

CHAPTER 1-23

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 1

TABLE OF CONTENTS

Marchantiaceae	1-23-3
<i>Marchantia</i>	1-23-3
<i>Marchantia berteroana</i>	1-23-4
Distribution	1-23-4
Aquatic and Wet Habitats	1-23-5
Physiology	1-23-6
Adaptations	1-23-7
Reproduction	1-23-7
Interactions	1-23-9
Fungal Interactions	1-23-9
Biochemistry	1-23-9
<i>Marchantia debilis</i>	1-23-10
Distribution	1-23-10
Aquatic and Wet Habitats	1-23-10
Adaptations	1-23-12
Reproduction	1-23-13
Biochemistry	1-23-13
<i>Marchantia emarginata</i>	1-23-13
Distribution	1-23-13
Aquatic and Wet Habitats	1-23-14
Adaptations	1-23-15
Reproduction	1-23-16
Fungal Interactions	1-23-17
Biochemistry	1-23-18
Culturing	1-23-19
<i>Marchantia inflexa</i>	1-23-19
Distribution	1-23-19
Aquatic and Wet Habitats	1-23-20
Physiology	1-23-21
Adaptations	1-23-22
Reproduction	1-23-23
Interactions	1-23-27
<i>Marchantia miqueliana</i>	1-23-27
Distribution	1-23-27
Aquatic and Wet Habitats	1-23-28
Adaptations	1-23-28
Biochemistry	1-23-28
<i>Marchantia paleacea</i>	1-23-28
Distribution	1-23-28
Aquatic and Wet Habitats	1-23-29
Physiology	1-23-31
Adaptations	1-23-33
Reproduction	1-23-34
Interactions	1-23-37
Biochemistry	1-23-39
Culturing	1-23-39
<i>Marchantia pappeana</i>	1-23-39
Distribution	1-23-39
Aquatic and Wet Habitats	1-23-40
Reproduction	1-23-41
Fungal Interactions	1-23-41

Biochemistry	1-23-42
Summary	1-23-42
Acknowledgments	1-23-42
Literature Cited	1-23-42

CHAPTER 1-23

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: MARCHANTIACEAE, PART 1



Figure 1. *Marchantia debilis* on emergent rocks in Madagascar. Photo courtesy of Catherine Reeb.

Marchantiaceae

Marchantia

Marchantia is widespread in the world. In the western Cascade Mountains, Oregon, USA, it is a pioneer **riparian** (relating to wetlands adjacent to rivers and streams) genus (Campbell & Franklin 1979). Several species in this genus are associated with wet habitats, with some occasionally becoming submersed.

Like most of the older taxa, this genus has a history of species synonyms (Bischler-Causse 1993). For example, of the 28 species described in Africa, Bischler-Causse reduced them to only 6, although another 8 remained unresolved.

Zheng *et al.* (2020a) have suggested that the morphology of the gemmae can be used to help in separation of the taxa, and that molecular analyses support these separations.

Bischler-Causse (1993) suggested that dispersal of at least some of the species seems to be limited by temperature extremes, but the species also require water throughout the year, free space, and light, thus limiting their success in much of the dry parts of the African continent. This distribution is further limited by the low level of sexual reproduction, relying on vegetative multiplication – a means that is more limited in dispersal distance.

Although *Marchantia polymorpha* (Figure 2) is by far the liverwort of choice, other species have been important

in unravelling the genetic and evolutionary history of liverworts. Marks *et al.* (2019a,b) presented the genome assembly for *Marchantia inflexa* (Figure 3-Figure 4) and found evidence suggesting that dehydration tolerance may be related to sex-specific genes in *Marchantia*. They found that the genes on the sex chromosomes experience greater diversifying selection than do the autosomal and organellar genes.



Figure 2. *Marchantia polymorpha* at tree base on bank of small river in Pfälzer Wald, Germany. Photo courtesy of Michael Lüth.



Figure 3. *Marchantia inflexa* females, a species where dehydration tolerance may be related to sex-specific genes. Photo by Amelia Merced, with permission.



Figure 4. *Marchantia inflexa* with gemmae. Photo by Alan R. Franck, through Creative Commons.

Ahmad (1981) described the historical studies on spore germination and gametophyte development in *Marchantia*.

Marchantia berteriana (Figure 5-Figure 7)

(syn. = *Marchantia cephaloscypha*, *Marchantia tabularis*)

Campbell (1965) reviewed some of the history of the nomenclature for this species. Another species recorded for New Zealand and described by Stephani (1883), namely *M. cephaloscypha*, is considered by Evans after examination of an original specimen to correspond with *M. berteriana* (Evans 1917). In Columbia, Herzog (1934) described the variety *polylepida*, but that is now considered to be *M. berteriana* as well.

Distribution

Marchantia berteriana (Figure 5-Figure 7) is known in Australia, New Zealand (Campbell 1965; Wikipedia 2021), Southern Africa (Perold 1995; Lüth & Schafer-Verwimp 2004; Phephu 2012a,b), South America (Costa Rica to the Antarctic Peninsula) (Hassel de Menendez 1962; Campbell 1965; Lüth & Schafer-Verwimp 2004), Antarctica (Davey 1997), and non-continental locations such as Papua New Guinea, Java, New Caledonia, and various smaller islands (Driessen 2009; Wikipedia 2021). Phephu (2012a) noted that this species is prevalent in the winter-rainfall region of South Africa, but it also grows in regions that receive summer rain in KwaZulu-Natal, Mpumalanga and Limpopo provinces.



Figure 5. *Marchantia berteriana* thallus. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 6. *Marchantia berteriana* thallus. Photo by Sarah Lloyd, with permission.



Figure 7. *Marchantia berteriana* vegetative thallus with gemmae cups. Photo by Clive Shirley, Hidden Forest, with permission.

Aquatic and Wet Habitats

Marchantia berteriana (Figure 5-Figure 7) lives in constantly damp, shaded areas (Figure 8) (Wikipedia 2021), including fresh water, waterfall splash zones, forest floors, and streambanks (Phephu 2012a,b). The species is widespread in New Zealand, especially near hot springs, and in southern Africa in swampy areas, **kloofs** (steep-sided wooded ravine or valley in Africa), gorges, and burned areas (Campbell 1965; Perold 1995). Li Zhang (pers. comm. 4 August 2022) found it growing in peatlands in Chile (Figure 9). It also occurs in peatlands in Colombia (Campos 2014). On the Juan Fernández Islands, it grows in expansive colonies on the mountain tops (Figure 10-Figure 11) where clouds most likely maintain its needed moisture levels.



Figure 8. *Marchantia berteriana* thallus growing on a damp soil bank. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 9. *Marchantia berteriana* in peatland in Puerto Williams, Chile. Photo courtesy of Li Zhang.



Figure 10. *Marchantia berteriana* soil habitat on Alejandro Selkirk Island, Juan Fernández Archipelago, Chile. Photo by Pato Novoa, through Creative Commons.



Figure 11. *Marchantia berteriana* habitat on Alejandro Selkirk Island, Juan Fernández Archipelago, Chile. Photo by Pato Novoa, through Creative Commons.

In geothermal areas in the Antarctic, *M. berteroa* (Figure 5-Figure 7) can occur at surface temperatures of 25-35°C and subsurface temperatures of 50-60°C, although these underground temperatures have no direct effect on the bryophytes (Convey & Lewis Smith 2006). Lewis Smith (2005a,b) found that on Deception Island in the South Shetland Islands, a geothermal gully included *Marchantia berteroa* (Figure 5-Figure 7) as one of the colonizers, forming a peripheral zone at the margin of the primary moss vegetation, living on fine moist compacted clay. He attributed its abundance to the "copiously produced and widely dispersed gemmae."

Halloy (1991) reported *Marchantia berteroa* (Figure 5-Figure 7) from heated areas (Figure 12) in the Andes, at 6000 m asl. These communities comprised the highest elevation of the known autotrophic communities on the planet.



Figure 12. Geothermal fissure and *Sphagnum*; heated areas in the Andes can be suitable habitats for *Marchantia berteroa*. Photo from a geothermal vent in Iceland, by Janice Glime.

Despite its seeming preference for wet habitats, it is a colonizer on soil following fire in Tasmanian mixed forests (Duncan & Dalton 1982) and also in southern Africa (Perold 1995). The rapid germination of the spores and rapid development of the gametophyte gives the species an advantage in this habitat. Brasell and Mattay (1984) found it as a colonizer in burned *Eucalyptus* forest (Figure 13) in Tasmania, where it accumulated a high concentration of potassium. In these forests, N, P, K, and Ca, but not Mg, all decreased with time following the fire. Brasell *et al.* (1986) found that *Marchantia berteroa* contributed significantly to nitrogen fixation in burned sites of southern Tasmania, greatly exceeding rates of bryophytes in unburned forests.



Figure 13. *Eucalyptus* forest at Sherbrooke, Victoria, Australia – fire-adapted forest where *Marchantia berteroa* often appears after fire. Photo by Patche99z, through public domain.

Duncan and Dalton (1982) showed that *Marchantia berteroa* spores germinated well on burned ground. The protonemal growth is more rapid than that of the non-colonizing species, giving the *M. berteroa* a chance to establish before other, more competitive species arrive.

Phephu (2012a) considers *Marchantia berteroa* to be important in nutrient cycles and erosion control, thus stabilizing the soil.

Physiology

Davey (1997) used measurements of respiration, photosynthesis, irradiance, and temperature to model the year-round net productivity of *Marchantia berteroa* (Figure 5-Figure 7), estimating a yearly net productivity of $823 \pm 75 \text{ mg C g}^{-1}$ ash-free dry weight. Desiccation was highly adverse to the thalli (Figure 14). Below a water content of 12 g g^{-1} ash-free dry weight the photosynthetic capacity was reduced. Recovery was only ca. 10% after dehydration and rehydration. Freezing also caused great photosynthetic reduction, although the model indicated that this species should be able to photosynthesize at sub-zero temperatures. Davey suggested that the photosynthetic capacity and freezing tolerance were likely to be seasonal.



Figure 14. *Marchantia berteroa* showing dying edges, suggesting drought damage. Note its low-lying habit on the mosses. Photo by Andrew Hodgson, with permission.

Despite that fact that the model indicates that freezing causes a great reduction in photosynthesis, the model suggests that photosynthesis at sub-zero temperatures is, nevertheless, likely (Davey 1997). It is suggested that seasonality in the photosynthetic capacity and the survival of these plants subjected to sub-zero temperatures might be important. However, their distribution is likely to be limited by available moisture.

Green and Lange (1995) found that the CO_2 compensation point is much lower for *Marchantia berteroa* (Figure 5-Figure 7) in 2% oxygen than for the other bryophytes they tested, and that the compensation points rise with a rise in temperature, resulting in inhibition (Figure 15). Photosynthesis at 21% oxygen [usual atmospheric oxygen concentration on Earth (National Geographic 2022)] is depressed compared to that at 2% oxygen (Figure 16), with the depression increasing at higher temperatures.

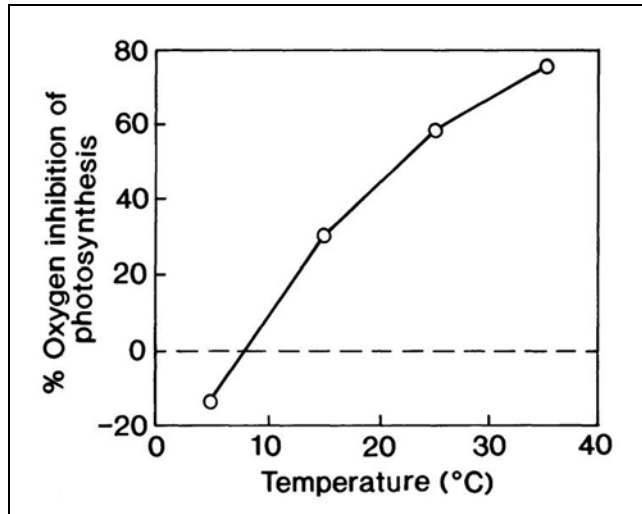


Figure 15. Temperature effect on oxygen inhibition in *Marchantia berteroana*. Modified from Green & Lange 1995.

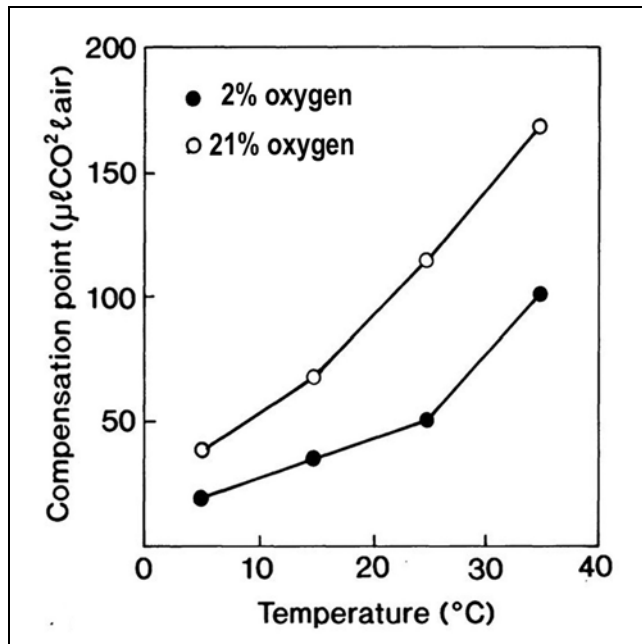


Figure 16. Temperature effect on CO₂ compensation point in *Marchantia berteroana*. Modified from Green & Lange 1995.

Adaptations

Marchantia berteroana (Figure 5-Figure 7) has scales on the lower surface, a common feature of the genus, but in this case they extend nearly to the margins (Phephu 2012a, b). These may be hyaline or colored reddish-brown (Campbell 1965). The thallus itself helps to maintain its moisture by its low-lying habit (Figure 14) that keeps it closer to the water in the soil and by reducing evaporation from the soil.

Like other members of *Marchantia*, the thalli have apical growing tips that are covered by scales (Figure 17). Presumably, these protect the important growing region from desiccation. When the older thallus dries out and dies, these apical areas can still retain living cells that can resume growth when favorable conditions return.



Figure 17. *Marchantia berteroana* thallus showing apical growing regions with apical scales covering them. Photo by Jan-Peter Frahm, with permission.

Reproduction

Marchantia berteroana (Figure 5-Figure 7) is **dioicous**, with a chromosome number of $n=9$ (Perold 1995; Phephu 2012a).

Males (Figure 18) are a bit larger than females (Figure 19-Figure 23) (Campbell 1965). In New Zealand, the antheridiophores (Figure 18) appear in August, followed in September by the archegoniophores (Figure 19-Figure 23).



Figure 18. *Marchantia berteroana* antheridiophore heads. Photo by Tom Thekathyl, with permission.



Figure 19. *Marchantia berteroana* with young archegoniophores. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 20. *Marchantia berteroana* with young archegoniophores before elongation. Photo by Clive Shirley, Hidden Forest, with permission.



Figure 23. *Marchantia berteroana* with elongated archegoniophores, demonstrating how large a population can become. Photo by Pato Novoa, through Creative Commons.



Figure 21. *Marchantia berteroana* with developing archegoniophores. Photo by Pato Novoa, through Creative Commons.



Figure 22. *Marchantia berteroana* mature archegonial head before sporangia are mature. Photo by Andrew Hodgson, with permission.



Figure 24. *Marchantia berteroana* archegoniophore heads with emerging open sporangia. Photo by Tom Thekathyl, with permission.

Markham *et al.* (1978) found that there is a "dramatic" change in flavonoid pattern of *Marchantia berteroana* (Figure 5-Figure 7) that accompanies sexual reproduction. Is this a consequence or an adaptation? It would be interesting to know the role of the change in compounds in reproduction. Markham and Porter (1975, 1978) found that the aurone aureusidin 6-O-glucuronide occurs in antheridiophores (Figure 18) of at least two species of *Marchantia*, one of which is *M. berteroana*. It is unknown from any other organ of the liverworts. In flowering plants it gives brighter yellow colors to the flowers (Nakayama 2022). Markham and Porter suggested parallel evolution in bryophytes and flowering plants, although the compound is not common even in flowering plants.

The sporophyte begins development the following spring, continuing through the summer (Phephu 2012a). Once it matures, its stalk elongates by absorbing water, causing the cells to stretch. This causes the sporangia to protrude from the archegonial head (Figure 24-Figure 25). When the sporangium breaks open, it exposes the spores and elaters (Figure 25). Wiggling of the elaters in response to humidity changes helps to disperse the spores. Once the spores are dispersed, the fragile stalk disintegrates.



Figure 25. *Marchantia berteriana* mature sporangia with elaters protruding. Photo by Tom Thekathyl, with permission.

On the Falkland Islands, *Marchantia berteriana* (Figure 5-Figure 7) forms extensive patches several meters in diameter, from sea level to mountain tops (Duckett *et al.* 2012). Although it seems typical for females of this species to dominate elsewhere (Garcia-Ramos *et al.* 2007; Groen *et al.* 2010a), these populations produced males and females in about equal proportion. Perhaps this sex ratio is regulated by environmental/climatic conditions?

We know that gemmae (Figure 26-Figure 27) are produced when the sexual reproduction is inactive. High humidity suppresses the production of these gemmae cups, but high temperatures (ca. 15°C) promote greater production of the cups (Chopra & Kumra 1988). Gemmae, and probably at times spores, are dispersed by water (Phephu 2012a).



Figure 26. *Marchantia berteriana* thallus forming a rosette, with gemmae cups. Photo by Tom Thekathyl, with permission.

Scott (1963) observed that plants of *Marchantia berteriana* (Figure 5-Figure 7) failed to produce gemmae cups (Figure 26-Figure 27) in New Zealand when pots were covered with glass or polyethylene sheets. He experimented with plants growing in a saturated atmosphere and demonstrated that it was indeed moisture that inhibited the development of gemmae cups. This

behavior permits the liverwort to divert its resources to sexual reproduction at a time when conditions are most favorable for that type of reproduction.



Figure 27. *Marchantia berteriana* thallus showing distinct pores and gemma cups. Photo by Tom Thekathyl, with permission.

Interactions

Marchantia berteriana (Figure 5-Figure 7) has close associations with at least several other organisms. Meeks (2018) reported associations with **Cyanobacteria**. Brasell *et al.* (1986) found that *Marchantia berteriana* exhibited high rates of acetylene reduction, indicating a high rate of nitrogen fixation, in populations from burned sites in southern Tasmania. **Cyanobacteria** are important contributors to nitrogen fixation. Activity was considerably greater than that for the same species when they occurred in the adjacent undisturbed forest. There was no significant relationship with temperature, moisture, organic matter, nitrogen, or phosphorus in these associations. I found no studies regarding nitrogen fixation association in wet habitat populations, but I would expect it to occur there as well.

