CHAPTER 1-15
AQUATIC AND WET MARCHANTIOPHYTA, PALLAVICINIALES

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Figure 1. Wetland habitat with ***Betula pubescens***, a habitat suitable for ***Pallavicinia lyellii***. Photo by Ingo2802, through Creative Commons.

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

SUBCLASS PELLIIDAE

Pallaviciniales: Hymenophytaceae

Hymenophyton flabellatum (Figure 2, Figure 4-Figure 6)

(syn. = *Symphyogyna flabellata*)

Hymenophyton flabellatum (Figure 2, Figure 4-Figure 6) has been treated variously by different researchers. Pfeiffer (2000) reviewed these differences in perspective and suggested that at least two distinct taxa of ***Hymenophyton*** exist in New Zealand and Tasmania. Pfeiffer *et al*. (2004) used molecular analysis to determine differences in populations and recognized four taxa in ***Hymenophyton***. Because of the differences in treatment through time, I have included all literature related to ***Hymenophyton flabellatum***, even if it has since been placed in a different species.

Figure 2. ***Hymenophyton flabellatum***, a species from Australia, New Zealand, and Tasmania. Photo by Ken Harris, EntSocVic, through Creative Commons.

Distribution

Hymenophyton flabellatum *s.l.* (Figure 2, Figure 4-Figure 6) has a Palaeoaustral distribution pattern, with populations known from Tasmania, New Zealand, and Australia. Pfeiffer (2000) recognized ***H. flabellatum*** and ***H. leptopodum*** (Figure 3) in New Zealand and ***H. mulleri*** collected from a river (Evans 1925) in Australia. ***Hymenophyton mulleri*** (*H. muelleri*) is not recognized by Söderström *et al.* (2016); TROPICOS (2021) includes it in ***Hymenophyton flabellatum***. The Tasmanian taxon might also be recognized as ***H. leptopodum***. The segregate ***Hymenophyton pedicellatum*** is known from South America (Pfeiffer *et al*. 2004). Segregates of ***H. flabellatum*** from New Caledonia, Fiji Islands, Colombia, and Chile (Evans 1925) have been variously treated as a member of ***H. flabellatum*** and as separate taxa (Pfeiffer 2000).

Figure 3. ***Hymenophyton leptopodum***, a segregate recognized in New Zealand. Photo by TePapa, through Creative Commons.

Figure 4. ***Hymenophyton flabellatum***. Photo by Niels Klazenga, with permission.

Figure 5. ***Hymenophyton flabellatum*** wet, growing on soil. Photo by Jan-Peter Frahm, with permission.

Figure 6. ***Hymenophyton flabellatum*** showing stipe and leafy plant. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

Hymenophyton flabellatum (Figure 2, Figure 4-Figure 6) occurs in Cool Temperate Victorian Rainforest streams (Downes *et al*. 2003; Carrigan 2008) found it in an unregulated creek in Australia. In New Zealand, Frogley and Glenny (2020) found it in a small creek bed. Braggins (1987) found it in a Tasmanian stream on clay and humus. Suren (1996) considered it to be obligately or facultatively aquatic in streams.

But ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) is not restricted to streams. In their biochemical study, Asakawa *et al*. (2001) noted that ***Hymenophyton flabellatum*** occurred on shaded wet soil (Figure 7), humus, and old logs in forests, usually in shade, and on banks beside streams and waterfalls (Figure 8). In ***Eucalyptus regnans*** forest (Figure 9) at Wallaby Creek, Victoria, Australia, ***Hymenophyton flabellatum*** occurred on very wet, sodden, white-rot logs sheltered on south sides of logs (Ashton 1986). Gibson (2006) reported it to be common in wet forests in Australia.

Figure 7. ***Hymenophyton flabellatum*** growing on soil. Photo by Jan-Peter Frahm, with permission.

Figure 8. ***Hymenophyton flabellatum*** on a vertical substrate. Such growth forms of shelves can occur in the splash of waterfalls. Photo from Manaaki Whenua – Landcare Research, with online permission.

Figure 9. ***Eucalyptus regnans*** forest in Australia, where one can find ***Hymenophyton flabellatum*** on very wet logs. Photo by Patche99z, through Creative Commons.

Adaptations

It is interesting that ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) has water-conducting elements (Figure 10-Figure 11) in its gametophytes (Burr *et al*. 1974; Campbell *et al*. 1975). These are axially elongated cells with no living contents and numerous perforations in their walls, making them unique among land plants. Hébant (1978) identified endoplasmic-reticulum cisternae associated with the differentiating pores and compared them to developing sieve pores in phloem of tracheophytes.

