern. Photo by Jan-Peter Frahm, with permission.

Figure 142. ***Riccardia multifida***. Photo by Manju Nair, through Creative Commons.

Figure 143. ***Riccardia multifida*** showing the pale color of a well hydrated colony. Photo by Hermann Schachner through Creative Commons.

Figure 144. ***Riccardia multifida*** showing a slightly darker phase. Photo by Jean Faubert, with permission.

Figure 145. ***Riccardia multifida***. Photo by Hermann Schachner, through Creative Commons.

Figure 146. ***Riccardia multifida***. Photo by Hermann Schachner, through Creative Commons.

Figure 147. ***Riccardia multifida*** growing on a vertical substrate. Photo by Michael Lüth, with permission.

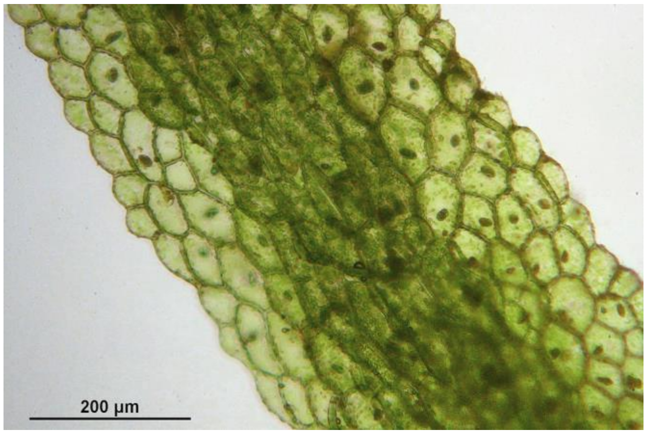

Figure 148. ***Riccardia multifida*** showing thallus with light-colored margins. Photo by Hermann Schachner, through Creative Commons.

Aquatic and Wet Habitats

Riccardia multifida (Figure 140-Figure 149) occurs on streambanks with frequent submergence and slow water, wet rocks and soil near fast streams (Watson 1919), and may invade partially into the constantly submerged zone (Watson 1915). Konstantinova *et al*. (2002) found it on soil near brooks (Figure 150) in the forest of the Upper Bureya River (Russian Far East). In northwest Portugal, it occurs in mountain streams (Vieira *et al.* 2005).

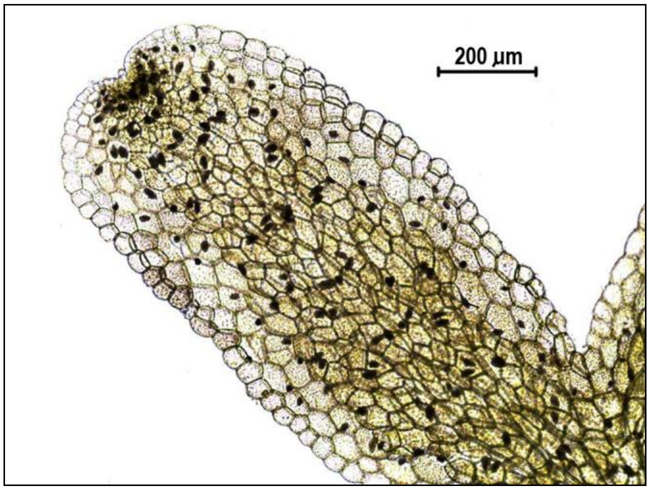

Figure 149. ***Riccardia multifida*** showing thallus with light-colored margins. Photo by Hugues Tinguy, with permission.

Figure 150. ***Riccardia multifida*** habitat. Photo by Hermann Schachner, through Creative Commons.

In the Himalayas, Singh and Singh (2017) report it from moist and shady places in dense mixed forest. Similarly, in Adjera, Georgia, on the coast of the Black Sea near the foot of the Lesser Caucasus Mountains, ***Riccardia multifida*** (Figure 140-Figure 149) occurs on stones and cliffs along streams in the broadleaved forest and in the waterfall spray zone, in partial shade, in broadleaved forests (Bakalin 2013).

