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Add *Blasia pusilla* slime papillae image

CHAPTER 1-17
AQUATIC AND WET MARCHANTIOPHYTA, ORDER BLASIALES

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Figure 1. ***Blasia pusilla*** forming a rosette on wet soil. Photo by Dale Vitt, with permission.

Nomenclature for this chapter is based primarily on Söderström *et al*. (2016). In addition, Lars Söderström provided me with correct names for species that I could not link to the names on that list. TROPICOS also permitted me to link names by tracking the basionym. I have ignored varieties, forms, and subspecies unless I could verify a current name for them. These unverifiable taxa have been included in the species.

To develop this list, I used my own bibliography, collected over the past 56 years, and Google Scholar. These papers soon led me to others. I do not pretend that this is complete. It includes streams, lakes, wetlands, and other wet substrata. It mostly ignores bogs and ignores fens, but nevertheless includes a few of these species because they were found in a wetland study. Bogs and poor fens have been treated in whole books and provide an extensive literature; fens seem somewhat less studied. They would require considerably more review and time. Thus I felt that less-reviewed topics, particularly the aquatic habitats with which I am most familiar, should be given priority.

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

MARCHANTIOPSIDA

Blasiidae – Blasiales

Blasiaceae

Blasia pusilla

Distribution

Blasia pusilla is a boreal-montane species (Dia & Not 1991). It occurs in Europe, West Greenland, North America, Asia (India, Kamchatka, China, Korea, Japan) (Rohret 1916; Schuster 1992). Schuster (1992) considers the Australian records to be errors.

It tends to form rosettes on its substrate (Figure 1-Figure 3).

Figure 2. ***Blasia pusilla*** habit on soil. Photo by Štěpán Koval, with permission.

Figure 3. ***Blasia pusilla*** habit, Mt. Robson, BC, Canada, 26 July 1980. Photo by Janice Glime.

Aquatic and Wet Habitats

Blasia pusilla (Figure 1-Figure 6) is not typically a submersed species. Holmes and Whitton (1975) considered it to be an "uncommon" member of the flora in the River Tweed. Jonsgard and Birks (1995) reported it from small streams in the Krakenes, Norway. In the Caucasian State Nature Reserve, Russia, it occurred in the dry river bed of the Bushujka River on silting rocks (Konstantinova *et al*. 2009).

Schuster (1992) comments that when ***Blasia pusilla*** (Figure 1-Figure 6) does occur in stream beds, it is almost always seasonal. Erosion and slippage seem to destroy most of the plants.

Nevertheless, the usual habitat of ***Blasia pusilla*** seems to be near water (Figure 6), occasionally submerged in some locations, but only facultatively aquatic.

Figure 4. ***Blasia pusilla*** rosette on sand, showing conspicuous ribs. Photo by Štěpán Koval, with permission.

Figure 5. ***Blasia pusilla*** on sand, with stellate gemmae. Photo by Štěpán Koval, with permission.

Figure 6. ***Blasia pusilla*** on wet soil. Photo by Kristian Peters, with permission.

River and stream banks seem to be among the most suitable habitats for ***Blasia pusilla*** (Figure 1-Figure 6). Sampson (1905) reported it from the bank of the River Dee in the UK. Paton (1967, 1971) reported it from gravelly detritus by a river and a clay stream bank in the UK. Rilstone (1949) found it on wet banks (Figure 1) in Cornwall, UK, but considered it to be rare. Fitzgerald and Fitzgerald (1966) reported it from schist detritus on rocks by the Glenedra River in northeast Ireland. Similarly, M'Ardle (1909) noted that it occurred among wet rocks in Ireland. Schumacher and Sivertsen (1987) found it on the banks of rivers, brooks, and rivulets in Norway, and Damsholt *et al*. (1984) reported it from along rills, along with ***Scapania paludosa*** (Figure 7) and ***Pellia neesiana*** (Figure 8).

Figure 7. ***Scapania paludosa***, a species that occurs with ***Blasia pusilla*** along rills in Norway. Photo by Hermann Schachner, through Creative Commons.

Figure 8. ***Pellia neesiana***, a species that occurs with ***Blasia pusilla*** along rills in Norway. Photo from Botany Website, UBC, with permission.

Váňa and Ignatov (1995) reported ***Blasia pusilla*** (Figure 1-Figure 6) from ravine slopes and on logs covered by alluvium in flood valleys, as well as creek bars, in the Altai Mountains of Asia. In the Komi Republic, Dulin (2014) found ***Blasia pusilla*** on inundated soil along the river bank, in pure patches (Figure 9) or with other liverworts. Sofronova reported it from banks of water courses in the Upper Course of the Indigirka River, East Yakutia (Sofronova 2018), and on stones near the Timpton River as well as rock outcrops there, sustaining in both river and stream banks that experience occasional floods (Sofronova 2017). In South Siberia it can be found in willow thickets along river and stream banks, sometimes mixed with ***Jungermannia pumila*** (Figure 10) and ***Scapania mucronata*** (Figure 11) (Czernyadjeva *et al*. 2013).

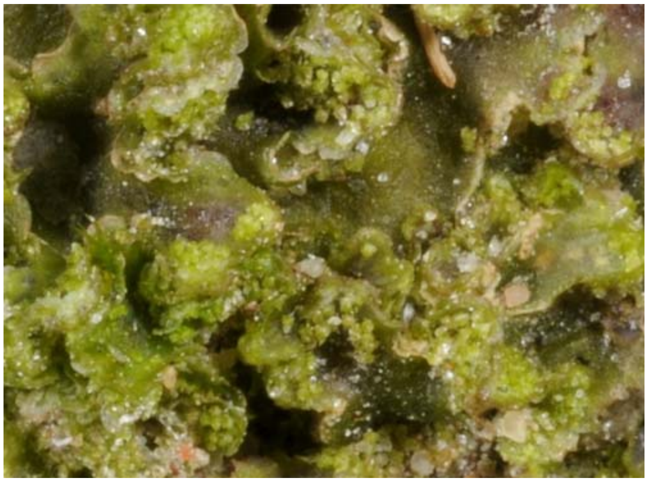

Figure 9. ***Blasia pusilla*** growing in pure patch on sand. Photo by Jouko Rikkinen, through Creative Commons.

Figure 10. ***Jungermannia pumila***, a species that occurs mixed with ***Blasia pusilla*** in South Siberia willow thickets. Photo by Michael Lüth, with permission.

Figure 11. ***Scapania mucronata***, a species that occurs mixed with ***Blasia pusilla*** in South Siberia willow thickets. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

In North America, Blomquist (1939) found ***Blasia pusilla*** (Figure 1-Figure 6) along the west branch of the New River in the Appalachian Mountains, USA. In the Arctic, it develops extensive cover, up to 75%, in the area flooded by glacial streams (Slack & Horton 2010). Skorepa (1968) found it on moist, shaded sandstone near a stream in southern Illinois, USA. Wagner (2009) reported it from moist sand (Figure 12-Figure 14) next to a creek in Oregon, USA, both solitary and mixed with other liverworts and with hornworts. It seems to like clay, occurring on clayey stream banks in Ohio, USA (Hall 1958). Hong (1978, 1980) reported it from wet rocks and soil in the North Cascades Range of Washington, USA.

Figure 12. ***Blasia pusilla*** in aging small, pure patches on sand. Photo by Jouko Rikkinen, through Creative Commons.

Figure 13. ***Blasia pusilla*** habit on sand. Photo by Jouko Rikkinen, through Creative Commons.

Figure 14. ***Blasia pusilla*** habit on sand with older thallus dying. Photo by Jouko Rikkinen, through Creative Commons.

Ditches (Figure 15) can offer similar conditions to streams, so the presence of ***Blasia pusilla*** (Figure 1-Figure 6) there might be expected. Taylor (1921) reported it from the sides of a ditch in Mount Desert, Maine, USA. Paton (1971) similarly found it on a ditch bank in the UK.

Figure 15. Drainage ditch in Germany, a habitat where one might find ***Blasia pusilla*** along the sides. Photo by Dirk Ingo Franke, through Creative Commons.

Waterfalls provide moist habitats where moisture-loving liverworts are able to survive (Figure 16). On Bering Island, Russia, ***Blasia pusilla*** (Figure 1-Figure 6) occurs on wet boulders in a waterfall canyon (Bakalin 2005). Gruber *et al*. (2005) found that in the area near Krimml Waterfalls of Austria, ***Blasia pusilla*** grows best in locations receiving spray from the waterfalls. Odland *et al*. (1991) found that following regulation of a river in Aurland, western Norway, cover by ***Blasia pusilla*** increased near the waterfall in the spray zone. The regulation reduced the spray precipitation by 98-100%, but there is still considerable spray near the waterfall.