Figure 10. ***Hymenophyton flabellatum*** showing ribs made of water-conducting elements. Photo by Arthur Chapman, through Creative Commons.

Figure 11. ***Hymenophyton flabellatum*** wet plants showing the prominent rib. Photo by Devaprayaga, through Creative Commons.

The plants of ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6Figure 14) are olive-green with fan-shaped fronds (Figure 12), crowded chloroplasts, small cells, and thick cell walls. The aquatic and wet habitat affiliations of this species puzzle me because they would seem to be adapted to drier habitats with their small cells, thick walls, and conduction system. Nevertheless, the fan-shaped fronds would most likely lose water easily (Figure 12-Figure 13), and they seem to handle both wet (Figure 11-Figure 12) and dry conditions (Figure 13).

Figure 12. ***Hymenophyton flabellatum*** showing signs of drying. Photo by Paul George, through Creative Commons.

Figure 13. ***Hymenophyton flabellatum*** dry plants. Photo by Robert Pergl, through Creative Commons.

Reproduction

The genus ***Hymenophyton*** (Figure 2, Figure 4-Figure 6Figure 14), as far as known, is **dioicous** (Figure 14) (Campbell *et al*. 1975; Crandall-Stotler *et al*. 2005). This image from Karen Renzaglia shows that at least sporophytes are known (Figure 15).

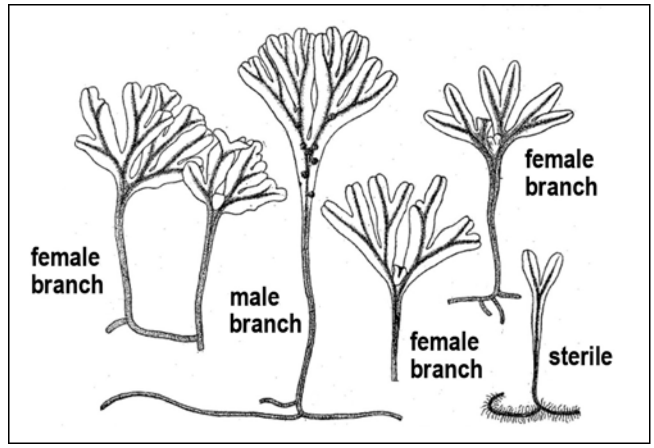

Figure 14. ***Hymenophyton flabellatum*** male, female, and sterile branches. Image modified from Evans 1925.

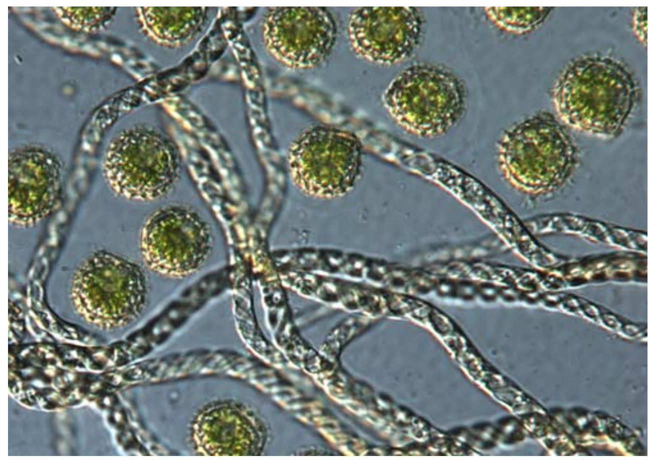

Figure 15. ***Hymenophyton*** spores and elaters. Photo by Karen Renzaglia, with permission.

Fungal Interactions

Johnson (1977) reported mycorrhizal infections of rhizoids in ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6). Ligrone *et al*. (2007) identified **Glomeromycotean** endophytes in New Zealand specimens. They concluded that **Glomeromycota** (Figure 16) lineages that form arbuscular mycorrhizae in a wide range of liverwort taxa have been derived by "host-shifting" from tracheophyte taxa (Figure 17) to liverworts.

Figure 16. ***Glomus coremioides*** (**Glomeromycota**); some members of this phylum form arbuscular mycorrhizae in liverworts such as ***Hymenophyton flabellatum***. Photo by Damon Tighe, through Creative Commons.