Fungal Interactions

Baylis (1970) found that *Marchantia berteriana* (Figure 5-Figure 7) formed mycorrhizal associations on unsteamed phosphorus-deficient soil. Baylis suggested that the fungi entered through the rhizoids. Johnson (1977) demonstrated that infection by members of the **Enogonaceae** in a New Zealand forest occurred in the lower part of the thallus and in rhizoids in *Marchantia berteriana*. These endophytes seemed to lack specificity, occurring in a variety of the tracheophytes tested. It is likely that many associations remain to be identified.

Biochemistry

This species does not have the large number of biochemical studies reported for some of the other *Marchantia* species. Markham and Porter (1975) provided early reports on the flavones isoscutellarein and hypolaetin 8-glucuronides in *Marchantia berteriana* (Figure 5-Figure 7). The composition and concentration of these change in response to seasonal changes and reproductive stage of the plant. Acacetin and its glycosides are absent when

gametangia are present (Markham *et al.* 1978). Instead, during the sexually active stage, the predominant flavonoids are 8-hydroxyapigenin and 8-hydroxyluteolin glycosiduronic acids. These latter flavonoids are absent during the stage of asexual reproduction when the acacetin and its glycosides achieve their most active concentrations.

Asakawa and Campbell (1982) found that the major components of terpenoids and bibenzyls in *M. berteriana* (Figure 5-Figure 7) are cuparene and (–)-2-hydroxycuparene. Cuvertino-Santoni *et al.* (2017) described a number of the volatile constituents.

***Marchantia debilis* (Figure 1, Figure 28-Figure 32)**

(syn. = *Marchantia chevalieri*)

Distribution

Marchantia debilis (Figure 28-Figure 32) is widespread in tropical Africa (Pócs & Lye 1999), where it is common north to south in the drier areas (Reeb *et al.* 2018).



Figure 28. *Marchantia debilis* on rock near water in Madagascar. Photo courtesy of Catherine Reeb.



Figure 29. *Marchantia debilis* in Madagascar, with archegoniophore. Photo courtesy of Catherine Reeb.



Figure 30. *Marchantia debilis* in Madagascar, showing dieback at the base of the thallus while the tips continue to grow. Photo courtesy of Catherine Reeb.



Figure 31. *Marchantia debilis* in Madagascar, showing numerous, overlapping thalli that help to conserve water. Photo courtesy of Catherine Reeb.



Figure 32. *Marchantia debilis* in Madagascar, growing on wet soil and rocks. Photo courtesy of Catherine Reeb.

Aquatic and Wet Habitats

Marchantia debilis (Figure 28-Figure 32) is more closely associated with water than some of the other species of *Marchantia* included here. It occurs on the edges of water in habitats like waterfalls, slow rivers (Figure 33-Figure 34), and ponds, on damp soil or rocks,

and sometimes experiences flooding, but it also occurs on terrestrial banks in both shaded and exposed areas (Reeb *et al.* 2018).



Figure 33. *Marchantia debilis* habitat on the riverbank in Madagascar. Photo courtesy of Catherine Reeb.



Figure 34. *Marchantia debilis* with *Riccia* on a riverbank in Madagascar. Photo courtesy of Catherine Reeb.

Hodgetts *et al.* (1999) similarly reported *Marchantia debilis* (Figure 28-Figure 32) from flushed rocks (Figure 35-Figure 36) in southern Africa. They are joined in this environment by the liverwort *Asterella bachmannii* (Figure 37), the mosses *Bryum alpinum* (Figure 38) and *Philonotis* spp. (Figure 39), and the hornworts *Anthoceros* spp. (Figure 40) and *Phaeoceros carolinianus* (Figure 41). *Marchantia debilis* also occurs on the soil and mud on river- and streambanks.



Figure 35. *Marchantia debilis* on rocks along riverbank in Madagascar. Photo courtesy of Catherine Reeb.



Figure 36. *Marchantia debilis* on rocks along riverbank in Madagascar. Photo courtesy of Catherine Reeb.



Figure 37. *Asterella bachmannii*, an associate of *Marchantia debilis* on flushed rocks in southern Africa. Photo by Ricky Taylor, through Creative Commons.



Figure 38. *Bryum alpinum*, an associate of *Marchantia debilis* on flushed rocks in southern Africa. Photo by Claire Halpin, with permission.



Figure 39. *Philonotis fontana*; several species of *Philonotis* associate with *Marchantia debilis* on flushed rocks in southern Africa. Photo by Claire Halpin, with permission.



Figure 40. *Anthoceros* sp., an associate of *Marchantia debilis* on flushed rocks in southern Africa. Photo by Bramadi Arya, through Creative Commons.



Figure 41. *Phaeoceros carolinianus*, an associate of *Marchantia debilis* on flushed rocks in southern Africa. Photo by Hermann Schachner, through Creative Commons.

Leonard (1994) found that *Marchantia debilis* (Figure 28-Figure 32) occurred on the periodically flooded parts of sandstone cliffs near Yanonge, Zaire, typically with *Garckea flexuosa* (Figure 42).

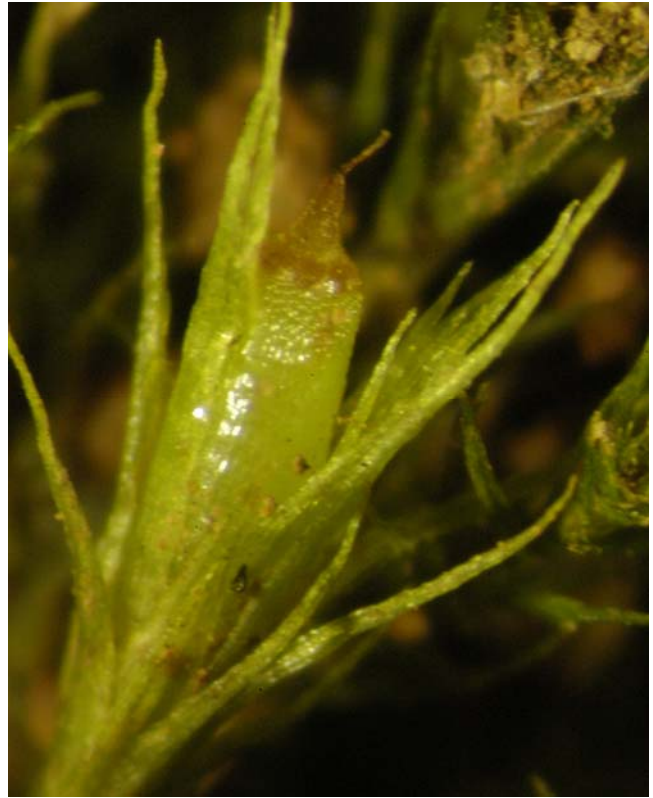


Figure 42. *Garckea flexuosa*, an associate of *Marchantia debilis* in the flooded parts of sandstone cliffs in Zaire. Photo by Manju C. Nair, through Creative Commons.

Adaptations

The adaptations of *Marchantia debilis* (Figure 28-Figure 32) involve the same structures as in other species of *Marchantia*. They have large air pores bordered with 5-8 rings of cells, with half projecting above the epidermis and half below into the photosynthetic air space (Reeb *et al.* 2018). The ventral scales occur in four rows and do not cover more than 30-50% of the thallus. These are purple, at least in the median portion of the thallus.

The thalli can grow over mosses (Figure 43), providing them with a water-retaining sponge that keeps them moist longer than just soil.



Figure 43. *Marchantia debilis* in Madagascar, growing with mosses that can help to retain moisture. Photo courtesy of Catherine Reeb.

Reproduction

As is typical for species of *Marchantia*, *Marchantia debilis* (Figure 28-Figure 32) is **dioicous** (Reeb *et al.* 2018). I have not found information on stimuli needed to produce archegoniophores (Figure 44-Figure 45) or antheridiophores or what their seasonal behavior is. Gemmae (Figure 46) serve as effective means of asexual reproduction.



Figure 44. *Marchantia debilis* with an archegoniophore, in Madagascar. Photo courtesy of Catherine Reeb.



Figure 45. *Marchantia debilis* archegoniophore in Madagascar, showing large pores. Photo courtesy of Catherine Reeb.



Figure 46. *Marchantia debilis* with gemmae cups, in Madagascar. Photo courtesy of Catherine Reeb.

Biochemistry

Anchang *et al.* (2016) reported a new methanol extract, marchantinquinone-l'-methyl ether, from *Marchantia debilis* (Figure 28-Figure 32). In addition it had three known bis-bibenzyls. Asakawa (2021) noted that *Marchantia debilis* produces large quantities of marchantin-type bis-bibenzyls. Anchang and Simonsen (2019) reported that extracts from both wet and dry liverworts were able to inhibit the bacteria *Staphylococcus aureus* and *Dermatophilus congolensis*, and the fungus *Aspergillus flavus*. On the other hand, the bacteria *Pseudomonas aeruginosa* and *Bacillus* spp. were inhibited by extracts from dry, but not wet, *Marchantia debilis*. This suggests that at least one of the inhibitory substances must be produced in response to desiccation.

Yongabi *et al.* (2016) reported that petroleum extracts from *Marchantia debilis* (Figure 28-Figure 32) could be used to treat at least some of the bacteria responsible for diabetic bacterial foot infections. This product has been marketed as BryoCreamTM. It had a 90% cure rate in three weeks.

Marchantia emarginata (Figure 47-Figure 53)

(syn. = *Marchantia palmata*, *Marchantia sumatrana*)

The taxonomic relationships of *Marchantia emarginata* (Figure 47-Figure 53) have recently been evaluated in India (Singh & Singh 2013) and Japan (Zheng & Shimamura 2021, 2022a).



Figure 47. *Marchantia emarginata* with enlarged terminal buds. Photo by Taiwan Mosses, through Creative Commons.

Distribution

Marchantia emarginata (Figure 47-Figure 53) is widespread, occurring in the Northern Hemisphere in Asiatic and Oceanic regions (Bischler-Causse 1989). Its distribution includes Borneo, China, Guam, Hong Kong, India, Indonesia Japan, Korea, Malaysia, Marianas, New Britain, New Caledonia, New Guinea, Philippines, Solomon Island, Sri Lanka, and Thailand (Bischler-Causse 1989; Siregar *et al.* 2020). In Malesia, it occurs from sea level to 1500 m asl, and Lu and Huang (2017) reported that it occurs below 1800 m asl, adding Taiwan to its distribution. Singh and Singh (2013) reported it for the first time in the Indian Himalayas. It is threatened in Singapore (Ho 2013).

Aquatic and Wet Habitats

Marchantia emarginata (Figure 47-Figure 53) occurs on walls of bays, in side brooks, on a large block in pouring water, in waterfalls, and in thermal acidic spray in the tropics (Ruttner 1955). In Sumatra, Siregar *et al.* (2020) found it on soil (Figure 48) and rocks (moist, damp or wet, shaded, semi-exposed places, riversides, creeks; Figure 49-Figure 50). Lu and Huang (2017) reported similar habitats in Taiwan, including damp soils up to 1800 m asl. As seen in the images, it occurs on the sides of drainage ditches (Figure 51-Figure 52) as well.



Figure 48. *Marchantia emarginata* male on soil. Photo by Ellen8355, through Creative Commons.



Figure 49. *Marchantia emarginata* on rocks in and beside stream. Photo courtesy of Tian-Xiong Zheng (NICH).

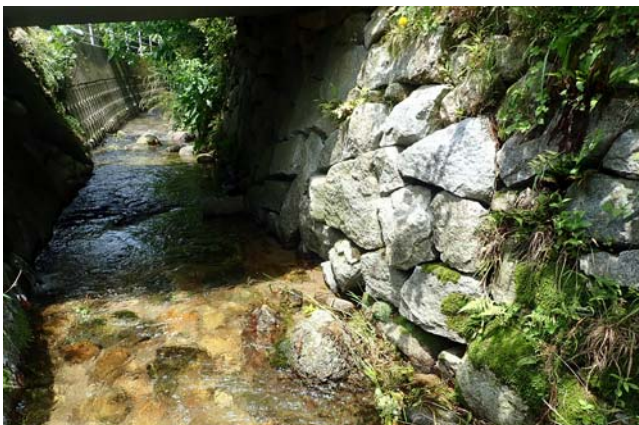


Figure 50. *Marchantia emarginata* on rocks along stream. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 51. *Marchantia emarginata* on rocks and concrete along ditch. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 52. *Marchantia emarginata* on rocks along ditch. Photo courtesy of Tian-Xiong Zheng (NICH).

But it can also occur on soil banks (Figure 53) if there is enough moisture. In southern China, this species is found frequently with *Dumortiera hirsuta* (Figure 54) on soil banks beside roads (Figure 55) (Li Zhang, pers. comm. 12 August 2022).



Figure 53. *Marchantia emarginata* ssp. *cuneiloba* on soil bank beside road. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 54. *Dumortiera hirsuta*, associate of *Marchantia emarginata* on roadside soil banks. Photo ©mutolisip, through Creative Commons.



Figure 55. *Marchantia emarginata* ssp. *tosana* with *Dumortiera hirsuta* (larger, hairy thalli). Photo courtesy of Li Zhang.

Tewari and Pant (1996) reported that *Marchantia emarginata* (Figure 47-Figure 53) grew along the borders of warm springs in hot spring areas of the Kumaon Himalaya, but was unable to grow in the hot, sulfurous springs.

Adaptations

This is not a truly aquatic bryophyte, but lives in habitats that can be wet part or most of the time, then experience drought when water levels recede. Hence we should expect adaptations that mediate these drier conditions.

Marchantia emarginata (Figure 47-Figure 53) has scales that are purple or pale-purple (see Figure 56) (Lu & Huang 2017). These contribute to water movement, absorption, and maintenance of hydration. One can only speculate about the advantages of the color. We have seen, in the chapter on light in Volume 1, that red pigments can be in higher concentrations in shade plants than in full sunlight (Melati *et al.* 2019). Furthermore, in the extreme shade of the rainforest, some forest floor tracheophytes have red or purple on the lower leaf surface, increasing the absorption of light at the upper end of the photosynthetic

action spectrum (Lee & Graham 1986). Hence, we can speculate that such a function might be operating in liverworts with purple scales. We need data to determine if the intensity of the color relates to the level of light in the habitat. I see no value to having this pigmentation on the ventral surface as a protection in high light. Do these scales somehow reflect light back to the photosynthetic tissue under low light conditions?



Figure 56. *Marchantia polymorpha* ssp. *ruderalis* scales showing purplish color of some *Marchantia* species. Photo by Des Callaghan, with permission.

Like other members of *Marchantia*, *M. emarginata* (Figure 47-Figure 53) has pores in the epidermis. These provide entry of CO₂ into the chamber beneath where photosynthetic filaments reside. And cuticular ridges around the pores are hydrophobic, preventing the entry of water that would greatly reduce the ability of CO₂ to enter the photosynthetic filaments.

Like many thallose liverworts, the thallus of *Marchantia emarginata* (Figure 47-Figure 53) often grows over mosses (Figure 57, Figure 61). These mosses provide a sponge-like base that helps to retain water longer than soil or pebbles alone, thus widening the habitat range of the liverwort.



Figure 57. *Marchantia emarginata* subsp. *tosana* growing on mosses. Photo from Taiwan Mosses, through Creative Commons.

Reproduction

Reproduction in *Marchantia emarginata* (Figure 47-Figure 53) follows that of other species in the genus. It is **dioicous** (Lu & Huang 2017). Cutting (1910) described the antheridial receptacles (Figure 58-Figure 59) of the species. A later description by Srinivasan (1939) suggests that it could actually be **protogynous** (female parts develop before male parts), with archegonial receptacles (Figure 60) developing first, then antheridial receptacles developing, a rather unusual order for bryophytes (see Vol. 1, Chapt. 3-2). Srinivasan describes the species as having receptacles that start as purely female, but soon one or more of the proliferations bear antheridia that grow out from the ventral surface. However, these proliferations once again become active lobes of the female receptacle. Srinivasan describes them as intermediate between an archegonium and an antheridium, later becoming typical antheridia. This observation leads him to the suggestion that the two reproductive structures are homologous. Nevertheless, the species is generally accepted as **dioicous**.



Figure 58. *Marchantia emarginata* males with antheridiophores. Photo by Ellen8355, through Creative Commons.



Figure 59. *Marchantia emarginata* males showing antheridial receptacles. Photo by Li Zhang, with permission.



Figure 60. *Marchantia emarginata* ssp. *tosana* females with archegonial heads. Photo courtesy of Li Zhang.

Asexual reproduction occurs by **gemmae** in cups (**cupules**) (Figure 61) (Ho 2013). In Singapore, these gemmae appear to be the primary means of reproduction, along with fragmentation and branching (see also Johnson 1958). On the other hand, Singh and Singh (2013) found no gemmae cups in the Himalayan material they studied, suggesting perhaps a climatic or photoperiod problem. We know that production of *Marchantia polymorpha* (Figure 2) gemmae are favored by short days (Carter & Romine 1969). If these conditions are coupled with the wrong temperatures, then the hormonal stimulus to produce gemmae might be absent.



Figure 61. *Marchantia emarginata* with gemmae. Photo by 楊玉鳳, through Creative Commons.

Kumra and Chopra (1989a,b) found that cytokinins (2iP, BAP, kinetin and zeatin) increased both growth and gemma cup formation in *Marchantia emarginata* (Figure 47-Figure 53) and were of decreasing effectiveness in that order. However, BAP is the most effective in increasing the number of gemmae. They also found (1989b) that vegetative growth and gemmae cup production were greatest in continuous light at 4500 lux, but were inhibited by applied auxins at most concentrations.

Li Zhang (pers. comm. 6 August 2022) sent me images of very unusual *Marchantia emarginata* ssp. *tosana* with

gemmae growing on the antheridiophore and archegoniophore (Figure 62-Figure 63). He concluded that the gemmae landed on these reproductive structures when the latter were young and the stalks had not yet elongated. These gemmae then were elevated as the antheridiophore and archegoniophore elongated. These two images represent two different populations in the same area. He considered that the high humidity in that location could make this unusual substrate possible. It also suggests that the inhibitor(s) to gemmae germination present in the thallus are absent in the archegoniophore and antheridiophore. But really, on the ends of the fingers of the antheridial head? It is interesting that the antheridial head does not have the typical shape seen in Figure 58.



Figure 62. *Marchantia emarginata* ssp. *tosana*, in Guangdong, S. China, with germinated gemmae and gemmae cups growing on male receptacle arms. Photo courtesy of Li Zhang.



Figure 63. *Marchantia emarginata* ssp. *tosana* with gemmaling on archegoniophore stalk, Guangdong, S. China. Photo courtesy of Li Zhang.

Fungal Interactions

Although I found little on fungal interactions for this species, Srinivasan (1939) reported fungal-forming **pycnidia** (flask-shaped fruiting body bearing conidiophores and conidia on interior and occurring in various imperfect fungi and Ascomycetes; Figure 64) in *Marchantia emarginata* (Figure 47-Figure 53). Srinivasan further suggested that the fungal attack might cause a change in the sex of the receptacle. This remains to be demonstrated experimentally, but with what we currently know about hormones from bacteria and fungi, and their influence on the development of bryophytes, this would be a worthwhile experiment.



Figure 64. *Phoma* (Coelomycetes) pycnidium. Some fungi have pycnidia that appear on *Marchantia emarginata*. Photo by Brawlings, through Creative Commons.

