CHAPTER 1-18
AQUATIC AND WET MARCHANTIOPHYTA, ORDER LUNULARIALES

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Figure 1. ***Lunularia cruciata*** with nearly mature gemmae cups, clearly showing the crescent shape of the cup. Photo by James Dickson, with permission.

MARCHANTIOPSIDA

Marchantiidae – Lunulariales

Lunulariaceae

Lunularia cruciata (Figure 1-Figure 13)

(syn. = *Lunularia thaxteri*)

Although ***Lunularia cruciata*** (Figure 1-Figure 13) and *L. thaxteri* can be morphologically distinct, these differences are due to environmental expressions (Bischler & Boisselier 1998). Their genetic markers indicate that they are the same species. Itouga *et al*. (2000) further described the genetic structure.

Distribution

Lunularia cruciata (Figure 1-Figure 13) is a common species in western Europe, being native around the Mediterranean (NBNatlas 2021). But it has spread through a wide range due to its propensity for growing in gardens and flower pots. It is easily spread by gemmae through horticultural watering regimes. Hence, one can also find it in California, USA (Whittemore 1982), in greenhouses in Australia, and in New Zealand (NBNatlas 2021). Not surprisingly, it is most common in urban areas and seems to be spreading northeastward in Europe with climate warming (Essl & Lambdon 2009; Skudnik *et al*. 2013a). Nevertheless, it is considered to be a rare liverwort away from the Mediterranean area. Skudnik *et al*. (2013b) reported that it had been considered rare or under threat in Slovenia, but their discovery of new locations suggested that instead it was a matter of under-recording.

Figure 2. ***Lunularia cruciata*** on soil. Photo from <www.aphotofauna.com>, with permission.

Figure 3. ***Lunularia cruciata*** habitat in Bhutan. Photo by David Long, with permission.

Figure 4. ***Lunularia cruciata*** with young gemmae cups. Photo by George Shepherd, through Creative Commons.

Figure 5. ***Lunularia cruciata*** showing numerous gemmae cups with gemmae beginning to disperse. Photo by Michael Lüth, with permission.

Figure 6. ***Lunularia cruciata***, almost entirely lacking gemmae cups. Photo from <www.aphotofauna.com>, with permission.

Figure 7. ***Lunularia cruciata*** in Europe. Photo by Michael Lüth, with permission.

Figure 8. ***Lunularia cruciata*** habitus. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 9. ***Lunularia cruciata*** in rock crevice, showing large pores in the thallus. Photo by Alexis Orion, through Creative Commons.

Figure 10. ***Lunularia cruciata*** with gemmae beginning to disperse. Photo by Hermann Schachner, through Creative Commons.

Figure 11. ***Lunularia cruciata*** with tiny gemmae cup sitting piggyback on another gemmae cup. Photo by Luis Nunes Alberto, through Creative Commons.

Figure 12. ***Lunularia cruciata*** with gemmae. Photo by Michael Lüth, with permission.

Figure 13. ***Lunularia cruciata*** with gemmae cups and lots of still-attached gemmae. Photo by Fotis Samaritakis, through Creative Commons.

This same horticultural transportation most likely accounts for the presence of ***Lunularia cruciata*** (Figure 1-

Figure 13) in Japan (Noguchi 1977; Taoda 1980). Taoda used it as a species indicating the degree of urbanization. It has also appeared in Kasmir of the Himalayas (Ismail *et al*. 2018). Other localities include Botswana and it is common in most of the southern African countries (Steel *et al*. 2004), Slovakia (Janovicova & Somogyi 1996), Germany (Frahm 1973), where it was fertile (Kirschner *et al*. 2010), Benslimane Region of Morocco where it is one of the two most common liverwort species (Elharech *et al*. 2018; Fadel *et al*. 2020), Nepal (Karki & Ghimire 2019), northeastern USA [Uva *et al*. (1997) considered it a weed], New York (Trigoboff 2000), British Columbia, Canada (Schofield 1997), and Central Chile (Gradstein & Cuvertino 2015).

Aquatic and Wet Habitats

Lunularia cruciata (Figure 1-Figure 13) has a relatively wide range of habitats (Yeates (1908). Ferreira *et al*. 2008) list it as a river species. It occurs midstream in the River Swale, Yorkshire, UK (Holmes & Whitton 1977a) and is mostly in the mid to lower River Tyne, UK (Holmes & Whitton 1981). It is among the commonest species in English and Welsh rivers (Scarlett & O'Hare 2006) In Thuringia, Germany, it is known in the ***Platyhypnidium*** (Figure 14)***-Fontinalis antipyretica*** (Figure 15) association, (Marstaller 1987). Özenoğlu Kiremit *et al*. (2007) found it on rocks and tree roots in a stream bed in Turkey. Konstantinova *et al*. (2009) found it on the bank of the Khosta River in the Caucasus of Russia. On Madeira Island, it occurs in mountain streams (Luis *et al*. 2015).

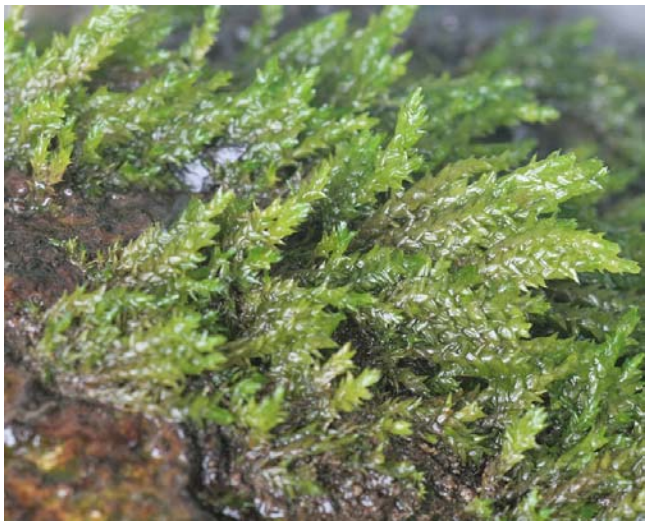

Figure 14. ***Platyhypnidium riparioides***, a species that is often an indicator of suitable habitat for ***Lunularia cruciata***. Photo by Hermann Schachner, through Creative Commons.

Figure 15. ***Fontinalis antipyretica***, an aquatic moss species that is often an indicator of suitable habitat for ***Lunularia cruciata***. Photo from Botany Website, UBC, with permission.

Yeates (1908) considers ***Lunularia cruciata*** (Figure 1-Figure 13) to be less hygrophilous than ***Marchantia polymorpha*** (Figure 16). The former is a suitable indicator of rich nutrients or eutrophic conditions in aquatic habitats (Werner 2001).

Figure 16. ***Marchantia polymorpha*** by water, a species that is more hygrophilous than ***Lunularia cruciata***. Photo by Hugues Tinguy, with permission.

But it is more likely that ***Lunularia cruciata*** (Figure 1-Figure 13) occurs near water, rather than in it, often wet or periodically inundated. It occurs on wet ground at the edge of waterfalls (Figure 17) in Morocco, as well as what Fadel *et al*. (2020) called small water surfaces.

Figure 17. Waterfall in Ireland, showing the effects of moisture from the falls that makes a suitable habitat for ***Lunularia cruciata***. Photo by Phil Armitage, through Wikimedia Commons.

Lunularia cruciata (Figure 1-Figure 13) occurs in damp places, on banks with frequent submergence and slow water (Figure 18-Figure 27) (Watson 1919), including the river bank of the River Tees, UK (Holmes & Whitton 1977b). In Germany it occurs increasingly in such natural habitats as brook banks (Borsdorf 1987; Bergl & Meinunger 1988). In Morocco, Saadi *et al*. (2020) found it both underwater and on soil and rocks near running water.

Figure 18. ***Lunularia cruciata*** on stream bank. Photo by Tom Kaye, through Creative Commons.

Figure 19. ***Lunularia cruciata*** forming shelves on rock by water. Photo by David Claro, through Creative Commons.

Figure 20. ***Lunularia cruciata*** on rock in stream. Photo by Andrew Melton, through Creative Commons.

Figure 21. ***Lunularia cruciata*** on stream bank. Photo by Gerrit Ohm, through Creative Commons.

Figure 22. ***Lunularia cruciata*** at base of log. Photo by Geerah, through Creative Commons.

Figure 23. ***Lunularia cruciata*** by water. Photo by S. Bushes, through Creative Commons.

Figure 24. ***Lunularia cruciata*** by water. Photo by Susan Marley, through Creative Commons.

Figure 25. ***Lunularia cruciata*** on rock by water. Photo by Thomas Koffel, through Creative Commons.

Figure 26. ***Lunularia cruciata*** by water. Photo by Ulysses M., through Creative Commons.

Figure 27. ***Lunularia cruciata*** on tree root near water. Photo by Maddi Song, through Creative Commons.

Figure 28. ***Lunularia cruciata*** with other bryophytes by water. Photo by Susan Marley, through Creative Commons.

Sometimes damp walls and slopes (Figure 29-Figure 31) provide suitable habitat. Armitage (1918) found ***Lunularia cruciata*** (Figure 1-Figure 13) on damp walls and bare earth banks on Madeira. Konstantinova *et al*. (2009) reported it at the base of limestone cliffs in the valley of the Khosta River, Caucasus, Russia. Garcia-Rowe and Saiz-Jimenez (1991) found it on vertical wet surfaces on Spanish cathedrals, where it could make it easier for tracheophytes to invade and damage the buildings with their roots.

Figure 29. ***Lunularia cruciata*** zone on slope. Photo by Stephen Thorpe, through Creative Commons.

Figure 30. ***Lunularia cruciata*** on clay bank. Photo by Susan Marley, through Creative Commons.

Figure 31. ***Lunularia cruciata*** habitat where it forms a zone on the substrate, probably related to water levels. Photo by Kate McCombs, through Creative Commons.

Springs are less common habitats. The only record I found was ***Lunularia cruciata*** (Figure 1-Figure 13) growing around a spring in Halstead, England (Lorenz 1910).

Wet soil in other locations is a more common habitat. Fadel *et al*. (2020) reported ***Lunularia cruciata*** (Figure 1-Figure 13) from rocky walls and wet soil (Figure 32-Figure 34) in Morocco. It was able to occupy limestone, schistose, and quartzite substrata. It was among the four most common species in wetlands. Salisbury (1962) considers it the commonest species on wet ground of gardens in the UK.

Figure 32. ***Lunularia cruciata*** with antheridial discs (dark brown) and gemmae cups, on wet soil. Photo by Michael Keogh, through Creative Commons.

Figure 33. ***Lunularia cruciata*** on clay. Photo by Mattia Manchetti, through Creative Commons.

Figure 34. ***Lunularia cruciata***, on soil, Waikite Pools Recreation Area, NZ, 16 July 1988. Photo by Janice Glime.

Karki and Ghimire (2019) reported ***Lunularia cruciata*** (Figure 1-Figure 13) as saxicolous (Figure 35-Figure 37) in Central Nepal, and locally rare. In some locations one can find it tucked into wet crevices (Figure 38-Figure 40) or on shale that is soaked with water (Figure 41) in the winter (Fadel *et al*. 2020).

Figure 35. ***Lunularia cruciata*** on rock. Photo by <www.aphotofauna.com>, with permission.

Figure 36. ***Lunularia cruciata*** on thin soil on rock. Photo by Zoltán Nagy, through Creative Commons.

