# **CHAPTER 1-25** AQUATIC AND WET MARCHANTIOPHYTA, **CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 3**

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# **CHAPTER 1-25 AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 3**



Figure 1. *Marchantia quadrata* on dripping cliff, a wet habitat with a more constant set of conditions than open areas. Photo courtesy of Keir Wefferling.

# <span id="page-1-2"></span><span id="page-1-0"></span>**Marchantiaceae, cont.**

## <span id="page-1-1"></span>*Marchantia quadrata* **[\(Figure 1](#page-1-2)[-Figure 5](#page-2-2))**

### (= *Preissia quadrata*)

Most readers may be more familiar with the synonym *Preissia quadrata*. However, Stotler and Crandall-Stotler (2017) have moved it to the genus *Marchantia* and this seems to be the name the bryological community has accepted. But Zheng & Shimamura (2022) just published a paper that once again offers support for the separation of this species into the genus *Preissia*. And they have added another species to that genus, *Preissia platycarpa*. This conclusion on their part is based on several differences in morphology, including the absence of gemmae cups and the presence of only one archegonium and sporophyte per arm in the female receptacle. This genus argument among bryologists seems to depend on the degree of difference accepted, both morphological and genetic, to define a different genus.



Figure 2. *Marchantia quadrata* showing frequent character of purple edges. Photo by Andy Hodgson, with permission.

<span id="page-2-1"></span><span id="page-2-0"></span>

Figure 3. *Marchantia quadrata* with young archegonial heads and distinct red-purple margins. Photo by Hermann Schachner, through Creative Commons.



Figure 4. *Marchantia quadrata* with expanded archegoniophores. Photo by Janice Glime.

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Figure 5. *Marchantia quadrata* thallus. Photo from Snappy Goat, through public domain.

<span id="page-2-4"></span><span id="page-2-2"></span>Boisselier-Dubayle *et al*. (1997) reported that there was an incongruence between molecular data and morphological characters in the **Marchantiales**. They recommended a weighting of the morphological character data and were able to resolve the contradictions by so doing. They suggested that this might mean that the molecular sampling is too limited.

#### **Distribution**

*Marchantia quadrata* [\(Figure 1](#page-1-2)-[Figure 5\)](#page-2-2) is known from Australia, Europe, Northern and Southern Asia, Central America, North America, Oceania, and South America (ITIS 2022). It was recently reported as new to Turkey (Şimşek *et al*. 2014).

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

 In North America, *Marchantia quadrata* ([Figure 1](#page-1-2)- [Figure 5\)](#page-2-2) occurs along calcareous rivers in Connecticut, USA (Nichols 1916). I have seen it at the top of a waterfall in shallow water on bedrock ([Figure 6\)](#page-2-3) in the Keweenaw Peninsula, Michigan, USA. Forrest (2018) found it at the edge of a stream at the top of Snowbird Mountain in Utah, USA. McNeilus and Sharp (1975) reported it from limestone bluffs with dripping water in Tennessee, USA. Nichols (1918) reported it along a rock ravine streambank, Cape Breton Island, Canada. In western Canada, it occurs submerged, in hemicalciphilous montane streams (Vitt *et al.* 1986) and also on streambanks [\(Figure 7\)](#page-2-4) (Glime & Vitt 1987).



Figure 6. *Marchantia quadrata* habitat in river gorge at top of falls, Keweenaw County, Michigan, USA. Photo by Janice Glime.



Figure 7. *Marchantia quadrata* growing with mosses beside water. Photo by Claire Halpin, with permission.

Watson (1919), in his discussion of aquatic bryophytes, reported that *Marchantia quadrata* [\(Figure 1-](#page-1-2) [Figure 5](#page-2-2)) usually occurs on rocks [\(Figure 8](#page-3-0)-[Figure 9\)](#page-3-1) (Watson 1919). Near Lacko in the Western Carpathians, it is part of the ground community in streams ([Figure 10\)](#page-3-2) (Mamczarz 1970). In the River Tweed, UK, it is not common (Holmes & Whitton 1975), but occurs on the river bank of River Tees, UK (Holmes & Whitton 1977a) and occurs in the upper upstream of River Swale, Yorkshire, UK (Holmes & Whitton 1977b). It is again infrequent in River Tyne, UK (Holmes & Whitton 1981).