Iqbal *et al.* (1988) described vesicular-arbuscular mycorrhizal fungi from both rhizoids and the ventral thallus parenchyma of *Marchantia emarginata* (Figure 47-Figure 53).

Fatma (2018) determined an endophytic mold in *Marchantia emarginata* (Figure 47-Figure 53) to be *Daldinia eschscholtzii*. (Figure 65-Figure 66).



Figure 65. *Daldinia eschscholtzii*, an endophytic fungal species that can occur in *Marchantia emarginata*. Photo by Petra White, through Creative Commons.



Figure 66. *Daldinia eschscholzii* ventral view. Photo by Byrain, through Creative Commons.

Biochemistry

Many biochemical studies have described the biochemical properties and potential uses of secondary compounds in the genus *Marchantia*. See Jantwal *et al.* (2019) for a review. The species *Marchantia emarginata* (Figure 47-Figure 53) may be less well known than the widespread *M. polymorpha* (Figure 67), but its biochemical studies are nevertheless numerous. Only a sampling will be presented here to suggest their ecological importance.



Figure 67. *Marchantia polymorpha* female with archegoniophores; this species is the typical example used for teaching about liverworts. Image copyright Stuart Dunlop <www.donegal-wildlife.blogspot.com>, with permission.

Yuan *et al.* (2021) demonstrated the presence of uridine diphosphate-dependent glycosyl transferases (UGTs) in *Marchantia emarginata* (Figure 47-Figure 53), noting the importance of flavonoid glycosides for their pharmaceutical activities. The value of pharmaceutical

compounds to the liverworts needs much experimental study. Are they merely a consequence of some other function or pathway, or do they defend the bryophytes against pathogens or herbivores?

Huang *et al.* (2010) isolated marchantin A, a bibenzyl ether, from *Marchantia emarginata* subsp. *tosana* (Figure 68). This secondary compound is able to induce **apoptosis** (death of cells which occurs as normal and controlled part of organism's growth or development) in human MCF-7 breast cancer cells. It furthermore has good anti-oxidant activity. Fatma (2018) likewise demonstrated anti-oxidant activity in this species. Antioxidants can be important in rehydration of bryophytes, countering the oxidative burst that often occurs (see for example Minibayeva & Beckett 2001).



Figure 68. *Marchantia emarginata* ssp. *tosana* females, a source of marchantin A. Photo from Taiwan Mosses, through Creative Commons.

Kumar *et al.* (2007) found that *Marchantia emarginata* could be used against tumors.

Wang *et al.* (2017) described the chemistry of the cuticle of *Marchantia emarginata* (Figure 47-Figure 53). They isolated the fatty ω -hydroxyacid/fatty alcohol hydroxycinnamoyl transferase (HFT) from the species and, based on a species of tobacco, suggested that its occurrence in the cells indicate that the **feruloylation** (subclass of carboxylic acid esterases that hydrolyze ester bonds between hydroxycinnamic acids and sugars present in plant cell walls) of the cutin monomers takes place in the cytoplasm. Bryophytes are often described as lacking cuticle, but **cutin** (insoluble polyester of C₁₆ and C₁₈ hydroxy fatty acids and main component of cuticle) is becoming well known in bryophytes. It appears that in bryophytes the cuticle is simply thinner than in tracheophytes.

Toyota *et al.* (2004) described the **sesquiterpene** alcohol 1,6-Humuladien-10-ol from *Marchantia emarginata* subsp. *tosana* (Figure 68). These **sesquiterpenes** are C₁₅-terpenoids comprised of three isoprene units. They are especially common in tracheophytes, but also are becoming well known in bryophytes (Awouafack *et al.* 2013). We know that sesquiterpenes can include essential oils and aromatic constituents; others are antimicrobial or provide protection against oxidative damage.

Alcoholic and acetonc extracts of *Marchantia emarginata* (Figure 47-Figure 53) indicated the presence of

carbohydrates, proteins, diterpenes, phytosterols, and anthocyanin, whereas flavonoids were present only in the alcoholic extract and phenol only in the acetonic extract (James *et al.* 2020). Alcohol extracts exhibited activity against the bacterium *Escherichia coli* (Figure 69) and both alcohol and acetone extracts against *Klebsiella pneumoniae* (Figure 70). However, neither alcohol nor acetone extracts exhibited activity against *Staphylococcus aureus* (Figure 71). This is unfortunate because this hospital scourge has become methicillin-resistant (Solberg 2000) and a new treatment is needed.

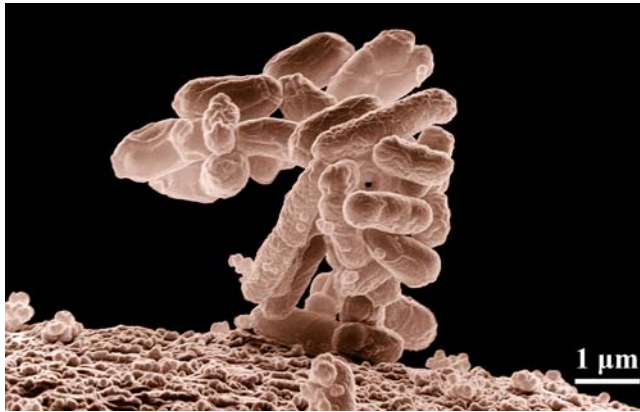


Figure 69. *Escherichia coli*, a bacterial species that is inhibited by alcohol extracts of *Marchantia emarginata*. Photo by USDA, through public domain.



Figure 70. *Klebsiella pneumoniae*, a bacterial species that is inhibited by both alcohol and acetone extracts of *Marchantia emarginata*. Photo from CDC, through public domain.

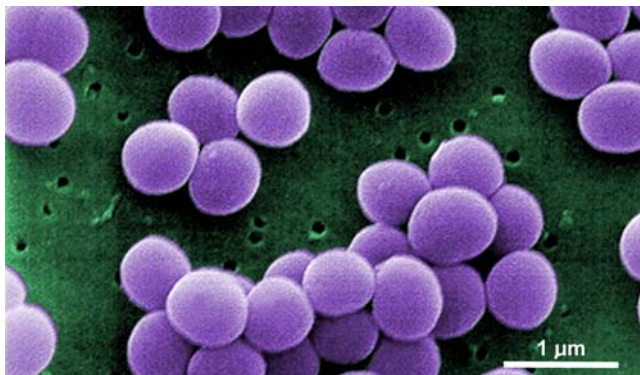


Figure 71. Colorized SEM of *Staphylococcus aureus*, a species that is not inhibited by alcohol or acetone extracts of *Marchantia emarginata*. Photo by Janice Haney Carr, CDC, through public domain.

Spermine is a polyamine in all **eukaryotic** (having nucleus with nuclear membrane) cells and is involved in cellular metabolism. The amino acid ornithine is its precursor. It is an essential growth factor in some bacteria as well.

Culturing

Chopra and Dhingra-Babbar (1986) studied the effects of various amino acids, complex organic substances, and active charcoal on the growth and development of *Marchantia emarginata* (Figure 47-Figure 53). The amino acid response was dependent on the concentration, with lower concentrations enhancing growth and higher ones inhibiting it. Glutamic acid, histidine, and methionine stimulated callus growth, whereas tryptophan induced thallus differentiation. Activated charcoal delayed callus formation and growth was extremely reduced. Coconut milk stimulated callus growth at 15% (v/v) and inhibited it at 25%.

Marchantia inflexa (Figure 72-Figure 74)

Despite its somewhat narrow tropical distribution, *Marchantia inflexa* (Figure 72-Figure 74) has received considerable attention regarding its sexual expression and the role of the environment in this expression. Marks *et al.* (2019a,b) revealed that those genes on sex chromosomes are subject to greater diversifying selection than those on autosomal (non-sexual) and organellar genes. This diversification occurs mostly among male-specific genes, whereas divergence of other sex-linked genes differs little from that of autosomal genes.

Distribution

Marchantia inflexa (Figure 72-Figure 74) is restricted to the Neotropics and bordering regions, from Central America and the Caribbean and from northern Venezuela to the southern United States (Marks *et al.* 2019a).



Figure 72. *Marchantia inflexa* thalli with brown scales covering apical growth regions. Photo by Scott Zona, with permission.



Figure 73. *Marchantia inflexa* with gemmae cups. Note brown scales covering the apical growth region. Photo by Alan R. Frank, through Creative Commons.



Figure 74. *Marchantia inflexa* showing large population of overlapping thalli. Photo by Alan R. Frank, through Creative Commons.

Aquatic and Wet Habitats

Marchantia inflexa (Figure 72-Figure 74) occurs mostly on streambank rocks (Figure 75-Figure 76) and soil (Figure 77-Figure 78) (Marks *et al.* 2019a).



Figure 75. *Marchantia inflexa* on rock. Note the meristematic tips on the branches, with brown scales covering them. Photo by Alan R. Frank, through Creative Commons.



Figure 76. *Marchantia inflexa* on streambank. Photo by Karen and Philip, through Creative Commons.



Figure 77. *Marchantia inflexa* on soil bank. Photo by Jeff Garner, through Creative Commons.



Figure 78. *Marchantia inflexa* on soil bank. Photo by Jeff Garner, through Creative Commons.



Figure 79. *Marchantia inflexa* population on soil bank where mosses can help it to maintain moisture. Photo by Alan R. Frank, through Creative Commons.

Physiology

water relations

Marks *et al.* (2019a,b) investigated dehydration tolerance, emphasizing differences between genetic lines, that allowed them to identify multiple dehydration-associated genes, two of which were sex-linked, suggesting that dehydration tolerance may be impacted by sex-specific genes. Identification of these genes permits the identification of gender when sexual expression is not present. Although the more common habitat for *Marchantia inflexa* (Figure 72-Figure 74) is on rock and soil surfaces along streambanks (Figure 79) in tropical forests, it can also colonize more exposed sites such as disturbed sites along roads.

Marks *et al.* (2019ab) explored the relationships to drought in five populations of *Marchantia inflexa* (Figure 72-Figure 74) in northern Trinidad and Tobago in the Republic of Trinidad. When grown in a common garden, the responses maintained the differences they had exhibited in their original habitats, indicating that they were genetically determined. They also found that males (Figure 86-Figure 87) had a lower desiccation tolerance than did females (Figure 88-Figure 89) in less exposed sites, but not in more exposed sites. The males furthermore exhibited more variation in morphology than did females, while females exhibited similar desiccation tolerance across the five sites.

Marks *et al.* (2021) identified stress responses to dehydration in *Marchantia inflexa* (Figure 72-Figure 74), including expression of LEA and ELIP genes and evidence of cell wall remodelling. They found, however, that there was little temporal synchronization of the responses across six genotypes. The researchers suggested that differences in timing of the transcriptional adjustments contribute to the variation seen among genotypes. Furthermore, developmental differences affect the relative tolerance of meristematic and differentiated tissues.

electrical responses

Measuring electrical responses in bryophytes is not a common activity, but such measures can be used to assess a plant's response to injury or environmental stimuli. Several studies have used *Marchantia inflexa* (Figure 72-Figure 74) as a subject. Cooper *et al.* (2022a) commented that the KCl-filled glass electrodes placed into plant tissues is subject to artifacts and is less reliable than the impedance method. Using the impedance method, one can detect plant injury and exposure to environmental compounds such as glutamate. This method was used successfully in *M. inflexa* by placing two impedance leads 2 cm apart into the thallus tissue, with a cut made to a third thallus between the two leads. Cooper *et al.* (2022b) found that the liverwort showed no electrical response to glutamate exposure, whereas *Arabidopsis thaliana* (Figure 80) and *Pisum sativum* (Figure 81) (both flowering plants) produced rapid depolarization upon exposure.



Figure 80. *Arabidopsis thaliana*, a species that, unlike *Marchantia inflexa*, experiences rapid depolarization upon exposure to glutamate. Photo by Stefan Lefnaer, through Creative Commons.



Figure 81. *Pisum sativum* var. *sativum*, a species that, unlike *Marchantia inflexa*, experiences rapid depolarization upon exposure to glutamate. Photo by Stefan Lefnaer, through Creative Commons.

Adaptations

Among the common adaptations is their ability to form dense mats that help to maintain moisture in the soil (Figure 82-Figure 83). But this ability to form mats brings its own problems of self-competition.



Figure 82. *Marchantia inflexa* with overlapping thalli that can help to conserve soil moisture. Photo by Scott Zona, with permission.



Figure 83. *Marchantia inflexa* with gemmae cups, showing closely contacting and overlapping thalli. Photo by Jamie Newman, through Creative Commons.

Crowley *et al.* (2005a) described three mechanisms for competition for space (Figure 82-Figure 83): **expansion** (spreading to unoccupied habitat), **lottery** (replacing dead competitors), and **overgrowth** (encroaching on competitors along zones of contact). For *Marchantia inflexa* (Figure 72-Figure 74), a local stable coexistence of the sexes requires the avoidance of this self-competition. This stable coexistence of the sexes seems to be possible in a narrow range of disturbance intensities, explaining ambiguous results in simulation studies (McLetchie *et al.*, 2002). Crowley *et al.* noted the importance of **contact inhibition** in this species. They considered that the improbability that a disturbance regime could maintain death rates within the high and restricted range is consistent with stable coexistence and that it indicates that long-term coexistence of the two genders may be dependent on processes operating at the scale of the metapopulation (Garcia-Ramos *et al.* 2002, 2007). Garcia-Ramos *et al.* (2002, 2007) indicated that single-sex populations were common and that males were rare. In the tropics the two sexes often coexisted in a single patch; in the USA only all-male or all-female populations were known. The spores were able to colonize disturbed sites, and large disturbed areas permitted

the colonization and coexistence by both sexes, with fertilization typically occurring between patches.

Reproduction

For a species that has few publications describing habitats, *Marchantia inflexa* (Figure 72-Figure 74) has an abundance of published reproductive studies, particularly related to the environmental conditions. Like the genus, the species is **dioicous**. Prominent among the studies are those related to environmental effects on sex ratio.

McLetchie and Puterbaugh (2000) noted that unisexual populations and female- or male-biased populations were common in this **dioicous** liverwort. Garcia-Ramos *et al.* (2002) found that whereas both sexes could coexist in a single patch in the tropics, in the USA only all-male or all-female populations are known. McLetchie and Puterbaugh (2000) found that sex-ratio patterns could be related to growth rates, number of meristematic regions (Figure 72-Figure 73), and asexual reproduction in the riverside populations they studied in Trinidad. Of the 209 patches they observed, 83% contained no sex-expressing thalli. Only 9% contained thalli of both sexes. The remainder were either entirely female-expressing (4%) or male-expressing (4%). Small patches were less likely to be expressing sexual reproductive structures. Shade (less canopy openness) also correlated with lower sexual expression. In those populations with expression of both sexes, the ratios of male (Figure 86-Figure 87) to female (Figure 88-Figure 89) ranged 0.22-0.80.

But what causes this variation? McLetchie and Puterbaugh (2000) found that females (Figure 88-Figure 89) of *Marchantia inflexa* (Figure 72-Figure 74) grew faster, produced more meristematic tips (Figure 73), and had lower levels of asexual reproduction (Figure 83-Figure 85) than did males (Figure 86-Figure 87). Furthermore, the number of meristematic tips exhibited a negative correlation with both asexual reproduction and growth rate. Hence, these factors could lead to female sex bias in reproductive colonies. A further factor in shifting toward female dominance is that populations that reproduce better asexually (*i.e.* males) are less likely to succeed under stressful conditions. These relationships position the species to produce more spores under stressful conditions and thus have a means to arrive at a different location where the stress might not be present.

McLetchie *et al.* (2002) followed with a study on the local sex-ratio dynamics using *Marchantia inflexa* (Figure 72-Figure 74) from rock surfaces and bark in Trinidad. These populations differed widely in their population sex ratios at the study site in the rainforest. They followed seven life history stages. In some stages the thalli became more abundant and extend over the substrate and each other in their quest for space (Figure 84-Figure 85). The sex ratio within a patch was not stable: at low to moderate disturbance levels, females gradually eliminated males. At high disturbance levels, males (Figure 86-Figure 87) eliminated females (Figure 88-Figure 89). This pattern was not dependent on whether sexual propagules (spores) could germinate within the patch, but germination of gemmae (Figure 84-Figure 85) within the patch had an important role. Hence, sexual reproduction, while unimportant within patches, is critical in spatial landscapes (Garcia-Ramos *et al.* 2002).



Figure 84. *Marchantia inflexa* with gemmae. Photo by Jeff Garner, through Creative Commons.



Figure 85. *Marchantia inflexa* with gemmae cups. Photo by Jamie Newman, through Creative Commons.

However, spores may be the primary means for recolonizing patches eliminated by large-scale disturbances (McLetchie *et al.* 2002). Once a patch became fully occupied, the production of the wind-dispersed spores was maximized. Once the colony became re-established, spore production declined and the sex ratio became increasingly more biased toward one or the other sex. Such scenarios support the concept that the sex ratio is determined at the **metapopulation** (group of spatially separated populations of same species which interact at some level; regional group of connected populations of species) level.

One question that arises is how does a species maintain sexually dimorphic pre-adult traits (Fuselier & McLetchie 2002). Fuselier and McLetchie noted that sexual dimorphism can influence the distribution of the sexes, the population sex ratios, the maintenance of the sex in populations, and the evolutionary potential of the species. Hence, in species like *Marchantia inflexa* (Figure 72-Figure 74), where sexual dimorphism results in greater growth and reproduction in females, the population could develop a female-biased sex ratio. Fuselier and McLetchie found that the sexes overlapped in habitat use. Furthermore, different populations exhibited differences in growth, asexual reproductive rates (Figure 84-Figure 85), degrees of sexual dimorphism, and the strength of their

among-trait correlations. The investment in growth and in asexual reproduction differed in single-sex and mixed-sex populations, but the degree of sexual dimorphism did not. The researchers concluded that the local environment may exert more influence than does the presence of the opposite sex in maintaining sexual dimorphism. Furthermore, between-sex correlations were not significant in the greenhouse common garden, but were significant in the field. Garcia-Ramos *et al.* (2002) found that males were able to persist longer in local populations due to minor disturbances such as drought.

Females (Figure 88-Figure 89) exhibited a cost for plasticity, whereas males (Figure 86-Figure 87) did not (Fuselier & McLetchie 2002). Among females, early sex-expressing individuals produced fewer gemmae cups than did late-expressing plants, supporting the concept that there is a tradeoff between the two modes of reproduction. These observations suggest that events during the life of the plant can influence its success at the local population level. These events can differ among the years of its life, making the success of a given population a somewhat random process dependent upon the changing conditions in the environment.



Figure 86. *Marchantia inflexa* males. Photo by Jeff Garner, through Creative Commons.

Fuselier and McLetchie (2004) explored several environmental parameters to determine if the two sexes exhibited different preferences. Using two populations in Trinidad and ten in the USA, they found no differences in preference for substrate, humidity, wind speed, or exposure among or within populations. However, in the USA, male populations (Figure 86-Figure 87) tended to occur under

more open canopies and in a wider light range than did females (Figure 88-Figure 89).



