CHAPTER 1-14
AQUATIC AND WET MARCHANTIOPHYTA, ORDER FOSSOMBRONIALES, PART 2

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Figure 1. ***Fossombronia pusilla***, a cosmopolitan species of moist soil and temporary ponds. Photo by Hugues Tinguy, with permission.

SUBCLASS PELLIIDAE, Fossombroniales part 2

Fossombronia mylioides (Figure 2-Figure 3)

Distribution

Thus far, ***Fossombronia mylioides*** (Figure 2-Figure 3) is known only from Iriomote Island, Japan (Higuchi 2016; Crandall-Stotler & Gradstein 2017), making it a narrow endemic.

Figure 2. ***Fossombronia mylioides***, an endemic of Iriomote Island, Japan. Photo by Masanabu Higuchi, National Museum, Japan, with permission.

Figure 3. ***Fossombronia mylioides***. Photo by Masanabu Higuchi, National Museum, Japan, with permission.

Aquatic and Wet Habitats

Fossombronia mylioides (Figure 2-Figure 3) is a riverine species, growing on open boulders covered with sandy soil, along the Urauchi and Nakama Rivers of Japan (Krayesky *et al*. 2005; Higuchi 2016; Crandall-Stotler & Gradstein 2017).

Fossombronia mylioides (Figure 2-Figure 3) also grows directly on moist rocks and stones in river beds and along streams (Figure 4-Figure 5) (Krayesky *et al*. 2005; Higuchi 2016). In these habitats it is sometimes submerged. It can also grow on vertical rock faces near the streams. In areas that flood, it may be mixed with ***Riccardia*** (Figure 6) (Higuchi 2016).

Figure 4. ***Fossombronia mylioides*** on rock in Japan. Photo by Masanabu Higuchi, National Museum, Japan, with permission.

Figure 5. ***Fossombronia mylioides*** on rock in Japan. Photo by Masanabu Higuchi, National Museum, Japan, with permission.

Figure 6. ***Riccardia multifida***; ***Riccardia*** is mixed with ***Fossombronia mylioides*** in areas that flood in Japan. Photo by Hermann Schachner, through Creative Commons.

Adaptations

Fossombronia mylioides (Figure 2-Figure 3) is light green, with dense, deep purple rhizoids that attach it firmly to its substrate (Higuchi 2016). The color suggests bright sun, but there are no data to suggest protection from high light.

Reproduction

Fossombronia mylioides (Figure 2-Figure 3) is **monoicous**, with archegonia and antheridia scattered on the dorsal surface of the stem (Higuchi 2016). Setae are quite short (2-3 mm). Sporophytes mature in March (Krayesky *et al*. 2005; Higuchi 2016).

The capsule dehiscence is somewhat unusual among bryophytes. Once the capsules dry, they dehisce irregularly from apex downward, lacking sutures or other weakened area for splitting (Figure 7) (Higuchi 2016). Instead the capsule walls form irregular fragments. The spores and elaters tend to clump together and fall as a group. Higuchi observed that the time required from the beginning of dehiscence to the spore dispersal is about 22 minutes. If you are able to observe it, consider yourself lucky.

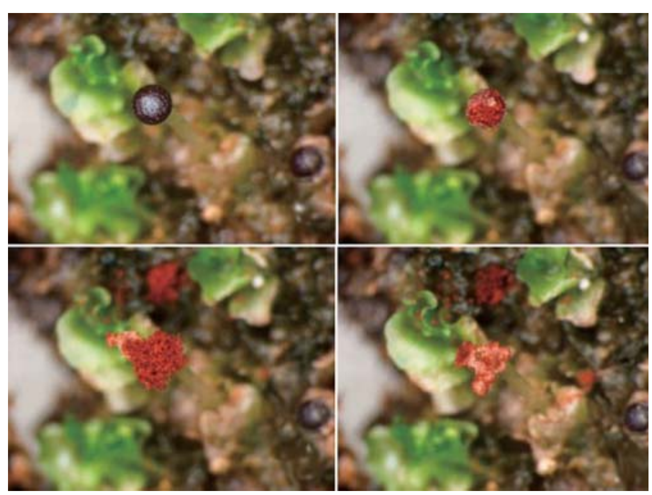

Figure 7. ***Fossombronia mylioides*** dehiscence and dispersal, shown here over 23 minutes. Photos by Masanabu Higuchi, National Museum, Japan, with permission.

Fossombronia peruviana

(syn. = *Fossombronia herzogii*; *Austrofossombronia peruviana*) (Crandall-Stotler *et al*. 1999)

Distribution

Fossombronia peruviana occurs in high elevation locations in the páramos and punas of the Andes (Crandall-Stotler & Gradstein 2017). Gradstein (2020) included it in the checklist for Ecuador; Müller (2016) reported it from Chile. Gradstein and Arbe (2003; Villagrán Moraga 2020) listed it for Bolivia and Villagrán Moraga (2020) for Venezuela and Peru.

Aquatic and Wet Habitats

Fossombronia peruviana occurs in consistently wet and aquatic habitats at high elevations in the Andean páramos and punas (Crandall-Stotler & Gradstein 2017), including high elevation mires in Latin America (Crandall-Stotler *et al*. 2019). Villagrán Moraga (2020) found it in the Chilean Altiplano wetlands. Gradstein and Pócs (2021) found the species to be characteristic of peaty soil along small streams and in mires of the páramo and puna, where it is sometimes submerged. Gradstein *et al*. (2016) reported it as usually submerged in pure, extensive mats in northern Chile. Although it is widespread, it is far from common.

Adaptations

Fossombronia peruviana is polymorphic, changing its form in response to its habitat (Crandall-Stotler *et al*. 2010). When submerged, it forms **mats**, but forms **turfs** rather than mats on soil. In the water they lack the purple rhizoids and are usually **sterile** (lacking reproductive organs).

Reproduction

Gradstein *et al*. (2016) found that most of the Chilean plants of ***Fossombronia peruviana*** were sterile. However, one plant was male with several groups of 10-12 naked antheridia on the midrib near the apex, where it is protected by strongly folded leaves. Capsules (Figure 8) are known, and the spores (Figure 9) resemble those of ***Fossombronia foveolata*** (Figure 10).