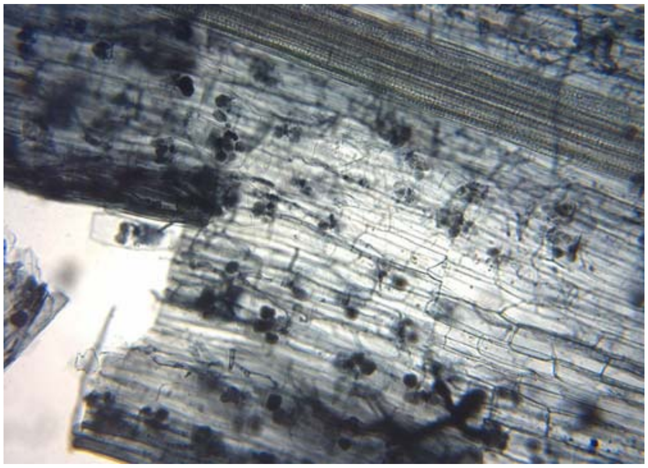

Figure 17. **Glomeromycota** arbuscular mycorrhiza in root of a tracheophyte. Photo by M. Sturmel, through public domain.

Figure 18. ***Eurema hecabe*** on ***Lespedeza bicolor***, a butterfly whose larvae are repelled by a compound that is present in ***Hymenophyton flabellatum***. Photo by Alpsdake, through Creative Commons.

Figure 19. *Arachniodes standishii*, a fern that produces the same antifeedant 1-(2, 4, 6-trimethoxy-phenyl)-but-2 (E)-en-1-one as that in ***Hymenophyton flabellatum***. Photo by Ecelan, through Creative Commons.

Biochemistry

Campbell *et al.* (1975) used chemical constituents to distinguish between ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) and ***H. leptopodum*** (Figure 3), concluding that they were both valid species. One of these differences is the presence of kaempferols in the latter but not in ***H. flabellatum***. Both species have flavone C-glycosides. Markham *et al.* (1976) further supported this conclusion based on flavonoid constituents.

Classen *et al.* (2019) reported arabinogalactan-proteins, compounds found in the extracellular matrix of ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) plants. These proteins have a small protein moiety that is usually rich in **hydroxyproline** (found in plant cell walls; serve as attachment points for glycan chains which are added as post-translational modifications). ***Hydroxyproline*** seems to have a major evolutionary role in liverworts, by regulating leaf and branch development (Basile 1990).

Toyota *et al.* (2009) identified 1-(2, 4, 6-trimethoxy-phenyl)-but-2 (E)-en-1-one, a known compound, as the cause of the hot-tasting, strongly pungent substance released when fragments of ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) are chewed. It is possible that this compound serves to discourage herbivores, but do the likely herbivores – arthropods – taste things the same way we do? In fact, Numata *et al.* (1984) demonstrated that its compound 1-(2, 4, 6-trimethoxy-phenyl)-but-2 (E)-en-1-one has antifeedant activity against the larvae of the yellow butterfly ***Eurema hecabe mandarina*** (Figure 18), although for that test it was extracted from *Arachniodes standishii* (Figure 19), a fern (see also Asakawa *et al.* 2001; Asakawa 2015).

Asakawa (2004) considered ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) to be one of the most chemically isolated liverworts so far examined. It was the only liverwort known to contain phenyl butanone. phenyl butanone in some fruits is used in perfumery and cosmetics (PubChem 2021).

It is not surprising that a liverwort so well endowed with noxious chemicals should offer protection against infections. Earl (2010) reported that ***Hymenophyton flabellatum*** (Figure 2, Figure 4-Figure 6) is commonly used medicinally.

Pallaviciniales: Pallaviciniaceae

Jensenia decipiens

(syn. = *Pallavicinia zollingeri*)

Schaumann *et al.* (2004) investigated DNA relationships in the genus ***Jensenia*** (Figure 20). They found a low level of variation both within and between taxa in the genus. On the other hand, the molecular data do support the separation of the genus ***Jensenia*** (Figure 20) from ***Pallavicinia*** (Figure 21-Figure 27). Forrest *et al.* (2005) further supported this separation and using cladistic methods concluded that ***Jensenia*** is monophyletic, thus a natural group. They considered its distribution to be the product of dispersal, not vicarious similarities.

Distribution

Jensenia decipiens is tropical, known from Sri Lanka (Farmer 1894; Long & Rubasinghe 2014), the Philippines, Malaysia (Grolle & Piippo 1986; Piippo & Tan 1992), Indonesia (Sumatra, Java, and Celebes) (Grolle & Piippo 1986; Piippo & Tan 1992; Gradstein *et al.* 2005), and

Papua New Guinea (Grolle & Piippo 1986; Enroth 1990; Piippo & Tan 1992), and more recently it has been reported from Malesia (Arianti & Gradstein 2007) and Japan (Schaumann *et al*. 2005).

Figure 20. ***Jensenia connivens***; ***Jensenia decipiens*** occurs on muddy stream banks. Photo by Bill Malcolm, with permission.

Aquatic and Wet Habitats

Jensenia decipiens in Ceylon occurs on muddy streambanks at 6200' (Farmer 1894). At lower elevations it outcompetes other plants with its profuse growth.