Figure 87. *Marchantia inflexa* males. Photo by Scott Zona, with permission.



Figure 88. *Marchantia inflexa* females. Photo by Jeff Garner, through Creative Commons.



Figure 89. *Marchantia inflexa* females. Photo by Jeff Garner, through Creative Commons.

Crowley *et al.* (2005b) postulated that the long-term coexistence of the sexes in *Marchantia inflexa* (Figure 72-

Figure 74) might be only temporary. They found that fragmentation is important in overgrowth competition. Stanley (2019) hypothesized that females (Figure 88-Figure 89) in bryophytes would show a greater competitive ability, thus at least in part accounting for the frequent female (Figure 88-Figure 89) bias in bryophyte sex ratio. In their greenhouse cultures of *M. inflexa*, they found that both sexes averaged 41% more growth if accompanied by the opposite sex than that of single-sex cultures. Their model predicted coexistence between the sexes, but that males (Figure 86-Figure 87), not females, would be in greater numbers, with a ratio of 3.2 males to 1 female.

Groen *et al.* (2010a) were surprised to find that males (Figure 86-Figure 87) of *Marchantia inflexa* (Figure 72-Figure 74), the gender that occurs in more tree-canopy openness, have lower chlorophyll *a:b* ratios than do females. Generally, a low chlorophyll *a:b* ratio, caused by more chlorophyll *b*, is an adaptation to shade. But both sexes had lower edge pore density in greater canopy openness; males had a weak positive correlation between edge pore density and light intensity (Groen *et al.* 2010b). Thus it appears that light intensity and canopy openness have opposing effects on edge pore density in males (Figure 86-Figure 87). The researchers suggest that males might be more responsive to water stress than are females (Figure 88-Figure 89). Females, on the other hand, have more support tissue, providing greater storage, and providing the resources needed for the female plants to support their sexual role.

Garcia-Ramos *et al.* (2007) noted that as a patch of *Marchantia inflexa* (Figure 72-Figure 74) persists through time, it is more likely to lose males (Figure 86-Figure 87) than females (Figure 88-Figure 89). This is due, at least in part, to the faster tissue growth of females. On the other hand, both sexes generally persist in the metapopulation, but with females predominating. Males had the advantage during patch filling, with their more abundant gemmae (Figure 84-Figure 85) providing an effective colonization strategy. Since males kept colonizing these available patches, they were maintained in the metapopulation. Similar maintenance of both sexes, particularly in small, highly disturbed populations where life-history traits and mortality differ between sexes, is likely to be a widespread phenomenon, particularly among dioicous bryophytes.

Using methods described by Chang *et al.* (2006), Fuselier (2008) found that geographically separated populations were significantly different. Single-sex populations of *M. inflexa* (Figure 72-Figure 74) in Oklahoma and Florida, USA form a distinct phenotypic group and it would be worthwhile to study physiological and developmental differences as well. Plants from single-sex and both-sex populations differed in their life history strategies. Those in single-sex populations invested more in growth than in asexual (gemmae; Figure 84-Figure 85) reproduction. While they produced as many sexual structures, they produced fewer gametangia per gametophore than did plants from both-sex populations, suggesting a possible chemical interaction among the plants. Characters of female plants (Figure 88-Figure 89) were positively correlated with geographic, nearest-neighbor distance. Characters of male plants (Figure 86-Figure 87) showed no relationship to geographic distance.

Dispersal is a logical choice for differences in population genders. Male plants produce more gemmae (Figure 84-Figure 85) and therefore should propagate more new plants near the parent colony. Female plants (Figure 88-Figure 89) produce spores and can therefore colonize areas at greater distances. But the gemmae, mostly falling within 1 m of the parent, have a greater chance of landing on a suitable substrate with suitable environmental conditions. To further complicate the picture, gemmae from males (Figure 86-Figure 87) (producing more males) have lower survivability than female gemmae due to desiccation (Stieha *et al.* (2014).

Brzyski *et al.* (2014) collected male and female plants from two strikingly different habitats within the same region: along natural sites (rivers) and along novel human-modified sites (roadsides). They used a common garden to demonstrate a strong sex by habitat interaction: male (Figure 86-Figure 87) and female (Figure 88-Figure 89) responses differed significantly by their source habitat. Road-collected females had higher growth and asexual reproduction compared to females from riverside habitats. In males, the pattern was not significant, but tended to be opposite to that of the females. The researchers found significant genetic differentiation between plants of the two habitats and found no evidence of individual differences in growth plasticity. However, there was a genotype effect for gemmae production. Although males and females did not differ genetically, river-collected plants with lower sexual potential were more diverse than roadside-collected plants. Could this be due to founder events, or are there selection pressures yet to be discovered? Nevertheless, these populations show that individual variation in reproduction is controlled by the interaction of genetics and environment.

Moore *et al.* (2016) questioned the selection for gamete dispersal and capture in clump water-holding capacity. In *Marchantia inflexa* (Figure 72-Figure 74), a dense tomentum-like mass of scales surrounds the archegonia (Figure 88-Figure 89), presumably retaining sperm-laden water. The male receptacle (Figure 86-Figure 87), on the other hand, has no scales and may serve as a dispersal splash platform (Figure 86).

Stieha *et al.* (2014) observed the productivity and dispersal of gemmae in *Marchantia inflexa* (Figure 72-Figure 74). Male plants produce more gemmae and more quickly than do female plants, but male plants have lower desiccation tolerance, leading to lower gemmae survival rates. They found that gemmae in this species can move up to 20 cm per minute in a light rain, permitting them to reach locations unoccupied by their parents. Models demonstrated that long-distance dispersal of gemmae is possible and they are likely to be successful if they stay moist. They warned that measurements of different stages to dispersal can be misleading about the survival of the sexes. Nevertheless, the gemmae are critical to the maintenance of both sexes.

Stieha *et al.* (2017) summarized the known mechanisms for maintaining both sexes to be "semi-independent dynamics of populations within a metapopulation. These semi-independent dynamics are influenced by dispersal and recolonization rates, which are affected by the spatial arrangement of populations." Using a mathematical model, Stieha and coworkers demonstrated

that at intermediate distances between populations, metapopulations maintained both sexes, and the spatial arrangement of populations changed the threshold at which one sex was lost. However, when populations were close to one another, one sex was eliminated and the single-sex metapopulation persisted through dispersal of asexual propagules. When populations were far apart, one sex was eliminated, and the metapopulation either went extinct due to lack of recolonization by asexual propagules or persisted because clumped populations facilitated recolonization. Hence, spatial arrangements are important in the maintenance or elimination of sexes in clonal organisms. This helps to explain the persistence of geographic parthenogenesis and the continuance of asexual species such as founder populations of dioicous species.

With so much known about the sexual behavior of *Marchantia inflexa* (Figure 72-Figure 74) populations, Walter (2015) set out to detect genetic evidence of sexual reproduction in sexual and asexual populations. She predicted that genetic variation would be higher in sexually reproducing populations when compared to asexually reproducing populations. In these haploid organisms, there is rapid selection for advantageous traits and rapid removal of deleterious ones. Sexual reproduction permits recombinations among the genes on different chromosomes, creating variability among offspring. Asexual reproduction such as gemmae produces a carbon copy of the parent. The results, using *Marchantia inflexa* (Figure 72-Figure 74), are fascinating. Bisexual populations are becoming more female biased (Figure 88-Figure 89), suggesting some mechanism of competition. The all-female populations have a low level of genetic diversity, implying that they have arisen mostly from asexual reproduction.

Brzyski *et al.* (2018) noted that sexual reproduction requires close proximity to potential mates. Clonal growth can increase this distance by carrying the reproductive structures farther from a neighboring plant of the opposite sex, thus reducing the probability of mating. The researchers calculated the spatial distributions as the likelihood that pairs of individuals were the same sex or genotype of *Marchantia inflexa* (Figure 72-Figure 74) and determined how the likelihood was affected by habitat patch size. In this species, asexual reproduction dominates within patches but could also occur between populations. Males (Figure 86-Figure 87) were more likely to occur near other males than the likelihood of females (Figure 88-Figure 89) being near other females, presumably reflecting the greater gemma production by males in *M. inflexa*. In small patches the likelihood of both sexes being near members of the same sex was greater than in large patches. In the large habitat patches, male genotypes were nearly 15% more likely to be near their own clone mates than were female plants. This difference is most likely due to differential survival or colonization. Thus, male plants were more likely to be aggregated clones than were females, particularly in large patches.

Based on earlier studies on differences in light preference, Lay *et al.* (2022) experimented with the effects of light intensity and quality on phytochromes in germination of gemmae of *Marchantia inflexa* (Figure 72-Figure 74). The germination responses of both sexual (spores) and asexual (gemmae) offspring were consistent

with a phytochrome-mediated event. This contrasts with germination in *M. polymorpha* (Figure 90) wherein photosynthesis mediates the event.



Figure 90. *Marchantia polymorpha* with gemmae in cups. Photo by Brenda Dobbs, through Creative Commons.

Stanley (2019) likewise found that in single-sex cultures, males had more asexual structures (gemmae) than in the mixed-sex cultures, with the reverse relationship for growth rate. Such an increase of asexual structures in single-sex cultures would increase the probability of encountering females. The reduction in growth is a tradeoff in resource allocation. The same pattern did not occur in the females.

These differences in behavior of males (Figure 86-Figure 87) in single- vs mixed-sex cultures suggest an interaction, perhaps hormonal, based on density of plants and presence of females (Figure 88-Figure 89). Stanley (2019) suggested that in this case there could be a change in sex ratio before the plants allocate their resources to sexual reproduction; this could also be caused by environmental conditions.

Such changes in sex ratio due to environmental conditions have been known in monoecious seed plants for some time. Freeman *et al.* (1981) found that in xeric conditions the males (Figure 86-Figure 87) were more prominent, whereas female (Figure 88-Figure 89) functions were more abundant on mesic sites. Similar results were found by Dawson and Elheringer (1993) for *Acer negundo* (box elder, Figure 91) in the Intermountain West, USA. In drought-prone habitats, the male:female ratio is 1.62:1, whereas in moist-streamside habitats (Figure 76) it is female (Figure 88-Figure 89) biased (0.65 male:1 female). By reviewing many publications, Golenberg and West (2013) indicated that environmental conditions could affect ethylene concentrations, which in turn affected other hormones in flowering plants, ultimately affecting the expression of sexual structures.

Blake-Mahmud and Struwe (2020) even found that sexual expression as male in the sexually plastic *Acer pensylvanicum* (striped maple, Figure 92-Figure 93) could be completely suppressed by wounding, with increasing likelihood of the sex changing to female as the severity of damage increased. Understanding such responses of bryophytes to environmental stresses is important to our

understanding of the changes we might expect as the climate becomes more stressful, particularly as drought increases and more severe weather events occur.



Figure 91. *Acer negundo* male flowers. Photo by Krzysztof Ziarnik, Kenraiz, through Creative Commons.



Figure 92. *Acer pensylvanicum* female flowers. Photo by Crosier, through Creative Commons.



Figure 93. *Acer pensylvanicum* male flowers. Photo by Ashley Bradford, through Creative Commons.

Interactions

Like many, probably most, other bryophytes, *Marchantia inflexa* (Figure 72-Figure 74) consorts with bacteria. The bacterial communities associated with bryophytes contribute to nutrient cycling, community interactions, and cost-benefit relationships of the individual organisms involved (Marks *et al.* 2018). There is evidence of nitrogen fixation by these associated bacteria from the early invasion of bryophytes on land (Knack *et al.* 2015).

Marks *et al.* (2018) compared the bacterial community between males (Figure 86-Figure 87) and females (Figure 88-Figure 89) of *Marchantia inflexa* (Figure 72-Figure 74) across habitats. They found an abundant and diverse community, even when grown in a common garden. Differences were present among habitats as well as between sexes. Marks and coworkers suggested that differences in communities between males and females may contribute to "subtle differences in both physiology and form," possibly contributing to their acclimation to the local environment. Females differed from males in having higher abundances of the bacterial order **Rhizobiales**, (Figure 142-Figure 143) an order known to have species that are able to fix nitrogen. At the same time, females had a lower abundance of nitrogen-fixing **Cyanobacteria** (Figure 94) compared to males.



Figure 94. *CylandrospERMUM* sp., a nitrogen-fixing member of **Cyanobacteria**. Photo from CSIRO ScienceImage, through Creative Commons.

Graham *et al.* (2018) noted that some bacterial associations with *Marchantia inflexa* (Figure 72-Figure 74) growing on streambanks (Figure 75) appear to have methane oxidation capabilities. Since streams are known sources of methane, albeit heterogeneous within the stream (Crawford *et al.* 2017), the bryophytes might have an important role in reducing this greenhouse gas.

Marchantia miqueliana

(syn. = *Marchantia cataractarum*)

Distribution

Marchantia miqueliana appears to be endemic to Java. Because of this narrow distribution, little has been published about it. Siregar *et al.* (2013) were unable to relocate it in Sumatra, a location that had been reported by Bischler-Causse (1989). Instead they found what they

considered to be a new species on soil in a wet place around the Dwi Warna waterfall at 1100 m asl.

Aquatic and Wet Habitats

Marchantia miqueliana occurs on the walls of bays and in the spray of waterfalls in the tropics (Ruttner 1955). Campbell (1908) likewise reported it from near a waterfall in Java.

Adaptations

Biochemistry

Despite its rarity, Campbell *et al.* (1979) listed flavonoids from *Marchantia miqueliana*. These included apogenin and flavone.

Marchantia paleacea (Figure 97-Figure 99)

(syn. = *Marchantia nitida*, *Marchantia nepalensis*)

Bischler (1986) sank a number of species into this one, based on type material, but warned that other records of these species do not necessarily belong to *Marchantia paleacea* (Figure 98-Figure 100).

Marchantia paleacea (Figure 97-Figure 99) usually is considered to have two subspecies, ssp. *paleacea* and ssp. *diptera* (Figure 95-Figure 96) (Zheng & Shimamura 2019; Zheng *et al.* 2020b). In China and Japan, *Marchantia paleacea* subsp. *paleacea* tends to be distributed in higher altitudes and latitudes compared to subsp. *diptera* (Zheng & Shimamura 2019). Zheng and coworkers (2020b) found that the two subspecies overlap in western Japan and may be able to interbreed there.



Figure 95. *Marchantia paleacea* ssp. *diptera* in Japan. Photo by Janice Glime.



Figure 96. *Marchantia paleacea* ssp. *diptera* females with capsules, Arimma, Japan. Photo by Janice Glime.

Distribution

Marchantia paleacea (Figure 97-Figure 99) is a widely distributed tropical and subtropical species, ranging through the West Indies, Mexico, Guatemala, Asia, Europe, Azores, and Africa (Svihla 1940). Country records include Andaman Islands, China, India, Japan, New Guinea, Ryukyus, southeastern Asia, Sri Lanka, and Taiwan (Lu & Huang 2017; Bischler-Causse 1989). Borovichev and Bakalin (2014) added it to the known Russian flora, stating that it is poorly known there. It is considered vulnerable in Italy (Poponessi *et al.* 2020) and rare in southern Africa (Perold 1995). In the Americas, it is known from the southern states of the USA, Mexico, and Central America (Bischler 1988).



Figure 97. *Marchantia paleacea* thallus growing in Europe. Photo by Jan-Peter Frahm, with permission.



Figure 98. *Marchantia paleacea* in Europe, showing reddening of margins. Photo by Michael Lüth, with permission.



Figure 99. *Marchantia paleacea* with red bases and distinct dichotomous branching. Photo by Dmitry Ivanov, through Creative Commons.



Figure 101. *Marchantia paleacea* with gemmae on rock wall at edge of subtropical laurel forest, Madeira. Photo by Des Callaghan, with permission.

Aquatic and Wet Habitats

Marchantia paleacea (Figure 97-Figure 99) can occur submersed in small pools, on the walls of bays, and in waterfalls in the tropics (Ruttner 1955). Lu and Huang (2017) reported subspecies *paleacea* to occur on damp soil from 300 to 2500 m asl in Taiwan. It can occur on wet rocks beside rivers and streams (Figure 100). Des Callaghan photographed it on a rock wall at the edge of a subtropical laurel forest in Madeira (Figure 101). Zheng and Shimamura (2022b) described this subspecies in Japan as growing on boulders, soil, concrete, or limestone walls in wet or shaded places. They provided a similar but slightly different habitat description of *Marchantia paleacea* ssp. *diptera* (Figure 95-Figure 96) on stones or soil in shaded or semi-shaded areas, anthropogenic regions, or near streams.

Bischler (1986) reported that *Marchantia paleacea* (Figure 97-Figure 99) had a high environmental tolerance, *i.e.* a wide niche, for soil factors, but that its climate tolerance was narrower.

In Oklahoma, USA, *Marchantia paleacea* (Figure 97-Figure 99) occurs on constantly moist, shaded rock outcrops within a few feet of water, on travertine deposits along streams (Figure 102-Figure 106), and on moist, shaded bluffs (Figure 107) (Little 1936). Images provided by members of Bryonet indicate that in some parts of the world it can occur elsewhere on wet banks (Figure 108-Figure 109), on the sides of drainage ditches (Figure 109-Figure 110), and in the splash of spring water (Figure 111-Figure 112) used for drinking.



Figure 100. *Marchantia paleacea* wet by river. Photo by Rafael Medina, through Creative Commons.

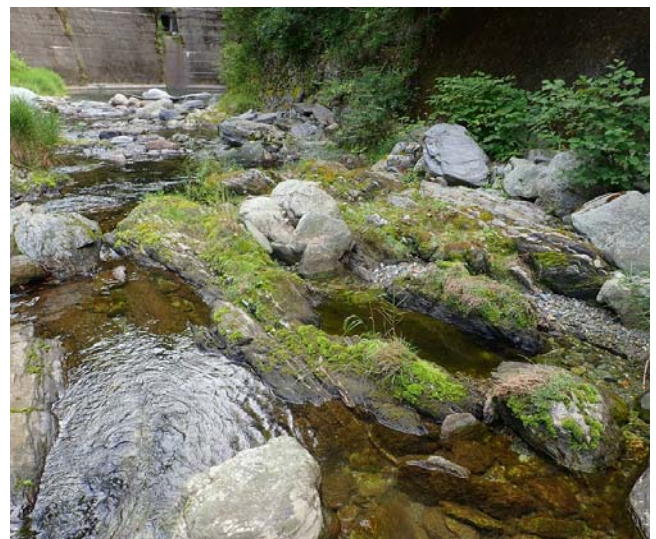


Figure 102. *Marchantia paleacea* on emergent rocks in stream. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 103. *Marchantia paleacea* on emergent rocks in stream. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 104. *Marchantia paleacea* on rocks at edge of stream. Photo courtesy of Tian-Xiong Zheng.



Figure 105. *Marchantia paleacea* on rocks in open stream. Photo courtesy of Tian-Xiong Zheng (NICH).

