

CHAPTER 1-19

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: AYTONIACEAE

TABLE OF CONTENTS

Aytoniaceae	1-19-2
<i>Asterella africana</i>	1-19-2
<i>Asterella khasyana</i>	1-19-5
<i>Mannia fragrans</i>	1-19-6
<i>Mannia triandra</i>	1-19-12
<i>Reboulia hemisphaerica</i>	1-19-17
Summary.....	1-19-34
Acknowledgments	1-19-34
Literature Cited	1-19-34

CHAPTER 1-19

AQUATIC AND WET MARCHANTIOPHYTA, CLASS MARCHANTIOPSIDA: AYTONIACEAE



Figure 1. A steep stream bank where one might find liverworts in the *Aytoniaceae*. Photo by Michael Lüth, with permission.

Many of the species in this subchapter are not typical wetland or aquatic species. They were, however, found in a wetland or aquatic study or other wet habitat.

Marchantiidae – Marchantiales

Aytoniaceae

Asterella africana (Figure 2-Figure 3)

(syn. = *Fimbriaria africana*)

This species can exhibit a large variability in spore and elater dimensions, but other morphological characters seem to be relatively constant (Figueiredo *et al.* 2006).

Distribution

Asterella africana (Figure 2-Figure 3) is known from southern Europe, Macaronesia, and Africa (Long 2005), with widespread distribution in northern Macaronesia, but rare in Europe and North Africa (Blockeel 2012). Casas (1998) listed it for Spain and the Balearic Islands. Rupidera Giraldo and Elias Rivas (1996) reported it from the Iberian Peninsula. Blockeel (2012) reported it from

Crete as new to Greece. It occurs on Madeira and mainland Portugal (Sérgio *et al.* 2001; Figueiredo *et al.* 2006; Sim-Sim *et al.* 2010; Luís *et al.* 2015). Frahm (2005) found it on 5 of the 9 islands of the Azores. Van Dort and Nieuwkoop (2003) reported it from the laurel forests of the Canary Islands. Aleffi (2005) listed it from Italy.



Figure 2. *Asterella africana* thallus. Photo by Jan-Peter Frahm, with permission.



Figure 3. *Asterella africana* on soil. Photo by Jan-Peter Frahm, with permission.

Aquatic and Wet Habitats

Long (2005) considered *Asterella africana* (Figure 2-Figure 3) to have hygromorphic characters, but Losada Lima and Beltran Tejera (1987) considered it mesophytic in the Canary Islands. On the Iberian Peninsula Sérgio and García (2009) found that *A. africana* was associated with moderate temperatures and high humidity.

Luís *et al.* (2010) consider *Asterella africana* (Figure 2-Figure 3) to be riparian in Madeira (Figure 4), where it occurs in mountain streams (Luís *et al.* 2015). Luís and coworkers (2010) found that riparian bryophytes are affected by the habitat and position in the stream, but not by the main aspect (northern versus southern slope).



Figure 4. Fog among the mountains on Madeira Island. Photo courtesy of Michael Stech.

In the Adelantado Forest on Tenerife, wet habitats and shady areas permit the establishment of bryophytes that are scarce elsewhere (Cedrés-Perdomo *et al.* 2017). Among these, *Asterella africana* (Figure 2-Figure 3) occupies slopes near the ravine, taking advantage of the wet conditions. It is also frequent on shady humid slopes of ravines on Tenerife (Losada Lima & Beltran Tejera 1987). Patiño *et al.* (2010) considered anthropogenic disturbances such as water pollution and canalization to be a threat to this species along streams on the Canary Islands.

With these moisture requirements, it is not surprising to find *Asterella africana* (Figure 2-Figure 3) in association with waterfalls. González-Mancebo and Hernández-García (1996) found *Asterella africana* to be abundant on rocks and soil near continuously flowing springs and waterfalls in the Canary Islands. Capelo *et al.* (2005) reported a similar habitat on basalt in a waterfall on Madeira Island.

In Crete, one can find *Asterella africana* (Figure 2-Figure 3) on wet schistose rock ledges near a stream, where it seems to be always saturated (Blockeel 2012). Dirkse (1995) reported that on the Canary Islands it prefers sheltered rocks with dripping water, especially laurel and pine forests. Van Dort and Nieuwkoop (2003) similarly found it in the laurel forests of the Canary Islands. In particular, they found it at the foot of damp walls, where it was accompanied by *Bryum donianum* (Figure 5).



Figure 5. *Bryum donianum*, a species that accompanies *Asterella africana* at the base of damp walls in the Canary Islands. Photo by Michael Lüth, with permission.

Sérgio *et al.* (2010) found *Asterella africana* (Figure 2-Figure 3) on wet slopes on Macaronesia, again in laurel forests. Dirkse and Bouman (1996) found *A. africana* in the wettest and darkest places on the Canary Islands. Hernández-García *et al.* (1995) considered it to be hydrophilic on the Islands, occurring in areas with low light and abundant drip.

Lava tube and pit cave entrances can provide interesting habitats for bryophytes. In the Azores, *Asterella africana* (Figure 2-Figure 3) seems to do well in such cave entrance habitats (Gabriel *et al.* 2008, 2011). It is possible that this habitat is a refugium because all recent records for *Asterella africana* are from cave entrances (Gabriel *et al.* 2008).

Physiology

Few studies discuss any aspect of the physiology of *Asterella africana*. Pedrotti (1996) considers the species to have "thermophilic tendencies."

Adaptations

Long (2005) compared the hygromorphic *Asterella africana* (Figure 2-Figure 3) to the xeromorphic *Asterella persica*. In *A. africana*, the thallus is thin with large air chambers, whereas in the xeromorphic *A. persica* the thallus is thick and leathery with spongy assimilation tissue that has small, irregular air chambers. This is consistent

with the conclusion that air chambers in bryophytes provide for better gas exchange, but are a source of water loss.

On the Canary Islands, humidity conditions, substrate dynamics, and vegetation disturbance are important in influencing the life strategies present (González-Mancebo & Hernández-García 1996). These researchers report that *Asterella africana* (Figure 2-Figure 3) is a long-lived species, a strategy they consider typical around continuously flowing springs and waterfalls on both rocks and soil. In the Canary Islands, they found that the perennial life strategy is best represented in the more humid forests.

By contrast, Lloret and González-Mancebo (2011) considered *Asterella africana* (Figure 2-Figure 3) to be a short-lived shuttle species in the Canary Islands. These differences are likely the result of sampling two different habitat conditions, with the Lloret and González-Mancebo study being an altitudinal study.

Reproduction

On the Canary Islands, from which one can find many records of the presence of *Asterella africana* (Figure 2-Figure 3), the breeding systems, climatic conditions, and rarity can have considerable influence on the fertility of the species.

Asterella africana (Figure 2-Figure 3) is **monoicous** (Figure 6) (Long 1999, 2005). More specifically, it is **paroiocous** (with archegonia and antheridia on same branch or stem) (Bischler-Causse & Long 1993). Losada Lima and Beltran Tejera (1987) found it fertile with archegonial heads (Figure 6-Figure 9) in the Canary Islands from February to July, and occasionally in November.



Figure 6. *Asterella africana* with young archegoniophores. Photo by Tim Waters, through Creative Commons.

Biochemistry

Although this species has a restricted distribution and is rare in many areas, the essential oils have been elucidated. The species of *Asterella* commonly produce intense scents (Ludwiczuk & Asakawa 2015). These odors are products of essential oils. Figueiredo *et al.* (2006) found that the essential oils were dominated by the monoterpene fraction (79-84%). These were

predominantly myrtenyl acetate (30-42%) and α -pinene (10-17%). Sesquiterpene and non-terpenoid fractions amounted to only 1-2% and 4-8%, respectively (see also Asakawa *et al.* 2013).



Figure 7. *Asterella africana* on Tenerife with young archegoniophores. Photo by Jonathan Sleath, with permission.



Figure 8. *Asterella africana* archegonial heads. Photo by Jan-Peter Frahm, with permission.



Figure 9. *Asterella africana* archegonial head with capsules. Photo by Jan-Peter Frahm, with permission.

***Asterella khasyana* (Figure 10-Figure 15)**(syn. = *Fimbriaria khasyana*; *Rhacotheca azorica*)**Distribution**

Asterella khasyana (Figure 10-Figure 15) is distributed in southeast Asia and tropical Africa (Long 2005). Its records include India, Pakistan, Nepal, Indochina, Indonesia, Bhutan, China, Philippines, and Thailand (Piippo 1990; Kaul *et al.* 1995; Piippo *et al.* 1997; Boonkerd *et al.* 2007; Singh & Singh 2008a; Daniels 2010; Piippo 2010; Singh *et al.* 2010; Piippo & Koponen 2013). It is common in the Great Himalayan National Park (Singh & Singh 2008a). Matcham (2000) found it in Uganda, Africa. Piippo and Koponen (2013) considered it to be present but very rare in Hunan Province, China.



Figure 10. *Asterella khasyana* with archegoniophores and drying thalli. Photo by Manju Nair, through Creative Commons.



Figure 11. *Asterella khasyana* with archegoniophores. Photo by David Long, with permission.

Aquatic and Wet Habitats

Habitats for *Asterella khasyana* (Figure 10-Figure 11) vary. Karki and Ghimire (2019) consider it to be terricolous and saxicolous in Central Nepal, where it is locally rare. Dixit and Kerketta (2019) likewise consider it terricolous in the Lafa Hills, Chhattisgarh, India. But it seems to be predominantly reported from wet habitats.

Matcham (2000) reported *Asterella khasyana* from a very wet cliff in Uganda.

For bryophytes such as *Asterella khasyana* (Figure 10-Figure 11) that tend to be moisture loving, waterfalls offer a suitable habitat. Not many species can withstand being in the strong flow of the falls themselves, but the moist stream or river bank that is in the spray zone is a suitable habitat for many of these moisture loving species. Long (2006) reported *Asterella khasyana* from wet rocks by a waterfall in the Himalayas.

In the Himalayas, *Asterella khasyana* (Figure 10-Figure 11) occurs on damp rocky banks by the road (Long 2006). It has a sufficiently wide moisture tolerance to be found in dry habitats as well as wet ones. Long (2006) found it in a steep valley with patches of evergreen broad-leaved forest in the Himalayas in areas that are not wet. Singh and Singh (2008a) even classify it as terrestrial in the Great Himalayan National Park, where it is common, but state that it grows in moist and shady places.

For those species that are tolerant of higher humidity, stream and river banks are suitable and often preferred habitats. Piippo and Koponen (2013) reported *Asterella khasyana* (Figure 10-Figure 11) from sand on a wet brook side in Hunan Province, China. But also in China, in Hunan, Piippo and Koponen (2013) report *A. khasyana* from secondary forests and on sandy forest slopes. Piippo and Koponen (2013) also reported it from a cliff in China, where it has a humus substrate. Its rarity in the province may reflect a lack of suitable habitat, but it is more likely the result of not having arrived yet.

Boonkerd *et al.* (2007) reported *Asterella khasyana* (Figure 10-Figure 11) on moist, sandy soil slopes and rocks in exposed areas of the lower montane forests in Thailand. Paudel (2019) found it commonly in terrestrial habitats in Kailali in the Far West Nepal, where it was among the few species found in both acidic and basic pH.

Adaptations

Asterella khasyana (Figure 10-Figure 11) seems to cope with its somewhat wide range of habitats by several adaptive strategies. Long (2005) considers its thin, delicate thallus with large air chambers in overlapping layers to be hygromorphic characters. It lacks photosynthetic filaments in these chambers. It would be interesting to compare these characters among a large number of populations from varying degrees of moisture.

In some terricolous habitats *A. khasyana* grows in association with leafy liverworts (Dixit & Kerketta 2019), most likely affording it a greater water retention in its habitat. Sreenath and Rao (2020) found that in Andhra Pradesh, India, the species forms irregular rosettes that are often associated with *Fissidens jungermannioides* and other acrocarpous mosses, again a habit that is likely to conserve moisture.

Reproduction

Asterella khasyana (Figure 10-Figure 11) is **monoicous**, with its androecia on the main thallus just behind the base of the archegoniophore (**paroiicous**) (Boonkerd *et al.* 2007). The archegonial heads (Figure 12-Figure 14) have distinct projections that may help in conservation of moisture, but we must also consider the possibility of light scattering to prevent damage to sporogenous tissue and developing spores.



Figure 12. *Asterella khasyana* with archegonial heads. Photo by David Long, with permission.



Figure 13. *Asterella khasyana* archegonial heads. Photo by Jan-Peter Frahm, with permission.



Figure 14. *Asterella khasyana* archegoniophores showing maturing sporangia looking like beaks. Photo by Jan-Peter Frahm, with permission.

The spores in *Asterella khasyana* (Figure 10-Figure 11) are large, ranging 65-78 μm in some Indian populations (Singh & Singh 2008b) and 80-90 μm in the Andhra Pradesh, India (Sreenath & Rao 2020). In Thailand, Boonkerd *et al.* (2007) reported a range of 75-90 μm . Alam *et al.* (2020) report spores that are 85-100 μm in southern India. Naveen *et al.* (2014) described the morphology spores of the species in India. It would be

interesting to know how the spore size relates to habitat and to dispersal ability in this species.

No specialized asexual reproductive structures are known in *Asterella* (Schuster 1992), but Chaturvedi and Eshuo (2012) described abnormal asexual reproduction in *Asterella khasyana* (Figure 10-Figure 11). This was accomplished by the development of new thalli from the archegonial head (Figure 15), a type of regeneration.

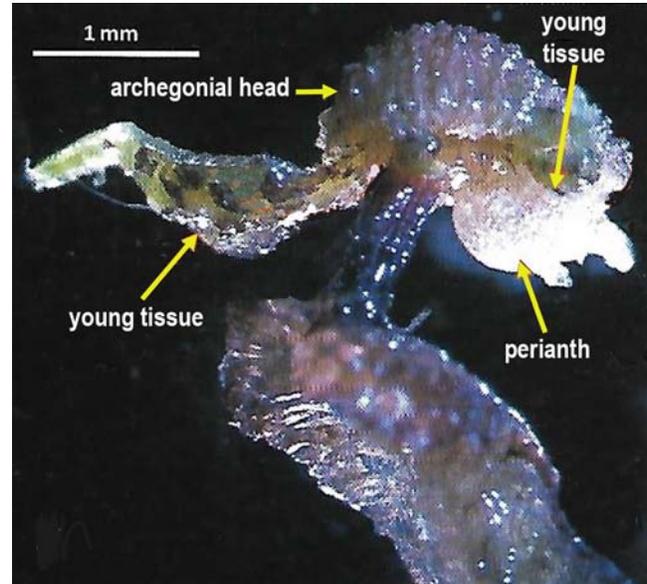


Figure 15. *Asterella khasyana* regeneration of archegonial head. Photo by Sunil Chaturvedi, with permission.

***Mannia fragrans* (Figure 16-Figure 18)**

(syn. = *Grimaldia fragrans*)

Distribution

Mannia fragrans (Figure 16-Figure 18) is widely distributed, but its distribution is disjunct (Schuster 1992). Portions of its distribution are relict. It is known in Asia (Himalayan Mountains, Korea, China, Japan), Europe, and scattered locations in North America (Schuster 1992; Choi *et al.* 2020), but it is relatively rare, despite its widespread distribution.



Figure 16. *Mannia fragrans* thallus with scales. Photo by Martin Hutten, with permission.



Figure 17. *Mannia fragrans* growing on the ground. Photo by Michael Lüth, with permission.



Figure 18. *Mannia fragrans* showing curling dry thalli. Photo by Michael Lüth, with permission.

When Oesau (2010) investigated the current presence of *Mannia fragrans* (Figure 16-Figure 18) in the lower valley of the River Nahe, Germany, they were able to confirm its previously known locations in conservation areas, but they warned that it is nevertheless endangered due to natural succession and damage by game animals.

Aquatic and Wet Habitats

Schuster (1992) describes both xeromorphic and mesomorphic ecotypes for *Mannia fragrans* (Figure 16-Figure 20). Conard (1940) refers to Iowa, USA, populations as distinctly xerophytic, growing in wooded areas or on stony hills in the prairie, but it is also frequent on rocks in half shade. Oesau (2010) found it in the arid region of the River Nahe in Germany.

Nevertheless, *Mannia fragrans* (Figure 16-Figure 20) occurs along calcareous rivers in Connecticut, USA (Nichols 1916).

Bakalin *et al.* (2019) reported a number of locations in Amur Province in Russia, but none of these was wet. Only mesic sandstone cliffs and crevices were somewhat moist.

In Poland *Mannia fragrans* (Figure 16-Figure 20) has been considered an endangered species (Piwowarczyk & Stebel 2012). Nevertheless, while it is threatened by succession of tracheophytes (Figure 21), it has been

released from the damage due to former grazing. The researchers describe it as "almost all over the slope above the Kamienna River in the village of Podgrodzie."



Figure 19. *Mannia fragrans* soil habitat. Photo by Michael Lüth, with permission.



Figure 20. *Mannia fragrans* on bank. Photo from Gencat, with online permission.



Figure 21. *Mannia fragrans* showing competing tracheophytes and lichens. Photo by Michael Lüth, with permission.

One habitat that seems to favor *Mannia fragrans* (Figure 16-Figure 20) is wind holes (Figure 22). Choi *et al.* (2020) report its presence on shaded rocks near the wind hole in broad-leaved deciduous forests in Korea. Bakalin *et al.* (2017) describe these as formations where the wind enters large holes tens of meters above, then goes underground, where it passes among wet stones and cliffs in areas with much lower temperatures due to evaporation of water from the stones. Therefore, at the exit hole, the air temperature may be about 10°C below that of the surrounding environment. This provides suitable habitat for several *Mannia* species.



Figure 22. Wind hole in Bihor Mts. in Transylvania, Romania. Note cryptogams growing on the interior walls. Photo courtesy of Tamás Pócs.