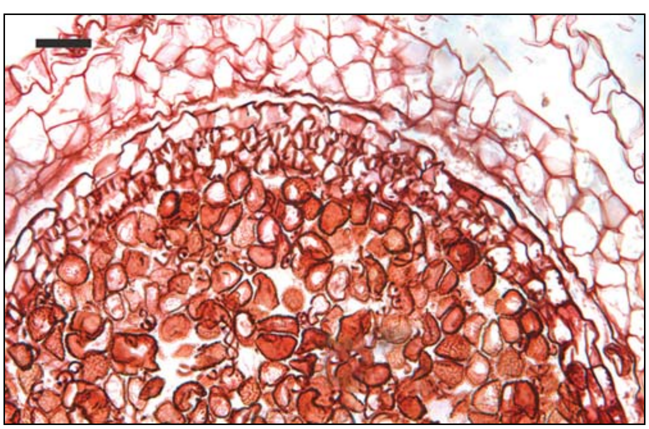

Figure 8. ***Fossombronia peruviana*** spore SEM. Photo by Barbara Crandall-Stotler, modified, with permission.

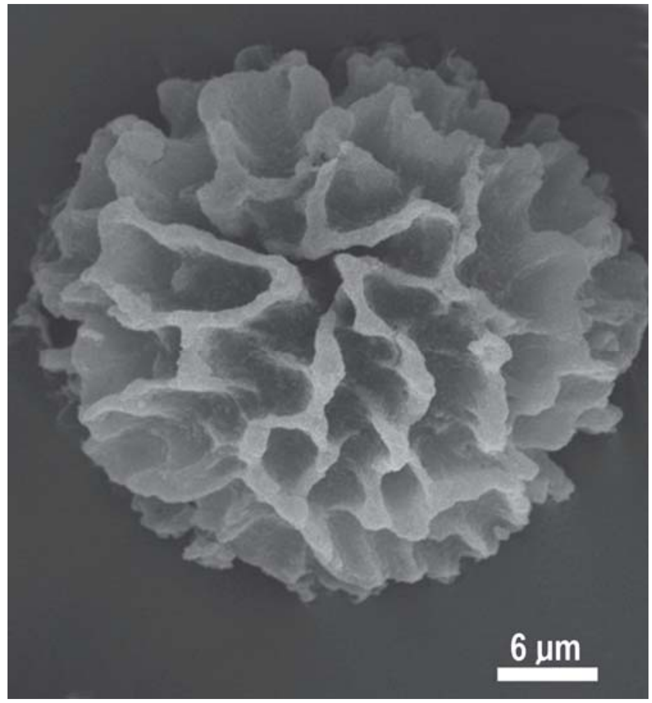

Figure 9. ***Fossombronia peruviana*** spore SEM. Photo by Barbara Crandall-Stotler, modified, with permission.

Figure 10. ***Fossombronia foveolata*** SEM of spore, showing its similarities to spores of ***Fossombronia peruviana***. Photo by Barbara Crandall-Stotler, with permission.

Fossombronia porphyrorhiza (Figure 11)

[syn. = *Fossombronia brasiliensis*, *Fossombronia salina*(?)]

With this species we suffer from confused taxonomy. My original introduction to it was through *Fossombronia salina* (Evans 1901), but that narrowly distributed species was named as a synonym of ***F. brasiliensis*** (Evans 1914). Later, ***F. brasiliensis*** was considered a synonym of ***F. porphyrorhiza*** (Figure 11) (Schaefer-Verwimp 2010; TROPICOS 2021), but ***F. salina*** was considered more related to ***F. foveolata*** (Figure 12) by the Stotler's (Lars Söderström, pers. comm. March 2021). Hence I shall try to keep the published name intact as I discuss these three taxa under the umbrella of ***Fossombronia porphyrorhiza***.

Figure 11. ***Fossombronia porphyrorhiza***, Chapada dos Guimaraes, Brazil. Photo courtesy of Denilson Peralta.

Figure 12. ***Fossombronia foveolata***. Photo by Kochibi, through Creative Commons.

Distribution

Fossombronia porphyrorhiza (Figure 11) is both common and widespread in the Neotropics (Mexico, West Indies, Central America, South America) (Crandall-Stotler & Bray 2019). But it also extends into the southeastern United States. Other publications place it as far north as Rhode Island and Connecticut, USA.

Fossombronia porphyrorhiza (Figure 11) extends from coastal regions of Connecticut and Rhode Island, USA, southward to the southeastern US, Puerto Rico, Cuba, Haiti, Dominican Republic, Isle of Pines near Cuba, and Trinidad, through Mexico and Central America to Brazil (Schuster 1992). Schäfer-Verwimp (1999) reported this species (as *Fossombronia brasiliensis*) from Dominica, Gradstein and Hekking (1979) from Colombia, and Schäfer-Verwimp and Reiner-Drehwald (2009) from Guadeloupe, West Indies. Söderström *et al*. (2013) listed it from Paraguay.

Aquatic and Wet Habitats

Peralta and Yano (2008) considered ***Fossombronia porphyrorhiza*** (Figure 11) to be both **rupicolous** (living among, inhabiting, or growing on rocks) and **terricolous** (living on soil or ground). Pereira Correia *et al*. (2015) likewise considered it to be rupicolous. But those substrate classifications can place it in both terrestrial and aquatic habitats.

Schuster (1992) considers ***Fossombronia porphyrorhiza*** (as *F. brasiliensis*; Figure 11) to be one of wide ecological distribution It occurs on moist exposed soil along ditches, exposed sandy-clayey soil in broken ground of old fields. on moist rocks, and as is common among liverworts of such moist but not submersed habitats, it can occur on dead wood.

Guerke (1971) found ***Fossombronia porphyrorhiza*** (as *F. brasiliensis*; Figure 11) on moist ditch banks along a dirt road in Louisiana, USA, Pôrto *et al*. in a similar habitat in Brazil, and Schäfer-Verwimp (1999) in Dominica, West Indies. Hermann (1959) found it on the open clay bank of a pond in the eastern USA. Redfearn (1979) found it in the Ozarks of Arkansas, USA, on moist vertical sandstone along creek margins. Haupt (1942) found it on a moist humus bank along a road in Costa Rica. Yano and Bastos (2004) found it on a river bank in Brazil.

Sometimes ***Fossombronia porphyrorhiza*** (Figure 11) satisfies its moisture needs by living near waterfalls on shaded rocks (Schäfer-Verwimp 1999). Redfearn (1980) reported ***Fossombronia porphyrorhiza*** from calcareous cedar glades in Missouri, Tennessee, and Texas, USA.

Breil (1996) reported a greater variety of habitats in the Virginia Piedmont, USA. Here ***Fossombronia porphyrorhiza*** (Figure 11) occurred in swamps, along streams, and both single and as mats on moist, clayey, compact soil of old fields. It often accompanies other species of seasonal habitats such as ***Riccia*** (Figure 13) or ***Sphaerocarpos*** (Figure 14). Gradstein and Weber (1982) likewise reported it from terrestrial habitats in the Galapagos Islands, and Stotler *et al*. (1998) reported it from an exposed soil bank where it was intermixed with mowed grass in Panama.