Figure 16. Waterfalls such as these create a constantly moist environment suitable for liverworts such as ***Blasia pusilla***. Photo by Fabian Michelangeli, through public domain.

Slopes often provide moist, shaded habitats (Figure 17-Figure 18). Rose (1950) found that ***Blasia pusilla*** was "plentiful" on a damp, north-facing bank on clayey sand in the UK. Dulin (2014) found it on "slightly matted loamy soil at a slope ledge" and on the vertical surface of a ground wall in the Komi Republic. Bakalin *et al*. (2016) found it on the moist soil or mineral ground of eroded slopes, where it typically occurred with ***Anthelia juratzkana*** (Figure 19), ***Calypogeia muelleriana*** (Figure 20), and ***Solenostoma hyalinum*** (Figure 21).

Figure 17. ***Blasia pusilla*** habitat on slope. Photo by Hermann Schachner, through Creative Commons.

Figure 18. ***Blasia pusilla*** habitat on slope. Photo by Hermann Schachner, through Creative Commons.

Figure 19. ***Anthelia juratzkana***, a species that occurs with ***Blasia pusilla*** on slopes in Russia. Photo by Hermann Schachner, through Creative Commons.

Figure 20. ***Calypogeia muelleriana***, a species that occurs with ***Blasia pusilla*** on slopes in Russia. Photo by Hugues Tinguy, with permission.

Figure 21. ***Solenostoma hyalinum*** with capsule, a species that occurs with ***Blasia pusilla*** on slopes in Russia. Photo by Michael Lüth, with permission.

In the Mt. Greylock region of Massachusetts, USA, Andrews (1904) found only a small specimen on a wet bank in the Notch. Lanfear (1933) found ***Blasia pusilla*** (Figure 1-Figure 6) on clay banks and shale in western Pennsylvania, USA. Conard (1940) likewise reported it from moist, shaded clayey banks, where it was rare, in Iowa, USA. Breil (1996) found it on moist, eroding loamy slopes in the Virginia Piedmont, USA.

The suitable slopes include a number of records along trails. Váňa and Ignatov (1995) reported it from wet clayish soil along both trails and roads in the Altai Mountains of eastern Asia. Czernyadjeva *et al.* (2017) found it, albeit rare, on a railway embankment, as did Dulin (2014, 2015) in the Komi Republic. Bakalin *et al.* (2013) found it on a moist clayish road rut, occurring in pure mats, in Adjara, Georgia. Ören *et al.* (2015) found it on a damp, steep, roadside slope in Turkey, where it was the most common bryophyte on the slope. Rikkinen (1992) reported it from shaded roadside banks and other disturbed sites in Finland. Blomquist (1939) reported ***Blasia pusilla*** (Figure 1-Figure 6) from a moist clay road bank in North Carolina, USA. Greenwood (1915) found it on damp soil by roadsides in Massachusetts, USA.

Springs are not often mentioned as habitats for ***Blasia pusilla*** (Figure 1-Figure 6), but then springs are less common habitats. Paton (1961) found it in the UK on a sandy track that remained moist by water from small springs. Wittlake (1950) found it under and around springs on a slope in Arkansas, USA. Similarly, seepage areas sometimes provide suitable habitats. Blockeel (2020) reported it from moist soil by a seepage in Greece.

Damp or wet soil is suitable, but few reports seem to identify that habitat for ***Blasia pusilla*** (Figure 1-Figure 6) (Macvicar 1902; Lanfear 1933; Paton 1967; Hong 1977, 1978). In their survey of the upper course of the Indigirka River in East Yakutia, Sofronova (2018) reported it from soil in the horsetail, moss shrub post-ice community. Among its damp soil habitats (Figure 22-Figure 24), Rilstone (1949) found it on clayey moors in Cornwall, UK, but it is rare.

Figure 22. ***Blasia pusilla*** on wet soil. Photo by Bernd Haynold, through Creative Commons.

Figure 23. ***Blasia pusilla*** large population on soil. Photo by Hermann Schachner, through Creative Commons.

Figure 24. ***Blasia pusilla*** on soil. Photo by Bernd Haynold, through Creative Commons.

Bogs don't seem to be a usual habitat for ***Blasia pusilla*** (Figure 1-Figure 6). The only record I have seen is that of

Macvicar (1902) for Meiller Bog in the Ben Lawers District, UK (Figure 25).

Figure 25. View from summit of Ben Lawers, UK, where ***Blasia pusilla*** occurs in a "bog" habitat. Photo by Scott Holland, through public domain.

Some plants of ***Blasia pusilla*** (Figure 1-Figure 6) are able to inhabit dune slacks (Figure 26) (Swann 1982; Persson & Pleijel 2008). These habitats occur between foredunes in low-lying depressions (Geographyinaction 2021). In the winter the plants can be close to or below the water level. Organic matter is slow to develop in slacks, but there is usually an impervious layer. Mosses (and possibly some liverworts) help to retain moisture. Other dune slacks remain as pools (Wikipedia 2021).

Figure 26. Dune slack in UK, a habitat where ***Blasia pusilla*** can occur. Photo by Gary Rogers, through Creative Commons.

The ability of ***Blasia pusilla*** (Figure 1-Figure 6) to colonize disturbed substrata has made it a successful pioneer species. When a former peat moor became agricultural land, bryophytes were able to colonize. For example, ***Blasia pusilla*** was among the pioneers in a maize field (Figure 27) when it remained untilled due to extremely wet weather (van den Bosch & Kersten 2004).

Figure 27. Muddy field in the UK, a potential site for the occurrence of ***Blasia pusilla***. Photo by Ian Peterson, through Creative Commons.

Drawdown of a lake in western Norway exposed a floodplain system with artificial islands (Odland 1997). During the first three years following construction, ***Blasia pusilla*** (Figure 1-Figure 6) was among the dominants able to colonize, but they disappeared or were greatly reduced after 8 years. The colonization by ***B. pusilla*** was not immediate, as ***Subularia aquatica*** (Figure 28) and small acrocarpous mosses dominated after one month, but this soon shifted to one in which ***Blasia pusilla*** was one of the dominants (Odland 1997; Odland & del Moral 2002).

Figure 28. ***Subularia aquatica***, a species that is a primary colonizer in a drawdown lake, preceding the colonization by ***Blasia pusilla***. Photo by J. C. Schou, with permission.

Blasia pusilla (Figure 1-Figure 6) is also present as a pioneer in the early successional stages of the Arctic tundra (Figure 29, where it reaches 75% in areas flooded by a glacial stream (Slack & Horton 2010). In even harsher conditions of a gold mining area of northeast Yakutia, ***Blasia*** was the only liverwort present (Sofronova 2019).

Figure 29. Arctic tundra, a habitat where ***Blasia pusilla*** can cover 75% of the ground in glacial melt areas. Photo by A. Dialla, through Creative Commons.

Various Russian records indicate that ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) is tolerant of more terrestrial, drier habitats as well (Figure 30). Sofronova found it on sand between rocks (Sofronova 2013), few plants on soil among ***Salix*** shrubs (Figure 31) (Sofronova 2015), and on decaying wood (Sofronova 2017), summarizing it as occurring in two main types of habitats in Yakutia: decaying wood and rocks. Dulin (2014) describes terrestrial habitats in the Komi Republic: matted loamy soil at slope ledge between inundated shrublet-moss spruce forest and pebbly bar; on slightly matted soil of roadside wall.

Figure 30. ***Blasia pusilla*** habitat on soil and roots. Photo by Michael Lüth, with permission.

Physiology

Nordhorn-Richter (1984) explored the presence of fluorescence in bryophytes, as seen with a compound microscope under UV light, including ***Blasia*** in her studies. She found that the receptacular gemmae (Figure 32) fluoresced yellow in UV light.

Smith (2002) examined rapid chlorophyll fluorescence induction in a number of bryophytes. ***Blasia pusilla*** (Figure 1-Figure 6) did not have outstanding values; its highest yield of PSII Fv/Fm was 0.78 ± 0.01.

Blasia pusilla (Figure 1-Figure 6) extends into the Arctic, surviving, for example, in the mountain tundra belt of Northeast Yakutia, Russia (Sofronova 2019). This area has permafrost, yet the liverwort is able to survive the long winters (Figure 33), probably mostly as gemmae.

Figure 31. ***Salix*** habitat, which can provide suitable habitat for ***Blasia pusilla***. Photo by Dennis Kalma, FEIS, through public domain.

Figure 32. ***Blasia pusilla*** gemmae from flask. Photo by Hermann Schachner, through Creative Commons.

Figure 33. ***Blasia pusilla*** frozen. Photo by Bernd Haynold, through Creative Commons.

