# CHAPTER 1-8 AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: JUBULINEAE, PART 2

## **TABLE OF CONTENTS**

Porellales – Suborder Jubulineae	. 1-8-	2
Lejeuneaceae, cont	. 1-8-	2
Drepanolejeunea hamatifolia	. 1-8-	2
Harpalejeunea molleri	. 1-8-	7
Lejeunea	1-8-1	2
Lejeunea aloba		
Lejeunea eckloniana	1-8-1	2
Lejeunea jurana	1-8-1	3
Lejeunea lamacerina	1-8-1	3
Lejeunea patens	1-8-1	8
Lejeunea polyantha	1-8-2	1
Lejeunea subaquatica	1-8-2	1
Lejeunea topoensis	1-8-2	1
Lopholejeunea nigricans	1-8-2	1
Myriocoleopsis	1-8-2	3
Myriocoleopsis fluviatilis	1-8-2	4
Myriocoleopsis gymnocoleopsis		
Myriocoleopsis minutissima		
Myriocoleopsis minutissima subsp. myriocarpa		
Myriocoleopsis vuquangensis		
Ptychanthus striatus var. intermedius		
Schusterolejeunea inundata		
Summary		
Acknowledgments		
Literature Cited	1-8-3	2

# CHAPTER 1-8 AQUATIC AND WET MARCHANTIOPHYTA, CLASS JUNGERMANNIOPSIDA, ORDER PORELLALES: JUBULINEAE, PART 2



Figure 1. Drepanolejeunea hamatifolia habitat on rocks by a rapid stream. Photo by Michael Lüth, with permission.

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

### Porellales – Suborder Jubulineae

### Lejeuneaceae, cont.

#### Drepanolejeunea hamatifolia (Figure 1-Figure 8)

#### Distribution

**Drepanolejeunea hamatifolia** (Figure 1-Figure 8) is an Atlantic species (Rhind 2010). It is, so far, restricted to the Atlantic coasts of Portugal (in laurel forests; Gutierres 2007), Spain (species of least concern; Sérgio *et al.* 2007), France (in Pyrénées; Dismier 1914), Ireland, England, Scotland (oceanic; Rothero 2003), and Macaronesia (Aleffi 2005). It is not known from Italy (Aleffi 2005), and it is known from only one site in continental Portugal (Cacciatori *et al.* 2015). To these records, Söderström and Pócs (2011) added South Africa. Sim-Sim *et al.* (2011) found it on Madeira Island.



Figure 2. *Drepanolejeunea hamatifolia*, a species of eastern Atlantic coastal regions. Photo by Hugues Tinguy, with permission.



Figure 3. *Drepanolejeunea hamatifolia* showing overlapping leaves. Photo by Michaela Sonnleitner, with permission.

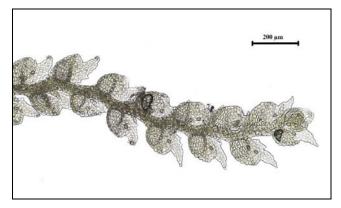


Figure 4. *Drepanolejeunea hamatifolia*. Photo by Hugues Tinguy, with permission.

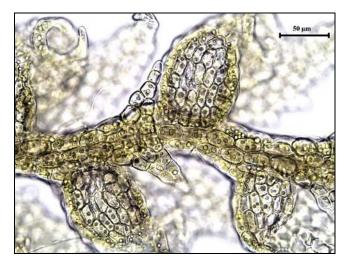


Figure 5. *Drepanolejeunea hamatifolia* showing underleaves. Photo by Hugues Tinguy, with permission.

Rothero (2003) considered **Drepanolejeunea** hamatifolia (Figure 2-Figure 8) to be rare in Europe, with the exception of Macaronesia and the Azores. In fact, Borges and Gabriel (2009) found it to be among the most common epiphyllous species in the Azores (see also Gabriel & Bates 2005).

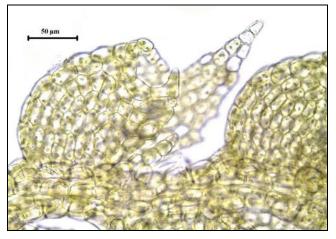


Figure 6. *Drepanolejeunea hamatifolia* leaf lobule. Photo by Hugues Tinguy, with permission.

#### **Aquatic and Wet Habitats**

Watson (1919)considered Drepanolejeunea hamatifolia (Figure 2-Figure 8) to be occasionally submerged (Figure 1), thus justifying its inclusion here. Hodgetts et al. (1999) reported it from streamside rocks in a ravine woodland at 1750 m asl in Lesotho, the Natal Drakensberg and the Orange Free State in southern Africa. In the UK, Rothero (2010) reported that it occurs on steep granitic rock of a ravine at 300 m asl. In Ireland, Jones (1954) found that it was "not uncommon" on basalt in deep, shady stream ravines. In Scotland, Long (2016) located it along a ravine. Damsholt et al. (1980) reported it from a wooded ravine in NW Scotland, where it occurred on moist, shaded rock faces. Brown (1954) found it in northeast Ireland on basalt in deep, shady stream ravines, where it was "not uncommon."

Rothero (2005) found it on large rocks in ravines of the Atlantic oakwoods. These rocks were regularly inundated, but did not suffer scouring. *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) formed a zone above the leafy liverwort *Lejeunea patens* (Figure 68-Figure 69) on these dark rocks (Figure 7-Figure 8).



Figure 7. *Drepanolejeunea hamatifolia* showing zonation patterns on boulder near a stream. Photo by Michael Lüth, with permission.



Figure 8. *Drepanolejeunea hamatifolia* on a wet rock. Photo by Barry Stewart, with permission.

Bosanquet (2015) discussed the effects of topography and rainfall on the distribution of Atlantic bryophytes in Wales. He recognized that rainfall in Wales ravines was not the sole driver of bryophyte diversity there. He considered that water courses and waterfalls were able to provide the mists that permitted the success of **hygrophilous** (humidity-demanding) bryophytes, in particular *Drepanolejeunea hamatifolia* (Figure 1-Figure 8). This species has a very patchy distribution due to its habitat restrictions. It is a desiccation-sensitive hyperoceanic species and is thus restricted to rocky cascades and other habitats that create a mist and moist environment.

Averis *et al.* (2012) found that those water courses that have the potential for electric power provide good habitats for *Drepanolejeunea hamatifolia* (Figure 1-Figure 8). Hence, if the construction of a power plant changes the mist and humidity of the area, the species is likely to become endangered there. Callaghan *et al.* (2019) found about 23% of colony losses following hydroelectric power development, including those changes to *Drepanolejeunea hamatifolia*, were due to larger bryophytes multiplying or invading and excluding them. The most aggressive of these was the moss *Ctenidium molluscum* (Figure 9).

But it appears that the requirement of mist or high humidity is not always the case. Schwarz and Schumm (2019) reported Drepanolejeunea hamatifolia (Figure 1-Figure 8) from the Canary Islands on dry, shaded to halfshaded bark (Figure 10), stone, or leaves. Likewise, on Tenerife in the Canary Islands, Gónzalez-Mancebo et al. (2004a) reported it as a pioneer epiphyte on Laurus azorica (Figure 11), occurring only in the Pijaral area, and with a low frequency. But laurel forests are typically humid and shady (Kürschner et al. 2007a). They are dominated by bryophytes that form mats (Figure 8) or fans and are perennial stayers or perennial shuttle species. Drepanolejeunea hamatifolia occurs in the laurel forests of Madeira Island with a thread life form. In the Azores, it occurs on stem bases in dense stands of *Persea* (Figure 12), Pittosporum (Figure 13), and Acacia (Figure 14) (Sjögren 2003). It also occurs as an epiphyte in laurel forests on the Madeira archipelago (Gutierres 2007). Bates (2012) found it on Cryptomeria (Figure 15) on the higher hills of the Azores, where it joins acidophilic bryophytic epiphylls. Patiño and González-Mancebo (2011) reported it from subtropical cloud forests in the Canary Islands, growing on ericaceous shrubs. All of these habitats are moist.





Figure 9. *Ctenidium molluscum* in rock canyon in Europe, a larger species that can overtake *Drepanolejeunea hamatifolia*. Photo by Michael Lüth, with permission.

Figure 10. *Drepanolejeunea hamatifolia* on bark in Bretagne. Photo by Michael Lüth, with permission.



Figure 11. Laurel forest (*Laurus azorica*), Macaronesia, on Flores Island. Photo by B. T. Varusko, through Creative Commons.



Figure 12. *Persea americana* with fruit; *Persea* can have *Drepanolejeunea hamatifolia* on bark at its base. Photo by M. Clara Salviano, through Creative Commons.



Figure 14. *Acacia saligna* on Cyprus; *Acacia* can have *Drepanolejeunea hamatifolia* on bark at its base. Photo by Anna Anichkova, through Creative Commons.



Figure 13. *Pittosporum coriaceum*; species in this genus can have *Drepanolejeunea hamatifolia* on bark at the base. Photo by Krzystof Ziarnek, through Creative Commons.

The epiphyllous habitat of *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) is not restricted to leaves of tracheophytes. It also occurs on other bryophytes, such as *Thamnobryum alopecurum* (Figure 16), another wet habitat species, in Killarney, Ireland (Kelly 1981). In the same woods, it grew on branches and upper parts of the trunk of yew trees, and Rose (1974) found it on oaks in Killarny. Similarly, Durfort (2015) found that this liverwort occurs as an epiphyte on mosses on tree trunks in Brittany, France. But it also occurs on rocks, old gorse, willows, birches, and larger trees in Brittany. Despite this variety of substrata, it is very rare in France.



Figure 15. *Cryptomeria japonica* in Azores, substrate for *Drepanolejeunea hamatifolia*. Photo by Mary Anne Melo, through Creative Commons.



Figure 16. *Thamnobryum alopecurum*, a substrate for *Drepanolejeunea hamatifolia*. Photo by Michael Lüth, with permission.

Proctor (1980) measured the radiation for *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) in several locations in the British Isles (North Wales and Yorkshire). In the wooded lowland habitats, peak irradiance occurred immediately before leaf expansion. Direct radiation was negligible in the ravine sites where *Drepanolejeunea hamatifolia* occurred.

Corley (1983) found *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) in the Inner Hebrides, where it occurred on boulders in the stream and rocks at the edge, accompanied by *Hyocomium armoricum* (Figure 17), *Thamnobryum alopecurum* (Figure 16), *Cololejeunea microscopica* (Figure 18), *Douinia ovata* (Figure 19), and *Colura calyptrifolia* (Figure 20).



Figure 17. *Hyocomium armoricum* in its common habitat where it might be accompanied by *Drepanolejeunea hamatifolia*. Photo by Dick Haaksma, with permission.



Figure 19. *Douinia ovata*, a species that might be accompanied by *Drepanolejeunea hamatifolia*. Photo by Des Callaghan, with permission.



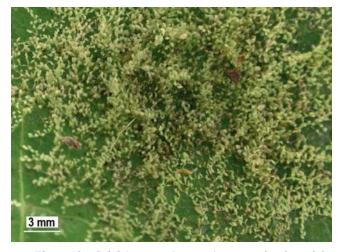


Figure 18. *Cololejeunea microscopica*, a species that might be accompanied by *Drepanolejeunea hamatifolia*. Photo by Jan-Peter Frahm, with permission.

But the reported habitats suggest that submersion is an unusual condition for the species. Instead, it occupies more terrestrial sites. Sim-Sim *et al.* (2011) report *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) as an epiphyte on Madeira Island, where it is an indicator species for the high-altitude *Erica* habitat (Figure 21). Roden *et al.* (2007) found it in the oak woods in the valley of the Owendalulleegh River in Ireland.

Figure 20. *Colura calyptrifolia*, a species that might be accompanied by *Drepanolejeunea hamatifolia*. Photo by Barry Stewart, with permission.



Figure 21. *Erica maderensis*; *Drepanolejeunea hamatifolia* is an indicator species for the high altitude *Erica* habitat on Madeira Island. Photo by Thomas Dellinger, through Creative Commons.