Figure 13. ***Riccia sorocarpa*** on wet soil, a species that occurs in the same seasonal habitats as ***Fossombronia porphyrorhiza***. Photo by Hermann Schachner, through Creative Commons.

Figure 14. ***Sphaerocarpos donnellii***; ***Sphaerocarpos*** species of seasonal habitats often accompany ***Fossombronia porphyrorhiza*** there. Photo by Belinda Lo through Creative Commons.

Reproduction

Although the species has been confused with ***Fossombronia angulosa*** (Figure 15), ***F. porphyrorhiza*** (Figure 11) is **monoicous** (Breil 1996), contrasting with the dioicous condition of ***F. angulosa***. Despite this monoicous condition, Haupt (1942) reported that whereas it had numerous antheridia and archegonia on a roadside in Costa Rica, it had few sporophytes. On the other hand, Schäfer-Verwimp (1999) found it with mature sporophytes in Dominica, West Indies. Its brown to yellow-brown spores have a wide size range of 38-55 µm (Crandall-Stotler & Bray 2019).

Could this lack of sporophytes be due to the collecting season, or to the wrong photoperiod or other environmental conditions for fertilization? Chin *et al*. (1987) explored the influence of photoperiod, temperature, and inorganic nitrogen source on reproduction and growth in ***Fossombronia porphyrorhiza*** (Figure 11). They found that at 18ºC it behaved as a short-day plant, requiring 6-12 hours of night for development of archegonia and antheridia. At 10ºC it was a quantitative short-day plant, producing more female gametangia, whereas at 18ºC it produced more male gametangia. Nitrate was more favorable to the production of gametangia than was ammonium. This may explain incomplete development of the reproductive structures, but the scarcity of sporophytes in Haupt's (1942) collections remains without explanation.

Figure 15. ***Fossombronia angulosa***, a dioicous species often confused with ***Fossombronia porphyrorhiza***. Photo by Jan-Peter Frahm, with permission.

Fossombronia typically produces tubers for asexual reproduction (Paton 1974, Schuster 1992), with leafy propagules being rare (Pôrto *et al*. 1999). But in Brazil Pôrto and coworkers found that ***Fossombronia porphyrorhiza*** (Figure 11) produced numerous fleshy green propagules with small leaves on the dorsal sides of stems.

Fungal Interactions

There seem to be no records of fungal associations with ***Fossombronia porphyrorhiza*** (Figure 11).

Biochemistry

I found a surprising absence of biochemical information on this species.

Fossombronia pusilla (Figure 16-Figure 20)

Fossombronia pusilla (Figure 16-Figure 20) has been included in ***Fossombronia angulosa*** (Figure 15) by a number of authors (Stotler *et al*. 2005). I have maintained the two taxa separately here.

Figure 16. ***Fossombronia pusilla***. Photo by David H. Wagner, with permission.

Figure 17. ***Fossombronia pusilla* var. *pusilla*** whole plant. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 18. ***Fossombronia pusilla***. Photo by Štěpán Koval, with permission.

Figure 19. ***Fossombronia pusilla*** forming dense clumps. Photo by Andras Keszei, with permission.

Figure 20. ***Fossombronia pusilla* var. *pusilla***. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Distribution

Fossombronia pusilla (Figure 16-Figure 20) is a cosmopolitan species (Crandall-Stotler & Bray 2019). In North America it is restricted to the west coast (California and Oregon). But it also occurs in South America (Chile); Europe: Germany (Schultze-Motel 1968), England (Callaghan & Ashton 2008), Ireland, Denmark, Italy, France (Gökler 1998), Bulgaria, Croatia, Greece, Macedonia, Romania, Serbia, Slovenia, Turkey (Blockeel *et al*. 2002, Papp & Erzberger 2007), Belgium, Czech Republic, Portugal, Sicily, Spain, Switzerland (Sérgio 1974), Russia (Borovichev & Bakalin 2017), Maltese Islands (Gradstein 1972), Madeira (Sérgio 1974); Asia: Japan (Higuchi 2016), India (Singh & Singh 2007; Alam 2011 – at > 2100 m); and Africa: Algeria (Gökler 1998), Tunisia (Sérgio 1974). Frahm (2005) reported it from the Azores. It also occurs in Papua New Guinea (Krayesky *et al*. 2005).

Aquatic and Wet Habitats

Fossombronia pusilla (Figure 16-Figure 20) occupies a variety of habitats on open soil (Crandall-Stotler & Bray 2019). It frequently grows over moist soil (Çetin 1999), remaining moist longer due to shade from nearby vegetation (Figure 21) (Crandall-Stotler & Bray 2019). Rilstone (1949) described it as frequent on bare, moist soil in Cornwall, UK. This is an apparent contrast with those colonies found by Osman *et al*. (2019) in Tunisia. They found that ***F. pusilla*** grew strictly on humus and litter there. Schultze-Motel (1968) found it on a loamy slope in Germany with ***Fissidens bryoides*** (Figure 22) and ***Brachythecium velutinum*** (Figure 23).

Figure 21. ***Fossombronia pusilla*** habitat in the shade of grass. Photo by Štěpán Koval, with permission.

Figure 22. ***Fissidens bryoides*** with capsules, a species that accompanies ***Fossombronia pusilla*** on loamy slopes in Germany. Photo by Dick Haaksma, with permission.

Figure 23. ***Brachythecium velutinum*** with capsules, a species that accompanies ***Fossombronia pusilla*** on loamy slopes in Germany. Photo by Michael Lüth, with permission.

Özenoğlu Kiremit *et al*. (2007) reported soil banks (Figure 24), stream banks, cave entrance, wet rocks, and stream beds as habitats for ***Fossombronia pusilla*** (Figure 16-Figure 20) in Antalya, Turkey. Casas *et al*. (1983) found it at the edges of a ravine in Spain.

Figure 24. ***Fossombronia pusilla*** habitat on a soil bank. Photo by Štěpán Koval, with permission.

In Italy, temporary ponds seem to be the best known habitat for ***Fossombronia pusilla*** (Figure 16Figure 17-Figure 20) (Puglisi *et al*. 2015 and others). In Sardinia, Italy, Cogoni *et al*. (2015) found it in temporary ponds, but it is critically endangered in Sardinia. In central Italy, Poponessi *et al*. (2016, 2018) found it associated with temporary ponds, where it was moderately abundant. It occurred on clayey-sandy waterlogged soil with ***Isoetes histrix*** (Figure 25) and in partially shaded pool systems along the borders of small ponds. It is, nevertheless, considered to be near threatened in Italy because of its scarcity in the country.

Figure 25. ***Isoetes histrix***, a species that accompanies ***Fossombronia pusilla*** on clayey-sandy, waterlogged soil in central Italy. Photo by Michel Garner, through Creative Commons.