Physiology

In *Mannia fragrans* (Figure 23-Figure 24) all cells survived 12 hours at 20°C and 15% humidity, making it the most desiccation-tolerant species among the 33 species reported (Clausen 1964). When in ice at -10°C, it was unable to survive for even two days, but when partly desiccated it did survive 2 days at -10°C. This suggests that when it is hydrated, there is likely to be membrane damage due to formation of crystals or cell expansion.



Figure 23. *Mannia fragrans* on soil in a dry state. Photo by Michael Lüth, with permission.



Figure 24. *Mannia fragrans* dry and curled. This might reduce moisture loss, but it could also reduce light damage in the dormant cells. Photo by Janice Glime. The dark color also helps to prevent light damage.

Adaptations

Sometimes *Mannia fragrans* grows with other bryophytes (Figure 25-Figure 26). This behavior can take advantage of the capillary water held by the adjoining bryophytes to maintain its own moisture longer.



Figure 25. *Mannia fragrans* with emerging archegoniophores and accompanying mosses. Photo by Angus Mossman, through Creative Commons.



Figure 26. *Mannia fragrans* with mosses, where it could benefit from their moisture retention. Michael Lüth, with permission.

In other cases, its own thalli tightly cover the ground (Figure 27), reducing evapotranspiration. This is probably useful in some habitats in preventing erosion and protecting soil organisms.



Figure 27. *Mannia fragrans* showing overlapping and tightly adhering thalli of a nearly pure colony. Photo by Michael Lüth, with permission.

One potential adaptation to obtaining and maintaining moisture is the presence of ventral scales (Figure 28). In other liverworts, these are known to provide capillary spaces that facilitate the uptake of water throughout the thallus.



Figure 28. *Mannia fragrans* ventral scale with transparent appendages. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Reproduction

The genus *Mannia* can be **dioicous** or **monoicous** (Choi *et al.* 2020). *Mannia fragrans* (Figure 29) is **polyoicous** (species being both monoicous and dioicous) (Schuster 1992). Hock *et al.* (2009) noted that colonizers that produce both sex organs are favored in selection because they ensure sexual reproduction when no partner is present. This is especially important for species like *Mannia fragrans* that have no specialized means of asexual reproduction.



Figure 29. *Mannia fragrans* with antheridial patches (dark brown) and young archegoniophores (pinkish red with scales, but it is hard to determine if they are on the same plant or on different plants. Photo by Jan-Peter Frahm, with permission.

The male branches or plants (Figure 30-Figure 31) produce patches of antheridia on the thallus surface. The phenology of these sexual structures, including the conditions that trigger their initiation, need to be studied.



Figure 30. *Mannia fragrans* on soil in NW Iowa, USA, with a few brown antheridial patches. Photo by Janice Glime.



Figure 31. *Mannia fragrans* with brown patches of antheridia. Photo by Janice Glime.

In *Mannia fragrans* (Figure 29), there is a strong female-biased sex ratio (Figure 32-Figure 35); sexual expression is high (Hock *et al.* (2008b). This high expression contributes to high fertilization rates and may account for its widespread distribution. But its relative rarity suggests that most arrival sites do not provide the conditions needed for establishment.



Figure 32. *Mannia fragrans* thalli with developing archegoniophores. Photo by Michael Lüth, with permission.



Figure 33. *Mannia fragrans* with beginning stages of archegoniophores and scales. Photo by Štěpán Koval, with permission.

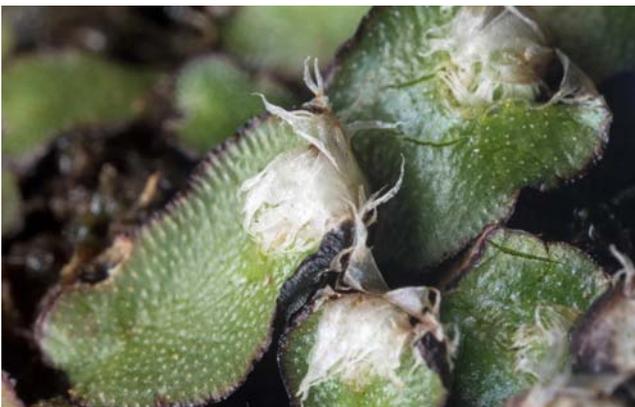


Figure 34. *Mannia fragrans* showing archegoniophore scales. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 35. *Mannia fragrans* archegonial heads with scales. Note the browning thalli that can leave small apical portions for potential dispersal. Photo by Aaron Carlson, through Creative Commons.

The archegoniophore is surrounded by white scales (Figure 34-Figure 38) that remain at the base when it elongates. Perhaps these help to maintain the proper moisture levels at the time of fertilization. Following sexual reproduction, there is further growth in male plants, but not in female plants/branches (Hock *et al.* 2009).



Figure 36. *Mannia fragrans* young archegonial head with scales. Photo by Aaron Carlson, through Creative Commons.



Figure 37. *Mannia fragrans* archegonial head with scales as it emerges from the thallus. Photo by Botanicalwanderer, through Creative Commons.



Figure 38. *Mannia fragrans* female lobes with only small apical portions of the thallus remaining. Photo by Samuel Brinker, through Creative Commons.

Despite the elevation of the sporangia on the extended archegoniophore (Figure 39), the large spores [60.0-82.0 μm (Figure 40) (Choi *et al.* 2020)] will mostly fall back to the same population. This results in significant differences between distant populations and signals negligible gene flow between them. There are numerous rare alleles and unique recombinations, indicating that at least occasional recombination and mutation do occur (Hock *et al.* 2009). In Japan, mature spores occur in early winter (Furuki 1992).



Figure 39. *Mannia fragrans* mature archegonial heads with dehiscent sporangia. Photo by Václav Dvořák, through Creative Commons.

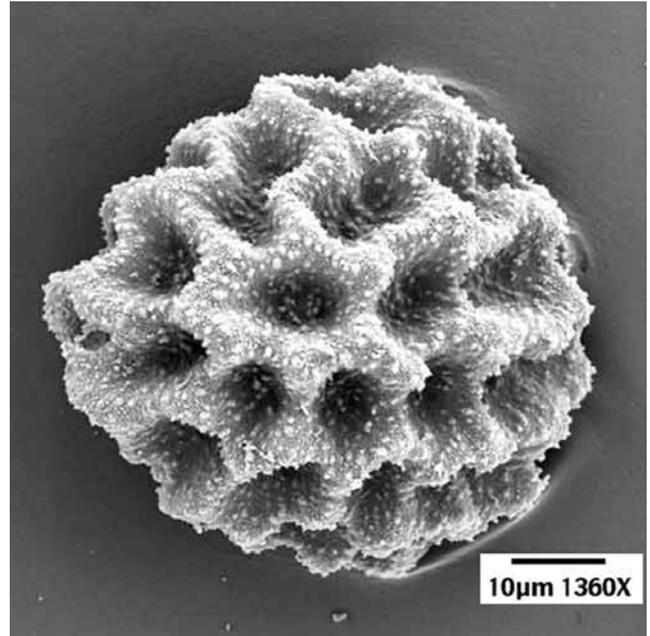


Figure 40. *Mannia fragrans* distal spore wall SEM. Photo by William T. Doyle, with permission.

Asexual reproduction in *Mannia fragrans* occurs commonly by fragmentation of thalli (Figure 41) (Hock *et al.* 2008b). But despite the high frequency of spore production, the genetic diversity within populations is low, suggesting that fragmentation is an important source of new plants (Hock *et al.* 2008b, 2009). Even when sexual reproduction occurs within the population, it is likely to occur between two identical genomes that have arisen through fragmentation.



Figure 41. *Mannia fragrans* with what appear to be dying older thalli with green apices and early stages of sexual structures. As these older parts of thalli die, they provide a means of fragmentation. During rain events, these smaller pieces of thalli could become dislodged, facilitating dispersal. This dispersal mechanism needs to be documented.

Hock *et al.* (2008a, b) used *Mannia fragrans* (Figure 41) to demonstrate that a diaspora bank can conserve genetic variability over generations and seasons. Propagules can remain in the soil for extended periods of time, then come to the surface following a disturbance, and grow, expressing the gene pool of previous points in time.

Fungal Interactions

De (2017) found that the **Glomeromycota** fungus *Planticonsortium tenue* (= *Glomus tenue*) grows in association with the gametophyte of *Mannia fragrans* (Figure 41). It primarily colonizes the smooth rhizoids, but can also live among the scales (Figure 28) and tuberculate rhizoids. From there, the fungus grows upward into the parenchyma cells of the thallus midrib and crosses the cell walls through the plasmodesmata. It is interesting that vesicles are able to develop in the smooth rhizoids and in the scales, but fail to develop in the tuberculate rhizoids. Within the thallus, the fungus occurs mostly intracellularly, forming vesicles and arbuscules in the midrib cells. Young cells are fungus free.

Biochemistry

As its name implies, *Mannia fragrans* (Figure 41) is usually aromatic, with the odor of cedar oil, although there seem to be some population variants (Choi *et al.* 2020). Schuster (1992) describes it as "oil cells frequent." Asakawa (2007) attributes the strong, sweet mossy odor to the cuparene-type sesquiterpene ketone, grimaldone.

Huneck *et al.* (1988a) reported pakynol as a macrocyclic bisbibenzyl diether from *Mannia fragrans* (Figure 41). Nogradi *et al.* (1990) later elaborated the synthesis of the compound in this species and Böcskei and Keserű (1994) described its crystal structure.

Huneck *et al.* (1988b) described the structure of the tricyclic sesquiterpenoid grimaldone in this species. Odrzykoski and Szweykowski (1981) found that *Mannia fragrans* (Figure 41) has only one form of glutamate dehydrogenase, but has two forms for glutamate-oxaloacetate transaminase.

Mannia triandra (Figure 42-Figure 43)

(syn. = *Mannia rupestris*)

There is a surprising number of publications on this species. Schill (2006) wrote a dissertation on the taxonomy and phylogeny of the genus *Mannia*.

Distribution

Mannia triandra (Figure 42-Figure 43) is a disjunct, circumpolar, subcontinental species from subarctic and subalpine regions (Müller *et al.* 2014), *i.e.* **arctomontane** (Borovichev & Bakalin 2016). Its distribution includes Europe [Montenegro (Duda 1965) and Albania, Austria, Bosnia, Bulgaria, Croatia, Czech Republic, France, Germany, Hungary, Italy, Macedonia, Poland, Romania, Russia, Slovakia, Slovenia, Sweden, Switzerland, Ukraine (Hugonnot & Offerhaus 2005; Sabovljević & Natcheva 2006; Müller *et al.* 2014)], North America (Greenland, Canada, USA), and Asia (China, Japan, Russia) (Müller *et al.* 2014). Schuster (1992) questions the Japanese record as probably another species. Furthermore, there seemed to be no recent records in Bosnia, Macedonia, or Slovenia (Sabovljević & Natcheva 2006; Ros *et al.* 2007; Alegro *et al.* 2019). However, in 2017, Krajšek and Martinčič reported several localities for it in Slovenia and cautioned that it is only visible in spring due to its ephemeral life cycle. Records for Spain appear to be based on problems of incorrect synonymy and Brugués *et al.* (2011) therefore excluded it from the flora there.



Figure 42. *Mannia triandra* on soil in Europe. Photo by Michael Lüth, with permission.



Figure 43. *Mannia triandra* thalli amid other bryophytes. Photo by Michael Lüth, with permission.

Mannia triandra (Figure 42-Figure 43) is a calcicole, concentrated mostly at low elevations in the Alps (Schuster 1992). Shershen *et al.* (2018) reported *M. triandra* from the Loud Thunder Forest Preserve in Illinois, USA. Conard (1940) reported it as rare in Iowa, USA.

Mannia triandra (Figure 42-Figure 43) is red-listed (threatened or endangered) in many of the countries where it occurs (Schumacker & Matriny 1995; Kučera & Váňa 2003; Colacino & Sabovijevec 2006; Martinčič 2009; Németh & Papp 2011; Dulin 2013; Zechmeister & Köckinger 2014; Borovichev & Bakalin 2016; Hodgetts *et al.* 2019).

Aquatic and Wet Habitats

Mannia triandra (Figure 42-Figure 43) is a species that occurs on Ca-rich or other basic substrata (Borovichev & Bakalin 2016). Hugonnot (2010) considers it to be a temporary hygrophile. Philippe (2013) says it is "absolutely not rupicolous," *i.e.*, it does not grow on rocks. Conard (1940) states that it is strictly xeric in Iowa, USA.

But this xerophytic habit is not universally true. In Hungary, Németh (2011) found *Mannia triandra* (Figure 42-Figure 43) growing with *Clevea* (= *Athalamia*) *hyalina* (Figure 44), *Myurella julacea* (Figure 45), and *Plagiobryum zieri* (Figure 46) on north-facing slopes

where it is shaded, humid, and "rather cool" (see also Németh & Papp 2011). It is mesothermophilic (Dierßen 2001). Philippe (2013) describes its habitat of Bonneville, France, as one that has a misty escarpment with a high spring humidity and dry summer. But none of the colonies occurred in habitats that were even temporarily oozing.



Figure 44. *Clevea hyalina*, a species that accompanies *Mannia triandra* in cavities of vertical rocks. Photo by Hugues Tinguy, with permission.



Figure 45. *Myurella julacea*, a species that accompanies *Mannia triandra* in cavities of vertical rocks. Photo by Michael Lüth, with permission.



Figure 46. *Plagiobryum zieri*, a species that accompanies *Mannia triandra* in cavities of vertical rocks. Photo by Tomas Hallingbäck, with permission.

Dürhammer (2017) finds *Mannia triandra* (Figure 42-Figure 43) on permanently humid substrata of calcareous rocks that are adequately lit. It is endangered in the damp cracks in the rock due to the rock climbers who tend to rest there or use them as footholds. It does especially well in humid rock overhangs, but that habitat is particularly fragile. Meinunger (1992) found that the same problems face populations in Germany. These habitats contrast with Philippe's (2013) assertion that it is not rupicolous, suggesting again that it may have population differences.

Borovichev and Andreeva (2009) found *Mannia triandra* (Figure 42-Figure 43) on limestone outcrops on the river bank in the Lapland Nature Reserve, Murmansk, Russia, where it was moist and shady.

Borovichev (2014) found that in the Murmansk Province of Russia, *Mannia triandra* (Figure 42-Figure 43) grows exclusively on calcareous substrates. Philippe (2013) describes *M. triandra* as **chasmophilic**, living in crevices of limestone escarpments. Alegro *et al.* (2019) reported it from small, earthy pits and cavities of vertical rocks, often accompanied by *Preissia quadrata* (Figure 47).



Figure 47. *Preissia quadrata* with archegoniophores, a species that often accompanies *Mannia triandra* in cavities on rocks. Photo by Oskar Gran, through Creative Commons.

Papp (1980) reported the only known location for *Mannia triandra* (Figure 42-Figure 43) in Hungary to be the base of a large limestone rock wall. Németh and Papp (2011) found it in cool, humid microhabitats of north-facing calcareous slopes in the Bükk Mountains of Hungary. Papp *et al.* (2007) reported it from limestone cliffs. In the Komi Republic of Russia, Dulin (2013) found it on ledges of southeast-facing outcrops (Figure 48-Figure 50).



Figure 48. *Mannia triandra* on rock in a large crevice. Photo by Renzo Salvo, through Creative Commons.



Figure 49. *Mannia triandra* in limestone rock crevice. Photo by Hugues Tinguy, with permission.



Figure 50. *Mannia triandra* on rock ledge. Photo by Oliver Dürhammer, through Creative Commons.

In the Korean Peninsula, *Mannia triandra* (Figure 42-Figure 43) occurs in wind holes (Figure 22) (Borovichev & Bakalin 2016). These cooler locations serve as refugia for rare alpine plants.

But often, *Mannia triandra* (Figure 42-Figure 43) occupies habitats that are not moist (Németh & Papp 2011). In the Bükk Mountains of Hungary, these include rock crevices on dolomite, soil (Figure 51) at the base of near vertical rock walls, and humus containing dolomite fragments between surface roots of small *Fagus sylvatica* (Figure 52) and *Fraxinus ornus* trees. Conard (1940) reported it from exposed dry rocks in wooded areas and on stony hills in the prairie in Iowa, USA.



Figure 51. *Mannia triandra* on soil. Photo by Hugues Tinguy, with permission.



Figure 52. *Fagus sylvatica* roots, providing a habitat where one might find *Mannia triandra*. Photo by Vegetator, through Public Domain.

Physiology

Dierßen (2001) described the ecological amplitude of European bryophytes, including *Mannia triandra* (Figure 42-Figure 43). Simmel *et al.* (2021) assigned an Ellenberg Indicator Value (EIV) for N of only 3, an indicator that it occurs on sites that are more or less infertile.

The range of habitats known for *Mannia triandra* (Figure 42-Figure 43) suggest that it has a relatively wide moisture tolerance (Figure 53). Its presence on rock surfaces indicate that it will get dried out at times (Figure 53).



Figure 53. *Mannia triandra* in a dry condition. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Mannia triandra (Figure 42-Figure 43) is a **short-lived shuttle species** (Orbán 1984; Németh & Papp 2011), permitting it to occupy transient habitats.

Mannia triandra (Figure 42-Figure 43) has well developed aerenchyma in the thallus (Figure 54), occupying 2-3 layers in the middle of the thallus and completely filling the wings (Borovichev & Bakalin 2016). These are, however, empty, having no photosynthetic filaments. Hence, they serve as reservoirs for CO₂, but can also increase evapotranspiration.

