CHAPTER 9-5

LIGHT: REFLECTION AND FLUORESCENCE

JANICE M. GLIME AND MAGDALENA TURZAŃSKA

TABLE OF CONTENTS

CHAPTER 9-5

LIGHT: REFLECTION AND FLUORESCENCE

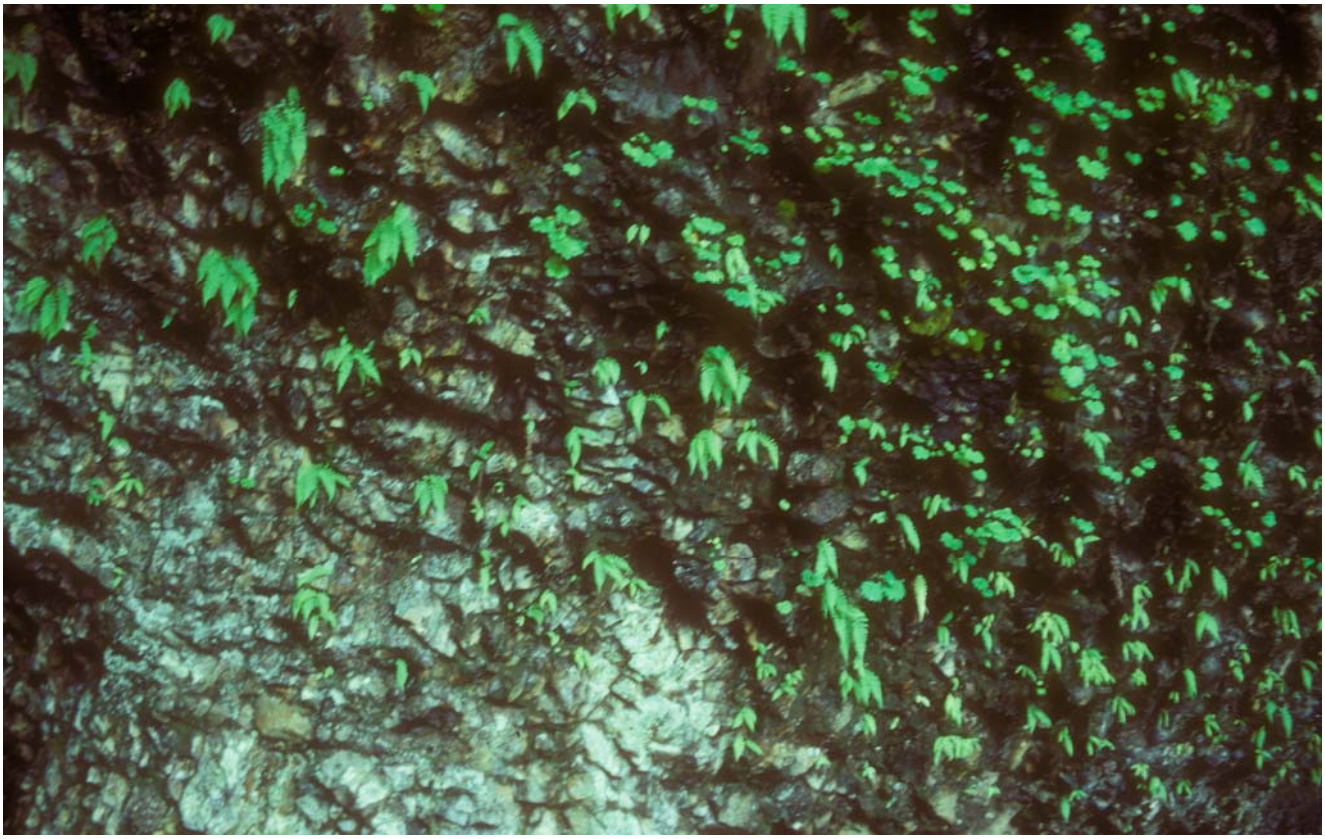

Figure 1. ***Schistostega pennata***, the luminous moss, growing on the roof of a cave in Rausu, Japan. Photo by Janice Glime.

Cave Mosses - Reflectance

Caves provide a classical example of gradients, with diminishing light and temperatures gradually descending or ascending from the mouth to an interior temperature near 10°C. As light diminishes, so does ability of the plant to meet its light compensation point. Thus, through this gradient, we see that flowering plants are the least tolerant, then ferns, followed by bryophytes, and last algae as the most tolerant (Dalby 1966b).

In non-commercial caves where light diminishes rapidly, or in buried lava caves, finding these bryophytes can be difficult and time consuming. Hanley (1982) used an echo sounder to locate bryophytes in caves and other dark areas such as deep lakes. However, in many caves, artificial lights provide sufficient illumination for algae, bryophytes, and ferns to succeed deep within the cave (Boros 1964). In fact, in many commercial caves, bryophytes have been considered to be a nuisance and measures have been taken to remove them, often using sodium hypochlorite. However, to avoid release of chlorine and other dangerous gases into caves, researchers tested hydrogen peroxide. But even the dilute 15% hydrogen peroxide necessary to remove bryophytes is destructive to fragile limestone formations, and the solution must be buffered with bits of limestone rock for at least 10 hours before its application (Faimon *et al*. 2003). I fail to understand why the bryophytes are considered offensive!

Schistostega pennata – Luminous Moss

No moss seems to be revered more than the clandestine cave moss ***Schistostega pennata*** (Figure 1-Figure 3), also known as dragon's gold (Berqvist 1991). Always a delight to find, its protonemata shine like emerald jewels from the darkness of a rock crevice or cave. So intriguing is this moss that the Japanese have a monument to it in Hokkaido (Iwatsuki 1977, Kanda 1988; Figure 2), where it grows in profusion in a cave barely large enough for a child to stand. At just the right position, you can see its marvelous reflections, but move the wrong way and they

are lost. The frond-like gametophyte and terminal sporophyte have none of that ethereal luminescent quality (Figure 3). Ignatov *et al*. (2012) examined the developmental pattern of this species and determined that it has sexual reproduction in September.

Figure 2. Monument to ***Schistostega*** in Hokkaido, Japan. Photo by Janice Glime.

Figure 3. ***Schistostega pennata*** plants showing their frond-like appearance and capsules at the end of the stem. Photo by Martin Hutten, with permission.

This unusual jewel-like property (Figure 4) is the result of the protonema (Gistl 1926). The cells are lens-shaped (Figure 7) and their upper surface is curved in such a way as to focus the light on the interior of the cell (Figure 6; Figure 5). This "normal" form is reached only when they grow in light that comes at all times from the same oblique direction. The chloroplasts orient themselves so that they are always at the most intensely lighted spot on the inner wall of the cell (Figure 7). If a change in the light direction occurs, as may happen seasonally, the chloroplasts can reposition themselves within one to three hours.

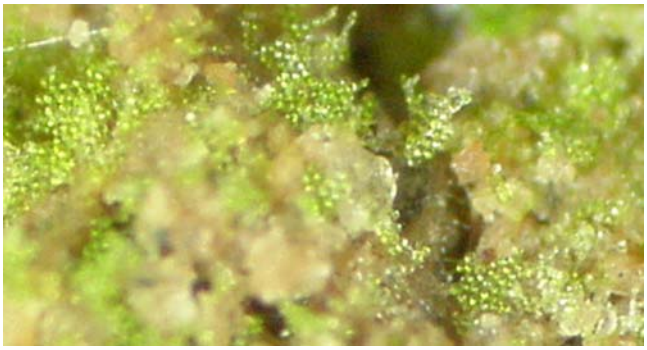

Figure 4. Protonemata of ***Schistostega pennata*** showing upright clumps. Photo courtesy of Misha Ignatov.

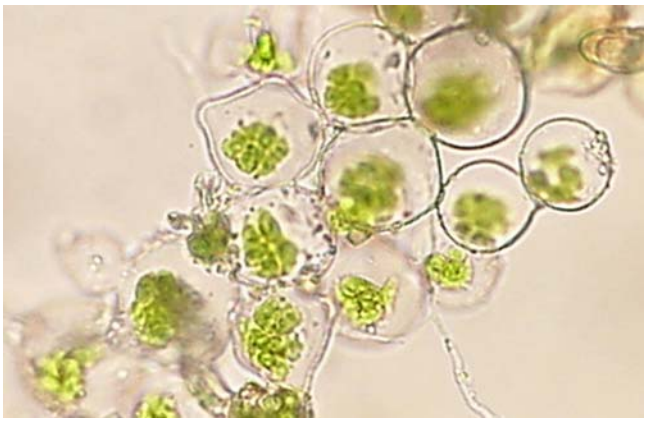

Figure 5. Protonema of ***Schistostega pennata*** showing lens-shaped cells. Photo courtesy of Misha Ignatov.

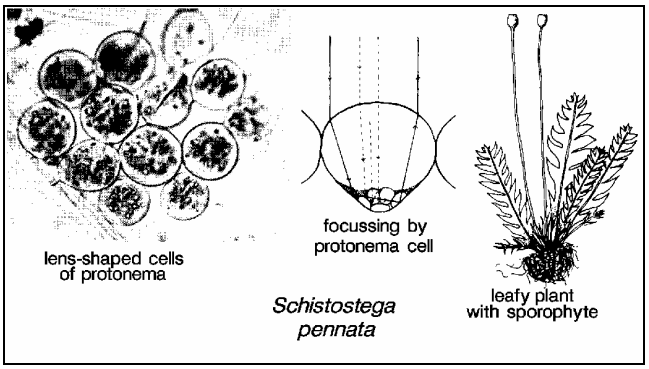

Figure 6. The cave moss, ***Schistostega pennata***, reprinted with permission from Zen Iwatsuki.

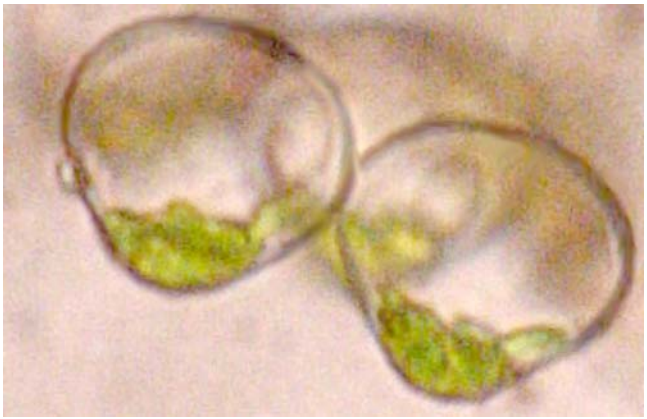

Figure 7. Lens-shaped cells of protonema of ***Schistostega pennata*** with chloroplasts arranged on one side of cell to focus light. Photo courtesy of Misha Ignatov.

Like Crum (1973), we find appeal in retelling the account by Kerner von Marilaun in *Pflanzenleben*, as translated by F. W. Oliver in *The Natural History of Plants*:

> "On looking into the interior of the cave, the background appears quite dark, and an ill-defined twilight only appears to fall from the center on to the side walls; but on the level floor of the cave innumerable golden-green points of light sparkle and gleam, so that it might be imagined that small emeralds had been scattered over the ground. If we reach curiously into the depth of the grotto to snatch a specimen of the shining objects, and examine the prize in our hand under a bright light, we can scarcely believe our eyes, for there is nothing else but dull lusterless earth and damp, mouldering bits of stone of yellowish-grey color! Only on looking closer will it be noticed that the soil and stones are studded and spun over with dull green dots and delicate threads, and that, moreover, there appears a delicate filigree of tiny moss-plants, resembling a small arched feather stuck in the ground [Figure 10]. This phenomenon, that an object should only shine in dark rocky clefts, and immediately lose its brilliance when it is brought into the bright daylight, is so surprising that one can easily understand how the legends have arisen of fantastic gnomes and cave-inhabiting goblins who allow the covetous sons of earth to gaze on the gold and precious stones, but prepare a bitter disappointment for the seeker of the enchanted treasure; that, when he empties out the treasure which he hastily raked together in the cave, he sees roll out of the sacks, not glittering jewels, but only common earth. . . . On the floor of rocky caves one may discern by careful examination two kinds of insignificant-looking plant-structures, one a web of threads studded with small crumbling bodies, and the other bluish-green moss-plants resembling tiny feathers. The threads form the so-called protonema, and the green moss-plants grow up as a second generation from this protonema ... the gleams do not issue from the green moss-plants, but only from their protonema."
>
> "From the much branched threads ... numerous twigs rise up vertically, bearing groups of spherical cells arranged like bunches of grapes. All the cells of a group lie in one plane, and each of these plants is at right angles to the rays of light entering through the aperture of the rocky cleft. Each of the spherical cells contains chlorophyll-granules, but in small number ... and they are always collected together on those sides of the cells which are turned towards the dark background of the cave.... Taken together, these chlorophyll-granules form a layer which under low power of the microscope appears as a round green spot ... the light which falls on such cells through the opening of a rocky cleft behaves like the light which reaches a glass globe at the further end of a dark room. The parallel incident rays which arrive at the globe are so refracted that they form a cone of light, and since the hinder surface of the globe is within this cone, a bright disc appears on it. If this disc, in which the refracted rays of light fall, is furnished with a lining, this also will be comparatively strongly illuminated by the light concentrated on it and will stand out from the darker surroundings as a bright, circular patch.... It is well worthy of notice that the patch of green chlorophyll-granules on the hinder side of the spherical cell extends exactly so far as it is illumined by the refractive rays, while beyond this region, where there is no illumination, no chlorophyll granules are to be seen. The refracted rays which fan on the round green spot are, moreover, only partially absorbed; in part they are reflected back as from a concave mirror, and these reflected rays give a luminous appearance. This phenomenon, therefore, has the greatest resemblance to the appearance of light which the eyes of cats and other animals display in half-dark places, only illumined from one side, and so does not depend upon a chemical process, an oxidation, as perhaps does the light from a glow-worm or of the mycelium of fungi which grow on decaying wood. Since the reflected light-rays take the same path as the incident rays had taken, it is clear that the gleams of the ***Schistostega*** can only be seen when the eye is in the line of the incident rays of light. In consequence of the small extent of the aperture through which the light penetrates into the rock cleft, it is not always easy to get a good view.... If we hold the head close to the opening, we thereby prevent the entrance of the light, and obviously in that case no light can be reflected. It is, therefore, better when looking into the cave to place one's self so that some light at any rate may reach its depth. Then the spectacle has indeed an indescribable charm."

The result of these very reflective chloroplasts in ***Schistostega pennata*** is that the protonema takes on the appearance of "goblin gold" and can create quite eerie effects (Figure 4-Figure 5; Figure 8-Figure 9).

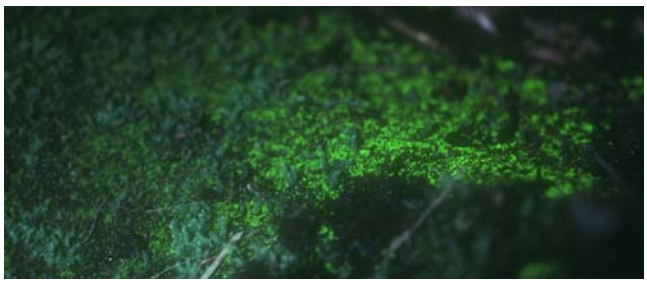

Figure 8. Luminous appearance of ***Schistostega pennata*** protonemata. Photo by Janice Glime.