In the Upper Peninsula of Michigan, USA, ***Riccardia multifida*** (Figure 140-Figure 149) occurs on gravelly bluffs along Lake Superior and on logs (Figure 151) in boggy woods (Evans & Nichols 1935). At Mountain Lake, Virginia, USA, it is "rather common" in wet sites (Sharp 1944). In West Virginia, it is one of the liverworts that occurs in McKinney's Cave (Ammons 1933). Burnham (1919) reported it from a "wet place" in the Lake George area, New York, USA. Trigoboff (2013) found that it could occur in massive clumps in Central New York on permanently wet creek rocks or dripping rocks at the sides of creeks, but nevertheless was never present at more than 2-3 spots along a creek. Fulford (1934) recorded it from shaded, swampy places in Kentucky, USA.

Figure 151. ***Riccardia multifida*** habitat where part of it is growing on decaying wood. Photo by Rick Ballard, through Creative Commons.

Few liverworts seem able to live in rich fens. In northwestern Europe, Kooijman and Westhoff (1995) found only two liverworts: ***Aneura pinguis*** (Figure 52-Figure 57) and ***Riccardia multifida*** (Figure 140-Figure 149), in these fens. Albinsson (1997) suggested that most liverworts require acidic, nutrient-poor sites.

Watson (1915) described zonation patterns in a Somerset heath (Figure 71). ***Riccardia multifida*** (Figure 140-Figure 149) occurs immediately above the zone of ***Aneura pinguis*** (Figure 52-Figure 57) and ***Pellia epiphylla*** (Figure 152). It sometimes extends downward into the latter zone. It also creates a definite zone in the furrows just at the water line.

Figure 152. ***Riccardia multifida*** on ***Pellia epiphylla***, an occurrence that can happen where it occurs adjacent to the ***Aneura pinguis*** and ***Pellia epiphylla*** zone in wet heath. Photo by Hermann Schachner, through Creative Commons.

In Arkansas, USA, Wittlake (1950) found it under and around the springs on the slope, accompanied by ***Aneura pinguis*** (Figure 52-Figure 57). On the Mahogany Hammocks, Everglades National Park, Florida, USA, ***Riccardia multifida*** (Figure 140-Figure 149) occurs on the low hammocks, but not on the high hammocks (Zona & Sadle 2017). These low hammocks have relatively continuous moisture in the soil. On the other hand, Haynes (1915) and McFarlin (1940) found ***Riccardia multifida*** on logs in wet places in Florida. Clebsch (1947) found it on a limestone face above Bellamy's Cave, Kentucky, USA.

In the Western Ghats, ***Riccardia multifida*** (Figure 140-Figure 149) occurs on tree buttresses near streams (Jyothilakshmi *et al*. 2016). Konstantinova *et al*. (2002) reported it from soil near a brook in the forest zone of the Upper Bureya River in the Russian Far East. Michael Lüth photographed it in a grass-sedge mire with other bryophytes (Figure 153-Figure 154).

Figure 153. ***Riccardia multifida*** occurring on soil amid grass. Photo by Michael Lüth, with permission.

Figure 154. ***Riccardia multifida*** with ***Scapania*** amid sedges. Photo by Michael Lüth, with permission.

Adaptations

In some wet habitats ***Riccardia multifida*** (Figure 140-Figure 149) forms dense **mats** (Figure 155-Figure 156). These seem to be able to change colors (Figure 155-Figure 156), but we need studies to show the environmental parameters that can cause these color changes and if they offer any advantage.

Riccardia multifida (Figure 140-Figure 149) does not seem to be well adapted to drying out. At 20ºC for 12 hours, only a few cells of ***R. multifida*** remained alive at 84% relative humidity (Clausen 1964). At 93% relative humidity about 3/4 of the cells remained alive.

Reproduction

Riccardia multifida (Figure 140-Figure 149) is **monoicous** (Singh & Singh 2017). The male and female branches are rarely **synoicous** (Perold 2001). Although Perold states that gemmae are unknown, Yang and Hsu had already described the germination of spores and gemmae of ***Riccardia multifida*** in 1967.