Sjögren (1993) considered **Drepanolejeunea** hamatifolia (Figure 1-Figure 8) to be a species with no substrate preference on the island of Corvo in the Azores. He also considered it to be a pioneer on bark. The species was able to colonize with thin carpets that were frequently split up by areas almost nude of bark. To add further to this lack of substrate preference, Schwarz and Schumm (2019) reported it from wet, shaded plastic pipe.

The invasive **Rhododendron ponticum** (Figure 22) in Atlantic oak woodlands impacted the oak woodland community (Maclean *et al.* 2017). However, **Drepanolejeunea hamatifolia** (Figure 1-Figure 8) seemed to have an affinity for these dense **Rhododendron** areas.



Figure 22. *Rhododendron ponticum*, a species whose invasion seemed to have a favorable impact on *Drepanolejeunea hamatifolia*. Photo by Rasbak, through Creative Commons.

#### Adaptations

Although it appears that *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) seems to be most common in moist microclimates, it is nevertheless also adapted to drier conditions. **Lobules** (water sacs) in this species help it to survive in the sometimes dry epiphytic habitat (Sim-Sim *et al.* 2005a).

Unlike the report by Kürschner *et al.* (2007a) that considered *Drepanolejeunea hamatifolia* (Figure 1-Figure 8) to be a **perennial stayer** or **perennial shuttle species**, other researchers considered it to be a **short-lived shuttle** species in the Canary Islands (González-Mancebo *et al.* 2004b; Lloret & González-Mancebo 2011; Patiño & González-Mancebo 2011), with 2% cover and 2.98% frequency (González-Mancebo *et al.* 2004b).

#### Reproduction

**Drepanolejeunea hamatifolia** can be **autoicous** or **dioicous** (Paton 1999), probably accounting for some of its morphological variability. The perianth has various projections from the folds, suggesting they might attach to an animal or trap air bubbles that help them to float. This requires experimentation and would necessitate the disarticulation of the perianth.

In running water, fragmentation is a frequent form of asexual reproduction. I would assume that this is facilitated by the caducous branches (Paton 1999) in *Drepanolejeunea hamatifolia* (Figure 1-Figure 8). Paton reported frequent sporophytes, but did not report gemmae.

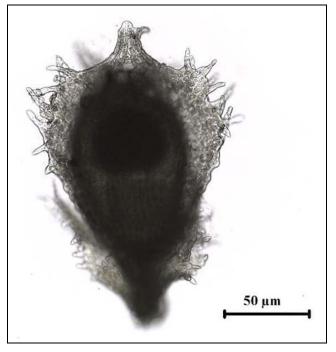


Figure 23. *Drepanolejeunea hamatifolia* perianth; note the spiny projections on the folds. Photo by Hugues Tinguy, with permission.

#### **Fungal Interactions**

Despite its association with ericaceous shrubs, known for the presence of mycorrhizae, there seem to be no records of mycorrhizal associations (Wang & Qiu 2006). Although the Ericaceae typically have mycorrhizae (Read & Stribley 1975; Specht 1979; Selosse *et al.* 2007), epiphytes such as this tiny liverwort usually do not.

#### Drepanolejeunea vandenberghenii

#### Distribution

Rwanda (Pócs 2021)

#### **Aquatic and Wet Habitats**

In Rwanda, *Drepanolejeunea vandenberghenii* occurs on dripping rocks, growing among *Sphagnum* and *Breutelia*; not known in submerged condition (Pócs 2021).

#### Adaptations

Plants of *Drepanolejeunea vandenberghenii* are yellowish to light brownish-green (Pócs 2021). This is in contrast to the blackish appearance of *D. vanderpoortenii* and suggests a difference in light intensity or quality.

#### Drepanolejeunea vanderpoortenii

#### Distribution

*Drepanolejeunea vanderpoortenii* is known only in Madagascar (Pócs 2021).

#### **Aquatic and Wet Habitats**

**Drepanolejeunea** vanderpoortenii occurs on streambed stones, often under water (Pócs 2021). Such locations include on wet boulders in streams in submontane rainforest and on streambed stones of Mahavoho River, at 220 m asl.

#### Adaptations

**Drepanolejeunea vanderpoortenii** has blackish pigmentation, julaceous habit, thick-walled stems (Pócs 2021). The blackish color and thick-walled stems could be adaptations to its rheophytic habitat (Gradstein & Vital 1975, Pócs 2010). I would suggest that the julaceous habit is also an adaptation against the abrasion caused by flowing water. I would predict that it causes less turbulence than other forms, and certainly less subject to abrasion than are keeled leaves.

#### Reproduction

The sexual and vegetative reproduction are both unknown at this time (Pócs 2021). It is likely that it experiences vegetative reproduction with dispersal by water flow.

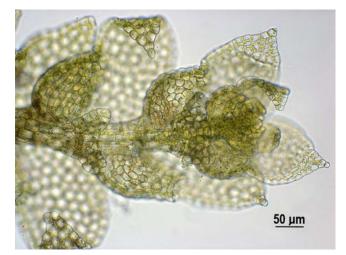


Figure 25. *Harpalejeunea molleri* underside. Photo by Blanka Aguero, with permission.

# *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38)

(syn. = Harpalejeunea ovata; Lejeunea molleri)

#### Distribution

*Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38) has had several synonyms (Grolle 1989) and there has been confusion about the use of some names (Schuster 1999). It is a widespread oceanic and suboceanic species from southern Norway south to Spain, Portugal, southern France, Tuscany, and Corsica (Sotiaux *et al.* 2007), the Canaries (Mancebo *et al.* 2007), and the Azores (Schuster 1980). In North America it extends from the Southern Appalachians from Virginia southward and outer Coastal Plain (Schuster 1980).

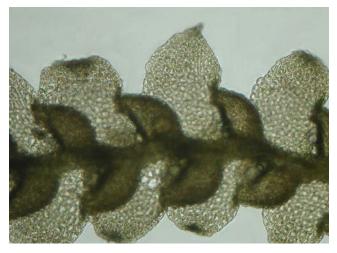


Figure 26. *Harpalejeunea molleri* showing leaf lobes that appear darker in this photo. Photo by Jan-Peter Frahm, with permission.



Figure 24. *Harpalejeunea molleri*, a species from both sides of the Atlantic in oceanic and suboceanic regions. Photo by Stan Phillips, through public domain.

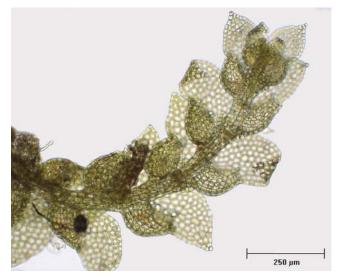


Figure 27. *Harpalejeunea molleri* subsp. *integra*. Photo by Blanka Aguero, with permission.



Figure 28. *Harpalejeunea molleri* subsp. *integra* giving a view of leaf insertion and leaf cells. Photo by Blanka Aguero, with permission.

#### **Aquatic and Wet Habitats**

Schuster (1980) describes the wetter habitats of *Harpalejeunea molleri* as shaded humid rocks, in swamps, along black-water streams, or on damp rocks. Dirkse (1985) reported it from sheltered wet volcanic rocks in the laurel forests (Figure 11) of the Canary Islands. González-Mancebo *et al.* (2004b) found it growing in areas with high mist in the laurel forests of the Canary Islands. Sim-Sim *et al.* (2005a) found *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38) growing with *Plagiochila exigua* (Figure 29) on moist rock surfaces and slopes near water courses on Madeira, but it also occurred epiphytically, often with *Frullania tamarisci* (Figure 30) and other bryophytes.



Figure 30. *Frullania tamarisci*, a species that occurs epiphytically with *Harpalejeunea molleri* on Madeira. Photo by Proyecto Musgo, through Creative Commons.

Rothero (2005) reported Harpalejeunea molleri (Figure 24-Figure 28, Figure 33-Figure 38) as a very small liverwort making a delicate green pattern (Figure 24) against the dark stone of large rocks in ravines. These rocks were regularly inundated, but escaped scouring. Bosanquet (2015) described seven hotspots in Wales, noting that these are located away from high-rainfall areas. These typically are in woodland ravines in locations with mist zones and periodic inundation, usually governed by areas of high upstream rainfall. These habitats include waterfalls and rocky cascades. Such areas are suitable habitats for Harpalejeunea molleri. Bosanquet considers this species to be desiccation intolerant. Pescott and Preston (2014) found that *Harpalejeunea molleri* in Britain and Ireland occurred with a group of species that experienced the most wet days. In hyperoceanic places in Scotland, Hodgetts et al. (2013) found it associated with Lejeunea mandonii (Figure 31) and other bryophytes on ash trees next to burns in ravines in a base-rich area. Denyer (2012) found it associated with crags that had calcareous seepage in the UK.



Figure 29. *Plagiochila exigua* growing with smaller liverworts such as *Harpalejeunea molleri*. Photo by Jan-Peter Frahm, with permission.



Figure 31. *Lejeunea mandonii*, a species that can occur with *Harpalejeunea molleri* on ash bark. Photo by Jan-Peter Frahm, with permission.

In Nova Scotia, *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38) occurs on the bases of the eastern white cedar *Thuja occidentalis* (Figure 32) in a swamp (Haughian & Neily 2020).



Figure 32. *Thuja occidentalis* in snow; *Harpalejeunea molleri* grows on the bases of this species in Nova Scotia. Photo by Peter M. Dziuk, with online permission.

Averis *et al.* (2011, 2012) considered that watercourses with hydroelectric potential are an important habitat for *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38). Since their declaration of concern for this species, Callaghan *et al.* (2019) found that following disturbance in the flow regime caused by a new hydroelectric power development, *Harpalejeunea molleri* was one of the first species to be diminished. *Harpalejeunea molleri* can be overtaken by larger bryophytes, especially *Ctenidium molluscum* (Figure 9).

Like so many of the wet habitat **Lejeuneaceae**, *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38) can occur on dry bark or stone in half-shaded to shaded habitats of Madeira Island (Schwarz & Schumm (2019). In these habitats, other very small liverworts often grow on it.

*Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38) occurs in small, yellowish-green patches (Schuster 1980). It can be found on bark and shaded humid rocks. In the North American Coastal Plain it is known only on bark, usually in swamps or deep, mesic, evergreen wood, often near or along black-water streams. But elsewhere it occurs on damp rocks, usually on shaded vertical sides of ledges or cliffs, less often on large boulders. It also occurs in relatively open xerophytic oakhickory-chestnut forests.

#### Adaptations

González-Mancebo *et al.* (2004b) considered *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38) to be a **short-lived shuttle** species on the forest floor of the laurel forest (Figure 11) in the Canary Islands. Kürschner *et al.* (2007a) considered it to be a **thread** (Figure 38) on the Canary Islands. At its small size, the threads can form a **mat**.

Biodiversity, ecology, and morphology of bryophytes are related (Fontinha *et al.* 2010). In Madeira, Fontinha and coworkers measured the variables related to the distribution of bryophytes and found that temperature, precipitation, altitude, species cover, presence of snow, substrate *p*H, microaspect, and topography could be related to the morphological characters of underleaf (Figure 33) and lobule surfaces, lobule width, lobe length (Figure 34), lobe surface, and length of median cells of the lobe (Figure 35) in several liverwort species, including *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38). **Trigones** (cell wall thickenings, especially where three cells join; Figure 36-Figure 37) don't seem to be one of these characters. In these habitats, *H. molleri* was associated with other liverwort species (Figure 38), including *Porella canariensis* (Figure 39), *P. inaequalis*, and *P. obtusata* (Figure 40).

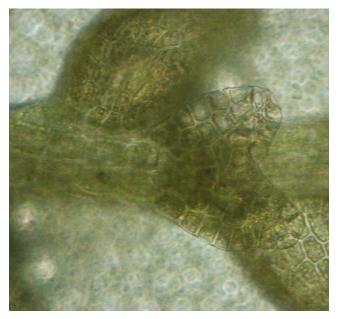


Figure 33. *Harpalejeunea molleri* underleaf. Photo by Jan-Peter Frahm, with permission.