Figure 9. Luminous protonemata of ***Schistostega pennata*** in natural light. Photo by Martin Hutten, with permission.

Figure 10. A single plant of ***Schistostega pennata*** among its protonemata, the "small arched feather." Photo by Des Callaghan, with permission.

In Japan, there is an opera written about this moss! The opera, written by Ikuma Dan, is based on a book of the same title, "Luminous Moss," by Taijun Takeda (Glime & Iwatsuki 1987). The story relates the tragedy of several sailors who were stranded by a blizzard on the northern island of Hokkaido. With no hope of escaping that remote northern tip of the island before spring to find food and shelter elsewhere, they hid in a cave. As their rations ran out and their fellow sailors died of starvation, they did the only thing they could to survive – they became cannibals. Finally, the captain alone remains. When he is brought to trial for his unthinkable acts, he reflects on the halo of green (the luminous moss) about the heads of each who has been a cannibal, but he tells the courtroom that the halo is visible only to those who have not been cannibals. He alludes to the cannibal in each of us as we struggle to survive among the millions of the world. Today a cave in Hokkaido is set aside as a memorial to protect this unusual moss (Kanda 1971, 1988; Figure 2).

Schistostega pennata (Figure 8-Figure 10) is widespread in the North Temperate Zone. Bowers (1968) and Conard (1938) have reported it from the Upper Peninsula of Michigan, where I have seen it growing on the roof of a cave behind a waterfall. Outside that same cave, I have observed the leafy gametophore, which resembles a tiny fern frond (Figure 11), growing on a small ledge of the rock wall, but protonemata there, if present, did not exhibit their highly reflective property. Bowley (1973) found the moss in several localities in Vermont, Champlin (1969) reported it from Rhode Island, Christy and Meyer (1991) from Wisconsin, Case (1975) found it in Alberta, Canada. Matsuda (1963) reported it in artificial caves in Japan. Perhaps the most unusual report is that of Koike (1989) who reported its culture in empty bottles in urban areas of Japan. Reinoso Franco *et al*. (1994) considered it to be an acidophile, at least on the Iberian Peninsula.

When I went to Germany, I was delighted to find ***Schistostega pennata*** (Figure 8-Figure 11) growing at the base of a boulder where it probably did not get direct sunlight except at sunset and most likely did not get direct rainfall very often either. Perhaps one reason for its success in such habitats is the presence of protonemal gemmae (Edwards 1978). In the Europe, ***Schistostega pennata*** also grows in rabbit holes (Glenny 2020).

Figure 11. ***Schistostega pennata*** showing frond-like branches of leafy gametophyte. Photo with permission from Botany Website, UBC, with permission.

Cyathodium

In the thallose liverwort genus ***Cyathodium*** (Figure 12), some species that grow in caves and similar low-light environments also emit a yellowish luminescence from their thalli (Crum 1973). These liverworts are tropical and subtropical and in China grow in karst caves (Zhang *et al*. 2004).

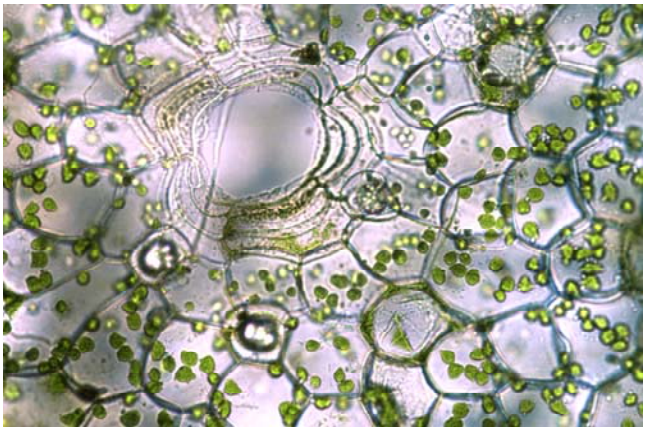

Figure 12. View through pore of ***Cyathodium cavernarum***, a thallose cave liverwort that emits a yellowish luminescence in caves. Photo by Noris Salazar Allen.

Mittenia plumula

In Australia, a similar moss, ***Mittenia plumula*** (Figure 13), lives on dimly lit, clay-covered rock ledges, at the entrances to wombat holes (Figure 14-Figure 15), and on tip-up mounds of fallen trees (Figure 16-Figure 17). The latter habitat makes the moss rather common after cyclone damage that causes trees to topple. In these locations, the moss lives on soil. Stone (1961, 1986) concluded that ***Mittenia*** belongs in the order **Schistostegales** with ***Schistostega*** (Figure 1-Figure 11). Both have a pinnate leaf arrangement, protonemata with similar luminescent properties, similar pale color of the leafy plant, and similar habitats.

Figure 13. ***Mittenia plumula*** showing leaves with bluish tint. Photo courtesy of David Glenny.

Figure 14. ***Mittenia plumula*** in wombat hole in Australia. Photo by Tony Markham, with permission. See <https://www.youtube.com/watch?v=PaXJTcaz1RE>.

Figure 15. ***Mittenia plumula*** growing in a wombat hole in Australia. Photos by Janice Glime.

Figure 16. ***Mittenia plumula*** habitat on tip-up mound. Photo courtesy of David Glenny.

Figure 17. ***Mittenia plumula*** protonemata on tip-up mound. Photo courtesy of David Glenny.

Mittenia plumula differs from ***Schistostega pennata*** by having protonemata with cylindrical filaments instead of spherical cells that act as a lens. Unlike ***Schistostega pennata*** (Figure 1-Figure 11), where the protonemal cells are spherical and are obviously acting as a lens, the

protonema of ***Mittenia plumula*** (Figure 18-Figure 20) is composed of cylindrical filaments and the chloroplasts are not on one side of each cell to take advantage of focused light. Nevertheless, under the compound microscope there is a faintly visible blue luminescence from the filament walls. This luminescence resembles the iridescence seen in some tropical plants of dark forest floors, for instance in ***Selaginella willdenowii*** (Figure 21).

Figure 18. ***Mittenia plumula*** protonemata in rabbit hole. Photo from Wildlife in the Marches at <www.youtube.com> .

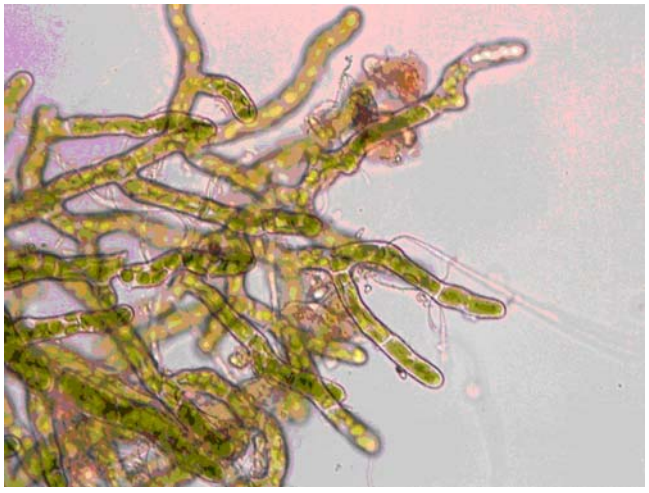

Figure 19. ***Mittenia plumula*** protonemata. Photo courtesy of David Glenny.

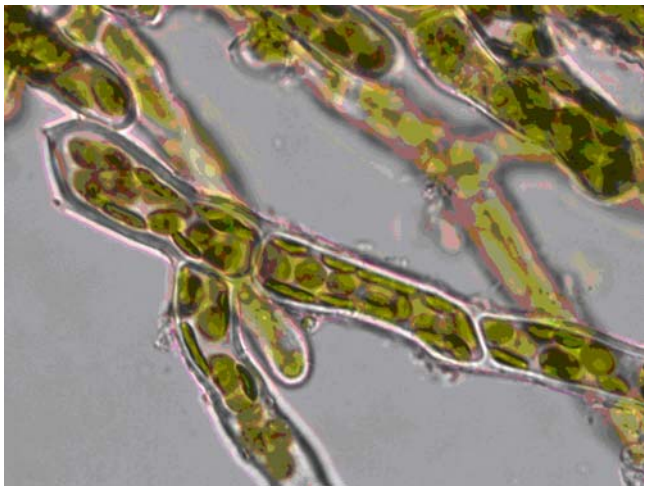

Figure 20. ***Mittenia plumula*** protonemata. Photo courtesy of David Glenny.

Figure 21. ***Selaginella willdenowii*** exhibiting **iridescence**. Photo courtesy of David Glenny.

Cave Communities

Growth of other bryophytes in caves far from a natural light source has been a source of fascination for both bryologists and non-bryologists all over the world, and these bryophytes often form zones around electric lights (Haring 1930). So fascinating are these plants of low light that their descriptions have appeared in non-botanical journals. Boros (1964) was able to publish a paper in the first volume of the *International Journal of Speleology* (**speleology** is the study of caves), reporting on mosses growing around electric light sources deep within a cave. Dalby (1966b) later published a similar article on their growth under reduced light in caves, this time in the first volume of *Studies in Speleology*. Numerous communities have been described from caves around the world: Shiomi (1973) in Japan; Maheu and Guerin (1935) in France; Rajczy (1979) in Greece; Ziober (1981), Komáromy *et al*. (1985), Rajczy *et al*. (1986), and Buczkó and Rajczy (1989) in Hungary; Lo Giudice & Privitera (1984) in Italian grottos; Stefureac (1985) in Romanian grottos; Weber (1989) for both animals and flora, including bryophytes, in two German caves and artificial caverns; Kubešová (2009) in the Czech Republic. Even *Science* has accepted articles on mosses in Virginia (USA) caverns, including the famous Luray Cavern (Lang 1941, 1943), and Prior (1961) again studied Luray Cavern mosses, publishing in *The Bryologist*.

Most cave bryophytes are not specific to these habitats. Reinoso Franco *et al*. (1994) have found ***Schistostega pennata*** with ***Isopterygium elegans*** (Figure 22; low-light species of canyons and crevices), ***Diplophyllum albicans*** (Figure 23; forest epiphyte), ***Calypogeia arguta*** (Figure 24), ***C. azurea*** (Figure 25; also an epiphyte), ***Pogonatum nanum*** (Figure 26), and ***Fissidens curnovii*** at a *p*H of 5.7 in caves.

Figure 22. ***Isopterygium elegans***, a species that is able to grow in low light. Photo by Michael Lüth, with permission.

Figure 23. ***Diplophyllum albicans***, a species that is able to grow in low light. Photo by Michael Lüth, with permission.

Figure 24. ***Calypogeia arguta***, a species that is able to grow in low light. Photo by Des Callaghan, with permission.

Figure 25. ***Calypogeia azurea***, a species that is able to grow in low light. Photo by Hermann Schachner through Creative Commons.

Figure 26. ***Pogonatum nanum***, a species that is able to grow in low light. Photo by J. C. Schou, with permission.

The widespread ***Fissidens taxifolius*** (Figure 27) grew in Crystal Caverns in Virginia, USA, and aroused the curiosity of a visitor who delivered it to Conard (1932). This moss grew on the damp ceiling, forming circles about 8" from several electric light bulbs, having appeared only a few years earlier. The moss looked normal, but the leaves were further apart than in typical specimens, not an unusual trait for a moss of low light.

Figure 27. ***Fissidens taxifolius***, a common moss that can grow on the ceiling of caves. Photo by Jan-Peter Frahm, with permission.

A variety of species seem to be capable of growing in caves. Buczkó & Rajczy (1989) reported nineteen bryophyte taxa from three caves in Hungary. Dalby (1966a) reported the occurrence of the **tufa**-former (rock former resulting in carbonates built upon bryophytes and other plants due to addition of photosynthetic oxygen to dissolved minerals), ***Eucladium verticillatum*** (Figure 39), in a poorly lit cave, also occurring in caves in Hungary (Buczkó & Rajczy 1989). In Crystal Cave, Wisconsin, Thatcher (1949) found ***Barbula unguiculata*** (Figure 28), ***Brachythecium populeum*** (Figure 29), ***Brachythecium salebrosum*** (Figure 30), ***Bryoerythrophyllum recurvirostrum*** (Figure 31), ***Bryum caespiticium*** (Figure 32), ***Bryum capillare*** (Figure 33), ***Ceratodon purpureus*** (Figure 34), ***Fissidens taxifolius*** (Figure 27), ***Leptodictyum riparium*** (Figure 35), ***Marchantia polymorpha*** (Figure 36), ***Plagiomnium cuspidatum*** (Figure 37), and ***Warnstorfia fluitans*** (Figure 38). Like Conard, Thatcher observed the leaves to be more distant than is typical.

Figure 28. ***Barbula unguiculata***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 29. ***Brachythecium populeum*** with capsules, a species that is able to grow in caves. Photo by Janice Glime.

Figure 30. ***Brachythecium salebrosum***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 31. ***Bryoerythrophyllum recurvirostrum***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 32. ***Bryum caespiticium*** with capsules, a species that is able to grow in caves. Photo by Bob Klips, with permission.

Figure 33. ***Bryum capillare***, a species that is able to grow in caves. Photo by Andrew Spink, with permission.

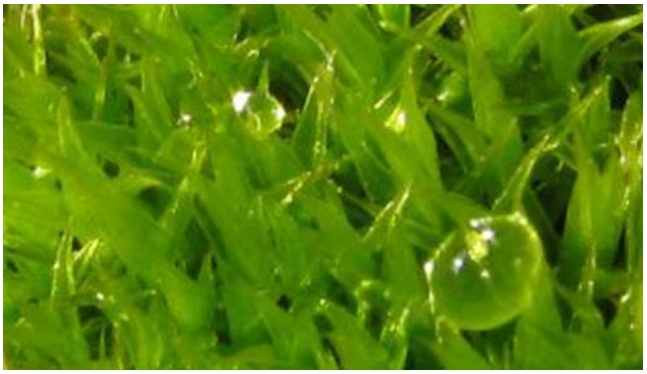

Figure 34. ***Ceratodon purpureus***, a species that is able to grow in caves. Photo by Jiří Kameníček, with permission.

Figure 35. ***Leptodictyum riparium***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 36. ***Marchantia polymorpha***, a species able to grow in caves. Photo from Botany Website, UBC, with permission.

Figure 37. ***Plagiomnium cuspidatum***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Figure 38. ***Warnstorfia fluitans***, a species that is able to grow in caves. Photo by Michael Lüth, with permission.

Komáromy *et al*. (1985) likewise found ***Eucladium verticillatum*** (Figure 39), a ***Brachythecium*** (***B. velutinum***), and two species of ***Fissidens*** [***F. dubius*** (Figure 40), ***F. pusillus*** (Figure 41)] in a cave. Within only one year from its first illumination, Howe Cavern in New York, USA, already was adorned with ***Amblystegium serpens*** (var. ***juratzkanum***; Figure 42), ***Amphidium mougeotii*** (Figure 43), ***Brachythecium rutabulum*** (Figure 44), ***Bryum caespiticium*** (Figure 32), ***Bryum capillare*** (Figure 33), ***Leptobryum pyriforme*** (Figure 45), and ***Marchantia polymorpha*** (Figure 36) encircling its new lights (Haring 1930). Buczkó and Rajczy (1989) found that ***Amblystegium serpens*** (=*A. juratzkanum* var. *juratzkanum*; Figure 42) was the most characteristic moss in several Hungarian caves, extending furthest from the cave entrance that provided the only light, surviving at only 232 lux. Niklas Lönnell reported to Bryonet (3 March 2010) that ***Eucladium verticillatum*** (Figure 39) introduced at an underground station in Stockholm, Sweden, thrives decades later on moist areas of the walls where artificial light is available.