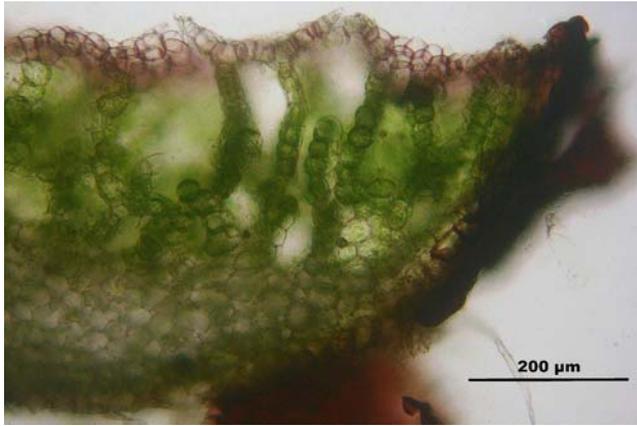


Figure 54. *Mannia triandra* thallus section showing air chambers and pores. Photo by Hermann Schachner, through Creative Commons.

Based on images I have seen, *Mannia triandra* (Figure 42-Figure 43) can grow with densely intermingled other bryophytes (Figure 55-Figure 56). Such a growth habit can help to maintain moisture for longer periods of time.



Figure 55. *Mannia triandra* with mosses, showing their dense growth that can help to retain water. Photo by Michael Lüth, with permission.



Figure 56. *Mannia triandra* with closely associated mosses and producing young archegoniophores. Photo by Michael Lüth, with permission.

Reproduction

Schuster (1992) describes *Mannia triandra* (Figure 42-Figure 43) as **dioicous**. However, Borovichev and Bakalin (2016) describe the androecia and gynoecia (Figure 57) as physically separated, with the androecia on the main thallus and not on the same branch as the female receptacle (Borovichev & Bakalin 2016).



Figure 57. *Mannia triandra* with brown androecia and a separate thallus or branch with one young archegoniophore (lower left). Photo by Štěpán Koval, with permission.

Hugonnot *et al.* (2017) found *Mannia triandra* fertile in May (Figure 57-Figure 60) in Saint-Maurin, France. Németh and Papp (2011) describe the life cycle of *M. triandra* in Hungary as thalli appearing in spring, producing spores in early spring, at which time its "small blue-green thalli" typically disappear during the dry season. The population size in any given year is very dependent on rainfall during its growing season. Müller *et al.* (2014) similarly found fluctuations in the population size from year to year. In 2008, one population occupied approximately 0.25 m². In 2009, it occupied only 5 dm². Then, in 2013, a rock was demolished and its area increased to at least 0.5 m². Similarly, Dürhammer (2017) found that the sporangia (Figure 61-Figure 67) numbers fluctuate considerably from year to year, perhaps driven by fluctuating weather conditions.



Figure 58. *Mannia triandra* with young archegoniophores showing the surrounding dense scales. Photo by Michael Lüth, with permission.



Figure 59. *Mannia triandra* with emergent archegoniophores and dead thalli. Photo by Štěpán Koval, with permission.



Figure 60. *Mannia triandra* young emergent archegoniophores and dying thallus. Photo by Hermann Schachner, through Creative Commons.



Figure 61. *Mannia triandra* archegoniophores with disintegrating thalli. Photo from Earth.com, with permission.



Figure 62. *Mannia triandra* archegoniophores with sporangia beginning to push scales surrounding them outward. Photo by Hugues Tinguy, with permission.



Figure 63. *Mannia triandra* archegoniophores beginning to elongate and sporangia beginning to emerge. Photo by Hugues Tinguy, with permission.



Figure 64. *Mannia triandra* with young capsules and elongated archegoniophores. Photo by Štěpán Koval, with permission.



Figure 65. *Mannia triandra* archegoniophores with mature capsules. Photo by Hermann Schachner, through Creative Commons.



Figure 66. *Mannia triandra* with mature sporangia. Photo by Paul G. Davison, with permission.



Figure 67. *Mannia triandra* underside of archegonial head showing mature sporangia. Photo by Paul G. Davison, with permission.

Spores (Figure 68) of *Mannia triandra* (Figure 42-Figure 43) are large [(55-)60-70(-75) μm] (Borovichev & Bakalin 2016). This is probably a major factor in its distribution. Since it is an annual species with no special asexual reproductive structures, it must rely on its spores, but being large, their dispersal is limited (Hugonnot & Celle 2012). As a result, it is not surprising that it is a poor competitor (Philippe 2013).

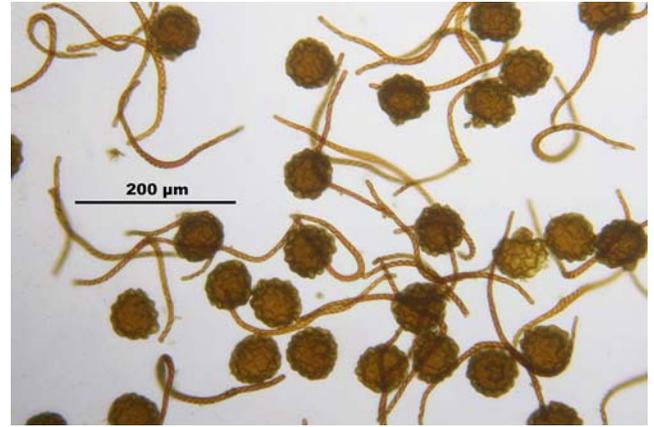


Figure 68. *Mannia triandra* spores and elaters. Photo by Hermann Schachner, through Creative Commons.

biochemistry

Mannia triandra (Figure 42-Figure 43) has numerous oil cells and has oil bodies that range 10-25 μm in diameter (Borovichev & Bakalin 2016). It nevertheless lacks the scent of cedar oil known in *Mannia fragrans* <<http://ecodb.bas.bg/rdb/en/vol11/Mantrian.html>>.

Reboulia hemisphaerica (Figure 69-Figure 76)

Stephani (1899) recognized *Reboulia hemisphaerica* (Figure 69-Figure 76) as a polymorphic species. It seems to have at least four genetically distinct races (Boisselier-Dubayle *et al.* 1998). Nevertheless, it exhibits less polymorphism than that generally attributed to mosses.

Hicks (1992) reported that three subspecies had been described for *Reboulia hemisphaerica* (Figure 69-Figure 76), differing in distribution of sex organs.



Figure 69. *Reboulia hemisphaerica* rosettes. Photo by Janice Glime.



Figure 70. *Reboulia hemisphaerica* in Europe. Photo by Michael Lüth, with permission.



Figure 73. *Reboulia hemisphaerica*. Photo by Janice Glime.



Figure 71. *Reboulia hemisphaerica*. Photo by Michael Lüth, with permission.



Figure 74. *Reboulia hemisphaerica* in Europe, with archegoniophores. Photo by Michael Lüth, with permission.



Figure 72. *Reboulia hemisphaerica* in Europe. Photo by Michael Lüth, with permission.



Figure 75. *Reboulia hemisphaerica* with purple edges. Photo by Allen Norcross, with permission.



Figure 76. *Reboulia hemisphaerica* in North America. Photo by Paul G. Davison, with permission.

Distribution

Reboulia hemisphaerica (Figure 69-Figure 76) is cosmopolitan (Piippo *et al.* 1997; Kürschner 2008) and is especially distributed in subtropical and temperate regions (Nieuwkoop 1996). *Reboulia hemisphaerica* is distributed in China, India, Japan, Korea, Nepal, Afghanistan, Pakistan, Java, Boning, New Zealand, Australia, Europe, Africa, Tahiti, North America, and South America (Singh & Singh 2002; Nair & Prajitha 2016).

Janovicová and Kubinská (2001) considered *Reboulia hemisphaerica* (Figure 69-Figure 76) to be both rare and threatened in the Biele Karpaty Mountains of Slovakia.

Aquatic and Wet Habitats

Reboulia hemisphaerica (Figure 69-Figure 76) is occasionally submerged (Watson 1919) and can occur in rivers (Ferreira *et al.* 2008). Konstantinova (2011) reported it from sandy soil between rocks in a dry stream bed in Dagestan, Russia. In the Uşak province of western Turkey it occurs on wet rocks (Gökler 2017). Hong (1977) found it on wet rocks in Montana, USA.

Reboulia hemisphaerica (Figure 69-Figure 76) occurs on the bank of the Banaz stream in the Uşak province of western Turkey (Gökler 2017). In the Izarene Massif of Rocco, it occurs on clayey soil on slopes (Figure 77) beside flowing water (Laouzazni *et al.* 2021). In Cyprus, it occurs under shrubs on the bank of a gully and on a steep bank by a stream in a deep valley (Blockeel 2003). Sharp (1939) found it on moist banks (Figure 1) in eastern Tennessee, USA. Konstantinova (2011) reported that *Reboulia hemisphaerica* subsp. *australis* occurs in Dagestan, Russia, in the gorge at the source of the Gunibka River on the bank. Some of its habitats on rocks and soil banks are shown in Figure 77-Figure 82.



Figure 77. *Reboulia hemisphaerica* with elongating archegoniophores on soil of a steep bank, Europe. Photo by Michael Lüth, with permission.



Figure 78. *Reboulia hemisphaerica* habitat on rocks. Photo by Michael Lüth, with permission.



Figure 79. *Reboulia hemisphaerica* on limestone cliff in Ohio, USA. Photo by Robert Klips, with permission.



Figure 80. *Reboulia hemisphaerica* on vertical face of rock. Photo by Michael Lüth, with permission.



Figure 81. *Reboulia hemisphaerica* habitat on steep soil bank with tree roots. Photo by Michael Lüth, with permission.



Figure 82. *Reboulia hemisphaerica* habitat on a soil bank. Photo by Michael Lüth, with permission.

Both streams and rivers can have floodplains. Many species have life cycles timed to take advantage of these ephemeral habitats. In the Virginia Piedmont, USA, the presence of *Reboulia hemisphaerica* (Figure 69-Figure 76) can indicate such a habitat where most of the species appear in late fall after leaf drop, regrowing from spores and dying soon after dispersing their spores (Breil 1977). These indicator species are sensitive to drying, yet typically require high light intensities.

Reboulia hemisphaerica (Figure 69-Figure 76) seems to have a preference for steep slopes (Figure 83-Figure 84). In the Netherlands, it is nearly always found on slopes up to 90° (Nieuwkoop 1996). Martin (1943) reported it from a cliff face in Ledges State Park, Iowa, USA. Miller and Thomson (1959) reported it from moist sandstone cliffs in Indiana, USA.



Figure 83. *Reboulia hemisphaerica* on a vertical face with soil over rock. Photo by Barry Stewart, with permission.



Figure 84. *Reboulia hemisphaerica* with archegoniophores on steep rocky slope. Photo by Michael Lüth, with permission.

Slopes and cliffs often have water trickling down them, or occur in canyons that remain humid. These provide suitable habitat for moisture-loving species of liverworts. In particular, cracks and crevices (Figure 85) provide protection and tend to remain moist longer than bare rock. *Reboulia hemisphaerica* (Figure 69-Figure 76) can occur in such locations (Sharp 1939; Crundwell & Nyholm 1979; Konstantinova 2011).



Figure 85. *Reboulia hemisphaerica* on rock ledge. Photo by Michael Lüth, with permission.

In the Netherlands, Nieuwkoop (1996) found that *Reboulia hemisphaerica* (Figure 69-Figure 76) preferred a loamy substrate (Figure 86), even if growing on a rock. These usually were on moist, loamy walls with light shade. Like the above members of the family Aytoniaceae, *Reboulia hemisphaerica* takes advantage of the cooler temperatures and greater moisture of wind holes (Figure 22) (Bakalin *et al.* 2017).



Figure 86. *Reboulia hemisphaerica* on soil. Photo by Štěpán Koval, with permission.

Reboulia hemisphaerica (Figure 69-Figure 76) exhibits a wide range of moisture tolerance, growing on slopes of ditches, on roadside banks, and along roads (Brown 1924). Jerath and Puja (2006) reported it as xeromorphic in the Shivalik Ecosystem of Punjab, India, but also growing in moist and exposed places. Nair and Prajitha (2016) found it on cut earth in the western Ghats of India. Singh and Singh (2002) found it on rocks in partially exposed places in India.

Province (2011) reported it in particular from basic schists and slate on rock outcrops among scrub vegetation in South-west Sichuan, China. Piippo and Koponen (2013) similarly found it in both primeval and secondary evergreen forests in northwestern Sichuan, China, in both open and shaded sites, on humus over rock (Figure 87) or stone, on cliffs, clay, and soil (Figure 88).



Figure 87. *Reboulia hemisphaerica* on soil over rock, Europe. Photo by Michael Lüth, with permission.



Figure 88. *Reboulia hemisphaerica* on soil. Photo by Jan-Peter Frahm, with permission.

Konstantinova *et al.* (2018) considered *Reboulia hemisphaerica* (Figure 69-Figure 76) to be a calcicole. It occurs in Russia on bare soil on mossy rock outcrops, on ledges (Figure 89-Figure 91) and in crevices, and even under rocks. Aleffi *et al.* (2005) listed it from rocks and escarpments in Italy. It finds similar habitats to be suitable in Morocco, including rock ledges with accumulated soil and bases of rocks (Ros *et al.* 2000), but Saadi *et al.* (2020) found it on siliceous soil in Morocco. Piippo and Tan (1992) found it on an abandoned wall in a shaded garden in the Philippines.



Figure 89. *Reboulia hemisphaerica* on rock ledges. Photo by Michael Lüth, with permission.



Figure 90. *Reboulia hemisphaerica* with archegoniophores on rock ledge. Photo by Michael Lüth, with permission.



Figure 91. *Reboulia hemisphaerica* with archegoniophores on rock ledge. Photo by Barry Stewart, with permission.

In Oklahoma, USA, *Reboulia hemisphaerica* (Figure 69-Figure 76) is the most frequent species of liverwort on dry rock outcrops (Little 1936) and also occurs on sandy soil (Sharp 1930). In Illinois, USA, it occurs on rocks, walls, and soil, including a sandstone wall (Spessard 1972; Simon 1977). Conard (1940) found it to be common on dry earth or rocks in Iowa, USA. At Mountain Lake, Virginia, USA, it similarly occurs on calcareous rocks and crevices (Sharp 1944).

In Myvatn, Iceland, *Reboulia hemisphaerica* (Figure 69-Figure 76) occurred as a pioneer on Krafla following the 1984 eruption (pers. obs. 1987). In just three years, it reached large populations (Figure 92-Figure 93).



Figure 92. *Reboulia hemisphaerica* in abundance during early succession on Krafla, Myvatn, Iceland, 3 years after 1984 eruption. Photo by Janice Glime.



Figure 93. *Reboulia hemisphaerica* succession on Krafla, Myvatn, Iceland, three years after the 1984 eruption. Photo by Janice Glime.

Physiology

Reboulia hemisphaerica (Figure 69-Figure 76) apparently has a wide moisture tolerance. Crundwell and Nyholm (1979) considered it to be one of the most drought-tolerant of the Turkish liverworts.

Reboulia hemisphaerica (Figure 69-Figure 76) exhibits growth and branching at moisture levels ranging 40-90%, with optimum growth at 70-80% (Vishvakarma & Kaul 1988a).

Xiang *et al.* (2010a) found that water stress affects the soluble sugar and proline, but has negligible effect on MDA. Calcium stress has even greater effects on sugar and proline. Low calcium results in a reduction in the accumulation of proline and soluble sugar, but as low calcium stress worsens their content gradually increases.

Hoffman and Gates (1970) demonstrated, using *Reboulia hemisphaerica* (Figure 69-Figure 76), that water loss proceeds rapidly in moist plants, with very low resistance. But as the water loss decreases, both convection and reradiation of energy become more important. At the same time, resistance increases in proportion to water loss. *Reboulia hemisphaerica* transpired for 2 hours under a radiation regime of 2.6 to 2.8 cal cm⁻² min⁻¹.

Reboulia hemisphaerica (Figure 69-Figure 76) has a mean water conductive rate of ~0.5 mm s⁻¹ (McConaha

1941). The areolation of its thallus greatly increases the surface through which water can be lost through the atmosphere by pores. A high phlobaphene content on the ventral surfaces helps to maintain a capillary film there among the tuberculate rhizoids and prevents water loss from the upturned thallus margins. McConaha demonstrated that a single water drop at one end of the thallus became distributed through the length of the thallus by its external capillary system. This water was immediately available to all absorptive surfaces. This external system provides a much more rapid transport than any known internal system. This seems to compensate successfully for the increased water loss due to areolation. In contrast to the description of McConaha, O'Hanlon (1928) describes the species with only a mere suggestion of air chambers and no air pores.

Takio *et al.* (1990) examined the chlorophyll content and photosynthetic rate in *Reboulia hemisphaerica* (Figure 69-Figure 76). They found that it possessed high levels of chlorophyll when cultured in light ($4\text{--}34 \mu\text{g mg}^{-1}$ dry weight). These plants likewise had a high photosynthetic rate of $10\text{--}94 \mu\text{mol O}_2 \text{ mg}^{-1} \text{ chlorophyll h}^{-1}$. Dark-grown cells exhibited these same high levels of chlorophyll and photosynthesis, contrasting sharply with the low chlorophyll levels in dark-grown *Barbula unguiculata* (Figure 94).



Figure 94. *Barbula unguiculata*. Photo by Kristian Peters, through Creative Commons.

Rao *et al.* (1979) reported on the assimilation of labelled carbon into amino acids for *R. hemisphaerica*. The CO_2 assimilation rate was lower than that of seed plants. The chlorophyll content of these populations (from moist locations in the Ooty Hills, India) was low, as was the chlorophyll *a:b* ratio, parameters that are typical of shade-loving species. Rao *et al.* (1979) reported that the Hill reaction rates of *R. hemisphaerica* was lower than that typically reported for seed plants.

Both dark-grown and light-grown cells of *Reboulia hemisphaerica* (Figure 69-Figure 76) exhibited high chlorophyll content ($4\text{--}34 \mu\text{g mg}^{-1}$ dry weight) after one year of culture on 2% glucose medium (Takio *et al.* 1990). Photosynthetic activity was likewise high in both ($10\text{--}84 \mu\text{mol O}_2 \text{ mg}^{-1} \text{ chlorophyll h}^{-1}$).