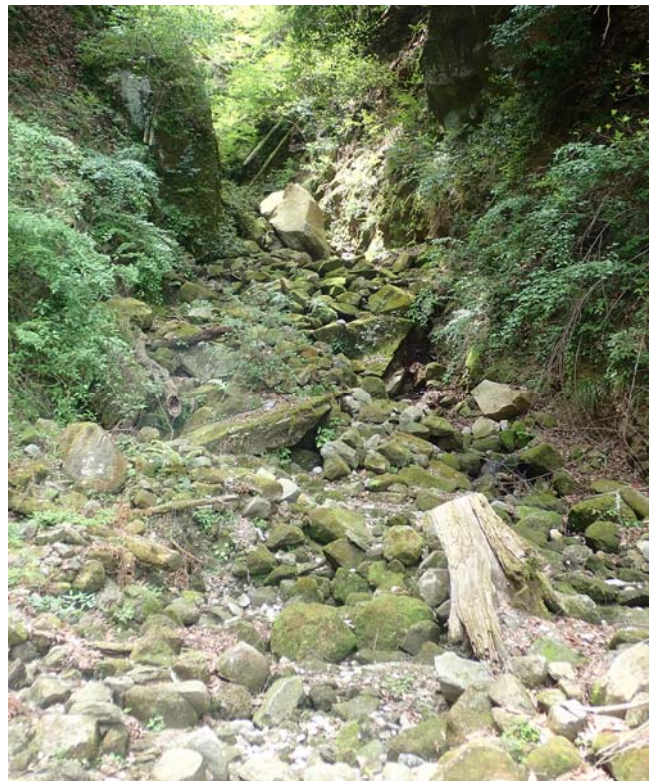


Figure 106. *Marchantia paleacea* on soil bank beside dry stream. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 107. *Marchantia paleacea* habitat on rocky bank in India. Michael Lüth, with permission.



Figure 108. *Marchantia paleacea* on a wet bank. Photo by Michael Lüth, with permission.



Figure 109. *Marchantia paleacea* on concrete wall of ditch. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 110. *Marchantia paleacea* on concrete wall of ditch. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 111. *Marchantia paleacea* on rocks near spring water pipe. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 112. *Marchantia paleacea* on rocks at spring. Photo courtesy of Tian-Xiong Zheng (NICH).

Physiology

Kaul *et al.* (1962) found that regenerating thalli of *Marchantia paleacea* (Figure 97-Figure 99) did not form protonemata, contrasting with regenerants of mosses. Liquid culture caused the production of more gemmae cups. Those gemmae germinated on solid media produced rhizoids, but those in liquid cultures did not, suggesting that these would not be able to attach if they germinated in water in nature. However, that might be remedied if the water level receded. Unlike observations for most *Marchantia*, gemmae frequently germinated within the cups.

Takio *et al.* (1988) demonstrated that *Marchantia paleacea* ssp. *diptera* (Figure 95-Figure 96) could synthesize chlorophyll in the dark as well as in the light in cell suspension culture. This ability continued for the one year of experiments. Doubling time (dry weight) required 1.2 days in the light, but 1.5 days in the dark. Could this behavior permit the species to survive and even grow while temporarily covered by litter or snow? Ngumi *et al.* (1990) further found that when the dark-grown cells were placed in the light, there was no lag phase before they were able to grow photoautotrophically. Their optimum light was 6 W m⁻² or higher in an atmosphere of 2.5% CO₂. Using *Marchantia paleacea* ssp. *diptera*, Taya *et al.* (1995) obtained "good growth" at 1% CO₂. They demonstrated both stimulatory and inhibitory light levels. At levels of 5.4-60 W m⁻² growth rate increased with light intensity; above 60 W m⁻² the rate decreased as the light intensity increased.

One has to ask what advantages a thallose liverwort has when it is able to grow heterotrophically in the dark. This would seem like a suitable trait for those in areas with snow, but this is a species (*Marchantia paleacea* ssp. *diptera*; Figure 95-Figure 96) that is mostly distributed in areas that do not see snow. Ngumi *et al.* (1990) grew it heterotrophically for two years, in the dark, then transferred it to light. The cells started to grow immediately, photoautotrophically, with no lag phase. Optimum growth occurred at 6 W m⁻² and above in an atmosphere of 25% (v/v) CO₂. The growth cycle exhibited high photosynthetic activity (7-88 mol O₂ per kg chlorophyll h⁻¹) with a high chlorophyll content of 17-25 g per kg dry weight. The cells once again returned to heterotrophic growth when placed in the dark.

Eguchi *et al.* (2002) investigated further and found that transfer of *Marchantia paleacea* var. *diptera* (Figure 95-Figure 96) to darkness resulted in a reversible repression in the gene coding for NADPH: protochloride oxidoreductase (EC 1.3.1.33). Further investigation suggested that the photosynthetic electron transport was involved in regulation of the stability of the por transcript involved in the reactions.

Nitrogen processing is also affected by light. Harada *et al.* (1993) found that when dark-grown cells were transferred to the light, the levels of activity of NaR and NiR activities decreased to about half those of cells remaining in the dark. When ammonium was the only nitrogen source supplied, activities of NiR, GS, and NADH-GOGAT were greatly reduced. Fd-GOGAT and GDH activities were not affected as greatly. But all this still begs the question how the dark production of chlorophyll is able to benefit the plant enough for the genes to remain in the population.

Many bryophytes are known for their ability to accumulate heavy metals. Concentrations of Pb, Cu, Ni, and Zn were higher in plant samples of *Marchantia paleacea* (Figure 97-Figure 99) from disturbed sites as compared to less disturbed sites in the Kumaon Hills, India (Sahu *et al.* 2014). Mn concentration, on the other hand, was higher in soil samples as compared to plant samples. Correlation analysis (r) was also performed to investigate the relationship between the soil samples and accumulation of metals in the plant. At the Bhowali taxi stand (Nainital),

Sahu and coworkers recorded significant accumulation ($P < 0.01$) of Pb, Cu, and Ni.

It appears that activation of enzymes might help to protect *Marchantia paleacea* ssp. *diptera* (Figure 95-Figure 96) from some heavy metals (Tanaka *et al.* 1995, 1996, 1998). The cytosolic Cu/Zn-superoxide dismutase is inactivated when the cells are copper deficient and reactivated when copper is added (Tanaka *et al.* 1995). The conversion from the active form to the inactive form of Cu/Zn-SOD by release of copper is the first step in the process of its degradation. Furthermore, a copper chelator causes transformation to the inactive form. Shiono *et al.* (2003) further found that the presence of copper decreases the accumulation of gene transcripts for Fe-SOD, but increases that for CuZn-SOD in a moss, whereas it produces little effect on the gene for Fe-SOD in the liverwort *Marchantia paleacea* ssp. *diptera*.

Shiono *et al.* (2003) found that whereas copper represses the expression of Fe-superoxide dismutase (Fe-SOD) in chloroplasts of the moss *Barbula unguiculata* (Figure 113), this is not the case in *Marchantia paleacea* ssp. *diptera* (Figure 95-Figure 96). Both are typical chloroplastic SODs, comparable to those in tracheophytes. The difference in *M. paleacea* var. *diptera* is that the copper has little effect on the gene for the Fe-SOD in the liverwort. Sakaguchi *et al.* (2004) found that instead the photosynthetic electron transport system differentially regulates the expression of the SOD genes in *M. paleacea* var. *diptera*.



Figure 113. *Barbula unguiculata*, a species in which copper represses the expression of Fe-superoxide dismutase (Fe-SOD) in chloroplasts. Photo by Michael Lüth, with permission.

Suzuki *et al.* (2001) explored the role of **phytochrome** (photoreceptor in plants; sensitive to light in red and far-red region of visible spectrum) and red/far-red reversibility in *Marchantia paleacea* ssp. *diptera* (Figure 95-Figure 96). Hata *et al.* (1997) found that the cell growth rate related so well to the light intensity that it could be used to calculate the light intensity. Chlorophyll content was inversely related to the light intensity.

Siregar *et al.* (2021) demonstrated strong antioxidant activity (LC50=25.25 µm mL⁻¹) for *Marchantia paleacea* (Figure 97-Figure 99). This is important during rehydration, when most bryophytes experience an oxidative

burst. It appears that the oxidative burst prevents bacteria from entering the cells, whereas the antioxidant prevents the high oxygen levels from harming the cells.

Marchantia paleacea (Figure 97-Figure 99) is one of the species that has been used as an indicator of heavy metals (Afroz & Srivastava 2009). Afroz and Srivastava found that it is a good accumulator, and therefore can be useful as an indicator species of heavy metals in the soil.

Sahu *et al.* (2014) similarly touted the use of *Marchantia paleacea* (Figure 97-Figure 99) as a bioindicator. Among their sites in the Kumaon Hills, they found that Pb, Cu, Ni, and Zn concentrations were higher from disturbed sites. Mn, on the other hand, was higher in soil samples than in the liverwort. Lead (Pb) exhibited a significantly higher concentration in the liverworts at a taxi stand.

Adaptations

Marchantia paleacea (Figure 97-Figure 99) requires a somewhat humid environment and can suffer from desiccation (Figure 114). Therefore, it survives with adaptations that permit it to live in places that are wet or sometimes submersed, but that also can become dry for days at a time.



Figure 114. *Marchantia paleacea* in a partially dry condition. Note that the terminal portions, where growth occurs, are still alive. Photo by Jan-Peter Frahm, with permission.

Marchantia paleacea (Figure 97-Figure 99), like other members of the genus, has pores (Figure 115) in the upper epidermis of the thallus, overlying air chambers that have photosynthetic filaments (Apostolakos *et al.* 1982). As noted earlier by Schönherr and Ziegler (1975), the cuticular ledges around the air pores prevent the entry of water into the thallus, thus permitting gas exchange without the interference of water within the thallus. The ledge has a surface of methyl and methylene groups and is covered by a layer of cutin. Schönherr and Ziegler considered these ridges to be "perfect" structures to protect against the entry of water.



Figure 115. *Marchantia paleacea* with gemmae cups, showing thallus pores. Photo by Efrain DeLuna, through Creative Commons.

Apostolakos and coworkers (Galatis *et al.* 1978b; Apostolakos *et al.* 1982; Apostolakos & Galatis 1985a,b,c) have provided us with a detailed study of the development of the air pores and air chambers in *Marchantia paleacea* (Figure 97-Figure 99).

Oil bodies can have multiple benefits to the liverwort plants. Oil bodies nearly fill the thallus cells they occupy in *Marchantia paleacea* (Figure 97-Figure 990) (Galatis *et al.* 1978c). The role of oil bodies was the subject of speculation for some time. Galatis *et al.* (1978a) provided an early assessment of the contents of oil bodies in *Marchantia paleacea*. They observed that the polysaccharidic material is first elaborated in the dictyosomes, then transferred into the oil bodies by their vesicles. Proteins appear to be absent in the oil bodies. However, phenolics and other aromatic compounds seem to be present, at least in the inner oil bodies. These observations suggest as the oil bodies serve as energy reserves and as sites of protective compounds such as phenolics.

One means of conserving water is to grow with overlapping thalli that reduce evaporation (Figure 116-Figure 118). Others grow on a mat of mosses (Figure 119). These mosses provide a sponge that keeps the water in proximity to the rhizoids and that further reduce evaporation from the soil.



Figure 116. *Marchantia paleacea* showing dense, overlapping thalli. Photo by Jan-Peter Frahm, with permission.



Figure 117. *Marchantia paleacea* with gemmae cup and overlapping thalli that reduce evaporation from the soil. Photo by Michael Lüth, with permission.



Figure 118. Overlapping thalli of *Marchantia paleacea* ssp. *diptera*. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 119. *Marchantia paleacea* growing over mosses in India. Photo by Michael Lüth, with permission.

Zheng and Shimamura (2019) suggested that the inward bent receptacle (Figure 120) of *Marchantia paleacea* ssp. *diptera* might help it to withstand the high temperatures and desiccation it experiences in its southern Japan distribution.



Figure 120. Females of *Marchantia paleacea* ssp. *diptera* showing inward bent margins of the female receptacle. Photo courtesy of Tian-Xiong Zheng (NICH).

Reproduction

Marchantia paleacea (Figure 97-Figure 99) is considered to be **dioicous** (Bischler 1986; Perold 1995; Lu & Huang 2017). Like other *Marchantia* species it develops antheridiophores (Figure 121-Figure 122) and archegoniophores (Figure 123-Figure 129). Other than these reproductive branches, the two sexes look the same (Bischler 1986). The life cycle is typical for species of *Marchantia*.



Figure 121. *Marchantia paleacea* male plants with antheridiophores. The two lower receptacles, at this stage looking like females, appear to be young male receptacles. Photo by Naufal Urfi Dhiya'ulhaq, through Creative Commons.



Figure 122. *Marchantia paleacea* males with antheridiophores. Note rows of antheridia on the fingers of the antheridial head. Photo by Naufal Urfi Dhiya'ulhaq, through Creative Commons.



Figure 125. Receptacles of *Marchantia paleacea* ssp. *diptera*, showing how dense these structures can be in the colony. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 123. *Marchantia paleacea* females showing archegonial heads. Photo by Jan-Peter Frahm, with permission.



Figure 126. *Marchantia paleacea* females with archegoniophores. Photo by Efrain DeLuna, through Creative Commons.



Figure 124. *Marchantia paleacea* females, Nichinan, Japan. Photo by Janice Glime.



Figure 127. *Marchantia paleacea* archegonial receptacle. Photo by Efrain DeLuna, through Creative Commons.



Figure 128. Receptacle of *Marchantia paleacea* ssp. *dipthera* with inward bent margins of the receptacle. Photo courtesy of Tian-Xiong Zheng (NICH).



Figure 129. *Marchantia paleacea* females with mature archegoniophores. Photo by 楊玉鳳, through Creative Commons.

Populations are usually small and do not increase in size rapidly (Bischler 1986). Growth seems to be limited by water availability. The lack of outcrossing may account for the limited variability of the species, the absence of ecotypes, and division into only two subspecies.

Male plants in nature are less frequent than female plants (Evans 1917; Bischler 1986). Near the borders of the range, males are almost completely absent (Bischler 1986).

Sporophytes can be found on the Azores islands and in the Caucasus mountains at fairly high elevations (Bischler 1986). Thus, male plants are present along with the females. Is it temperature that controls males, or do they have a dispersal limitation?

But even when both males and females are growing intermixed, only 25-42% of the females produce sporangia (Bischler 1986). Nevertheless, Bischler wondered why it was so high when both sperm and archegonia were elevated on stalked structures. But evidence presented in this chapter demonstrates that sperm, easily splashed, swim

directly to the archegoniophore and may even be carried upward by the same means that water moves upward.

With so few males, especially in some areas, *Marchantia paleacea* (Figure 97-Figure 99), relies to a great degree on gemmae (Figure 130-Figure 135) for local spread. As the gemmae age, the gemmae cups may disintegrate (Figure 136-Figure 138).



Figure 130. *Marchantia paleacea* with gemmae cups. Photo through Creative Commons.



Figure 131. *Marchantia paleacea* with gemmae cups in India. Note the conspicuous pores. Photo by Michael Lüth, with permission.



Figure 132. *Marchantia paleacea* with purple margins (suggesting stress) and gemmae cups. Photo by Maria Emília Martins, through Creative Commons



Figure 133. *Marchantia paleacea* with gemmae. Photo by Jan-Peter Frahm, with permission.



Figure 134. *Marchantia paleacea* with gemmae cups. Photo by Jan-Peter Frahm, with permission.



Figure 135. *Marchantia paleacea* gemmae cup. Photo by 楊玉鳳, through Creative Commons.



Figure 136. *Marchantia paleacea* with deteriorating and nearly empty gemmae cups in Europe. Photo by Michael Lüth, with permission.



Figure 137. *Marchantia paleacea* in Bhutan, with disintegrating gemmae cups. Photo by David Long, with permission.



Figure 138. *Marchantia paleacea* from India showing reddening of borders and disintegrating gemmae. Photo by Michael Lüth, with permission.

Interactions

Bacterial Interactions

Using cultures from gemmae of *Marchantia paleacea* (Figure 97-Figure 99), Alcaraz *et al.* (2018) isolated members of *Bryobacter*, *Lysobacter* (Figure 139),

Methylobacterium (Figure 140), *Paenibacillus* (Figure 141), *Pirellula*, *Rhizobium* (Figure 142-Figure 143), and *Steroidobacter* from the thalli. These bacteria are known to promote plant growth, degrade complex exudates, fix nitrogen, use and convert methylene, and suppress disease.

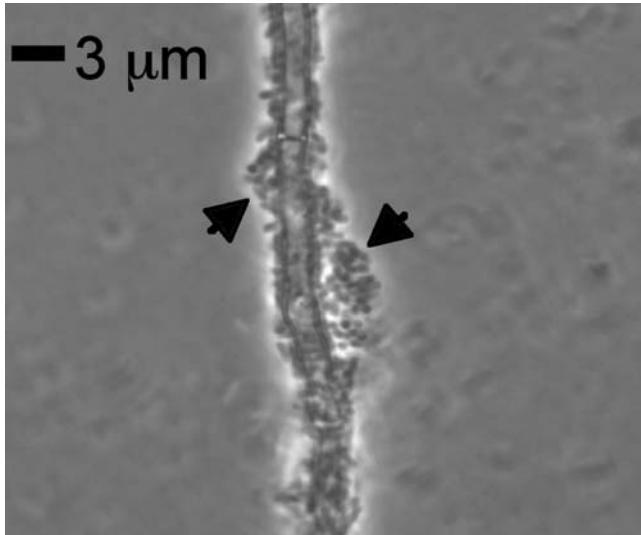


Figure 139. *Lysobacter* sp. hyphae, a genus associated with *Marchantia paleacea*. Photo by Don Kobayashi, through Creative Commons.

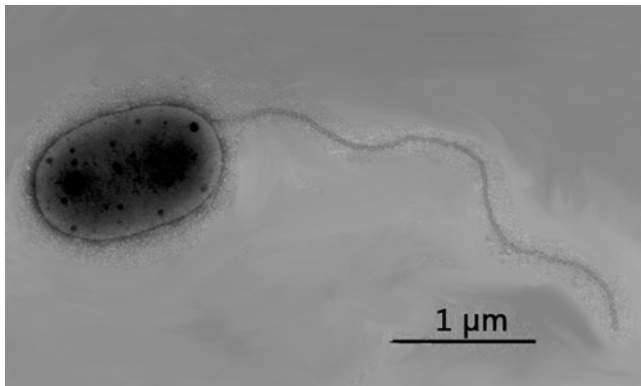


Figure 140. *Methylobacterium jeotgali*, member of a genus associated with *Marchantia paleacea*. Photo from Aslam *et al.* 2007, through Creative Commons.