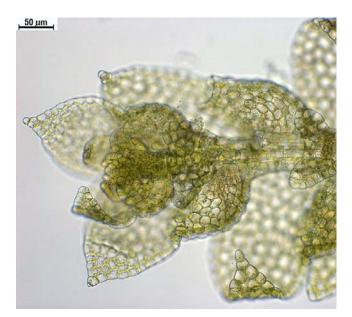


Figure 34. *Harpalejeunea molleri* subsp. *integra* showing lobes on ventral side. Photo by Blanka Aguero, with permission.

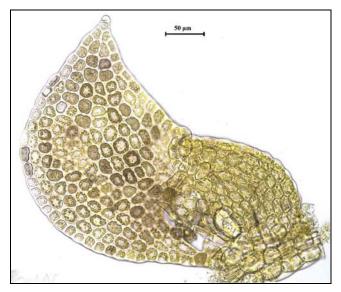


Figure 35. *Harpalejeunea molleri* leaf showing lobe. Photo by Hugues Tinguy, with permission.



Figure 38. *Harpalejeunea molleri* growing as a thread on larger liverworts. Photo by Jan-Peter Frahm, with permission.

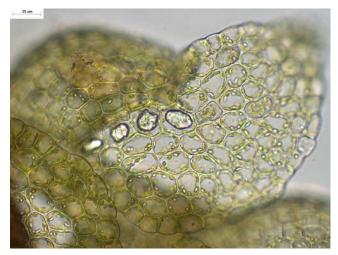


Figure 36. *Harpalejeunea molleri* subsp. *integra* leaf and leaf lobe cells. Photo by Blanka Aguero, with permission.

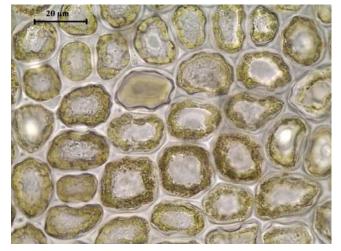


Figure 37. *Harpalejeunea molleri* leaf cells with trigones. Photo by Hugues Tinguy, with permission.



Figure 39. *Porella canariensis*, a species that associates with *Harpalejeunea molleri*. Photo by Jan-Peter Frahm, with permission.



Figure 40. *Porella obtusata*, a species that associates with *Harpalejeunea molleri*. Photo by Stan Phillips, through public domain.

#### Reproduction

*Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38) is **dioicous**, usually sterile, usually without asexual reproduction.

#### **Fungal Interactions**

There seems to be little information about the interactions of *Harpalejeunea molleri* (Figure 24-Figure 28, Figure 33-Figure 38), although it seems to occur at least some of the time with other bryophytes (Figure 41). However, Vital *et al.* (2000) found that it can grow on the fungus *Hyphodontia* sp. (Figure 42), a capability of other liverworts as well.



Figure 41. *Harpalejeunea molleri* mixed with other bryophytes. Photo by Michael Lüth, with permission.



Figure 42. *Hyphodontia sambuci* overgrown by leafy liverworts, one of which can be *Harpalejeunea molleri*. Photo by Roger Griffith, through public domain.

# *Lejeunea* (Figure 43-Figure 44, Figure 47-Figure 51, Figure 61-Figure 71)

#### (syn. = *Neopotamolejeunea*)

S. Robbert Gradstein (November 2011) related to me that multiple species in the genus *Lejeunea* (Figure 43-Figure 44, Figure 47-Figure 51, Figure 61-Figure 71) are common in Andean streambeds. The genus has lobes that approach the structure of lobules. Both terms are used in the literature.

#### Lejeunea aloba

(syn. = Eulejeunea aloba, Rectolejeunea aloba, Rectolejeunea submersa)

#### Distribution

*Lejeunea aloba* occurs in the tropics. Records include Nilgiri Hills (Verma & Rawat 2013), Jog Falls (Schwarz

2013) and other locations in India (Shah & Gujar 2016; Singh & Singh 2016). It occurs in the African countries of Kenya (Chuah-Petiot & Pócs 2003; Enroth *et al.* 2019) and Rwanda (Biedinger & Fischer 1996). Söderström *et al.* (2014) included in the flora of Java.

#### **Aquatic and Wet Habitats**

Ruttner (1955) included *Lejeunea aloba* in his treatment of aquatic taxa of the tropics. But little seems to be known of its ecology. Biedinger and Fischer (1996) reported it in their epiphytic study in Rwanda. Malombe *et al.* (2016) found it growing as an epiphyll in the edges of Afromontane fragmented forests. Rashid *et al.* (2012) noted its altitudinal range in the Kashmir state of India to be 800-1100 m.

#### Lejeunea eckloniana (Figure 43-Figure 44)

#### Distribution

Lejeunea eckloniana (syn. = Lejeunea holtii; Figure 43-Figure 44) has been reported in South Africa (Jones 1974), Cape Verde Islands, Teneriffe, Sierra Leone and Angola to Kenya, Tanzania, Cape, and to the Mascarenes (widespread; Pócs 1993), Ethiopia (Hylander et al. 2010), Ghana (Hodgetts et al. 2016), Taita Hills region, Kenya (Enroth et al. 2019), Bioko Island in Equatorial Guinea (Müller & Pócs 2007), Réunion Island (Ah-Peng & Bardat 2005), India (Schwarz 2013; Singh & Pócs 2016; Kasiani et al. 2019), Portugal (Sérgio et al. 2012; Cacciatori et al. 2015), Azores (Gabriel & Bates 2005; Frahm 2006), Macaronesia (Sérgio 1978), Canary Islands (González-Mancebo & Hernández-García 1996), Pico Branco-Porto Santo Island, Madeira (rare; Lobo 2008; Ruas et al. 2015), Malaysia and Indonesia (Kasiani et al. 2019), UK (rare; Pescott 2016; Bosanquet et al. 2018), Ireland (endangered; Kingston 2012).



Figure 43. *Lejeunea eckloniana*, a mostly tropical species in the Eastern Hemisphere and that can occur at waterfalls. Photo by Jan-Peter Frahm, with permission.

#### **Aquatic and Wet Habitats**

*Lejeunea eckloniana* (Figure 43-Figure 44) seldom occurs as a true aquatic, but it usually prefers damp habitats. Watson (1919) reported it from waterfalls in Europe. Dirkse (1985) found it on sheltered wet volcanic

1-8-13

rocks in the laurel forest (Figure 11) of the Canary Islands, Luís *et al.* (2015) found it in mountainous streams on Madeira Island. And Sim-Sim *et al.* (2005b) found it was a frequent part of the flora in the vicinity of temporary lagoons and swamps in the Madeira Archipelago. But Schwarz and Schumm (2019) reported it from wet to dry shaded stone or bark in the Madeira Island. In the Canary Islands, González-Mancebo and Hernández-García (1996) found it to be frequent in the laurel forest, but only occasional in the *Erica-Myrica* (Figure 45) woodland. On the other hand, in the Azores Gabriel and Bates (2005) found it to be a characteristic epiphyte, but it occurred where there was lower water availability and higher bark *p*H.



Figure 44. *Lejeunea eckloniana*. Photo by Jan-Peter Frahm, with permission.



Figure 45. *Myrica* on Canary Islands. Photo through Creative Commons.

Bosanquet *et al.* (2018) considered *Lejeunea eckloniana* (Figure 43-Figure 44) to be a rare hyperoceanic species in British Atlantic woodlands. Crundwell *et al.* (1994) reported that it occurs on a *Pittosporum* (Figure 13) trunk near a stream, but also in small quantities among the moss *Andoa berthelotiana* (Figure 46) on rocks at a roadside in the UK. In the Iberian Peninsula, it is likewise quite rare except in the oceanic flora in semi-natural woodlands (Franco *et al.* 2003).



Figure 46. *Andoa berthelotiana*, a moss that may have small quantities of *Lejeunea eckloniana* growing with it. Photo by Pedro Cardoso, with permission through Azoresbioportal.

#### Adaptations

*Lejeunea eckloniana* (Figure 43-Figure 44) seems to be best adapted to epiphylly, with small stems, imbricate leaves, and lobules, but no papillae (Kraichak 2012), perhaps reflecting its occurrence in both wet and dry habitats. Sim-Sim *et al.* (2005a) noted the use of water sacs to adapt the species to the variable water conditions. Its oil bodies are minute, with only 2-4 per cell (Kis & Pócs 1997). But the species is variable in other ways, with innovations in particular varying (Jones 1979).

#### Reproduction

*Lejeunea eckloniana* (Figure 43-Figure 44) is monoicous (Jones 1974).

#### Lejeunea juruana

(syn. = Neopotamolejeunea uleana, Potamolejeunea ulena)

Lejeunea juruana is endemic to Andean Brazil (Gradstein & Reiner-Drehwald 2007). It is a specialized rheophyte, occurring as rare in the rainforest on leaves of trees or shrubs in rivers (Bastos & Gradstein 2020). In this habitat it is periodically submerged. In the lowland rainforest, it is likewise periodically submerged, but can occur on rock and pendent on branches of shrubs in the rivers.

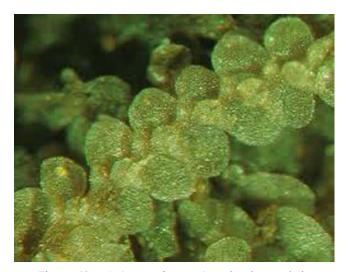
#### Lejeunea lamacerina (Figure 47-Figure 51)

#### Distribution

Lejeunea lamacerina (Figure 47-Figure 51) is a Holarctic species with a North American and a European/Macaronesian clade (Heinrichs *et al.* 2013; Lee *et al.* 2016; Bastos & Gradstein 2020), where it represents a euoceanic element (Vieira *et al.* 2005). Bastos and Gradstein (2020) reviewed the genus in Brazil and concluded that this species probably does not occur there. Although Schumacker and Váña (2000) originally considered it to be a European/Macaronesian endemic, Cogoni *et al.* (2002) included North America, as well as Japan, Siberia, and Iceland in its distribution. They found it to be of limited occurrence in Italy. Blockeel (2004) expanded its known localities in Italy. Heinrichs *et al.* (2012) reported it from the Canary Islands. Vieira *et al.*  (2004) considered it to be a relic on Macaronesia due to its worldwide distribution. Özenoğlu and Gökler (2002) reported it from Turkey in the Dilek Peninsula National Park. In the Azores, it occurs on all nine islands (Frahm 2005).

Figure 47. *Lejeunea lamacerina*, a Holarctic species often found in mountain streams. Photo by Andy Hodgson, with permission.

In North America, as subsp. *gemminata* (Figure 64), it is known from Newfoundland and Nova Scotia in Canada, south to Georgia, USA (Schuster 1980). Miller (1964) reported this subspecies from Hocking Co., Ohio. Schuette and Krayesky (2014) reported the subspecies from Wayne Co., Pennsylvania. Briscoe *et al.* (2009) reported it from Maine.



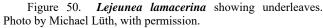




Figure 48. *Lejeunea lamacerina*, a species often living in spray from rapids and waterfalls. Photo by David T. Holyoak, with permission.

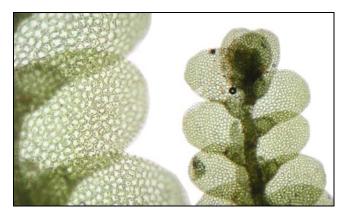


Figure 49. *Lejeunea lamacerina*, showing lobes. Photo by Michael Lüth, with permission.