Figure 37. ***Lunularia cruciata*** on thin soil on rock. Photo by Zoltán Nagy, through Creative Commons.

Figure 38. ***Lunularia cruciata*** with gemmae cups (**left**) + ***Marchantia polymorpha*** (**right**) among rocks. Photo by Michael Lüth in Europe, with permission.

Figure 39. ***Lunularia cruciata*** in rock crevice. Photo by Attila Oláh, through Creative Commons.

Figure 40. ***Lunularia cruciata*** in rock crevice. Photo by Alexis Orion, through Creative Commons.

Figure 41. ***Lunularia cruciata*** on wet rock. Photo by Loverworts, through Creative Commons.

Based on its other habitats, it is not surprising that ***Lunularia cruciata*** (Figure 1-Figure 13) is able to occupy the rich alluvium associated with temporary ponds (Fadel *et al*. 2020).

This opportunistic liverwort also lives by paths and roadsides. Skudnik *et al*. (2013b) found it on damp soil by paths and roadsides in Slovenia. Likewise, Yeates (1908) noted its presence on the banks of roadside water channels, but also on boulders in deep-seated valley beds, at the bottom of old walls and outhouses, and even on shaded banks where it was often hidden by brambles. Özenoğlu Kiremit *et al*. (2007) found it on soil banks along the road in Antalya, Turkey.

It appears that the most common habitat for the introduced populations is related to horticulture. ***Lunularia cruciata*** (Figure 1-Figure 13) is common in greenhouses (Figure 42) and gardens, where sprinkling systems and garden hose water facilitate dispersal of gemmae from the gemmae cups. Perold (1993) reported the species from old gardens, nurseries, and forested areas in southern Africa, where it is most likely introduced. Bergl and Meinunger (1988) reported that it was introduced to Central Europe through greenhouse cultures used to supply market gardens, churchyards, and parks (Frahm 1973). Schofield (1997) noted that in British Columbia, Canada, it occurs almost exclusively in gardens. Similarly, in Chile, it occurs in urban areas (Gradstein & Cuvertino 2015). A picture by Merav Vonshak suggests that it might occur in spruce forests (Figure 43).

Salisbury (1962) lists ***Lunularia cruciata*** (Figure 1-Figure 13) as a troublesome weed in gardens of the UK. Its frequency in such habitats is 40%! It does well in sunken paths and greenhouses as well (Augier 1966; Coudreuse *et al*. 2005).

Figure 42. ***Lunularia cruciata*** on soil in a flower pot in greenhouse in Ripley, Michigan, USA, with mosses. Photo by Janice Glime.

Figure 43. ***Lunularia cruciata*** amid spruce needles. Photo by Merav Vonshak, through Creative Commons.

Armitage (1918) found ***Lunularia cruciata*** (Figure 1-Figure 13) on open ground and bare earth banks as well as shady mountain ground, on Madeira. Gradstein (1972) reported it from the Maltese Islands on the thin soil layer of a sheltered floor enclosure of a temple. Steel *et al*. (2004) considered it to be one of the world's commonest liverworts and a common inhabitant of man-made and disturbed environments in Botswana. Lo Giudice *et al*. (1997) found it to be common in urban areas and relatively indifferent to substrate hardness. It can also occur on soil under shrubs and small trees (Özenoğlu Kiremit *et al*. 2007; Saadi *et al*. 2020).

Physiology

Lunularia cruciata (Figure 1-Figure 13) was the subject of a number of early physiological studies. Crocker (1912) evaluated its tropisms and concluded that, contrary to the conclusions of Weinert (1909), the rhizoids of growing gemmae are positively gravitropic, as are those of the thallus. Bischoff (1912) supported this argument by concluding that the absence of motile starch in the rhizoids does not negate the statolith theory and suggests that other bodies in the cell could accomplish this role of sensing the direction of gravity.

Temperature effects on ***Lunularia cruciata*** (Figure 1-Figure 13) could benefit from more study. It appears that not only is ***Lunularia cruciata*** spreading to more northern habitats, perhaps as a result of global warming, but it seems to be attaining more frost tolerance. Bergl and Meinunger (1988) contend that its expansion to the north is due to the establishment of frost-resistant types. In Japan, plants in cultivated locations are likewise frost-resistant (Fletcher 1982). Warming temperatures also can play a role in gemma germination (Schwabe 1990).

Lunularia cruciata has both rhizoids (Figure 44) and scales that contribute to its external capillary movement of water (McConaha 1941). This species has two types of rhizoids (Figure 45). The smooth rhizoids are partially enclosed by the ventral scales and may contact the substrate. The tuberculate rhizoids originate beneath the scales and create numerous connected capillary strands that parallel the thallus, creating a "rapid" distribution system for water uptake throughout the thallus.

Figure 44. ***Lunularia cruciata*** ventral side showing rhizoids clinging to soil. Photo by Pat Enright, through Creative Commons.

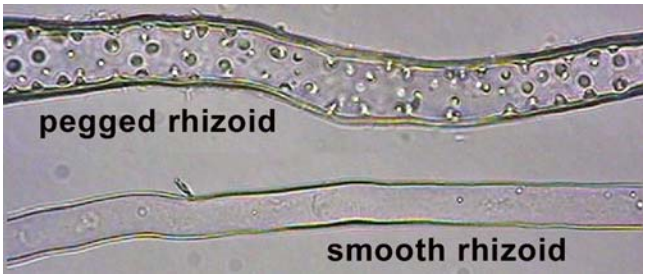

Figure 45. Pegged and smooth rhizoids of ***Conocephalum conicum***; ***Lunularia cruciata*** has the same two types. Photo by Paul Davison, with permission.

By contrast, the upper surface of ***Lunularia cruciata*** (Figure 1-Figure 13) is designed to keep water out, at least through the pores (Figure 46-Figure 47) (Schönherr & Ziegler 1975). The air pores are surrounded by hydrophobic ledges (Figure 48) that constrict the entrance. This permits only liquids with a contact angle of zero^{o} with the hydrophobic ledge to enter.

Figure 46. ***Lunularia cruciata*** showing pores. Photo by Steven Bodzin, through Creative Commons.

Figure 47. ***Lunularia cruciata*** showing pores. Photo by Mike, through Creative Commons.

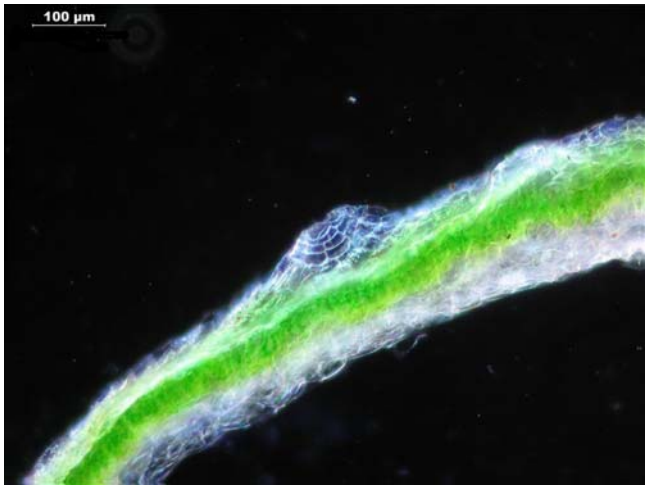

Figure 48. ***Lunularia cruciata*** thallus and pore longitudinal section. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Giordano *et al*. (1985, 1989) reported the presence of a hyaline parenchyma in the thallus of ***Lunularia cruciata*** (Figure 1-Figure 13). These have wall thickenings with large primary pit fields between them and numerous plasmodesmata-derived pores. These differ from the parenchymatous cells of the midrib, where the plasmodesmata-derived pores occur in small, sparse groups. The researchers suggest that the reticulate pattern has a role in the water-holding capacity and lateral distribution of water, using both **symplastic** (inside cell membrane) and **apoplastic** (space outside plasma membrane) pathways.

Deltoro *et al*. (1998) listed ***Lunularia cruciata*** (Figure 1-Figure 13, Figure 49) as a desiccation-intolerant bryophyte. At low water content they showed low efficiency of photosynthetic conversion, closed down their photosystem II reaction centers, and exhibited weak nonphotochemical quenching. They were unable to restore photochemical activity after desiccation. The large leakage of potassium suggests membrane damage.

Figure 49. ***Lunularia cruciata*** with gemmae, growing in a flower pot in a greenhouse where it gets watered regularly. Photo by Janice Glime.

Nevertheless, ***Lunularia cruciata*** (Figure 1-Figure 13) responds to long days by increasing its resistance to drought (Valio *et al*. 1969; Schwabe 1990, 2019). When moved from moist conditions to relative humidity levels of 90%, the liverwort dies (Figure 50). However, after long-day treatment, it can be dried for years and still survive. The rapidity of drying is likely to be important.

Figure 50. ***Lunularia cruciata*** dieback. It may still have some living tissue that will come back. Photo by Jon Sullivan, through Creative Commons.

Fredericq (1966) first examined the effects of photoperiod on growth in ***Lunularia cruciata*** (Figure 1-Figure 13). Lunularic acid increases with long-day treatment of ***Lunularia cruciata*** (Valio & Schwabe 1970). Its concentration changes rapidly in response to day-length change. The inhibition of growth in this species is linearly related to the concentration of the acid, with very high

concentrations being lethal. Sabovljević and Marka (2009) verified these day-length relationships in the field. Abscisic acid could not be detected in the species (Valio & Schwabe 1970), but lunularic acid appears to have the same functions (Yoshikawa *et al*. 2002).

Wilson and Schwabe (1964) found that red light induces dormancy and far-red reverses it. This suggests that phytochrome is involved in the response. But this is contradicted by the effect of short exposures (15 seconds) of far-red light that alone causes significant growth inhibition. They surmised that the far-red light could elicit the formation of some of the P 730 form of phytochrome. In experiments, ***Lunularia cruciata*** (Figure 1-Figure 13) exhibited photoreversibility like that in ***Marchantia polymorpha*** (Figure 16), but with a weaker response to far-red light than that of ***M. polymorpha*** (Fredericq 1966). Huault (1980) found that phytochrome was involved in the germination of propagules in ***Lunularia cruciata***.

The optimum day length for growth in ***Lunularia cruciata*** (Figure 1-Figure 13) is 8 hours (Schwabe & Valio 1970b). Continuous light causes growth to cease, with a rapid onset of dormancy. The effects of red vs far-red light depended on the duration and frequency and intervening light quality. Furthermore, growth promoters of tracheophytes generally inhibit ***Lunularia***, or have little effect.

Liverworts use lunularic acid where other plants use ABA as a dormancy hormone and, apparently, to help prepare them for drying, as shown in ***Lunularia cruciata*** (Figure 1-Figure 13) (Schwabe 1990). Schwabe and Nachmony-Bascomb (1963) found that long days induce dormancy and short days break it in this species. All parts of the thallus are able to register day length, including the young gemmae (Figure 51) in the cup. However, temperature interacts strongly with the photoperiod, making it difficult to determine the critical day length. High temperature (24ºC) in continuous light rapidly induces dormancy – within 6 days. During this dormancy, the plants have a greater capacity to resist drought; actively growing thalli die in a reduction to 80% relative humidity.

Figure 51. ***Lunularia cruciata*** with gemmae; the thallus and gemmae both respond to day length. Photo by Damon Tighe, through Creative Commons.