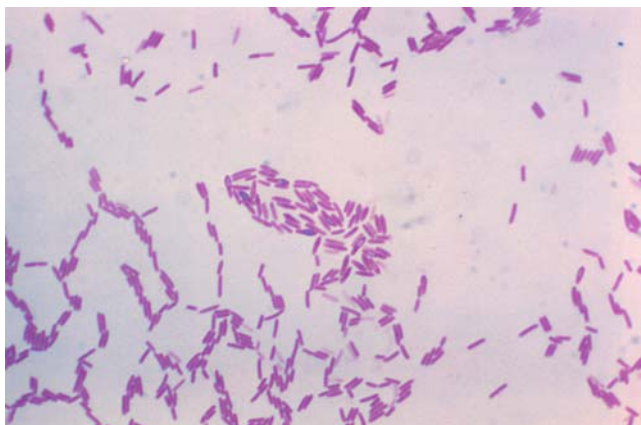


Figure 141. *Paenibacillus polymyxa*; some members of this genus are associated with *Marchantia paleacea*. Photo from CDC, through public domain.



Figure 142. *Rhizobium* root nodule on *Vicia faba* roots; *Rhizobium* is a known associate of *Marchantia paleacea*. Photo by Whitney Cranshaw, through Creative Commons.



Figure 143. *Rhizobium* showing typical red color of nodules. Photo from CSIRO, through Creative Commons.

On the other hand, as in many liverworts, Pinfang *et al.* (2001) found that *Marchantia paleacea* (Figure 97-Figure 99) alcohol extracts were active against the Gram-positive bacterium *Bacillus subtilis* (Figure 144).

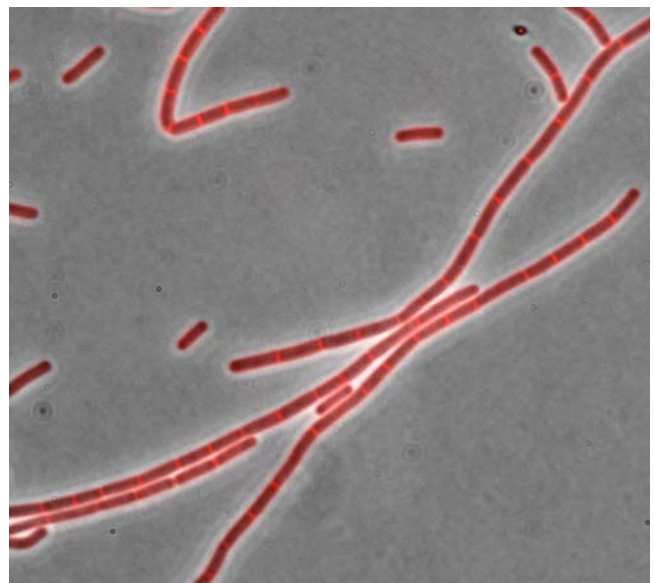


Figure 144. *Bacillus subtilis* stained with Nile Red, a species that is inhibited by alcohol extracts of *Marchantia paleacea*. Photo by EditorInTheRye, through Creative Commons.

In their study of 52 bryophyte species, Banerjee and Sen (1979) found that *Marchantia paleacea* (Figure 97-Figure 99) exhibited the broadest spectrum of antibiotic activity against the 12 microorganisms tested.

Fungal Interactions

Fungi have played a major role in the nutrition of land plants, and *Marchantia paleacea* (Figure 98-Figure 100) is no exception to these benefits. But they also contribute to this relationship. Rich *et al.* (2021) found that in the relationship between this species and its arbuscular mycorrhizal fungi, lipids are transferred from the liverwort to the fungus. Bouwmeester (2021) likewise found that liverwort lipids served to "entice" fungi into the mutualism and were essential to its establishment.

When gemmae (Figure 130-Figure 138) from this liverwort were cultured with tracheophyte roots, it took only 18 days for the liverwort to exhibit arbuscules, indicating fungal colonization (Kobae *et al.* 2019). These arbuscular mycorrhizal fungi entered through the rhizoids.

Field *et al.* (2019) identified the presence of both **Glomeromycotina** and **Mucoromycotina** fungal groups in *Marchantia paleacea* (Figure 97-Figure 99). They found that dual partnerships, hosting two different fungal species, provided complementarity both in greater nutrient pool use and greater allocation of photosynthate to the fungal partners. The partners seemed to provide different functions and the researchers argue for this complementarity as a reason for the success of multiple fungal partners in the plant kingdom. In this case, only the **Mucoromycotina** provided liverworts with substantial access to algal N, unrelated to atmospheric CO₂ concentration. Both fungal symbionts increased P uptake, but **Glomeromycotina** were often more effective.

Kodama *et al.* (2021) identified carotenoid-derived strigolactones in *Marchantia paleacea* (Figure 97-Figure 99). These compounds are known to both serve as hormones to regulate growth and development and to serve as rhizosphere-signalling molecules that induce a symbiotic relationship with arbuscular mycorrhizal fungi. However evidence suggests that in *Marchantia paleacea* the receptor needed for it to serve as a hormone is absent. It does, on the other hand, seem to serve as a mycorrhizal signalling device.

Other Interactions

It appears that *Marchantia paleacea* (Figure 97-Figure 99) might even have allelopathic effects on tracheophytes. Wang *et al.* (2013) found that secondary metabolites, in particular bibenzyls, from callus cultures of this species could inhibit seedling growth of the flowering plant *Arabidopsis thaliana* (Figure 80), with a dose-dependent response.

Biochemistry

Takio *et al.* (1998) found that expression of the cDNA that encodes the NADPH:protochlorophyllide oxidoreductase in *Marchantia paleacea* ssp. *diptera* (Figure 95-Figure 96) is light-dependent, whereas in most tracheophytes it is light-independent.

So *et al.* (2002) verified the presence of marchantin C, isoriccardin C, and the phenanthrene derivative, 2-hydroxy-3,7-dimethoxyphenanthrene in *Marchantia paleacea* (Figure 97-Figure 99). They also described the structures of two novel cyclic bis (bibenzyls), isoriccardinquinone A and B.

Yuan *et al.* (2021) characterized three genes for uridine diphosphate-dependent glycosyl transferases (DBRs) in this species. Wu *et al.* (2018) isolated and characterized two double bond reductases (DBRs). These enzymes are capable of catalyzing the NADPH-dependent reduction of the α,β -unsaturated double bond. The two reductases differed in their behavior and temperature optima. This was the first report of a microbial type of DBR in any plant. Both enzymes are important in protection against environmental stress in liverworts.

Mukhia *et al.* (2014) demonstrated that *Marchantia paleacea* (Figure 97-Figure 99) exhibited potential antioxidant activity and the existence of a variety of phytochemicals involved in scavenging activities.

Sakurai *et al.* (2016) identified the monocyclic monoterpene aldehyde, perillaldehyde, as the major component of volatiles, comprising about 50% of the volatiles in *Marchantia paleacea* subsp. *diptera* (Figure 95-Figure 96). This represents the first report of a perillaldehyde in a liverwort. Minor volatiles included α -selinene, β -selinene, β -caryophyllene, β -pinene, and limonene. But what do they do for the liverwort?

We have named a number of secondary compounds here, but in many cases their role for the liverwort is unclear. It is presumed that most of these serve in protection against pathogens and herbivores, but some might simply be intermediates in a pathway toward another needed compound. Others are apparently part of the ability to survive drought.

The antimicrobial properties (Xia *et al.* 2001) of many of these compounds may be of use to them. Examples include action against the Gram-positive bacterium *Bacillus subtilis* (Figure 144). Xia *et al.* (2001) isolated 2-hydroxy-3, 7-dimethoxyphenanthrene, marchantin C, and isoriccardin C from *Marchantia paleacea* (Figure 97-Figure 99).

Culturing

Awasthi *et al.* (2012) compared sterilization techniques in culturing *Marchantia paleacea* (Figure 97-Figure 99) and several other thallose liverworts. They found the best results with 1% sodium hypochlorite solution for 8-10 seconds. They used repeated sub-culturing to ultimately achieve aseptic cultures. All of these species grew well in half strength Knop's macronutrients + Nitsch's trace elements with 10 ppm freshly prepared ferric citrate under the continuous illumination of 4,500-5,000 lux at 20 \pm 2°C.

Marchantia pappeana (Figure 147)

Distribution

Marchantia pappeana (Figure 145) is widely distributed in tropical Africa. Bischler-Causse (1993) reported it from the Cape Verde Islands to Ethiopia and south to southern Africa, generally at an elevational range of 1000-2500 m. Its distribution in southern Africa

includes the Northern Province, Northern Transvaal, and Eastern Transvaal, Gauteng [PWV], Swaziland, Kwazulu-Natal, eastern [Orange] Free State, and Lesotho (Perold 1995). Müller (1995) recorded it for Zaire. Manyanga and Perold (2004) listed it for Zimbabwe. Enroth *et al.* (2019) recorded it from the Mwatate River in Kenya (see also Chuah-Petiot 2001). The World Flora Online (2022) simply describes the distribution as tropical Africa.



Figure 145. *Marchantia pappeana* along ditch in Ranomafana National Park, Madagascar. Photo courtesy of Catherine Reeb.

Aquatic and Wet Habitats

Marchantia pappeana (Figure 145) often grows in the same localities as *M. debilis* (Figure 28-Figure 36), including vertical soil banks of streams (Figure 146-Figure 148), at waterfalls, at sluice canals, rarely on rotting wood or on rocks, in open grassland, or in forests, sometimes in deep shade (Perold 1995; World Flora Online 2022).

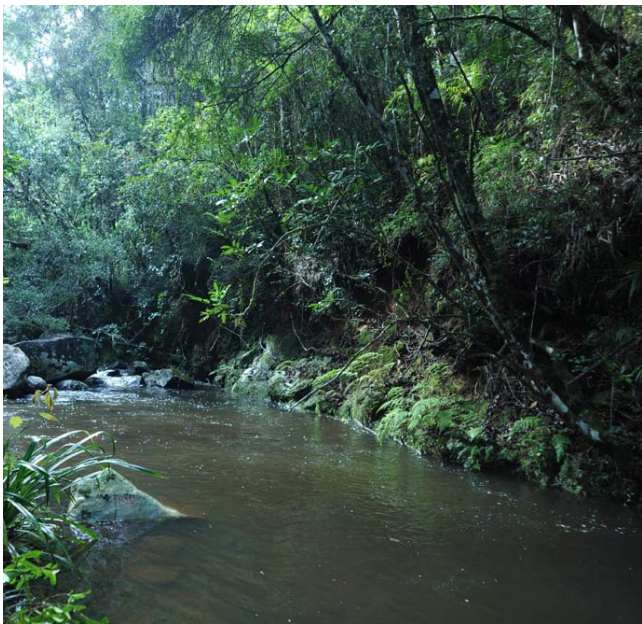


Figure 146. *Marchantia pappeana* habitat on Zahamean riverbanks, Madagascar. Photo courtesy of Catherine Reeb.



Figure 147. *Marchantia pappeana* habitat on Zahamean riverbanks, Madagascar. Photo courtesy of Catherine Reeb.



Figure 148. *Marchantia pappeana* habitat on Zahamean riverbanks, Madagascar. Photo courtesy of Catherine Reeb.

Wigginton (2013) considered *Marchantia pappeana* (Figure 145) on Ascension Island to be a plant that grows mostly on rocks and soil (Figure 146-Figure 149), rarely on tree roots. Catherine Reeb (pers. comm. August 2022) has found it on the walls of ditches (Figure 149).



Figure 149. *Marchantia pappeana* along ditch in Ranomafana National Park, Madagascar. Photo courtesy of Catherine Reeb.

Reproduction

Marchantia pappeana (Figure 145) is **dioicous** (Perold 1995). Male plants produce antheridiophores; females produce archegoniophores (Figure 150). But sometimes male branches appear on the female receptacle (World Flora Online 2022).



Figure 150. *Marchantia pappeana* with archegoniophores along ditch in Ranomafana National Park, Madagascar. Photo courtesy of Catherine Reeb.

Sporangia are elevated on the archegoniophore (Figure 151). These disperse spores that are aided by wiggling elaters (Figure 152) as moisture changes occur.



Figure 151. *Marchantia pappeana* habitat on Zahamena riverbanks, Madagascar. Photo courtesy of Catherine Reeb.



Figure 152. *Marchantia pappeana* with mature sporangia dispersing spores, along ditch in Ranomafana National Park, Madagascar. Photo courtesy of Catherine Reeb.

Like other species of *Marchantia*, gemmae (Figure 153-Figure 154) are important means of asexual reproduction. Their hormone system curtails production of gemmae cups when sexual development begins. Of the 50 specimens Perold (1995) examined, 62% had cupules, 20% had antheridiophores, and 34% had archegoniophores; only 6% had both cupules and sexual structures.



Figure 153. *Marchantia pappeana* with gemmae cups, in river in Zahamena, Madagascar. Photo courtesy of Catherine Reeb.



Figure 154. *Marchantia pappeana* with gemmae cups and distinct pores in river in Zahamena, Madagascar. Photo courtesy of Catherine Reeb.

Fungal Interactions

Strullu-Derrien *et al.* (2014) indicated that the fungal associations in *Horneophyton ligneri* from Rhynie Chert closely resemble the **Glomeromycota** symbionts in *Marchantia pappeana*. Field *et al.* (2015) found that the **Glomeromycota** found in *Marchantia pappeana* (Figure 155-Figure 156) were similar to the structures of the typical arbuscular mycorrhizae occurring in flowering plants. This species lacks studies on the benefits to *Marchantia pappeana* and its partner(s) in this association.

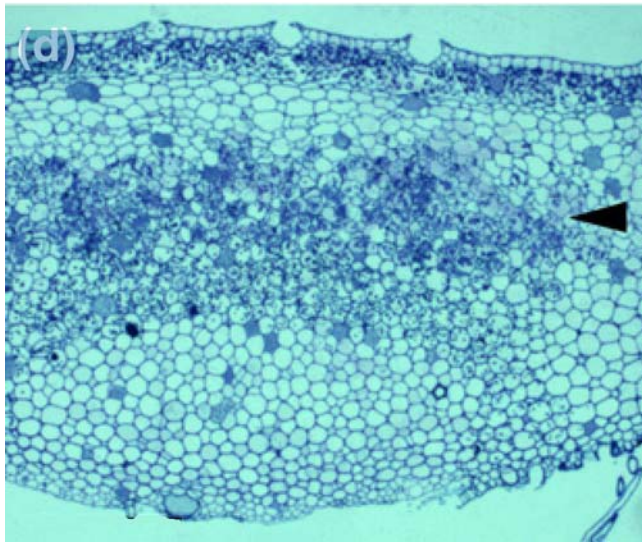


Figure 155. *Marchantia pappeana* mid thallus colonized by **Glomeromycota**. Modified from Strullu-Derrien *et al.* 2014, with permission from Jeff Duckett.

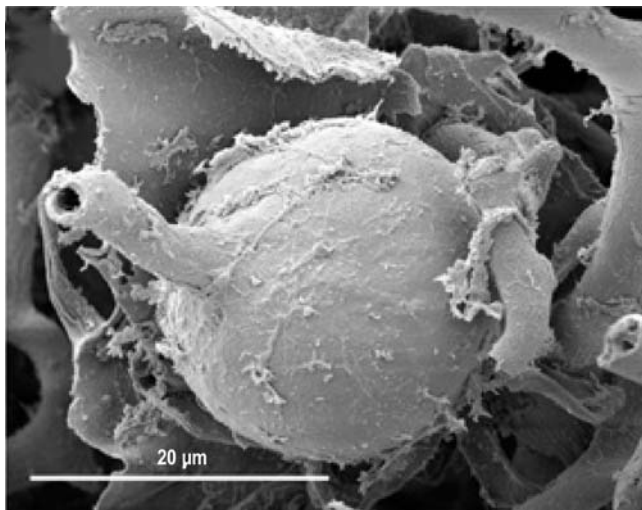


Figure 156. *Marchantia pappeana* colonized by **Glomeromycota** with detail of large vesicle. Modified from Strullu-Derrien *et al.* 2014, with permission from Jeff Duckett.

Biochemistry

Despite its somewhat narrow distribution, *Marchantia pappeana* (Figure 146) has experienced several biochemical studies. Linde *et al.* (2016) reported that sesquiterpene hydrocarbons are characteristic of this species (see also Combrinck *et al.* 2015). Linde *et al.* (2016) found that crude extracts of *M. pappeana* from South Africa (as well as *Pallavicinia lyellii*) had the highest level of antibacterial activity against *Escherichia coli* among the nine liverworts tested. Much remains for us to learn about the role of these sesquiterpenes for the liverwort.

Summary

The species of *Marchantia* covered in this subchapter are those of wet habitats. They may become

submersed occasionally during flooding events, but they do not normally live submersed. To survive in these habitats, they are protected by a thick thallus with air chambers to permit CO₂ entry. Oil bodies serve as a storage organ for polysaccharides and for secondary compounds that help prevent herbivory and protect the thallus from pathogens. A ridge of cutin around the pore prevents water entry. Scales on the lower surface help to move water to the thallus and to retain it in capillary spaces. Some rhizoids anchor the thallus while others help in directing water to the thallus on the lower surface.

They all have gemmae, which seem to be their primary means of reproduction. Yet some are able to colonize rapidly after a fire, suggesting that they are also dispersed by spores. The longevity of spores and gemmae has not been tested.

Secondary compounds, mostly sesquiterpenes and flavonoids, help to protect the plants from herbivory and pathogens.

Acknowledgments

Lars Söderström helped me with puzzling nomenclature. Masaki Shimamura alerted me to nomenclature problems in *Marchantia paleacea* vs. *M. polymorpha* in some important publications. Li Zhang sent me a variety of papers and reviewed my treatment of *Marchantia emarginata*. Catherine Reeb introduced me to *Marchantia debilis* and *M. pappeana* as species of wet habitats and provided me with many images and habitat information. Thank you to Tian-Xiong Zheng and for sending me much needed images. And thank you to the many photographers who have given me blanket permission to use their images or who have put them in Creative Commons.

Literature Cited

- Afroz, A. and Srivastava, S. C. 2009. *Marchantia paleacea* Bert. as an indicator of heavy metal pollution. Indian J. Forest. 32: 465-470.
- Ahmad, S. M. 1981. A historical outline of researches on spore germination and gametophyte development in Marchantiales with special reference to Indian studies. Misc. Bryol. Lichenol. 9: 49-54.
- Alcaraz, L. D., Peimbert, M., Barajas, H. R., Dorantes-Acosta, A. E., Bowman, J. L., and Arteaga-Vázquez, M. A. 2018. *Marchantia* liverworts as a proxy to plants' basal microbiomes. Sci. Rept. 8(1): 1-12.
- Anchang, K. Y. and Simonsen, H. T. 2019. Developments and perspectives in bryophyte biotechnology in Sub-Saharan Africa. In: Jacob-Lopes, E. and Zepka, L. Q. (eds.). Biotechnology and Bioengineering. IntechOpen.
- Anchang, K. Y., Novaković, M., Bukvički, D., and Asakawa, Y. 2016. Bis-benzyls from the Cameroon liverwort *Marchantia debilis*. Nat. Prod. Comm. 11: 1317-1318.
- Apostolakis, P. and Galatis, B. 1985a. Studies on the development of the air pores and air chambers of *Marchantia paleacea* II. Ultrastructure of the initial aperture formation with particular reference to cortical microtubule organizing centers. Can. J. Bot. 63: 744-756.