Figure 39. ***Eucladium verticillatum***, a tufa-forming moss. Photo by Michael Lüth, with permission.

Figure 40. ***Fissidens dubius***, a known cave dweller. Photo by Bernd Haynold, through Creative Commons.

Figure 41. ***Fissidens pusillus***, a species known to live in caves. Photo by Michael Lüth, with permission.

Figure 42. ***Amblystegium serpens***, a common cave moss in Hungary. Photo by Michael Lüth.

Figure 43. ***Amphidium mougeotii***, a species that colonized within one year around lights in a cave. Photo by Michael Lüth, with permission.

Figure 44. ***Brachythecium rutabulum*** with capsules, a species that colonized around lights in a cave within one year. Photo by Tim Waters, through Creative Commons.

Figure 45. ***Leptobryum pyriforme***, an invader of bare soil in caves. Photo by Michael Lüth.

Tufa formers such as ***Eucladium*** (Figure 39) (von der Dunk & von der Dunk 1980), ***Barbula*** (Figure 28), and ***Didymodon*** (Figure 46) are found in many of these caves, since the caves are usually limestone, and tufa formers must be adapted to relatively dim light to survive the calcium carbonate covering they must endure.

Figure 46. Tufa-forming ***Didymodon tophaceus***, a former of didymodontoliths. Note carbonates at base encrusted on older stems. Photo by Michael Lüth, with permission.

With all these reports, it is not unexpected then that Koponen (1977) reported mosses at a depth of 176 m in a mine at Vihanti, Finland. The surprising fact is that the mosses he found are the very light-tolerant ***Ceratodon purpureus*** (Figure 34) and ***Pohlia nutans*** (Figure 47). But then, these two mosses seem to do well in extremes, as long as it is not too hot.

Jedrzejko and Ziober (1992) illustrated the effects of light on the species composition of moss communities and the ability of mosses to survive at low light intensities with their study of bryophytes in seven Polish caves. More than 50% of the bryophyte flora occurred where they had full access to daylight. As the investigators went deeper into the caves, the number of species decreased, but with 1.3% of the species occurring only in the darkest zone.

Figure 47. ***Pohlia nutans***, a widespread moss that frequents caves and mines. Photo by Michael Lüth.

Rockhouses

Rockhouses are really just small caves created by deep recesses in bedrock cliffs. But despite their smaller size, they can create conditions much different from those of their surroundings outside the cavity. They tend to be buffered from extremes in both temperature and moisture, with cold blasts emanating in the summer and protection from severely cold winds in the winter. Nevertheless, despite their moderate climate, their low light levels greatly restrict the potential flora. It is therefore interesting that the greatest affinities of these floras are with the tropics (Farrar 1998). While the species in the rockhouses tend to be endemic to the eastern United States, the conditions created for them mimic the low light intensities of the dense rainforests. It is possible that the climatic moderation of the rockhouses might have permitted adapted plant groups to persist here since the time when a tropical/subtropical climate existed in the eastern US during the Pre-Pleistocene. It is in these secluded habitats that a number of endemic ferns reside, but the most numerous plants are the bryophytes. Farrar considered both groups to be preadapted to this habitat by their vegetative reproduction and their ability to have net photosynthetic gain in very low light.

Responses to Low Light in Caves

If you have ever picked up a board from your lawn, you know how thin and long the grass stems can be. This elongation response by plants in low light is termed **etiolation**. Dunham and Lowe (1927) described etiolation of bryophytes in caves and among boulders in New England, USA. But at least some light should be present, right? Nevertheless, Fries (1945) succeeded in growing the mosses ***Funaria hygrometrica*** (Figure 48) and ***Leptobryum pyriforme*** (Figure 45) from protonemata on inorganic media in total darkness. Thus, it would appear that some growth can occur, using the plant's reserves, even in the absence of light.

Rajczy (1978-1979) chose to experiment with growing mosses in total darkness of a cave. He used two common Hungarian species, ***Atrichum undulatum*** (Figure 50) and ***Plagiomnium ellipticum*** (Figure 51), which he planted in flowerpots along with their original soil. These were placed in a cave where the climate is very constant, having a temperature of 9.5 ±1ºC and 95-100% relative humidity. ***Plagiomnium ellipticum*** rapidly became brown and within three months had produced long, fine, vertical, leafless stems of 4-6 cm length. ***Atrichum undulatum***, on the other hand, remained green for two years. Its chloroplasts increased from a mean of 8.8 to 10.3 per cell from May to October. In the cave both species had a much higher ratio of dark CO_2 fixation that did the control samples from normal light (Table 1). One interesting event in Rajczy's experiment was that isopods (***Mesoniscus graniger***; Figure 49) consumed all the dead material of the plants. The mosses soon grew pale, then partly brown.

Figure 48. ***Funaria hygrometrica***, a species that is able to grow without a media carbon source in the dark. Photo by Michael Lüth, with permission.

Table 1. Incorporation of CO_2 into moss biomass in caves compared to controls. From Rajczy 1978-1979.

$^{14}CO_2$ Incorporation				
	Net Activity (cmp/leaf)			Contrib dk
	total fix	dark fix	light fix	fix to total fix
Atrichum undulatum				
control	898	85	813	9%
cave sample	174	81	93	47%
Plagiomnium ellipticum				
control	3790	340	3450	9%
cave sample	550	220	330	40%

Figure 49. ***Mesoniscus graniger***, an isopod consumer of dead mosses. Photo by Richard Kovács, through Creative Commons.

When ***Atrichum undulatum*** (Figure 50) cells were examined with the electron microscope after four months of experiment (September), the chloroplasts differed considerably from those of the control plants. The size of the grana had increased but their number decreased and they were arranged mostly at the periphery of the chloroplast. There were no starch grains. Then, in March, there was a most unexpected change. The chloroplasts contained starch once more and the grains appeared to be identical to those of the control plants. Thylakoids (Figure 52) were even thinner than in September, and only 1-2 stroma thylakoids were present. From 3 to 10 broad, low grana were present.

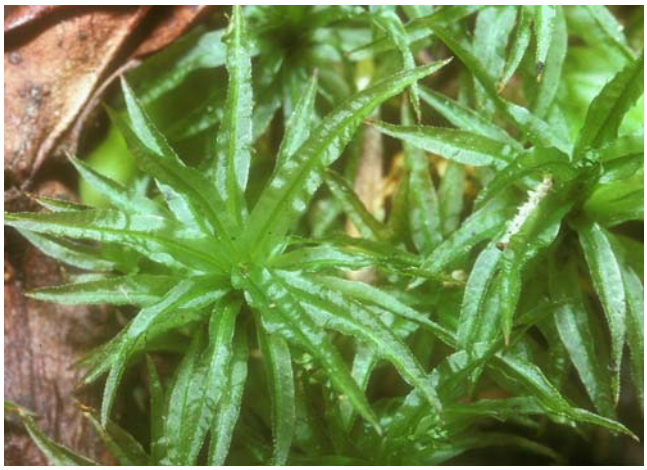

Figure 50. ***Atrichum undulatum***, a species that acclimates to living in caves. Photo by Janice Glime.

Figure 51. ***Plagiomnium ellipticum***, a species that seems unable to live in the low light of caves. Photo by Michael Lüth, with permission.

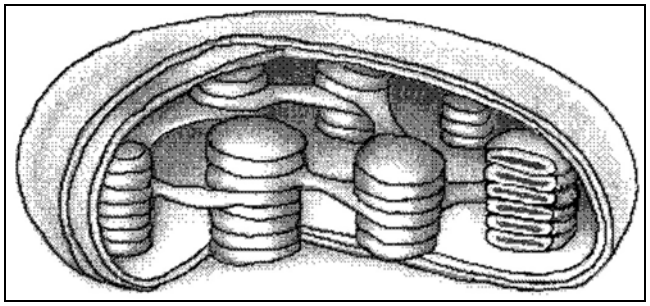

Figure 52. Chloroplast with cutaway view to show inner and outer membrane, stacks of thylakoids that form grana, and connecting stroma. Drawing by Janice Glime

Surprisingly, ***Plagiomnium ellipticum*** (Figure 51) also had starch grains in March. However, these were not like those of their control plants. Some were far larger, and most chloroplasts lacked them. Most of the chloroplast envelopes were torn up.

In April, samples taken from the cave to the lab had measurable photosynthesis, although they had no exposure to light prior to the time of measurement. For ***Atrichum undulatum*** (Figure 50), photosynthesis reached 15-20% of that in the controls. Both species retained some photosynthetic activity for the two years of the experiment, but that of ***Atrichum undulatum*** was greater.

Rajczy (1978-1979) interpreted these results to mean that the mosses were subsisting on heterotrophic energy sources. He could find no other explanation for the sudden appearance of starch after 10 months in the cave. Furthermore, he cited the dark-culturing experiments of Servettaz (1913), Pringsheim and Pringsheim (1935), and Fries (1945) to support his position. Could the mosses be using electromagnetic rays? symbiosis? chemosynthesis? Cave algae are known to subsist using these unusual methods of obtaining energy (Kol 1966; Hadju 1979). And why did both species [***Atrichum undulatum*** (Figure 50) and ***Plagiomnium ellipticum*** (Figure 51)] have starch grains in March when the grains had disappeared earlier? Did some endogenous rhythm, lacking stimulus by photoperiod or temperature, trigger a change in metabolic activity?

Reflectance in the Desert

In desiccation-tolerant species, surface properties often change. This can result in a change in surface reflectance, as exemplified in the xerophytic moss ***Syntrichia ruralis*** (Figure 53) (Hamerlynck *et al*. 2000). In this species, distinct differences occur in the ability to establish thermal dissipation of excess light energy throughout a range of light levels, helping to protect the sensitive chlorophyll and DNA.

Figure 53. ***Syntrichia ruralis***, a species that changes its optical properties when dry vs wet. Photo by Jan-Peter Frahm, with permission.

In the Antarctic, surface reflectance properties differed over a range of water content, but did not correlate with pigment content (Lovelock and Robinson 2002). Nevertheless, the photochemical reflectance was correlated with the concentrations of active xanthophyll-cycle pigments and the photosynthetic light use efficiency as

measured by chlorophyll fluorescence. The water content had a strong influence on both the amplitude and position of the red-edge and may itself cause the differences in reflectance. Continuous high levels of xanthophyll pigments indicate the continual high light levels.

Fluorescence and Other Light Emissions

(coauthored with Magdalena Turzańska)

Definitions

Wikipedia defines **fluorescence** as "emission of light by a substance that has absorbed light or other electromagnetic radiation of a different wavelength." One little-known property of at least some bryophytes is their ability to fluoresce various colors in UV light. Lichenologists are familiar with this property in lichens (Figure 54-Figure 55), using it as an identification tool (Hale 1956). Bees know it in flowers (we call them nectar guides), being attracted to fine lines of marsh marigold (*Caltha palustris* – Figure 56-Figure 57) and black patches of oriental poppy (*Papaver orientale* – Figure 58) petals and by their emission of fluorescence in the UV light of the sun. In fact, Talamond *et al*. (2015) consider **autofluorescence** to be abundant in plant cells. But bryologists seem rarely to use it

Figure 54. The lichen *Xanthoria polycarpa* in natural light. Photo through Creative Commons.

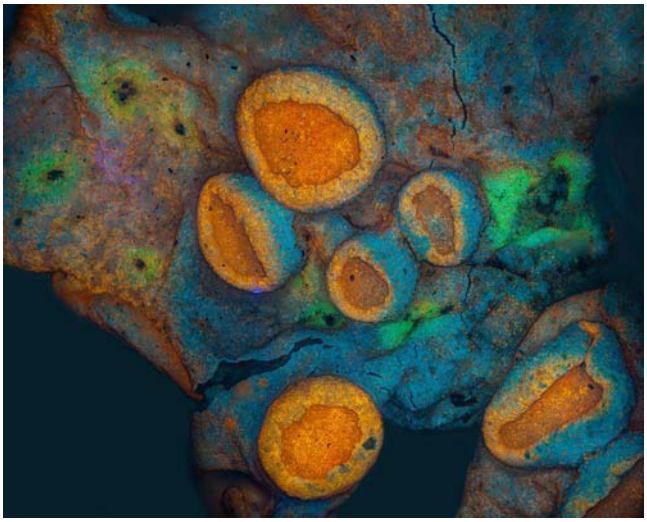

Figure 55. *Xanthoria polycarpa* showing fluorescence in UV light. Photo by Walter Machielsen, with permission.

Figure 56. *Caltha palustris*, a species whose flowers appear yellow to us, but that reflect UV rays seen by bees. Photo by H. Zell, through Creative Commons.

Figure 57. *Caltha palustris* in UV light, showing UV-reflecting lines. Photo courtesy of Dave Kofranek.

Figure 58. The oriental poppy (*Papaver orientale*) has patches that appear black to us, but that reflect UV light that is visible to bees, guiding them to the center of the flower where the pollen and stigma reside. Photo by Janice Glime.

Fluorescence should not be confused with **bioluminescence**. Fireflies have bioluminescence. Some dinoflagellates (think red tides) have bioluminescence. This is a form of chemiluminescence produced by living organisms. It requires a light-emitting molecule (**luciferin**)

and an enzyme (**luciferase**), wherein the enzyme catalyzes the oxidation of the luciferin. The luciferin and its associated enzyme differ among species. The reaction may also require **ATP** (energy-carrying molecule, adenosine triphosphate). In **luminescence**, something adds energy, causing an electron to get bounced from one orbital to another, emitting light, then decaying back down (Jerry Jenkins, Bryonet 23 April 2022). Bioluminescence is not known in land plants, but since it is present in some bacteria, it is possible that we have not discovered it in some bacteria-bryophyte associations. **Triboluminescence** results from mechanical energy such as crushing sugar cubes or rubbing quartz crystals. Heat produces **incandescence** (emitted from hot body as result of high temperature, *e.g.* incandescent light bulb).

Phosphorescence (microsecond decay that changes spin state, causing prolonged emission of light even in darkness) is a form of luminescence that results from the absorption of radiation (such as light or electrons) and continues for a noticeable time after these radiations have stopped. We have seen these in various items that glow in the dark after being exposed to light. I have seen them on cards with a cross or on ceilings to look like stars.

Fluorescence is not seen by the human eye during the day because our eyes are less sensitive to those short wave lengths and the longer "visible" light waves keep us from seeing it. However, with the right equipment, *i.e.* a UV light source, we can detect it. The discovery of a liverwort that was fluorescing precipitated one of the longest running threads on Bryonet.