Adaptations

Blasia pusilla can dry out (Figure 34). This seems to be common at the end of the growing season, but gemmae are able to carry it over to the next spring. But it also has some adaptations to help it in its water relations.

Figure 34. ***Blasia pusilla*** with flasks, somewhat dry. Photo by Bob Klips, with permission.

Blasia pusilla (Figure 1-Figure 6) develops strands of thick-walled cells (Figure 35) that provide both mechanical support and conducting tissue (Rohret 1916). The plants can grow in pure mats (Figure 36) or with other liverworts (Wagner 2009; Dulin 2014; Sofronova 2017), both providing a reduction in water loss.

Figure 35. ***Blasia pusilla*** discolored, probably due to aging or sun exposure, and showing the strands that provide mechanical support and conduits for water. Photo by Štěpán Koval, with permission.

Figure 36. ***Blasia pusilla*** large population on soil. Photo by Hermann Schachner, through Creative Commons.

Reproduction

Allsopp and Ilahi (1971) described the morphology of ***Blasia pusilla*** (Figure 1-Figure 6). ***Blasia pusilla*** is typically seasonal, resulting from considerable dieback (Figure 37) in the winter months (Schuster 1992). This occurs both in submersed locations and out of water. Its reappearance in the spring results from its prolific production of gemmae (two types) and spores from its numerous sporophytes.

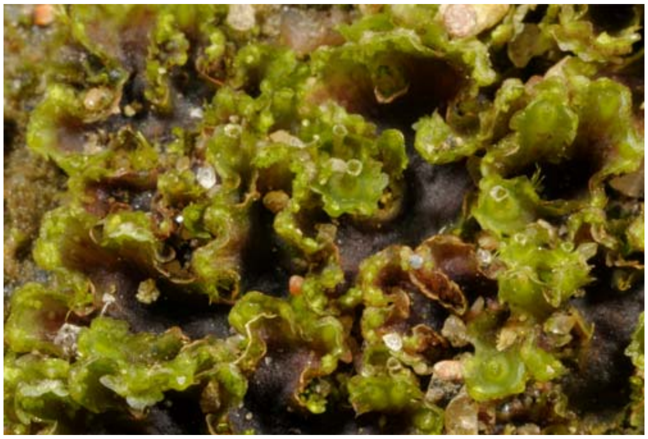

Figure 37. ***Blasia pusilla*** with older thallus dying. Photo by Jouko Rikkinen, through Creative Commons.

Blasia pusilla (Figure 1-Figure 6) is **dioicous**. Rohret (1916) describes the male plants as being more slender and deeply lobed than the female plants. Antheridia occur in a row on each side of the midrib in small lobes of the thallus (Figure 38). Ten to twelve archegonia (Figure 39) are produced near the tip, but the continued growth of the apex causes them to eventually reside near the middle of the thallus length. Ultimately, the sex organs are imbedded in the thallus (Figure 39) due to overgrowth by the thallus. Despite the numerous archegonia, typically only one sporophyte develops on a single thallus. Despite its dioicous condition, it can produce abundant sporophytes (Figure 40-Figure 46) in at least some locations (Rohret 1916; Schuster 1992; Breil 1996).

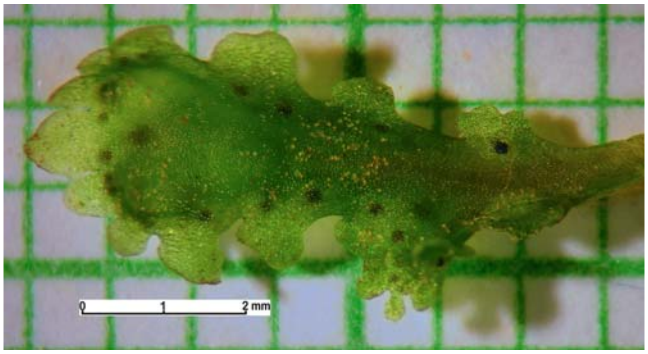

Figure 38. ***Blasia pusilla*** male thallus with small antheridial lobes at bottom. Photo courtesy of David H. Wagner.

Figure 39. ***Blasia pusilla*** archegonium imbedded in thallus. Photo courtesy of David H. Wagner.

Figure 40. ***Blasia pusilla*** with emerging capsules. Photo by Kristian Peters, with permission.

Figure 41. ***Blasia pusilla*** capsules. Photo by Rafael Medina, with permission.

Figure 42. ***Blasia pusilla*** with mature capsules. Photo by Jouko Rikkinen, through Creative Commons.

Figure 43. ***Blasia pusilla*** with mature capsules. Photo by Jouko Rikkinen, through Creative Commons.

Figure 44. ***Blasia pusilla*** with mature and dehisced capsules. Photo by Jouko Rikkinen, through Creative Commons.

Figure 45. ***Blasia pusilla*** with dehisced capsules, showing tangled elaters. Photo by Jouko Rikkinen, through Creative Commons.

Figure 46. ***Blasia pusilla*** with open capsules. Photo by Rafael Medina, with permission.

Wagner (2009) reported the presence of male plants and females with sporophytes near Sutton Creek in Oregon, USA. Rohret (1916) reported that sex organs of ***Blasia pusilla*** are formed in the summer in Iowa, USA. But it appears that this timing differs by location, probably relating to factors associated with latitude. Fertilization of ***Blasia pusilla*** (Figure 1-Figure 6) occurs in the spring in England, Scotland, Wales, and North Carolina, USA (Duckett & Renzaglia 1993). Sporophytes develop during the summer months and the parent gametophytes die (Figure 42) (Duckett & Renzaglia 1993). Spores are shed in the spring, indicating that the sporophyte must overwinter on the dead gametophyte (Rohret 1916; Duckett & Renzaglia 1993; Shimamura *et al*. 2006). The death of the gametophyte before the sporophyte matures is unique to ***Blasia***. The cell division in the seta is completed by early autumn and the cells are packed with amylochloroplasts (Duckett & Renzaglia 1993). The capsule produces sporocytes with abundant protein bodies. These researchers suggest that day length probably controls the initiation of the sex organs in spring and dormancy of sporophytes in autumn. On the other hand, they suggest that it is higher temperatures that govern the sporophyte maturation. Both sporogenesis and seta elongation occur in early spring in Japan (Shimamura *et al*. 2006). Spores are large (35-50 µm). Udar and Srivastava (1983) provide SEM micrographs of the spores of ***Blasia*** and discuss the reproductive biology.

Van Zanten (2005) noted the rarity of sporophytes on ***Blasia pusilla*** (Figure 1-Figure 6) in The Netherlands. But when he was able to find ripe capsules, it was not spring, but November. He attributed the increase in plants with capsules to a greater search intensity. He also noted that the increase in capsules did not affect the production of gemmae.

Renzaglia and Duckett (1987) described the spermatogenesis of ***Blasia pusilla*** (Figure 1-Figure 6) in detail. Bartholomew (1986) described the sporeling development of ***Blasia pusilla***, noting that the spores are endosporic, but not precocious. Germination is initiated by imbibition of water, causing the spores to swell to 50-60 µm. Differences in temperature and light regimes (18ºC, 18:6 light dark & 3000-3500 lux; 18ºC, 12:12 light dark & 500 lux; 10ºC & 18:6 light dark, 1300 lux) had no effect on spore germination or development except to alter the rate. Bartholomew-Began (2009) explored the development of the sporeling in another member of Blasiales (***Cavicularia***; Figure 47) and found that the pattern of development is unique to ***Cavicularia*** and ***Blasia***.

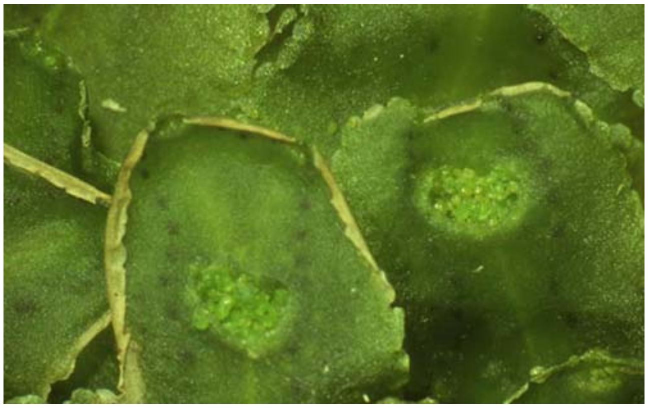

Figure 47. ***Cavicularia densa*** with ***Nostoc*** colonies forming a row on each side of the gemmae cups. Photo from Digital Museum Hiroshima University, with permission.