#### **Aquatic and Wet Habitats**

In Tuscany and Piedmont, Italy, Lejeunea lamacerina (Figure 47-Figure 51) grows on damp rocks along the Riu Rica Bianca (Cogoni et al. 2002) and is "not rare" on rocks in streams of the Apuanian Alps (Frahm 2013). Vieira et al. (2005) reported it as rare in the Portuguese mountain stream habitats, where it is either seasonally immersed or receives splash or spray (Figure 50-Figure 51). It also occurs in Portugal on dripping schistose wall (Vieira et al. 2004) and deeply shaded steep dripping granitic surfaces (Vieira et al. n.d.). On Madeira Island it occurs in mountain streams (Luís et al. 2015). Sim-Sim et al. (2005b) found it on Madeira Island on shaded rocks and rocky slopes near streams and ravines; it typically was associated with Plagiochila punctata (Figure 52). In the laurel forest (Figure 11) slope communities, it occurs along shaded rivulets, often with other liverworts. It had a 1.4% frequency in the stream, but a 27.1% frequency on the stream bank (Luís et al. 2010). Haury (1995) found it at a Breton (France) brook, a stream that also had Platyhypnidium riparioides (Figure 53) and Leptodictyum riparium (Figure 54). On Islay, the southernmost of the Inner Hebrides islands of Scotland, it occurs on wet, shaded rocks in a gully on the north coast (Birks & Adam 1978). In Turkey it occurs on tree roots and straight rocks, as well as damp shaded rocks, especially base-rich substrata, and not so often on the sheltered stream banks and tree trunks (Özenoğlu & Gökler 2002).



Figure 50. *Lejeunea lamacerina*, showing a common stream habitat. Photo by Michael Lüth, with permission.



Figure 51. *Lejeunea lamacerina* on boulders in a stream -a common habitat for this species. Photo by Michael Lüth, with permission.



Figure 52. *Plagiochila punctata*, a species often associated with *Lejeunea lamacerina* on shaded rocks and rocky slopes near streams and ravines on Madeira Island. Photo by Stan Phillips, through public domain.

Vieira *et al.* (2012) considered *Lejeunea lamacerina* (Figure 47-Figure 51) to be especially important in the northwestern streams of Portugal. These streams are their best habitat in the country, but these researchers considered them to be among the "most threatened" by a warming climate, thermal pollution, and changed hydrological regimes. Heras *et al.* (2002) reported it from humid, acidic conditions in the Botanical Garden of Madrid, Spain.



Figure 53. *Platyhypnidium riparioides*, a species that often occurs in the same streams as *Lejeunea lamacerina* in Breton, France. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 54. *Leptodictyum riparium*, a species that often occurs in the same streams as *Lejeunea lamacerina* in Breton, France. Photo by Štěpán Koval, with permission.

But like so many of the **Lejeuneaceae**, *Lejeunea lamacerina* (Figure 47-Figure 51) also occurs as an epiphyte. Kelly (1981) reported it to be frequent on epiphytic mosses in Killarney, southwest Ireland. Sim-Sim *et al.* (2011) found it on all the tree species on Madeira Island.

One of the habitats of *Lejeunea lamacerina* (Figure 47-Figure 51), at least in the Azores, is in lava tubes (Figure 55) and volcanic pits, where it is a frequent species (Gabriel *et al.* 2008). In central Spain, Luceño *et al.* (2017) occurs on the wet granites in the alder grove forest. Ravines with *Prunus lusitanica* (Figure 56) there serve as refugia for oceanic species such as this.



Figure 55. Volcanic cave (lava tube) at Algar do Carvão, on Terceira Island, Portugal. Photo by Vitor Oliveira, through Creative Commons.



Figure 56. *Prunus lusitanica* epiphytes, which can include *Lejeunea lamacerina*, using these trees as refugia in ravines in the Azores. Photo by Krzysztof Ziarnek, through Creative Commons.

Pescott (2019) found it on drystone wall in the UK. Gökler (1998) found it on stones at 1200 m asl in the Altindere Valley National Park of Turkey. In Maine, USA, the subsp. *gemminata* (Figure 64) occurs on serpentine rock (Briscoe *et al.* 2009).

Like so many members of this family, *Lejeunea lamacerina* (Figure 47-Figure 51) occurs on a wide range of habitats. These include thin patches on rock and bark in damp to almost dry locations (Schuster 1980). Kürschner *et al.* (2007a, b) found that on Madeira Island it was among the dominant epiphytes in the laurel (Figure 11) and ericaceous forests (Figure 57). In the Canary Island subtropical cloud forests, it is the only species that is "distinctive" of the laurel forests (Patiño & González-Mancebo 2011). On Corvo in the Azores, Sjögren (1993) found that *Lejeunea lamacerina* is among the most frequent in the epiphyllous associations and also occurs in the epiphytic associations (Figure 56). It occurs as a primary invader in areas of almost nude bark on *Erica* (Figure 57) and *Juniperus* (Figure 58).

Kürschner *et al.* (2007b) found that *Lejeunea lamacerina* (Figure 47-Figure 51) is able to survive under minimal light in the Madeira laurel (Figure 11) and ericaceous forests (Figure 57). These forests exhibit deep shade and constantly humid conditions.



Figure 57. *Erica azorica*, in a genus where *Lejeunea lamacerina* can be a primary invader in the Azores. Photo by Felix Gertz, through Creative Commons.



Figure 58. *Juniperus cedrus*, in a genus where *Lejeunea lamacerina* can be a primary invader in the Azores. Photo by H. Zell, through Creative Commons.

In the Leyre valley of southwestern France, *Lejeunea lamacerina* (Figure 47-Figure 51) arrived after a mud wash with only a slight salt and nutrient enrichment (Hugonnot 2010). Mosses, particularly *Dichelyma capillaceum* 

(Figure 59), trapped and retained the mud, creating a suitable habitat for the *L. lamacerina*.



Figure 59. *Dichelyma capillaceum*, a species that traps mud during flooding, providing a suitable habitat for *Lejeunea lamacerina* in southwestern France. Photo by Michael Lüth, with permission.

In The Netherlands, van der Pluijm *et al.* (2015) reported that *Lejeunea lamacerina* (Figure 47-Figure 51) is usually found on rocks in or near streams that are sheltered by forests in lowland valleys. They suggested that this area is humid and provides protection from frost and drought. But their new find was epiphytic in a relatively open landscape, occurring at 1.5 m height on an oak (*Quercus robur*; Figure 60) stem.



Figure 60. *Quercus robur* in Dartmoor, UK; *Lejeunea lamacerina* grows on its trunks in The Netherlands. Photo by Alex Jane, through Creative Commons.

#### Adaptations

The life form of *Lejeunea lamacerina* is typically that of a **small mat** (Figure 61-Figure 62) (Sim-Sim *et al.* 2003, 2005b; Kürschner *et al.* 2007a; Patiño *et al.* 2009). Its life strategy in the Madeiran laurel (Figure 11) and ericaceous forests (Figure 57) is that of a **long-lived shuttle**, surviving in minimal light (Kürschner *et al.* 2007b). Schuster (1980) described these mats as thin, whitish to pale yellowish green, occurring in patches or scattered on rock or bark.



Figure 61. *Lejeunea lamacerina* (yellowish patches) forming mats on a rock. Photo by Michael Lüth, with permission.



Figure 62. *Lejeunea lamacerina* forming a mat. Photo by Michael Lüth, with permission.

*Lejeunea lamacerina* can exhibit modified form in some environments (Figure 63). This can be expressed as very slender stems with small leaves, and when shaded the leaves can be longer than usual (BAP 2001).



Figure 63. *Lejeunea lamacerina* exhibiting a shelf-like growth form. Photo by George G., through Creative Commons.

Kraichak (2012) describes its epiphyllous characteristics as being **monoicous** (facilitating sexual reproduction) and having imbricate leaves (Figure 65) and

lobules (Figure 66) to retain water, but at the same time it lacks the advantage of neoteny and asexual reproductive structures.

#### Reproduction

*Lejeunea lamacerina* (Figure 47-Figure 51) is **autoicous** and has no specialized asexual reproduction (Schuster 1980); the female perianth of subsp. *gemminata* is shown in Figure 64. Nevertheless, van der Pluijm *et al.* (2015) found buds of young plants on the margin or lamina of old weathered leaves. They suggested that these probably act as a means of vegetative propagation.

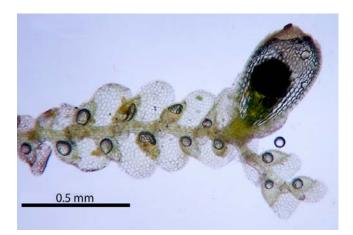


Figure 64. *Lejeunea lamacerina* subsp. *gemminata*, with perianth. Photo by Ken McFarland and Paul Davison, with permission.



Figure 66. *Lejeunea lamacerina* showing underleaves and leaf lobes. Photo by David T. Holyoak, with permission.

#### **Fungal Interactions**

No studies have found any mycorrhizal relationships (Wang & Qiu 2006), but once more the small size may account for a lack of studies.

#### Biochemistry

*Lejeunea lamacerina* has a few small oil bodies per cell (Figure 67), indicating the presence of secondary compounds. Due to its small size, it is not surprising that biochemical studies are few. Asakawa *et al.* (2018) used chemical relationships of sesquiterpenoids to argue for its relationship among several Japanese species.

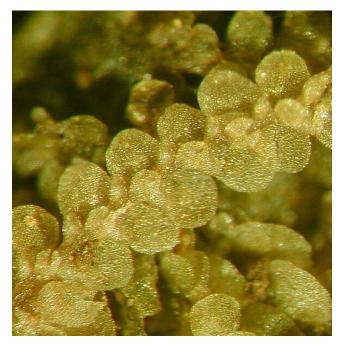


Figure 65. *Lejeunea lamacerina* showing imbricate leaves, lobules, and underleaves. Photo by Michael Lüth, with permission.

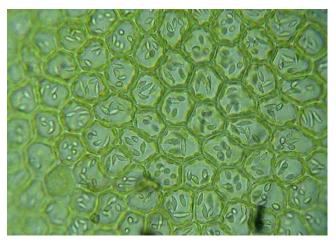


Figure 67. *Lejeunea lamacerina* leaf cells showing oil bodies. Photo by David T. Holyoak, with permission.

#### Lejeunea patens (Figure 68-Figure 69)

(syn. = Crossotolejeunea polyantha, Neopotamolejeunea polyantha, Potamolejeunea polyantha)

*Lejeunea patens* (Figure 68-Figure 69) has experienced misidentification in various geographic areas. Confusion between *Lejeunea patens* and other similar liverwort species and confusion in its synonymy in its various locations makes records of its occurrence incomplete and sometimes misleading (see Söderström *et al.* 2007). For example, Miller (1964) considered *Lejeunea patens* Lindb. (Frye and Clark, 1947) to be the same as *Lejeunea lamacerina* Gott. ex. Steph. ssp. *gemminata* Schuster (Figure 64), but Söderström *et al.* 2016) consider both to be valid species.



Figure 68. *Lejeunea patens* on a boulder beside the river near Swallow Falls, Wales. Photo by Janice Glime.

#### Distribution

Lejeunea patens (Figure 68-Figure 69) has an Atlantic-Mediterranean distribution (Damsholt 2017). The species has been reported from Spain (Sérgio *et al.* 2007), Portugal (Sérgio *et al.* 2007; Cacciatori *et al.* 2015). Yamaguchi *et al.* (2005) found it in Indonesia in two unburned plots. Bakalin (2019) reported it from the Caucasus of western Russia. Bosanquet *et al.* (2018) reported it from the British Atlantic woodland. It is known in Britain and Norway (Barbour (1903; Frahm 2012), Ireland, Bretagne in France, the Iberian Peninsula, and the Faroe Islands (Frahm 2012). Hugonnot *et al.* (2013) reported it from the Massif Central in France.

Frahm (2005) reported it from eight of the nine Azorean islands, occurring in the Madeira laurel forests (Figure 11) (Sim-Sim *et al.* 2005a,b; Ruas *et al.* 2015). Gil and Guerra (1981) found it at Sierras de Algeciras in the Iberian Peninsula. Casas *et al.* (1983) found it at l'Alt Empordà in Spain. Poponessi and Aleffi (2016) listed it for the Sardinian region of Italy, Macaronesia, Spain, France, Madeira, Portugal, and Turkey. They termed it a Mediterranean-mountain hemiboreal species.