Lei *et al.* (2010) explored the responses of photosystem II in *Reboulia hemisphaerica* (Figure 69-Figure 76) to nitrogen deposition. Increased N concentrations (40 and $60 \text{ kg h}^{-1} \text{ m}^{-2} \text{ a}^{-1}$) caused changes in chlorophyll fluorescence and reduced the energy-trapping capacity per unit area. It furthermore changed the redox states, destroyed electron flow especially beyond the Q-A, disabling that energy absorption and necessitating its consumption by fluorescence and heat. Liu *et al.* (2009) also explored N effects on this species and found both photosynthetic rate and starch concentration were lower at N concentrations of 20 and $40 \text{ kg h}^{-1} \text{ m}^{-2}$ than at the control levels or at $60 \text{ kg h}^{-1} \text{ m}^{-2}$. On the other hand, the total N in the tissue changed inversely. Both the inducible and constituted nitrate reductase activity were very low in all treatments, suggesting that it is unable to use nitrates. Potassium ion leakage increased significantly when the N addition increased to $60 \text{ kg N h}^{-1} \text{ m}^{-2}$, suggesting membrane damage.

Vishvakarma and Kaul (1986) explored the temperature tolerance of *Reboulia hemisphaerica* (Figure 69-Figure 76). Morais and Becker (1991) cultured *Reboulia hemisphaerica* and found that it grew best on agar with 0.5% sucrose and an 18 h light: 6 h dark regime. Callus could be induced by phytohormones (2 mg L^{-1} a-naphthylacetic acid + 1 mg L^{-1} kinetin) or by 4% glucose. Once cultures differentiated, there was a tenfold increase in sesquiterpene production. No sesquiterpenes were produced in dark cultures, but 5-hydroxy-7,8,4'-trimethoxyflavone was present. In light cultures, apigenin *n*-7,4'-dim ethylether was the only flavonoid produced.

Xiang *et al.* (2010b) evaluated the effects of heavy metals on *Riccardia hemisphaerica* (Figure 69-Figure 76) from cavern rock and soil on walls. They found that *R. hemisphaerica* actually exhibited depletion levels of Ca in the Three Gorges karst region, whereas some mosses exhibited either strong or relative enrichment in their tissues. It exhibited no enrichment of Mg, whereas the moss *Thuidium cymbifolium* (Figure 95) did. *Reboulia hemisphaerica* did, however, show a strong enrichment by Zn.



Figure 95. *Thuidium cymbifolium*, a species that can experience Mg enrichment. Photo by Chris Alice Kratzer, through Creative Commons.

Adaptations

One aspect that may account for the wide range of habitats for *Reboulia hemisphaerica* (Figure 69-Figure 76) is its ability to form pure mats or to grow with other bryophytes (Figure 96-Figure 97) (Konstantinova *et al.* 2018). The accompanying bryophytes can act like a sponge to retain moisture that could maintain suitable conditions for *R. hemisphaerica*, whereas pure mats can completely cover the substrate and reduce evapotranspiration.



Figure 96. *Reboulia hemisphaerica* growing over mosses. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.



Figure 97. *Reboulia hemisphaerica* with mosses and archegoniophores. Photo by Michael Lüth, with permission.

Reboulia hemisphaerica (Figure 69-Figure 76) has air chambers (Figure 98-Figure 100) that form an extensive system of air spaces separated by thin partitions (Dupler 1921; Haupt 1921a). These have air pores (Figure 99-Figure 101) on the upper surface, but no filaments, and thus serve primarily for gas exchange. Dupler (1921) describes them as very elongated air chambers that extend lengthwise along the midrib region. They radiate from there toward the thallus margins. They are in a single layer just below the surface and presumably facilitate CO₂ exchange in internal photosynthetic cells.

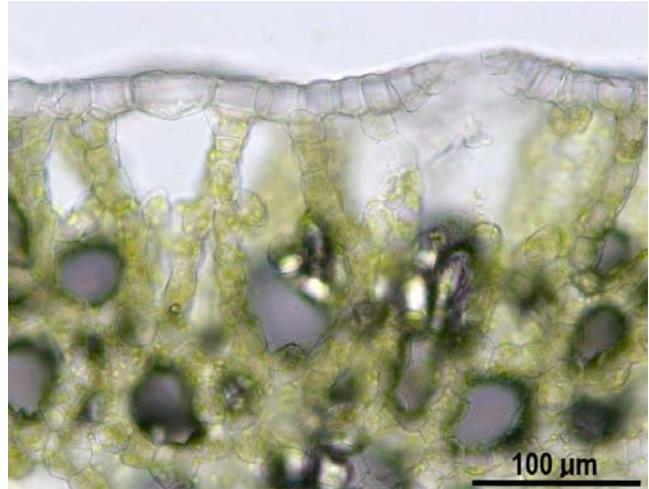


Figure 98. *Reboulia hemisphaerica* section showing air chambers. Photo by Jia-Dong Yang, through Creative Commons.



Figure 99. *Reboulia hemisphaerica* air chambers and pore. Photo by Hugues Tinguy, with permission.

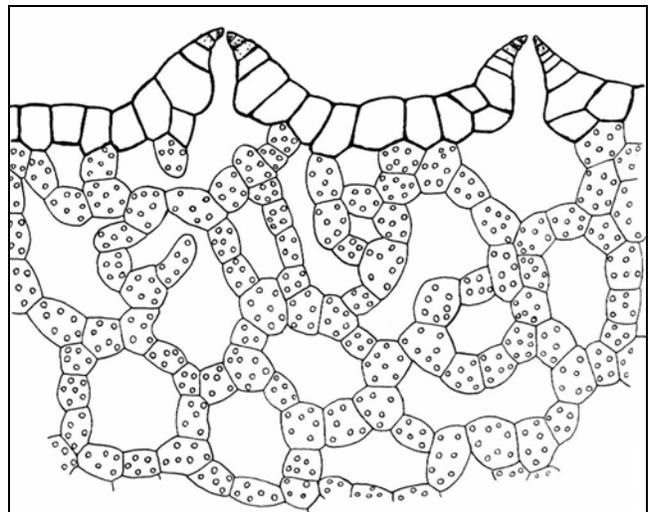


Figure 100. *Reboulia hemisphaerica* air chambers and pores. From Haupt 1921a.

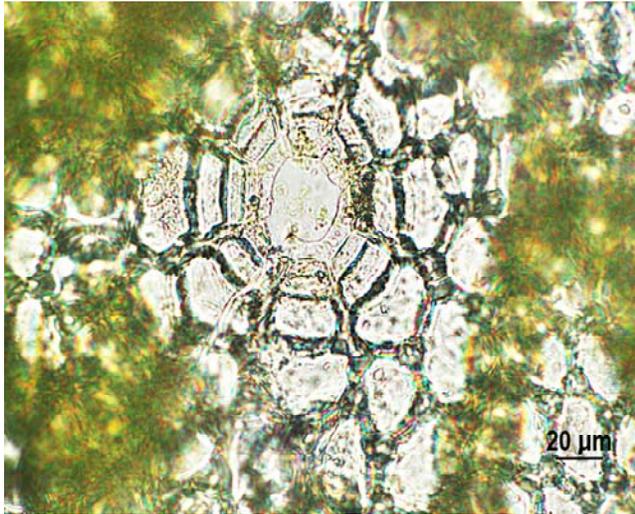


Figure 101. *Reboulia hemisphaerica* thallus pore. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Having pores (Figure 99-Figure 101) presents its own set of problems. They are advantageous for gas exchange, but not only do they allow water to leave the thallus, they also can allow water to enter. In species like *Reboulia hemisphaerica* (Figure 69-Figure 76), these pores have hydrophobic ledges that not only constrict the size of the pore, but that also repel water, preventing water from entering the plant during downpours or other water events Schönherr & Ziegler (1975). For water to enter, it must have a contact angle of 0° with the ledge. It would be interesting to see the difference in photosynthetic rate if these chambers were injected with water to fill the spaces.

Watson (1919) noted that when *Reboulia hemisphaerica* (Figure 69-Figure 76) grows on wet ground it has fewer rhizoids than when it grows in drier situations. This suggests that more rhizoids help to facilitate the movement and uptake of water, as noted above for other members of the family. Daniels (1998) cites the complex morphology along with tuberculate and smooth rhizoids, scale leaves (Figure 102), and well defined assimilatory and storage zones as xerophytic adaptations in *R. hemisphaerica*.

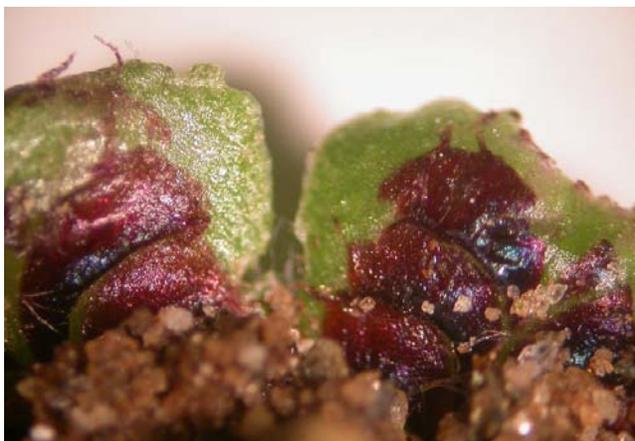


Figure 102. *Reboulia hemisphaerica* ventral side with scales (reddish). Photo by Blanka Aguero, through Creative Commons.

Reproduction

Haupt (1921a) described *Reboulia hemisphaerica* (Figure 69-Figure 76) as **monoicous** (Figure 103-Figure 107) in Midwestern USA. It is **protandrous** (antheridia develop before archegonia; Figure 105-Figure 106). Generally, 2-3 antheridial groupings develop in succession before the archegonia develop. The antheridia and archegonia occur in separate groups on the dorsal thallus surface.



Figure 103. *Reboulia hemisphaerica* male and female reproductive structures. Photo by Bob Klips, with permission.



Figure 104. *Reboulia hemisphaerica* with sexual structures. Photo by Ed Leathers, with permission.



Figure 105. *Reboulia hemisphaerica* with antheridia but no visible archegoniophores. Photo by Michael Lüth, with permission.



Figure 106. *Reboulia hemisphaerica* with male (brown) and female (green) sex organs. Photo by Ed Leathers, with permission.



Figure 107. *Reboulia hemisphaerica* with young archegoniophores and mosses that probably help in moisture retention. Photo by Barry Stewart, with permission.

Dupler (1922a) considered the male receptacle and antheridium to be plastic, including both primitive and advanced characteristics. It is typically dorsal and posterior to the female receptacle (Figure 108-Figure 118) that terminates the branch. It is sessile or on a very short stalk, a feature that places it close to the archegonial head before elongation of the latter on its stalk.



Figure 108. *Reboulia hemisphaerica* young archegoniophores in Europe. Photo by Michael Lüth, with permission.



Figure 109. *Reboulia hemisphaerica* young archegoniophores in Europe. Photo by Michael Lüth, with permission.



Figure 110. *Reboulia hemisphaerica* archegoniophores in Europe. Photo by Michael Lüth, with permission.



Figure 111. *Reboulia hemisphaerica* with young archegoniophores. Photo by Li Zhang, with permission.



Figure 112. *Reboulia hemisphaerica* archegonial heads. Photo by Heino Lepp, Australian National Botanic Gardens <www.anbg.gov.au>, with online permission.



Figure 115. *Reboulia hemisphaerica* with elongated archegoniophores. Photo by Michael Lüth, with permission.



Figure 113. *Reboulia hemisphaerica* archegonial heads. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.



Figure 116. *Reboulia hemisphaerica* with emerging archegoniophores. Photo by Štěpán Koval, with permission.



Figure 114. *Reboulia hemisphaerica* with emerged archegoniophores in Europe. Photo by Michael Lüth, with permission.



Figure 117. *Reboulia hemisphaerica* with emerging archegoniophores and still green thalli. Photo by Malcolm Storey <www.discoverlife.org>, with online permission.



Figure 118. *Reboulia hemisphaerica* with archegoniophores and dying thalli. Photo by Štěpán Koval, with permission.

Udar and Chandra (1964) reported anomalous female receptacles in *Reboulia hemisphaerica* (Figure 69-Figure 76). One aberrant type produced branch stalks of the archegoniophores. A second aberrant type was just the opposite, producing no stalks or nearly sessile archegonial heads. Furthermore, Chandra (1963) reported compound female receptacles.

Miduno (1937) described the spermatozoids of *Reboulia hemisphaerica* (Figure 69-Figure 76). These typically had two cilia, although they also found five with three cilia. Other variations in size of the spermatozoid and relative length of the cilia were present.

Among the variations in the life cycle of *Reboulia hemisphaerica* (Figure 69-Figure 76) are differences in oicy. Since Haupt (1921a) published his descriptions of Midwestern, USA, populations, differences among populations have led to the description of subspecies. The subspecies of *R. hemisphaerica* differ in the distribution of their sexual organs (Hicks 1992). The typical variety is **paroiuous**, whereas the three more recent subspecies are **dioicous** and two **autoicous** ones with differences in male receptacle size. Konstantinova (2011) reported that populations in the eastern Caucasus of Russia were **autoicous**. However in the entire country of Russia, one can find **paroiuous**, **autoicous**, and **dioicous** populations (Bakalin 2008). Schuster (1992) considered all these to be one species, but Bakalin (2008) considers them to need further study. Itouga *et al.* (2005) noted that *R. hemisphaerica* had been subdivided into seven subspecies based on sexual condition, a strong indicator of genetic diversity. They recognized three subspecies in Japan, including the autoicous subsp. *orientalis*, subsp. *acrogyna*, and a new to Japan **paroiuous** subsp. *hemisphaerica*. In addition to differences in oicy, spore maturation times differed. In subsp. *acrogyna* spores matured in summer, whereas in subsp. *hemisphaerica* and subsp. *orientalis*, they matured in spring.

The emergence of the archegoniophore of *Reboulia hemisphaerica* (Figure 69-Figure 76) does not occur until the sporophytes are nearly mature (Haupt 1921a). Archegonia appear in autumn and fertilization occurs then. The embryo develops immediately, but the sporophyte

(Figure 119-Figure 123) does not mature until the following spring, necessitating survival through the winter.



Figure 119. *Reboulia hemisphaerica* with immature capsules. Photo by Jiří Kameníček (BioLib, Obázek), with permission.



Figure 120. *Reboulia hemisphaerica* with archegoniophores and emergng sporangia. Photo by Jan-Peter Frahm, with permission.



Figure 121. *Reboulia hemisphaerica* with mature black sporangia. Photo by Michael Lüth, with permission.



Figure 122. *Reboulia hemisphaerica* archegoniophores with young capsules and mature capsules. Photo by Adolf Ceska, with permission.



Figure 123. *Reboulia hemisphaerica* archegonial head with scales and capsules that have shed their spores. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Allsopp (1964) found that whereas male gametangiophores developed on media with 1% glucose, female gametangiophores developed on sugar-free media. Could these differences in energy needs serve to induce their formation at different times?

Rao and Das (1968) found a sharp rise in the respiratory rate and a doubling of the C:N ratio as *Reboulia hemisphaerica* (Figure 69-Figure 76) transformed from the vegetative to female reproductive phase. At that time, the plants exhibited enhanced levels of endogenous IAA (indole-3-acetic acid), RNA, and protein. During antheridial formation the plants exhibited a reverse trend and exhibited no appreciable change in the C:N ratio (see also Hartmann & Weber 1990).

As noted by Haupt (1921a), *Reboulia hemisphaerica* (Figure 69-Figure 76) is fertilized in autumn in southern Wisconsin and northern Illinois, USA (O'Hanlon 1928); Dupler (1922b) likewise reported fertilization in October. In early spring (8 March) the plants are still dormant (O'Hanlon 1928). Woodburn (1919) determined that both egg and sperm nuclei are in a resting condition in the early stages of fusion. When transplanted indoors on 29 October, *R. hemisphaerica* regenerated new branches but failed to exhibit elongation of the archegoniophore (O'Hanlon 1928). The plants exhibited an inverse relationship between amount of regeneration and development within the receptacle. Most thalli produce fewer than three mature sporophytes per head, but can produce up to nine.

As one might expect, *Reboulia hemisphaerica* (Figure 69-Figure 76) has a lower gene flow with increasing distance ($Nm = -0.0009 \times \text{km}^{1.1}$) (Itouga *et al.* 2002). The mean value for populations in East Asian populations was only 0.609. Thus, the genetic variation was high, as would be predicted for species that reproduce only by spores. Slatkin (1985) considers that Nm values <1 usually imply that genetic drift has been a major contributor to the distribution of genetic variation. Itouga and coworkers found that the break point for Nm values <1 was 125 km. Dispersal of spores beyond 100 km was negligible. Itouga and coworkers agree that the degree of genetic differentiation within monoicous marchantialean species is correlated with dispersal distances of sperm and rates of self-fertilization. Nevertheless, the dioicous *Asterella wallichiana* (Figure 124) and monoicous *R. hemisphaerica* showed similar levels of gene flow in this study.



Figure 124. *Asterella wallichiana*, a dioicous liverwort with gene flow levels similar to those of the monoicous *Reboulia hemisphaerica*. Photo by Forestowlet, through Creative Commons.

Woodburn (1919) described the union of egg and sperm and the early developmental stages of the ensuing sporophyte. Dupler (1922b) also described the early embryogeny of *Reboulia hemisphaerica* (Figure 69-Figure 76). The embryo begins immediate development following fertilization. There is considerable variation in the development of the early embryo, with accompanying variations in habitat, archegoniophore, and other morphological variations. By winter, the sporogenous tissue is becoming differentiated. However, the sporophyte does not mature until the following May or June. Brown found *Reboulia hemisphaerica* fruiting "profusely" in a variety of places in Georgia (in the Caucasus region).