It is possible for ***Blasia pusilla*** (Figure 1-Figure 6) to reproduce aposporously in culture (Matzke & Raudzens 1968; Raudzens & Matzke 1968). Particular cells of the elongating seta can remain alive. After 3.5-6 weeks these can at times in the right conditions give rise to diploid gametophytes. These gametophytes develop in appearance like those with only one set of chromosomes. Normal gametophytes have n=9; the ones produced by apospory have n=18. They can produce archegonia, but not antheridia. Matzke and Raudzens consider that this type of apospory could not occur in the field.

Allsopp and Ilahi (1971) described regeneration in ***Blasia pusilla*** (Figure 1-Figure 6). An early description of the asexual reproduction in ***Blasia pusilla*** was provided by Buch in 1907. ***Blasia pusilla*** produces two types of gemmae in addition to spores (During 2001a). The stellate gemmae (Figure 48-Figure 55) form on the dorsal side of the thallus and the globose gemmae (Figure 56-Figure 68) are produced in receptacles (Buch 1907; Duckett & Renzaglia 1993; Paton 1999; Laaka-Lindberg *et al*. 2003). Those produced in the flask-like receptacles exhibit a yellow fluorescence in UV light (Nordhorn-Richter 1984)

Figure 48. ***Blasia pusilla*** with stellate gemmae. Photo by David T. Holyoak, with permission.

Figure 49. ***Blasia pusilla*** with stellate gemmae. Photo by Martin Hutten, with permission.

Figure 50. ***Blasia pusilla*** with stellate gemmae. Photo by Shaun Pogacnik, through Creative Commons.

Figure 51. ***Blasia pusilla*** with stellate gemmae. Photo by Jouko Rikkinen, through Creative Commons.

Figure 52. ***Blasia pusilla*** with stellate gemmae (**arrow**) on surface and ***Pellia*** on left (**arrow**). Photo by Paul Davison, with permission.

Figure 53. ***Blasia pusilla*** with stellate gemmae, habit on sand. Photo by Jouko Rikkinen, through Creative Commons.

Figure 54. ***Blasia pusilla*** showing stellate gemmae arranged on the thallus margins. Photo courtesy of David H. Wagner.

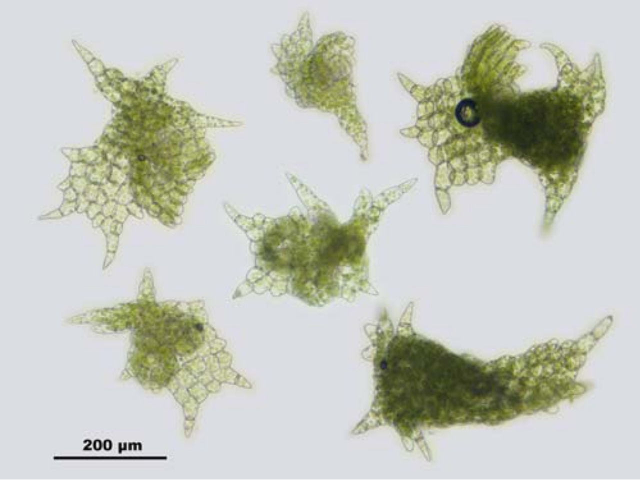

Figure 55. ***Blasia pusilla*** stellate gemmae. Photo by Hermann Schachner, through Creative Commons.

The globose gemmae (Figure 56-Figure 68) from the receptacles are able to persist in diaspore banks. Both kinds of gemmae of ***Blasia pusilla*** (Figure 1-Figure 6) are multicellular, with each cell containing a large nucleus and many oil bodies (Rohret 1916). I have been unable to find any other report of oil bodies in the gemmae of ***Blasia pusilla***.

Figure 56. ***Blasia pusilla*** with numerous flask-like receptacles containing gemmae. Photo by Dick Haaksma, with permission.

Figure 57. ***Blasia pusilla*** side view of gemmae flasks. Photo by Jouko Rikkinen, through Creative Commons.

Figure 58. ***Blasia pusilla*** side view of habit with gemmae flasks. Photo by Jouko Rikkinen, through Creative Commons.

Figure 59. ***Blasia pusilla*** showing numerous gemmae flasks. Photo by Hermann Schachner, through Creative Commons.

Figure 60. ***Blasia pusilla*** with flask-like gemmae receptacles and exuding gemmae. Photo by Tim Faasen, with permission.

Figure 61. ***Blasia pusilla*** habit with moisture. Photo by Jouko Rikkinen, through Creative Commons.

Figure 62. ***Blasia pusilla*** with flasks of gemmae and gemmae exuding from flask. Photo by Hermann Schachner, through Creative Commons.

Figure 63. ***Blasia pusilla*** with gemmae in flask and mucilage exuding from tips. Photo by Hermann Schachner, through public domain.

Figure 64. ***Blasia pusilla*** gemmae on flask. Photo by Štěpán Koval, with permission.

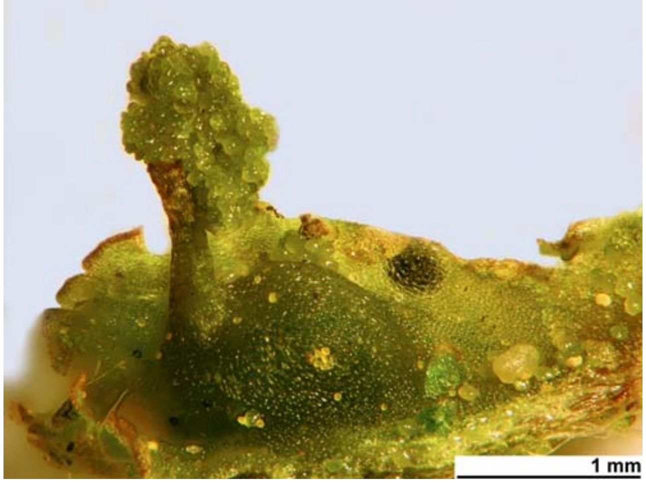

Figure 65. Gemmae flask of ***Blasia pusilla*** with gemmae exuding from the opening. Photo courtesy of David Wagner.

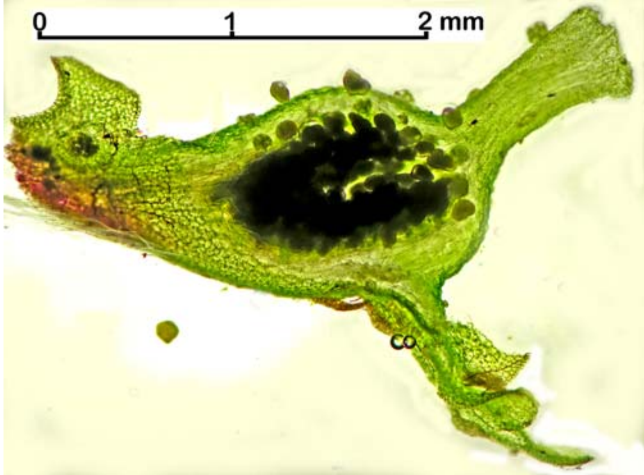

Figure 66. View of gemmae flask of ***Blasia pusilla***, showing globose gemmae inside and on its surface. Photo courtesy of David Wagner.

Figure 67. ***Blasia pusilla*** with gemmae in neck of flask. Photo by Hermann Schachner, through Creative Commons.

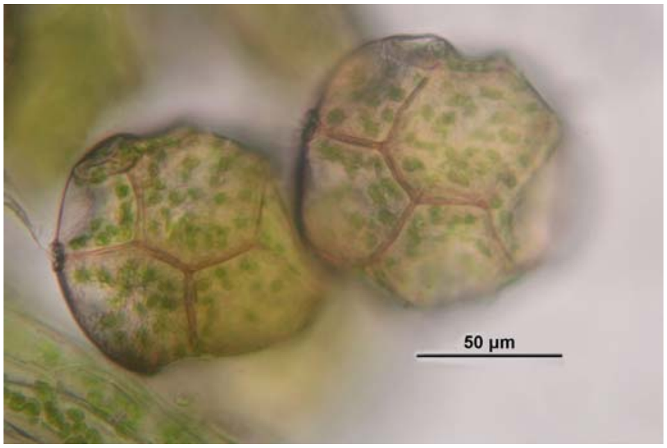

Figure 68. ***Blasia pusilla*** gemmae from flask. Photo by Hermann Schachner, through Creative Commons.

As the globose gemmae (Figure 56-Figure 68) in the flask-like receptacles of ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) develop, the mucilage papillae secrete a slimy substance that enters the flask cavity (Rohret 1916). As the mature gemmae break from their stalks, they become imbedded in the viscid liquid. Pressure of the growing gemmae, and probably entrance of water into the flask, causes the mucilage to swell and exude from the flask neck (Figure 63-Figure 67). When the gemma begins to grow, the young plant benefits from the energy stored in the gemma (Figure 68). As the old thalli die, the gemmae and young plants are permitted to reach the soil. The gemmae can be shed during most of the year. These globose gemmae of ***Blasia pusilla*** have large oil droplets, and these may help the gemmae survive the winter to replace winter-damaged plants.