<span id="page-3-2"></span>

Figure 8. *Marchantia quadrata* on wet rock at edge of stream. Photo by Andy Hodgson, with permission.

<span id="page-3-3"></span><span id="page-3-0"></span>

Figure 9. *Marchantia quadrata* on rock at waterfall, Michigan, USA. Photo by Janice Glime.



Figure 10. *Marchantia quadrata* with archegoniophores, growing on soil. Photo by Hermann Schachner, through Creative Commons.

Lee and Greenwood (1976) reported that *Marchantia quadrata* ([Figure 1-](#page-1-2)[Figure 5\)](#page-2-2) was able to occupy calcareous waste deposits in the UK in areas where there were no natural calcareous substrata.

*Marchantia quadrata* ([Figure 1-](#page-1-2)[Figure 5](#page-2-2)) occurs in the travertine *Cratoneuron* ([Figure 11](#page-3-3)) association in the Lorraine River, Belgium, (de Sloover & Goossens 1984), in streams in Greece (Papp 1998), and at springs in the Tara river canyon and Durmitor area, Montenegro (Papp & Erzberger 2011).



Figure 11. *Cratoneuron filicinum*, a species associated with *Marchantia quadrata* on travertine rock. Photo by Hermann Schachner, through Creative Commons.

<span id="page-3-1"></span>Contrasting with these limestone habitats, Haupt (1926) reported *Marchantia quadrata* [\(Figure 1-](#page-1-2)[Figure 5\)](#page-2-2) on thin soil [\(Figure 10](#page-3-2)) over granitic rocks, particularly along stream banks. It tends to occur in drier situations than *Marchantia polymorpha* [\(Figure 12\)](#page-4-0) or *Conocephalum* [\(Figure 13](#page-4-1)[-Figure 14](#page-4-2)), but they can occur intermixed. Nevertheless, it can occur close to the water ([Figure 15](#page-4-3)-[Figure 17](#page-4-4)).



Figure 12. *Marchantia polymorpha* gemmae cups in Europe; *Marchantia quadrata* prefers drier conditions than does *M. polymorpha*. Photo by Michael Lüth, with permission.



Figure 15. *Marchantia quadrata* on stream bank. Photo by Scot Loring, through Creative Commons.

<span id="page-4-3"></span><span id="page-4-0"></span>

Figure 13. *Marchantia quadrata* with archegoniophores on wet canyon wall by stream at Hocking Hills, Ohio, USA. Note the *Conocephalum cf. salebrosum* at the bottom of the view, illustrating the presence of *Marchantia quadrata* in a higher zone above the water. Photo by Janice Glime.

<span id="page-4-4"></span><span id="page-4-2"></span><span id="page-4-1"></span>

Figure 14. *Marchantia quadrata* with archegoniophores stacked on canyon wall at Hocking Hills, Ohio, USA, growing next to *Conocephalum salebrosum*. Photo by Janice Glime.



Figure 16. *Marchantia quadrata* on wet rock. Photo by Andy Hodgson, with permission.



Figure 17. Wet *Marchantia quadrata* near falls at Tahquamenon Falls, Michigan, USA. Photo by Janice Glime.

In the Netherlands, *Marchantia quadrata* ([Figure 1](#page-1-2)- [Figure 5\)](#page-2-2) occurs on the **trilveen** (Kooijman & During 1989). The **trilveen** [\(Figure 18\)](#page-5-0) is a bog that is a rare, with thin, extremely soft "soil" and vegetation type with sedges and grass roots. It floats on water or soft mud and occurs in low moor areas such as peat meadows.



Figure 18. Trilveens in The Netherlands. Note the person pushing one across the water surface. Photo from Wikiwand, through Creative Commons.

<span id="page-5-0"></span>Keir Wefferling found it growing on dripping sandstone cliffs in Wisconsin, USA ([Figure 1](#page-1-2)[-Figure 5,](#page-2-2) [Figure 19\)](#page-5-1).

<span id="page-5-3"></span>

Figure 19. *Marchantia quadrata* (**bottom**) forming a zone above the base of a dripping cliff in Wisconsin, USA. Photo courtesy of Keir Wefferling.

<span id="page-5-4"></span><span id="page-5-1"></span>In Turkey *Marchantia quadrata* [\(Figure 1-](#page-1-2)[Figure 5\)](#page-2-2) occurs on moist calcareous rocks ([Figure 20\)](#page-5-2) of the subalpine zone (Şimşek *et al*. 2014).