Thomas and Silcox (1983) explored the effects of various biological compounds on IAA effects and proton efflux in ***Lunularia cruciata*** (Figure 1-Figure 13). They suggested that **lysis** (breakage by rupture of cell wall or membrane) of cells may be caused by conversion of starch reserves to solutes that create greater osmosis, rather than protoplast swelling.

LaRue and Narayanaswami (1955, 1957; Narayanaswami 1957) determined that IAA inhibits the germination of gemmae of ***Lunularia cruciata*** (Figure 1-Figure 13) in the lab. They also demonstrated that if the gemmae remained in the thallus cups, they did not germinate (Figure 52), but if the thallus was cut close to the cup, germination could occur. Removal of the upper half of the thallus, above the gemma cup, caused the gemmae in the cups to germinate. Mutilations elsewhere on the thallus did not cause the gemmae to germinate. Hence, it appears that the apical growing region produces the growth inhibitors. This would be an ecologically advantageous trait, permitting resources to promote growth until unfavorable conditions stopped it. Lack of further production of the inhibitor would then permit the gemmae to germinate and provide a means of surviving such conditions as drying out.

Figure 52. ***Lunularia cruciata*** with dormant gemmae resting on thallus. Photo by Martin Hutten, with permission.

Schwabe and Valio (1970a) later demonstrated that the gemmae themselves exhibit self-inhibition through a substance produced in the growing tip. This inhibitor has greater production in short days compared to that in long-day dormancy conditions. Furthermore, the growing conditions determine how much inhibitor diffuses away. Dry conditions, for example, can elicit the morphological changes of incipient dormancy.

There are three life cycle stages that can become dormant in ***Lunularia cruciata*** (Figure 1-Figure 13): mature thallus, gemma, and spore. Plants from Israel that have dried in the air produce adventitious branches ventrally from the region immediately behind the meristem. That meristem fails to resume growth. Dormant gemmae, on the other hand, resume growth when removed from the cup.

Lunularia cruciata (Figure 1-Figure 13) succeeds and maintains growth at very low light intensities (Nachmony-Bascomb & Schwabe 1963). The gemmae are also able to grow at the same low light intensities. Initial growth of the gemmae is due only to the expansion of the cells. It would be interesting to learn whether they take advantage of sunflecks (Figure 53).

Figure 53. ***Lunularia cruciata*** with sunflecks that might give it bursts of photosynthesis. Photo by Siznax, through Creative Commons.

Gemmae cup production is markedly diminished by high temperatures above 12ºC (Nachmony-Bascomb & Schwabe 1963). Thallus growth is severely limited by lack of P; N can also restrict growth to a very low level.

The first sign of growth from dormant gemmae of ***Lunularia cruciata*** (Figure 1-Figure 13) is development of rhizoids (Valio & Schwabe 1969). Temperature and light are important in controlling this development. As long as the days are long, a wide range of temperatures is suitable. When gemmae have been illuminated for 2 hours in white light, then transferred to darkness, about 50% of the gemmae produce rhizoids, and only at 20-25ºC. No rhizoid production occurs in total darkness, but the gemmae remain alive for at least 6 months.

Fernández-Marín *et al*. (2009) found that darkness induced the xanthophyll cycle in ***Lunularia cruciata*** (Figure 1-Figure 13) as a response to dehydration.

Pollution

Lunularia cruciata (Figure 1-Figure 13) is known as a toxitolerant species (Daly 1970; Gilbert 1970). Gilbert (1971) found that it is SO_2-resistant. It has the advantage of being able to transform quickly from its more susceptible protonema stage to the more protected and resistant thallus stage (LeBlanc & Rao 1975).

Vieira *et al*. (n.d.) found that ***Lunularia cruciata*** (Figure 1-Figure 13) was among the most tolerant liverworts to water pollution and increased *p*H and conductivity. In their study, this species occurred at a mean height of 30 cm above the water. Basile *et al*. (2017) similarly found the species to be very tolerant of air pollution.

Other studies have examined the effects of heavy metals on ***Lunularia cruciata*** (Figure 1-Figure 13). Basile (1993) examined the localization of lead in the cells and tissues. Carginale *et al*. (2004) found that cadmium accumulation in this species was both dose and time dependent. This metal accumulated preferentially in hyaline parenchyma and at the base of the gemmae cups. In the cells, it accumulated in the vacuoles and cell walls. These accumulations were accompanied by an increase of sulfur in the vacuoles of the stressed cells. The researchers suggested that the excess sulfur in the vacuoles may have been facilitated by stress-induced phytochelatins. Ultrastructural changes also occurred at sublethal levels of cadmium: alteration of the fine structure of cells and induced alterations of the chloroplast structure. Both apical thallus growth and gemma germination were inhibited, following a dose-dependent response.

Basile *et al*. (2017) reported that in the Land of Fires, ***Lunularia cruciata*** (Figure 1-Figure 13) exhibited high values of Al, Cd, Cr, Cu, Hg, Ni, Pb in its tissues. Reactive Oxygen Species (ROS) were high and the plants exhibited antioxidant activity and DNA damage. Basile and coworkers likewise found that phytochelatins served as good biomarkers of metal pollution. Further exploration indicated that detrimental pollution was indicated by a significant increment in heat shock protein (Hsp70) expression and occurrence and modifications in the chloroplast ultrastructure. Basile *et al*. (2005) found that accumulation of cadmium, one of the most toxic metals in the environment, affected DNA expression. The enzyme cystathionine γ-synthase is upregulated by Cd. Three other genes are downregulated.

Nothing is ever simple in biology. Alam and Sharma (2012) found that responses could change. Nevertheless, the responses indicated an increase in heavy metal air pollutants in the summer, a change that could be missed by ordinary pollution monitoring.

Lower exposures to radiation elicited damage to gemmae apical cells (Miller 1968). Apical cells of gemmae of ***Lunularia cruciata*** (Figure 1-Figure 13) are larger than other cells. However, radiation exposure had no different effect on energy absorption per chromosome in gemmae apices than it did in vegetative cells.

Degola *et al*. (2014) questioned why the phytochelatin synthase enzyme evolved long before pollution became a problem. This pre-adaptive enzyme would seemingly not be needed in ancient organisms to sequester excess cadmium or arsenic. Therefore, they looked for essential functions. They hypothesized that there was a need to regulate trace element homeostasis and to minimize the risk of exposure to toxic concentrations of certain metals even in pre-plant organisms such as **Charophyta** (***Nitella mucronata***; Figure 54).

Figure 54. ***Nitella mucronata***, an alga species that is likely to regulate trace element homeostasis. Photo by Kristian Peters, through Creative Commons.

Adaptations

Thalli of ***Lunularia cruciata*** (Figure 1-Figure 13) are large and flat, forming overlying patches (Figure 55) or even extensive turfs (Perold 1993; Steel *et al*. 2004). Or they can grow with other mosses and liverworts (Figure 56-Figure 61) that help to maintain moisture. Such growth arrangements can help to conserve water. They have numerous rhizoids that help them remain attached in the disturbed habitats they frequent. As already noted the scales and rhizoids also move water to all locations on the thallus, and pores facilitate the movement of water between cells both apoplastically and symplastically.

Figure 55. ***Lunularia cruciata*** on soil, forming overlapping patches. Photo by George Shepherd, with permission.

Figure 56. ***Lunularia cruciata*** with mosses. Photo by Duarte Frade, through Creative Commons.

Figure 57. ***Lunularia cruciata*** with mosses on soil. Photo by Martin Hutten, with permission.

Figure 58. ***Lunularia cruciata*** with mosses. Photo from <www.aphotofauna.com>, with permission.

Figure 59. ***Lunularia cruciata*** with mosses. Photo from <www.aphotofauna.com>, with permission.

Figure 60. ***Lunularia cruciata*** with mosses. Photo from <www.aphotofauna.com>, with permission.

Figure 61. ***Lunularia cruciata*** with mosses. Photo from <www.aphotofauna.com>, with permission.

Reproduction

It appears that ***Lunularia cruciata*** (Figure 1-Figure 13) relies primarily on gemmae. It is a **dioicous** perennial (Perold 1993; Steel *et al*. 2004) and its spread through horticultural shipments seems to have created populations with only one sex. In fact, it rarely has sexual reproduction in the UK (Benson-Evans & Hughes 1955; Blackstock 2018). One factor seemed to be the cold winters, which were tolerable to female plants (Figure 62), but male-expressing plants (Figure 63-Figure 66), and consequently sporophytes (Figure 67), were restricted to the southern parts of England and Wales.

Figure 62. ***Lunularia cruciata*** developing archegoniophores. Photo by Fotis Samaritakis, through Creative Commons.

Figure 63. ***Lunularia cruciata*** male plants with antheridial discs (dark patches) and splash cups. Photo from <www.aphotofauna.com>, with permission.

Figure 64. ***Lunularia cruciata*** with antheridial discs. Photo by Rutger Barendse, Saxifraga, through Creative Commons.

Figure 65. ***Lunularia cruciata*** with antheridial discs. Photo by Ricardo Ferreiro Sanjurjo, through Creative Commons.

Figure 66. ***Lunularia cruciata*** with antheridial discs. Photo by Tricia Stewart, through Creative Commons.

Figure 67. ***Lunularia cruciata*** female plants with developing sporophytes in the archegoniophore receptacle lobes. Photo by Stavros Apostolou, through Creative Commons.

Benson-Evans and Hughes (1955) reported that ***Lunularia cruciata*** (Figure 1-Figure 13) requires a low temperature regime before the production of sexual organs, a physiological function similar to **vernalization** (cooling process that facilitates initiation of growth stage, such as initiation of sexual organs or gemma germination) in tracheophytes. Nevertheless, as Blackstock (2018) notes, both genders are known in more northern localities. Even sporophytes have a wider distribution than previously thought. The limited sporophyte production is in part due to the dioicous condition, but also to a female-biased sex ratio. Since warmer conditions have arrived, it appears that fertility has increased. In northwest Wales, sexual reproduction has benefitted from prolonged and synchronous production of archegonia and antheridia (Figure 63-Figure 66). Yeates noted in 1908 that it seems to reproduce best in the even temperatures of greenhouses, with most of its reproduction by gemmae. In fact, the thalli disappear in winter and reappear in spring, whereas the gemmae survive through winter, presumably accounting for most of the reappearance in spring.

But vernalization does not seem to be the only factor. Benson-Evans (1964) found that ***Lunularia cruciata*** (Figure 1-Figure 13) grew best and produced gametangia at 21ºC in long days (18 hours), but not at either 10ºC or in short days (6 hours).

Sporophyte production (Figure 67-Figure 80) in ***Lunularia cruciata*** (Figure 1-Figure 13) is so rare outside the Mediterranean that finding it is often considered worthy of publication. Such records include Chalaud (1931), Rousseau (1955), Goodman (1956) for South Wales, and Ahayoun *et al*. (2008) for Morocco. The sporophytes are elevated on an **archegoniophore** (stalk that elevates archegonia), with four occurring on each **receptacle** (expanded portion of archegoniophore bearing sporangia).

Figure 68. ***Lunularia cruciata*** with emerging archegoniophores and developing capsules. Photo by Ken-Ichi Ueda, with permission.