Figure 155. ***Riccardia multifida*** with pale green portions and pinkish portions. Photo by Michael Lüth, with permission.

Figure 156. ***Riccardia multifida*** showing two clumps with one brownish pink and one pale pink-green. Photo by Michael Lüth, with permission.

Benson-Evans (1964) found that gametangial production in ***Riccardia multifida*** (Figure 140-Figure 149) was a long-day response. Light intensities above 16 lux in the field also correlated with gametangial production.

Steil (1923) described the structure of the antherozoid in ***Riccardia multifida*** (Figure 140-Figure 149). Rushing *et al*. (1995) have described the blepharoplast of the spermatid.

Presence of sporophytes is known from a number of locations (Figure 157-Figure 159).

Figure 157. ***Riccardia multifida*** with young sporophyte. Photo by Paul G. Davison, with permission.

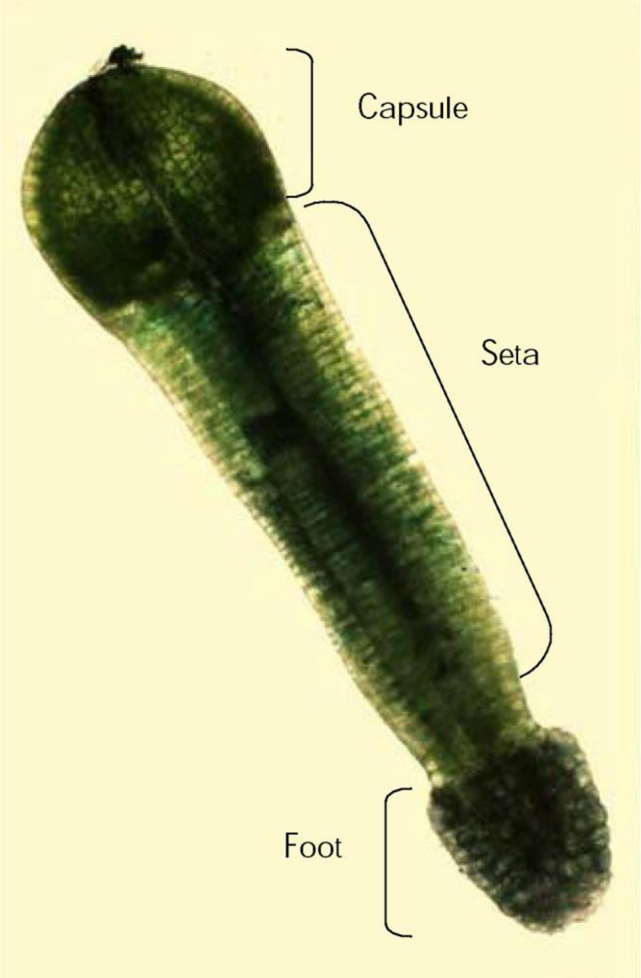

Figure 158. ***Riccardia multifida*** sporophyte before elongation. Image by Karen Renzaglia, with permission.

The chromosome number in the genus is *n*=9 + m (Zheng & Zhu 2008).

Fungal Interactions

In ***Riccardia multifida*** (Figure 140-Figure 149), Krause *et al*. (2011) were unable to find any fungal hyphae of tulasnelloid (**Basidiomycota**) fungi in living liverwort host cells. However, fungi had colonized dead cells. More commonly, the fungi occurred outside the thallus and on the adjacent substrate. In the liverwort, uncolonized living cells exhibited thick-walled cortical cells and ovoid, starch-filled chloroplasts. These chloroplasts were absent in the colonized cells. The hyphae on the dead cells proved to be those of **Ascomycetes**. Krause *et al*. (2011) found that the differences in colonization patterns among species in the genus differed from each other, supporting the hypothesis that the host regulates the pattern of colonization by the fungus.

Figure 159. ***Riccardia multifida*** with capsules and fully elongated setae. Photo from Botany Website, UBC, with permission.