In another study, Filippino (2018) reported ***Fossombronia pusilla*** (Figure 16-Figure 20) from Mediterranean temporary ponds, describing the ponds as small and shallow bodies of water isolated from permanent water bodies and undergoing periodic flooding and drought. ***Fossombronia pusilla*** is one of the bryophyte species found there, but it is considered critically endangered.

In Oregon, USA, it grows on moist soil in disturbed sites like road cuts, along trail cuts, but also in open natural habitats (Wagner 2006).

Fadel *et al*. (2020) found that in the Benslimane region of Morocco ***Fossombronia pusilla*** (Figure 16-Figure 20) was mostly present in wet crevices of limestone blocks, but also occurred in wetlands where the soil is humid (Figure 26) for a large part of the year and has a rich alluvium. In the Michlifen crater, they found it on shaded rock.

Gradstein (1972) similarly reported ***Fossombronia pusilla*** (Figure 16-Figure 20) from sheltered crevices in limestone rock of the Maltese Islands, where it was accompanied by ***Tortella inflexa*** (Figure 27). Papp and Erzberger (2007) found it on base-rich rock in Turkey. On the other hand, Hill *et al*. (2007) note that ***Fossombronia pusilla*** occurs on moderately acid soil that is constantly moist or damp, but not permanently waterlogged.

In addition to its wet habitats, it has been found on bark in Ohio, USA (Austin 1869).

Adaptations

Fossombronia pusilla (Figure 16-Figure 20) is a hygrophytic, solitary, creeping shuttle species (Filippino 2018). This life cycle strategy is suitable in particular for its temporary pond habitats. In Oregon, USA, it is a winter ephemeral that disappears in the summer (David H. Wagner, pers. comm. 18 April 2021).

In some cases it grows with other bryophytes (Figure 28) that may help it to hold moisture, but it is also possible that they can outcompete it.

Figure 26. ***Fossombronia pusilla* var. *pusilla*** on moist soil. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 27. ***Tortella inflexa***, a species that grows with ***Fossombronia pusilla*** in crevices of limestone rock on the Maltese Islands. Photo by Dick Haaksma, with permission.

Figure 28. ***Fossombronia pusilla* var. *pusilla*** mixed with other bryophytes. Photo by Malcolm Storey, <DiscoverLife.org>, with online permission.

It has purple rhizoids (Figure 29), but their adaptive value, if any, is unknown.

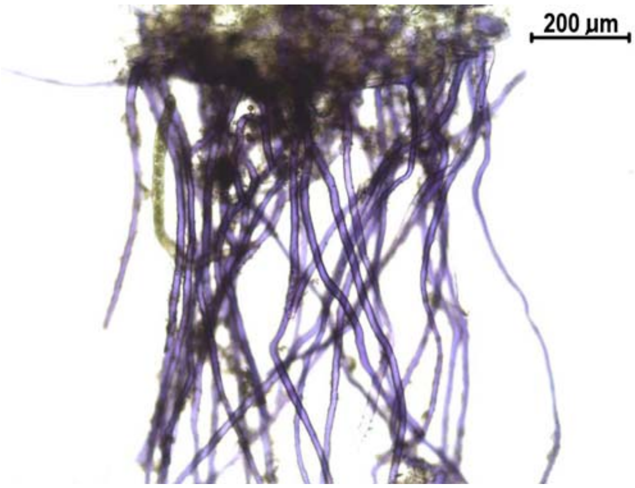

Figure 29. ***Fossombronia pusilla*** purple rhizoids. Photo by Hugues Tinguy, with permission.

Reproduction

Fossombronia pusilla (Figure 16-Figure 20) is **monoicous** (Crandall-Stotler & Bray 2019). The antheridia (Figure 30-Figure 32) and archegonia are intermixed. Wilson (1911) noted that the first mention of spermatozoids in plants was that of Schmiedel in 1747, for this species, accompanied by a description of their movement. The images I have found of the capsules show both immersed capsules and capsules with elongated setae. In both cases, one can find both brown (Figure 33-Figure 36) and black (Figure 37-Figure 43) capsules. Dehiscence is an irregular pattern of cell breakup (Figure 44-Figure 45). The spores (Figure 46-Figure 47) have a wide size range (38-58 µm) and are yellowish brown to dark brown (Crandall-Stotler & Bray 2019). The chromosome number is *n*=8 (Mehra 1938).

Figure 30. ***Fossombronia pusilla*** with small yellow antheridia showing. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 31. ***Fossombronia pusilla* var**. ***pusilla*** with antheridia. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

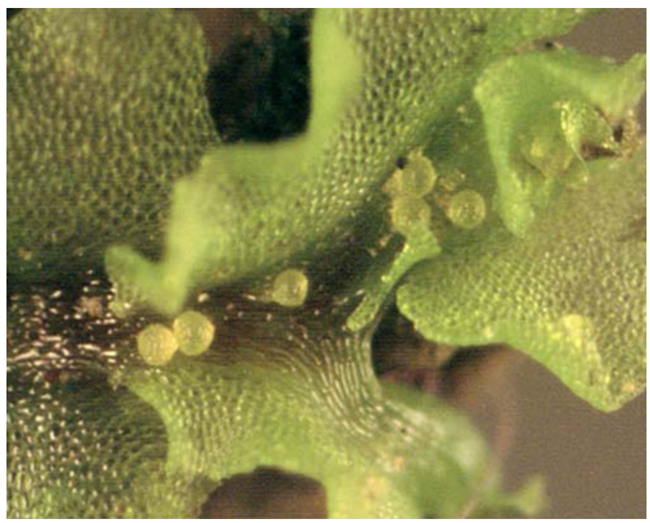

Figure 32. ***Fossombronia pusilla* var. *pusilla*** with antheridia. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 33. ***Fossombronia pusilla*** with capsules. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 34. ***Fossombronia pusilla* var. *pusilla*** with capsules. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 35. ***Fossombronia pusilla* var. *pusilla*** with capsules. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 36. ***Fossombronia pusilla* var. *pusilla*** with capsules. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 37. ***Fossombronia pusilla*** with capsules. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 38. ***Fossombronia pusilla*** with capsules. Photo by Clive Shirley, Hidden Forest, with permission.

Figure 39. ***Fossombronia pusilla*** with capsules. Photo by David T. Holyoak, with permission.

Figure 40. ***Fossombronia pusilla*** with capsules, growing with ***Dicranella varia*** and ***Trichodon cylindrica***. Photo by Barry Stewart, with permission.

Figure 41. ***Fossombronia pusilla*** perianth and capsules. Photo by Štěpán Koval, with permission.

Figure 42. ***Fossombronia pusilla*** capsules with elongated seta. Photo by Štěpán Koval, with permission.