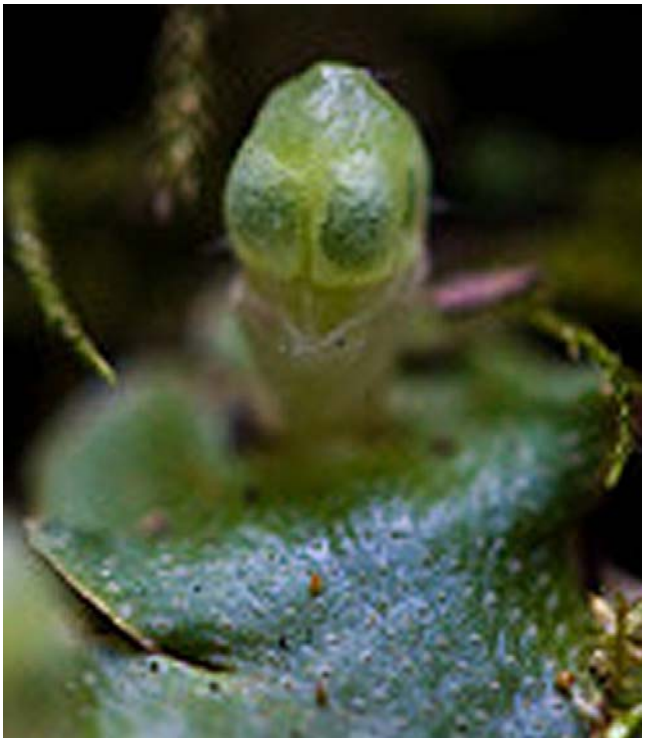

Figure 69. ***Lunularia cruciata*** with archegoniophore with developing sporophytes. Photo by Ken-Ichi Ueda, with permission.

Figure 70. ***Lunularia cruciata*** with archegoniophores, showing how common the archegoniophores can be in some locations. Photo by Stephen Thorpe, through Creative Commons.

Figure 71. ***Lunularia cruciata*** with mature archegoniophore. The few plants provide limited opportunity for fertilization. Photo by Loverworts, through Creative Commons.

Figure 72. ***Lunularia cruciata*** with fully elongated archegoniophore and nearly mature capsules. Photo by loverworts, through Creative Commons.

Figure 73. ***Lunularia cruciata*** with archegoniophores, in Israel. Photo by Jael Orgad, with online permission.

Figure 74. ***Lunularia cruciata*** with archegoniophores growing on vertical wall. Note the thallus dieback. Photo by Debbi Brusco, through Creative Commons.

Figure 75. ***Lunularia cruciata*** archegoniophore with four nearly mature capsules. Photo by loverworts, through Creative Commons.

Perold (1995) noted that ***Lunularia cruciata*** (Figure 1-Figure 13) responded to photoperiod in its native Israel, but this could not be determined in the field for New Zealand plants because of the much lower winter temperatures in New Zealand. On the other hand, Sérgio and Viana (1973) considered the availability of water as a possible limiting factor for development of sporophytes, based on the distribution of plants producing sporophytes. This would also explain the greater incidence of sexual reproduction in the Mediterranean climate.

Saxton (1931) described the archegoniophore and sporophyte (Figure 67-Figure 80) of ***Lunularia cruciata*** (Figure 1-Figure 13). I note here that many authors have avoided the term **archegoniophore** for this species, referring instead to the **receptacle**, which should be the expanded top portion of the archegoniophore. Kirschner *et al*. (2010) recorded the first sighting of sporophytes in Germany in the botanical garden in Main. They were able to observe all developmental stages, beginning with antheridial receptacles in early spring, followed by archegonial receptacles somewhat later in spring. Sporophytes developed in late summer.

Shinn (1902) presented a rather different picture of sexual reproduction of ***Lunularia cruciata*** (Figure 1-Figure 13) in California, USA. The first fertile plants appeared in April on the drier parts of shaded soil on the greenhouse floor. These bore many small, white, tuft-like sheaths (Figure 76) covering the young archegonial receptacles. Unlike most bryophytes (antheridia usually develop first), the antheridia developed two weeks later. These were on the same plants of this "**dioicous**" thallus! But they did occur on different divisions of the thallus. By 9 May, capsules appeared, while others were just beginning to emerge from the scales of the sheaths.

Figure 77. ***Lunularia cruciata*** with mature capsules, three of which are dehiscing. Photo by Fotis Samaritakis, through Creative Commons.

Figure 76. ***Lunularia cruciata*** with white sheaths where archegoniophores will emerge. Note the adjacent male plants. Carminda Santos, through Creative Commons.

Spores (Figure 77-Figure 80) of ***Lunularia cruciata*** (Figure 1-Figure 13) are "very small" (Perold 1993), a feature that should facilitate their long-distance dispersal but that would carry with it little reserved food to give the germaling a boost. They are either green or brown and smooth, so perhaps photosynthesis helps them to get a start. Kumar and Kapila (2003) reported a chromosome number of n=9.

Figure 78. ***Lunularia cruciata*** dehiscing capsules showing masses of spores and elaters. Photo by Fotis Samaritakis, through Creative Commons.

Figure 79. ***Lunularia cruciata*** dehisced capsules. Photo by Ken-Ichi Ueda, with permission.

Figure 80. ***Lunularia cruciata*** with sporophytes dispersing spores. Photo by Ken-Ichi Ueda, with permission.

The gemmae of ***Lunularia cruciata*** (Figure 1-Figure 13) occur in pocket-like gemmae cups (Figure 81) (Brodie 1951). The gemmae themselves are **lenticular** (lens-shaped; Figure 82), a common shape for gemmae in cups, and can be splashed for about 60 cm.

Yeates (1908) noted that gemmae are coated with an adhesive mucilage that could readily attach to the coats of animals, hence accomplishing dispersal. Furthermore, rats disperse them to gullies and sewers that further disperse them by moving water. They could also attach to bird's feet, but there are no data on their survival as the birds fly through the cooler atmosphere.

Sussman (1965) attributed the success of many bryophytes, especially ***Lunularia cruciata*** (Figure 1-Figure 13), to the resistant nature of their tissues and gemmae (Figure 83-Figure 96). Such bryophyte species have high regenerative capacity and gemmae have good desiccation resistance. This permits them to spread widely around the world without the production of spores. And for this species, they often spread as hitchhikers in horticultural shipments.

Figure 81. ***Lunularia cruciata*** with gemmae firmly tucked into the cups. Photo from Botany Website, UBC, with permission.

Figure 82. ***Lunularia cruciata*** showing the lenticular shape of the gemmae. Photo by Martin Hutten, with permission.

Figure 83. ***Lunularia cruciata*** with young gemmae cups, showing how quickly they can appear on a young thallus that is still small. Photo by Ken-ichi Ueda, through Creative Commons.

Figure 84. ***Lunularia cruciata*** with crescent-shaped gemmae cups. Photo by David T. Holyoak, with permission.

Figure 85. ***Lunularia cruciata*** gemmae tightly arranged in crescent-shaped cup. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 86. ***Lunularia cruciata*** gemmae cup with discoid gemmae. Photo by Andras Keszei, with permission.

Figure 87. ***Lunularia cruciata*** gemmae in cup, showing collected water and suggesting that the gemmae are not ready for dispersal. Photo by Bernard De Cuyper, with permission.

Figure 88. ***Lunularia cruciata*** thallus section through gemmae cup. Arrow indicates one of the gemmae. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

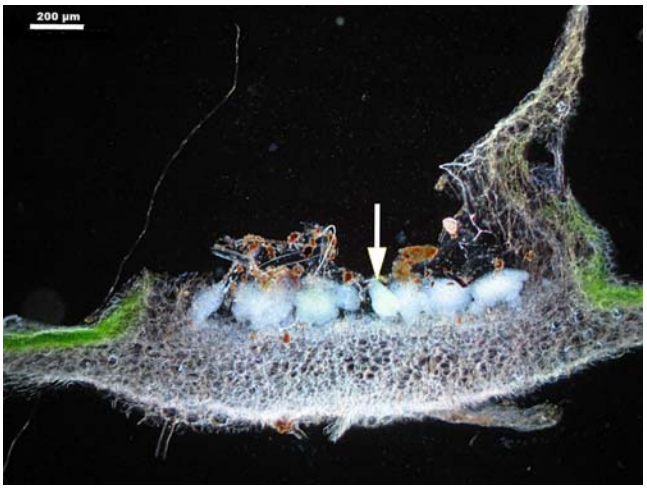

Figure 89. ***Lunularia cruciata*** gemmae cup cross section. **Arrow** indicates one of the gemmae. Note that the gemmae are attached and must break loose prior to dispersal. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 90. ***Lunularia cruciata*** with a few gemmae that have broken loose. Photo by Michael Lüth, with permission.

Figure 91. ***Lunularia cruciata*** gemmae cup with one escaped gemma. Photo by Ralf Wagner <www.dr-ralf-wagner.de>, with permission.

Figure 92. ***Lunularia cruciata*** with mature gemmae ready for dispersal. Those on the thallus will not germinate there. Photo by Jan-Peter Frahm, with permission.

Figure 93. ***Lunularia cruciata*** with some gemmae resting on the thallus, but not germinating. Photo by Michael Lüth, with permission.

Figure 94. ***Lunularia cruciata*** showing many dormant gemmae resting on the thallus, away from the gemmae cup. Photo by Jan-Peter Frahm, with permission.

Figure 95. ***Lunularia cruciata*** gemmae that have broken loose and are ready for dispersal. Photo by Walter Obermayer, with permission.

Figure 96. ***Lunularia cruciata*** and young plants, probably from gemmae. Photo by S. Bush, through Creative Commons.

Itouga *et al*. (2002) compared genetic differentiation in four species of East Asian liverworts. They found that the highest gene flow occurred in ***Conocephalum japonicum*** (Figure 97), a dioicous species that relies on spores, and was lowest in ***Lunularia cruciata*** (Figure 1-Figure 13), a dioicous species that relies on gemmae. ***Lunularia cruciata*** showed strong population differences, whereas ***Conocephalum japonicum*** showed little, further supporting the greater gene flow in the latter. In general, however, it was the monoicous species that exhibited the greatest population differences.

Following these, studies appeared on factors affecting the sexual cycle (Longton 1990) and morphology of the sporophyte of ***Lunularia cruciata*** (Figure 1-Figure 13) (Shimamura & Deguchi 2002).

Figure 97. ***Conocephalum japonicum*** with antheridial discs. Photo by David Long, with permission.

The persistence of gemmae permits the species to appear in disturbed areas. Biggs and Wittkuhn (2006) found diaspores of ***Lunularia cruciata*** (Figure 1-Figure 13) in litter samples, but not in soil samples. Disturbance can bring diaspores such as gemmae to the surface, where they can get light and germinate (Figure 98).

Figure 98. ***Lunularia cruciata*** germinating gemma. Photo from Plant Actions, with permission from Eugenia Ron Alvarez and Tomas Sobota.

Longton (1990) summarized the sexual reproduction problems in ***Lunularia cruciata*** (Figure 1-Figure 13). It readily produces both sexes and sporophytes in its native Mediterranean area. However, in areas where it has more recently become established, most likely by human dispersal through horticulture, sporophytes are rare. In Europe and California, USA, this is apparently due to insufficient moisture in summer to facilitate fertilization or sporophyte development. In temperate regions, it appears that climatic conditions are unsuitable for gametangial formation. Gametangia may occasionally appear in such temperate areas as southern Britain, but this may be due to aberrant weather that more closely resembles that of the Mediterranean area. It is also possible that the required long-day stimulation for gametangial development is not coupled with the right temperature (15-21ºC) or moisture availability. Based on observations, it appears that a warm period is needed to initiate antheridia in Britain, thus initiating them in late summer, followed by a cool period of winter when they become dormant. It also appears that the conditions needed to stimulate growth and reproduction differ geographically. In Israel, short days (winter) stimulate growth, during the more humid time of year, and the plants become dormant in the dry summer. But in Britain it is long days that stimulate growth. Clearly there are physiological races among these scattered populations. It appears that it has survived despite the mismatched timing because of its production of gemmae.