Jiao *et al*. (2013) determined the chemical structures of compounds obtained from ***Penicillium*** sp. (Figure 160-Figure 161) that lived endophytically in ***Riccardia multifida*** (Figure 140-Figure 149). When tested, these compounds showed significant **allelopathic** effects (phenomena by which organisms produce one or more biochemicals that influence germination, growth, survival, and reproduction of other organisms) that retarded germination of ***Arabidopsis thaliana*** seeds (Figure 162-Figure 163). It would be interesting to test the allelopathic effects of this liverwort-fungus combination in nature. For a tiny plant this could provide a powerful competitive advantage against the larger tracheophytes.

Figure 160. ***Penicillium italicum*** and ***Penicillium digitatum*** growing on an orange. A species of ***Penicillium*** lives in cells of ***Riccardia multifida***. Compounds made by the fungus during this association can inhibit germination of ***Arabidopsis thaliana***. Photo by George Barron, with permission.

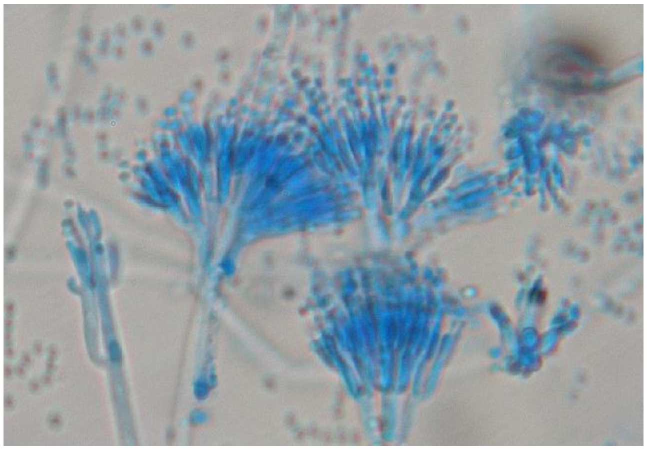

Figure 161. ***Penicillium*** sp. as seen under the microscope. Photo by Carlos de Paz, through Creative Commons.

Figure 162. ***Arabidopsis thaliana*** seeds, a species whose germination is inhibited by the ***Penicillium*** species that lives in cells of ***Riccardia multifida***. Photo by Stefan Lefnaer, through Creative Commons.

Figure 163. ***Arabidopsis thaliana***. Photo by Brona, through Creative Commons.

Biochemistry

The oil bodies are not evenly distributed, being absent or rare in the dorsal and ventral epidermal cells, absent in as much as 70% of the marginal cells, but present in internal cells (Perold 2001). They are mostly single, but occasionally two per cell.

Yoshida *et al*. (1997; Ge 2007) reported bisbibenzyls and other compounds from ***Riccardia multifida*** (Figure 140-Figure 149). They were able to isolate a new cyclic bisbibenzyl dimer from the variety ***decrescens***.

The aromatic ethers riccardin A and riccardin B have been isolated from ***Riccardia multifida*** (Figure 140-Figure 149) (Salamani 1978; Asakawa *et al*. 1983). These compounds, isolated from ***R. multifida***, have cytotoxic properties (Asakawa *et al*. 1983; Chandra *et al*. 2017).

Tori *et al*. (1985) used NMR spectra to identify new macrocyclic bis(bibenzyls) in ***Riccardia multifida*** (Figure 140-Figure 149).

Riccardia multifidoides

Distribution

Riccardia multifidoides is a tropical species that seems to be either rare or poorly known.

Aquatic and Wet Habitats

In the tropics, Ruttner (1955) reported ***Riccardia multifidoides*** as submersed in ponds and on the wall of a bay. But in the Philippines, Furuki (2006) reported it only from fallen logs.

Reproduction

Riccardia multifidoides is **monoicous** (Furuki 2006).

Riccardia parvula

Distribution

Riccardia parvula is known from the Philippines, Malay Peninsula, Borneo, Sumatra, and Java.