Figure 43. ***Fossombronia pusilla*** *var.* ***pusilla*** capsule. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

Figure 44. ***Fossombronia pusilla*** with dehiscing capsules. Photo by Heino Lepp, with online permission.

Figure 45. ***Fossombronia pusilla* var. *pusilla*** with dehisced capsules. Photo by Malcolm Storey, DiscoverLife.org, with online permission.

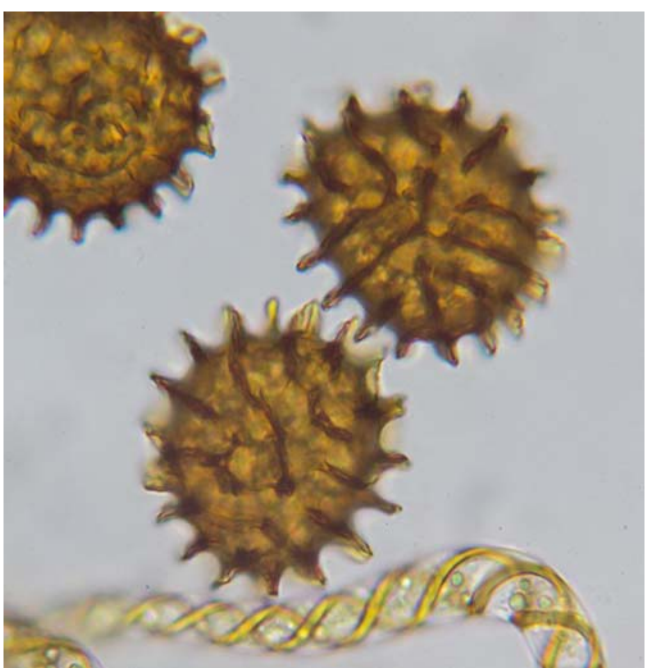

Figure 46. ***Fossombronia pusilla*** spores and elater. Photo by Štěpán Koval, with permission.

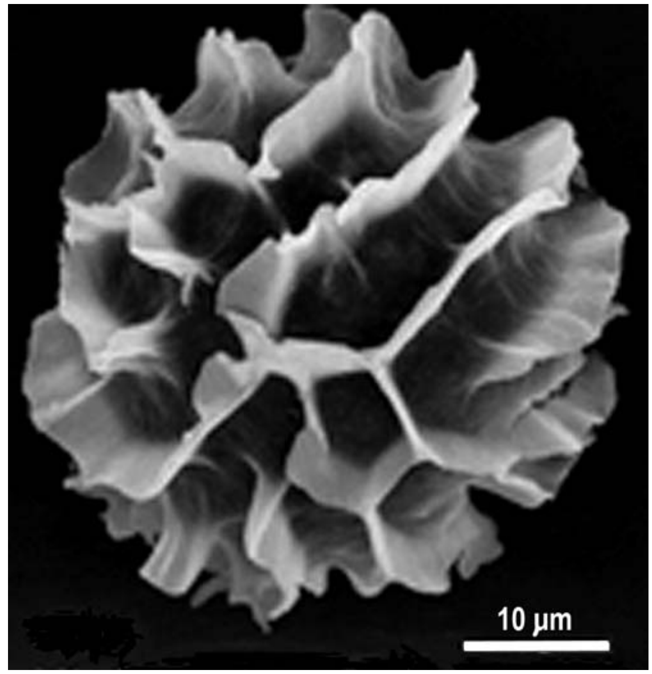

Figure 47. ***Fossombronia pusilla*** SEM of spore. Photo by Piyanart Suankeaw, through Creative Commons.

In California and Oregon, ***Fossombronia pusilla*** is **perennial** by means of fleshy, persistent tuberous stems (Figure 48) (Crandall-Stotler & Bray 2019). Otherwise, it appears that no specialized asexual reproductive structures exist.

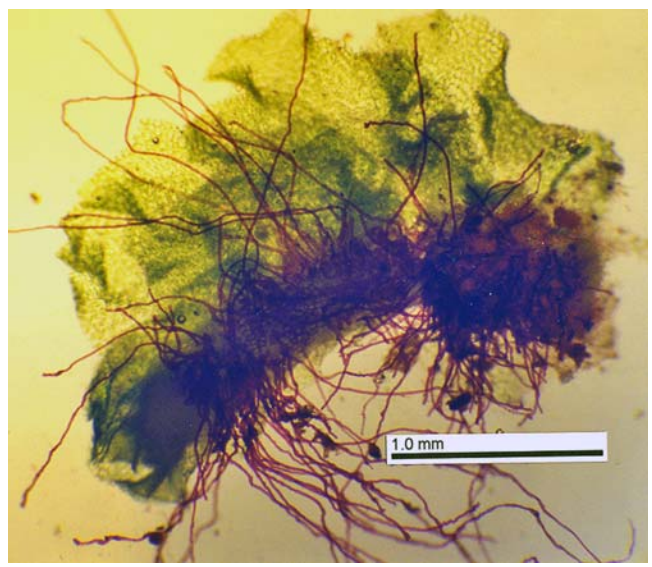

Figure 48. ***Fossombronia pusilla*** thallus showing purple rhizoids and perennial fleshy stem. Photo by David H. Wagner, with permission.

Ono (1973) reported the induction of callus formation in cultured ***Fossombronia pusilla***.

Fungal Interactions

Christie *et al*. (1985) used soluble carbohydrates of ten axenically cultured liverwort species to demonstrate that these are synthesized by the liverworts and not by fungal hyphae that are present with the field populations. They were unable to rule out the fungal production of hexitol by fungal endophytes of the liverworts tested, but none was found in ***Fossombronia pusilla*** (Figure 16-Figure 20). Vesicular-arbuscular endophytic fungi were present in the field where ***F. pusilla*** was collected, but a symbiotic or parasitic relationship remained to be demonstrated.

Rimington *et al.* (2019) examined evolution and symbiotic networks in symbioses between **Mucoromycotina** fungi and liverworts. Network analysis permits us to visualize and quantify how network members interact, showing which plants interact with which fungi. The researchers found that these networks are dominated by specialists, not generalists. ***Fossombronia pusilla*** (Figure 16-Figure 20) was the only connector hub in all three networks and was the most important member of all three symbiotic networks. They suggested that many of the liverwort associations might be facultative.

Biochemistry

I have found no descriptions of the oil bodies, but Figure 49 has what appear to be spherical oil bodies.