Haupt (1921b) found that the archegoniophore begins to elongate in early spring (Figure 125), about the last week of March, in Indiana, USA. The sporogenous tissue resumes development, but there is no indication at that time as to which will become spores and which elaters. By the first part of May, these cells break apart from each other, form an abundance of mucilage, and spore mother cells and elaters are clearly distinguishable.



Figure 125. *Reboulia hemisphaerica* with developing archegoniophores and dying older thalli. Photo by Štěpán Koval, with permission.

Blair (1926) describes meiosis in *Reboulia hemisphaerica* (Figure 69-Figure 76). She notes only 16 chromosomes arriving at each pole. However, several authors (Sha *et al.* 2003; Itouga *et al.* 2005) have since determined the chromosome number for *R. hemisphaerica* to be $n=9$, a typical number in liverworts.

Patidar *et al.* (1987) reported 2410 spores (Figure 126-Figure 127) per capsule in *Reboulia hemisphaerica* (Figure 69-Figure 76). Schuster (1966) earlier reported 2500 per capsule (see also O'Hanlon 1930). These large (70-80 μm) spores germinate in about five days when in suitable conditions of fairly good light and plenty of moisture (O'Hanlon 1930). They remain completely viable for at least five months.

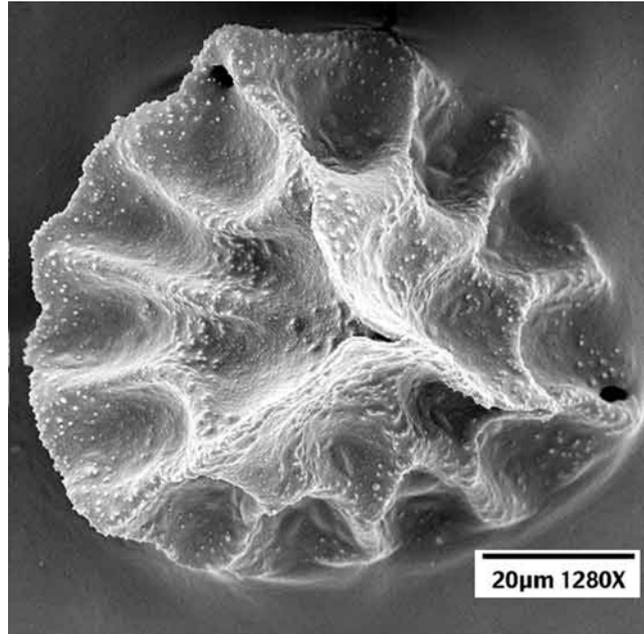


Figure 126. *Reboulia hemisphaerica* spore SEM. Photo by William T. Doyle, with permission.

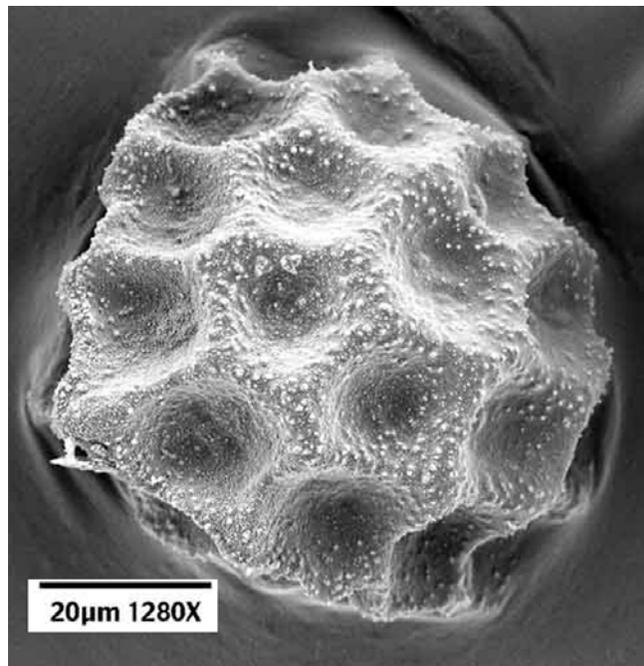


Figure 127. *Reboulia hemisphaerica* distal spore wall SEM. Photo by William T. Doyle, with permission.

Reboulia hemisphaerica (Figure 69-Figure 76) produces a tangle of white, sticky filaments (Figure 128) below the capsule (Frank 2015). These appear to aid in spore dispersal in a rather unusual way. They make a bryophyte version of masking tape. The springtail *Bourletiella hortensis* (Figure 129) peruses the capsule area and comes away with bits of the sticky filaments on its body. And to these, spores are attached. Frank suggests that not only do springtails aid dispersal through these adhered filaments, but that other animals could easily contribute as well.



Figure 128. *Reboulia hemisphaerica* archegoniophores with mature sporangia in Europe. Note the white filaments hanging below the capsules. Photo by Michael Lüth, with permission.



Figure 129. *Bourletiella hortensis*, a springtail that facilitates spore dispersal in *Reboulia hemisphaerica* by getting sticky filaments with adhering spores stuck to its body. Photo by Andy Murray, through Creative Commons.

Vishvakarma and Kaul (1987) studied the effects of such conditions as duration, quality, and intensity of light on spore germination in *Reboulia hemisphaerica* (Figure 69-Figure 76). Inoue (1960) reported that blue and red light were the most effective in promoting rhizoid development, and far-red and green caused less activity. However, germ tube development was just the opposite of rhizoid development, being relatively short in blue and red light but elongating remarkably in far-red and green.

Vishvakarma and Kaul (1988b) found that the optimum pH for both germination and thallus growth was 6, but vegetative growth occurred in the range of 3.0-7.0. Germination was more restricted at pH 5-7. Differences between germination requirements and growth tolerances could explain the absences of species in some areas where we expect them.

O'Hanlon (1930) noted that the first stage in spore germination of *Reboulia hemisphaerica* (Figure 69-Figure 76) is the emergence of a germ tube and a single rhizoid. The author provides details of subsequent cell divisions

leading up to bud formation. Rhizoids form on the ventral side of the protonema, establishing its dorsiventrality. Low intensity causes the germ tubes to be extremely long or to give rise to secondary and even tertiary germ tubes. Hartmann and Weber (1990) reviewed the literature on control of germination in this and other species of liverworts.

Vishvakarma *et al.* (1987) showed that percentage spore germination of *Reboulia hemisphaerica* (Figure 69-Figure 76) was enhanced by the addition of Mg in the liquid culture medium.

Not all bryophytes are known to produce callus tissue. Allsopp (1957) reported the first success in obtaining unlimited callus-like growth in liverworts, one of which was *Reboulia hemisphaerica* (Figure 69-Figure 76). This technique is often useful for mass producing desired chemical from bryophyte tissues.

Koevenig (1973) investigated reproductive physiology of *Reboulia hemisphaerica* (Figure 69-Figure 76). Archegoniophores elongate in late spring in Kansas. Under long days (12 hr light, 12 hr dark, or 16 hr light, 8 hr dark), pre-elongation archegoniophores elongated completely within two weeks at both 15 and 25°C. But in short days (8 hr light, 16 hr dark) no elongation occurred. Cold temperature (5°C) slowed elongation. Adding plant growth hormones (IAA, NAA, BA, GA) to heads failed to stimulate to normal lengths in short days. Koevenig suggested that perhaps the hormones could facilitate elongation but could not initiate it. (See also Szein *et al.* 1997).

Brown and Lemmon (1990) elucidated the mitotic apparatus of *Reboulia hemisphaerica* (Figure 69-Figure 76). They concluded that the mitotic apparatus in this species demonstrates a transition between algae and land plants.

Nehira and Nakagoshi (1987) reported that after removal of bryophytes in an urban environment, the same community became re-established in 1-2 years. Pleurocarpous mosses and thalloid liverworts such as *Reboulia hemisphaerica* (Figure 69-Figure 76) regenerated faster than did acrocarpous mosses. This regrowth occurred primarily in spring and autumn, but there was little seasonal variation in the amount of available airborne diaspores.

Role

Bryophytes such as *Reboulia hemisphaerica* (Figure 69-Figure 76) often serve as substrates for algae, especially diatoms (Ando 1978). These algae and other microorganisms provide food for visiting invertebrates. But the bryophytes themselves can serve as food (Konstantinov *et al.* 2019). The flea beetle *Distigmoptera borealis* (Figure 130) was recently discovered eating *R. hemisphaerica*. Imada and Kato (2016) reported on larvae of the fly *Litoleptis* on bryophytes and described six new species, all thallus-miners of liverworts. *Litoleptis küiensis* (Figure 131), *L. niyodoensis*, *L. himukaensis*, and *L. izuensis* are all thallus miners on *Reboulia hemisphaerica* and only that species.



Figure 130. *Distigmoptera borealis*, a beetle that consumes *Reboulia hemisphaerica* thalli. Photo from CBG Photography Group, Centre for Biodiversity Genomics, through Creative Commons.



Figure 131. *Litoleptis kiienensis* larva, an inhabitant of *Reboulia hemisphaerica*. Photo courtesy of Yume Imada.

Biochemistry

Reboulia hemisphaerica (Figure 69-Figure 76) was an early subject of biochemical studies. Furusawa *et al.* (2006) isolated and described structures of new cyclomylytayne and ent-chamigrane-type sesquiterpenoids from *Reboulia hemisphaerica* subsp. *australis*. Morais *et al.* (1988, 1991) described a gymnomitrane-type sesquiterpenoid and two derivatives from cultures of this species. Keserü and Nogradi (1995) reported riccardins. Warmers and König (1999, 2000) reported gymnomitrone from plants in nature and described its synthesis. Wei *et al.* (1995) described five new sesquiterpenoids and three new marchantin-type compounds and elucidated their structures. Sakai *et al.* (1999) were able to describe the synthesis (+)-cyclomylytayne-5 α -ol from *Reboulia hemisphaerica* from Taiwan.

Toyota *et al.* (1999) found and described the structure of four new sesquiterpenes from *Reboulia hemisphaerica* (Figure 69-Figure 76), as well as isolating nine compounds that were already known. Warmers and König (2000) identified the biosynthesis of the gymnomitrane-type sesquiterpene in this species.

Reboulia hemisphaerica (Figure 69-Figure 76) has chemotypes (Ludwiczuk *et al.* (2008). The researchers found two "totally different chemical compositions" in two different locations in Tokushima, Japan, whereas those from the same location had very similar chemical composition, indicating genetic isolation of the two populations. They noted that *R. hemisphaerica* has sesquiterpenoids and acetogenins.

Asakawa and Matsuda (1982) isolated riccardin C from *Reboulia hemisphaerica* (Figure 69-Figure 76) – a secondary compound that appears to be widespread among thallose liverworts. Wang *et al.* (2011a) found four new phenolic glycosides in this species in China and described their structures as rebousides. Wang *et al.* (2011b) described the configuration of isoriccardin C and riccardin D isolated from this species.

Kwon *et al.* (2019) were able to describe the entire chloroplast genome of *Reboulia hemisphaerica* with its 122,596 base pairs with 87 protein-coding genes, eight rRNAs, and 36 tRNAs. These indicated a close relationship to *Dumortiera hirsuta* (Figure 132).



Figure 132. *Dumortiera hirsuta*, a close relative of *Reboulia hemisphaerica*, based on chlorophyll DNA. Photo by Lin Kyan, with permission.

There have been at least some traditional medical uses of bryophytes (Du 1997). Sabovljević *et al.* (2016) noted that *Riccardia hemisphaerica* (Figure 69-Figure 76) is sold in Chinese markets. It has been cited numerous times related to potential medicinal uses of its compounds. Belcik and Wiegner (1980) reported good antibacterial activity in culture, reinforcing the findings of Banerjee and Sen (1979), who considered it to be one of the most active bryophytes against bacteria.

Becker (1990) pointed out the need for *in vitro* plant cultures when the desired plant product has a high price or conventional production of the plant causes problems. Liverwort culture meets the second criterion, but the science is new and although many medicinally active compounds are known, development of their commercial use is negligible. Kandpal *et al.* (2016) further noted the need for new antibiotic compounds because of the increasing evolution of antibiotic-resistant bacterial strains.

While one extract may inhibit bacteria or have other medicinal properties, a different extract solvent of the same compound(s) may exhibit no activity (Zehr 1990). Although this is a serious consideration in making ecological interpretations, it is usually not a serious problem for medicinal applications. Furthermore, effectiveness differs among bacteria species. Zehr showed that *Bacillus subtilis* (Figure 133-Figure 134) and *Escherichia coli* (Figure 135) were the most susceptible bacteria tested while *Enterococcus faecalis* (Figure 136) experienced the least inhibition.

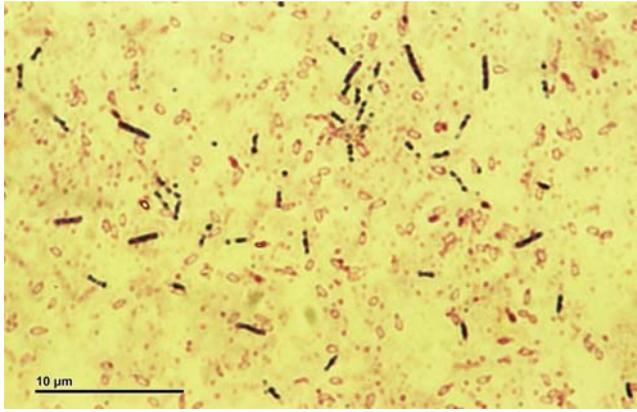


Figure 133. *Bacillus subtilis*, a bacterial species that is inhibited by extracts of *Reboulia hemisphaerica*. Photo by Josef Reischig, through Creative Commons.

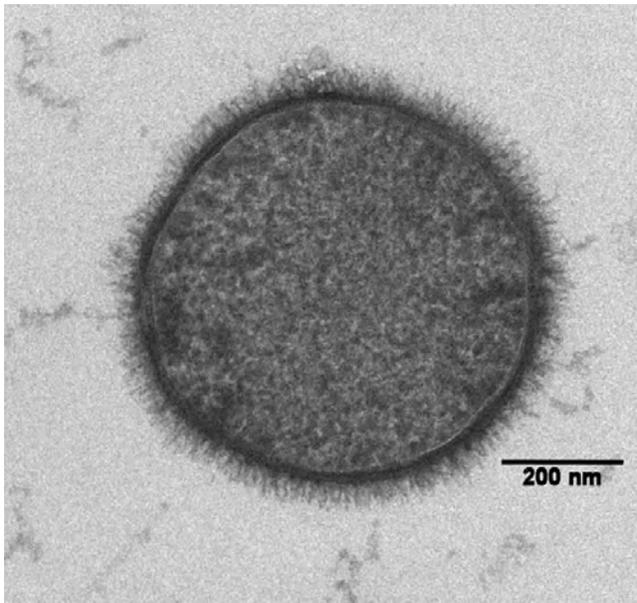


Figure 134. *Bacillus subtilis*, a bacterial species that is inhibited by extracts of *Reboulia hemisphaerica*. Photo by Allonweiner, through public domain.

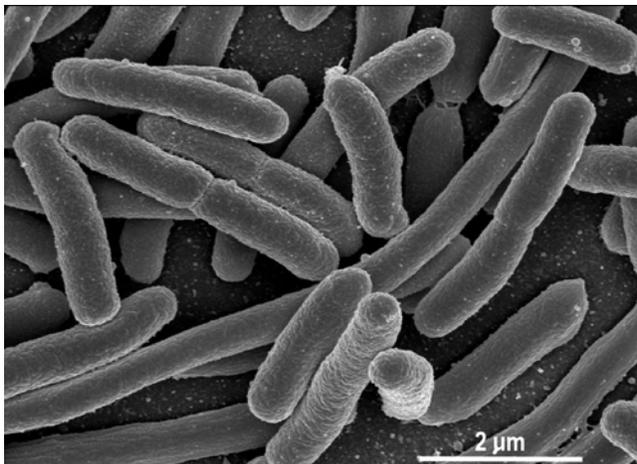


Figure 135. *Escherichia coli*, a bacterial species that is inhibited by extracts of *Reboulia hemisphaerica*. Photo from Rocky Mountain Laboratories, through public domain.

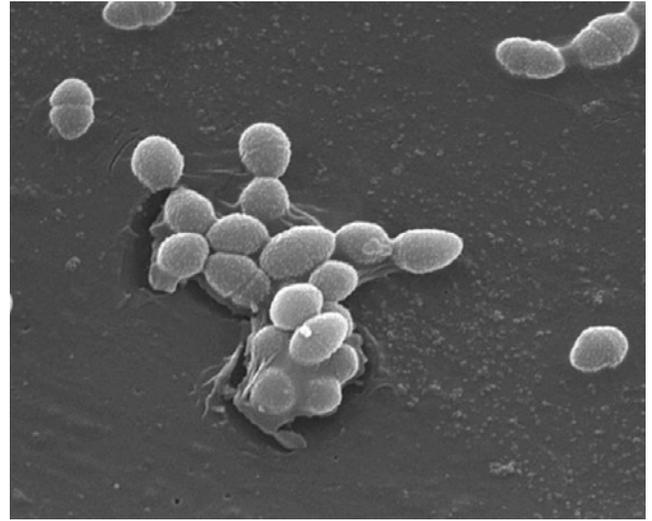


Figure 136. *Enterococcus faecalis* SEM, a species of bacteria that is more resistant than others in study to extracts of *Reboulia hemisphaerica*. Photo from CDC, through public domain.

Following these early studies, a number of additional studies confirmed antibacterial and medicinal activity in *Reboulia hemisphaerica* (Figure 69-Figure 76) (Joshi 1995; Ko *et al.* 1995; Du 1997).

Ko *et al.* (1995) isolated marchantinquinone, from *Reboulia hemisphaerica* (Figure 69-Figure 76), a compound known to inhibit lipid peroxidation and to serve as a free radical scavenger. Liao *et al.* (2000) reported that marchantinquinone from *R. hemisphaerica* inhibited platelet aggregation and ATP release stimulated by thrombin. Harrowven *et al.* (2005) found that Riccardin C, manufactured by *Reboulia hemisphaerica* exhibited cytotoxicity against nasal epidermoid carcinoma cells in culture as well as inhibiting HIV-1 reverse transcriptase.