Ruttner (1955) reported ***Jensenia decipiens*** from the wall of a bay in the tropics. Piippo and Tan (1992) reported it from wet crevices of a trail in very deep shade in the Philippines.

Adaptations

Jensenia decipiens grows erect from a creeping rhizome. Its branches are thus tree-like (van der Gronde 1980). This would be a disadvantage in locations that dry, but in a moist environment it could provide greater access to CO_2 and possibly to light for photosynthesis.

Reproduction

Jensenia decipiens and all members of the genus thus far described are **dioicous** (van der Gronde 1980). Farmer (1894) described details of its development, including the gametophyte, archegonia, sporophyte, and spores.

Moore (1906) questioned the account of sporogenesis provided by Farmer (1894) and suggested that it was not unique, as suggested by the Farmer account, but was instead consistent with that known for other plants, including other liverworts.

The branching pattern of ***Jensenia decipiens*** is rather unusual. It appears to be dichotomous, but on closer inspection, the terminal bud occurs between the paired branches, and remains and grows, as in **monopodial** branching (having a central axis from which other branches arise, as in a spruce tree).

Pallavicinia

Pallavicinia can occur as a **rheophyte** (plant that lives in fast-moving water currents in environment where few other organisms can survive) in the wet tropics of SE Asia (Akiyama 1992).

Pallavicinia indica

Distribution

Pallavicinia indica is known from India, Java, Nepal, Sri Lanka, Sumatra, and Tahiti (Campbell 1908; Herzog 1942; Pradhan & Joshi 2009; Long & Rubasinghe 2014; Lavate *et al*. 2015; Manju *et al*. 2015). Specimens reported from China appear to belong to ***Pallavicinia levieri*** (Mamontov *et al.* 2015).

Aquatic and Wet Habitats

Pallavicinia indica occurs on **tuff** (porous volcanic rock) wall, waterfalls in tropics (Ruttner 1955). This species does not seem to prefer wet habitats. Nair and Prajitha (2016) reported the habitat of ***Pallavicinia indica*** as "land cuttings."

Pallavicinia levieri (Figure 21)

Distribution

Pallavicinia levieri (Figure 21) is an Asian temperate-tropical mountain species. It is known from Cambodia, China, Japan, Vietnam, Indonesia, Philippines, and Papua New Guinea (Grolle & Piippo 1984, 1986; Mamontov *et al*. 2015).

Figure 21. ***Pallavicinia levieri*** with leafy liverworts, from Guangdong, China. Photo by Li Zhang, with permission.

Aquatic and Wet Habitats

Ruttner (1955) reported ***Pallavicinia levieri*** (Figure 21) as aquatic from the tropics (Ruttner 1955). Mamontov *et al*. (2015) reported that it occurs along river beds of primeval forests, along stream beds and slopes in secondary mixed evergreen forests, and in deep gorges. In Cambodia it occurs on wet cliffs near waterfalls.

Reproduction

Pallavicinia levieri (Figure 21) is **dioicous** (Figure 22-Figure 23) (Mamontov *et al.* 2015). Campbell and Williams (1914) provide a morphological study.

Figure 22. ***Pallavicinia levieri*** with perianths and young sporophytes, from Hainan, China. Photo by Rui-Liang Zhu, with permission.

Figure 23. ***Pallavicinia levieri*** with perianth and other bryophytes. Photo by Li Zhang, with permission.

Biochemistry

Hashimoto *et al*. (1993, 1995) repotted that the major component of ***Pallavicinia levieri*** (Figure 22-Figure 23) is sacculatal, a pungent diterpene dialdehyde (Asakawa 1982). It also produces pallavicinol and a rare chettaphanin-type diterpenoid. It has a pungent (-)-polygodial that is a strong piscicide (Asakawa 1990). Furthermore, killie-fish (*Oryzia latipes*) die within 2 hours when exposed to a solution of 0.4 ppm of sacculatal, and within 20 minutes at 1 ppm of sacculata and 1/3 1/3-hydroxysacculatal (Asakawa 1998).

Pallavicinia lyellii (Figure 24-Figure 27)

(syn. = *Pallavicinia radiculosa*)

Distribution

Pallavicinia lyellii (Figure 24-Figure 27) is a subcosmopolitan, temperate-tropical species (Stebel *et al*. 2018). It occurs in western and central parts of Europe, Asia, North, Central, and South America, northern and central Africa, and some areas in the Southern Hemisphere. Nevertheless, it is rare in Europe. Lavate *et al*. (2015) detailed its country locations, including Bermuda, Brazil, Cuba, England, Europe, Jamaica, Japan, Java, Kansaie, Moluccas, New Zealand, Philippines, Ryukya (Ryukyu?), Singapore, Sri Lanka, and West Indies.