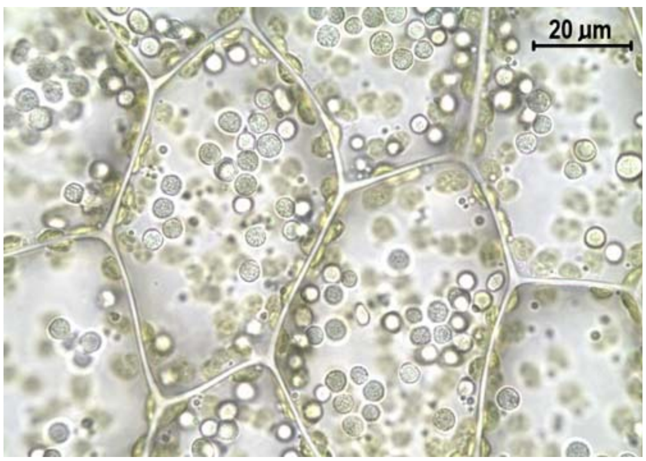

Figure 49. ***Fossombronia pusilla*** cells with what appear to be oil bodies. Photo by Hugues Tinguy, with permission.

Sauerwein *et al.* (1992) noted the difficulty in investigating secondary compounds in small liverworts such as ***Fossombronia pusilla*** (Figure 16-Figure 20). It is difficult to collect sufficient material, so they cultured it in the lab. They found that it grew well on Gamborg B5 solid medium, but the liverworts died in liquid media. When the researchers added vitamin B_{12} to the liquid media, growth was stimulated and the liverwort produced terpenes. These included diterpenedialdehydes perrottetianal A, B and 8-hydroxyperrottetianal A. They also reported santonin for the first time in a bryophyte. Grammes *et al.* (1994) identified three new terpenes, again using cultured gametophytes.

When Sauerwein and Becker (1990) cultured ***Fossombronia pusilla*** (Figure 16-Figure 20) from spores, they produced the same secondary substances as those measured in collected material. They identified perrottetianal A and B and α-(-)-santonin. They also identified seven terpenes and found that terpenes isolated from a petrol ether extract exhibited antibacterial activity.

Spiteller *et al.* (2002) found that whereas both the bacterium *Streptomyces* sp. and liverwort ***Fossombronia pusilla*** (Figure 16-Figure 20) produced geosmin, they used different pathways. Dickschat *et al.* (2005) also found that geosmin was manufactured by the Myxobacteria *Myxococcus xanthus* and *Stigmatella aurantiaca*. These likewise followed a different pathway from that used by ***Fossombronia pusilla***.

Fossombronia renateae

Distribution

Fossombronia renateae has a narrow distribution in southern Africa, where there are only two known locations (Perold 1999).

Aquatic and Wet Habitats

At Lone Creek Falls in southern Africa, ***Fossombronia renateae*** grows between rocks on soil that is kept moist by spray from the waterfalls (Perold 1999). It is accompanied there by ***Bryum alpinum*** (Figure 50) and ***Entosthodon limbatus*** (as *Funaria limbata*).

Figure 50. ***Bryum alpinum***, a species that accompanies ***Fossombronia renateae*** in the spray of waterfalls in southern Africa. Photo by David T. Holyoak, with permission.

Adaptations

Fossombronia renateae forms creeping, dense, crowded stands or is intimately to loosely mixed with mosses (Perold 1999). Both habits could help to conserve moisture during dry periods and permit slow drying that is more likely to prepare the liverwort for surviving the dry conditions.

Reproduction

Fossombronia renateae is **dioicous** (Perold 1999). Nevertheless, both sexes were seen and Perold was able to find a few dehisced capsules retained from the previous season.

Biochemistry

Oil bodies in ***Fossombronia renateae*** are few (4-6 per cell, 5 µm diameter) (Perold 1999).

Fossombronia texana (Figure 51)

(syn. = *Fossombronia mexicana*)

Distribution

Fossombronia texana (Figure 51) is known from Texas, Oklahoma, Missouri, and Arkansas (Timme & Redfearn 1997; Atwood & Brinda 2019), but its distribution is poorly known, causing its endangered status to be "no status rank" (NatureServe Explorer 2021). In addition to these USA sites, it occurs in Mexico, Cuba, and Bermuda (Crandall-Stotler & Bray 2019).

Aquatic and Wet Habitats

Atwood and Brinda (2019) reported ***Fossombronia texana*** (Figure 51) from a bridge over a creek. It also occurs on shaded dolomite ledges along the creek and generally is a calciphile on limestone near streams.

Fossombronia texana (Figure 51) forms loose to dense mats over calcareous boulders (limestone, marl, or travertine) in or next to rivers, where they are frequently inundated (Crandall-Stotler & Gradstein 2017). Crandall-Stotler and Bray (2019) consider it to be restricted to calcareous substrata. On loose marl it can form dense carpets. Its sites are often in shaded riverine habitats. Others are on drip walls of the Interior Highlands at low to moderate elevations.

Among north temperate ***Fossombronia*** species, only ***Fossombronia texana*** (Figure 51) forms mats directly on rocks along waterways, which at times become submerged (Bray 2001).

Figure 51. ***Fossombronia texana***. Photo by Bob O'Kennon, through Creative Commons.

Adaptations

The **mat** life form (Crandall-Stotler & Gradstein 2017) of ***Fossombronia texana*** (Figure 51) most likely helps it to conserve water in its streamside habitat where moisture can become less available in the summer. It may also help to reduce drag during times when it becomes inundated.

Reproduction

Fossombronia texana (Figure 51) is **monoicous** (Atwood & Brinda 2019) with antheridia scattered along with archegonia (Crandall-Stotler & Bray 2019). Therefore, production of capsules (Figure 52) is not limited by distance between the sexes. The spores are large (42-57 µm). It lacks tubers at the stem apices (Atwood & Brinda 2019), an asexual reproductive means known in some other species of ***Fossombronia***.

Figure 52. ***Fossombronia texana*** with capsules. Photo by Bob O'Kennon, through Creative Commons.

Fossombronia wondraczekii (Figure 53-Figure 54)

Distribution

Fossombronia wondraczekii (Figure 53-Figure 54) is widely circumboreal (Aleffi & Esposito 2005; Poponessi *et al*. 2015), scattered in North America (Crandall-Stotler & Bray 2019) and elsewhere, but widespread (Poponessi *et al*. 2015). It extends from eastern Greenland, south to the Appalachians, and west to Ohio and Indiana in North America. It is also present in Iceland, Europe, northern Africa, Australia, and New Zealand. Poponessi *et al*. (2015) added Cyprus, Mauritius, Réunion, Siberia, and Sri Lanka. Ştefãnuţ and Goia (2012) listed it for Romania. It is usually not common, and in the Western Carpathians of Poland it is in the protected and threatened category (Stebel & Vončina 2017).

Figure 53. ***Fossombronia wondraczekii***, a species that occurs in both hemispheres. Photo by Hugues Tinguy, with permission.