<span id="page-5-2"></span>Figure 20. *Marchantia quadrata* growing among calcareous rocks. Photo by Michael Lüth, with permission.

I have also seen the species on a rock ledge of a cliff in New York, USA ([Figure 21](#page-5-3)). It can occur on rock and cavern walls [\(Figure 22](#page-5-4)[-Figure 26](#page-6-1)).



Figure 21. *Marchantia quadrata* on ledge in New York, USA. Photo by Janice Glime.



Figure 22. *Marchantia quadrata* on rocky bank at Tahquamenon Falls, Michigan, USA. Photo by Janice Glime.



Figure 23. *Marchantia quadrata* on calcareous rock. Photo by Michael Lüth, with permission.



Figure 24. *Marchantia quadrata* on rock in NW Iowa, USA. Associated mosses can help it to retain moisture. Photo by Janice Glime.

<span id="page-6-2"></span>

Figure 25. *Marchantia quadrata* with archegoniophores on rock. Photo by Michael Lüth, with permission.

<span id="page-6-3"></span><span id="page-6-0"></span>

Figure 26. *Marchantia quadrata* on a rock depression – a common habitat for the species. Photo by Oskar Gran, through Creative Commons.

<span id="page-6-1"></span>Others have found it in open areas on soil, as seen in these pictures by Michael Lüth ([Figure 27](#page-6-2)[-Figure 28](#page-6-3)).



Figure 27. *Marchantia quadrata* with archegoniophores, growing on open soil. Photo by Michael Lüth, with permission.



Figure 28. *Marchantia quadrata* with archegoniophores, growing on soil in the location shown above. Photo by Michael Lüth, with permission.

#### **Physiology**

Tyler *et al*. (1995) found that soluble phosphate was important to the occurrence of *Marchantia quadrata* [\(Figure 1-](#page-1-2)[Figure 5](#page-2-2)) on limestone soil. It produced 7 times as much biomass when phosphate was added to the soil. Perhaps this is due to the ability of the calcium carbonate of the limestone to be an effective binder of phosphate (Yanamadala 2005). Furthermore, the liverwort is likely to be phosphate limited without the high levels of phosphate. The mix of  $CaCO<sub>3</sub>$  and phosphate could also encourage certain bacteria, particularly nitrogen-fixing bacteria, that are beneficial to the liverwort. The reaction with limestone further releases water and  $CO<sub>2</sub>$ , the latter being a limiting factor in submersed plants:

2 H<sub>3</sub>PO<sub>4</sub> + 3 CaCO<sub>3(ag)</sub> 
$$
\rightarrow
$$
 Ca<sub>3</sub>(PO<sub>4</sub>)<sub>2(s)</sub> + 3 CO<sub>3</sub><sup>-2</sup> + H<sup>+</sup>  
2 H<sup>+</sup> + CO<sub>3</sub><sup>-2</sup>  $\rightarrow$  H<sub>2</sub>O<sub>(1)</sub> + CO<sub>2(d)</sub>

Fletcher (1982) reported that *Marchantia quadrata* [\(Figure 1](#page-1-2)-[Figure 5\)](#page-2-2) was among the *Marchantia* species from several areas that sustained no frost damage when other bryophytes suffered blackening, bleaching, or growth cessation in cultivation down to -5.5ºC. In nature, it can survive winter under the snow and ice in the 5-6 months of snow cover in the Keweenaw Peninsula, Michigan, USA [\(Figure 29\)](#page-7-1).

<span id="page-7-3"></span>

Figure 29. Snow covering *Marchantia quadrata* habitat at top of Manganese Falls, Keweenaw County, Michigan, USA. Photo by Janice Glime.

<span id="page-7-4"></span><span id="page-7-1"></span>Heat is less kind, but it can have reversible damage effects on *Marchantia quadrata* [\(Figure 1](#page-1-2)-[Figure 5\)](#page-2-2) (Weis *et al*. 1986). Mild heat treatment suppresses photosynthesis. More severe heat causes irreversible damage of PSII similar to that known in tracheophytes. Exposure to high but sublethal temperatures does not increase the heat stability of these liverworts, indicating an extremely low heat-hardening capacity.