Figure 24. ***Pallavicinia lyellii*** showing its typical life form. Photo by Jan-Peter Frahm, with permission.

Figure 25. ***Pallavicinia lyellii*** showing the ribbon-like life form. Photo by Jan-Peter Frahm, with permission.

Figure 26. ***Pallavicinia lyellii*** with narrow ribbons that suggest low light. Photo by Clive Shirley, Hidden Forest <hiddenforest.co.nz>, with permission.

Figure 27. ***Pallavicinia lyellii*** mat. Photo by Clive Shirley, Hidden Forest <hiddenforest.co.nz>, with permission.

Aquatic and Wet Habitats

Pallavicinia lyellii (Figure 24-Figure 27) occurs in thermal acidic sprays in the tropics (Ruttner 1955). In northwest Portugal it occurs on steep, water-dripping schist surfaces or moist clayey streambanks between herbs, in shaded or moderately exposed places in low altitudes (Vieira *et al.* 2005). It can also occur in marshes, as photographed by Des Callaghan (Figure 28-Figure 29), where the grasses and sedges provide protection from moisture loss. It forms small patches mixed with other bryophytes such as ***Aneura pinguis*** (Figure 30), ***Solenostoma hyalinum*** (Figure 31), and ***Fissidens polyphyllus*** (Figure 32) in mountain streams.

Figure 28. Marshy habitat where ***Pallavicinia lyellii*** occurs. Photo by Des Callaghan, with permission.

Figure 29. ***Pallavicinia lyellii*** among grasses in marshy habitat. Photo by Des Callaghan, with permission.

Figure 30. ***Aneura pinguis***, a species that occurs with ***Pallavicinia lyellii*** in small patches in mountain streams. Photo by Hermann Schachner, through Creative Commons.

Figure 31. ***Solenostoma hyalinum***, a species that occurs with ***Pallavicinia lyellii*** in small patches in mountain streams. Photo by Michael Lüth, with permission.

Figure 32. ***Fissidens polyphyllus***, a species that occurs with ***Pallavicinia lyellii*** in small patches in mountain streams. Photo by David T. Holyoak, with permission.

Stebel *et al*. (2018) found that in Poland ***Pallavicinia lyellii*** (Figure 24-Figure 27) prefers damp or considerably wet habitats (Figure 33-Figure 37) and even grows in semi-aquatic conditions (Düll 1992). It grows on acidic to moderately acidic substrata and can live in moderately bright habitats (Stebel *et al*. 2018), but it is also very shade tolerant, as exemplified by its growth **under** a carpet of ***Sphagnum*** spp. (Figure 34) (Düll 1992; Dierβen 2001; Ellenberg & Leuschner 2010). Its light tolerance permits it to grow in open "bogs (Figure 35)," bog alder (***Alnus glutinosa***, Figure 36) or birch (***Betula pubescens***, Figure 37) forests, and beside wooded acid streams on moist soil (Figure 38), leaf litter, decaying wood (Figure 39), damp rocks (Figure 40), and rarely on exposed tree roots (Smith 1990; Dierβen 2001; Lavate *et al.* 2015; Mamontov *et al.* 2015). It doesn't seem to tolerate competition and thus is well-served by disturbed habitats with the right moisture.

Figure 33. ***Pallavicinia lyellii*** habitat at Cadnam Bog. Photo by Des Callaghan, with permission.

Figure 34. ***Pallavicinia lyellii*** under ***Sphagnum***. Photo by Gill Stevens, with permission from BBS website.

Figure 35. Bohemia bog with ***Sphagnum cuspidatum*** and ***S. denticulatum***. Photo by Jonathan Sleath, with permission.

Figure 36. ***Alnus glutinosa*** habitat where there is a suitable light level for ***Pallavicinia lyellii*** to grow. Photo by Sten Porse, through Creative Commons.

Figure 37. ***Betula pubescens*** habitat where there is a suitable light level for ***Pallavicinia lyellii*** to grow. Photo by Ingo2802, through Creative Commons.

Figure 38. ***Pallavicinia lyellii*** in a wet habitat. Photo by Michael Lüth, with permission.

Figure 39. ***Pallavicinia lyellii*** on wet, rotting log. Photo by Richard Orr, with permission.

Figure 40. ***Pallavicinia lyellii*** habitat. Photo by Michael Lüth, with permission.

Lavate *et al*. (2015) described the thallus of ***Pallavicinia lyellii*** (Figure 24-Figure 27) as **terricolous** (growing on soil or on ground) and **rupicolous** (growing on or among rocks), listing its habitats in India as moist soil on rocks, banks of freshwater streams (Figure 41), and cut surfaces as an associate with other liverworts. The relative humidity in these locations is typically 70-80%.