In North America, Barbour (1903) found that *Lejeunea patens* (Figure 68-Figure 69) occurs in Newfoundland and Nova Scotia and northern borders of the USA. Andrews (1921) reported it from several locations in North Carolina. Evans (1923) added Maine, New Hampshire, Vermont, Massachusetts, and Connecticut, USA.

#### **Aquatic and Wet Habitats**

*Lejeunea patens* (Figure 68-Figure 69) can be occasionally submerged (Watson 1919) and occurs in rivers (Ferreira *et al.* 2008). Cros (1982) found it on rocks in the Escalonada torrent of the Balearan Islands in the Mediterranean.

More likely one can find it on damp, shaded rocks in such locations as gorges (Poponessi & Aleffi 2016). Sim-Sim *et al.* (2003) reported it from rocks, boulders, and stone walls that were in either sheltered or exposed habitats (Figure 70) along water courses. These formed loose to dense patches, often with other bryophytes, on moist rock surfaces and slopes near the water (Figure 71). In the Faroe Islands, *Lejeunea patens* (Figure 68-Figure 69) occurs in rocky ravines or clefts where species richness is greater than in any other habitat in the Faroes (Damsholt 2017). In Turkey, Ezer *et al.* (2009) found it in humid locations.

In gorges in France, Hugonnot *et al.* (2016) report it from shaded and dry walls that have an accumulation of organic matter. They describe its habitat as having moderate shade with a "certain quantity" of light. In Bretagne, northern France, Durfort (2015) found it in ravines, wooded ridges, and mountainous areas with high atmospheric humidity.

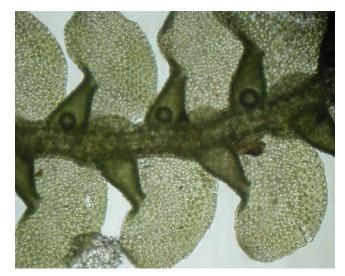


Figure 69. *Lejeunea patens* showing leaf lobes and underleaves. Photo by Jan-Peter Frahm, with permission.



Figure 70. *Lejeunea patens* habitat on vertical boulder surfaces. Photo by Michael Lüth, with permission.



Figure 71. *Lejeunea patens* on boulder near Swallow Falls, Wales, growing with *Thamnobryum alopecurum* in a humid environment. Photo by Janice Glime.

The habitat for *Lejeunea patens* (Figure 68-Figure 69) is clearly broadly defined, but usually in places with nearly constant humidity. It has even been found, but rarely, in a salt marsh in Britain (Adam 1976). In the Madeira Archipelago, Sim-Sim *et al.* (2005b) found it growing as an epiphyte where it was humid and shady in the laurel forest (Figure 11). It also often occurred with *Plagiochila exigua* (Figure 29) in **loose turfs** on moist rocks and slopes near water courses.

Long and Williams (2007) found that the intense shading of **Rhododendron ponticum** (Figure 22) causes the complete loss of a number riparian bryophytes. Only occasional patches of **Lejeunea patens** (Figure 68-Figure 69) on sheltered boulder faces are present. They assumed that this species could be washed in from stands living higher up on the rock face. Several reports mention that it tends to occur in brighter areas.

Lorenz (1924) found *Lejeunea patens* (Figure 68-Figure 69) on Mt. Desert Island, Maine, USA, on trees, rocks and the northern white cedar, *Thuja occidentalis* (Figure 32) – a swamp forest species.

#### Adaptations

The wide range of habitats is supported by the humidity and temperature tolerance of this species from the Faroes. In his experiments, Clausen (1964) found that at 43% and 51% relative humidity, half the cells of Lejeunea patens (Figure 68-Figure 69) were dead, but at 63% humidity, all cells remained alive. It did best between 70% and 100% rh with a temperature of ~35°C and 60% relative humidity at 20°C. All died at ~45°C at all humidities and at 20°C with 10% rh. These parameters placed it close to the middle among the liverwort species from various northern locations in the experiments. When maintained in ice at -10°C for 2-5 days, about 3/4 of the cells remained alive, but the dead cells were mostly at the shoot apices. After 11-12 days, all cells were dead. However, if it was partly desiccated over sugar, all cells remained alive for 5 days. At -40°C, all cells were dead in 1 day.

*Lejeunea patens* (Figure 68-Figure 69) can modify its form in different environments, sometimes having very slender stems with small leaves (BAP 2001). When so attenuated, shaded stems can produce leaves that are longer than usual.

#### Reproduction

Lejeunea patens (Figure 68-Figure 69) is autoicous (Evans 1902; Hugonnot et al. 2016). In the Faroe Islands, Damsholt (2017) found that perianths were frequent, but despite its autoicous sexuality, it only occasionally produces sporophytes there. Perhaps the climate is unsuitable for the antheridia or for sperm transfer for this species that extends southward to the Mediterranean. It is possible that the signals for antheridial and archegonial maturation are out of sync. On the other hand, even in Galicia in northwestern Spain, the species is frequent, but sporophytes are encountered only occasionally (Reinoso 1985). And in the gorges of the Rhue in France it does not produce sporophytes at the studied site, nor does it have any specialized vegetative propagation (Hugonnot et al. 2016).

#### Role

Des Callaghan (pers. comm.) has found rotifers (Figure 72) living among the mats of *Lejeunea patens* (Figure 68-Figure 69) in Wales (Figure 73).

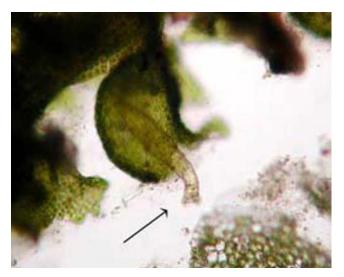


Figure 72. *Frullania*, showing how a rotifer can live in a lobule such as those found in *Lejeunea patens*. Photo courtesy of Andi Cairns.



Figure 73. *Lejeunea patens* – home of rotifers near Swallow Falls, Wales, mixed with the moss *Thamnobryum alopecurum*. Photo by Janice Glime.

#### Biochemistry

The species has larger oil bodies, usually 4-6 per cell, up to 10. Biochemical studies seem to be lacking. Wang and Qiu (2006) were unable to find any records of mycorrhizae associated with *Lejeunea patens* (Figure 68-Figure 69), but is this the result of biochemical inhibition, or just lack of study?

#### Lejeunea polyantha

Confusion quickly arises in finding information on this species because there are two taxa that have had this name (homonyms): *Lejeunea polyantha* Mont. and *Lejeunea polyantha* Mitt. – the homonym (TROPICOS 2020). At times like this I regret not including authors in the text of this book.

#### Distribution

(syn. = Crossotolejeunea polyantha, Neopotamolejeunea polyantha, Potamolejeunea polyantha)

*Lejeunea polyantha* occurs in South America (Reiner-Drehwald 1999), including Brazil and Venezuela (Gradstein & Reiner-Drehwald 2007; Bastos & Gradstein 2020).

#### Aquatic and Wet Habitat

I must admit that this species did not appear in my search for aquatic species. But, as I found information on other species, this one showed up as being a rheophyte, occurring in lowland rainforests and being periodically submerged on rock and pendent on branches of shrubs in rivers (Reiner-Drehwald 2000a, b; Bastos & Gradstein 2020).

#### Lejeunea subaquatica

*Lejeunea subaquatica* seems to be a barely known species, but it is still recognized by Söderström *et al.* (2016).

The only wet/aquatic record I have found thus far is for its occurrence in the tropics at 10-20 cm above water level (Ruttner 1955).

#### Lejeunea topoensis

#### Distribution

*Lejeunea topoensis* is a rare Andean species, occurring in Brazil and Ecuador (Gradstein & Reiner-Drehwald 2007; Bastos & Gradstein 2020). It has an interesting disjunction between the Andes and the Atlantic coastal region in Brazil (Gradstein & Reiner-Drehwald 2007).

#### Aquatic and Wet Habitats

Lejeunea topoensis is a rheophyte, occurring in fast water and often submerged (Gradstein & Reiner-Drehwald 2007). In Ecuador it grows on the dwarf shrub Cuphea bombonasae (Figure 74) where it forms large mats (Gradstein & Benitez 2014). In Brazil they found it in a spring bog, growing submerged in running water. Gradstein *et al.* (2011) found it in great abundance in torrential water currents of the Topo River in the Ecuadorian Andes.



Figure 74. *Cuphea bombonasae*, substrate for *Lejeunea topoensis*. Photo from <swbiodiversity.org>, through Creative Commons.

#### Adaptations

*Lejeunea topoensis* is green when fresh, forming large **mats** (Gradstein & Reiner-Drehwald 2007).

#### Reproduction

Lejeunea topoensis is very fertile, a benefit of its autoicous condition. The seta is articulate (having joint between two separable parts), probably contributing to its dispersal in running water. Its oil bodies are numerous (20-30 per cell) and thus small. The spores are green and germination is **precocious** (occurring early – germinating within capsule). The spores are irregular in shape with a surface covered with small granules and rosettes, perhaps giving the spores better flotation. Long-distance spore dispersal is quite possible, based on experiments by van Zanten and Gradstein (1988). This premise is supported by molecular phylogenetic studies in other species (Heinrichs *et al.* 2005, 2006).

#### **Biochemistry**

Ludwiczuk and Asakawa (2014) used fingerprinting of secondary metabolites to show that *Lejeunea topoensis* lacks isolepidozene, pingiusanes, fusicoccanes, and monocyclofarmesanes that are found in many of the genera of the **Lejeuneaceae**. No vegetative propagules were observed, but fragmentation remains a possibility.

#### Lopholejeunea nigricans (Figure 75-Figure 78)

(syn. = *Heterolejeunea javanica*)

*Lopholejeunea nigricans* Figure 75-Figure 78) has lots of synonyms (Staples & Imada 2006), an expected outcome for this species with lots of variation.

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Figure 75. *Lopholejeunea nigricans* showing variation in leaf color. Photo by Jia-dong Yang, through Creative Commons.



Figure 76. *Lopholejeunea nigricans* habit showing leaf lobes. Photo by Michaela Sonnleitner, with permission.

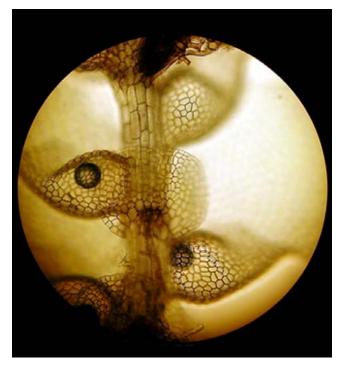


Figure 77. *Lopholejeunea nigricans* underleaves and lobes. Photo by Michaela Sonnleitner, with permission.

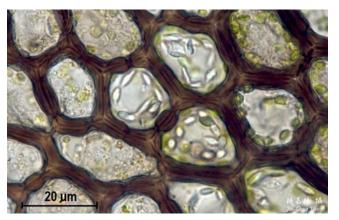


Figure 78. *Lopholejeunea nigricans* leaf cells showing oil bodies. Photo by Jia-dong Yang, through Creative Commons.

#### Distribution

Lopholejeunea nigricans (Figure 75-Figure 78) is a widespread pantropical species (Müller et al. 2011; Kornochalert et al. 2012; do Carmo & Peralta 2016). In Asia it is known from Bangladesh, Bhutan, Borneo, Cambodia, China, Hong Kong, India, Indonesia, Japan, Malaysia, Myanmar, Nepal, Papua New Guinea, Philippines, Taiwan, Thailand, Vietnam, and Yemen (Zhu & Gradstein 2005; Schwarz 2013). Kürschner and Ochyra (2003) found it in the Arabian Peninsula. Kornochalert et al. (2012) added much more information on the species in Thailand. Pócs and Chantanaorrapint (2016) reported it among non-epiphyllous species from several lowland areas in Thailand. Rajesh and Manju (2014) reported it from both lowlands and midlands in Kerala, India. In Sulawesi, an Indonesian island, Ariyanti and Gradstein (2007) found it in both lowland and montane regions. Zhu et al. (1998) added Zhejiang Province in China.