#### **Adaptations**

<span id="page-7-0"></span>*Marchantia quadrata* [\(Figure 1](#page-1-2)[-Figure 5](#page-2-2)) has a thallus that is multiple cells in thickness [\(Figure 30](#page-7-2)[-Figure 31](#page-7-3)). The upper layer and the epidermis cells ([Figure 32](#page-7-4)) contain chloroplasts, but these are absent in the cells surrounding the pores (Walker & Pennington 1939). The thickness is likely to aid in moisture retention during drought periods.

<span id="page-7-5"></span><span id="page-7-2"></span>

Figure 30. *Marchantia quadrata* thallus section showing photosynthetic cells on top and scales hanging from the ventral side. Photo by Hermann Schachner, through Creative Commons.



Figure 31. *Marchantia quadrata* section showing distinctive photosynthetic layer on top. Rhizoids hang from the ventral surface. Photo by David Wagner, with permission.



Figure 32. *Marchantia quadrata* thallus showing epidermis with pores. Photo from Bioimages, through Creative Commons.

Rhizoids ([Figure 33](#page-7-5)) are known to create capillary spaces that conduct water in the **Marchantiales**. McConaha (1941) suggests that the more numerous rhizoids present in *Marchantia quadrata* [\(Figure 1-](#page-1-2)[Figure](#page-2-2)  [5](#page-2-2)) compensate for its less compact arrangement of the capillary system. It also does not have its capillary system over the wings of the thallus to the extent seen in *Marchantia s.s.* Thallus areolation in *M. quadrata* exposes a greater surface to water loss despite having pores that are able to achieve partial closure; there is little regulation of the transpiration.



Figure 33. *Marchantia quadrata* thallus cross section with scales and rhizoids projecting from the lower surface. Photo by Kristian Peters, with permission.

Like other *Marchantia* species, *M. quadrata* [\(Figure](#page-1-2)  [1](#page-1-2)-[Figure 5\)](#page-2-2) has both smooth and pegged rhizoids [\(Figure](#page-7-5)  [33](#page-7-5)) as well as appendaged scales ([Figure 33](#page-7-5)[-Figure 34\)](#page-8-0) on the lower surface (Cavers 1904). Presumably, these serve the same functions in conduction as those of *M. polymorpha* ([Figure 12](#page-4-0)).



<span id="page-8-0"></span>Figure 34. *Marchantia quadrata* ventral scale. Photo by Hugues Tinguy, with permission.

Like other species of *Marchantia*, *M. quadrata* [\(Figure 1-](#page-1-2)[Figure 5\)](#page-2-2) has air pores [\(Figure 35](#page-8-1)[-Figure 43\)](#page-9-0) in the thallus that permit more rapid gas exchange than the thallus epidermis does (Haupt 1926). In this species, the pore is barrel-shaped with cells in four or five tiers ([Figure](#page-8-2)  [38,](#page-8-2) [Figure 40,](#page-9-1) [Figure 43\)](#page-9-0) (Walker & Pennington 1939). The upper opening is always wide open ([Figure 40,](#page-9-1) [Figure](#page-9-2)  [41,](#page-9-2) [Figure 43](#page-9-0)), but the inner part is narrower and can be closed ([Figure 41](#page-9-2)-[Figure 43\)](#page-9-0). Each cell of the basal tier, referred to by Walker and Pennington as **motor cells**, has a papilla which projects freely inward. The papilla has a thinner wall than the remainder of the motor cell. Movements of the papillae are responsible for changes in the size of the opening.

<span id="page-8-2"></span><span id="page-8-1"></span>

Figure 35. *Marchantia quadrata* showing epidermis with pores. Photo by Jan-Peter Frahm, with permission.



Figure 36. *Marchantia quadrata* thallus portion showing pores. Photo by Kristian Peters.



Figure 37. *Marchantia quadrata* thallus showing pore viewed from ventral surface. Photo by David Wagner, with permission.



Figure 38. *Marchantia quadrata* thallus section showing air spaces, photosynthetic cells, and pore. Photo by David Wagner, with permission.



Figure 39. *Marchantia quadrata* pore showing cuticular ridge (grey). Photo by Hugues Tinguy, with permission.



Figure 40. *Marchantia quadrata* thallus section showing closed pore, photosynthetic layer, and purple ventral side. Photo by Hermann Schachner, through Creative Commons.

<span id="page-9-1"></span><span id="page-9-0"></span>

<span id="page-9-2"></span>Figure 41. *Marchantia quadrata* pore closing. Note that the motor cell on the right is not functioning, presumably due to injury. Image modified from Walker & Pennington 1939.