- Apostolakos, P. and Galatis, B. 1985b. Studies on the development of the air pores and air chambers of *Marchantia paleacea*, III. Microtubule organization in preprophase-prophase initial aperture cells – formation of incomplete preprophase microtubule bands. *Protoplasma* 128: 120-135.
- Apostolakos, P. and Galatis, B. 1985c. Studies on the development of air pores and air chambers of *Marchantia paleacea* IV. Cell plate arrangement in the initial aperture cells. *Protoplasma* 128: 136-146.
- Apostolakos, P., Galatis, B., and Mitrakos, K. 1982. Studies on the development of the air pores and air chambers of *Marchantia paleacea*: 1. Light microscopy. *Ann. Bot.* 49: 377-396.
- Asakawa, Y. 2021. Application of phytochemicals from bryophytes to foods, cosmetics, and medicine. *Bildiri Özetleri Kitabı* 11. In: Nazar, N., Bhamra, S. K., Masiero, E., Arroo, R., and Sgamma, T. Characterisation of trichomes morphology and density in the genus *Ocimum* L. 51st International Symposium on Essential Oils.
- Asakawa, Y. and Campbell, E. O. 1982. Terpenoids and bibenzyls from some New Zealand liverworts. *Phytochemistry* 21: 2663-2667.
- Aslam, Z., Lee, C. S., Kim, K.-H., Im, W.-T., Ten, L. N., and Lee, S.-T. 2007. *Methylobacterium jeotgali* sp. nov., a nonpigmented, facultatively methylotrophic bacterium isolated from jeotgal, a traditional Korean fermented seafood. *Internat. J. Syst. Evol. Microbiol.* 57: 566-571.
- Awasthi, V., Nath, V., and Asthana, A. K. 2012. *In vitro* regeneration and micropropagation of some liverworts from vegetative explants. *Natl. Acad. Sci. Lett.* 35(1): 7-12.
- Awouafack, M. D., Taneb, P., Kuetec, V., and Eloffa, J. N. 2013. Sesquiterpenes from the medicinal plants of Africa. *Pharmacology and chemistry*. In: Kuate, V. (ed.). *Medicinal Plant Research in Africa*. Elsevier, New York, pp. 33-103.
- Banerjee, R. D. and Sen, S. P. 1979. Antibiotic activity of bryophytes. *Bryologist* 82: 141-153.
- Baylis, G. T. S. 1970. Root hairs and phycomycetous mycorrhizas in phosphorus-deficient soil. *Plant Soil* 33: 713-716.
- Bischler, H. 1986. Geographic variation and species structure in *Marchantia paleacea* Bertol. *Hikobia* 9: 345-351.
- Bischler, H. 1988. *Marchantia paleacea* Bertol. – karyotype analysis. *Beih. Nova Hedw.* 90: 95-100.
- Bischler-Causse, H. 1989. *Marchantia* L. The Asiatic and Oceanic taxa. *Bryophyt. Biblio.* 38: 1-317.
- Bischler-Causse, H. 1993. *Marchantia* L. The European and African taxa. *Bryophyt. Biblio.* 45: 129 pp.
- Blake-Mahmud, J. and Struwe, L. 2020. When the going gets tough, the tough turn female: Injury and sex expression in a sex-changing tree. *Amer. J. Bot.* 107: 339-349.
- Borovichev, E. A. and Bakalin, V. A. 2014. A survey of Marchantiales from the Russian Far East III. Note on *Marchantia paleacea* Bertol. *Arctoa* 23: 25-28.
- Bouwmeester, H. J. 2021. Plant lipids enticed fungi to mutualism. *Science* 372: 789-790.
- Brasell, H. M. and Mattay, J. P. 1984. Colonization by bryophytes of burned *Eucalyptus* forest in Tasmania, Australia: Changes in biomass and element content. *Bryologist* 87: 302-307.
- Brasell, H. M., Daviesandj, S. K., and Mattay, P. 1986. Nitrogen fixation associated with bryophytes colonizing burnt sites in Southern Tasmania, Australia. *J. Bryol.* 14: 139-149.
- Brzyski, J. R., Taylor, W., and McLetchie, D. N. 2014. Reproductive allocation between the sexes, across natural and novel habitats, and its impact on genetic diversity. *Evol. Ecol.* 28: 247-261.
- Brzyski, J. R., Stieha, C. R., and Nicholas McLetchie, D. 2018. The impact of asexual and sexual reproduction in spatial genetic structure within and between populations of the dioecious plant *Marchantia inflexa* (Marchantiaceae). *Ann. Bot.* 122: 993-1003.
- Campbell, A. G. and Franklin, J. F. 1979. Riparian vegetation in Oregon's western Cascade Mountains: Composition, biomass, and autumn phenology. *Bulletin* 14. Coniferous Forest Biome, Ecosystem Analysis Studies, U.S./International Biological Program, 90 pp.
- Campbell, D. H. 1908. Collecting liverworts in Java. *Torreyia* 8(5): 103-110.
- Campbell, E. O. 1965. *Marchantia* species of New Zealand. *Tuatara* 13(2): 122-126.
- Campbell, E. O., Markham, K. R., Moore, N. A., Porter, L. J., and Wallace, J. W. 1979. Taxonomic and phylogenetic implications of comparative flavonoid chemistry of species in the family Marchantiaceae. *J. Hattori Bot. Lab.* 45: 185-199.
- Campos, L. V. 2014. Liverworts and mosses diversity of peatlands from Nevado del Tolima, Colombia. *Caldasia* 36: 217-229.
- Carter, J. L. and Romine, K. G. 1969. The effects of long and short photoperiods on the rate of growth and gemmae cup production in *Marchantia polymorpha* L. *Trans. Kans. Acad. Sci.* 72(1): 98-107.
- Chang, E. H., Fuselier, L., and Malott, M. 2006. Ecological genomics: Analyzing genetic data from liverworts using ISSRs and the CEQ 8000. *FASEB J.* 20: A908-A908.
- Chopra, R. N. and Dhingra-Babbar, S. 1986. Studies on callus induction, its growth and differentiation in *Marchantia palmata* Nees. I. Effect of some amino acids, complex organic substances and activated charcoal. *J. Hattori Bot. Lab.* 60: 193-202.
- Chopra, R. N. and Kumra, P. K. 1988. *Biology of Bryophytes*. New Age International Publishers; Wiley & Sons, NY, 350 pp.
- Chuah-Petiot, M. S. 2001. Contribution to the bryoflora of Kenya. *Trop. Bryol.* 20: 31-38.
- Combrinck, S., Linde, J., Ludwiczuk, A., Vuuren, S. Van, Rooy, J. Van, and Mokgalaka, N. S. 2015. Chemical constituents and biological properties of liverworts from South Africa. *Plant. Med.* 81(16): PM_101.
- Convey, P. and Lewis Smith, R. I. 2006. Geothermal bryophyte habitats in the South Sandwich Islands, maritime Antarctic. *J. Veg. Sci.* 17: 529-538.
- Cooper, R. L., Thomas, M. A., and McLetchie, D. N. 2022a. Impedance measures for detecting electrical responses during acute injury and exposure of compounds to roots of plants. *Meth. Protocols* 5(4): 56, 19 pp.
- Cooper, R. L., Thomas, M. A., Vascassenno, R. M., Brock, K. E., and McLetchie, D. N. 2022b. Measuring electrical responses during acute exposure of roots and rhizoids of plants to compounds using a flow-through system. *Meth. Protocols* 5(4): 62.
- Crawford, J. T., Loken, L. C., West, W. E., Crary, B., Spawn, S. A., Gubbins, N., Jones, S. E., Streigl, R. G., and Stanley, E. H. 2017. Spatial heterogeneity of within-stream methane concentrations. *J. Geophys. Res. Biogeosci.* 122: 1036-1048.
- Crowley, P. H., Davis, H. M., Ensminger, A. L., Fuselier, L. C., Jackson, J. K., and McLetchie, D. N. 2005a. A general model of local competition for space. *Ecol. Lett.* 8(2): 176-188.

- Crowley, P., Stieha, C. R., and McLetchie, D. N. 2005b. Overgrowth competition, fragmentation and sex-ratio dynamics: A spatially explicit, sub-individual-based model. *J. Theor. Biol.* 233(1): 25-42.
- Cutting, E. M. 1910. On androgynous receptacles in *Marchantia*. *Ann. Bot.* 24: 349-357.
- Cuvertino-Santoni, J., Asakawa, Y., Nour, M., and Montenegro, G. 2017. Volatile chemical constituents of the Chilean bryophytes. *Nat. Prod. Comm.* 12: 1929-1932.
- Davey, M. C. 1997. Effects of physical factors on photosynthesis by the Antarctic liverwort *Marchantia berteroa*. *Polar Biol.* 17(3): 219-227.
- Dawson, T. E. and Ehleringer, J. R. 1993. Gender-specific physiology, carbon isotope discrimination, and habitat distribution in boxelder, *Acer negundo*. *Ecology* 74: 798-815.
- Driessen, M. 2009. Dalco Creek – 15 March 2009 Excursion report. *Tasmanian Field Nat. Club Bull.* 334: 4.
- Duckett, J., Russell, S., Upson, R., and Tangney, R. 2012. Lower plants inventory and conservation in the Falkland Islands. *Field Bryol.* 106: 32-42.
- Duncan, D. and Dalton, P. L. 1982. Recolonisation by bryophytes following fire. *J. Bryol.* 12: 53-63.
- Eguchi, S., Takano, H., Ono, K., and Takio, S. 2002. Photosynthetic electron transport regulates the stability of the transcript for the protochlorophyllide oxidoreductase gene in the liverwort, *Marchantia paleacea* var. *diptera*. *Plant Cell Physiol.* 43: 573-577.
- Enroth, J., Pócs, T., He, X., Nyqvist, P., Stam, Å., Malombe, I., and Rikkinen, J. 2019. An annotated checklist of the bryophytes of Taita Hills region, Kenya. *Acta Musei Siles. Sci. Nat.* 68: 53-66.
- Evans, A. W. 1917. The American species of *Marchantia*. *Trans. Conn. Acad.* 21: 201-313.
- Fatma, F. N. 2018. Isolasi metabolit sekunder isolat MEC 2 dari kapang endofit lumut hati *Marchantia emarginata* Reinw., Blume and Nees. Bachelor's thesis, Fakultas Ilmu Kesehatan UIN Syarif Hidayatullah Jakarta.
- Field, K. J., Pressel, S., Duckett, J. G., Rimington, W. R., and Bidartondo, M. I. 2015. Symbiotic options for the conquest of land. *Trends Ecol. Evol.* 30: 477-486.
- Field, K. J., Bidartondo, M. I., Rimington, W. R., Hoysted, G. A., Beerling, D., Cameron, D. D., Duckett, J. G., Leake, J. R. and Pressel, S. 2019. Functional complementarity of ancient plant-fungal mutualisms: contrasting nitrogen, phosphorus and carbon exchanges between *Mucoromycotina* and *Glomeromycotina* fungal symbionts of liverworts. *New Phytol.* 223: 908-921.
- Freeman, D. C., McArthur, E. D., Harper, K. T., and Blauer, A. C. 1981. Influence of environment on the floral sex ratio of monoecious plants. *Evolution* 35: 194-197.
- Fuselier, L. 2008. Variation in life history characteristics between asexual and sexual populations of *Marchantia inflexa*. *Bryologist* 111: 248-259.
- Fuselier, L. and McLetchie, N. 2002. Maintenance of sexually dimorphic pre-adult traits in *Marchantia inflexa* (Marchantiaceae). *Amer. J. Bot.* 89: 592-601.
- Fuselier, L. and McLetchie, D. N. 2004. Microhabitat and sex distribution in *Marchantia inflexa*, a dioicous liverwort. *Bryologist* 107: 345-356.
- Galatis, B., Apostolakis, P., and Katsros, C. 1978a. Histochemical studies on the oil bodies of *Marchantia paleacea* Bert. *Protoplasma* 97: 13-29.
- Galatis, B., Apostolakis, P., and Katsros, C. 1978b. Ultrastructural studies on the oil bodies of *Marchantia paleacea* Bert. I. Early stages of oil-body cell differentiation: Origination of the oil body. *Can. J. Bot.* 56: 2252-2267.
- Galatis, B., Katsaros, C., and Apostolakis, P. 1978c. Ultrastructural studies on the oil bodies of *Marchantia paleacea* Bert. II. Advanced stages of oil body differentiation: Synthesis of lipophilic material. *Can. J. Bot.* 56: 2268-2285.
- Garcia-Ramos, G., Stieha, C., McLetchie, N., and Crowley, P. 2002. Maintenance of sexes under metapopulation dynamics: Modeling a liverwort case. Abstracts of the 87th Annual Meeting of the Ecological Society of America and the 14th Annual International Conference of the Society for Ecological Restoration, August 4-9, 2002, Tucson, AZ. Accessed on 3 July 2004, at <<http://abstracts.co.allenpress.com/pweb/esa2002/document/?ID=18119>>.
- Garcia-Ramos, G., Stieha, C., McLetchie, D. N., and Crowley, P. H. 2007. Persistence of the sexes in metapopulations under intense asymmetric competition. *J. Ecol.* 95: 937-950.
- Golenberg, E. M. and West, N. W. 2013. Hormonal interactions and gene regulation can link monoecy and environmental plasticity to the evolution of dioecy in plants. *Amer. J. Bot.* 100: 1022-1037.
- Graham, L. E., Graham, J. M., Wilcox, L. W., Cook, M. E., Arancibia-Avila, P., and Knack, J. J. 2018. Evolutionary roots of plant microbiomes and biogeochemical impacts of nonvascular autotroph-microbiome systems over deep time. *Internat. J. Plant Sci.* 179: 505-522.
- Green, T. G. A. and Lange, O. L. 1995. Photosynthesis in poikilohydric plants: A comparison of lichens and bryophytes. Chapt. 16. In: Schulze, D.-E. and Caldwell, M. M. (eds.). *Ecophysiology of Photosynthesis*. Springer, Berlin, pp. 319-341.
- Groen, K. E., Stieha, C. R., Crowley, P. H., and McLetchie, D. N. 2010a. Sex-specific plant responses to two light levels in the liverwort *Marchantia inflexa* (Marchantiaceae). *Bryologist* 113: 81-89.
- Groen, K. E., Stieha, C. R., Crowley, P. H., and McLetchie, D. N. 2010b. Sex-specific plant responses to light intensity and canopy openness: Implications for spatial segregation of the sexes. *Oecologia* 162: 561-570.
- Halloy, S. 1991. Islands of life at 6000 m altitude: The environment of the highest autotrophic communities on Earth (Socompa Volcano, Andes). *Arct. Alp. Res.* 23: 247-262.
- Harada, M., Takio, S., and Takami, S. 1993. Nitrogen-assimilating enzymes in chlorophyllous cells of the liverwort, *Marchantia paleacea* var. *diptera*, grown in the dark. *J. Plant Physiol.* 141: 527-532.
- Hassel de Menendez, G. G. 1962. Estudio de last Anthocerotales y Marchantiales de la Argentina. *Op. Lill.* 7: 1-297.
- Hata, J. I., Toyo-oka, Y., Taya, M., and Tone, S. 1997. A strategy for control of light intensity in suspension culture of photoautotrophic liverwort cells, *Marchantia paleacea* var. *diptera*. *J. Chem. Eng. Japan* 30: 315-320.
- Herzog, T. 1934. Die Bryophyten der Andenreissen von C. Troll (Bolivia, Columbia, Panama), 36 pp.
- Ho, B. C. 2013. The liverwort genus *Marchantia* L. (Marchantiophyta: Marchantiopsida) in Singapore, with a new species record. *Nat. Singapore* 6: 187-190.
- Hodgetts, N. G., Matcham, H. W., and Duckett, J. G. 1999. Bryophytes collected in Lesotho, the Natal Drakensberg and the Orange Free State, southern Africa. *J. Bryol.* 21: 133-155.