Uses

Aside from sometimes being welcome in a garden (but more likely considered a weed), ***Lunularia cruciata*** (Figure 1-Figure 13) has been used in making maize beer (Franquemont *et al.* 1990; Harris 2008).

Pande *et al*. (2004) found that extracts of ***Lunularia cruciata*** (Figure 1-Figure 13) inhibited germination of seeds of the legume ***Indigofera heterantha*** (Figure 99) and non-legume ***Impatiens scabrida*** (Figure 100). The inhibition was greater at lower concentrations than at higher ones. Initiation of germination was also delayed more in lower concentrations. Likewise, seedling growth was suppressed. As in most of these allelopathic studies, we need to demonstrate that the same inhibition occurs in the presence of whole plants of ***Lunularia cruciata*** and that the solvent alone does not contribute to the inhibition.

Or perhaps dying plants could leach the inhibitors in concentrations similar to those from the macerated plants. A further question is the ability of the soil to bind the inhibitor in the field, rendering it useless against these tracheophytes.

Figure 99. ***Indigofera heterantha***, a species whose seed germination is inhibited in the lab by extracts from ***Lunularia cruciata***. Photo by Dinesh Valke, through Creative Commons.

Figure 100. ***Impatiens scabrida***, a species whose seed germination is inhibited in the lab by extracts from ***Lunularia cruciata***. Photo by Paganum, through Creative Commons.

Schwabe (1990) found that an internal accumulation of lunularic acid could inhibit the growth of ***Lunularia cruciata*** (Figure 1-Figure 13). Schwabe also suggested that lunularic acid from the parent plant served to inhibit the germination of gemmae while still residing on the parent (Figure 101-Figure 102). As already noted, IAA could serve this function. On the other hand, despite leakage of lunularic acid to the soil, evidence suggests that it is not accumulated there, thus permitting gemmae to germinate once leaving the parent plant surface.

Figure 101. ***Lunularia cruciata*** with dormant gemmae on thallus. Photo by Martin Hutten, with permission.

Figure 102. ***Lunularia cruciata*** with dormant gemmae on thallus. Photo by Martin Hutten, with permission.

Herbivory

It is clear from some of the images posted that ***Lunularia cruciata*** (Figure 1-Figure 13) experiences herbivory (Figure 103). This could be from slugs, pillbugs, or insects. And perhaps even birds might nibble the edges.

Figure 103. ***Lunularia cruciata*** showing herbivory (**lower right**). Photo by Des Callaghan, with permission.

Interactions

Bacteria most likely play a larger role in bryophyte development than we have supposed. ***Methylobacterium*** (Figure 104) is able to inhabit the surfaces of plants, including ***Lunularia cruciata*** (Figure 1-Figure 13) (Kutschera & Koopmann (2005). While there, they secrete cytokinines that are able to promote growth of gemmae on agar plates. There seemed to be no effect on the seed plants tested, and Kutschera and Koopmann hypothesized that these bacteria have a role in normal development and regulation in ***Lunularia cruciata*** in nature.

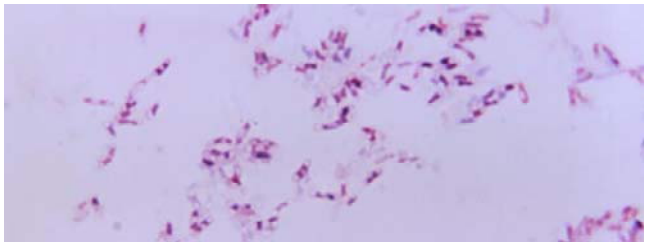

Figure 104. ***Methylobacterium***, a bacteria species that can live on the surfaces of ***Lunularia cruciata***. Photo by R. E. Weaver, CDC, through public domain.

Sahu *et al*. (2013) observed that the green alga ***Stichococcus bacillaris*** (Figure 105) occurred as a contaminant on laboratory cultures of ***Lunularia cruciata*** (Figure 1-Figure 13) on soil in growth chambers. They found that presence of the alga suppressed the growth of the liverwort, an example of algal allelopathy.

Figure 105. ***Stichococcus bacillaris*** on rotting wood, a green alga species that can be allelopathic to ***Lunularia cruciata***. Photo by James K. Lindsey, with permission.

Bukvicki *et al*. (2021) determined that bis-bibenzyl perrottetin F was isolated from ***Lunularia cruciata*** (Figure 1-Figure 13) by the fungus ***Aspergillus niger*** (Figure 106). This compound exhibits inhibitory activity against the bacteria ***Pseudomonas aeruginosa*** (Figure 107) PAO1 and ***Staphylococcus aureus*** (Figure 108) at concentrations of 100 µm to 450 µm. It also has "remarkable ability" to inhibit the synthesis of bacterial quorum-sensing signal molecules. These results suggest that this biological combination could provide a fast and effective way of producing bioactive substances.

Figure 106. ***Aspergillus niger***, a fungus that is able to isolate bis-bibenzyl perrottetin F from ***Lunularia cruciata***. Photo through public domain.

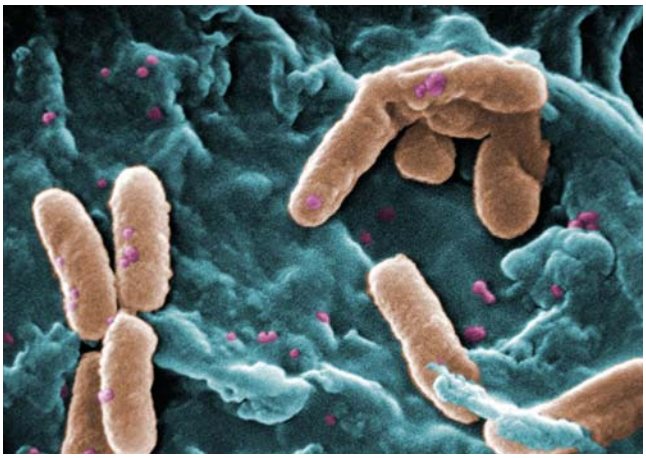

Figure 107. ***Pseudomonas aeruginosa***, colorized SEM. This is a bacterial species that is inhibited by bis-bibenzyl perrottetin F isolated by ***Aspergillus niger*** from ***Lunularia cruciata***. Photo by Janice Haney Carr, CDC, through public domain.

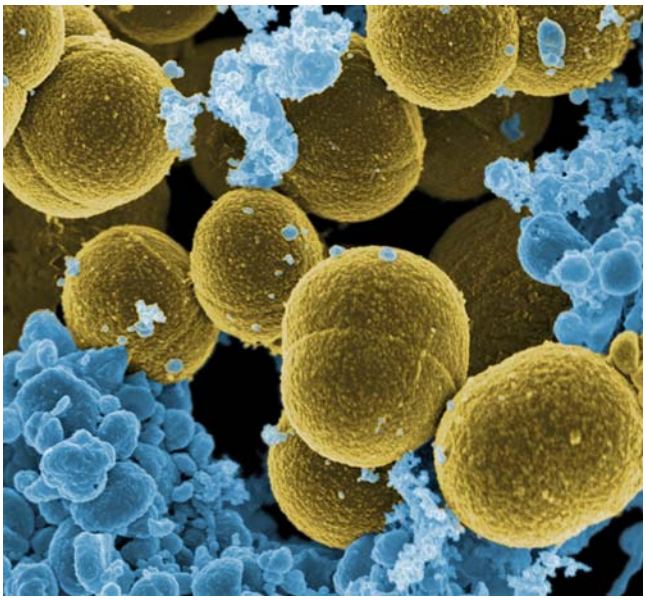

Figure 108. ***Staphylococcus aureus***, colorized SEM. This is a bacterial species that is inhibited by bis-bibenzyl perrottetin F isolated by ***Aspergillus niger*** from ***Lunularia cruciata***. Photo by Frank DeLeo, NIH, through public domain.

Lunularia cruciata (Figure 1-Figure 13) can be colonized by the oomycete pathogenic fungus ***Phytophthora palmivora*** (Figure 109) (Carella & Schornack 2018). The hyphae colonize the air chambers in the dorsal photosynthetic layer, and they may sometimes be associated with ventral epidermal cells and rhizoids (Figure 110). However, the fungus is never associated with the central storage region.

Figure 109. ***Phytophthora palmivora*** mycelia on papaya that has been damaged by herbivory. Photo by Scot Nelson, through Creative Commons.

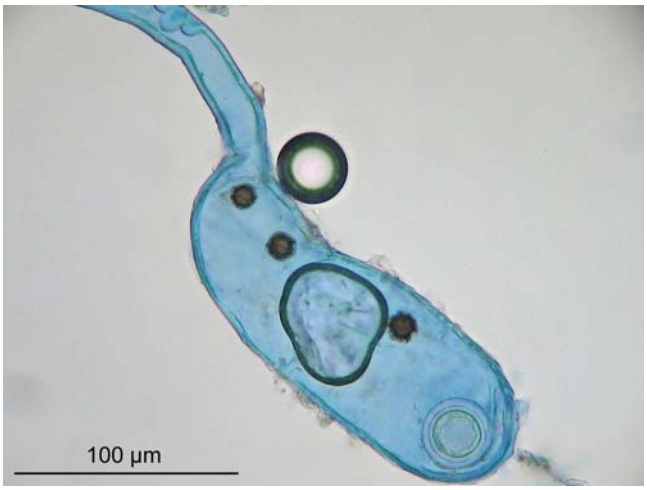

Figure 110. ***Lunularia cruciata*** inflated rhizoid. Photo by Jan Eckstein, with permission.

One of the most common groups of fungi in association with bryophytes is the **Glomeromycota**, a phylum of fungi that produce arbuscular mycorrhizal associations almost exclusively with bryophyte plants and tracheophyte roots. Among their habitats, they include wetlands and salt marshes.

Rhizophagus irregularis (Figure 111) is a symbiotic fungus in **Glomeromycota** that can colonize the thalli of ***Lunularia cruciata*** (Figure 1-Figure 13) (Carella & Schornack 2018). During the symbiosis, the fungus acts to up-regulate the transcriptome genes of the liverwort (Delaux *et al*. 2015). Delaux *et al*. conclude that the green alga ancestor of land plants was preadapted for symbiotic associations. This was followed in early land plants by gene duplication that permitted additional pathways, enabling a fully functional arbuscular mycorrhizal symbiosis.

Figure 111. ***Rhizophagus irregularis*** in the roots of the bean ***Vicia faba***; it is a symbiotic fungus that can colonize the thalli of ***Lunularia cruciata***. Photo by Mylène Durant, through Creative Commons.

Lunularia cruciata (Figure 1-Figure 13) is one of the bryophyte species in which the **Glomeromycota** mycorrhizae develop (Fonseca *et al*. 2006). Fonseca and coworkers cultured ***Rhizophagus irregularis*** (syn.=***Glomus intraradices***; Figure 111) and ***Glomus proliferum*** (see Figure 112), then introduced them to ***Lunularia cruciata***. The fungi produced external hyphae and spores similar to those found associated with roots.