Jerry Jenkins (Bryonet 23 April 2022) provided us with a detailed description of the light emissions from organisms. For example, he noted that the light emitted by ***Zygodon rupestris*** (=***Zygodon viridissimus* var. *rupestris***; Figure 59), shared by Ken Kellman (Bryonet 21 April 2022), could be **fluorescence** or **phosphorescence**. These cannot be distinguished just by using a UV flashlight.

Figure 59. ***Zygodon rupestris***, a species known for blue fluorescence. Photo by Jonathan Sleath, with permission.

It is intriguing that the ***Zygodon rupestris*** (Figure 59) does not emit this light when dry (Ken Kellman, Bryonet 21 April 2022). Kellman suggested that perhaps in the dry state the UV light is blocked from entering the cells and thus there is no stimulation. This could be possible due to structural changes that make the dry cells less transparent. A second possibility is that UV light is able to enter the cell, but that the change in structure due to drying makes it impossible for the emitted visible light to get out for us to see. Jenkins (Bryonet 23 April 2022) suggested that it is also possible that it is fluorescence that is quenched or red-shifted out of the visible range in the dry moss. This could be caused by neighboring molecules or by binding to membranes [or cell walls?]. Those neighbors can affect the energy levels and frequency of light emission of the excited electrons. (See Wilson & Hastings 2013 for more detail on the mechanism of fluorescence.)

Jerry Jenkins (Bryonet 23 April 2022) ultimately concluded that it was **photoluminescence** (which includes fluorescence) that emitted light from ***Zygodon rupestris*** (Figure 59) when irradiated with UV. The incoming UV photon interacts with an orbiting electron, causing it to achieve an excited state. Some of the photon energy is transferred to the electron. The remainder is used in vibrations and rotation. As the electron decays, it emits a photon, but with less energy than that of the incoming photon. Thus, the light has a longer wavelength and is shifted toward the red end of the spectrum into the visible spectrum.

Compounds That Fluoresce

The specific compounds in bryophytes that fluoresce have not been studied extensively. However, we know more about those in tracheophytes. Wolfbeis (1985) listed the following compounds from leaves that emit blue-green fluorescence: alkaloids (berberine, quinine, lysergic acid), aurones, chalcones, chromones, coumarins (umbelliferone, esculetin, scopoletin), flavones (except 5-hydroxyflavones), flavins (FMN, FAD, riboflavin), flavonols, furocumarins (psoralen), hydroxycinnamic acids (caffeic, ferulic, sinapic), isoflavones, nicotinamides (NADH, NADPH), phenolic acids (salicylic, gentisic, ellagic), polyenes (phytofluen), pterines (folic acid, dihydrofolate), quinones (phyllohydroquinone), stilbenes (resveratrol), other coenzymes (pyridoxal-5'-phosphate), and degradation products (kynurenine, polyadenylic acid).

The internal environment can modify the fluorescent response, including such factors as temperature, viscosity, spatial constraints, *p*H, polarity, and presence of quenchers, such as heavy metals and oxygen, influencing the spectral characteristics and yield (Cerovic *et al*. 1999).

Parts That Fluoresce

Chlorophyll fluorescence is well known in algae and plants, including bryophytes (Shi *et al*. 1992; Proctor & Smirnoff 2011), giving an indication of the health of the plant by its ability to emit light from its active chloroplasts (*e.g.* Csintalan *et al*. 1999; Deltoro *et al*. 1999; Arróniz-Crespo 2008). As in tracheophytes and algae, the chlorophyll of bryophytes fluoresces red in UV light. In the hornwort ***Anthoceros*** sp., the chlorophyll fluoresces a brilliant red whereas the cell walls fluoresce blue (Figure 60-Figure 64). In ***Fontinalis antipyretica***, the cell wall fluoresces yellow, contrasting with the red chloroplasts (Figure 65). A similar contrast is present in ***Sphagnum***, with photosynthetic cells showing red chlorophyll fluorescence and cell walls showing a blue-green fluorescence in UV light (Figure 66-Figure 68). In ***Funaria hygrometrica***, there is a strong chlorophyll fluorescence, but the cell walls seem to lack any

fluorescence visible in the UV light of a microscope (Figure 69).

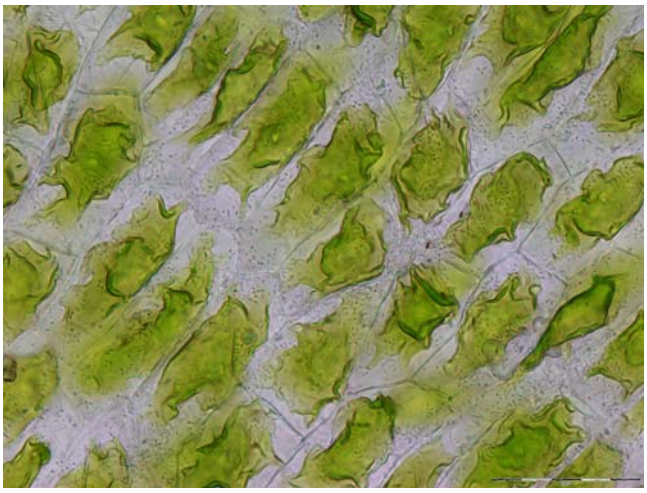

Figure 60. ***Anthoceros*** sp. gametophyte cells in white light. Photo by Magdalena Turzańska.

Figure 61. ***Anthoceros*** sp. gametophyte red chlorophyll fluorescence and cell walls fluorescing blue. Photo by Magdalena Turzańska.

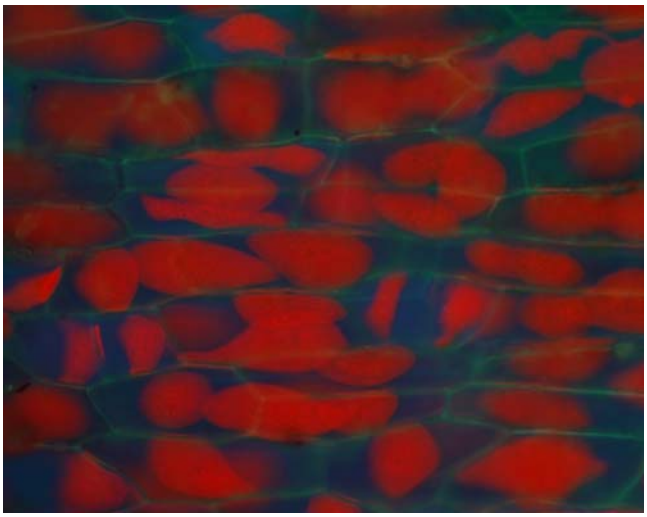

Figure 62. ***Anthoceros*** sp. gametophyte red chlorophyll fluorescence and cell walls fluorescing blue. Photo by Magdalena Turzańska.

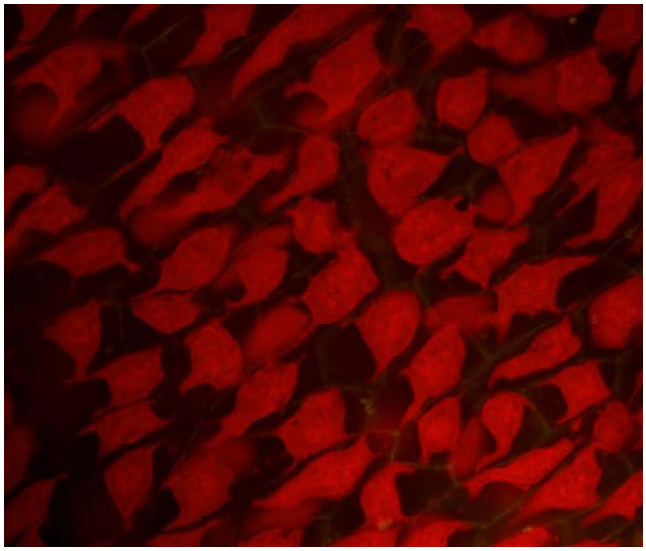

Figure 63. ***Anthoceros*** sp. gametophyte red chlorophyll fluorescence and cell walls fluorescing blue. Photo by Magdalena Turzańska.

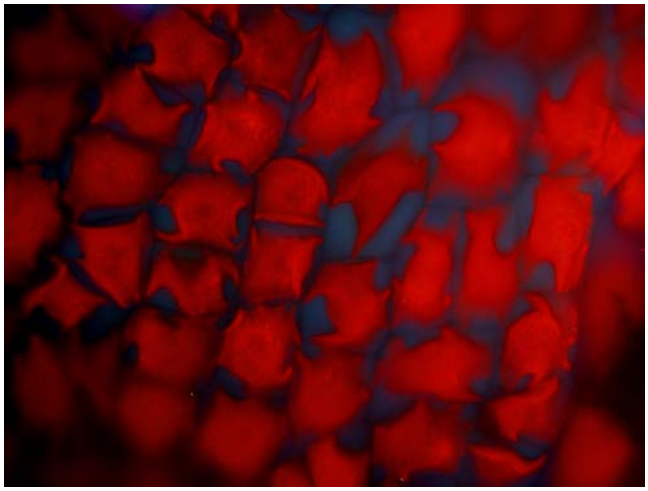

Figure 64. ***Anthoceros*** sp. gametophyte red chlorophyll fluorescence and cell walls fluorescing blue. Photo by Magdalena Turzańska.

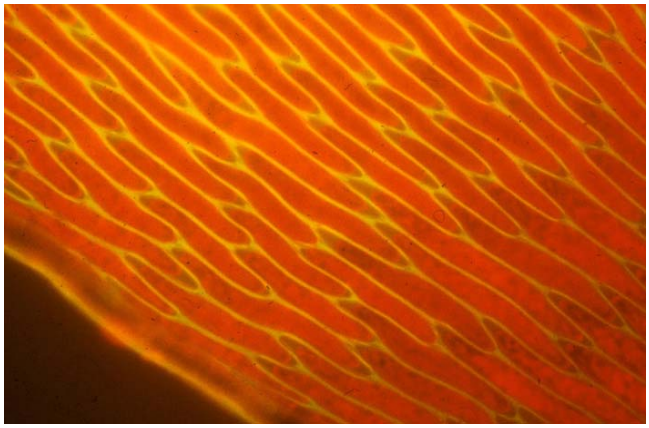

Figure 65. ***Fontinalis antipyretica*** cell wall showing yellow fluorescence, contrasting with the red of the chlorophyll fluorescence. Photo by Janice Glime.

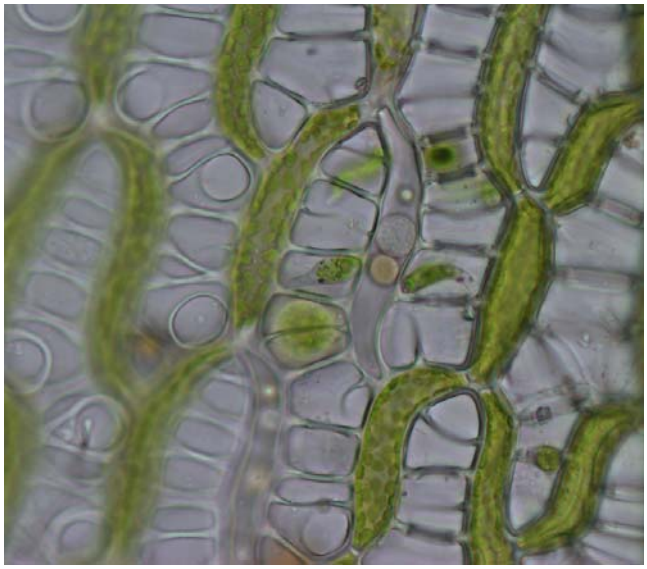

Figure 66. ***Sphagnum*** sp. leaf with algae in hyaline cells. Photo by Magdalena Turzańska.

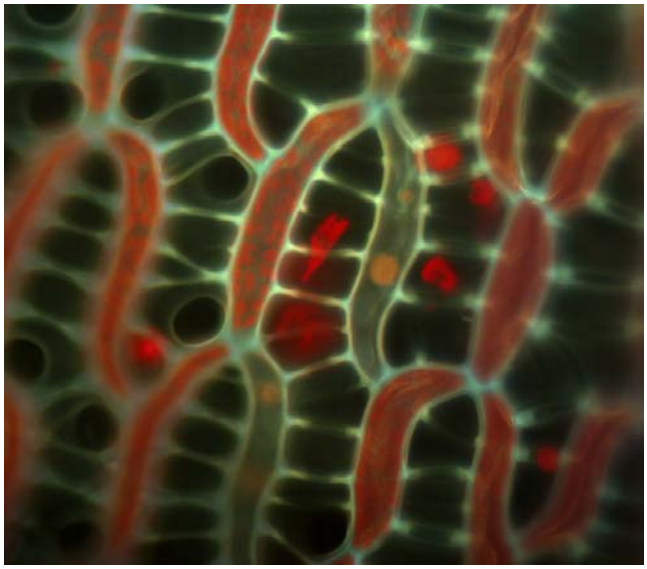

Figure 67. ***Sphagnum*** sp. leaf fluorescence of the leaf in Figure 66 with algae fluorescing red in hyaline cells and cell walls fluorescing greenish. Photo by Magdalena Turzańska.

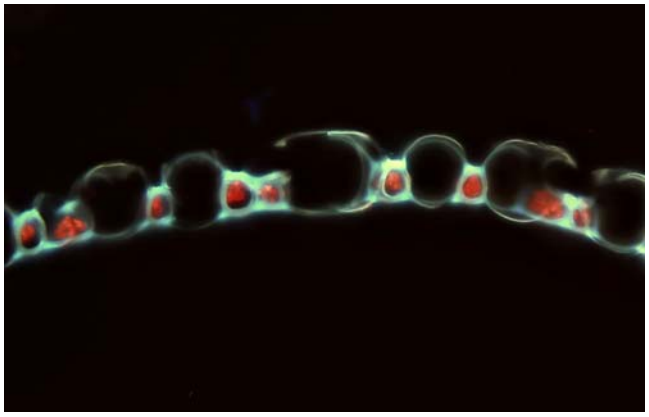

Figure 68. ***Sphagnum*** sp. leaf fluorescence in cross section with chlorophyll fluorescing red and cell walls fluorescing green in UV light. Photo by Magdalena Turzańska.

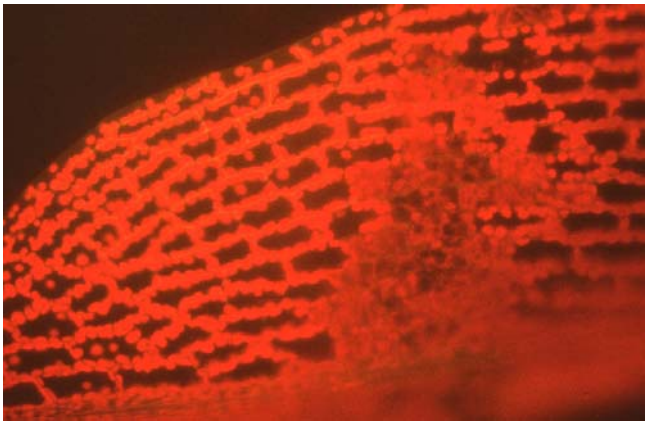

Figure 69. ***Funaria hygrometrica*** leaf chlorophyll fluorescence, showing the typical red fluorescence of that molecule. Note that the cell walls lack fluorescence under the UV light of a microscope. Photo by Janice Glime.