Figure 41. ***Pallavicinia lyellii*** growing streamside in Spain. Photo by Michael Lüth, with permission.

In Maryland, USA, ***Pallavicinia lyellii*** (Figure 24-Figure 27) occurs on soil, rotten wood (Figure 39), and tree bases in a stream valley (Glime 1966). In Florida, USA, White and Judd (1985) found it among the most conspicuous bryophytes at a ravine and adjacent uplands.

Sometimes ***Pallavicinia lyellii*** (Figure 24-Figure 27) seems to benefit from the shade of grasses, as observed by Gill Stevens at Wimbledon Downs (Figure 42-Figure 43).

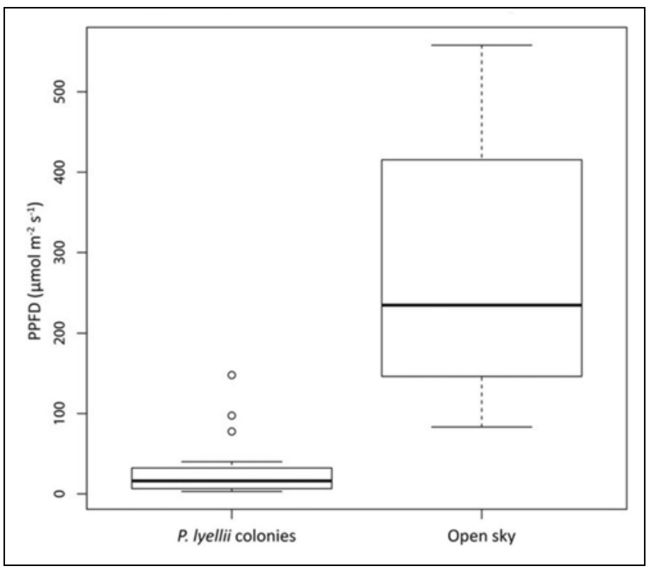

Figure 42. ***Pallavicinia lyellii*** photosynthetic photon flux density (PPFD), beneath canopies of ***Molinia caerulea*** and 1 m above (open sky), demonstrating the effect of cover on the liverwort. n = 20. Image by Des Callaghan, with permission.

Adaptations and Physiology

Pallavicinia lyellii (Figure 24-Figure 27) is a **short-lived shuttle** species (Smith 2006). This strategy permits it to inhabit the disturbed sites where it can enjoy the lack of competition.

Stebel *et al*. (2018) consider ***Pallavicinia lyellii*** (Figure 24-Figure 27) to be a **hemicryptophyte** (perennial plant having overwintering buds located at soil surface). It is sensitive to dehydration, but it has a prominent midrib that conducts water and that Stebel *et al*. and others (Dierβen 2001; Pence *et al.* 2005) suggest may serve as a buffer against the rapid loss of water. In some habitats it grows with other bryophytes (Figure 44) (Vieira *et al*. 2005; Lavate *et al*. 2015), another potential mechanism for conserving water (Stebel *et al*. 2018). But it can also grow in solitary, dense mats, as seen in Figure 45.

Figure 43. ***Pallavicinia lyellii*** at base of ***Molinia caerulea*** at Wimbledon Commons, UK. Photo by Gill Stevens, from BBS website, with permission.

Figure 44. ***Pallavicinia lyellii*** with mosses and other plants. Photo by Blanka Aguera, with permission.

Figure 45. ***Pallavicinia lyellii*** on stream bank, North Carolina. Photo by Janice Glime.

Charissou and Hugonnot (2020) note that ***Pallavicinia lyellii*** (Figure 24-Figure 27) pioneers moist clods but it is especially sensitive to desiccation. Pence *et al.* (2005) found that a pretreatment for one week with 10 µM ABA improved survival of desiccation in ***Pallavicinia lyellii***. ***Pallavicinia lyellii*** was less responsive to ABA treatment than the aquatic ***Riccia fluitans*** (Figure 46), but more responsive than the more terrestrial ***Marchantia polymorpha*** (Figure 47). Untreated ***Pallavicinia lyellii*** took 120 minutes to reach the same level of desiccation as that reached by ***Riccia fluitans*** in 45 minutes (11%). ABA did not change the rate of drying in these two species, but it slowed the drying rate significantly in ***Marchantia polymorpha***. Treated plants also exhibited an increase in total soluble carbohydrates.

Figure 46. ***Riccia fluitans***, a species that more commonly floats in ponds and other quiet waters. Photo by Christian Fischer, through Creative Commons.