Figure 112. ***Glomus*** sp.; ***Glomus*** species are all obligate arbuscular mycorrhizal (AM) fungi; ***G. proliferum*** forms this relationship with ***Lunularia cruciata***. Photo by Reiner Richter, through Creative Commons.

But that is not evidence of a symbiotic relationship, so Fonseca and Berbara (2008) used Koch's postulates to determine if they formed a symbiotic relationship. They found that fungi in cultured liverwort thalli were able to extend into a compartment of the Petri dish where they obtained phosphorus and to translocate that phosphorus

into the liverwort. The liverwort responded with increased dry weight, greater AM fungi spore production, and higher liverwort total phosphorus content. However, the researchers suggested that the energy requirements to maintain the symbiosis may limit its symbiotic advantage in the field. Fonseca and Berbara considered the relationship of endophytic ***Rhizophagus irregularis*** (Figure 111) and ***Glomus proliferum*** (see Figure 112) with ***Lunularia cruciata*** (Figure 1-Figure 13) to be a parasitic/opportunistic partnership rather than a mutualistic symbiosis.

The thalli of ***Lunularia cruciata*** (Figure 1-Figure 13) reveal major anatomical traits of mycorrhizal associations (arbuscules, coils, arbusculate coils and vesicles) when infected with ***Glomus proliferum*** (Figure 112) (Fonseca & Berbara 2008; Fonseca *et al*. 2009a). But colonized liverwort thalli exhibited a reduction in biomass in comparison with axenic thalli, supporting the conclusion that the relationship is parasitic (Fonseca *et al*. 2009a, b; Figueiredo 2010). Fonseca *et al*. 2009a) determined that those liverwort plants that did not fare well already had sufficient phosphorus, thus giving all the benefit to the fungus. This does not rule out the possibility of benefit to the liverwort in conditions where phosphorus is limiting because of the ability of the fungus to scavenge phosphorus from a much larger area than that available to the liverwort alone. Furthermore, significant reductions in growth of infected compared with uninfected cultured plants did not arise until 86 and 106 days of infection (Figueiredo 2010).

Fonseca *et al*. (2013) introduced laboratory methods for culturing ***Rhizophagus clarus*** (Figure 113) (syn.=***Glomus clarum***) and ***Gigaspora margarita*** (also in the **Glomeromycota**; Figure 114) with ***Lunularia cruciata*** (Figure 1Figure 4-Figure 13). *In vitro* cultures of ***Rhizophagus clarus*** and ***Gigaspora margarita*** were grown with ***Lunularia cruciata*** on macro and micronutrients with a layer of activated charcoal in the upper agar layer (Fonseca *et al*. 2014). Both fungal species reached maturity in less than 150 days and were still viable after more than 500 days. Container size was the only limiting factor for growth of the liverwort. Both fungal species colonized the midrib parenchyma. ***Gigaspora margarita*** developed relatively small, shallow colonies, apparently limited by its distribution within the plant. Penetration by this species occurs mainly through new entry points by its external hyphae from neighboring thalli and not by invasion from cell to cell. The higher level of colonization by ***Rhizophagus clarus*** most likely resulted from the internal growth of the fungi along the midrib parenchyma toward the thallus apical meristem. The production of spores occurred primarily among the rhizoids, developing between overlapping thalli and over the thalli (Fonseca *et al*. 2013). The pattern of development was similar to that seen in ***Rhizophagus irregularis*** (Figure 111) and ***Glomus proliferum*** (see Figure 112).

Nobre *et al.* (2013) found that inoculated thalli of ***Lunularia cruciata*** (Figure 1-Figure 13) achieved their peak absolute growth rate at 39 days after inoculation with ***Glomus proliferum*** (Figure 112), whereas those not inoculated required 42 days, suggesting a benefit to the liverwort under the growing conditions of the experiment. The liverwort exhibited a relative growth rate of 0.074 and 0.387 $cm^2\ cm^{-2}\ d^{-1}$, respectively. Addition of 20 and 80 mg carbon L^{-1} of humic acid had a positive influence on the growth of ***L. cruciata***.

Figure 113. ***Rhizophagus clarus***, a fungus that is able to colonize the midrib parenchyma of ***Lunularia cruciata***. Photo by Silvani Vanesa, Fernández Bidondo Laura, and Fracchia Sebastián, BGIV, through Creative Commons.

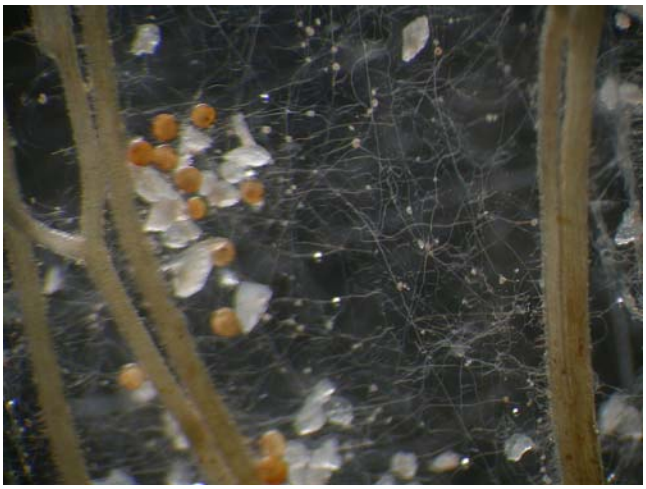

Figure 114. ***Gigaspora margarita***, a fungus that is able to form small colonies in the thallus of ***Lunularia cruciata***. Photo by Mike Geuther, through Creative Commons.

Desirò *et al*. (2013) renewed the story of big fleas have little fleas by demonstrating that the **Glomeromycota** inhabiting ***Lunularia cruciata*** (Figure 1-Figure 13) in a botanical garden were themselves inhabited by coccoid Gram-positive parasitic endobacterium related to the class **Mollicutes (**Figure 115**)**.

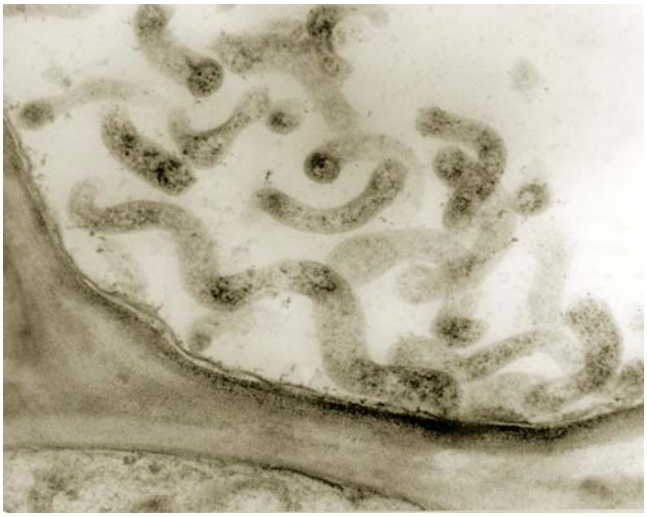

Figure 115. TEM image of ***Spiroplasma*** sp. (in class **Mollicutes**) from corn phloem. Photo through Creative Commons.

Auret (1930) first reported an endophytic fungus in ***Lunularia cruciata*** (Figure 1-Figure 13) in South Africa (only females were present). The fungi resided below the assimilating tissue and in the rhizoids. The mycelium exhibited branched, septate hyphae with granular contents, and they formed vesicles, arbuscules, and sporangioles, but none of the cells of the field-grown plants exhibited fructifications. However, when grown on glucose or protein agar, the fungus produced thin, hyaline hyphae that began to form pycnidia by the tenth day. These matured into flask-shaped structures with a beak or neck. Auret described this as a new species, ***Phoma lunulariicola*** (Figure 116-Figure 117). The relationship did not appear to harm the liverwort beyond the cells that were infected.

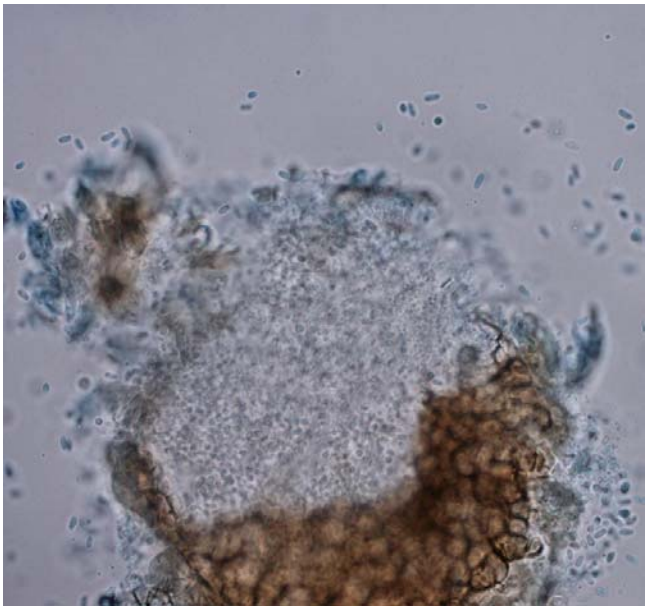

Figure 116. ***Phoma herbarum***; ***Phoma lunulariicola*** is an endophytic fungus in ***Lunularia cruciata***. Photo by Cesar Calderon, through Creative Commons.

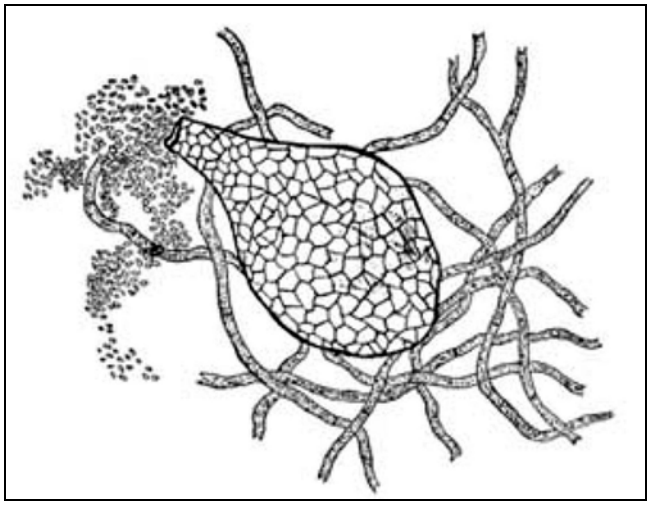

Figure 117. ***Phoma lunulariicola*** from ***Lunularia cruciata***, showing flask of spores. Modified from Auret 1930.

Ridler (1923) also observed the relationship. The fungus occurred in a single strand of cells along the thickened midrib area toward the surface of ***Lunularia cruciata*** (Figure 1-Figure 13). The liverwort partially digests the fungus, causing the fungus to form arbuscules and sporangioles. Its growth is restricted henceforth. The liverwort starch disappears after the fungus enters, benefitting the fungus. The liverwort does not seem to be harmed, agreeing with the description given by Auret (1930). Ridler also concluded that it was a species of ***Phoma*** (Figure 116-Figure 117).