The use of fluorescence to detect the damage to chlorophyll has been established for some time (Proctor 2003). These uses include indication of effects of various intensities of desiccation (Proctor 2003) and of metal contaminant locations within the cell, as shown in ***Fontinalis antipyretica*** (Figure 70-Figure 71) (Chorvatova *et al*. 2021).

Figure 70. ***Fontinalis antipyretica***, an aquatic moss with cell wall fluorescence under UV light and a species where one can trace metals using fluorescence. Photo by Hermann Schachner, through Creative Commons.

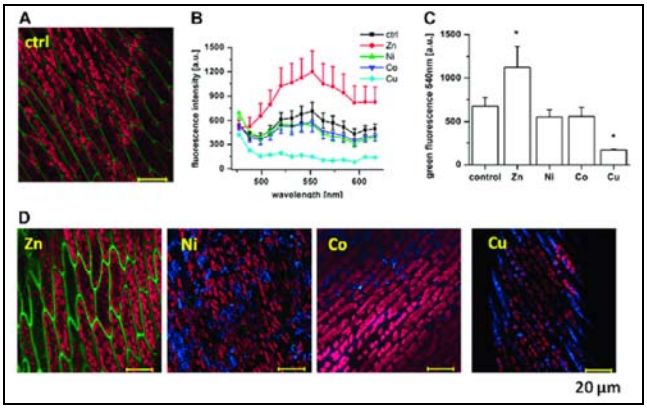

Figure 71. Fluorescence of various metals in ***Fontinalis antipyretica*** located by UV light. From Chorvatova *et al*. 2021.

Various parts of bryophytes are known to fluoresce. Ridgway and Larson (1966) reported on the usefulness of the fluorescence technique to follow sporogenesis in the hornwort ***Anthoceros*** sp. (Figure 72-Figure 76). Similar changes in color seem to occur in ***Riccia*** sp. (Figure 77-Figure 80). Using a UV microscope enables us to examine the development and greening of spores (Figure 78-Figure 79), protonemal bud initiation, callose distribution to find phloem-like elements, callose in cross walls of leptoids, events leading to egg formation, events following fertilization (Sarafis 1971; Brandes 1967), and locating elusive propagules (Nordhorn-Richter 1984 a,b,c, 1985 a,b, 1988).

Figure 72. ***Anthoceros punctatus***, member of a genus in which fluorescence permits us to follow development of spores, at least in some species. Photo by Jonathan Sleath, with permission.

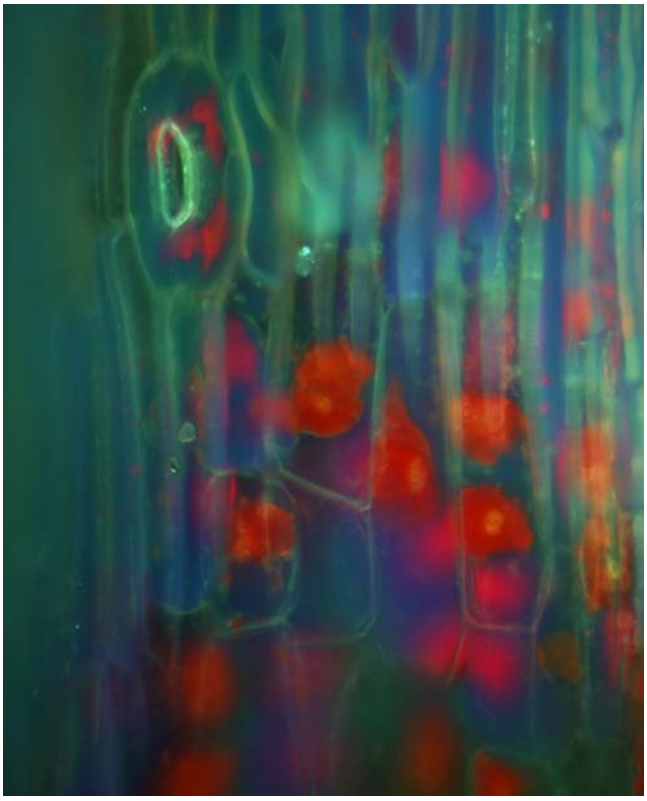

Figure 73. ***Anthoceros*** sp. sporophyte fluorescence showing greenish cell walls and red of chlorophyll in developing spores. Photo by Magdalena Turzańska.

Figure 74. ***Anthoceros*** sp. sporophyte fluorescence. Note the clarity of the stomatal openings. Photo by Magdalena Turzańska.

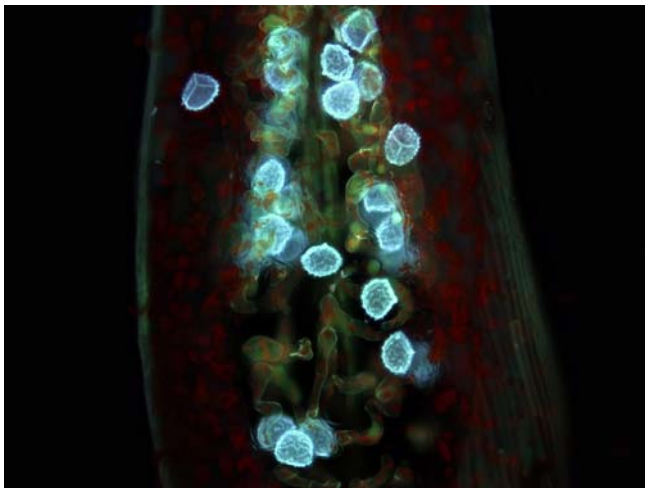

Figure 75. ***Anthoceros*** sp. sporophyte showing blue spore fluorescence. Photo by Magdalena Turzańska.

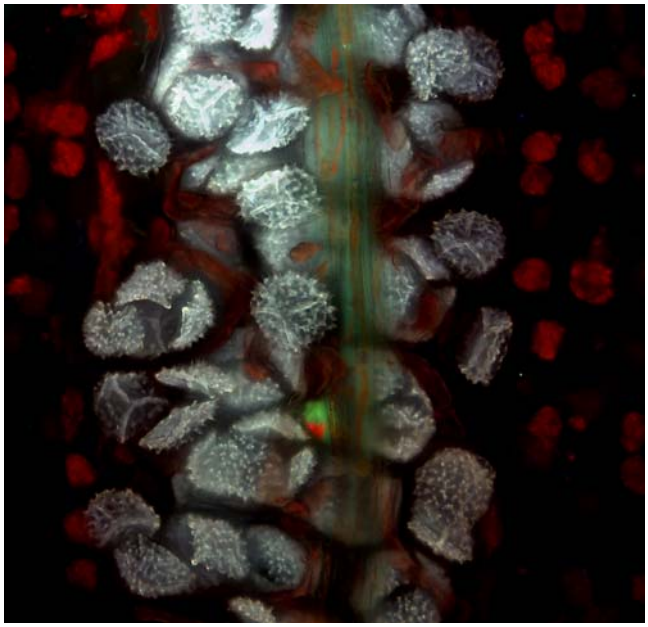

Figure 76. ***Anthoceros*** sp. sporophyte showing pale fluorescence. Photo by Magdalena Turzańska.

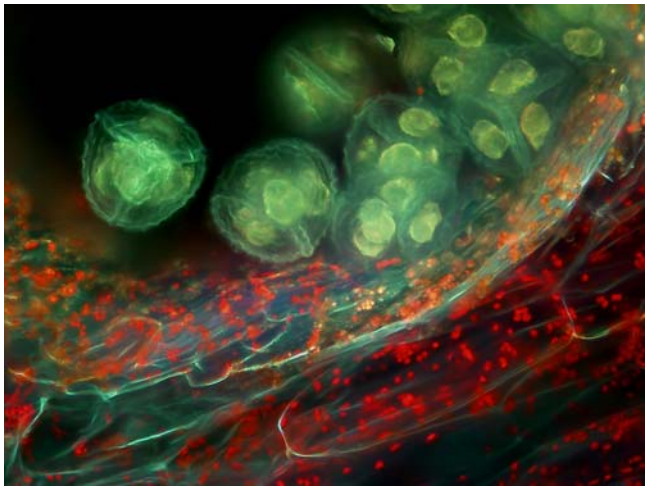

Figure 77. ***Riccia cavernosa*** young sporangium with green fluorescence of young spores. Photo by Magdalena Turzańska.

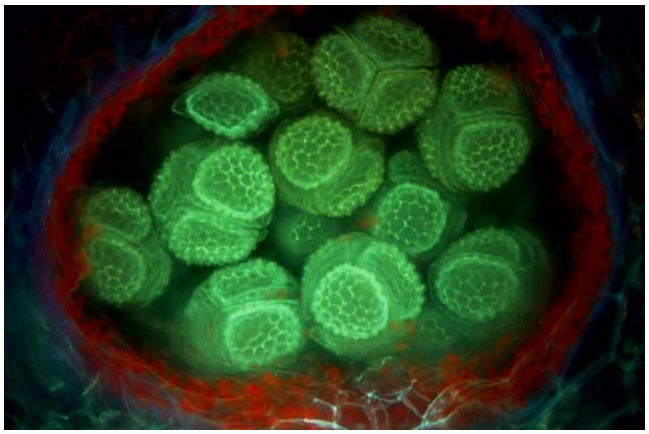

Figure 78. ***Riccia*** sorocarpa sporangium with spore tetrads showing green fluorescence and decoration on the spores and nuclei no longer visible through the spore wall. Photo by Magdalena Turzańska, with permission.

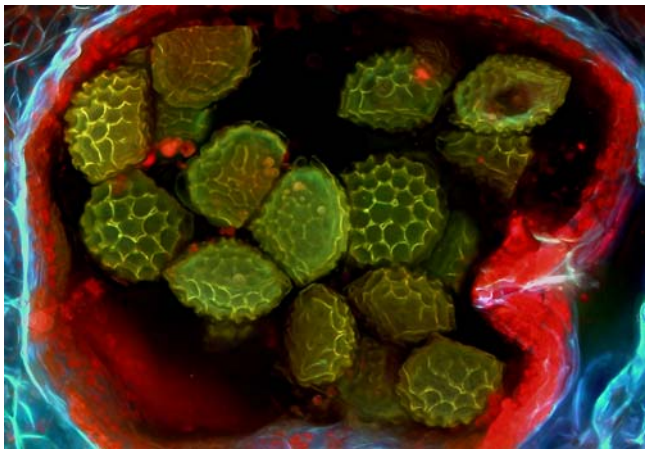

Figure 79. ***Riccia*** sp. mature spores fluorescing differently from younger spores in Figure 78. Photo by Magdalena Turzańska, with permission.

The change in color of the cell walls in spore tetrads to those of the mature spores in ***Riccia*** sp. suggests that the compounds present change with maturity. The sporangia stand out from the coloring of the thallus internal cell walls in ***Riccia*** (Figure 80).

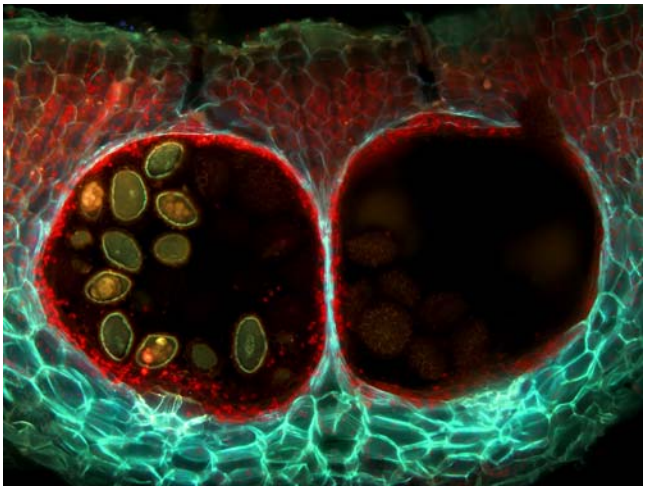

Figure 80. ***Riccia*** sporangia with red chlorophyll fluorescence and blue-green thallus cell wall fluorescence. Spore walls are fluorescing gold. Photo by Magdalena Turzańska.

My first encounter with the phenomenon of **fluorescence** in bryophytes was on a field trip in Europe where I entered in conversation with Gisela Nordhorn-Richter. She had stopped at a display of microscopes at her university just because the poor guys didn't have many visitors. She took her research organisms, members of the genus ***Pohlia*** (Figure 81-Figure 82), to test the quality of the microscopes, one of which had UV light capabilities. To her amazement, gemmae lit up all over the place, displaying far more than she had been able to see without the UV aid. She then looked at other species and found that this was a good tool to help in determining number and shape, enabling her to delineate species more easily (Nordhorn-Richter 1984 a,b,c, 1985 a,b, 1988).

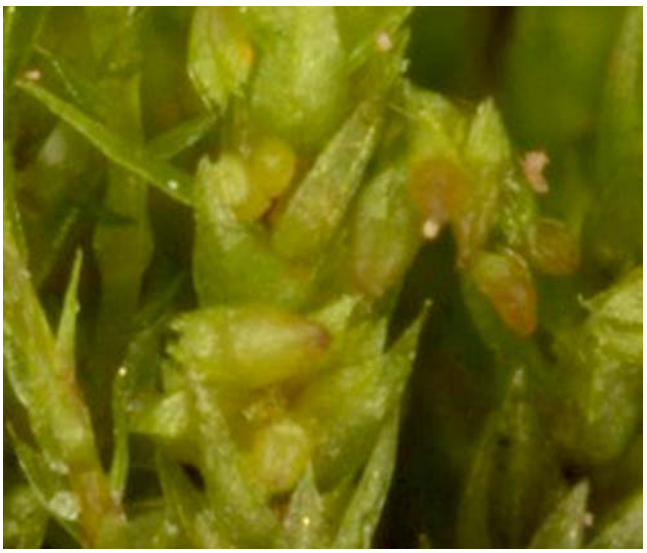

Figure 81. ***Pohlia bulbifera*** showing location of bulbils – structures that can be located in UV light by their fluorescence. Photo by Jan-Peter Frahm, with permission.

Figure 82. ***Pohlia bulbifera*** bulbils that fluoresce, making them easier to locate. Photo by Des Callaghan, with permission.

An image of a gemma of ***Lunularia cruciata*** (Figure 83-Figure 84) from Robin Young indicates that this structure fluoresces blue in UV light. Furthermore, the gemmae of ***Zygodon rupestris*** fluoresce blue (Figure 147). Gemmae can provide multiple colors, including a golden shade in liverworts ***Calypogeia*** sp. (Figure 85), ***Metzgeria*** sp. (Figure 86), and ***Radula complanata*** (Figure 87), and mosses ***Aulacomnium androgynum*** (Figure 88) and ***Tetraphis pellucida*** (Figure 89-Figure 90). The gemmae of ***Tetraphis pellucida*** suggest that the fluorescence color changes with age.

Figure 83. ***Lunularia cruciata***, a species with fluorescing gemmae. Photo by David Holyoak, with permission.