Figure 54. ***Fossombronia wondraczekii*** with capsule before seta elongation. Photo by Dick Haaksma, with permission.

Aquatic and Wet Habitats

Aleffi and Esposito (2005) characterized ***Fossombronia wondraczekii*** as mesohygrophilous, photo-sciaphilous, and terricolous. ***Fossombronia wondraczekii*** (Figure 53-Figure 54) is mostly restricted to moist soil habitats in low to moderate elevations (Crandall-Stotler & Bray 2019). These are often disturbed habitats. It typically grows intermixed with other bryophytes or forms small rosettes on moist soil where it is shaded by nearby vegetation. Ştefănuţ and Maria (2018) found it with other bryophytes near a slow-flowing stream and Stebel (2015) found it on wet soil near a ditch, both in Poland. Sotiaux *et al*. (2007) reported it from ground along a streamlet in Corsica, France, growing with ***Bryum alpinum*** (Figure 50).

In the Nilgiri Hills of India, ***Fossombronia wondraczekii*** (Figure 53-Figure 54) grows in dense patches on moist and exposed rocks and soil-covered rocks along with other terrestrial mosses (Figure 55) (Alam 2011). ***Fossombronia wondraczekii*** occurs on calcareous stony soil (Figure 56) in the Balearic Islands (Sáez *et al*. 2006).

Figure 56. ***Fossombronia wondraczekii*** growing on stony soil. Photo by Tom Neily, through Creative Commons.

Like a number of other members of ***Fossombronia***, ***Fossombronia wondraczekii*** (Figure 53-Figure 54) occurs along the edge of ponds, especially in Italy, giving it a spotty and local distribution (Poponessi *et al*. 2016).

It is not unusual to find members of ***Fossombronia*** in temporary habitats. In the Western Carpathians, ***Fossombronia wondraczekii*** (Figure 53-Figure 54) occurs with other rare species in fallow fields (Armata 2005). Klama and Górski (2018) similarly found it in wet fields, stubble fields, and fallow fields (Figure 57) in Poland, as well as moderately used forest ground roads. Sotherton and Self (2000) reported it from lowland farmland in the UK. These records suggest that it benefits, for a short period of time at least, from the lack of competition in disturbed habitats. This suggestion is further supported by its ability to colonize burned soil in moist depressions in southern Italy (Aleffi & Esposito 2005). Its rapid maturation and high level of spore dispersal aid in its colonization of such disturbed areas.

Figure 55. ***Fossombronia wondraczekii*** growing with mosses. Photo by Michael Lüth, with permission.

Figure 57. ***Fossombronia wondraczekii*** on dry mud, typical of seasonally flooded habitats. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission.

Adaptations

The habit of ***Fossombronia wondraczekii*** to grow among other bryophytes (Figure 58) (Crandall-Stotler & Bray 2019) most likely keeps this moisture-loving species moist longer, reducing both frequency and duration of desiccation.

Figure 58. ***Fossombronia wondraczekii*** habitat on soil, growing with mosses that may help to conserve moisture. Photo by Hugues Tinguy, with permission.

The dense patches are yellowish-green to green (Figure 59). In patches no bigger than a dime it grows "like a bunch of unkempt, light green, Victorian ruffles (Figure 60) with distinctive bright violet rhizoids growing from the undersides of horizontal stems" (Trigoboff 2012). Because of its small areas of growth, Hill *et al*. (2007) distinguish it as a "patch" rather than a mat.

Figure 59. ***Fossombronia wondraczekii***, showing yellowish-green color and small patch. Photo by Bernd Heynold, through Creative Commons.

Figure 60. ***Fossombronia wondrazeckii*** habitat on calcareous soil, showing patchy growth pattern. Photo by Bernd Heynold, through Creative Commons.

Reproduction

Fossombronia wondraczekii (Figure 53-Figure 54) is **monoicous** with its antheridia (Figure 61) scattered among and intermixed with the archegonia (Alam 2011; Crandall-Stotler & Bray 2019). It apparently lacks asexual reproductive structures and regenerates by spores (Figure 62-Figure 68) (Aleffi & Esposito 2005). One of its advantages toward arriving in disturbed habitats and in spreading somewhat rapidly is its high dispersal ability (Sotiaux *et al*. 2006). Brown and Lemmon (1993) described the development of the spores in detail.

Figure 61. ***Fossombronia wondraczekii*** with a few visible yellow antheridia. Photo by Štěpán Koval, with permission.

Figure 62. ***Fossombronia wondraczekii*** patch with capsules. Photo by Michael Lüth, with permission.

Figure 63. ***Fossombronia wondraczekii*** with nearly mature capsules. Photo by Michael Lüth, with permission.

Figure 64. ***Fossombronia wondraczekii*** with capsules in multiple stages of maturity and dehiscence. Photo by Bob Klips, through Creative Commons.

Figure 65. ***Fossombronia wondraczekii*** capsules with collapsed setae, showing how numerous they can be. Photo by Shaun Pogacnik, through Creative Commons.

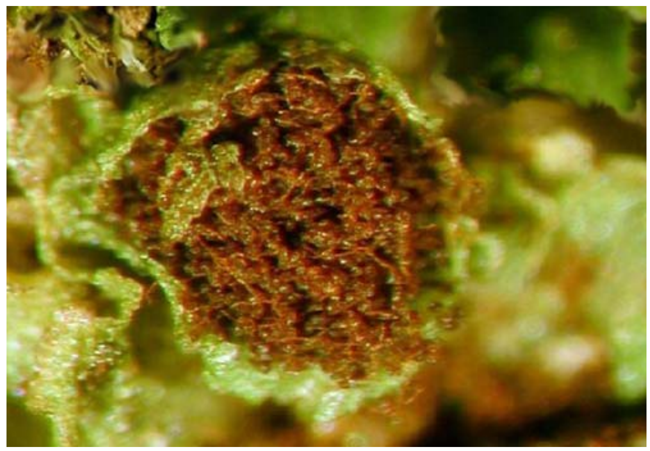

Figure 66. ***Fossombronia wondraczekii*** open sporangium exposing spores and elaters. Photo by Michael Lüth, with permission.

Figure 67. ***Fossombronia wondraczekii*** spores and elaters. Photo by Shaun Pogacnik, through Creative Commons.

Figure 68. ***Fossombronia wondraczekii*** spore and elater. Photo by Bob Klips, through Creative Commons.

Trigoboff (2012) reported ripe capsules on 5 December in Central New York, UA. There were shed spores, and many plants were bleached, with a "ghostly" appearance. On 10 January, he considered the plants to be "legally dead." Despite this unseemly condition, there were bits of green tissue, some unripe capsules, and a few unopened capsules with mature spores. The usual time for capsule (Figure 62-Figure 65) production of ***Fossombronia wondraczekii*** in central New York is 15 September to 15 October, with peak spore discharge 25 September to 5 October (Schuster 1949).