Asakawa (1998; 2007) cited a number of potential medical uses for *Reboulia hemisphaerica* (Figure 69-Figure 76), including treatment of blotches, external wounds, and bruises, and hemostasis. Tosun *et al.* (2016) and Chandra *et al.* (2017) expanded on this list, including uses to cure cuts, burns, wounds, bacteriosis, pulmonary tuberculosis, neurasthenia, fractures, convulsions, scalds, uropathy, inflammation, fever, and pneumonia. Tosun *et al.* (2016) further elaborated on the specific means of wound healing. Önder and Özenoğlu (2019) found that extracts of *R. hemisphaerica* were effective against three different cancer cell lines.

A variety of potential uses emerged in laboratory cultures of *Reboulia hemisphaerica* (Figure 69-Figure 76) (Gao *et al.* 2009; Asakawa 2013; Tosun *et al.* 2013). Harada *et al.* (2013) reported its potential for the treatment of cardio-vascular diseases, including arteriosclerosis. Even pet treatments are possible, with *R. hemisphaerica* inhibiting carrageenan-induced paw edema (Tosun *et al.* 2013).

Kandpal *et al.* (2016) found the extract of *R. hemisphaerica* (Figure 69-Figure 76) to be the most effective bryophyte species tested against *Escherichia coli* (Figure 135), *Bacillus cereus* (Figure 137), and *Pseudomonas aeruginosa* (Figure 138). The researchers found a correlation between total phenol and flavonoid contents and the antioxidant activity.

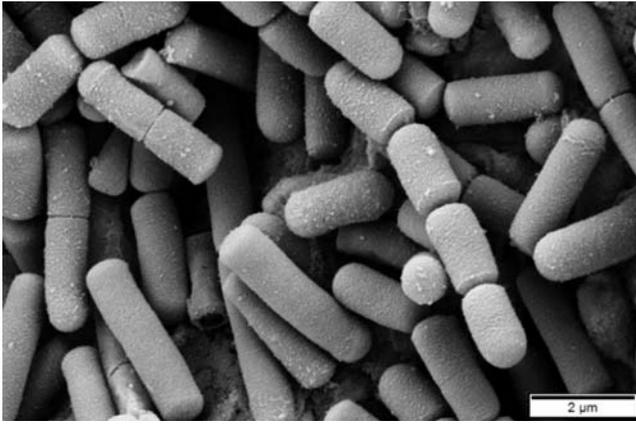


Figure 137. *Bacillus cereus* SEM, a bacterial species that is inhibited by extracts of *Reboulia hemisphaerica*. Photo by Mogana Das Murtey and Patchamuthu Ramasamy, through Creative Commons.

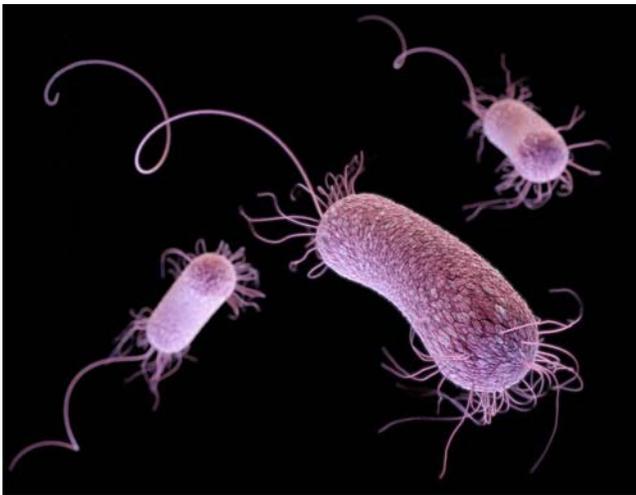


Figure 138. *Pseudomonas aeruginosa*, a bacterial species that is inhibited by extracts of *Reboulia hemisphaerica*. Photo from CDC, through public domain.

Summary

The Aytoniaceae does not have members that are typically submersed, but several species are at least tolerant of being constantly wet from water spray or other source of water. Their habitats include waterfall spray, streamside, dripping cliffs and ledges, wet soil and wind holes, but also various substrata in mesic forests. The latter habitat provides cool, moist air that permits Arctic species to survive in temperate regions. On the other hand, many of these species occur in the mountains, especially in Macaronesia.

The members of **Aytoniaceae** included here tend to endure a wide range of habitats, including a wide range of moisture conditions. They have air spaces that permit CO₂ exchange and rhizoids and scales that facilitate water uptake. Sexual condition varies, even within a species, but no gemmae or other specialized asexual reproductive structures are present. Most of the species die from the posterior end after fertilization, but grow from the apex.

Acknowledgments

Lars Söderström helped me find the current acceptable names for taxa. Bryonettors helped me find images of wind holes.

Literature Cited

- Alam, A., Sharma, V., Verma, P. K., and Kumar, K. 2013. Scanning electron microscopy of some selected south Indian taxa of Marchantiales (Bryophyta: Hepaticae). *Arch. Bryol.* 190: 1-6.
- Aleffi, M. 2005. New check-list of the Hepaticae and Anthocerotae of Italy. *Fl. Medit.* 15: 485-566.
- Aleffi, M., Campisi, P., Cogoni, A., Cortini Pedrotti, C., Flore, F., Perego, S., Sguazzin, F., and Tacchi, R. 2005. Contributo alla conoscenza della flora briologica delle Murge Tarantine (Taranto, Puglia): La Gravina di Petruscio ed il Bosco delle Pianelle. *Inform. Bot. Ital.* 37: 1137-1144.
- Alegro, A., Šegota, V., Rimac, A., Kiebacher, T., Prlić, D., Sedlar, Z., Sedlar, Z., and Papp, B. 2019. New and noteworthy bryophyte records from Croatia. *Cryptog. Bryol.* 40(2): 5-13.
- Allsopp, A. 1957. Controlled differentiation in cultures of two liverworts. *Nature* 179: 681-682.
- Allsopp, A. 1964. The metabolic status and morphogenesis. *Phytomorphology* 14: 1-27.
- Ando, K. 1978. Moss diatoms in Japan (2). *Jap. J. Phycol.* 26: 125-130.
- Asakawa, Y. 1998. Biologically active compounds from bryophytes. *J. Hattori Bot. Lab.* 84: 91-104.
- Asakawa, Y. 2007. Biologically active compounds from bryophytes. *Pure Appl. Chem.* 79: 557-580.
- Asakawa, Y. 2013. Chemical constituents of bryophytes: Chemical diversity, biological activity, and chemosystematics. Conference of the International Association of Bryologists, 15-19 July 2013 at Natural History Museum, London, UK.
- Asakawa, Y. and Matsuda, R. 1982. Riccardin C. a novel cyclic bibenzyl derivative from *Reboulia hemisphaerica*. *Phytochemistry* 21: 2143-2144.
- Asakawa, Y., Ludwiczuk, A., and Nagashima, F. 2013. Chemical constituents of bryophytes: Bio- and chemical diversity, biological activity and chemosystematics. In: Kinghorn, A. D., Falk, H., and Kobayashi, J. (eds.). *Progress in the Chemistry of Organic Natural Products*, vol. 95. Springer-Verlag, Vienna, pp. 1-796.
- Bakalin, V. A. 2008. New liverwort records from Primorsky Territory. 2. *Arctoa* 17: 221-226.
- Bakalin, V. A., Butorina, E. V., and Klimova, K. G. 2017. The Hepaticae and Anthocerotae of Kedrovaya Pad' Nature Reserve – an intact enclave of East Manchurian flora in Russia. *Bot. Pacif.* 6(1): 23-29.
- Bakalin, V. A., Stupnikova, T. V., and Klimova, K. G. 2019. New input to the knowledge of the liverwort flora of Amur Province (the Russian Far East). *Бюллетень Ботанического сада-института ДВО РАН* 22: 28-35.
- Banerjee, R. D. and Sen, S. P. 1979. Antibiotic activity of bryophytes. *Bryologist* 82: 141-153.
- Becker, H. 1990. Terpene production by liverworts of *in vitro* cultures. In: Nijkamp, H. J. J., Plas, L. H. W. van der, and Aartrijk, J. van. (eds.). *Progress in Plant Cellular and Molecular Biology. Current Plant Science and Biotechnology in Agriculture*, Vol 9. Springer, Dordrecht, pp. 609-613.

- Belcik, F. P. and Wiegner, N. 1980. Antimicrobial activities or antibiosis of certain eastern U.S. liverwort, lichen and moss extracts. *J. Elisha Mitchell Sci. Soc.* 96: 94.
- Bischler-Causse, H. and Long, D. G. 1993. Taxonomic results of the BRYOTROP-Expedition to Zaire and Rwanda. *Trop. Bryol.* 8: 53-54.
- Blair, M. C. 1926. Sporogenesis in *Reboulia hemisphaerica*. *Bot. Gaz.* 81: 377-400.
- Blockeel, T. L. 2003. New records of bryophytes from Cyprus. *Bocconea* 16: 105-113.
- Blockeel, T. L. 2012. Notes on the bryophytes of the schistose valleys of western Crete, including *Asterella africana* new to Greece, and an assessment of the conservation status of *Rhamphidium purpuratum* and *Jungermannia handelii*. *J. Bryol.* 34: 292-296.
- Böcskei, Z. and Keserü, G. M. 1994. Crystal structure and conformation of pakyonol, a macrocyclic bis (bibenzyl) constituent of *Mannia fragrans*. *J. Chem. Soc. Perkin Trans. 2*: 595-597.
- Boisselier-Dubayle, M. C., Lambourdiere, J., and Bischler, H. 1998. Taxa delimitation in *Reboulia* investigated with morphological, cytological, and isozyme markers. *Bryologist* 101: 61-69.
- Boonkerd, T., Pollawatn, R., Chantanaorrapint, S., and Lai, M. J. 2007. A Note on *Asterella khasyana* (Griff.) Pandé, KP Srivast. and Sultan Khan (Marchantiales, Aytoniaceae) in Thailand. *Trop. Nat. Hist.* 7(2): 109-113.
- Borovichev, E. A. 2014. Checklist of liverworts of the Lapland State Nature Biosphere Reserve (Murmansk Province, Russia). *Folia Cryptog. Eston.* 51: 1-11.
- Borovichev, E. A. and Andreeva, E. N. 2009. New findings of liverwort in Murmansk region 2. *Arctoa* 18: 249-287.
- Borovichev, E. A. and Bakalin, V. A. 2016. On *Mannia triandra* (Aytoniaceae, Marchantiophyta) in Eastern Asia. *Herzogia* 29: 59-65.
- Breil, D. A. 1977. Bryophytes of the Virginia Piedmont floodplains. *Castanea* 42: 308-315.
- Brown, M. S. 1924. Hepatics in Georgia. *Bryologist* 27: 31-34.
- Brown, R. C. and Lemmon, B. E. 1990. Polar organizers mark division axis prior to preprophase band formation in mitosis of the hepatic *Reboulia hemisphaerica* (Bryophyta). *Protoplasma* 156: 74-81.
- Brugués, M., Infante, M., and Cros, R. M. 2011. Anotaciones sobre hepáticas de España. *Bol. Soc. Español. Biol.* 36: 3-8.
- Capelo, J., Sequeira, M., Jardim, R., Mesquita, S., and Costa, J. C. 2005. The vegetation of Madeira Island (Portugal). A brief overview and excursion guide. *Quercetea* 7: 95-122.
- Casas, C. 1998. The Anthocerotae and Hepaticae of Spain and Balearic Islands: A preliminary checklist. *Orsis* 13: 17-26.
- Cedrés-Perdomo, R. D., Losada-Lima, A., González-Montelongo, C., Arencibia, M. C. L., and Pérez-Vargas, I. 2017. Flora briológica del Bosque del Adelantado (El Rosario, Tenerife). *Vieraea* 45: 313-322.
- Chandra, V. 1963. On the occurrence of compound female receptacles in *Reboulia hemisphaerica* (L.) Raddi. *Curr. Sci.* 32: 372-373.
- Chandra, S., Chandra, D., Barh, A., Pandey, R. K., and Sharma, I. P. 2017. Bryophytes: Hoard of remedies, an ethno-medicinal review. *J. Trad. Comple. Med.* 7: 94-98.
- Chaturvedi, S. K. and Eshuo, K. 2012. Abnormal asexual reproduction in *Asterella khasyana* (Griff.) Pande KP Srivast and Sultan Khan (Marchantiophyta: Hepaticae) from Nagaland. *Internat. J. Plant Repro. Biol.* 4: 89-92.
- Choi, S. S., Bakalin, V. A., Park, S. J., Sim, S. H., and Hyun, C. W. 2020. Unrecorded liverwort species from Korean flora III. New data on the distribution of *Mannia* Opiz (Marchantiophyta). *Korean J. Plant Tax* 50: 227-231.
- Clausen, E. 1964. The tolerance of hepatics to desiccation and temperature. *Bryologist* 67: 411-417.
- Colacino, C. and Sabovijevic, M. 2006. Bryophyte flora of Albania: A preliminary check-list. *Cryptog. Bryol.* 27(4): 1-30.
- Conard, H. S. 1940. Thirty Iowa liverworts. *Proc. Iowa Acad. Sci.* 47: 97-99.
- Crundwell, A. C. and Nyholm, E. 1979. Some additions to the bryophyte flora of Turkey. I. Hepaticae. *J. Bryol.* 10: 479-489.
- Daniels, A. E. D. 1998. Ecological adaptations of some bryophytes of the Western Ghats. *J. Ecobiol.* 10: 261-270.
- Daniels, A. E. D. 2010. Checklist of the bryophytes of Tamil Nadu, India. *Arch. Bryol.* 65: 1-117.
- De, A. B. 2017. Association of *Glomus tenue* (Greenall) Hall with the hepatic *Mannia fragrans* (Balb.) Frye & Clark. *Internat. J. Adv. Res. Biol. Sci.* 4(8): 51-58.
- Dierßen, K. 2001. Distribution, ecological amplitude and phytosociological characterization of European bryophytes. *Bryophyt. Biblioth.* 56. J. Cramer, Berlin-Stuttgart, 289 pp.
- Dirkse, G. M. 1995. Remarks on the bryophytes of the Canary Islands. *Bol. Mus. Mun. Fuchal Suppl.* 4: 211-217.
- Dirkse, G. M. and Bouman, A. C. 1996. A revision of *Rhynchostygiella* (Musci, Brachytheciaceae) in the Canary Islands. *Lindbergia* 20: 109-121.
- Dixit, A. K. and Kerketta, M. A. 2019. Richness of Thaloid liverworts in Bilaspur, Achanakmar-Amarkantak Biosphere Reserve and Lafa hills, Chhattisgarh (India). *Plant Sci. Today* 6: 287-298.
- Dort, K. W. van and Nieuwkoop, J. A. W. 2003. De bryologische excursie naar Gran Canaria in 1996. *Buxbaumia* 64: 11-27.
- Du, Z.-X. 1997. A study of medicinal bryophytes used in Guangxi Province, S China. *Chenia, Contrib. Cryptog. Biol.* 3-4: 123-124.
- Duda, J. 1965. Beitrag zur Erforschung der Lebermoose Jugoslawiens. [Contribution to research on the liverworts of Yugoslavia.]. *Acta Bot. Croat.* 24: 79-82.
- Dulin, M. V. 2013. Liverworts of the Ilych River valley (Komi Republic). *Arctoa* 22: 35-40.
- Dupler, A. W. 1921. The air chambers of *Reboulia hemisphaerica*. *Bull. Torrey Bot. Club* 48: 241-252.
- Dupler, A. W. 1922a. The male receptacle and antheridium of *Reboulia hemisphaerica*. *Amer. J. Bot.* 9: 285-295.
- Dupler, A. W. 1922b. Early embryogeny of *Reboulia hemisphaerica*. *Bot. Gaz.* 74: 143-157.
- Dürhammer, O. 2017. FFH-Moose in Bayern. Arten und Lebensräume. [FFH mosses in Bavaria. Species and habitats.]. *Anliegen Nat.* 39(2): 47-50.
- Ferreira, M. T., Aguiar, F. C. F., Rodríguez-González, P., Albuquerque, A., and Sérgio, C. 2008. Manual Para a Avaliação Biológica da Qualidade da Água Em Sistemas Fluviais Segundo a Directiva Quadro da Água. Protocolo de amostragem e análise para os macrófitos. [Manual for Biological Assessment of Water Quality in River Systems under the Water Framework Directive. Sampling and Analysis Protocol for Macrophytes.]. Ministério Do Ambiente, Do Ordenamento Do Território e Do Desenvolvimento Regional, 18 pp.