Bartholomew-Began and Jones (2005) described the receptacular gemma (Figure 56-Figure 68) development of ***Blasia pusilla*** (Figure 1Figure 2-Figure 6). These discoid to ellipsoid, stalked gemmae are produced within the flask-shaped receptacle. The gemma has distinct tiers of thick-walled cells with margins of lateral column of thin-walled cells. Germination does not occur until the gemmae are free from the receptacle. In fact, During (2001b) found that the disc-like gemmae do not seem to be able to germinate right away after they are dispersed, a condition that permits them to find their way into diaspore banks.

The globose receptacular gemmae (Figure 56-Figure 68) of ***Blasia pusilla*** (Figure 1-Figure 6) are present on both male and female plants (CRB 1908). However they are rare if the female is developing embryos. The apical brood-buds are common in summer; gemmae do not seem to germinate in summer or autumn, but instead are dormant until spring, when they can form new plants. Shoots arise from one side of the gemma, not both.

During (2001c) considers the production of two kinds of gemmae to be beneficial for ruderal species such as ***Blasia pusilla*** (Figure 1-Figure 6). The stellate gemmae (Figure 48-Figure 55) bring along their own nitrogen-fixing ***Nostoc*** symbiont in the two auricles (Duckett & Renzaglia 1993). These gemmae are also in possession of large amylochloroplasts (During 2001c). They are produced throughout the growing season, but are unable to survive the cold of winter. The more globose receptacular gemmae (Figure 56-Figure 68) are filled with starch, proteins, and lipids, but no ***Nostoc***. Unlike the stellate gemmae, they are not released until late summer or autumn, survive the winter, and germinate in spring. These cold-resistant gemmae are suitable for diaspore banks. When they are brought to the surface, they do not germinate right away. This could cause them to be missed in some diaspore studies since identification is usually based on germination. Perhaps they are waiting for the right combination of temperature, day length, and light intensity, or maybe requiring a cold period first.

Role

In the Mt. Kurikoma district of Japan, Chiba and Kato (1969) explored the testacean (protozoa) community associated with bryophytes. They found that these communities related to the habitat of the bryophytes, with ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) among those that formed a suitable substrate for the protozoans.

Symbiotic Interactions

Most of the cyanobacterial symbiotic associations in the bryophytes are with the genus ***Nostoc*** (Watts *et al*. 1999). Although ***Nostoc*** partners are common in the **Anthocerotophyta**, this is not the case among the **Marchantiopsida**. Only two species of **Marchantiopsida** are known to harbor ***Nostoc*** (Figure 69) symbionts: ***Blasia pusilla*** (Figure 1Figure 2-Figure 6; Figure 70) and ***Cavicularia densa*** (Figure 47), both in **Blasiidae** (Rikkinen & Virtanen 2008). It is interesting that these species lack fungal symbionts (Adams & Duggan 2008; Rikkinen & Virtanen 2008; Liepiņa 2012), although they can have non-symbiotic fungal inhabitants.

Figure 69. ***Nostoc punctiforme***, a **Cyanobacterium** that can live symbiotically in ***Blasia pusilla***. Photo by Eduardo Zuñiga, through Creative Commons.

Figure 70. ***Blasia pusilla*** showing ***Nostoc*** colonies. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

The ***Nostoc*** (Figure 69-Figure 70) of ***Blasia pusilla*** occurs extracellularly (Jackson *et al*. 2012) in auricles on the ventral surface (Figure 71-Figure 77) along the midrib (Adams 2002), thus receiving some protection from bright light and from desiccation. These ***Nostoc*** colonies cause areas of dark spots visible along the thallus (Adams *et al*. 2006). The assurance of transfer of these symbionts to the next generation is accomplished by the occurrence of the ***Nostoc*** in the lobes of the stellate gemmae (Figure 48-Figure 55) (Duckett & Renzaglia 1993; Rikkinen & Virtanen 2008). Rodgers and Stewart (1977) found that this symbiosis works well under moist conditions, but not in waterlogged or desiccated conditions. In their experiments, Rikkinen and Virtanen (2008) found that 95 out of 100 of the stellate gemmae produced cyanobacterial colonies within 3 months in culture.

Figure 71. ***Blasia pusilla*** side view of habit showing ***Nostoc*** colonies on ventral side. Photo by Jouko Rikkinen, through Creative Commons.

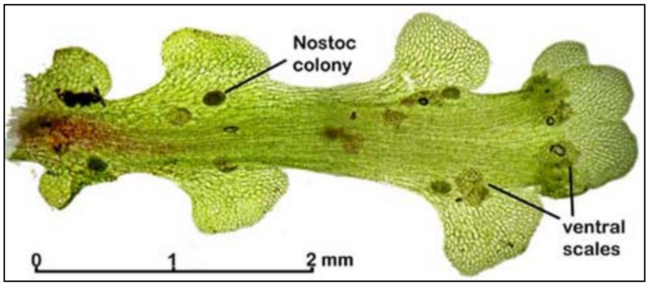

Figure 72. ***Blasia pusilla*** labelled to show location of ***Nostoc***. Photo by David H. Wagner, with permission.

Figure 73. ***Blasia pusilla*** showing ***Nostoc*** as darker patches on the lobes. Photo by Bernd Haynold, through Creative Commons.

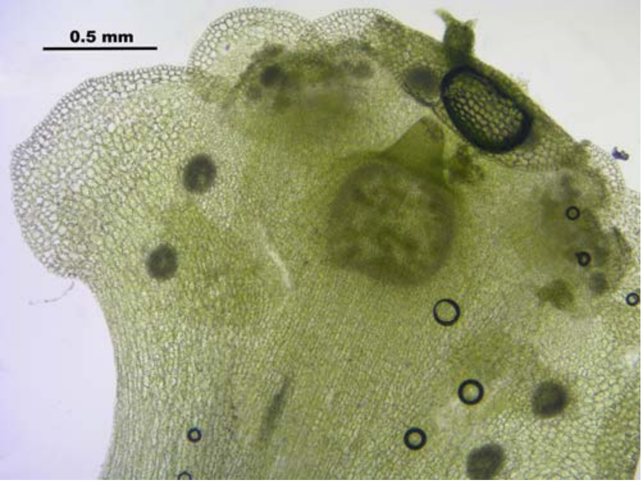

Figure 74. ***Blasia pusilla*** with ***Nostoc*** colonies. Photo by Hermann Schachner, through Creative Commons.

Duckett and Renzaglia (1993) found that viability differed between the non-symbiotic receptacular gemmae (Figure 78) and the symbiotic stellate gemmae (Figure 79). The stellate gemmae contain starch, but are short-lived. The receptacular gemmae, on the other hand, contain proteins and lipids and remain viable for a long time. The stellate gemmae, with their symbionts and starch, are able to secure their initial development and produce plants with symbiotic nitrogen fixation in a short time. The receptacular gemmae, by surviving longer, had more opportunity to obtain a ***Nostoc*** partner from the soil (Figure 80-Figure 82).

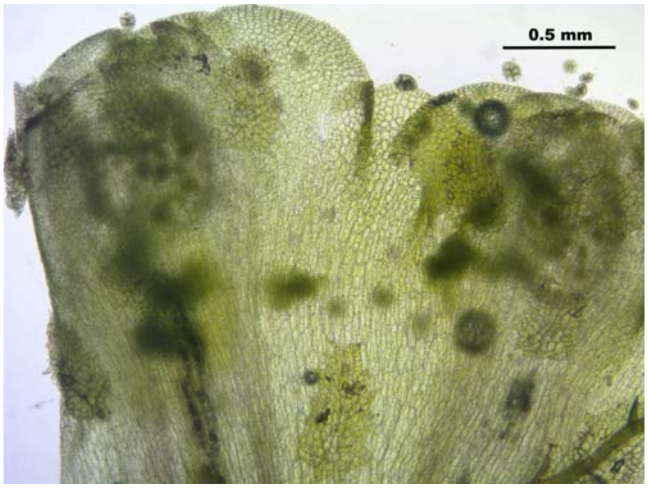

Figure 75. ***Blasia pusilla*** with ***Nostoc*** colonies and gemmae (globose especially at margins of thallus). Photo by Hermann Schachner, through Creative Commons.