Figure 42. *Marchantia quadrata* pore closing. Image modified from Walker & Pennington 1939.



Figure 43. *Marchantia quadrata* thallus section showing pore and chamber beneath it with photosynthetic filaments. Photo by Hermann Schachner, through Creative Commons.

Growth occurs at the apical notch, which is covered by a small scale that is usually purplish [\(Figure 44](#page-9-2)[-Figure 45](#page-10-1)). The thallus can dry out or senesce while the reproductive branches continue to grow [\(Figure 46\)](#page-10-2). Red coloration on the thallus margins ([Figure 47\)](#page-10-3) is common in this species and could indicate that it has experienced stress.



Figure 44. *Marchantia quadrata* in Europe, showing purple covers of the apical growing region. Photo by Michael Lüth, with permission.



Figure 45. *Marchantia quadrata* in Europe, showing purple covers of the apical growing region. Photo by Michael Lüth, with permission.

<span id="page-10-1"></span><span id="page-10-0"></span>

<span id="page-10-2"></span>Figure 46. *Marchantia quadrata* archegoniophores and dying thallus, showing the ability of archegoniophores to persist even when the thallus is senescing or dying. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

<span id="page-10-3"></span>

Figure 47. *Marchantia quadrata* with red margins, indicating stress. Photo by Allen Norcross, with permission.

One feature that seems to lack documentation for liverworts, but present in *Marchantia quadrata* [\(Figure 1](#page-1-2)- [Figure 5](#page-2-2)), is the presence of scattered sclerotic cells in the ventral part of the thallus (Haupt 1926). These are elongated, thick-walled, dark brown, fiber-like cells with pointed ends. Their significance is not clear. Cavers (1904) suggests that their primary function is conduction and storage of water. These fibers are absent in the plants that grow in a moist atmosphere (Haupt 1926).

Isolated mucilage cells can be found in all parts of the thallus, but mucilage canals are absent (Haupt 1926). Starch grains seem only to accumulate in the older female receptacles where they presumably are available to the growing sporophytes. Oil globules occur in the apical region, particularly in the epidermal cells, and in the epidermis of the receptacles.

#### **Reproduction**

*Marchantia quadrata* ([Figure 1-](#page-1-2)[Figure 5\)](#page-2-2) is usually considered to be **dioicous** (Haupt 1926). However, Haupt (1926) also found a few **monoicous** plants, comprising about 1% of the material studied. Zheng and Shimamura (2022) furthermore noted that dioicous plants are known to be widely distributed in the temperate boreal region and monoicous plants are usually found in the Arctic (Schuster 1972, 1985, 1992; Long & Crandall-Stotler 2020). Are these different races, or different expression of genes in the cold Arctic with its long summer days?

However, all the Japanese *M. quadrata* plants that Zheng and Shimamura (2022) examined and found during fieldwork were **monoicous**. Because the growing season of archegoniophores and antheridiophores is different and the archegoniophores do not grow unless fertilization is successful (Haupt 1926) it is easy to falsely conclude that one sex is absent in the population.

In spring in Japan, thalli with young antheridiophores arise from the apex of the ventral side of previous thalli with a well-stalked female receptacle bearing sporophytes Zheng and Shimamura (2022). In summer, a new thallus with a new archegoniophore occurs in the same way from the underside of the apex of the previous thalli with a wellstalked male receptacle and the oldest archegoniophore withers after spore dispersal. That is, each time a new branch is formed, the sexuality alternates. Only by following the same population throughout the year can the true sexuality condition be determined.

Usually the antheridia are produced on a separate stalk, the **antheridiophore** [\(Figure 48-](#page-11-0)[Figure 50\)](#page-11-1), and archegonia are produced on **archegoniophores** ([Figure 51](#page-11-2)-[Figure 58\)](#page-12-0). When the plants are **monoicous**, antheridia occur on the upper surface of the anterior portion of the receptacle and the archegonia occur on the under side of the posterior portion (Haupt 1926). Haupt, presumably in North America, found that antheridia begin to appear in late spring, with archegonia developing somewhat later in early summer.



Figure 48. *Marchantia quadrata* antheridiophores. Photo from Bioimages, through Creative Commons.