Reproduction

Pallavicinia lyellii (Figure 24-Figure 27) is **dioicous** (Figure 48) (Stebel *et al.* 2018). Sex distribution varies between populations (Figure 49). Both males and females often occur together (Figure 48-Figure 57). Vieira *et al.* (2005) reported that the species was fertile in a Portuguese stream habitat in March. These plants had mature perigonia (Figure 52-Figure 57) and sporophytes (Figure 58-Figure 59).

Figure 47. ***Marchantia polymorpha***, a species that usually does not occur under water. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 48. ***Pallavicinia lyellii*** showing inter-mixed female (**red arrows**) and male (**white arrows**), **black** fertilized. Photo by Des Callaghan, with permission.

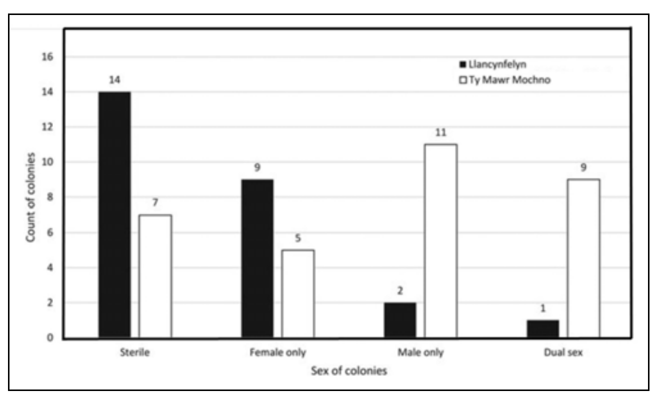

Figure 49. ***Pallavicinia lyellii*** sex distribution in 2 populations in Wales, showing differences in two locations. Modified from Des Callaghan, with permission.

Figure 50. ***Pallavicinia lyellii*** male. Photo by Blanka Aguera, with permission.

Figure 53. ***Pallavicinia lyellii*** female with laciniate scales that surround a group of archegonia. Photo by Des Callaghan, with permission.

Figure 51. ***Pallavicinia lyellii*** male with antheridia. Photo by Tom Thekathyil, with permission.

Figure 54. ***Pallavicinia lyellii*** with laciniate scales surrounding an emerging perianth. Photo by Jan-Peter Frahm, with permission.

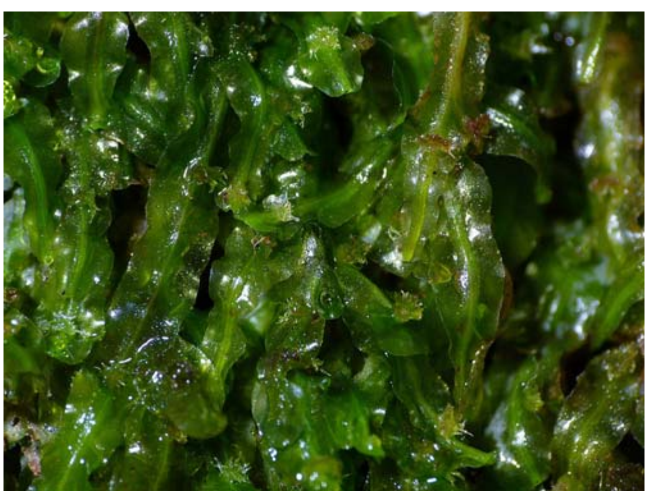

Figure 52. ***Pallavicinia lyellii*** wet, with archegonia. Photo by Shyamal L, through Creative Commons.

Figure 55. ***Pallavicinia lyellii*** with senescing branches. Photo by Jeremy Collison, through Creative Commons.

Figure 56. ***Pallavicinia lyellii*** perianths. Photo by Blanka Aguero, with permission.

Figure 57. ***Pallavicinia lyellii*** young sporophyte still inside perianth (**arrow**). Photo courtesy of Des Callaghan.

Figure 58. ***Pallavicinia lyellii*** with emerging sporophytes. Photo by Jan-Peter Frahm, with permission.

Figure 59. ***Pallavicinia lyellii*** with dehisced capsule. Photo by John Bradford, with permission.

Biochemistry

The oil bodies (Figure 60) of ***Pallavicinia lyellii*** (Figure 24-Figure 27) are small, numerous per cell, and very variable in shape (Juslén *et al*. 2021). Ebner (2016) expressed surprise that despite the great variety of natural products in liverworts, he was only able to find already known compounds, including terpenes, fatty acids, and sterols in ***Pallavicinia lyellii***.