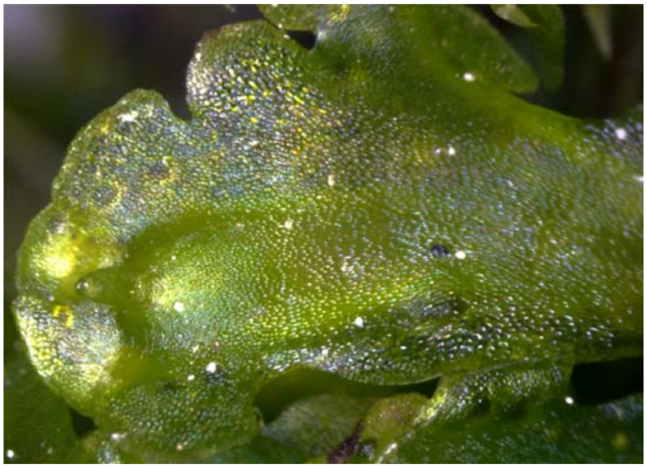

Figure 76. ***Blasia pusilla*** showing ***Nostoc*** in dark patches. Photo by Jouko Rikkinen, through Creative Commons.

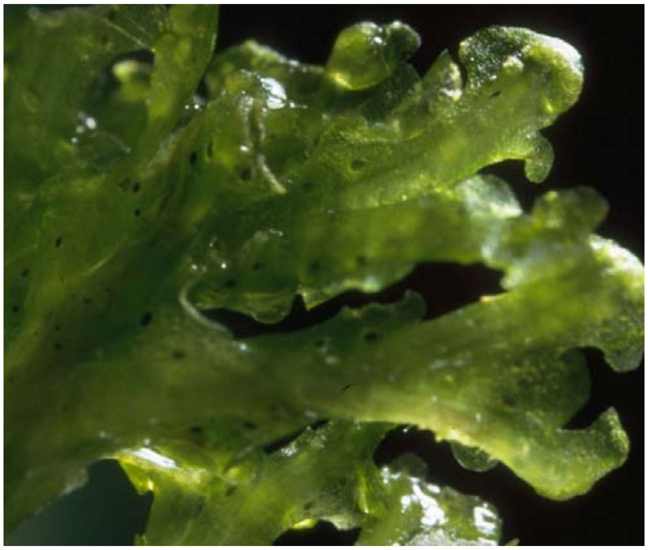

Figure 77. ***Blasia pusilla*** showing ***Nostoc*** colonies. Photo by Jan-Peter Frahm, with permission.

Figure 78. ***Blasia pusilla*** with flasks of gemmae. Photo by Hugues Tinguy, through Creative Commons.

Figure 79. ***Blasia pusilla*** with stellate gemmae. Photo by Jouko Rikkinen, through Creative Commons.

Figure 80. ***Nostoc commune*** on soil, a potential source for symbionts for ***Blasia pusilla***. Photo by Yamamaya, through Creative Commons.

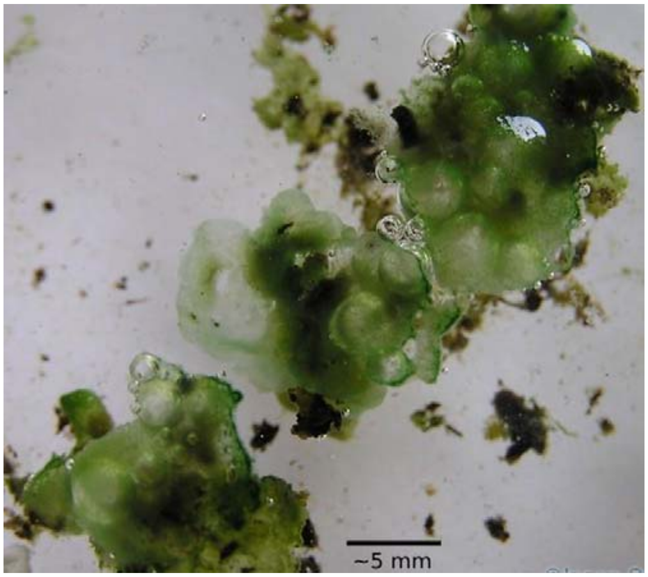

Figure 81. ***Nostoc*** free-living colonies. Photo by Jason Oyadomari, with permission.

Figure 82. Free-living ***Nostoc*** colonies. Photo by Jason Oyadomari, with permission.

Meeks (1990) described the colonization and establishment of ***Nostoc*** in ***Blasia pusilla*** (Figure 73-Figure 77), including both structural and metabolic changes that result from the symbiosis. There has been some controversy over the location of the ***Nostoc*** in pits (Davison 2009), attributing them to pits on the thallus. However, Davison argues that pits and open holes do not exist in ***Blasia pusilla***. The ***Nostoc*** actually occurs in the cavities formed by the slime papillae (Adams 2002; Solheim *et al.* 2004). These occur in auricles – as almost spherical structures.

Kimura and Nakano (1990) found that the ***Nostoc*** is only invasive when it is in its motile, hormogonial (describing mobile filaments) stage (Figure 83, Figure 84). Knight and Adams (1996; Adams 2002) found that when ***Blasia pusilla*** is deprived of N, it releases extracellular signals that trigger hormogonia to form; at the same time, these signals serve as a highly effective attractant to facilitate the hormogonia in finding the thallus. The ability of these shorter hormogonia to glide makes it possible for them to move to the sites where they can become symbionts (Adams 2002). This invasion induces morphological changes in the cavities it invades.

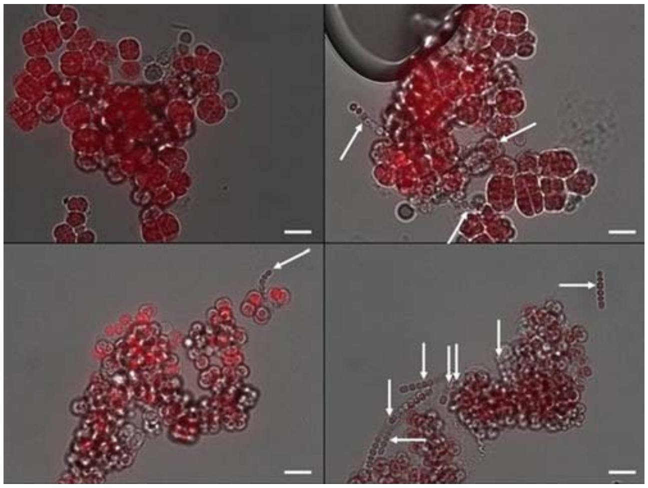

Figure 83. ***Chlorogloeopsis fritschii*** forming hormogonia, the mobile stage that is able to invade the thallus of liverworts such as ***Blasia pusilla***. Photo by Benjamin L. Springstein, Fabian Nies, and Tal Dag, through Creative Commons.

Nilsson *et al*. (2006) found that the extracts of both symbiotic plants such as ***Blasia pusilla*** (Figure 73-Figure 77) and non-symbiotic plants such as rice all elicited positive **chemotaxis** (directional movement in response to chemical) by the two ***Nostoc*** strains tested. The chemotaxis is reduced by increased temperature and darkness but stimulated by phosphorus and iron starvation or elevated salt concentrations. Sugars also stimulated chemotaxis, but flavonoids and amino acids had no effect. Díaz *et al*. (2011) suggested that **lectins** could be expected to promote the symbiont cellular dispersal. They demonstrated that it causes ***Nostoc*** to differentiate mobile cells that are attracted to the lectins. However, the ***Nostoc*** does not form filaments (Figure 82) before its chemotropic movement in response to lectins.

Once infection of the ***Blasia pusilla*** (Figure 73-Figure 77) thallus has occurred, the developmental pathway of the symbiont must switch from hormogonia development (Figure 83) to heterocyst (Figure 84) differentiation (Adams 2002). That means it must have a mechanism for repressing further hormogonia formation, which is genetically programmed. Once the symbiotic association has formed, the ***Nostoc*** produces **heterocysts (**Figure 84-Figure 85) (Herrero *et al*. 2004), which are the sites of the extensive nitrogen fixation. Gorelova *et al.* (1996) provided protocol that made it possible to study this symbiont development.

Figure 84. ***Nostoc*** with heterocysts (arrow). Photo by Jason Oyadomari, with permission.

Rodgers and Stewart (1977) reported that in ***Blasia pusilla*** (Figure 73-Figure 77) the 2-week-old colonies had a 20% heterocyst (Figure 84) frequency, whereas by six weeks this had increased to 48%. Production of heterocysts in symbiotic conditions can be 10-20 times that found free-living ***Nostoc*** (Adams 2002). Rodgers and Stewart (1977) found a heterocyst frequency of the free-living isolates to be 3-6%, but in their study this increased to 30% or more when they were symbiotic in ***Blasia***. ***Nostoc*** colonies develop in the slime cavities of the ***Blasia*** thallus within 72 hours. These colonies stretch the cells of the cavities. Filamentous protrusions develop on the liverwort cavity wall and penetrate the ***Nostoc*** colonies, forming a labyrinth of wall ingrowths in the ***Nostoc*** cells (Duckett *et al*. 1977), thus increasing the surface area of contact with the host by about 30% within 4 weeks (Rodgers & Stewart 1977), presumably facilitating transfer of the nitrogen compounds.