<span id="page-11-0"></span>

Figure 49. *Marchantia quadrata* antheridiophores. Photo from Bioimages, through Creative Commons.

the plants expressed sexual structures; in 18 hours of light this increased to 80%. Light of 16.1-87.6 lux was suitable for gametangia development. However, when the temperature was dropped to 10ºC in 18 hours light, the plants exhibited few sexual structures and had slow growth. These were even more limited at both 10ºC and 21ºC in 6 hours light. This species is, however, mostly influenced by photoperiod, operative within a somewhat broad temperature range (Longton 1990).

Both sexual organs continue to form during the entire growing season, with young archegonial receptacles in northern New York, USA, appearing as late as the end of September (Haupt 1926). On 24 September, Haupt observed that nearly all of the plants had the same sexual condition. The male nucleus was within the egg and in contact with the egg nucleus, but not yet fused. These archegonial receptacles overwinter with sporogenous tissue that has just differentiated. In the spring, growth of the sporophytes continues and the female receptacle stalk continues growth. In this location, the spores mature in June.



<span id="page-11-2"></span>

Figure 50. *Marchantia quadrata* antheridiophores. Photo from Bioimages, through Creative Commons.

<span id="page-11-1"></span>Benson-Evans (1964) reported that in the UK *Marchantia quadrata* ([Figure 1-](#page-1-2)[Figure 5](#page-2-2)) is a long-day plant for sexual reproduction. In 16 hours of light, 66% of

Figure 51. *Marchantia quadrata* with developing archegoniophores. Photo by Hermann Schachner, through Creative Commons.



Figure 52. *Marchantia quadrata* with developing archegoniophores. Photo by Claire Halpin, with permission.



Figure 53. **Marchantia quadrata** with developing archegoniophore. Photo by Hermann Schachner, through Photo by Hermann Schachner, through Creative Commons.



Figure 54. *Marchantia quadrata* with expanding archegoniophores. Photo by Jan-Peter Frahm, with permission.

<span id="page-12-0"></span>

Figure 55. *Marchantia quadrata*, showing numerous fertile plants at Pictured Rocks, Michigan, USA. Photo by Janice Glime.



Figure 56. *Marchantia quadrata* young (at tip) and older archegoniophores in Europe. Photo by Michael Lüth, with permission.



Figure 57, *Marchantia quadrata* with extended archegoniophores. Note white scales showing at the margins. Photo by Hermann Schachner, through Creative Commons.



Figure 58. *Marchantia quadrata* with mature archegoniophores, showing how numerous they can be. Photo by Michael Lüth, with permission.

When the sporangia mature, they protrude from the archegonial head ([Figure 59](#page-13-0)[-Figure 63\)](#page-13-1). They burst and elaters wiggle among the spores [\(Figure 64](#page-13-2)-[Figure 65\)](#page-14-8) in response to moisture changes, in some cases helping the spores to exit the capsule, but in others entangling them in clusters of tangled elaters.



Figure 59. *Marchantia quadrata* with mature archegoniophores. Photo by Michael Lüth, with permission.

<span id="page-13-0"></span>

Figure 60. *Marchantia quadrata* mature archegoniophores with green thalli in Europe. Photo by Michael Lüth, with permission.

<span id="page-13-2"></span><span id="page-13-1"></span>

Figure 61. *Marchantia quadrata* archegoniophores with emerging sporangia. Photo by Michael Lüth, with permission.



Figure 62. *Marchantia quadrata* mature archegonial head with sporangia. Photo by Des Callaghan, with permission.



Figure 63. *Marchantia quadrata* archegoniophore with emerging sporangia and elaters. Photo by Bob Klips, with permission.



Figure 64. *Marchantia quadrata* spores and elaters. Photo by Hermann Schachner, through Creative Commons.

<span id="page-14-3"></span><span id="page-14-2"></span>

<span id="page-14-8"></span><span id="page-14-4"></span>Figure 65. SEM of *Marchantia quadrata* distal spore wall. Photo by William T. Doyle, with permission.

<span id="page-14-5"></span>Unlike other members of the **Marchantiaceae**, *M. quadrata* [\(Figure 1](#page-1-2)[-Figure 5](#page-2-2)) has no gemmae (Boisselier-Dubayle & Bischler 1997; Zheng *et al*. 2020). Nevertheless, members of an individual colony were genetically identical, suggesting vegetative reproduction was important, achieved by growth and division of the thalli. There was little indication of any genetic exchange between colonies growing in proximity.