Aquatic and Wet Habitats

Riccardia parvula occurs in waterfalls in the tropics (Ruttner 1955). In the Philippines, this species in known only from rotten logs (Furuki 2006). Nevertheless, rotten logs hold moisture longer than early stage logs, thus suggesting its preference for moisture.

On Mount Patuha, West Java, Indonesia, ***Riccardia parvula*** occurs on soil in disturbed forest adjacent to Situ (Lake) Patenggang, 1500 m asl (Gradstein *et al*. 2010).

Reproduction

Riccardia parvula is **dioicous** (Furuki 2006). Furuki (2001) has described the capsules and spores. The spores are 12.5-15 µm in diameter.

Riccardia singapurensis

The status of this species is controversial (Furuki & Tan 2013).

Distribution

Riccardia singapurensis occurs in Singapore (Zhu *et al*. 2018) and Australia (North Queensland) (Furuki & Tan 2013). It is rather common in Malesia and adjacent regions (Furuki & Tan 2013). Horing (2017) added it to the flora of Malaysia.

Aquatic and Wet Habitats

Riccardia singapurensis occurs on wet rocks and fallen logs in forests or along streams (Furuki & Tan 2013).

Adaptations

Thalli of ***Riccardia singapurensis*** are small, green to brownish green when fresh. Geotropic stolons give it a structure to survive unfavorable conditions and help the colony to spread (Furuki & Tan 2013). Rhizoids are scattered on the ventral surface of the prostrate thallus, providing a means of cementing itself to rocks.

Reproduction

Riccardia singapurensis is h**eteroicous** with male and **paroicous** branches, but male branches are rare and female branches are unknown (Furuki & Tan 2013). However paroicous branches are common. Gemmae are rare.

Biochemistry

Oil bodies of ***Riccardia singapurensis*** are pale brownish, composed of granules, globose to elliptical (Furuki & Tan 2013). The species lacks biochemical studies.

Riccardia subexalata

(syn. = *Aneura subexalata*)

Distribution

The only record I found for this species was the report by Ruttner (1955) that it occurs in the tropics.

Aquatic and Wet Habitats

This is one of those species listed as aquatic in the tropics by Ruttner (1955).

Riccardia tenuis

(syn. = *Aneura tenuis*)

Distribution

Riccardia tenuis is known from the tropics (Ruttner 1955). But otherwise, little seems to be known about it.

Aquatic and Wet Habitats

Riccardia tenuis occurs in waterfalls in the tropics (Ruttner 1955).

Riccardia tjibodensis

Distribution

Like the previous species, little is known about this species except the report by Ruttner (1955) that it occurs in the tropics.

Aquatic and Wet Habitats

Riccardia tjibodensis occurs in waterfalls in the tropics (Ruttner 1955).

Riccardia wettsteinii

Several varieties are known for this species.

Distribution

Riccardia wettsteinii is known from its type specimen from Java (Pócs 1976-77).

Aquatic and Wet Habitats

Riccardia wettsteinii occurs on the wall of a bay in the tropics (Ruttner 1955), presumably in Java.

Summary

The **Aneuraceae** has a number of members that live in wet habitats, but few that live submersed. The most remarkable member is ***Aneura mirabilis***, a completely parasitic species that partners with a fungus (***Tulasnella*** sp.) and a tree, especially birch trees. Other members of the genus can have fungal partners or epiphytc fungi, but ***Aneura mirabilis*** is the only liverwort that totally lacks chlorophyll.

Members of ***Aneura*** often differ in thickness of the thallus that within the species can represent different cryptic species.

Lobatiriccardia is a much less known genus, but its separation from ***Aneura*** seems justified. It occurs in the Southern Hemisphere and the tropics. Its wetland species are mostly not submersed, occurring in bogs, streambanks, decaying logs, but occasionally submersed.

Riccardia can be found from the tropics to both polar regions. Some species occur in cold alpine streams; others occur at stream margins and on emergent rocks. The genus occupies a wide range of wet habitats.

Acknowledgments

Lars Söderström helped me find the current acceptable names for a number of older taxa.

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