- Huang, W.-J., Wu, C.-L., Lin, C.-W., Chi, L.-L., Chen, P.-Y., Chiu, C.-J., Huang, C.-Y., and Chen, C.-N. 2010. Marchantin A, a cyclic bis (bibenzyl ether), isolated from the liverwort *Marchantia emarginata* subsp. *tosana* induces apoptosis in human MCF-7 breast cancer cells. *Cancer Lett.* 291(1): 108-119.
- Iqbal, S. H., Nasim, G., and Jahan, S. 1988. II. Vesicular-arbuscular [sic] mycorrhizal fungi associated with a bryophyte: *Marchantia palmata*. *Biologia (Lahore)* 34: 275-278.
- James, J. M., Aiswarya, M. S., and Vishnupriya, K. S. 2020. A comparative phytochemical and antibacterial analysis of two selected liverworts (*Lunularia cruciata* (L.) Dum ex. Lindb. and *Marchantia emarginata*) of Kerala. *Plant Arch.* 20: 6959-6965.
- Jantwal, A., Rana, M., Joshi Rana, A., Upadhyay, J., and Durgapal, S. 2019. Pharmacological potential of genus *Marchantia*: A Review. *J. Pharmacog. Phytochem.* 8: 641-645.
- Johnson, A. 1958. An account of the thallose liverworts found in Malaya. *Malay. Nat. J.* 13: 52-69 + 1 pl.
- Johnson, P. N. 1977. Mycorrhizal Endogonaceae in a New Zealand forest. *New Phytol.* 78: 161-170.
- Kaul, K. N., Mitra, G. C., and Tripathi, B. K. 1962. Responses of *Marchantia* in aseptic culture to well-known auxins and antiauxins. *Ann. Bot.* 26: 447-466.
- Knack, J. J., Wilcox, L. W., Delaux, P. M., Ané, J. M., Piotrowski, M. J., Cook, M. E., Graham, J. M., and Graham, L. E. 2015. Microbiomes of streptophyte algae and bryophytes suggest that a functional suite of microbiota fostered plant colonization of land. *Internat. J. Plant Sci.* 176(5): 405-420.
- Kobae, Y., Ohtomo, R., Morimoto, S., Sato, D., Nakagawa, T., Oka, N., and Sato, S. 2019. Isolation of native arbuscular mycorrhizal fungi within young thalli of the liverwort *Marchantia paleacea*. *Plants* 8(6): 142.
- Kodama, K., Rich, M. K., Yoda, A., Shimazaki, S., Xie, X., Akiyama, K., Mizuno, Y., Komatsu, A., Luo, Y., Suzuki, H., Kmeoka, H., Libourel, C., Keller, J., Sakakibara, K., Nishiyama, T., Nakawa, T., Mashiguchi, K., Uchida, K., Yoneyama, K., Tanaka, Y., Yamaguchi, S., Shimamura, M., Delaux, P.-M., Nomura, T., and Kyoizuka, J. 2021. An ancestral function of strigolactones as symbiotic rhizosphere signals. *bioRxiv*. <<https://doi.org/10.1101/2021.08.20.457034>>.
- Kumar, K., Nath, V., and Asthana, A. K. 2007. Concept of bryophytes in classical text of Indian ethnobotanical prospective. In: Nath, V. and Asthana, A. K. (eds.). *Current Trends in Bryology*. Bishen Singh Mahendra Pal Singh. Dehra Dun, India, pp. 215-220.
- Kumra, S. and Chopra, R. N. 1989a. Effect of some cytokinins on growth and gemma cup formation in *Marchantia palmata* Nees. *J. Hattori Bot. Lab.* 67: 331-334.
- Kumra, S. and Chopra, R. N. 1989b. Studies on growth and gemma cup formation in *Marchantia palmata* Nees. *Beitr. Biol. Pflanzen* 64: 243-252.
- Lay, C. M., Sindall, M., McLetchie, S. K., and McLetchie, D. N. 2022. Sexual and asexual offspring germination in a tropical liverwort is mediated by phytochromes. *Bryologist*, 125: 328-336.
- Lee, D. W. and Graham, R. 1986. Leaf optical properties of rainforest sun and extreme shade plants. *Amer. J. Bot.* 73: 1100-1108.
- Léonard, J. 1994. La végétation périodiquement inondée des falaises gréseuses de Yanonge (Yangambi-Kisangani, Zaïre). *Bull. Natl. Plant. Belg.* 63: 101-123.
- Lewis Smith, R. I. 2005a. The thermophilic bryoflora of Deception Island: unique plant communities as a criterion for designating an Antarctic Specially Protected Area. *Antarc. Sci.* 17(1): 17-27.
- Lewis Smith, R. I. 2005b. Bryophyte diversity and ecology of two geologically contrasting Antarctic islands. *J. Bryol.* 27: 195-206.
- Linde, J., Combrinck, S., Vuuren, S. Van, Rooy, J. Van, Ludwiczuk, A., and Mokgalaka, N. 2016. Volatile constituents and antimicrobial activities of nine South African liverwort species. *Phytochem. Lett.* 16: 61-69.
- Little, E. L. 1936. The liverworts of Oklahoma. *Bryologist* 39: 25-34.
- Lu, Y. W. and Huang, S. F. 2017. *Marchantia* L. (Marchantiaceae-Marchantiophyta) in Taiwan. *Taiwania* 62(1): 55-62.
- Lüth, M. and Schafer-Verwimp, A. 2004. Additions to the bryophyte flora of the Neotropics. *Trop. Bryol.* 25: 7-17.
- Manyanga, P. and Perold, S. M. 2004. A checklist of Zimbabwean bryophytes. In: Perold, S. M. (ed.). *Southern African Botanical Diversity Network Report No. 21*, 20 pp.
- Markham, K. R. and Porter, L. J. 1975. Isoscutellarein and hypolaetin 8-glucuronides from the liverwort *Marchantia berteriana*. *Phytochemistry* 14: 1093-1097.
- Markham, K. R. and Porter, L. J. 1978. Production of an aurone by bryophytes in the reproductive phase. *Phytochemistry* 17: 159-160.
- Markham, K. R., Moore, N. A., and Porter, L. J. 1978. Changeover in flavonoid pattern accompanying reproductive structure formation in a bryophyte. *Phytochemistry* 17: 911-913.
- Marks, R. A., Smith, J. J., Cronk, Q., and McLetchie, D. N. 2018. Variation in the bacteriome of the tropical liverwort, *Marchantia inflexa*, between the sexes and across habitats. *Symbiosis* 75(2): 93-101.
- Marks, R. A., Smith, J. J., Cronk, Q., Grassa, C. J., and McLetchie, D. N. 2019a. Genome of the tropical plant *Marchantia inflexa*: implications for sex chromosome evolution and dehydration tolerance. *Sci. Repts.* 9(1): 1-13.
- Marks, R. A., Pike, B. D., and Nicholas McLetchie, D. 2019b. Water stress tolerance tracks environmental exposure and exhibits a fluctuating sexual dimorphism in a tropical liverwort. *Oecologia* 191: 791-802.
- Marks, R. A., Smith, J. J., VanBuren, R., and McLetchie, D. N. 2021. Expression dynamics of dehydration tolerance in the tropical plant *Marchantia inflexa*. *Plant J.* 105(1): 209-222.
- McLetchie, D. N. and Puterbaugh, M. N. 2000. Population sex ratios, sex-specific clonal traits and tradeoffs among these traits in the liverwort *Marchantia inflexa*. *Oikos* 90: 227-237.
- McLetchie, D. N., García-Ramos, G., and Crowley, P. H. 2002. Local sex-ratio dynamics: A model for the dioecious liverwort *Marchantia inflexa*. *Evol. Ecol.* 15: 231-254.
- Meeks, J. C. 2018. Cyanobacterial-bryophyte associations. *CRC Handbook of Symbiotic Cyanobacteria*, pp.43-63.
- Melati, R., Sugito, Y., Aini, N., and Nihayati, E. 2019. Quality optimization of Luja plant (*Peristrophe bivalvis* Merrill) by means of light intensity manipulation and identification of substance with pigment potential. *Biosci. Res.* 16(2): 1660-1667.
- Minibayeva, F. and Beckett, R. P. 2001. High rates of extracellular superoxide production in bryophytes and lichens, and an oxidative burst in response to rehydration following desiccation. *New Phytol.* 152: 333-341.

- Moore, J. D., Kollar, L. M., and McLetchie, D. N. 2016. Does selection for gamete dispersal and capture lead to a sex difference in clump water-holding capacity? *Amer. J. Bot.* 103: 1449-1457.
- Mukhia, S., Mandal, P., Singh, D. K., Singh, D., and Choudhury, D. 2014. *In-vitro* free-radical scavenging potential of three liverworts of Darjeeling Himalaya. *Internat. J. Pharm. Sci. Res.* 5: 4552-4561.
- Müller, F. 1995. Neue und bemerkenswerte Moosfunde aus Zaire. *Trop. Bryol.* 10: 81-90.
- Nakayama, T. 2022. Biochemistry and regulation of aurone biosynthesis. *Biosci. Biotech. Biochem.* 86: 557-573.
- National Geographic. 2022. Atmosphere Resource Library, encyclopedic entry. Accessed 26 August 2022 at <<https://education.nationalgeographic.org/resource/atmosphere>>.
- Ngumi, V. W., Takio, S., and Takami, S. 1990. Photoautotrophic growth in cell suspension culture from the liverwort, *Marchantia paleacea* var. *diptera*. *J. Plant Physiol.* 137: 25-28.
- Perold, S. M. 1995. Studies in the Marchantiales (Hepaticae) from southern Africa 9. The genus *Marchantia* and its five local species. *Bothalia* 25: 183-204.
- Phephu, Nonkululo. 2012a. *Marchantia berteroaana* | PlantZ Africa. <http://opus.sanbi.org/bitstream/20.500.12143/3591/1/MarchantiaBerteroana_PlantZAfrica.pdf>.
- Phephu, Nonkululo. 2012b. *Marchantia berteroaana*. PlantZAfrica.com. Accessed 4 August 2022 at <<http://pza.sanbi.org/marchantia-berteroana>>.
- Pócs, T. and Lye, K. A. 1999. New records and additions to the hepatic flora of Uganda 2. *Trop. Bryol.* 17: 23-34.
- Reeb, C., Marline, L., Rabeau, L., Andriamanantena, A., Andriamiarisoa, R. L., Ranarijaona, H. L., and Pócs, T. 2018. A survey of Marchantiales from Madagascar. *Acta Biol. Plant. Agr.* 6(1): 3-72.
- Rich, M. K., Vigneron, N., Libourel, C., Keller, J., Xue, L., Hajheidari, M., Radhakrishnan, G. V., Ru, A. le, Diop, S. I., Conti, E., Duijsings, D., Batut, A., Faouder, P. le, Kodama, K., Kyojuka, J., Sallet, E., Bécard, G., Rodriguez-Franco, M., Ott, T., Bertrand-Michel, J., Oldroyd, G. D., Szövényi, P., Bucher, M., and Delaux, P. M. 2021. Lipid exchanges drove the evolution of mutualism during plant terrestrialization. *Science* 372: 864-868.
- Ruttner, F. 1955. Zur Ökologie tropischer Wassermoos. [On the ecology of tropical water moss.]. *Arch. Hydrobiol. (Suppl.)* 21: 343-381.
- Sahu, V., Nath, V., Asthana, A. K., and Yunus, M. 2014. *Marchantia paleacea* Bertol. as quantitative biomonitor of atmospheric heavy metals deposition. *J. Recent Adv. Appl. Sci.* 29: 22-27.
- Sakaguchi, S., Fukuda, T., Takano, H., Ono, K., and Takio, S. 2004. Photosynthetic electron transport differentially regulates the expression of superoxide dismutase genes in liverwort, *Marchantia paleacea* var. *diptera*. *Plant Cell Physiol.* 45: 318-324.
- Sakurai, K., Tomiyama, K., Kawakami, Y., Ochiai, N., Yabe, S., Nakagawa, T., and Asakawa, Y. 2016. Volatile components emitted from the liverwort *Marchantia paleacea* subsp. *diptera*. *Nat. Prod. Comm.* 11(2): 1934578X1601100232.
- Schönherr, J. and Ziegler, H. 1975. Hydrophobic cuticular ledges prevent water entering the air pores of liverwort thalli. *Planta* 124: 51-60.
- Scott, G. A. 1963. Suppression of gemma-cups in *Marchantia* by high humidity. *Nature* 200: 1123-1123.
- Shiono, T., Nakata, M., Yamahara, T., Matsuzaki, M., Deguchi, H., and Satoh, T. 2003. Repression by Cu of the expression of Fe-superoxide dismutase of chloroplasts in the moss *Barbula unguiculata* but not in the liverwort *Marchantia paleacea* var. *diptera*. *J. Hattori Bot. Lab.* 93:141-153.
- Singh, D. and Singh, D. K. 2013. An Appraisal of the genus *Marchantia* in India with a note on *Marchantia emarginata* subspecies *emarginata* in Indian Himalayan Region. *Proc. Nat. Acad. Sci., India B Biol. Sci.* 83(1): 15-26.
- Siregar, E. S., Ariyanti, N. S., and Tjitrosoedirdjo, S. S. 2013. The liverwort genus *Marchantia* (Marchantiaceae) of Mount Sibayak North Sumatra, Indonesia. *Biotropia* 20(2): 73-80.
- Siregar, E. S., Pasaribu, N., and Sofyan, M. Z. 2020. Morphological Study on *Marchantia emarginata* Reinw., Blume et Nees in North Sumatra Indonesia. In: *Proceedings of the International Conference of Science, Technology, Engineering, Environmental and Ramification Researches (ICOSTEERR 2018) - Research in Industry 4.0*, pp. 1073-1075.
- Siregar, E. S., Pasaribu, N., and Sofyan, M. Z. 2021. Antioxidant activity of liverworts *Marchantia paleacea* Bertol. from North Sumatra Indonesia. In: *IOP Conference Series: Earth and Environmental Science* 713, No. 1, p. 012061. IOP Publishing.
- So, M. L., Chan, W. H., Xia, P. F., and Cui, Y. 2002. Two new cyclic bis(bibenzyl)s, isoriccardinquinone A and B from the liverwort *Marchantia paleacea*. *Nat. Prod. Lett.* 16(3): 167-171.
- Solberg, C. O. 2000. Spread of *Staphylococcus aureus* in hospitals: Causes and prevention. *Scand. J. Infect. Dis.* 32: 587-595.
- Srinivasan, K. S. 1939. On the developmental morphology of androgynous receptacles in *Marchantia palmata* Nees. *Proc. Indian Acad. Sci. B* 10(1): 88-97. Springer India.
- Stanley, Z. 2019. Relative competitive abilities, intersexual overyielding, and population sex ratio changes in a bryophyte. M.S. thesis. University of Kentucky. Accessed 19 August 2022 at <https://uknowledge.uky.edu/biology_etds/60/>.
- Stephani, F. 1883. Einige neue Lebermoose. *Hedwigia* 22: 49-52.
- Stieha, C. R., Middleton, A. R., Stieha, J. K., Trott, S. H., and McLetchie, D. N. 2014. The dispersal process of asexual propagules and the contribution to population persistence in *Marchantia* (Marchantiaceae). *Amer. J. Bot.* 101: 348-356.
- Stieha, C., García-Ramos, G., Nicholas McLetchie, D., and Crowley, P. 2017. Maintenance of the sexes and persistence of a clonal organism in spatially complex metapopulations. *Evol. Ecol.* 31: 363-386.
- Strullu-Derrien, C., Kenrick, P., Pressel, S., Duckett, J. G., Rioult, J. P., and Strullu, D. G. 2014. Fungal associations in Horneophyton ligneri from the Rhynie Chert (c. 407 million year old) closely resemble those in extant lower land plants: Novel insights into ancestral plant-fungus symbioses. *New Phytol.* 203: 964-979.
- Suzuki, T., Takio, S., Yamamoto, I., and Satoh, T. 2001. Characterization of cDNA of the liverwort phytochrome gene, and phytochrome involvement in the light-dependent and light-independent protochlorophyllide oxidoreductase gene expression in *Marchantia paleacea* var. *diptera*. *Plant Cell Physiol.* 42: 576-582.
- Svihla, R. D. 1940. An extension of the range of *Marchantia paleacea* Bertol. *Bryologist* 43: 167-168.
- Takio, S., Takami, S., and Hino, S. 1988. Photosynthetic ability of dark-grown *Marchantia paleacea* cells in suspension culture. *J. Plant Physiol.* 132: 195-198.

- Takio, S., Nakao, N., Suzuki, T., Tanaka, K., Yamamoto, I., and Satoh, T. 1998. Light-dependent expression of protochlorophyllide oxidoreductase gene in the liverwort, *Marchantia paleacea* var. *diptera*. *Plant Cell Physiol.* 39: 665-669.
- Tanaka, K., Takio, S., and Satoh, T. 1995. Inactivation of the cytosolic Cu/Zn-superoxide dismutase induced by copper deficiency in suspension-cultured cells of *Marchantia paleacea* var. *diptera*. *J. Plant Physiol.* 146: 361-365.
- Tanaka, K., Takio, S., Yamamoto, L., and Satoh, T. 1996. Purification of the cytosolic CuZn-superoxide dismutase (CuZn-SOD) of *Marchantia paleacea* var. *diptera* and its resemblance to CuZn-SOD from chloroplasts. *Plant Cell Physiol.* 37: 523-529.
- Tanaka, K., Takio, S., Yamamoto, L., and Satoh, T. 1998. Characterization of a cDNA encoding CuZn-superoxide dismutase from the liverwort *Marchantia paleacea* var. *diptera*. *Plant Cell Physiol.* 39: 235-240.
- Taya, M., Miya-Oka, M., Toyo-Oka, Y., Kino-Oka, M., Tone, S., and Ono, K. 1995. Growth characteristics of liverwort cells, *Marchantia paleacea* var. *diptera*, in a photoautotrophic suspension culture. *J. Ferment. Bioeng.* 80: 580-585.
- Tewari, S. D. and Pant, G. 1996. Bryophytes of hot water carbonated sulphur springs of Kumaon Himalaya. *Bryol. Times* 90: 1-2.
- Toyota, M., Omatsu, I., Braggins, J., and Asakawa, Y. 2004. New humulane-type sesquiterpenes from the liverworts *Tylimanthus tenellus* and *Marchantia emarginata* subsp. *tosana*. *Chem. Pharm. Bull.* 52: 481-484.
- Walter, C. 2015. Detecting genetic evidence of sexual reproduction in sexual and asexual populations. *Kaleidoscope* 28: 100. Accessed 19 August 2022 at <<https://uknowledge.uky.edu/cgi/viewcontent.cgi?article=1330&context=kaleidoscope>>.
- Wang, L., Wang, L. N., Zhao, Y., Lou, H. X., and Cheng, A. X. 2013. Secondary metabolites from *Marchantia paleacea* calluses and their allelopathic effects on *Arabidopsis* seed growth. *Nat. Prod. Res.* 27: 274-276.
- Wang, P. P., Liu, H., Gao, S., and Cheng, A. X. 2017. Functional characterization of a hydroxyacid/alcohol hydroxycinnamoyl transferase produced by the liverwort *Marchantia emarginata*. *Molecules* 22(11): 1854.
- Wigginton, M. J. 2013. *Marchantia pappeana*. New national and regional bryophyte records. 37. *J. Bryol.* 35: 290-305.
- Wikipedia. 2021. *Marchantia berteriana*. Accessed 7 August 2022 at <https://en.wikipedia.org/wiki/Marchantia_berteriana#:~:tex>.
- Wu, Y.-F., Zheng, H.-B., Liu, X.-Y., Cheng, A.-X., and Lou, H.-X. 2018. Molecular diversity of alkenal double bond reductases in the liverwort *Marchantia paleacea*. *Molecules* 23(7): 1630.
- Xia, P., Li, Z., So, M.-L., Chan, W.-H., and Wong, W.-Y. 2001. Studies on the antimicrobial chemical composition of Hong Kong liverwort *Marchantia paleacea* Bertol. *Nat. Prod. Res. Dev.* 13(5): 15-17.
- Yongabi, K. A., Novaković, M., Bukvički, D., Reeb, C., and Asakawa, Y. 2016. Management of diabetic bacterial foot infections with organic extracts of liverwort *Marchantia debilis* from Cameroon. *Nat. Prod. Comm.* 11: 1333-1336.
- Yuan, J.-C., Xiong, R.-L., Zhu, T.-T., Ni, R., Fu, J., Lou, H.-X., and Cheng, A.-X. 2021. Cloning and functional characterization of three flavonoid O-glucosyltransferase genes from the liverworts *Marchantia emarginata* and *Marchantia paleacea*. *Plant Physiol. Biochem.* 166: 495-504.
- Zheng, T.-X. and Shimamura, M. 2019. Morphological discrimination of the two subspecies of *Marchantia paleacea* Bertol. (Marchantiaceae, Marchantiophyta) and their geographical distribution patterns in Japan. *Hikobia* 18: 65-69.
- Zheng, T.-X. and Shimamura, M. 2021. Taxonomic re-evaluation of *Marchantia emarginata* subsp. *tosana* and related taxa in Japan. *Bryol. Res.* 12(6): 163-163.
- Zheng, T.-X. and Shimamura, M. 2022a. Taxonomic reevaluation of the Japanese *Marchantia* taxa belonging to sect. *Papillatae* of subg. *Chlamidium* (Marchantiaceae). *Bryologist* 125: 135-147.
- Zheng, T.-X. and Shimamura, M. 2022b. Taxonomic revision of the genus *Marchantia* (Marchantiaceae) in Japan and the redefinition of the genus. *Hattoria* 13: 33-77.
- Zheng, T.-X., Inoue, Y., and Shimamura, M. 2020a. Morphology of gemmae, an overlooked taxonomic trait in the genus *Marchantia* L. (Marchantiaceae). *Bryologist* 123: 601-610.
- Zheng, T.-X., Inoue, Y., and Shimamura, M. 2020b. The phylogenetic data supporting the segregation of *Marchantia paleacea* species complex into sub-species level. *Bryol. Res.* 12(3): 91-92.