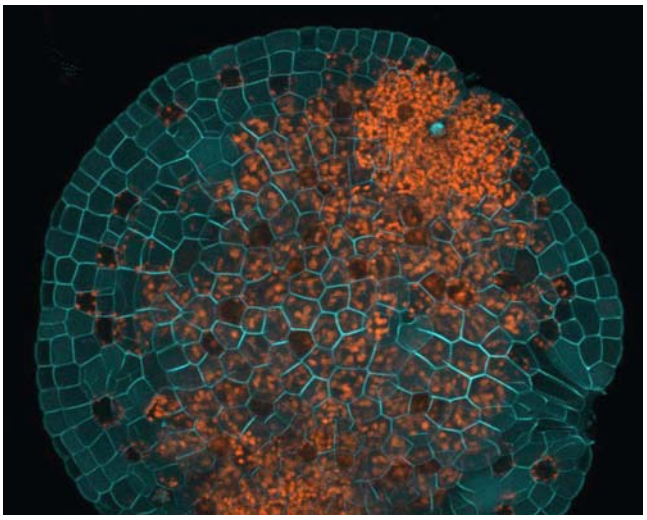

Figure 84. ***Lunularia cruciata*** gemma fluorescing. Photo by Robin Young, with permission.

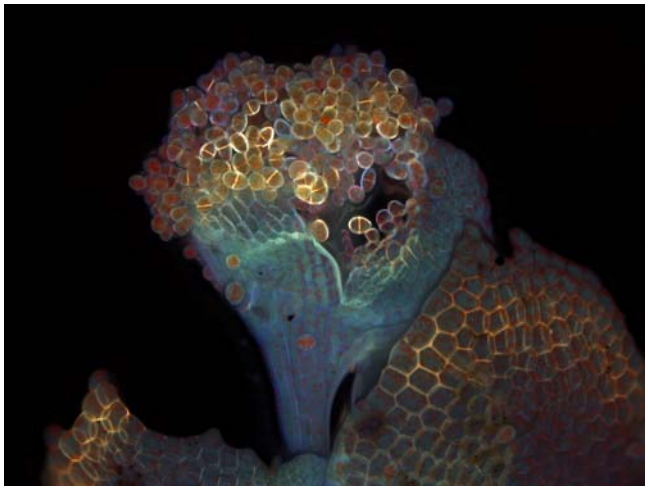

Figure 85. ***Calypogeia*** sp. gemmae with wall fluorescence. Photo by Magdalena Turzańska.

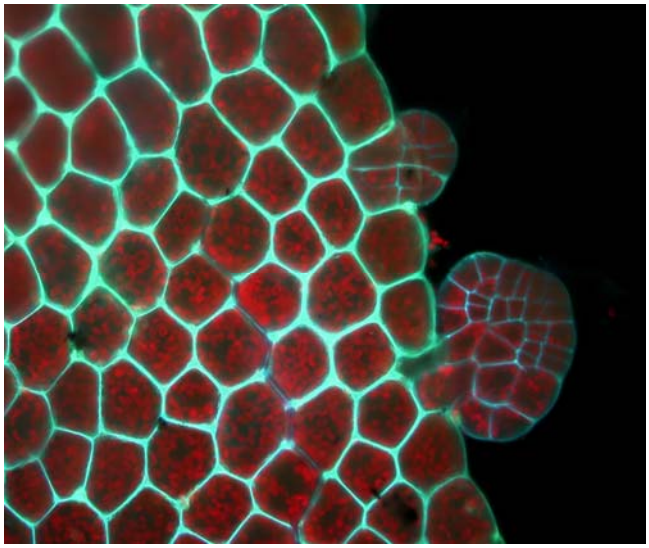

Figure 86. ***Metzgeria*** sp. showing fluorescence of cell walls, including that of marginal gemmae. It appears that the conspicuousness of the gemmae depends on the concentration of the fluorescing substance. Photo by Magdalena Turzańska.

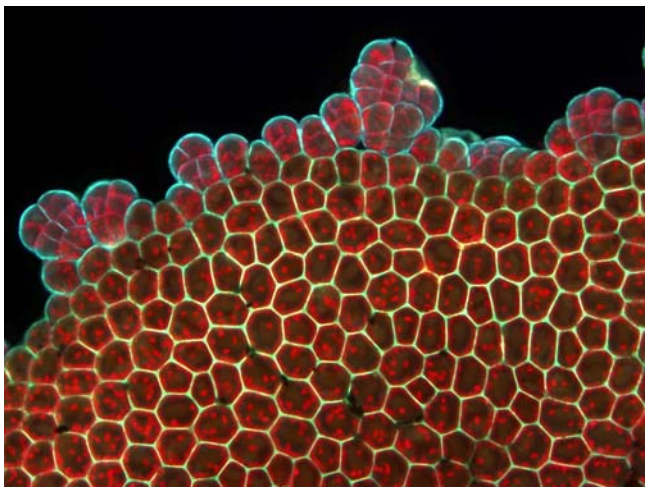

Figure 87. ***Radula complanata*** yellow leaf cell wall fluorescence with blue-green gemma cell wall fluorescence. Photo by Magdalena Turzańska.

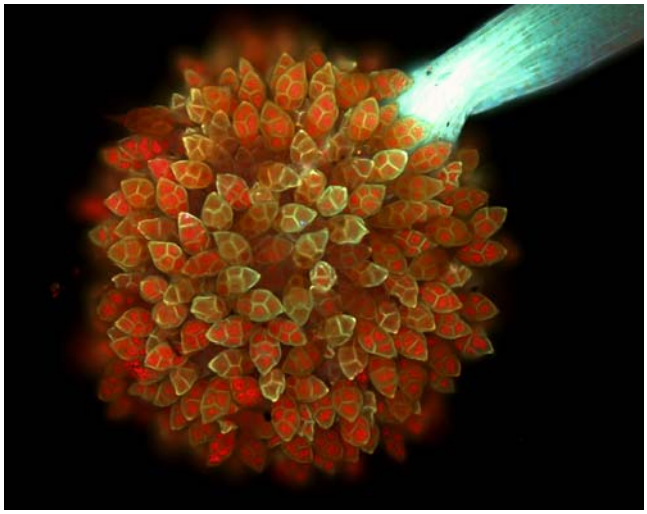

Figure 88. ***Aulacomnium androgynum*** gemmae with wall and chlorophyll fluorescence. Photo by Magdalena Turzańska.

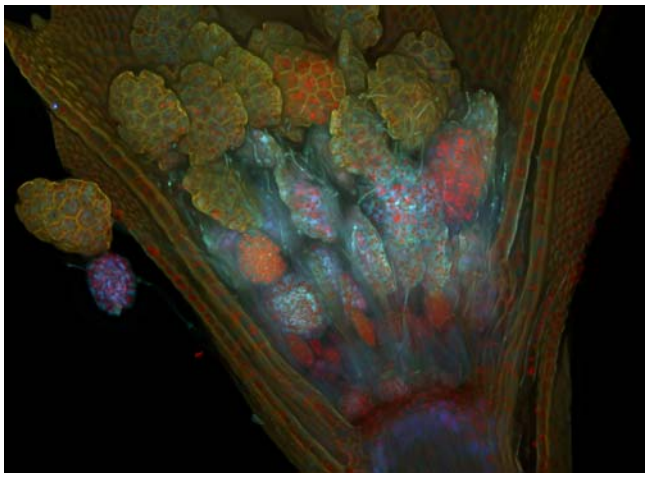

Figure 89. ***Tetraphis pellucida*** gemmae cup fluorescence showing golden cell walls of cup and multiple colors of gemmae, presumably indicating different ages. Photo by Magdalena Turzańska.

Figure 90. ***Tetraphis pellucida*** gemma fluorescence showing golden cell walls, red chloroplasts, and something blue. Photo by Magdalena Turzańska

Even branch buds can become more obvious because of a deep chlorophyll fluorescence. This is illustrated in ***Physcomitrella patens*** (Figure 91).

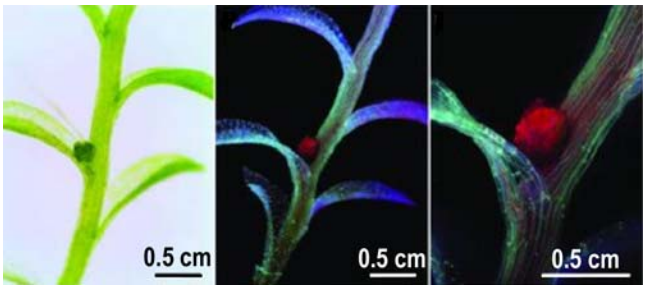

Figure 91. ***Physcomitrella patens*** normallight and fluorescence showing greenish leaf cell walls and bright red of bud due to dense chlorophyll. Photo modified from Beata Zagórska-Marek, with permission; published in American Journal of Botany with Creative Commons attribution <https://creativecommons.org/licenses/by/4.0/#>.

Merced and Renzaglia (2017) used fluorescence as a tool in viewing the stomata of a variety of bryophytes. In a species of ***Bartramia*** (Figure 92-Figure 93) the guard cells fluoresce red due to chloroplasts, but the rest of the capsule has a blue-green color in UV light. They also showed the coloration in UV light for ***Orthotrichum*** sp. (Figure 94-Figure 95), ***Physcomitrium*** sp. (Figure 96-Figure 97), and ***Polytrichum*** sp. (Figure 98).

Figure 92. ***Bartramia pomiformis*** with capsules. Photo by Northern Forest Atlas, with permission through Jerry Jenkins.

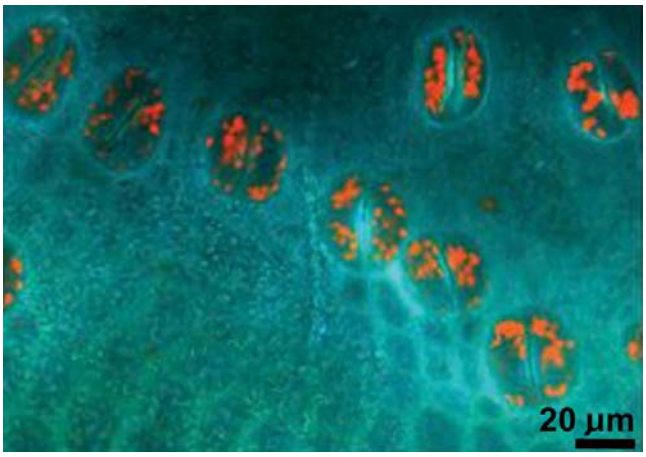

Figure 93. ***Bartramia*** guard cells with chloroplasts and cell walls fluorescing. Photo from Merced & Renzaglia 2017, with permission.

Figure 94. ***Orthotrichum alpestre***, in a genus where guard cells are of taxonomic importance. Photo by Michael Lüth, with permission.

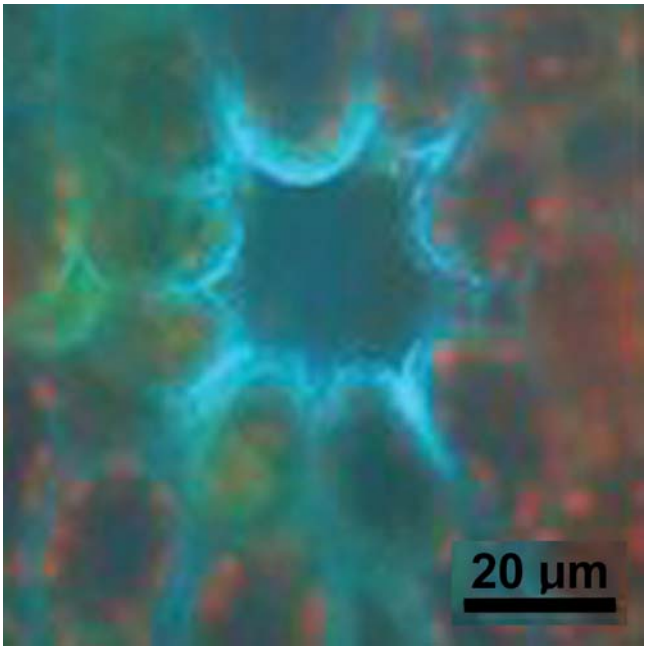

Figure 95. ***Orthotrichum*** guard cells with chloroplasts and cell walls fluorescing in UV light. Photo modified from Merced & Renzaglia 2017, with permission.

Figure 96. ***Physcomitrium patens*** showing capsules Photo by Hugues Tinguy, with permission.

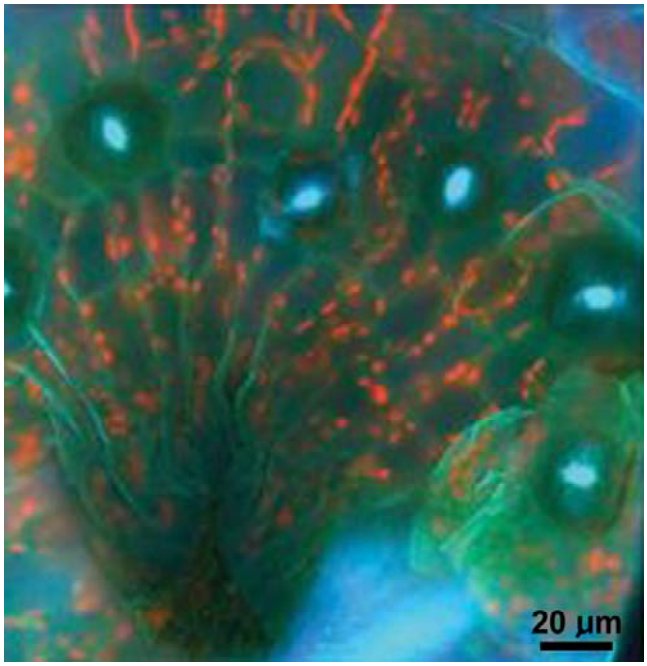

Figure 97. ***Physcomitrium*** guard cells and chloroplasts (**orange**) in fluorescence microscopy. Photo from Merced & Renzaglia 2017, with permission.

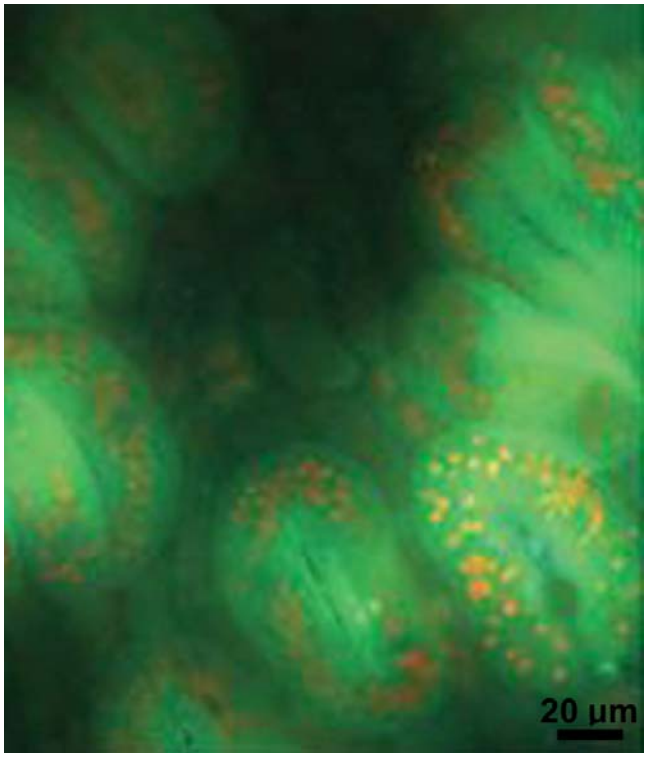

Figure 98. ***Polytrichum*** guard cells with chloroplasts (orange) using fluorescence microscopy. Photo from Merced & Renzaglia 2017, with permission.