In ***Blasia pusilla*** (Figure 73-Figure 77), these specialized cells are formed as a response to limiting nitrogen conditions in the cell and are initiated by specialized genes (Herrero *et al*. 2004). In the ***Nostoc*** the **heterocysts**, as their name implies, are different from the other cells. They are able to reduce atmospheric nitrogen by providing an oxygen-free environment in which the nitrogenase enzyme can function (Wolk *et al*. 1994). This anoxic condition is achieved by both increased respiration and lack of photosynthesis in the heterocyst. The heterocyst loses the ability to fix CO_2, but products needing additional carbon can be supplied by the bryophyte (Duckett *et al*. 1977; Herrero *et al*. 2004). The heterocysts are unable to divide, but they perform an important function for the ***Nostoc***, and in turn, for the liverwort partner. They reduce N_2, readily available from the atmosphere, to ammonium (Figure 85) (Adams 2002) that is then incorporated into amino acids, particularly glutamine (Stewart & Rodgers 1978; Wolk *et al*. 1994). The symbiotic colonies of ***Nostoc*** in ***Blasia pusilla*** (Figure 73-Figure 77) are more effective at converting the nitrogen to a usable form (ammonia) than those that are free-living. This is rapidly transferred to the liverwort thallus, increasing the liverwort yield by 300-500% in 30 days.

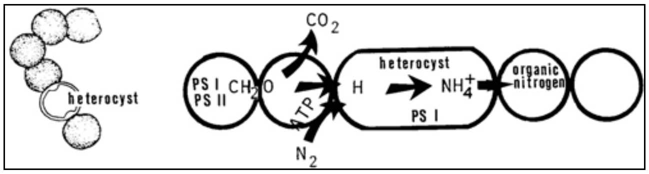

Figure 85. Heterocyst of ***Anabaena***, a member of the **Cyanobacteria,** showing the nitrogen fixation pathway. Drawing by Janice Glime.

Although ammonia (NH_3) is the immediate product of the nitrogen reduction, it is toxic and is quickly converted to harmless amino acids (Figure 85). It is unclear if the transfer to the photosynthetic cells of the ***Nostoc*** filaments (and probably the liverwort) is by ammonia or by glutamine (derived from the glutamate) and possibly other amino acids – or both (Stewart & Rodgers 1978; Wolk *et al*. 1994). It appears that the ***Nostoc*** is dependent on the ***Blasia*** for its fixed carbon. Stewart and Rodgers (1977) found that excised ***Nostoc*** colonies had only a negligible ability to fix CO_2, but that in the cavities of ***Blasia pusilla***

(Figure 73-Figure 77) they receive fixed carbon from the thallus of the liverwort. Further details of the biochemical pathway are provided by Chapman *et al.* (2008) and Duggan *et al.* (2013).

The mechanism of transfer of reduced nitrogen from the heterocyst is a source-sink relationship (Wolk *et al.* 1994; Meeks 2009). The carbohydrate serves as the reductant and the abundant reduced nitrogen (NH_4) is transferred to other cells due to a concentration gradient. Once the reduced nitrogen is incorporated into biological compounds, those compounds and the cells that contain them become sinks.

Rodgers (1978) described the conditions favorable to the ***Nostoc*** symbiosis in ***Blasia pusilla*** (Figure 73-Figure 77). As an endophyte, ***Nostoc*** has greater nitrogenase activity at lower *p*H levels than those suitable for the free-living form. On the other hand, the symbiont requires a higher light level than the free living form. Below 10ºC, the ***Nostoc*** has low activity in either growth condition, but the free-living form has high activity above 12ºC, whereas the endophyte requires 17ºC for such levels of activity. The free-living form is also more tolerant of desiccation, although both have protective mucilage.

Rodgers and Stewart (1977) identified ***Nostoc sphaericum*** (Figure 86) in the populations of ***Blasia pusilla*** (Figure 73-Figure 77) they examined. Although ***Nostoc punctiforme*** (Figure 69) is able to inhabit both ***Blasia pusilla*** and ***Anthoceros*** (Figure 87-Figure 89) species in the lab, different strains occupy ***Blasia*** and ***Anthoceros*** in the field (Leizerovich *et al.* 1990). In the lab, a strain of ***Nostoc punctiforme*** is able to colonize and form a symbiont with ***Blasia pusilla***, but the lab strain of this ***Nostoc*** species has not been identified from any of these liverworts in the field (Rikkinen & Virtanen 2008). Further studies indicate that there is a "moderate level of spatial and temporal continuity" by some of the ***Nostoc*** strains in the ***Blasia pusilla-Nostoc*** symbioses (Costa *et al.* 2001). Jackson *et al.* (2012) demonstrated that three arabinogalactan proteins (AGP) were common to widely diverse cyanobacterial partnerships.

Figure 86. ***Nostoc sphaericum***, "the caviar of the Andes" and also a symbiont of ***Blasia pusilla***. Antonio W. Salas, through Creative Commons.

Figure 87. ***Anthoceros***, NZ, showing bluish green color that suggests the presence of **Cyanobacteria**. Photo by Clive Shirley, Hidden Forest <hiddenforest.co.nz>, with permission.

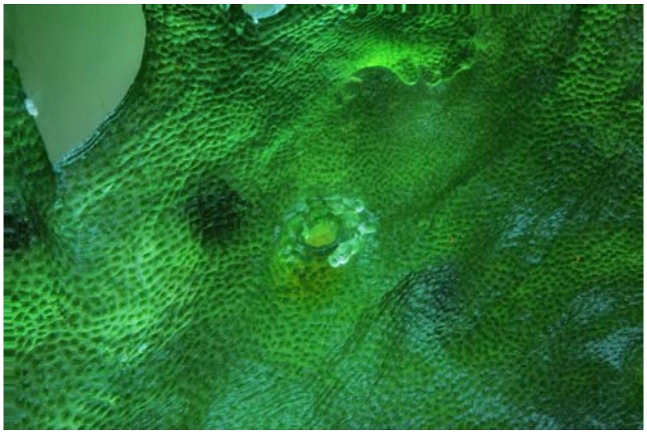

Figure 88. ***Anthoceros punctatus*** pore and ***Nostoc*** colony. Photo by Des Callaghan, with permission.

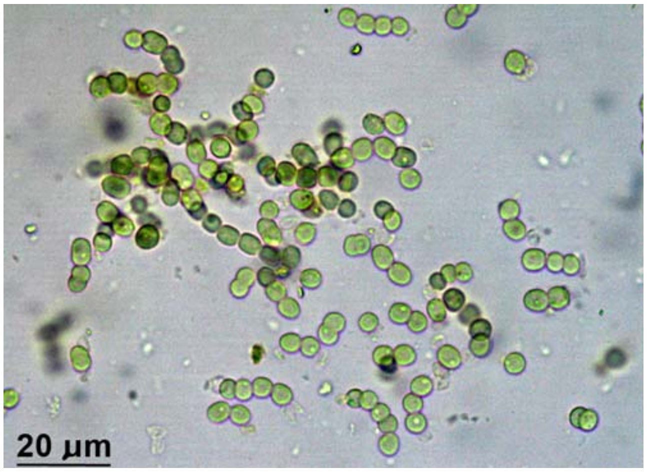

Figure 89. ***Nostoc*** from ***Anthoceros agrestis***, showing the breakup of hormogonia and scarcity of heterocysts during early colonization. Photo by Ralf Wagner <www.dr-ralf-wagner.de>.

In axenic cultures, all but one of the free-living ***Calothrix*** spp. (Figure 90), ***Chlorogloeopsis*** spp. (Figure 83), and ***Nostoc*** spp. (Figure 69, Figure 84, Figure 86) (all **Cyanobacteria**) were able to join in a symbiotic relationship with both ***Blasia pusilla*** (Figure 73-Figure 77) and ***Phaeoceros*** sp. (Figure 91) (West & Adams 1997). By contrast, the strains of **Cyanobacteria** found as symbionts in the field where not found free-living in those locations. Furthermore, none of the symbiotic strains were found at more than one sample site.

Figure 90. ***Calothrix parietina***, a **Cyanobacterium** in a genus that can inhabit ***Blasia pusilla***. Photo from Algae Base, through Creative Commons.

Figure 91. ***Phaeoceros laevis*** with a bluish-green color suggesting the presence of its ***Nostoc*** partner. Photo by Oliver S., through Creative Commons.