Haerida *et al.* (2010) found that *Lopholejeunea nigricans* (Figure 75-Figure 78) has a moderately wide distribution in West Java, occurring in both lowland and montane habitats (200-1700 m asl). Hodgetts *et al.* (2016) found it in the Eastern Region of Ghana. Hedderson *et al.* (2015) reported it from 1274 m asl in Mozambique and Wigginton (2001) from Malawi (up to 1635 m asl). It has been reported from Réunion Island off the eastern coast of Africa in the Indian Ocean (Ah-Peng & Bardat 2005) and the Central African island country of São Tomé and Príncipe. Carreon *et al.* (2016) added it to the Philippines. It also occurs in the Hawaiian Islands (Staples & Imada 2006).

In the Neotropics, *Lopholejeunea nigricans* (Figure 75-Figure 78) is known from Brazil (da Costa 2003; Peralta & Yano 2008; Visnadi 2009), Cocos Island in Costa Rica (Dauphin 1999), a tropical lowland cloud forest in central French Guiana (Gradstein 2006), Bolivia (Fuentes & Churchill 2005), and Peru (Drehwald 2003).

#### **Aquatic and Wet Habitats**

**Lopholejeunea nigricans** (Figure 75-Figure 78) occurred in a water spout of a tuff wall in the tropics (Ruttner 1955). Zhu and Gradstein (2005) reported that it occurs up to 1200 m asl in Asia, occasionally occurring on stones in running water. Hodgetts *et al.* (2016) reported it

from damp, shaded rocks by streams in Ghana, where it is locally abundant at 350-630 m asl. In India, Das and Sharma (2013) reported it from the bank of the River Boleswar at 70 m asl, as well as on loose moist soil of rock crevices. In Malawi, Wigginton (2001) found it on rocks beside rivers and streams. Müller *et al.* (2011) found it in the central African island country of São Tomé and Príncipe on exposed hardwood roots along a river. In Equatorial Guinea, Sánchez and Pérez (1998) found it both on rocks and bark near streams at 5-75 m asl.

The habitats of *Lopholejeunea nigricans* (Figure 75-Figure 78) are rather variable, including tree bases, roots, trunks, branches, shrubs, lianas, stumps, decaying logs, rocks, soil, occasionally on stones in running water, or on living leaves, from sea level to 2900 m asl (Zhu & Gradstein 2005). Hodgetts *et al.* (2016) found it forming small colonies in earthy rock crevices in the eastern region of Ghana.

Records for *Lopholejeunea nigricans* (Figure 75-Figure 78) on rock seem less frequent than epiphytic records except in or near water. Hedderson *et al.* (2015) found it on a small boulder in the *Streptocarpus* (Figure 80) forest on Mabu Mountain in Mozambique (Figure 81). Wigginton (2001) reported it from rocks, including granite, close to rivers. Müller *et al.* (2011) found it on soil and litter over volcanic rock where it received filtered light.

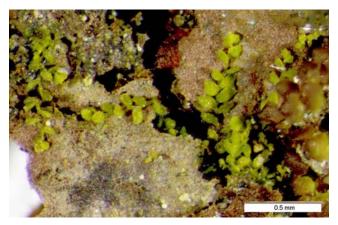


Figure 79. *Myriocoleopsis minutissima*, a species that grows on *Lopholejeunea nigricans*. Photo by Blanka Aguero, with permission.



Figure 80. *Streptocarpus* sp.; *Lopholejeunea nigricans* has been found in the *Streptocarpus* forest on Mabu Mountain in Mozambique. Photo by Mokkie, through Creative Commons.



Figure 81. Mount Mabu, Mozambique, where one can find *Lopholejeunea nigricans* on small boulders in the *Streptocarpus* forest. Photo by Conradie *et al.* 2016, through Creative Commons.

#### Adaptations

Sass-Gyarmati (2015) considered *Lopholejeunea nigricans* (Figure 75-Figure 78) to be the most variable species in the genus *Lopholejeunea*. For example, in some cases the lobules may be reduced (Zhu & Gradstein 2005). In a moist environment these modifications include reduced female bract lobules, weakly laciniate perianths, and very small leaf lobules. These modifications have resulted in the description of several species that are now considered synonyms.

*Lopholejeunea nigricans* (Figure 75-Figure 78) forms mats (Figure 75) (Batista & Santos 2016) and has a dark pigmentation (de Oliveira 2018). De Oliveira found that the dark pigmentation was significantly more frequent among liverworts in the canopy and significantly less at the tree bases. This dark coloration (Figure 75) presumably protects the canopy liverworts from the bright light there.

#### Reproduction

Lopholejeunea nigricans (Figure 75-Figure 78) has both monoicous and dioicous sexuality, giving it the advantages of both ease of fertilization and diversity of cross fertilization. He and Zhu (2011) found that the spore output from Lopholejeunea nigricans was 936-1254 from a tree trunk population. But it lacks asexual reproduction. De Oliveira (2018) suggested that the absence of overrepresentation of asexual propagules in canopy liverworts challenges the current views of bryophyte strategy, especially in the canopy. But Zhu and Gradstein (2005) found that Lopholejeunea nigricans accomplishes asexual reproduction with caducous (falling off easily) or fragmenting leaves.

#### Myriocoleopsis (Figure 79, Figure 87-Figure 91)

*Myriocoleopsis* (Figure 79, Figure 87-Figure 91) can be found in Andean streambeds (S. Robbert Gradstein pers. comm. 3 November 2011). Discovery of the molecular relationship of *Cololejeunea vuquangensis* with *Myriocoleopsis* has also placed the genus in Asia from Vietnam as *Myriocoleopsis vuquangensis* (Pócs 2010). For a discussion of species and their affinities in this genus, see Pócs (2010).

In this genus, the development of robust stems seems to be an adaptation to the periodic submergence it experiences (Reiner-Drehwald & Gradstein 1995). Gradstein *et al.* (2018) noted that it exhibits **neoteny** with perpendicular leaf segmentation, absence of underleaves, and stem with only one row of medullary cells.

But Myriocoleopsis (Figure 79, Figure 87-Figure 91) also is epiphyllous (Yu et al. 2013), a habitat much more subject to drying conditions. Yu and coworkers described the rheophytic relatives of these epiphyllous species, including Myriocoleopsis. They found that the rheophytic taxa differed from epiphyllous species by having creeping stolons, robust stems, and long androecial spikes, and they considered these characters adaptive for running water. In addition to its epiphyllous substrata, the genus also occurs on rock (Gradstein et al. 2014), where these adaptations also could be beneficial, but especially on rocks in running water. Wilson et al. (2007) noted that rheophytes from unrelated taxonomic groups are driven to parallel development, resulting in similar adaptations to habitats of swiftly flowing water and regular flooding. These included long, robust stems with pinnate branching and numerous, small gametoecial branches on both sides of the stem.

#### Myriocoleopsis fluviatilis

(syn. = *Myriocoleopsis puiggarii*)

#### Distribution

*Myriocoleopsis fluviatilis* is endemic in Brazil (Gradstein & da Costa 2003; da Costa and dos Santos 2009), where it is classified as endangered (da Costa and dos Santos 2009; de Gasper *et al.* 2012), and thus threatened in the world (Hallingbäck and Hodgetts (2000).

#### **Aquatic and Wet Habitats**

*Myriocoleopsis fluviatilis* grows on rocks and shrubs that are periodically submerged in rivers (Gradstein & da Costa 2003). It is "very rare" and occurs at 150-1300 m asl in Brazil. It grows primarily on bare rocks or small rocky cliffs in the middle and along the edges of the River Pardo (Gradstein & Vital 1975). But it also grows on the bases of low shrubs, always in exposed places in or near running water, in or near a river with small waterfalls and rapids and a rocky bottom. The species is only found in exposed places in or near running water.

*Myriocoleopsis fluviatilis* colonizes bare rocks and small rocky cliffs in the middle and edges of the River Pardo (Gradstein & Vital 1975). The life form is a **mat**, which forms a dense, pale greenish growth. It has short, creeping, stoloniform primary stems and secondary stems that are ascending to erect, up to 3 cm long.

Continuous submergence is not suitable for the health of the plants. After a period of 5-15 days of submergence, leafy shoots die and only the stoloniferous stems survive (Gradstein & Vital 1975).

#### Adaptations

Gradstein *et al.* (2003a) ascribed the thicker stems with more numerous rows of cells to adaptations for the rheophytic habitat of *Myriocoleopsis fluviatilis*. This species is also neotenous, but I know of no experimental study that shows any rheophytic advantage to this developmental strategy. It is common among epiphylls and among some aquatic **Lejeuneaceae**, as seen above.

#### Reproduction

Despite its autoicous sexuality, sporophytes develop only on plants that occur on emerged substrates, a phenomenon that has been noted for a number of other flowing-water bryophytes (Gradstein & Vital 1975). It has multicellular disciform gemmae that arise from the leaf surfaces, but these are rare.

#### Role

In the continuously wet habitat of this species, many diatoms find a suitable home on the liverworts: *Melosira* (in great number; Figure 82), *Gomphonema* (Figure 83), *Synedra* (Figure 84), *Cymbella* (Figure 85), and some Naviculaceae (Figure 86) (Gradstein & Vital 1975).



Figure 82. *Melosira* sp., a genus that can occur on *Lopholejeunea nigricans* in wet habitats. Photo by Yuuji Tsukii, with permission.



Figure 83. *Gomphonema* sp., a genus that can occur on *Lopholejeunea nigricans* in wet habitats. Photo by Yuuji Tsukii, with permission.

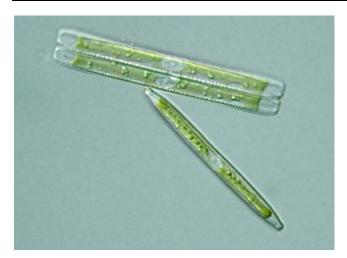


Figure 84. *Synedra cf. ulna*, in a genus that can occur on *Lopholejeunea nigricans* in wet habitats. Photo by Yuuji Tsukii, with permission.



Figure 85. *Cymbella cf. lanceolata*, in a genus that can occur on *Lopholejeunea nigricans* in wet habitats. Photo by Yuuji Tsukii, with permission.

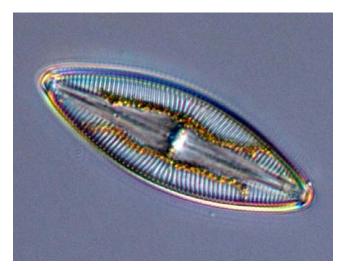


Figure 86. *Navicula* (Naviculaceae), in a genus that can occur on *Lopholejeunea nigricans* in wet habitats. Photo by Phyto'pedia – The Phytoplankton Encyclopaedia Project, through Creative Commons.

#### Myriocoleopsis gymnocolea

(syn. = Myriocoleopsis riparia)

#### Distribution

*Myriocoleopsis gymnocolea* is known from Argentina (Reiner-Drehwald & Gradstein 1995; Gradstein & da Costa 2003), Bolivia (Gradstein *et al.* 2003b), Brazil (Reiner-Drehwald & Gradstein 1995; Gradstein *et al.* 2003a; dos Santos & da Costa 2010; do Carmo *et al.* 2018), and Ecuador (Gradstein & da Costa 2003; Gradstein *et al.* 2004; Pócs 2010; Benitez & Gradstein 2011; Gradstein 2020).

In Ecuador *Myriocoleopsis gymnocolea* occurs at 500-1300 m asl (León-Yanez *et al.* 2006; Gradstein 2020), 100-1300 m asl in Brazil (Gradstein & da Costa 2003), 100-1300 m asl in Argentina (Reiner-Drehwald 1995).

#### **Aquatic and Wet Habitats**

Like *Myriocoleopsis fluviatilis*, this species occupies periodically submerged rocks in rivers (Gradstein & da Costa 2003). Reiner-Drehwald (1995) found *Myriocoleopsis gymnocolea* above a waterfall, where it is sometimes submerged, but primarily on rocks that are periodically submerged. The species occurs in the center and on the banks of rivers, typically in rapid currents. The rapid currents provide splash that keep it moist in its emergent positions.