In addition to the fluorescence of stomata in the sporophyte, it appears that the gametophyte thallus and the cells surrounding the pores of ***Conocephalum conicum*** (Figure 99-Figure 101) and ***Marchantia polymorpha*** (Figure 102) also exhibit fluorescence.

Figure 99. ***Conocephalum conicum*** showing raised pores. Photo by Dick Haaksma, with permission.

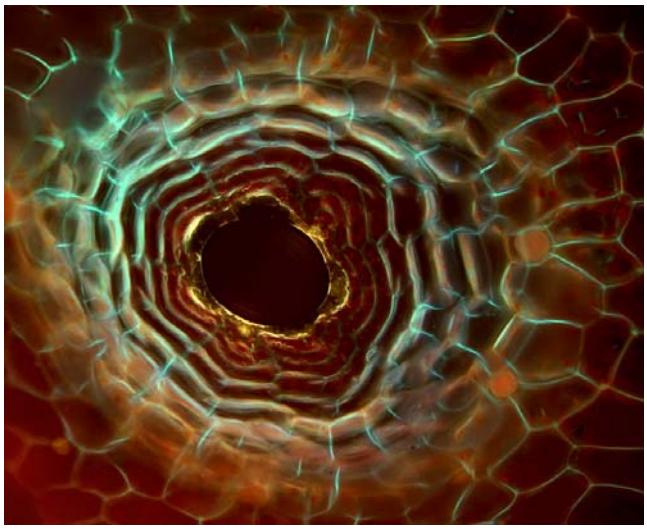

Figure 100. ***Conocephalum conicum*** pore fluorescence. This image has been enhanced by increasing the color contrast using Photoshop. Photo by Magdalena Turzańska, with permission.

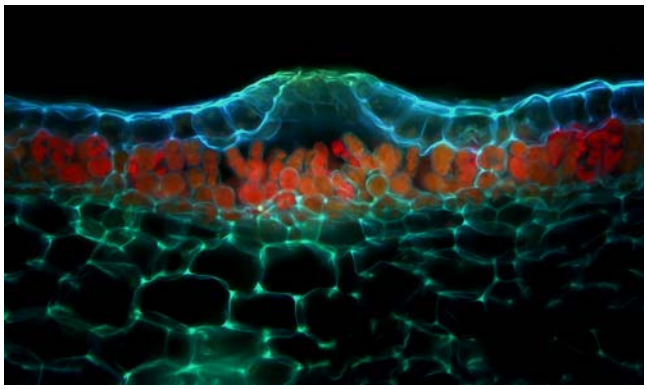

Figure 101. ***Conocephalum conicum*** thallus section showing pore and fluorescence. Note the bright red chlorophyll in photosynthetic cells under the epidermis. Photo by Magdalena Turzańska.

Little has been published about fluorescence of sexual structures. Nevertheless, in her photographic images Magdalena Turzańska illustrates that the antheridia (Figure 103-Figure 108) and archegonia (Figure 109-Figure 110) and associated paraphyses can exhibit a colorful display.

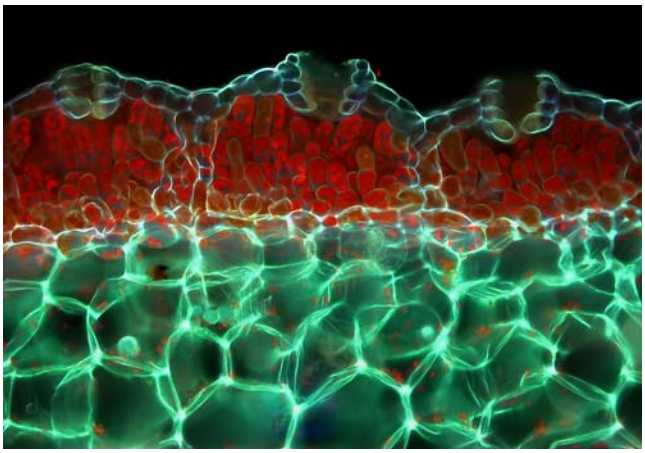

Figure 102. ***Marchantia polymorpha*** thallus section showing fluorescing pore, chlorophyll fluorescence, and fluorescing thallus tissue. Photo by Magdalena Turzańska.

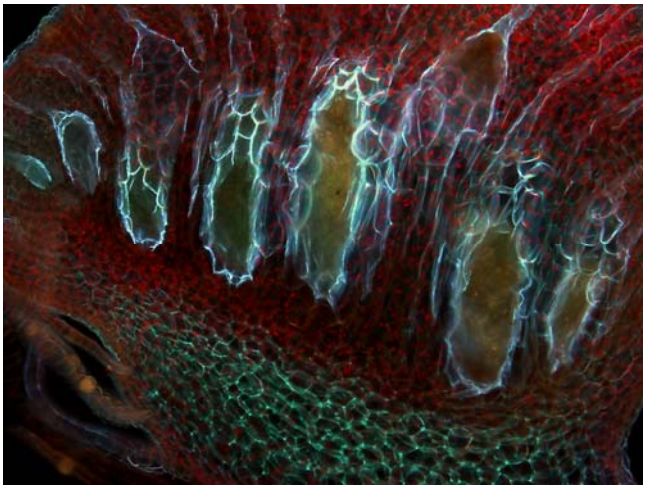

Figure 103. ***Conocephalum conicum*** antheridia showing fluorescence of their walls, chlorophyll in surrounding cells, and green walls of non-photosynthetic thallus cells. Photo by Magdalena Turzańska.

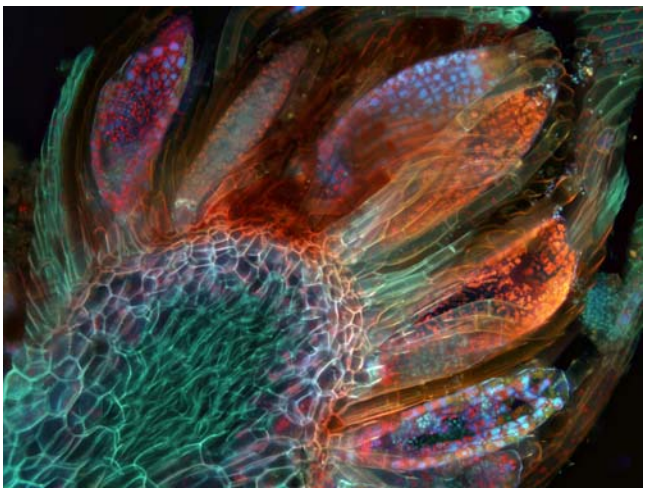

Figure 104. Moss antheridia fluorescence providing a colorful contrast to that of the stem. Photo by Magdalena Turzańska, with permission.

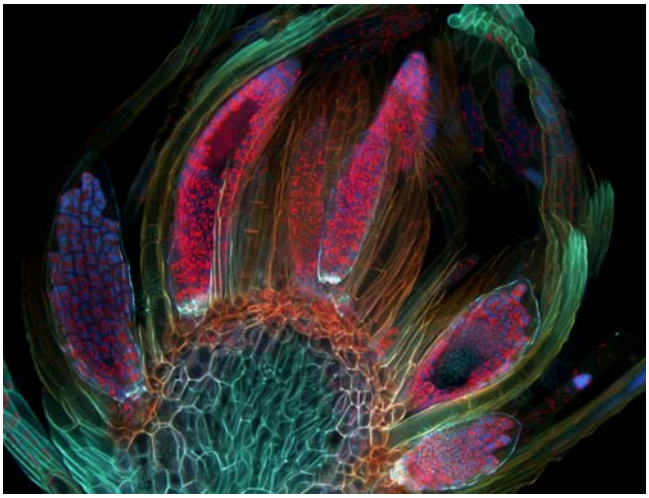

Figure 105. Moss antheridia fluorescence with intense coloration. Photo by Magdalena Turzańska.

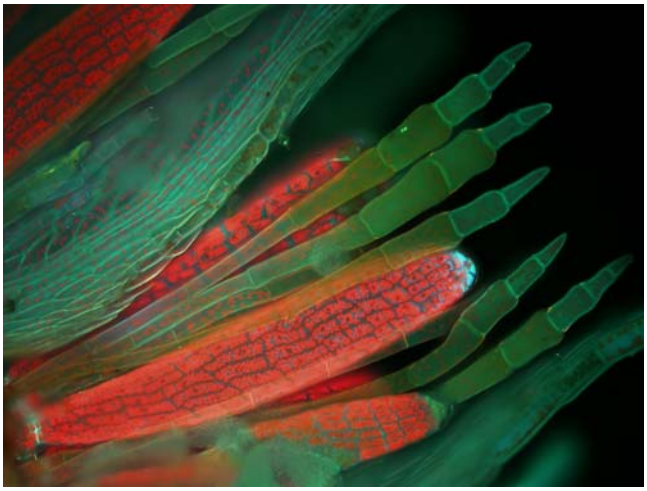

Figure 106. ***Mnium hornum*** antheridia fluorescence barely visible at tips due to chlorophyll fluorescence; paraphyses have strong green fluorescence. Photo by Magdalena Turzańska.

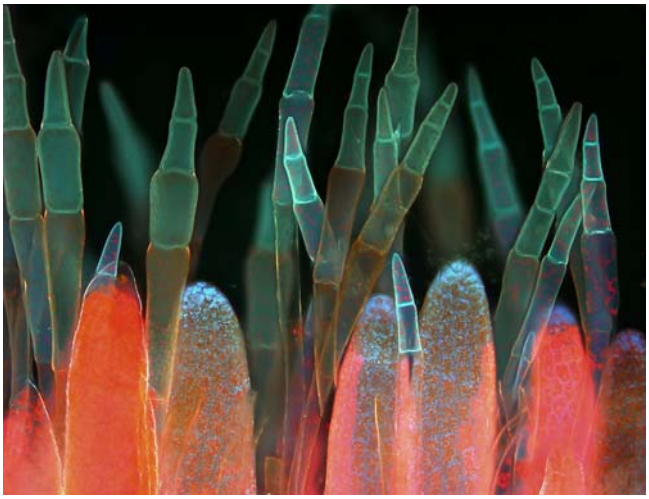

Figure 107. ***Mnium hornum*** antheridia and paraphyses fluorescing. Photo by Magdalena Turzańska, with permission.

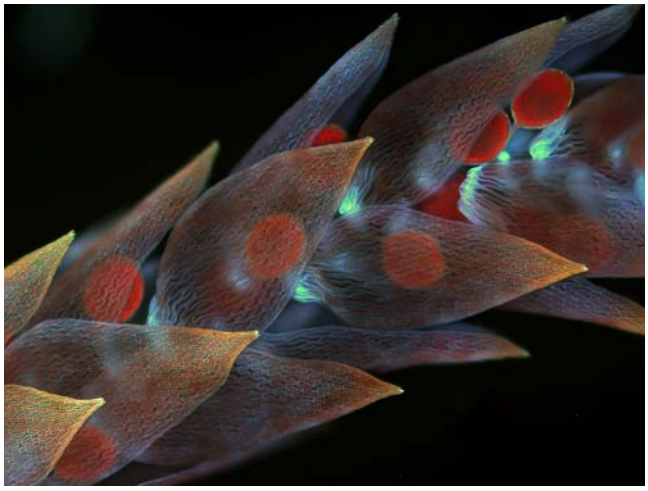

Figure 108. ***Sphagnum*** sp. antheridia showing fluorescence in UV light. Photo by Magdalena Turzańska.

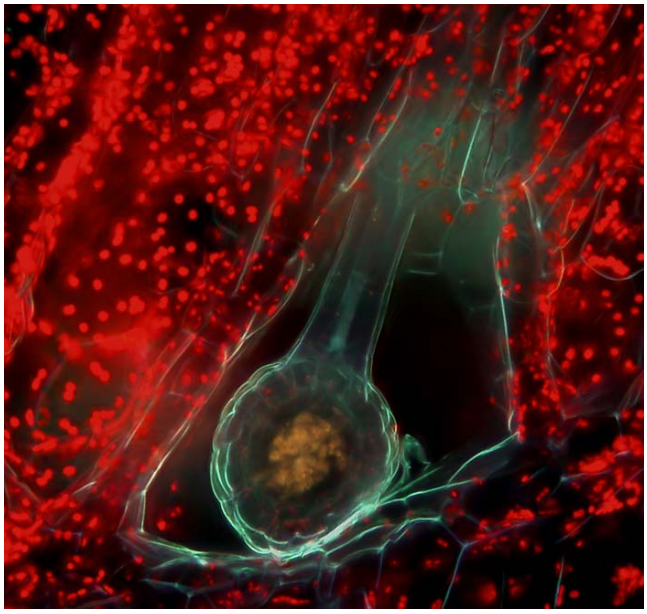

Figure 109. ***Riccia*** sp. archegonium fluorescence, surrounded by chlorophyll fluorescence of the thallus. Photo by Magdalena Turzańska.

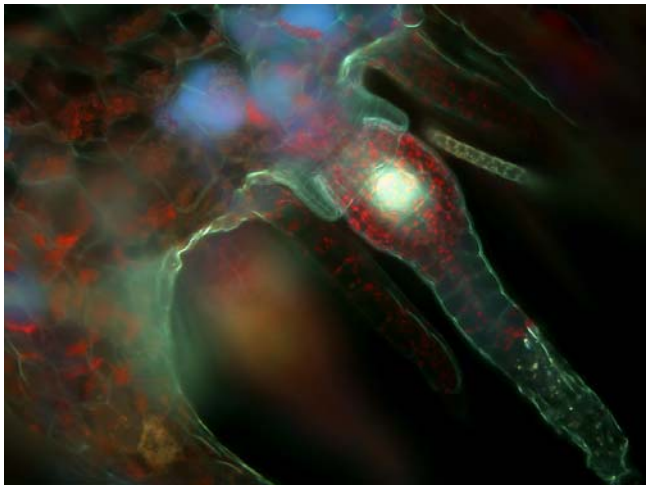

Figure 110. ***Marchantia polymorpha*** archegonium green fluorescence with red chlorophyll fluorescence at base and bright egg. Photo by Magdalena Turzańska.

The fluorescence of sporophytes seems to be largely unknown. The only images I have seen are those of Magdalena Turzańska for ***Phascum*** sp. (Figure 111) and ***Sphagnum*** sp. (Figure 112) The latter appears to lack capsule fluorescence, but exhibits it in the pseudopodium. It would be interesting to see if the fluorescence of spores and capsule are more common in species lacking a peristome, perhaps serving to attract arthropod dispersal vectors.