Liaimer *et al*. (2016) further elaborated on the diversity of **Cyanobacteria** strains. They claimed that ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) recruits its symbiotic ***Nostoc*** partner from the soil nitrogen-fixing strains. They found that those from an agricultural community exhibited negative allelopathic interactions, but such was not the case in an undisturbed site. The **Cyanobacteria** did not exhibit antimicrobial activity, but four of the isolates were cytotoxic to human cells. Interestingly, the symbiotic recruits commonly produced microcystin, a toxic compound, but it was not commonly produced in the free-living community. Could this be an additional herbivore deterrent for the liverwort?

The bryophyte-**Cyanobacteria** symbiosis, by providing usable nitrogen compounds, is an important contributor to the environment (Solheim *et al*. 2004).

Interactions with Fungi

As already noted, ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) is not known to have any fungal endophytes (Liepiņa 2012). On the other hand, they do have parasitic inhabitants. Redhead (1981) reported ***Blasiphalia pseudogrisella*** (**Basidiomycota**; Figure 92) from the rhizoids. Hallgrímsson (1981) found this fungus to be frequent on river banks in Iceland and concluded that it is probably always associated with ***Blasia pusilla***.

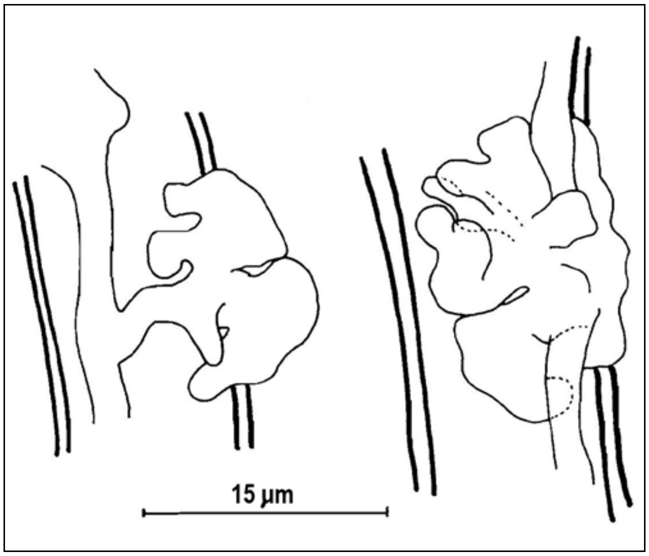

Figure 92. Appressoria of ***Blasiphalia pseudogrisella*** on rhizoids of ***Blasia pusilla***. Drawing modified from Scott Redhead 1981.

Persson and Pleijel (2008) reported the rare species ***Bryoscyphus marchantiae*** (discomycete; Figure 93) as a parasite on ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) in dune slacks (Figure 26).

Figure 93. ***Bryoscyphus marchantiae*** on liverwort; this species is able to parasitize ***Blasia pusilla***. Photo by Iain Munro, through Creative Commons.

The mushroom ***Blasiphalia pseudogrisella*** (Figure 94) in the Arctic and alpine Northern Hemisphere is known only from ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) (Antonin & Noordeloos 2001). Hyphae appearing to be identical to those of this mushroom formed clasping pads (**appresoria**) on the rhizoids of ***Blasia pusilla***.

Furthermore, gemmae of the liverwort had a sparse covering of fungal spores matching those of the mushroom. Some of these seemed to have infected the gemmae. In other cases, dispersed gemmae had short rhizoids covered with fungal appressoria. Antonin and Noordeloos suggested that the gemmae could be vectors for dispersing the fungus.

Figure 94. **Blasiphalia pseudogrisella** growing with bryophytes. Photo by Rénee Lebeuf, through public domain.

Biochemistry

Blasia pusilla (Figure 1Figure 2-Figure 6) is one of those liverworts that apparently lacks oil bodies (Figure 95-Figure 96) (Schuster 1992; Millar *et al*. 2007; He *et al*. 2013). On the other hand, Rohret (1916) reported numerous oil bodies from the gemmae. Whether they are in the oil bodies or not, a number of compounds have been recognized from this species, but their antibiotic activity is limited (Millar *et al*. 2007).

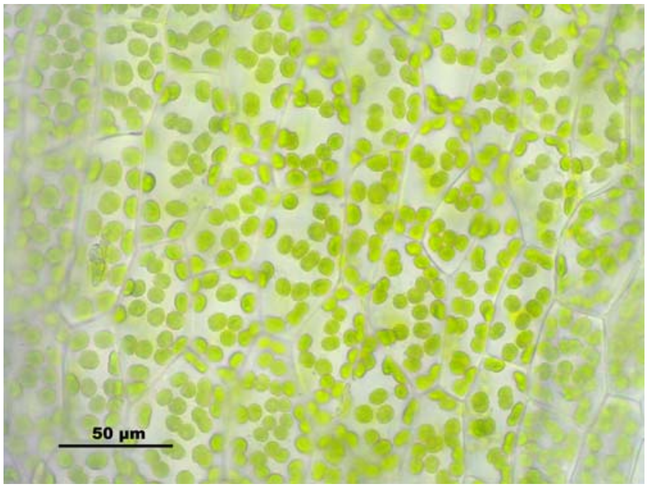

Figure 95. ***Blasia pusilla*** cells with chloroplasts, but lacking oil bodies. Photo by Hermann Schachner, through Creative Commons.

Hashimoto *et al.* (1993) reported riccardin C, riccardin F, and orsellinic acid methyl ester from ***Blasia pusilla*** (Figure 1-Figure 6). Viennois *et al*. (2011) found that riccardins from this species are natural antagonist compounds.

Four phenolic novel cyclic bisbibenzyl dimers, six bibenzyl derivatives, apigenin 7-O-β-d-glucoside, shikimic acid, and five orsellinic acid derivatives were isolated from ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) (Hashimoto *et al*. 1994; Yoshida *et al*. 1996). Asakawa (1994) reported that the cyclic bis-bibenzyl dimers of this species exhibit inhibitory activity against plant growth. Could this help maintain a habitat with limited competition for this species that seems to thrive best in disturbed habitats and as a pioneer?

Axenic ***Blasia pusilla*** (Figure 1Figure 2-Figure 6) extract is able to produce bioactive compounds. These retard fungal sporulation, but thus far there is no indication that they are able to inhibit bacterial growth (Millar *et al*. 2007). Furthermore, Asakawa (2008) reported moderate cytotoxicity against KB cells and only weak activity against HIV-RT. Millar *et al.* (2007) suggest that antimicrobial activity is greater in taxa with oil bodies; this would limit the medicinal value of ***Blasia pusilla***.

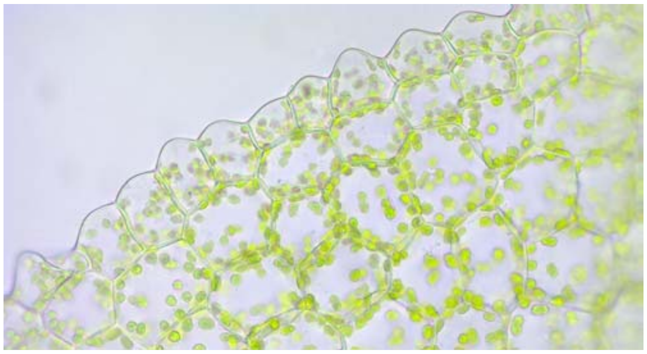

Figure 96. ***Blasia pusilla*** marginal cells with chloroplasts and no oil bodies. Photo by Hermann Schachner, through Creative Commons..

Summary

Blasia pusilla is the only species representing the **Blasiales** on wet substrates. It is rarely submerged, but can live in mires, streambanks, spray of waterfalls, fens, bogs, and similar wet habitats. It does well on disturbed substrata and is often an early pioneer. In these habitats, it benefits from persistent ovoid gemmae that can remain in the diaspore bank. Its ***Nostoc*** partner helps it to meet its fixed nitrogen needs. It is also able to spread through use of its stellate gemmae that get a head start with their own ***Nostoc*** colonies. The ovoid gemmae get their ***Nostoc*** partner from the soil.

Blasia pusilla is dormant through dieback in winter, the attached sporophyte is dormant in winter, and gemmae remain dormant while on the thallus. Both gemma germination and production of sexual structures are dependent on signals from the environment. Water triggers spore germination, but day length and temperature seem unimportant. Day length may affect initiation of sex organs and dormancy of sporophytes, but higher temperatures seem to affect sporophyte maturation.

Blasia pusilla has no symbiotic fungal partners, but they do harbor surface fungi and parasitic fungi. The absence of antibiotic effects against bacteria may be the result of lacking oil bodies.

Acknowledgments

Lars Söderström helped me find the current acceptable names for a number of older taxa. I have also benefitted from discussions with him on conventions in naming of some structures. David Wagner provided me with important images of reproductive structures.

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