The species can occur as an epiphyte at the base of small shrubs and on river banks, occupying a niche similar to that of *M. fluviatilis* (Reiner-Drehwald 1995).

#### Adaptations

*Myriocoleopsis gymnocolea* exhibits traits that we have seen in previous rheophytic members of the **Lejeuneaceae**. It is **monoicous** and neotenous (Kraichak 2012), the latter a character that needs further investigation to determine its advantages in the aquatic environment. In fast water, this may permit it to remain small, thus creating little or no drag, while also permitting sexual structures to develop. The guarantee of a wet film over the plants at the right time would facilitate its ability to transfer sperm from antheridia to archegonia in this monoicous species.

*Myriocoleopsis gymnocolea* has thin stems with only 5 rows of cortical cells (Reiner-Drehwald & Gradstein 1995). Yu et al. (2014) considered certain remarkable characters to include its dimorphic stems with creeping stolons and erect leafy axes arising from them, reduced lobules, and long male spikes. The reduced lobules are often expressed in rheophytic species. In addition, they noted the absence of underleaves, another character that could be part of the neotenous development of many aquatic Lejeuneaceae. It might be interesting to examine the differences in hydroxyproline (component of plant hormones essential for growth, cell differentiation, and defense) concentrations surrounding the leaves in the aquatic environment (see Basile 1967). Could it be that the condition of immersion changes the concentrations of this component, thus affecting development? This could be accomplished by reduced diffusion in water.

#### Reproduction

*Myriocoleopsis gymnocolea* is **monoicous** (Kraichak 2012).

### Role

*Myriocoleopsis gymnocolea* serves as a suitable substrate for diatoms (Figure 82-Figure 86) and other algae (Reiner-Drehwald 1995).

#### Biochemistry

Despite its small size, Ludwiczuk *et al.* (2013) examined chemical relationships in the Lejeuneaceae, including this species. *Myriocoleopsis gymnocolea*, like a number of members of this family, has only pinguisanes and not isolepidozenes, fusicoccanes, or monocyclofarmesanes. The researchers considered this chemistry to be a marker of the subtribe Cololejeuneinae.

Like other members of the genus, *Myriocoleopsis* gymnocolea lacks lepidozanes, fusicoccanes, monocyclofarnesanes, having only pinguisanes (Coulerie *et al.* 2015), strengthening its relationship to those species of Lejeuneaceae not placed in *Myriocoleopsis*.

#### *Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91)

(syn. = *Cololejeunea minutissima*)

#### Distribution

*Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) was originally described as a species of *Cololejeunea* (see Chapt. 1-7 in this volume), but has been moved to *Myriocoleopsis* (Yu *et al.* 2014). It is a widespread pantropical species (Cañiza *et al.* 2016; Hodgetts *et al.* 2020) that is distributed in North America from Virginia and Tennessee to Florida and Texas (Stotler & Crandall-Stotler 2017). It is also known from Central America, South America, western and central Europe, central and eastern Asia, and Australia (Stotler & Crandall-Stotler 2017; Hugonnot (2019), southern Africa and South Indian Ocean islands (Bischler 2004; Hugonnot 2019).



Figure 88. *Myriocoleopsis minutissima* with perianth. Photo by Hugues Tinguy, through Creative Commons.





Figure 87. *Myriocoleopsis minutissima* in a large patch on rock. Photo by Hugues Tinguy, with permission.

Figure 89. *Myriocoleopsis minutissima*, showing large leaf lobes. Photo by Hugues Tinguy, through Creative Commons.



Figure 90. *Myriocoleopsis minutissima* showing large lobes. Photo by Blanka Aguero, with permission.

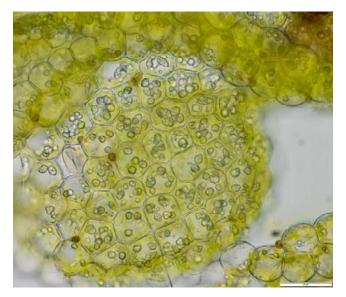


Figure 91. *Myriocoleopsis minutissima* leaf cells with oil bodies. Photo by Blanka Aguero, with permission.

In Europe *Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) exhibits a Mediterranean-oceanic character (Düll 1983). European records include Madeira Island (Schwarz & Schumm 2019), Montseny massif in the Iberian Peninsula (very rare; Sáez *et al.* 2018), Corsica (Hugonnot 2019), Sicily (Dia *et al* 2017), and France (Hugonnot *et al.* 2017; Hugonnot & Simont 2018). It is rare in the Mediterranean region, occurring in the Azores, Canary Islands, Cape Verde Islands, Madeira, Croatia, Greece, Italy, Montenegro, Portugal, Serbia, and Spain (Hugonnot 2019).

In Asia *Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) is known from Vietnam (Shu *et al.* 2016), Singapore (Zhu *et al.* 2018), southern Thailand (Pócs and Chantanaorrapint 2016), Lebanon in southwestern Asia (Hugonnot 2019), and Sabah in Malaysian Borneo (Pócs *et al.* 2020).

Wigginton (2018) found *Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) in the flora of Africa and the African islands. Enroth *et al.* (2019) included it in the checklist of the Taita Hills region of Kenya, noting that it is widely distributed in sub-Saharan Africa. Hugonnot (2019) included it in the flora of Algeria and Tunisia in northern Africa.

In Central and South America, Ristow *et al.* (2015) reported *Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) from Brazil. It occurs in Ecuador (Gradstein 2020) and Paraguay (Cañiza *et al.* 2016). Schäfer-Verwimp and van Melick (2016) reported it from Jamaica and Stotler and Crandall-Stotler (2017) from Bermuda.

*Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) has a varied altitudinal range. It has a known altitudinal range of 1500-2800 m asl in Ecuador (Gradstein 2020). In Malaysian Borneo, it occurs in the mossy cloud forest at 1900-1940 m asl (Pócs *et al.* 2020). On the Iberian Peninsula it occurs at 750 m. It is known from lowlands in Thailand, where it has expanded into the warm temperate, oceanic areas (Pócs & Chantanaorrapint 2016).

#### **Aquatic and Wet Habitats**

*Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) has little claim to the aquatic environment, but it is at least tolerant of a humid environment, living in "well preserved" humid riparian forests of Paraguay, where it is an epiphyte on the corky bark of *Chloroleucon tenuiflorum* (Figure 92) (Cañiza *et al.* 2016). Most records for *Myriocoleopsis minutissima* (Figure 79, Figure 87-Figure 91) present it as an epiphyte.



Figure 92. *Chloroleucon tenuiflorum*, a species of humid riparian forests of Paraguay and substrate for *Myriocoleopsis minutissima*. Photo by CECOAL, through Creative Commons.

#### Reproduction

*Myriocoleopsis minutissima* is **autoicous**. Images of perianths are in Figure 93-Figure 95. It produces large gemmae (Figure 96) with 16-48 cells, mostly on the lobes, but sometimes on the leaf periphery.



Figure 93. *Myriocoleopsis minutissima* with perianths and archegonia. Photo by Blanka Aguero, with permission.

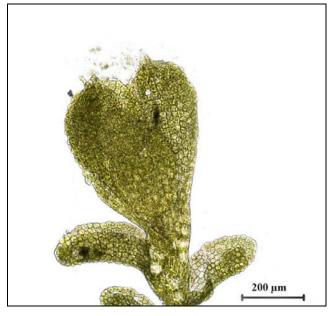


Figure 94. *Myriocoleopsis minutissima* perianth. Photo by Hugues Tinguy, through Creative Commons.



Figure 95. *Myriocoleopsis minutissima* with archegonium showing reddish neck. Photo by Blanka Aguero, with permission.

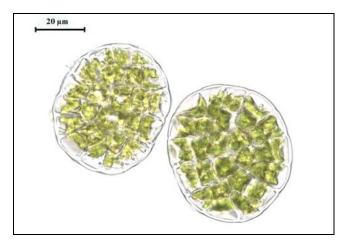


Figure 96. *Myriocoleopsis minutissima* gemmae. Photo by Hugues Tinguy, through Creative Commons.

#### Myriocoleopsis minutissima subsp. myriocarpa

#### Distribution

Like the subspecies *minutissima* (Figure 79, Figure 87-Figure 91), *Myriocoleopsis minutissima* subsp. *myriocarpa* is widespread in the tropics (Hodgetts *et al.* 2020). It is thus pantropical, with records in Europe, North America, and South America. Gradstein (2020) found it in Ecuador at 100-3000 m asl.

#### **Aquatic and Wet Habitats**

In Florida, USA, *Myriocoleopsis minutissima* subsp. *myriocarpa* occurs in mahogany (*Swietenia mahogani*) hammocks (Figure 97), in Everglades National Park (Schuster 1971; Zona & Sadle 2017). These are islands of trees in wetlands or on slopes between wetlands and uplands. Those serving as home for this species are low hammocks, surrounded by marshland (Schuster 1971).



Figure 97. *Swietenia mahagoni* hammock, Everglades. Photo by Miguel Vieira, through Creative Commons.

#### Myriocoleopsis vuquangensis

#### Distribution

*Myriocoleopsis* was considered a Neotropical genus until Pócs (2010) reported it from Vietnam in southeast Asia. Wilson *et al.* (2007) used molecular evidence to identify similarities of *Cololejeunea vuquangensis* to the Neotropical *Myriocoleopsis* (Figure 79, Figure 87-Figure 91), causing its transfer to *Myriocoleopsis vuquangensis*. In the Neotropics it is known from the Nangaritza River in Ecuador (Pócs 2010).

#### **Aquatic and Wet Habitats**

This species has more qualifications as a wetland species, living as a rheophyte on twigs of the euphorbiaceous shrub *Homonoia riparia* (Figure 98) (Pócs 2010). In its known Asian home, this species of *Myriocoleopsis* (Figure 79, Figure 87-Figure 91) exists on the bush vegetation on riverbed shoals where it gets inundated twice a year during the monsoons. These shrubs occur in groups on river banks, rocky (fast-running) stream beds, and along the coast. Soil in these locations is usually

(temporarily) inundated, in some areas for months, creating a humid or wet environment.



Figure 98. *Homonoia riparia*, a rheophyte that can support *Myriocoleopsis vuquangensis* on its twigs, where they are occasionally inundated. Flora of Peninsular India, through Creative Commons.

#### Adaptations

Like other *Myriocoleopsis* (Figure 79, Figure 87-Figure 91) species, *Myriocoleopsis vuquangensis* has both creeping stolons and erect leafy stems (Pócs 2010).

#### Reproduction

*Myriocoleopsis vuquangensis* is monoicous, with male branches and "very abundant" perianths (Pócs 2010).

# *Ptychanthus striatus* var. *intermedius* (see Figure 99-Figure 101)

#### (syn. = *Ptychanthus intermedius*)

Although *Ptychanthus striatus* var. *intermedius* was described in 1934 by Verdoorn as *Ptychanthus intermedius*, I have not been able to find much ecological information on it under either name, so the information contained here is for the species *Ptychanthus striatus* (Figure 99-Figure 101).



Figure 99. *Ptychanthus striatus*. Photo by Jia-dong Yang, through Creative Commons.



Figure 100. *Ptychanthus striatus*, dry, growing on a vertical surface in Bhutan. Photo by David Long, with permission.



Figure 101. *Ptychanthus striatus* ventral side showing underleaves and perianths. Photo by Boon Chuan Ho, courtesy of Rob Gradstein.

#### Distribution

**Ptychanthus striatus** (Figure 99-Figure 101) is a variable species (Gradstein 1985). Singh and Singh (2016) noted that the species **Ptychanthus striatus** has many synonyms. He (1997) considered it to have worldwide distribution, especially in the Palaeotropics (Gradstein 1985), but it appears to be absent in the Western Hemisphere. It was considered to occur in warm temperate regions including South Africa, the Himalayas, Japan, and Australasia (Gradstein & Inoue 1980). Pócs *et al.* (2007) summed its distribution up as widespread in the whole Indopacific region.