#### **Fungal Interactions**

<span id="page-14-6"></span><span id="page-14-0"></span>Haupt (1926) reported intracellular fungi in the lower part of the *Marchantia quadrata* ([Figure 1](#page-1-2)-[Figure 5](#page-2-2)) thallus (see also Golenkin 1902). These occur mostly along the median line and are more abundant in older tissues. This fungal zone frequently occupies one-half to two-thirds the thickness of the thallus, sometimes reaching the air chambers. In the ventral region, the hyphae form parallel strands that extend longitudinally. Above this area they form compact tangled masses inside the shorter thallus cells.

#### **Biochemistry**

<span id="page-14-7"></span><span id="page-14-1"></span>Gorham (1977) reported the presence of lunularic acid in all parts of *Marchantia quadrata* ([Figure 1](#page-1-2)[-Figure 5\)](#page-2-2). This presence was greatest in continuous light. Gorham suggested that either the lunularic acid was not inhibited in continuous light or the inhibition was overcome by products of photosynthesis.

König *et al*. (1996) reported that the main constituent of a southern German chemotype of *Marchantia quadrata* [\(Figure 1](#page-1-2)-[Figure 5\)](#page-2-2) is the labile sesquiterpene hydrocarbon germacrene C. These researchers also observed several rare ent-sesquiterpenes as major constituents.

Asakawa *et al*. (1997) reported a number of sesquiterpenes and the cyclic bis(bibenzyls) riccardin B and neomarchantin A from *Marchantia quadrata* [\(Figure 1](#page-1-2)- Figure 5[\).](#page-2-2) 

#### *Marchantia treubii*

(syn. = *Marchantia sciaphila*)

#### **Distribution**

Siregar *et al*. (2013) reported on *Marchantia treubii* from Sumatra. This species is among the most common *Marchantia* species on Mount Sibayak, found from lowland to high altitude. It is relatively widespread in Indonesia (Sumatra, Java, Lesser Sunda Island), Borneo, and Malaysia (Bischler-Causse 1989; Chuah-Petiot 2011).

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

*Marchantia treubii* occurs in the spray of waterfalls in the tropics (Ruttner 1955). *Marchantia treubii* occurs on soil and rocks in open places and semi-shaded places in Indonesia (Siregar *et al*. 2013; Haerida 2017). Raihan *et al*. (2018) reported that this liverwort occurs almost everywhere on rocks at their study area at Peucari Bueng Jantho Waterfall in the Aceh Besar District of Indonesia.

Azwir *et al*. (2022) reported its environmental parameters from Mesjid Raya in Indonesia. The site was humid, with *p*H ranging 4.9-7.3 (mean 6.3) and a low light intensity of 0.07-0.09 lux, mean of 0.08 lux. Since the light intensity also affects the temperature and humidity, this indicates lower temperatures and higher humidity in its habitat.

#### **Adaptations**

Most of the adaptations described for other species of *Marchantia* apply here. *Marchantia treubii* from Indonesia had purplish lines on the thallus and fine hair at the edge (Raihan *et al.* 2018). I was unable to find much specific information on this species.

#### **Reproduction**

Fritsch (1991) reported a chromosome count of n=9 for *Marchantia treubii*. It is **dioicous** (Siregar *et al*. 2013). Raihan *et al.* (2018) found *Marchantia treubii* with gemmae cups as well as sporophytes in Indonesia, exhibiting female receptacles with 3-5 lobes.

#### **Summary**

*Marchantia quadrata* was classified in the genus *Preissia* and might return there. It lacks gemmae, but occurs in similar habitats to some of the *Marchantia* species. Its distribution is similar (Australia, Europe, Northern and Southern Asia, Central America, North America, Oceania, and South America). It occurs on wet rocks and soil of stream banks, waterfalls, and dripping cliffs, including limestone. It benefits from phosphates, especially on limestone. It survives winter under the snow, but does not do well in high temperatures. Its adaptations are similar to those of other *Marchantia* species, with thick thallus, pores, photosynthetic chambers, rhizoids that either anchor or provide capillary spaces for conduction, and scales that help move and conserve water.

*Marchantia treubii* occurs in a small, tropical portion of Asia. It is best known from waterfalls, but in some areas of Indonesia it is the most common liverwort on the mountain. It is dioicous and has gemmae.

#### <span id="page-15-0"></span>**Acknowledgments**

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