- Figueiredo, A. C., Barroso, J. G., Pedro, L. G., Fontinha, S. S., Sim-Sim, M., Sérgio, C., Luís, L., and Scheffer, J. J. C. 2006. *Asterella africana* (Mont.) A. Evans grown on Madeira and in mainland Portugal: Morphological data and composition of the essential oil. *Flav. Frag. J.* 21: 534-538.
- Frahm, J. P. 2005. An evaluation of the bryophyte flora of the Azores. *Trop. Bryol.* 26: 57-79.
- Frank, K. D. 2015. Apparent dispersal of *Reboulia hemisphaerica* (Aytoniaceae) by springtails. *Bartonia* 67: 85-89.
- Furuki, T. 1992. Ecological notes and distribution range of *Mannia fragrans* (Balbis) Frye et Clark in Japan. *Proc. Bryol. Soc. Japan* 5(10): 158-160.
- Furusawa, M., Hashimoto, T., Noma, Y., and Asakawa, Y. 2006. Isolation and structures of new cyclomyltayne and ent-chamigrane-type sesquiterpenoids from the liverwort *Reboulia hemisphaerica* and their biotransformation by the fungus *Aspergillus niger*. *Chem. Pharmaceut. Bull.* 54: 996-1003.
- Gabriel, R., Pereira, F., Borges, P. A. V., and Constância, J. P. 2008. Indicators of conservation value of Azorean caves based on its bryophyte flora at cave entrances. In: Espinasa-Pereña, R. and Pint, J. (eds.). *Proc. X, XI and XII International Symposia on Vulcanospeleology, Association for Mexican Cave Studies (AMCS), Bull. 19, Sociedad Mexicana de Exploraciones Subterráneas (SMES), Bol. 7. XI International Symposium on Vulcanospeleology, Pico Island, Azores, May 12-18, 2004*, pp. 114-118.
- Gabriel, R., Homem, N., Couto, A. B., Aranda, S. C., and Borges, P. A. 2011. Azorean bryophytes: A preliminary review of rarity patterns. *Açoreana: Revista de Estudos Açoreanos, Suppl.* 7: 149-206.
- Gao, J., Li, X., Lv, B.-B., Sun, B., Zhu, C.-J., and Lou, H.-X. 2009. LC-DAD/MS/MS detection of macrocyclic bisbibenzyls from the liverwort *Reboulia hemisphaerica* and the cell-based screening of their microtubule inhibitory effects. *Chinese J. Nat. Med.* 7(2): 123-128.
- Gökler, İ. 2017. Contributions to the liverworts flora of Uşak province. *Anatolian Bryol.* 3(1): 19-24.
- González-Mancebo, J. M. and Hernández-García, C. D. 1996. Bryophyte life strategies along an altitudinal gradient in El Canal y los Tiles (La Palma, Canary Islands). *J. Bryol.* 19: 243-255.
- Harada, K., Makino, K., Shima, N., Okuyama, H., Esumi, T., Kubo, M., Hioki, H., Asakawa, Y., and Fukuyama, Y. 2013. Total synthesis of riccardin C and (\pm)-cavicularin via Pd-catalyzed Ar-Ar cross couplings. *Tetrahedron* 69: 6959-6968.
- Harrowven, D. C., Woodcock, T., and Howes, P. D. 2005. Synthesis of cavicularin and riccardin C: Addressing the synthesis of an arene that adopts a boat configuration. *Synfacts* 17: 3967-3969.
- Hartmann, E. and Weber, M. 1990. Photomodulation of protonemal development. Chapt. 3. In: Chopra, R. N. and Bhatla, S. C. *Bryophyte Development: Physiology and Biochemistry*. CRC Press, Ann Arbor, pp. 33-54.
- Haupt, A. W. 1921a. Gametophyte and sex organs of *Reboulia hemisphaerica*. *Bot. Gaz.* 71: 61-74.
- Haupt, A. W. 1921b. Embryogeny and sporogenesis in *Reboulia hemisphaerica*. *Bot. Gaz.* 71: 446-453.
- Hernández-García, C. D., González-Mancebo, J. M., and Losada-Lima, A. 1995. Contribución al estudio florístico de cuevas artificiales (galerías) en la isla de Tenerife (Islas Canarias). II. [Contribution to the floristic knowledge of artificial caves (water tunnel) on the island of Tenerife (Canary Islands). II.]. *Vieraea* 24: 143-152.
- Hicks, M. L. 1992. Queensland liverworts: *Reboulia* Raddi. *J. Hattori Bot. Lab.* 71: 113-117.
- Hock, Z., Szövényi, P., Schneller, J. J., Tóth, Z., and Urmi, E. 2008a. Bryophyte diaspore bank: A genetic memory? Genetic structure and genetic diversity of surface populations and diaspore bank in the liverwort *Mannia fragrans* (Aytoniaceae). *Amer. J. Bot.* 95: 542-548.
- Hock, Z., Szövényi, P., Schneller, J. J., Urmi, E., and Tóth, Z. 2008b. Are sexual or asexual events determining the genetic structure of populations in the liverwort *Mannia fragrans*? *J. Bryol.* 30: 66-73.
- Hock, Z., Szövényi, P., Schneller, J. J., Urmi, E., and Tóth, Z. 2009. Population genetic consequences of the reproductive system in the liverwort *Mannia fragrans*. *Plant Ecol.* 202: 123-134.
- Hodgetts, N. G., Cáliz, M., Englefield, E. *et al.* 2019. A miniature world in decline: European Red List of Mosses, Liverworts and Hornworts. IUCN, Brussels, 88 pp.
- Hoffman, G. R. and Gates, D. M. 1970. An energy budget approach to the study of water loss in cryptogams. *Bull. Torrey Bot. Club* 97: 361-366.
- Hong, W. S. 1977. Thalloid Hepaticae of Montana and phytogeographical relationships to neighboring states and provinces. *Bryologist* 80: 270-278.
- Hugonnot, V. 2010. Mousses et hépatiques de Païolive (Ardèche et Gard, France). [Mosses and Liverworts of Païolive (Ardèche and Gard, France).] *Bull. Soc. Bot. Centre-Ouest, n.s.* 34: 1-293.
- Hugonnot, V. and Celle, J. 2012. Fiche de *Mannia triandra* (Scop.) Grolle. [File of *Mannia triandra* (Scop.) Grolle.]. Fédération des Conservatoires botaniques nationaux.
- Hugonnot, V. and Offerhaus, B. 2005. Nouvelles localités de *Mannia triandra* (Scop.) Grolle. Écologie et répartition en France. [New localities of *Mannia triandra* (Scop.) Grolle. Ecology and distribution in France.]. *J. Bot. Soc. Bot. France* 29: 63-68.
- Hugonnot, V., Vanderpert, H., and Granato, L. 2017. Les bryophytes du complexe pétrifiant de Saint-Maurin (La Palud-sur-Verdon, Alpes-de-Haute-Provence) Approche conservatoire. *Bull. Soc. Linn. Provence* 68: 87-96.
- Huneck, S., Connolly, J. D., Rycroft, D. S., and Woods, N. 1988a. Pakyonol, a macrocyclic bisbibenzyl diether from the liverwort *Mannia fragrans*. *J. Chem. Res.* 1988: 78-79.
- Huneck, S., Connolly, J. D., Freer, A. A., and Rycroft, D. S. 1988b. Grimaldone, a tricyclic sesquiterpenoid from *Mannia fragrans*. Crystal structure analysis. *Phytochemistry* 27: 1405-1407.
- Imada, Y. and Kato, M. 2016. Bryophyte-feeding of *Litoleptis* (Diptera: Rhagionidae) with descriptions of new species from Japan. *Zootaxa* 4097: 41-58.
- Inoue, H. 1960. Studies on spore germination and the earlier stages of gametophyte development in the Marchantiales. *J. Hattori Bot. Lab* 23: 148-191.
- Itouga, M., Yamaguchi, T., and Deguchi, H. 2002. Gene flow and genetic differentiation in four East Asian liverwort species. *J. Hattori Bot. Lab.* 92: 199-209.
- Itouga, M., Kato, Y., Deguchi, H., Ono, Y., and Sakakibara, H. 2005. Genetic diversity, sexual condition and branching pattern within *Reboulia hemisphaerica* (Marchantiales; Hepaticae) in Japan. *Hikobia* 14: 251-261.
- Janovicová, K. and Kubinská, A. 2001. Present state of the bryophyte diversity in the Protected Landscape Area Biele Karpaty (western Carpathians, Slovakia). *Biologia* 56: 33-41.

- Jerath, N. and Puja, J. C. (eds.). 2006. Biodiversity in the Shivalik Ecosystem of Punjab, India. Punjab State Council for Science and Technology, Chandigarh. Bishen Singh Mahendra Pal Singh 23-A, Dehra Dun, India, pp. 234-244 + 2 pp. plates.
- Joshi, D. Y. 1995. Antibacterial activity of *Reboulia hemisphaerica* (L.) Raddi. *J. Indian Bot. Soc.* 74: 321-322.
- Kandpal, V., Chaturvedi, P., Negi, K., Gupta, S., and Sharma, A. 2016. Evaluation of the antibiotic and biochemical potential of bryophytes from Kumaun Hills and Taral Belt of Himalayas. *Internat. J. Pharm. Pharmaceut. Sci.* 8: 65-69.
- Karki, S. and Ghimire, S. K. 2019. Bryophytes of Suspa-Kshamawoti, Dolakha District, Central Nepal. *J. Plant Res.* 17: 21-18.
- Kaul, A., Jain, D., and Pareek, A. 1995. *Asterella khasiana* Griff. A new record for Pachmarhi. In: Kumar, S. S. (ed.). *Recent Studies on Indian Bryophytes*. Bishan Singh Mahendra Pal Singh, Dehradun, India, pp. 249-252.
- Keserü, G. M. and Nogradi, M. 1995. The chemistry of macrocyclic bis (bibenzyls). *Nat. Prod. Rept.* 12: 69-75.
- Ko, F. N., Liao, C. H., and Wu, C. L. 1995. Marchantinquinone, isolated from *Reboulia hemisphaerica*, as inhibitor of lipid peroxidation and as free radical scavenger. *Chem.-Biol. Interact.* 98(2): 131-143.
- Koevenig, J. L. 1973. Effect of photoperiod, temperature, and plant growth hormones on initiation of archegoniophore elongation in the thalloid liverwort *Reboulia hemisphaerica*. *Bryologist* 76: 501-504.
- Konstantinov, A. S., Linzmeier, A. M., Morais, A. C. C., Palmer, M. W., Scheffer, S. J., and Lewis, M. L. 2019. Discovery of the first Nearctic moss-eating flea beetle, *Distigmoptera borealis* Blake, 1943 (Coleoptera: Chrysomelidae: Galerucinae: Alticini). *Coleop. Bull.* 73: 599-610.
- Konstantinova, N. A. 2011. Contribution to the hepatic flora of the Republic of Dagestan (Eastern Caucasus, Russia). *Arctoa* 20: 175-182.
- Konstantinova, N. A., Mamontov, Y. S., and Savchenko, A. N. 2018. On the liverwort flora of Tunkinskiy National Park (Republic of Buryatia, Russia). *Arctoa* 27: 131-139.
- Krajšek, S. S. and Martinčič, A. 2017. The confirmed presence of *Mannia triandra* (Aytoniaceae) liverwort in Slovenia. *Hladnikia* 40: 18-25.
- Kučera, J. and Váňa, J. 2003. Check- and red list of bryophytes of the Czech Republic. *Preslia* 175: 193-222.
- Kürschner, H. 2008. Biogeography of south-west Asian Bryophytes – with special emphasis on the tropical element. *Turkish J. Bot.* 32: 433-446.
- Kwon, W., Min, J., Kim, Y., and Park, J. 2019. The complete chloroplast genome of *Reboulia hemisphaerica* (L.) Raddi (Aytoniaceae, Marchantiophyta). *Mitochondrial DNA Part B*, 4(1): 1459-1460.
- Laouzazni, H., Zaza, J., Dahmani, J., and Belahbib, N. 2021. Contribution to the knowledge of the bryophytic flora of the Izarene Massif (Ouezzane Region, North-West Morocco). *Plant Arch.* 21: 260-268.
- Lei, C., Liu, W., Liu, B., and Zhang, Y. 2010. Responses of photosystem II of *Reboulia hemisphaerica* to nitrogen deposition. *Acta Sci. Nat. Univ. Sunyatseni*, 01.
- Liao, C. H., Ko, F. N., Wu, C. L., and Teng, C. M. 2000. Antiplatelet effect of marchantinquinone, isolated from *Reboulia hemisphaerica*, in rabbit washed platelets. *J. Pharm. Pharmacol.* 52: 353-359.
- Little, E. L. 1936. The liverworts of Oklahoma. *Bryologist* 39: 25-34.
- Liu, B.-Y., Liu, W.-Q., Lei, C.-Y., and Zhang, Y.-S. 2009. Physiological responses of three bryophyte species of South China to simulated nitrogen deposition. *Chinese J. Plant Ecol.* 33: 141-149.
- Lloret, F. and González-Mancebo, J. M. 2011. Altitudinal distribution patterns of bryophytes in the Canary Islands and vulnerability to climate change. *Flora* 206: 769-781.
- Long, D. G. 1999. Studies on the genus *Asterella*. IV. *Asterella grollei* sp. nov., a new species from eastern Asia related to the American *A. palmeri*. *Bryologist* 102: 169-178.
- Long, D. G. 2005. Studies on the genus *Asterella* (Aytoniaceae) VI: Infrageneric classification in *Asterella*. *J. Hattori Bot. Lab.* 97: 249-261.
- Long, D. G. 2006. Notes on Himalayan Hepaticae 3: New records and extensions of range for some Himalayan and Chinese Marchantiales 1. *Cryptog. Bryol.* 27: 119-129.
- Losada Lima, A. and Beltran Tejera, E. 1987. Estudio de la flora briológica del Monte de Agua García y Cerro del Lomo (Tenerife, Islas Canarias). [Study of the bryological flora of Monte de Agua García and Cerro del Lomo (Tenerife, Canary Islands)]. *An. Jard. Bot. Madrid* 44: 233-254.
- Ludwiczuk, A. and Asakawa, Y. 2015. Chemotaxonomic value of essential oil components in liverwort species. A review. *Flav. Frag. J.* 30: 189-196.
- Ludwiczuk, A., Nagashima, F., Gradstein, R. S., and Asakawa, Y. 2008. Volatile components from selected Mexican, Ecuadorian, Greek, German and Japanese liverworts. *Nat. Prod. Comm.* 3(2): 133-140.
- Luis, L., Bergamini, A., Figueira, R., and Sim-Sim, M. 2010. Riparian bryophyte communities on Madeira: Patterns and determinants of species richness and composition. *J. Bryol.* 32: 32-45.
- Luis, L., Bergamini, A., and Sim-Sim, M. 2015. Which environmental factors best explain variation of species richness and composition of stream bryophytes? A case study from mountainous streams in Madeira Island. *Aquat. Bot.* 123: 37-46.
- Martin, J. N. 1943. Some of the available hepatics and their location in the vicinity of Iowa State College. *Proc. Iowa Acad. Sci.* 50: 229-234.
- Martinčič, A. 2009. Contributions to the bryophyte flora of Republic of Macedonia. *Hacquetia* 8(2): 97-114.
- Matcham, H. 2000. Tropical Bryology Group: Visit to Uganda, 1998. *Bull. Brit. Bryol. Soc.* 74: 55-59.
- McConaha, M. 1941. Ventral structures effecting capillarity in the Marchantiales. *Amer. J. Bot.* 28: 301-306.
- Meinunger, L. 1992. Endangered bryophytes in the eastern part of Germany. *Biol. Conserv.* 59: 211-214.
- Miduno, T. 1937. Zytologische untersuchungen der Bryophyten. III. Die Morphologie des Spermatozoids von *Reboulia hemisphaerica*. *Cytologia, Fujii Jub.* 2: 970-976.
- Miller, H. A. and Thomson, J. W. 1959. The 1958 foray of the American Bryological Society. *Bryologist* 62: 67-73.
- Morais, R. M. and Becker, H. 1991. Growth and secondary product formation of *in vitro* cultures from the liverwort *Reboulia hemisphaerica*. *Zeit. Nat. C.* 46: 28-32.
- Morais, R. M. S. C., Harrison, L. J., and Becker, H. 1988. (+)-Gymnomitr-8(12)-en-9a-ol and (R)-(-)-8,11-Di-hydro-a cuparenone. Two novel sesquiterpenoids from the liverwort *Reboulia hemisphaerica*. *J. Chem. Res. (Synop.)* 1988: 380-381.
- Morais, R. M. S. C., Harrison, L. J., and Becker, H. 1991. A gymnomitrane-type sesquiterpenoid from *in vitro* cultures of *Reboulia hemisphaerica*. *Phytochemistry* 30: 1013-1014.