Giordano *et al*. (1999) recorded the interactions between the lichen ***Cladonia foliacea*** (Figure 118) and ***Lunularia cruciata*** (Figure 1-Figure 13). The interaction by the lichen caused a delay in protonemal growth and reduction in the number of thallose plants produced. Internally, the cytoplasm obtained a granular appearance with many microvesicles in the protonema, enlarged periplasmic space, and changes in chloroplast shape.

Figure 118. ***Cladonia foliacea***, a lichen that causes a delay of protonemal growth and reduces the number of thalli produced in ***Lunularia cruciata***. Photo by J. C. Schou, with permission.

Basile *et al*. (2011) tested the effect of essential oils from the flowering plant ***Sideritis italica*** (**Lamiaceae**; Figure 119) on thallus and rhizoid growth and gemma development of ***Lunularia cruciata*** (Figure 1-Figure 13). Leaf oil was more active than was flowerhead oil, causing

inhibition of gemma development and browning, and inhibiting apical growth of the thallus of ***L. cruciata***.

Figure 119. ***Sideritis italica***, a species from which the essential oils inhibit gemma development and browning, and they inhibit apical growth in the thallus of ***Lunularia cruciata***. Photo by Andrea Moro, through Creative Commons.

Biochemistry

Lunularia cruciata (Figure 1-Figure 13) exhibits "conspicuous oil bodies" (Lepp & Lawson 1984). These are susceptible to damage from pollutants. In elevated vanadium levels, they change color from light brown to black.

Lunularia cruciata (Figure 1Figure 4-Figure 13) has been the subject of many physiological studies, so it is no surprise that it has been a subject of many biochemical studies as well. As early as 1940, Lugg determined that the amide tyrosine and tryptophan contents of the proteins of the main photosynthesizing tissues of ***Lunularia cruciata*** presented the same magnitude as those in seed plants.

Because of the micro-organisms that inhabit the surfaces of bryophytes, it is necessary to make certain that compounds identified actually were produced by the bryophyte and not the inhabitants. Christie *et al*. (1985) determined that the carbohydrates produced by axenically cultured ***Lunularia cruciata*** (Figure 1-Figure 13) were the same as those identified from field populations, especially alditols.

Lunularic acid, an ABA-like inhibitor and stress hormone, was named for its discovery in ***Lunularia cruciata*** (Figure 1-Figure 13) (Pryce & Kent 1971). Thus far, this hormone is almost unique to liverworts, and is notably absent from mosses (Pryce 1972). Yoshikawa *et al*. (2002) demonstrated the similarity of lunularic acid to ABA in both the physiological responses it elicits and in its apparent ability to bind to the same receptor in tracheophytes.

One of the early reports is the presence of sucrose phosphatase in ***Lunularia cruciata*** (Figure 1Figure 4-Figure 13) (Hawker & Smith 1984). This is evolutionarily significant because in all species tested it has been absent in red and brown algae and from fungi.

Markham and Porter (1974) identified luteolin 3′,4′-di-O-β-d-glucuronide as the major flavonoid in ***Lunularia cruciata*** (Figure 1-Figure 13) and at that time unique to this species. They also found luteolin 3′-O-β-d-glucuronide. James *et al*. (2020) reported the presence of carbohydrates, proteins, diterpenes, phytosterols, and anthocyanin, but flavonoids did not appear in the alcoholic or acetonic extracts.

Jocković *et al*. identified luteolin-7-O-glucoside and quercetin from extracts of ***Lunularia cruciata*** (Figure 1-Figure 13). Quercetin is a common plant flavonol in fruits, vegetables, leaves, seeds, and grains. It is reputed to bolster the immune system, to reduce hot flashes, and to serve as an antioxidant in humans. However, it is short-lived in humans, with a half life of only 1-2 hours, and the FDA warns that many of the claims for its beneficial effects to humans have not been validated.

Bryophytes present unique problems for biochemical analysis. Many species are quite small and it is difficult to get enough plants for analysis (Mukhia *et al*. 2019). Some are only available in a particular season; others have restricted geographic distribution or are rare. Hence, Mukhia *et al*. propagated ***Lunularia cruciata*** (Figure 1-Figure 13) for this purpose, using gemmae. This was a good choice because of its ability to grow in gardens over a large portion of the planet. They validated this approach by comparing its pharmacological properties with those of naturally grown plants. This endeavor revealed nine key compounds present in both lab-grown and field-grown plants. This verified that both *in vitro* and naturally grown plants produced antioxidant and anti-diabetic activity, thus making it feasible to culture this species for both experimental and clinical use.

The antibiotic activities of many liverworts against bacteria are well known. Joshi (1993) investigated antibacterial properties of ***Lunularia cruciata*** (Figure 1-Figure 13). Basile *et al*. (1993) explored the effects of a-D-oligogalacturonides on the production of antibiotic substances. Basile *et al*. (1998a) determined the minimum concentrations of extracts needed to illicit antibiotic activity against 13 bacterial strains and compared these with standard antipharmaceutical antibiotics. The extracts were effective against both Gram-positive and Gram-negative bacteria.

Sorbo *et al*. (2004) found significant antibacterial activity by ***Lunularia cruciata*** (Figure 1-Figure 13) extracts against the Gram-positive ***Staphylococcus aureus*** (Figure 108), ***Streptococcus*** sp. (Figure 120), and ***Enterococcus*** sp. (Figure 121) The activity against Gram-negative ***Proteus mirabilis*** (Figure 122), ***Pseudomonas aeruginosa*** (Figure 107), ***Escherichia coli*** (Figure 123), ***Salmonella*** sp. (Figure 124), and ***Klebsiella*** sp. (Figure 125) was especially good. The extracts also exhibited antioxidant activity, apparently due to A catechin and its derivatives. By contrast, Russell (2010) found no visible

antibiotic activity against the Gram-negative ***Escherichia coli*** (Figure 123) or ***Klebsiella pneumoniae*** (Figure 125). Nevertheless, ***Lunularia cruciata*** exhibited the most significant antibacterial activity among the 14 bryophyte species tested.

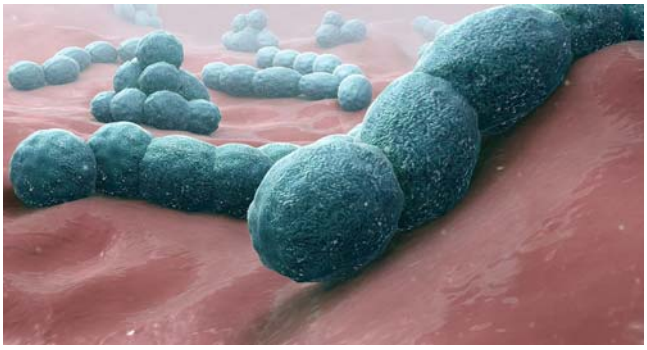

Figure 120. ***Streptococcus pneumoniae***; ***Lunularia cruciata*** exhibits significant antibacterial activity against ***Streptococcus*** sp. Photo from <www.scientificanimations.com>, through Creative Commons.

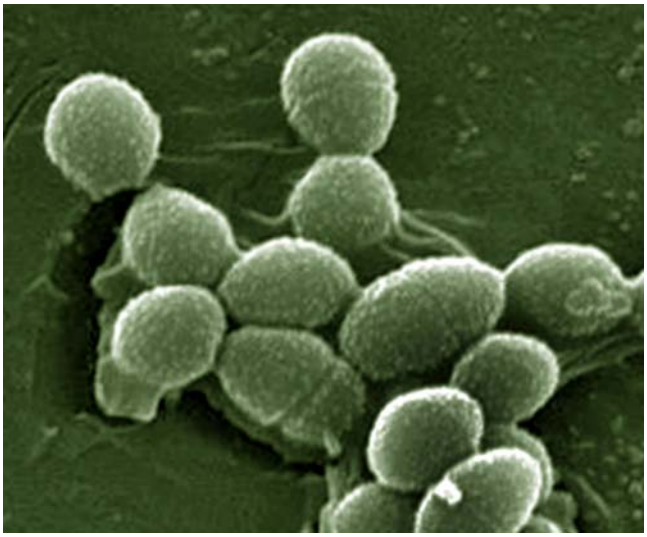

Figure 121. ***Enterococcus faecalis***; ***Lunularia cruciata*** exhibits significant antibacterial activity against ***Enterococcus*** sp. Photo by Janice Haney Carr, CDC, public domain.

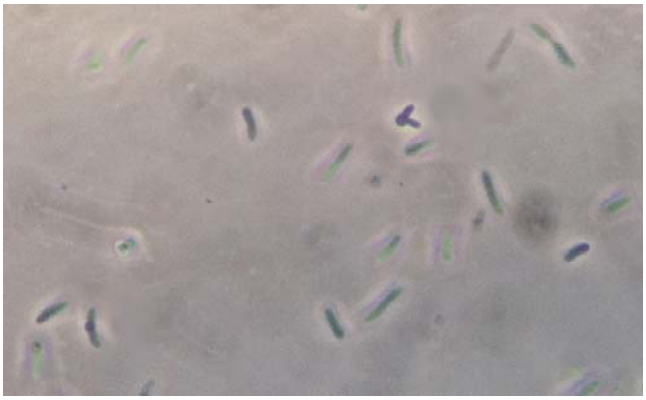

Figure 122. ***Proteus mirabilis*** suffering from Penicillin exposure. In early stages the bacteria are thickened in the middle (**lower left**). Later they fold into a V shape (**upper right**) just before lysis. Extracts from ***Lunularia cruciata*** are especially good at inhibiting the bacterium ***Proteus mirabilis***. Photo by Geoman3, through Creative Commons.

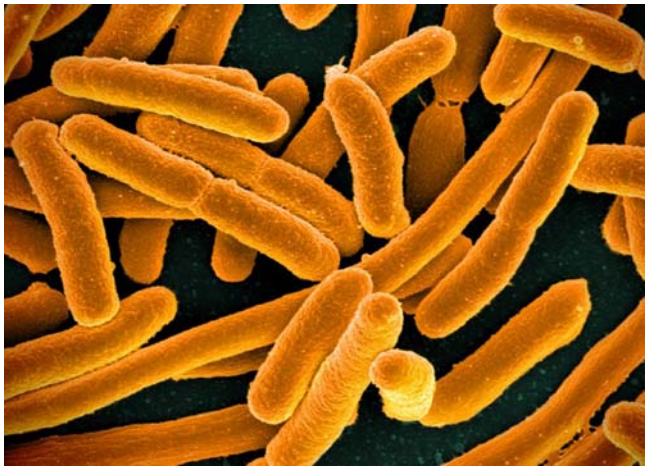

Figure 123. ***Escherichia coli*** colored SEM image, a species that does not seem to be affected by extracts from ***Lunularia cruciata***. Photo from NIAID, through Creative Commons.

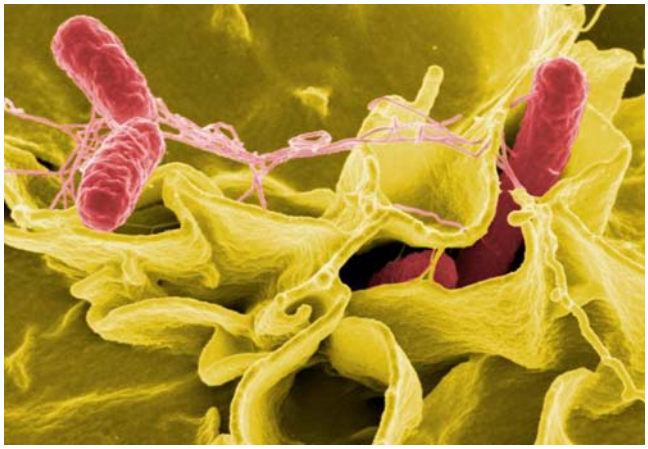

Figure 124. Colored SEM image of ***Salmonella*** invading cells; at least some members of this genus are unaffected by extracts from ***Lunularia cruciata***. Photo from NIAID, through Creative Commons.