Srivastava and Sharma (1995) described the development and morphology of the ***Fossombronia wondraczekii*** sporelings. There were three types of development, with the most common one being filamentous, septate germ-tubes.

Biochemistry

Feld *et al.* (2005) identified five new sacculatane diterpenoids in ***Fossombronia wondraczekii*** (Figure 53-Figure 54).

Fossombronia wrightii (Figure 69)

Distribution

Fossombronia wrightii (Figure 69) occurs in the Carribean (ITIS 2021).

Aquatic and Wet Habitats

Like ***Fossombronia texana*** (Figure 51), ***Fossombronia wrightii*** (Figure 69) forms mats over calcareous boulders in or next to rivers, where they are frequently inundated (Crandall-Stotler & Gradstein 2017). Freire and Stotler (2007) reported it to be riparian on rocks in Cuba.

Adaptations

As do most of the wet habitat ***Fossombronia*** species included in this chapter, ***F. wrightii*** (Figure 69) forms **mats**, in this case on calcareous boulders. Once again, we can assume that it helps to conserve water during dry periods, but it would also reduce drag during periods of high water when it becomes inundated. At such times, the flow of rivers is likely to be rapid.

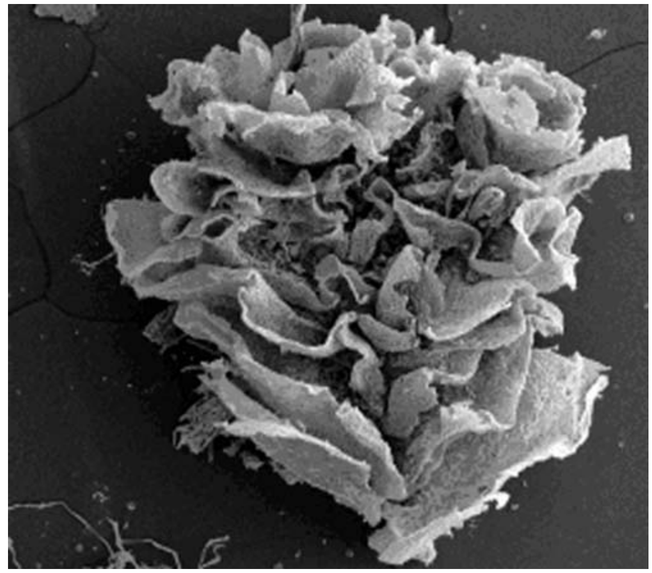

Figure 69. ***Fossombronia wrightii*** SEM, a riparian Carribean species. Photo courtesy of Virginia Freire.

Reproduction

Fossombronia wrightii (Figure 69) has known sporophytes (Figure 70) and produces spores without tubercles (Figure 71), but it is not known if it is **dioicous** or **monoicous** because no antheridia have been found (Virginia Freire, pers. comm. 24 April 2021). It forms fleshy tubers (Figure 72) that undoubtedly help it to spread where it has become established. They could also serve as dispersal agents at times of inundation, having a greater likelihood of survival than the leafy plant.

Figure 70. SEM of ***Fossombronia wrightii*** with sporophyte and tuber. Photo courtesy of Virginia Freire.

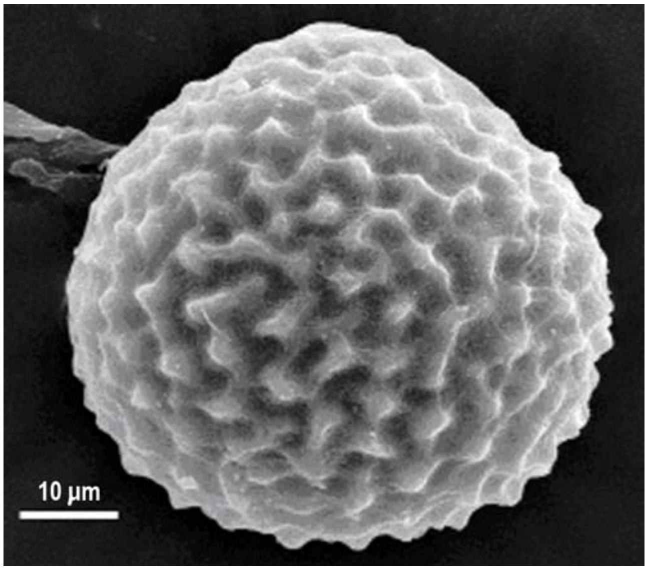

Figure 71. ***Fossombronia wrightii*** spore SEM. Photo courtesy of Virginia Freire.

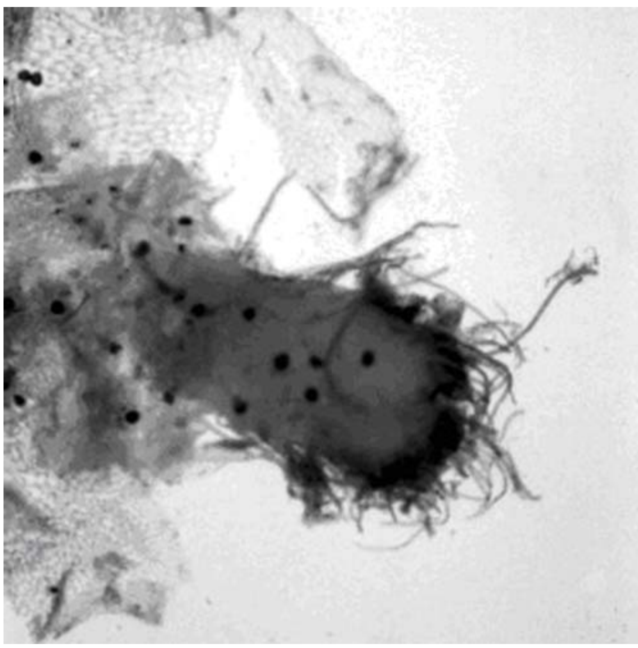

Figure 72. SEM of ***Fossombronia wrightii*** tuber. Photo courtesy of Virginia Freire.

Summary

Some of the species in this subchapter are at least periodically submerged (*e.g.* ***Fossombronia mylioides***), but most of the species can occur in wet habitats that can dry out. The adaptations seem to be physiological, permitting it to survive both submersion and drying out. For example, ***Fossombronia pusilla*** grows in temporary ponds. Some grow with other bryophytes, thus benefitting from reduced water loss; others benefit from forming large, closely overlapping mats. Some of the aquatic species are confined to high elevations in the Andes.

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