- Müller, F., Günther, K.-F., Hentschel, J., and Long, D. G. 2014. Erstfund von *Mannia triandra* (Aytoniaceae, Hepaticae) Für den Harz und Sachsen-Anhalt. [First record of *Mannia triandra* (Aytoniaceae, Hepaticae) in the Harz Mts and Saxony-Anhalt (Germany).] *Herzogia* 27: 147-156.
- Nair, M. C. and Prajitha, B. 2016. Systematic Studies on Bryophytes of Northern Western Ghats in Kerala. Final Report. Council order no. (T) 155/WSC/2010/KSCSTE dtd. 13.09.2010. Malabar Botanical Garden, Kerala, India, 97 pp.
- Naveen, S., Afroz, A., Rawat, K. K., and Verma, P. K. 2014. Spore morphology of some south Indian species of *Asterella* P. Beauv. (Marchantiophyta). *J. Amer. Sci.* 10(4s): 18-24.
- Nehira, K. and Nakagoshi, N. 1987. Reproductive processes of bryophytes in an urban environment. *Symp. Biol. Hung.* 35: 269-278.
- Németh, C. 2011. Bryofloristical data from the Transdanubian Mountain Ranges, Bakony and Vértes Mts (Hungary). *Stud. Bot. Hung.* 42: 5-22.
- Németh, C. and Papp, B. 2011. *Mannia triandra* in the Transdanubian Range (Hungary). *Stud. Bot. Hung.* 42: 23-29.
- Nichols, G. E. 1916. The vegetation of Connecticut. V. Plant societies along rivers and streams. *Bull. Torrey Bot. Club* 43: 235-264.
- Nieuwkoop, J. 1996. *Reboulia hemisphaerica* L. Raddi terug in Nederland Met opmerkingen over de mosflora van De Hoge Fronten. [*Reboulia hemisphaerica* L. Raddi back in the Netherlands With comments about the moss flora of De Hoge Fronten.]. *Buxbaumia*, 40(1): 37-40.
- Nogradi, M., Vermes, B., Jaktar-Peredy, M., and Novikov, V. P. 1990. Synthese von Pakyonol, einem macrocyclischen Bis(bibenzylether) aus *Mannia fragrans*. [Synthesis of pakyonol, a macrocyclic bisbibenzyl ether from *Mannia fragrans*.]. *Liebigs Ann. Chem.* 1990: 299-302.
- Odrzykoski, I. and Szweykowski, J. 1981. An interesting enzymatic polymorphism in some European populations of the liverwort *Mannia fragrans* (Balbis) Frye and Clark. In: Szweykowski, J. (ed.). *New Perspectives in Bryotaxonomy and Bryogeography*. Bryological Meeting, Poznan, 26.-29.6.1980, pp. 33-37.
- Oesau, A. 2010. Neue Untersuchungen zur Verbreitung von *Mannia fragrans* (Balb.) Frye & L. Clark im unteren Nahetal (Rheinland-Pfalz). [New investigations concerning the distribution of *Mannia fragrans* (Balb.) Frye & L. Clark in the lower valley of the River Nahe (Rhineland-Palatinate).]. *Arch. Bryol.* 63: 1-5.
- O'Hanlon, M. E. 1928. Notes on *Reboulia hemisphaerica*. *Bryologist* 31: 47-51.
- O'Hanlon, M. E. 1930. Gametophyte development in *Reboulia hemisphaerica*. *Amer. J. Bot.* 17: 765-769.
- Önder, A. and Özenoğlu, H. 2019. Evaluation of cytotoxic effects on ethereal extracts of some selected liverworts. *FABAD J. Pharm. Sci.* 44: 119-125.
- Orbán, S. 1984. A magyarországi mohák stratégiai és TWR értékei. [Life strategies and TWR values of Hungarian bryophytes]. *Az Egri Ho Si Minh Tanárképző Főiskola Füzetei* NS 17: 755-765.
- Papp, B. 2008. Selection of important bryophyte areas in Hungary. *Folia Cryptog. Eston.* 44: 101-111.
- Papp, B., Ódor, P., and Szurdoki, E. 2007. Monitoring of moss species I. PROJECT. Monitoring of protected and endangered species, 6 pp.
- Patidar, K. C., Solanki, C. M., and Kaul, A. 1987. Spore output in Marchantiales. *Bryologist* 90: 251-252.
- Patiño, J., Hylander, K., and González-Mancebo, J. M. 2010. Effect of forest clear-cutting on subtropical bryophyte communities in waterfalls, on dripping walls, and along streams. *Ecol. Appl.* 20: 1648-1663.
- Paudel, M. 2019. Floristic Composition and Diversity of Bryophytes Along an Altitudinal Gradient in Kailali, Far West Nepal. M.S. thesis, Central Department of Botany, Institute of Science and Technology Tribhuvan University Kirtipur, Kathmandu, Nepal, 69 pp.
- Pedrotti, C. C. 1996. Aperçu sur la bryogéographie de l'Italie. [Overview of the bryogeography of Italy.]. *Bocconea* 5: 301-318.
- Philippe, M. 2013. Observations de taxa bryophytiques nouveaux ou listés rouges pour la Franche-Comté. Observations of new or red listed bryophytic taxa for Franche-Comté.]. *Champion. Les Nouvelles Archives de la Flore jurassienne et du nord-est de la France*, 11: 69-78.
- Piippo, S. 1990. Annotated catalogue of Chinese Hepaticae and Anthocerotae. *J. Hattori Bot. Lab.* 68: 1-192.
- Piippo, S. 2010. Bryophyte flora of the Hunan Province, China. 15. Genera *Asterella*, *Fossombronia*, *Isotachis*, *Jubula* and *Metzgeria* (Aytoniaceae, Fossombroniaceae, Balantiopsaceae, Jubulaceae and Metzgeriaceae). In: Koponen, T., Piippo, S., and Reinikka, E. (eds.). *Dr. Ming-Jou Lai Memorial Volume*. *Acta Bryolichenol. Asiat.* 3: 145-150.
- Piippo, S. and Koponen, T. 2013. Bryophyte flora of Hunan Province, China. 16.: Complex thalloids (Marchantiopsida, Hepaticae). *Festschrift for Tamás Pócs on the occasion of his 80th birthday*. *Polish Bot. J.* 58: 179-192.
- Piippo, S. and Tan, B. C. 1992. Novelty for the Philippine hepatic flora. *J. Hattori Bot. Lab.* 72: 117-126.
- Piippo, S., He, X. L., and Koponen, T. 1997. Hepatics from northwestern Sichuan, China, with a checklist of Sichuan hepatics. *Ann. Bot. Fenn.* 34: 51-63.
- Piowarczyk, R. and Stebel, A. 2012. Stanowisko wątrobowca *Mannia fragrans* w Podgrodziu koło Ćmielowa (Wyżyna Małopolska). [The site of the liverwort *Mannia fragrans* in Podgrodzie near Ćmielów (Małopolska Upland).]. *Chrońmy Przyrodę Ojczystą* 68(3): 219-224.
- Province, S. 2011. Bryophyte exploration of South-west Sichuan, China. *Field Bryol.* 103: 32-39.
- Rao, M. P. and Das, V. S. R. 1968. Metabolic changes during reproductive development in liverworts. *Z. Pflanzenphysiol.* 59: 87-99.
- Rao, K. R., Kumar, N. R., and Reddy, A. N. 1979. Studies of photosynthesis in some liverworts. *Bryologist* 82: 286-289.
- Ros, R. M., Cano, M. J., Muñoz, J., and Guerra, J. 2000. Contribution to the bryophyte flora of Morocco: The Jbel Toubkal. *J. Bryol.* 22: 283-289.
- Ros, R. M., Mazimpaka, V., Aleffi, M., Blockeel, T. L., Cano, M. J., Cros, R. M., Dia, M. G., Dirkse, G., M El Saadawi, W., Erdağ, A., Ganeva, A., González-Mancebo, J. M., Herrstadt, I., Khalil, K., Kürschner, H., Lanfranco, E., Losada-Lima, A., Refai, M. S., Rodríguez-Núñez, S., Sabovljević, M., Sérgio, C., Shabbara, H., Sim-Sim, M., and Söderström, L. 2007. Hepatics and anthocerotae of the Mediterranean, an annotated checklist. *Cryptog. Bryol.* 28: 351-437.
- Rupidera Giraldo, J. L. and Elias Rivas, M. J. 1996. *Asterella africana* (Mont.) Evans (Aytoniaceae, Hepaticae) en la Península Ibérica, novedad para la brioflora de Europa Continental. *Cryptog. Bryol. Lichénol.* 17: 195-201.
- Saadi, K., Dahmani, J., Zidane, L., and Belahbib, N. 2020. Contribution to the bryoflora inventory of Jbel Tazekka

- (Middle Eastern Atlas, Morocco): New data on the presence of new, rare or abundant species. *Plant Arch.* 20: 4639-4647.
- Sabovljević, M. and Natcheva, R. 2006. A check-list of the liverworts and hornworts of Southeast Europe. *Phytol. Balcan.* 12: 169-180.
- Sabovljević, M. S., Sabovljević, A. D., Ikram, N. K. K., Peramuna, A., Bae, H., and Simonsen, H. T. 2016. Bryophytes – an emerging source for herbal remedies and chemical production. *Plant Gen. Res.* 14: 314-327.
- Sakai, H., Hagiwara, H., Ito, Y., Hoshi, T., Suzuki, T., and Ando, M. 1999. Total synthesis of (+)-cyclomyltalan-5 α -ol isolated from the taiwanese liverwort *Reboulia hemisphaerica*. *Tetrahedron Lett.* 40: 2965-2968.
- Schill, D. B. 2006. Taxonomy and phylogeny of the liverwort genus *Mannia* (Aytoniaceae, Marchantiales). Ph.D. thesis, University of Edinburgh, Scotland.
- Schönherr, J. and Ziegler, H. 1975. Hydrophobic cuticular ledges prevent water entering the air pores of liverwort thalli. *Planta* 124: 51-60.
- Schumacker, R. and Matriny, Ph. 1995. Threatened bryophytes in Europe in Macronesia. In: E.C.C.B. (eds.). Red Data book of European bryophytes. Part. 2. Trondheim, pp. 29-193.
- Schuster, R. M. 1966. The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian, Vol. 1. Columbia University Press, NY, 802 pp.
- Schuster, R. M. 1992. The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian. Vol. 5. Field Museum of Natural History, Chicago.
- Sérgio, C. and Garcia, C. 2009. Noteworthy range extensions of two *Aneura* (Jungermanniopsida, Metzgeriales) species new for the Iberian Peninsula: *Aneura maxima* (Schiffn.) Steph. and *A. pseudopinguis* (Herzog) Pócs. *Cryptogamie* 30: 207-215.
- Sérgio, C., Cros, R. M., Brugués, M., and Garcia, C. 2001. A brioflora de enclaves com *Prunus lusitanica* L. no Parque Natural da Serra da Estrela. *Bol. Soc. Españ. Briol.* 18(19): 5-14.
- Sérgio, C., Sim-Sim, M., and Luís, L. 2010. *Atrichum androgynum* (Müll. Hal.) A. Jaeger in Portugal, Azores and Madeira, new to the European bryoflora. *Cryptog. Bryol.* 31: 281-288.
- Sha, W., Cao, T., and Gao, Y.-C. 2003. Chromosome numbers of twelve species of bryophytes from China. *J. Syst. Evol.* 41: 258-262.
- Sharp, A. J. 1930. Bryophytes of southeastern Oklahoma I. A preliminary list with notes. *Bryologist* 33: 45-55.
- Sharp, A. J. 1939. Taxonomic and ecological studies of eastern Tennessee bryophytes. *Amer. Mid. Nat.* 21: 267-354.
- Sharp, A. J. 1944. Some Hepaticae from the Mountain Lake Region of Virginia. *Bryologist* 47: 29-36.
- Shershen, E., Gilliland, C., and Medina, R. 2018. Bryophytes of Loud Thunder Forest Preserve, with an updated checklist of the bryoflora of Rock Island County, Illinois. *Evansia* 35: 36-42.
- Simmel, J., Ahrens, M., and Poschlod, P. 2021. Ellenberg N values of bryophytes in Central Europe. *J. Veg. Sci.* 32: e12957, 20 pp.
- Simon, T. M. 1977. Saxicolous Bryophytes of Coles and Clark Counties. M. S. Thesis, Eastern Illinois University, Charleston, Illinois, 237 pp.
- Sim-Sim, M., Fontinha, S., Luís, L., Lobo, C., and Stech, M. 2010. The Selvagens Islands bryoflora and its relation with islands of the Madeira and Canary Islands Archipelagos. *Nova Hedw.* 138: 187-199.
- Singh, S. K. and Singh, D. K. 2002. Contribution to the liverworts of Gobind National Park, Uttaranchal, India. *Nelumbo* 44: 99-118.
- Singh, D. K. and Singh, S. K. 2008a. Diversity in liverworts and hornworts of Great Himalayan National Park, Western Himalaya, India. In: Mohamed, H., Baki, B. B., Nasrulhaq-Boyce, A., and Lee, P. K. Y. (eds.). *Bryology in the New Millennium*. University of Malaya, Kuala Lumpur, pp. 57-81.
- Singh, D. K. and Singh, S. K. 2008b. Scanning electron microscopic studies on sporoderm of some Indian liverworts and hornworts. In: Mohamed, H., Baki, B. B., Nasrulhaq-Boyce, A., and Lee, P. K. Y. (eds.). *Bryology in the New Millennium*. University of Malaya, Kuala Lumpur, pp. 291-317.
- Slatkin, M. 1985. Gene flow in natural populations. *Ann. Rev. Ecol. Syst.* 16: 393-430.
- Söderström, L., Hagborg, A., Konrat, M. von, Bartholomew-Began, S., Bell, D., Briscoe, L., Brown, E., Cargill, D. C., Costa, D. P., Crandall-Stotler, B. J., Cooper, E. D., Dauphin, G., Engel, J. J., Feldberg, K., Glenney, D., Gradstein, S. R., He, X., Heinrichs, J., Hentschel, J., Ilkiu-Borges, A. L., Katagiri, T., Konstantinova, N. A., Larrain, J., Long, D. G., Nebel, M., Pócs, T., Puche, F., Reiner-Drehwald, E., Renner, M. A. M., Sass-Gyarmati, A., Schäfer-Verwimp, A., Moragues, J. G. S., Stotler, R. E., Sukkharak, P., Thiers, B. M., Uribe, J., Váña, J., Villarreal, J. C., Wigginton, M., Zhang, L., and Zhu, R.-L. 2016. World checklist of hornworts and liverworts. *PhytoKeys* 59: 1-828.
- Spessard, L. L. 1972. The Bryophytes of Shelby County. M. S. Thesis, Eastern Illinois University, Charleston, Illinois, 430 pp.
- Sreenath, A. and Rao, B. R. P. 2020. Eleven species of liverworts as new distributional records to Bryoflora Andhra Pradesh, India. *Biosci. Discov.* 11(3): 111-120.
- Stephani, F. 1899. *Species Hepaticarum* 1. Geneva.
- Sztein, A. E., Cohen, J. D., and Cooke, T. J. 1997. Further studies of auxin metabolism in lower land plants. *Amer. J. Bot. (Abstr. Suppl.)* 84(6): 22-23.
- Takio, S., Akita, C., Ngumi, V. W., and Takami, S. 1990. Photosynthetic ability in dark-grown *Reboulia hemisphaerica* and *Barbula unguiculata* cells in suspension culture. *Plant Cell Rept.* 8: 575-578.
- Tosun, A., Küpeli Akkol, E., Süntar, I., Özenoğlu Kiremit, H., and Asakawa, Y. 2013. Phytochemical investigations and bioactivity evaluation of liverworts as a function of anti-inflammatory and antinociceptive properties in animal models. *Pharmaceut. Biol.* 51: 1008-1013.
- Tosun, A., Süntar, İ., Keleş, H., Kiremit, H. Ö., Asakawa, Y., and Akkol, E. K. 2016. Wound healing potential of selected liverworts. *Turk. J. Pharm. Sci.* 13: 285-291.
- Toyota, M., Konoshima, M., and Yoshinori, A. 1999. Terpenoid constituents of the liverwort *Reboulia hemisphaerica*. *Phytochemistry* 52: 105-112.
- Udar, R. and Chandra, V. 1964. On some anomalous female receptacles of *Reboulia hemisphaerica* (L.) Raddi. *J. Indian Bot. Soc.* 43: 521-528.
- Vishvakarma, K. S. and Kaul, A. 1986. Temperature tolerance of *Plagiochasma appendiculatum* and *Reboulia hemisphaerica* on comparative basis. *Yushania* 3: 1-6.
- Vishvakarma, K. S. and Kaul, A. 1987. Response of duration, quality and intensity of light on the spore germination of *Plagiochasma appendiculatum* and *Reboulia hemisphaerica* on comparative basis. *Yushania* 4: 1-4.

- Vishvakarma, K. S. and Kaul, A. 1988a. Influence of moisture levels on growth of *Plagiochasma appendiculatum* Lehm. et Lindb. and *Reboulia hemisphaerica* (L.) Raddi on a comparative basis. *Cryptog. Bryol. Lichénol.* 9: 337-341.
- Vishvakarma, K. S. and Kaul, A. 1988b. Culture studies on *Plagiochasma appendiculatum* Lehm. et Lindenb. and *Reboulia hemisphaerica* (L.) Raddi populations of Pachmarhi (central India) in relation to pH on a comparative basis. *Cryptog. Bryol. Lichénol.* 9: 129-135.
- Vishvakarma, K. S., Kaul, A., and Sharma, D. K. 1987. Culture studies on spore germination of two liverworts. *Yushania* 4: 1-4.
- Wang, L. N., Guo, D. X., Wang, S. Q., Wu, C. S., Rehman, M. U., and Lou, H. X. 2011a. Phenolic glycosides from the Chinese liverwort *Reboulia hemisphaerica*. *Helveti. Chim. Acta* 94: 1146-1152.
- Wang, L. N., Xie, C. F., Zhu, X. S., Fan, P. H., and Lou, H. X. 2011b. Determination of atropisomeric configurations of macrocyclic bisbibenzyls by HPLC-CD/UV and quantum chemical calculations. *J. Asian Nat. Prod. Res.* 13: 312-318.
- Warmers, U. and König, W. A. 1999. Gymnomitrane-type sesquiterpenes of the liverworts *Gymnomitrium obtusum* and *Reboulia hemisphaerica*. *Phytochemistry* 52: 1501-1505.
- Warmers, U. and König, W. A. 2000. Biosynthesis of the gymnomitrane-type sesquiterpenes in liverworts. *Phytochemistry* 53: 645-650.
- Watson, W. 1919. The bryophytes and lichens of fresh-water. *J. Ecol.* 7: 71-83.
- Wei, H.-C., Ma, S.-J., and Wu, C.-L. 1995. Sesquiterpenoids and cyclic bisbibenzyls from the liverwort *Reboulia hemisphaerica*. *Phytochemistry* 39: 91-98.
- Woodburn, W. L. 1919. Preliminary notes on the embryology of *Reboulia hemisphaerica*. *Bull. Torrey Bot. Club* 46: 461-464.
- Xiang, J., Zhao, F., Fang, Y. P., and Chen, J. 2010a. Effects of calcium and water stress on physiological and biochemical indexes of bryophytes. *Environ. Sci. Technol.* 33: 70-74.
- Xiang, J., Li, Z.-Z., Fang, Y.-P., Wu, G., Li, W., and Fan, Y.-Y. 2010b. Analysis of Ca, Mg and Zn contents in bryophytes from different geological settings. *Proc. Environ. Sci.* 2: 1422-1428.
- Zechmeister, H. G. and Köckinger, H. 2014. Die Moosflora des Wildnisgebietes Dürrenstein. *Silva Fera* 3: 47-52.
- Zehr, D. R. 1990. A simplified technique for assaying the production of bacteriostatic compounds by hepatics. *Lindbergia* 16: 128-132.