Gradstein and Inoue (1980) also included Central Africa to the western Pacific, with several records indicating that *Ptychanthus striatus* (Figure 99-Figure 101) occurs in Africa (Bizot & Pócs 1974; Frahm 1994; Braun *et al.* 2004; Müller 2006). Müller (2006) even considered it to be widely distributed in tropical Africa. However, using both morphology and molecular characteristics, Ahonen *et al.* (2005) and Pócs and Luke (2007) considered all African records of *Ptychanthus striatus* to be the separate species *Ptychanthus africanus*.

Thiers (1990) and Haerida *et al.* (2010) reported *Ptychanthus striatus* (Figure 99-Figure 101) from

Australia. It also has been found in Java and Sumatra (Verdoorn 1933), Peninsular Malaysia, Borneo, Sulawesi, Moluccas, Philippines, West Irian, New Zealand, Pacific Islands, India, Sri Lanka, Taiwan, Indochina, and China (Haerida *et al.* 2010). Kornochalert *et al.* (2012) reported its presence in Thailand. Additional Asian records include China (He 1997), including Sichuan (Piippo *et al.* 1997) and Yunnan (Han *et al.* 2010), Western Ghats in India (Pócs *et al.* 2007), and southern India (as *Spruceanthus wiggintonii*; Wang *et al.* 2014). The finding that *Ptychanthus africanus* replaces it in Africa and the Himalayas suggests that the remaining populations should be re-examined to determine whether they indeed all belong to *Ptychanthus striatus* (Figure 99-Figure 101).

Haerida *et al.* (2010) reported *Ptychanthus striatus* (Figure 99-Figure 101) in both lowlands and montane habitats at elevations ranging 1000-2400 m asl. Kornochalert *et al.* (2012) reported its range from 50-2480 m asl in Thailand. Frahm (1994) reported it at less than 1500 m on Mt. Kahuzi, Zaire. Pócs *et al.* (2007) found it at 2350 m asl in the Western Ghats in India. It even is considered common in the Himalayas at altitudes below 4000 m asl (Zhu & Long 2003), but those records might actually represent *Ptychanthus africanus* (see Singh & Singh 2008). Hence, the altitudinal ranges described here need to be verified following a more thorough assessment of the species.

#### **Aquatic and Wet Habitats**

It doesn't appear that *Ptychanthus striatus* (Figure 99-Figure 101) is particularly aquatic. Ruttner (1955) listed *Ptychanthus striatus* var. *intermedius* as aquatic in the tropics. Thiers (1990) reported *Ptychanthus striatus* (Figure 99-Figure 101) as growing especially near waterfalls (Figure 102) and steep escarpments in Australia, where the species forms large, "festooning" bodies in the mist that keeps these areas humid. In India, Singh and Singh (2008) reported the species *Ptychanthus africanus* as rare from moist places where it grew on rocks on a thin layer of soil.

*Ptychanthus striatus* also occurs in a variety of terrestrial habitats, including grassland (Gradstein & Inoue 1980), forest epiphytes (Müller 2006; Pócs *et al.* 2007), and on rocks (Kornochalert *et al.* 2012).

Several studies have examined the impact of heavy metals on Ptychanthus striatus (Figure 99-Figure 101). Shakya et al. (2008a, b) found that the metal accumulation in P. striatus increased with metal concentration in the water. Copper had a significant inhibition of both chlorophyll a and b. Similarly, zinc and lead accumulation caused a significant decrease in chlorophyll. Thev suggested that the greater loss of chlorophyll from P. striatus than from moss species in the experiments may have been caused by relatively more K<sup>+</sup> efflux in the leafy liverwort than in the mosses. However, there was no significant decrease in chlorophyll when the liverworts were exposed to copper, zinc, and lead together. The metals zinc and copper exhibited leaching in P. striatus, indicating that they occur on exchange sites under hydrated conditions. Competition for these exchange sites might explain the lowered toxicity when the three metals were provided together. These results are consistent with the presence of the species only in clean sites, not those contaminated with heavy metals. This study has led to the use of *P. striatus* and other bryophytes in determining heavy metal loading near roads (Shakya *et al.* 2012).

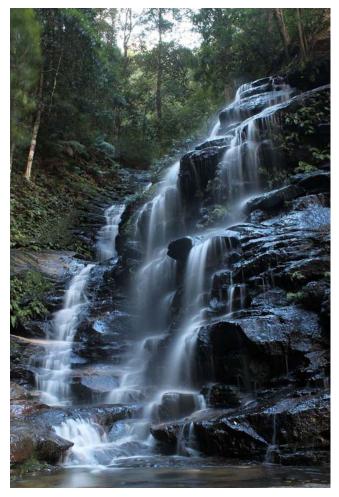


Figure 102. Waterfalls at Wentworth, Australia, a habitat where one might find *Ptychanthus striatus*. Photo by Jack Brogan, through Creative Commons.

#### Adaptations

*Ptychanthus striatus* (Figure 99-Figure 101) is a robust species, up to 10 cm long, contrasting with the many tiny members of the **Lejeuneaceae**. These plants are either pendent or stand up away from their substrate.

#### Reproduction

**Ptychanthus striatus** is autoicous (see perianths in Figure 103) (Haerida *et al.* 2010), contrasting with its sister species, **Ptychanthus africanus**, in which **dioicous** specimens "are not rare" (Bizot & Pócs 1974). The spore output of **Ptychanthus striatus** is high (up to 5750) among the Chinese Lejeuneaceae (He & Zhu 2011).

#### Biochemistry

**Ptychanthus striatus** (Figure 99-Figure 101) has 6-10 grayish-yellow oil bodies per cell (Figure 104) (Singh *et al.* 2008). These presumably are sites of concentrations of a number of secondary compounds. This species has one of the longest lists of biochemical studies. Such studies include the isolation and description of structures of a number of sesquiterpenoids (Takeda *et al.* 1982, 1983;

Nabeta *et al.* 1998, 2000; Wu *et al.* 2015), isolation and structure of diterpenoids such as ptychantins with elaboration of their synthetic pathway (Hashimoto *et al.* 1995, 1999; Hagiwara & Nozawa 2009; Wu *et al.* 2015). Like many of the **Lejeuneaceae**, it produces several pinguisane-type sesquiterpenes and striatene, but is poor in diterpenes (Gradstein *et al.* 1985).



Figure 103. *Ptychanthus striatus* with perianths. Photo by Jan-Peter Frahm, with permission.

#### Schusterolejeunea inundata

# (syn. = Cladocolea inundata, Lejeunea inundata, Potamolejeunea sprucei)

*Schusterolejeunea inundata* is the only known species in *Schusterolejeunea* (Grolle 1980; Söderström *et al.* 2016).

#### Distribution

Schusterolejeunea inundata is a rare Amazonian endemic (Gradstein & Costa 2003; Gradstein & Costa 2003; Dauphin et al. 2008; Désamoré et al. 2014; Costa et al. 2017; Sierra et al. 2018). It was known only along the Rio Negro of Brazil (da Silva 2019) and Venezuela (Sierra et al. 2018). The latest records show it from Venezuela (Moreno 1992; Söderström et al. 2020), Brazil (Gradstein & da Costa 2003; da Silva 2019), the Guianas (Gradstein & Hekking 1985; Gradstein et al. 1990; Gradstein & da Costa 2003; Söderström et al. 2020), Surinam (Söderström et al. 2020), Guyana (Söderström et al. 2020), Ecuador (Gradstein et al. 2018), and Peru (Gradstein & da Costa 2003; Söderström et al. 2020).

#### Aquatic and Wet Habitats

*Schusterolejeunea inundata* occurs in Andean streambeds as a rheophyte on branches of trees, roots, and rocks that occur in these beds in undisturbed lowlands up to 100 m asl (Gradstein *et al.* 1990; Gradstein & da Costa 2003). Hallingbäck and Hodgetts (2000) considered it an indicator of undisturbed lowland rainforest.

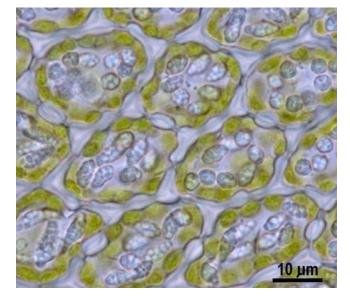


Figure 104. *Ptychanthus striatus* leaf cells with oil bodies. Photo by Jia-dong Yang, through Creative Commons.

In addition to the exploration of secondary compounds, other biological pathways were explored. Karunagoda *et al.* (Karunagoda *et al.* 2001, Karunagoda & Nabeta 2004) elucidated the biosynthesis of the phytyl side-chain of chlorophyll *a* using this species.

*Ptychanthus striatus* (Figure 99-Figure 101) is among the liverworts that have shown antidiabetic activity and antioxidant activity (Mukhia *et al.* 2015), as well as antigfungal activity against human pathogens (Dikshit *et al.* 1982). Other fungal interaction studies seem to be lacking.



Figure 105. *Schusterolejeunea inundata* with sediments imbedded in it from inundation. Photo from BioPortal, through Creative Commons.

Schusterolejeunea inundata occurs with Ceratolejeunea temnantha (Figure 106) in large mats in seasonal habits on rocks, lower portions of tree trunks, twigs, and roots in running water of seasonally inundated black-water forest habitats. It can also occur on river banks (Gradstein *et al.* 2011). Gradstein *et al.* (2001) described it as a liverwort of lakes and rivers in Amazonia.

#### Adaptations

Schuster (1990) considered the genus *Schusterolejeunea* to be among the most **apomorphic** (having novel evolutionary trait) of the liverwort genera (see also Vanderpoorten *et al.* 2010, 2012; Gradstein *et al.* 

2011). This is among the **stenotypic** genera (those with 1-3 species) (Schuster 1990; Désamoré *et al.* 2014). Gradstein *et al.* (2011) contend that habitat specialization drives the evolution of unusual characters in such species as *Schusterolejeunea inundata*. Such characters in this species are highly specialized for living in and out of water as the water level changes, permitting them to live on emergent vegetation and river banks.



Figure 106. *Ceratolejeunea temnantha* on tree roots, a habitat also occupied by *Schusterolejeunea inundata*. Photo by Juan Carlos Villarreal, with permission.

Gradstein *et al.* (2001) describe the rheophytic adaptations of *Schusterolejeunea inundata*. These include creeping rhizomes, thick stems, and "superfertility" (Thiers 1988). The species lacks **neoteny**, a common character of epiphylls, but one that seems to be mostly absent among species that become submersed.

### Summary

Most of the Lejeuneaceae are not true aquatics, but many do occur in wetlands and very humid habitats. Splash from waterfalls and rapids in streams are often the source of such water. Many have wide substrate tolerances, particularly for both rocks and bark, and many also occur as epiphylls. And many, like Lejeunea lamacerina and L. patens, have a wide moisture tolerance, from drying out to being submersed for short periods. This variety of habitat conditions leads to environmental forms that confound understanding of the taxonomy. Most Lejeuneaceae form mats, but some species are larger and have other growth forms. Many are dioicous, thus seldom producing sporophytes, but fragmentation and gemmae often provide an adaptive alternative. Their moisture retention allows many of them to provide suitable habitats for diatoms.

There seem to be almost no reports of these from polar regions, but they do often occur on mountains, some to relatively high elevations.

**Drepanolejeunea hamatifolia** is a desiccationsensitive hyperoceanic species that is restricted to rocky cascades and similarly wet habitats. Humidity maintenance is sometimes achieved by growing on other bryophytes. *Harpalejeunea molleri* is one of the species from moist habitats such as swamps, but not typically submerged. Many species, like *Lejeunea lamacerina* in mountain streams, are seasonally submersed.

Some *Myriocoleopsis* species can occupy rocks in streams that become inundated, but they occur more commonly as epiphytes in moist forests, mahogany hammocks, and other damp locations.

**Ptychanthus striatus** can form substrata suitable for nitrogen-fixing **Cyanobacteria**, as can a number of other moist-habitat bryophytes. Lobules/lobes in some, perhaps many, of the **Lejeuneaceae** can serve as watery habitats for rotifers.

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