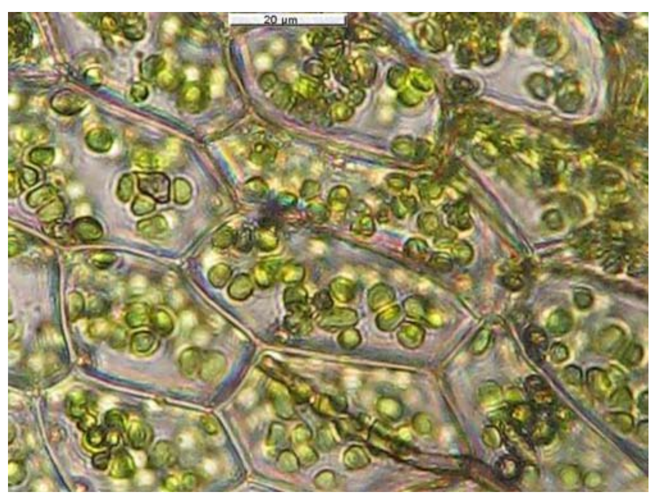

Figure 60. ***Pallavicinia lyellii*** thallus cells, showing the difficulty of observing oil bodies. Photo by Tom Thekathyil, with permission.

Adler (1983) identified the 4-desmethylsterol fraction in ***Pallavicinia lyellii*** (Figure 24-Figure 27). Rajan and Murugan (2010) extracted ascorbate peroxidase from

Pallavicinia lyellii. This enzyme performed optimally at 40ºC. The authors suggested that this pathway may contribute to desiccation tolerance in ***P. lyellii***.

Williams *et al*. (2016) found that ***Pallavicinia lyellii*** (Figure 24-Figure 27) has remarkable inhibitory activity against bacterial pathogens. Subhisha and Subramoniam (2005) reported antifungal activity by a steroid from this species. Extracts of ***Pallavicinia lyellii*** inhibited ***Pseudomonas aeruginosa*** (bacterium; Figure 61) and exhibited the greatest antibacterial activity against ***Escherichia coli*** (Figure 62) among the nine liverworts tested (Linde *et al*. (2016).

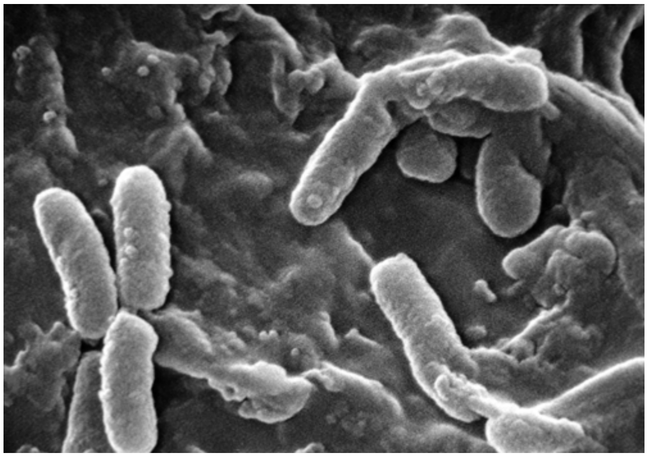

Figure 61. ***Pseudomonas aeruginosa*** SEM. Photo by Janice Haney Carr, CDC, through public domain.

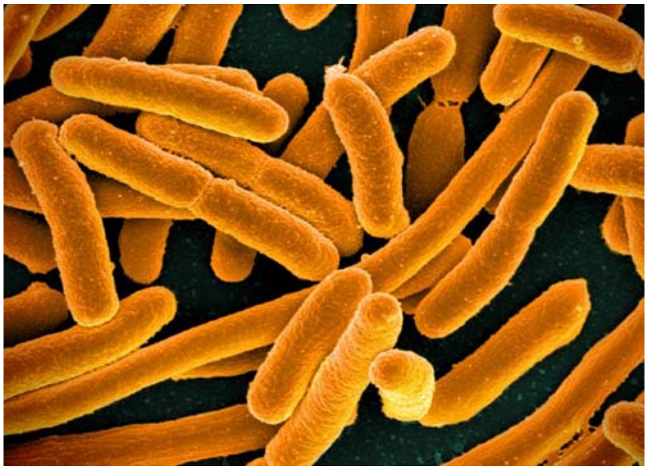

Figure 62. ***Escherichia coli*** SEM with color added. Photo by Niaid, through Creative Commons.

Summary

These members of the **Pallaviciniales** are at best facultatively aquatic. On the other hand, they like moist habitats such as stream banks, wet cliffs, and the spray of waterfalls. ***Hymenophyton flabellatum*** is able to form a mycorrhizal relationship with fungi in **Glomeromycota**. No fungal relationships seem to be known in the **Pallaviciniaceae** included here.

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