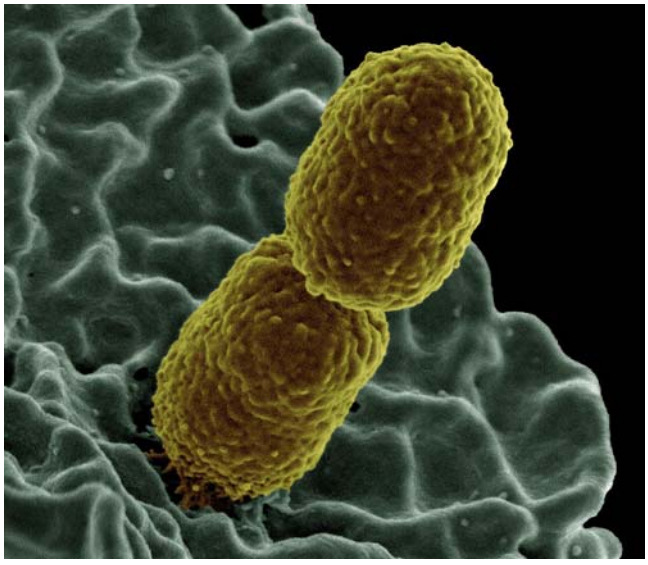

Figure 125. ***Klebsiella pneumoniae*** colored SEM image, a species that does not seem to be affected by extracts from ***Lunularia cruciata***. Photo from NIAID, through Creative Commons.

Dhondiyal *et al*. (2013) reported "substantial" antibiotic activity by ***Lunularia cruciata*** (Figure 1-Figure 13) extracts against five pathogenic species of bacteria [***Agrobacterium tumefaciens*** (Figure 126), ***Xanthomonas phaseoli*** (Figure 127), ***Escherichia coli*** (Figure 123), ***Bacillus subtilis*** (Figure 128), and ***Dickeya dadantii*** (Figure 129)]. This occurred in all four crude organic extracts against all five bacteria species. The extracts proved to be very effective against these bacteria when compared to the standard antibiotic ampicillin. But these results must be viewed with caution. While they provide evidence that the liverwort has medicinal properties, the aqueous extracts had no antibiotic effects, suggesting that the plants may not be protected by these natural compounds in nature. Furthermore, based on conflicting reports discussed above, we need to assess the role of the solvents as well as temperature, light, and nutrient conditions in altering the antibiotic effectiveness.

Figure 126. ***Agrobacterium tumefaciens*** causing a gall at the tree base. Photo by Jerzy Opioła, through Creative Commons.

Figure 127. ***Xanthomonas phaseoli*** infecting leaves of the bean ***Phaseolus vulgaris***; ***Lunularia cruciata*** exhibits significant antibiotic activity against this bacterial species. Photo by Howard F. Schwartz, through Creative Commons.

Lunularia cruciata (Figure 1-Figure 13) alcoholic and acetonic extracts are very active against ***Klebsiella pneumoniae*** (Figure 125) (James *et al*. 2020). ***Escherichia coli*** (Figure 123) is inhibited by both acetone and alcohol extracts. ***Staphylococcus aureus*** (Figure 108) is inhibited only by acetone extracts, whereas alcohol extracts elicit no inhibition. The researchers suggested that lunularic acid may be the reason for greater inhibitory responses to ***Lunularia cruciata*** extracts than to ***Marchantia emarginata*** (Figure 130) extracts.

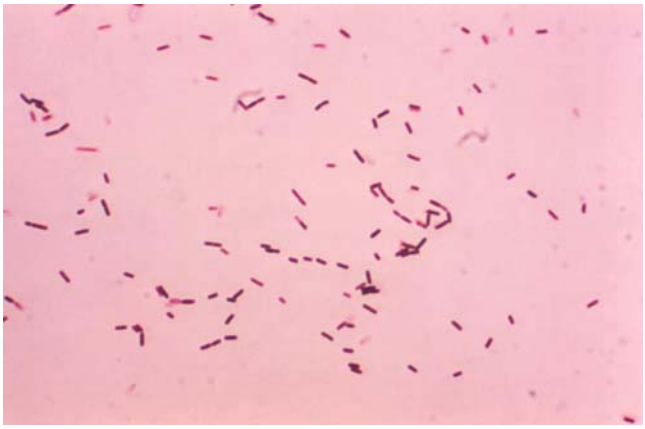

Figure 128. ***Bacillus subtilis*** with Gram stain; ***Lunularia cruciata*** exhibits significant antibiotic activity against this species. Photo by W. D. Clark, CDC, through public domain.

Figure 129. ***Dickeya dadantii*** infecting ***Allium cepa*** (onion); ***Lunularia cruciata*** exhibits significant antibiotic activity against this bacterial species. Photo by Scot Nelson, through Creative Commons.

Figure 130. ***Marchantia emarginata***, a species that elicits less inhibitory response than does ***Lunularia cruciata***. Photo by Li Zhang, with permission.

Basile *et al*. (1998a) tested the minimum concentrations of extracts of ***Lunularia cruciata*** (Figure 1-Figure 13) needed to illicit antibiotic activity against 2 fungal species, but they found no antifungal activity among the strains tested.

Although extracts of ***Lunularia cruciata*** (Figure 1-Figure 13) in organic solvents proved to be very effective on the tested bacteria, none of the extracts had any effect against the three pathogenic fungi [***Alternaria alternata*** (Figure 131), ***Sclerotinia sclerotiorum*** (Figure 132), and ***Pyricularia oryzae*** (Figure 133)] tested (Dhondiyal *et al*. 2013).

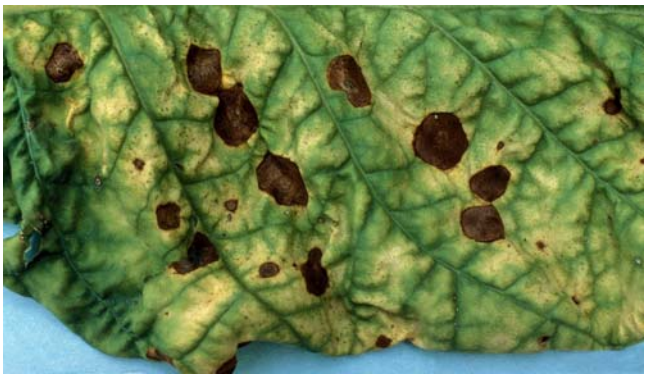

Figure 131. ***Alternaria alternata*** on tobacco leaf (***Nicotiana tabacum***), a species of fungi that is immune to extracts of ***Lunularia cruciata***. Photo by R. J. Reynolds Tobacco Company, through Creative Commons.

Figure 132. ***Sclerotinia sclerotiorum*** on bean, ***Phaseolus vulgaris***, a fungus species that is immune to extracts of ***Lunularia cruciata***. Photo by Jymm, through Creative Commons.

Figure 133. ***Pyricularia oryzae*** from rice, a fungus species that is immune to extracts of ***Lunularia cruciata***. Photo by Donald Groth, USDA Forest Service, through public domain.

Basile *et al*. (1991, 1993, 1998b) tested the ability of α-d-oligogalacturonides (OG) to induce antibiotic activity, using the fern ***Nephrolepis*** sp. (Figure 134) as a model system. This compound can occur naturally in the soil as a product of biological components. The experiments demonstrated that indeed the antibiotic activities can be induced, at least in the fern. Further testing indicated that extracts from wild-grown ***Lunularia cruciata*** (Figure 1-Figure 13) likewise inhibited the growth of all bacterial strains tested, whereas extracts from the axenically grown plants in the presence of α-d-oligogalacturonides were able to inhibit only three of the tested bacterial strains. Basile and coworkers concluded that the OG mixture induces the production of fewer antibiotic compounds compared to inducing compounds typically found in the soil. This does not rule out the possibility of more specific compounds being produced in response to OG.

Figure 134. ***Nephrolepis exaltata***, in a genus that produces the same α-d-oligogalacturonides (OG) as those of ***Lunularia cruciata***, compounds that can induce production of antibiotic compounds. Photo by Mokkie, through Creative Commons.

Sorbo *et al*. (2004) showed allelopathic activity by 7 pure flavonoids of ***Lunularia cruciata*** (Figure 1-Figure 13). In this case, they inhibited root development of the radish, ***Raphanus sativus*** (Figure 135). These same flavonoids presented severe allelopathic activity against spore germination and growth of the moss ***Tortula muralis*** (Figure 136).

Figure 135. ***Raphanus sativus*** (radish), a species whose roots are inhibited by flavonoids from ***Lunularia cruciata***. Photo by Rasbak, through Creative Commons.

Figure 136. ***Tortula muralis***, a moss species for which both spore germination and growth are severely inhibited by flavonoids from ***Lunularia cruciata***. Photo by Björn S., through Creative Commons.

Compounds from ***Lunularia cruciata*** (Figure 1-Figure 13) have other potential medical applications. An acetone extract is effective, causing significant changes in light emissions from whole blood phagocytes and polymorphonuclear leukocytes, providing inhibitory activity (Ielpo *et al*. 1998). The researchers postulated that the activity could be caused by compounds such as flavonoids or sesquiterpenes. In further experiments, Ielpo *et al*. (2000) demonstrated that both raw extracts and purified flavonoids exhibited activity against leukocytes.

Novakovic *et al*. (2019) isolated seven new bisbibenzyls from ***Lunularia cruciata*** (Figure 1-Figure 13), some of which are rare in nature. They demonstrated that riccardin G exhibited cytotoxic activity against the A549 cell line for lung cancer.

Summary

Lunularia cruciata is primarily a Mediterranean species, but it has spread to many places in the world through the horticulture trade. In many of these places sexual reproduction is rare or non-existent and gemmae provide the primary means of spread. It occurs in wet habitats, but is sometimes known from streams. Such moist habitats are provided by waterfalls, stream and river banks, moist slopes and dripping cliffs, springs, mires, seepage, wet soil, dune slacks, and roadside ditches. But it can in some circumstances venture farther from water, especially in gardens and greenhouses. It does especially well in greenhouses and gardens, perhaps due to dispersal gemmae by the watering regime.

Lunularia cruciata was the subject of a number of early physiological studies – finding positive gravitropism, conduction in midrib cells and between scales and rhizoids, hydrophobic pores, greater growth in response to short day length, desiccation hardening in long days, high temperatures and continuous light induce dormancy, lunularic acid protects against drought, inhibition of gemma germination by the thallus, and effects of higher temperatures on inhibiting gemmae.

Lunularia cruciata is highly resistant to pollution, but it can accumulate heavy metals and thus serves as a biological monitor. Flat, overlapping thalli and accompanying other bryophytes help to maintain moisture.

Various compounds in ***Lunularia cruciata*** are effective in inhibiting growth of bacteria. Fungi form various relationships from surface colonies to beneficial to parasitic. ***Lunularia cruciata*** has allelopathic properties against some seeds.

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.

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