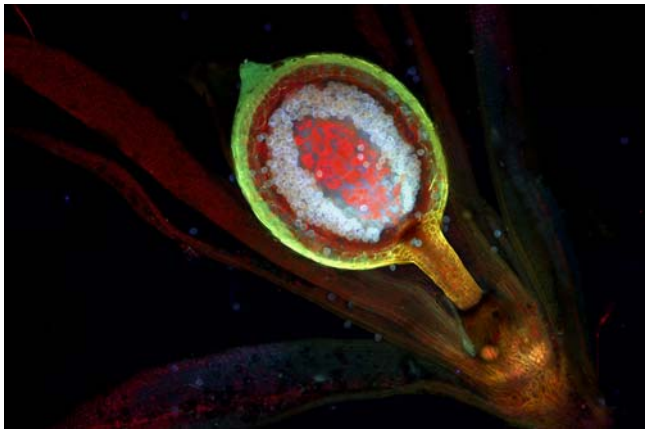

Figure 111. ***Phascum*** sp. fluorescence of capsule and spores in capsule with no peristome. Photo by Magdalena Turzańska.

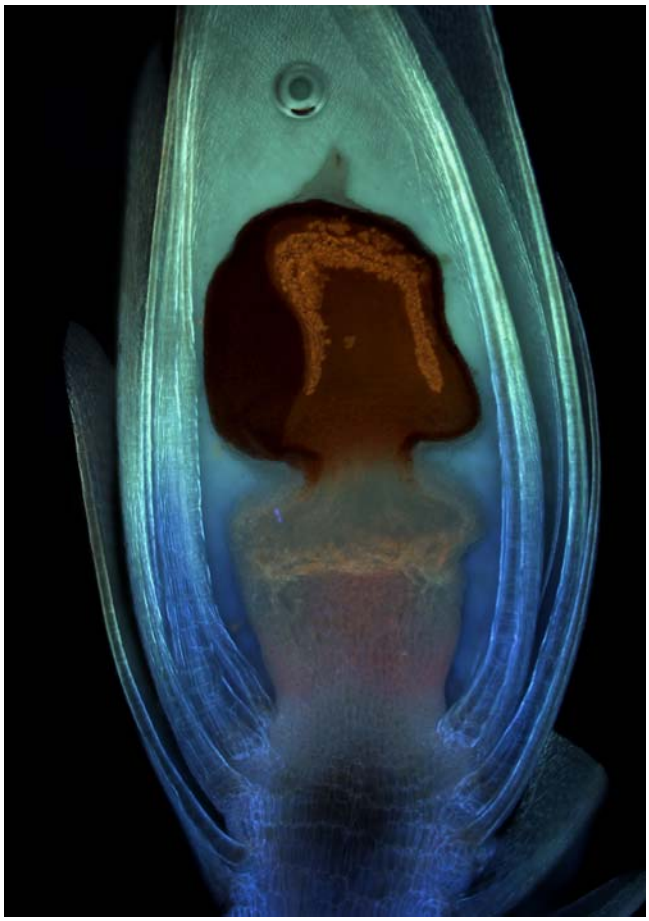

Figure 112. ***Sphagnum*** sp. fluorescence with capsule apparently not fluorescing, but the developing pseudopodium has some pink, green, and greenish fluorescence. Photo by Magdalena Turzańska.

In liverworts, the spores are nestled among elaters that may help to loosten and expel the spores from the capsules. These, too, can fluoresce (Figure 113-Figure 114). Since I have few records, it is too early to determine if this is a common character in liverwort elaters. I have even fewer examples of fluorescence in peristomes (Figure 115).

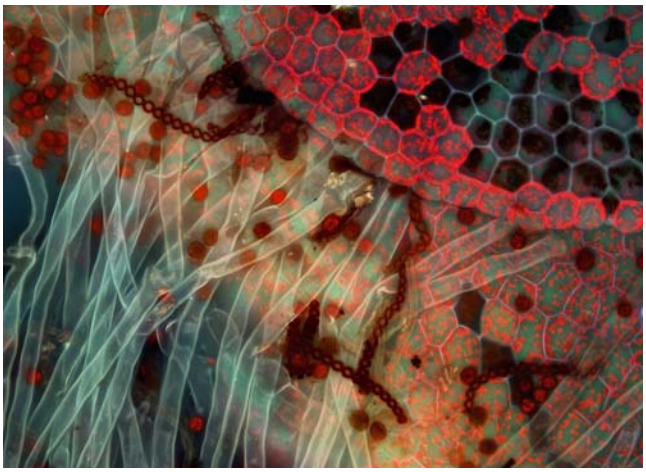

Figure 113. ***Marchantia*** elater dark red fluorescence in UV light. Photo by Magdalena Turzańska.

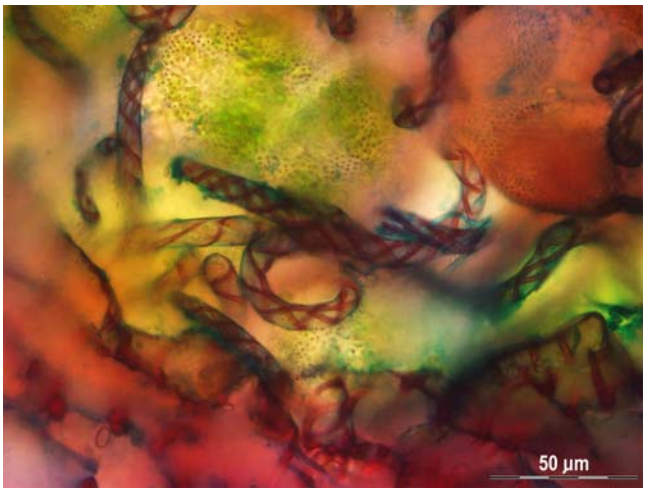

Figure 114. ***Pellia*** elater dark red fluorescence in UV light. Photo by Magdalena Turzańska.

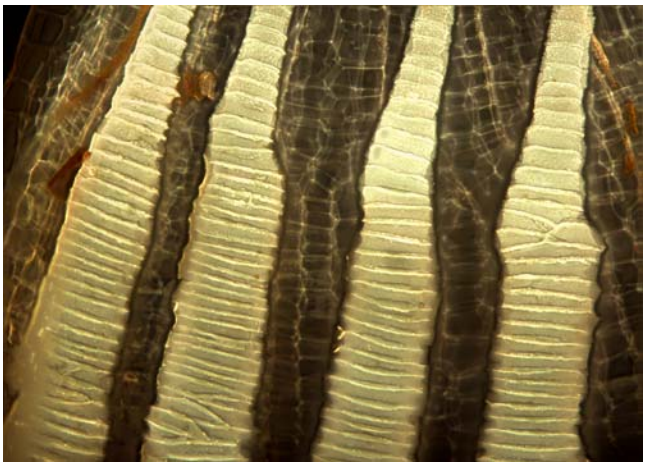

Figure 115. Moss peristome golden fluorescencein UV light. Photo by Magdalena Turzańska.

In addition to the fluorescence of the plant parts, it is often possible to distinguish the presence of epiphytes more easily using UV light. This can be seen in Figure 66-Figure 67 for algae on ***Sphagnum***, in Figure 116-Figure 117 for **Cyanobacteria** on ***Hylocomium splendens***, and ***Blasia pusilla*** (Figure 118-Figure 121). Can it be used as well to detect and help identify bacteria on the bryophytes?

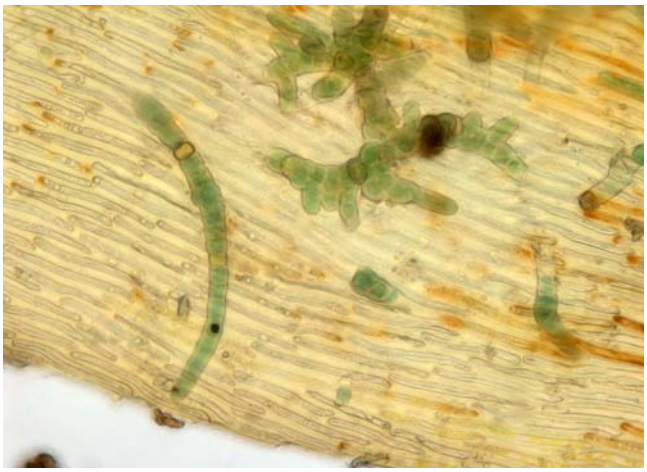

Figure 116. ***Hylocomium splendens*** with ***Stigonema*** (**Cyanobacteria**). Photo by Magdalena Turzańska.

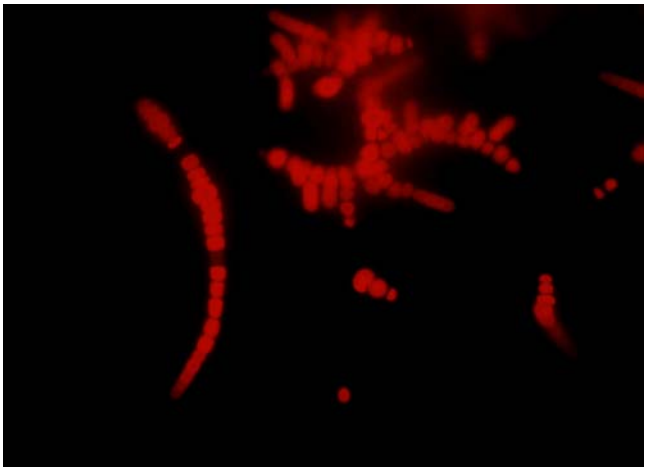

Figure 117. ***Stigonema*** (**Cyanobacteria**) on ***Hylocomium splendens*** fluorescence. Photo by Magdalena Turzańska.

Figure 118. ***Blasia pusilla Nostoc*** colonies. Photo by Magdalena Turzańska.

Figure 119. ***Blasia pusilla*** with ***Nostoc*** (**Cyanobacteria**). Photo by Magdalena Turzańska.

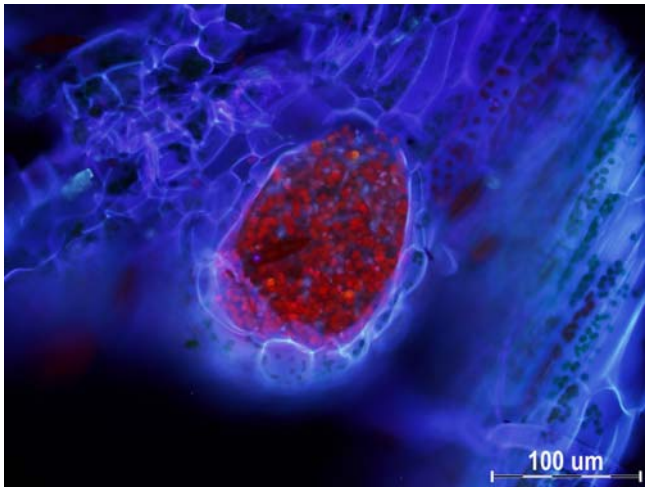

Figure 120. ***Blasia pusilla*** blue fluorescence of thallus and red **Cyanobacteria** fluorescence. Photo by Magdalena Turzańska.

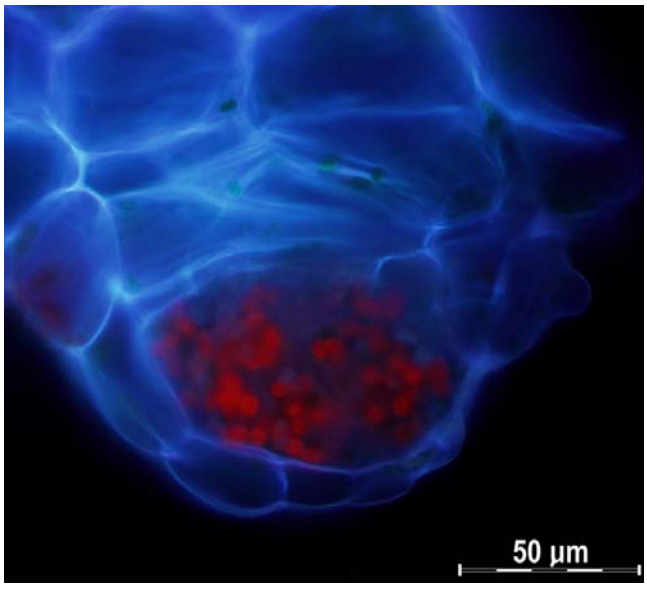

Figure 121. ***Blasia pusilla*** with red fluorescence of **Cyanobacteria** and blue thallus fluorescence. Photo by Magdalena Turzańska.

Which Species Fluoresce?

For some reason, the method of viewing bryophytes with UV light has been neglected. It was not until Dale Kruse inquired about bryophyte fluorescence on Bryonet (25 March 2011) that the subject again surfaced: "I just returned from a trip to Puerto Rico where I visited the rainforests of the Caribbean (El Yunque) National Forest. A 'non-bryological' employee there suggested there were fluorescent mosses in the forests of El Yunque. I did a quick search on the web and found very little information. I have seen fluorescent lichens but not mosses." Bryologists responded with skepticism, suggesting it was a fungus or bacterium (or possibly a lichen). Then Michael Lüth responded (Bryonet 26 March 2011): "We saw a fluorescent ***Frullania dilatata*** (Figure 122-Figure 124) on an excursion, when someone held a fluorescent lamp to a tree searching for some lichens." And Michael was able to show us proof (Figure 123).

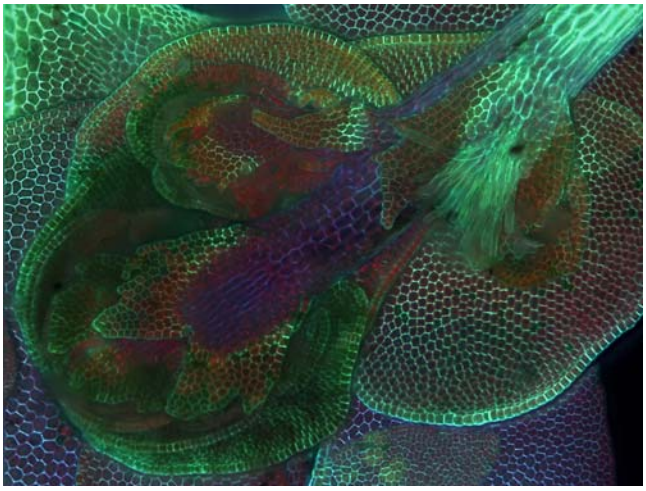

Figure 124. ***Frullania dilatata*** green cell wall fluorescence. Photo by Magdalena Turzańska.

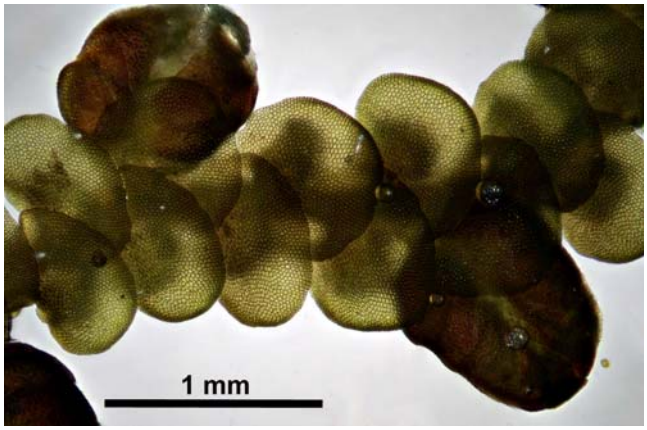

Figure 122. ***Frullania dilatata***, a species that exhibits purple fluorescence. Photo by Claire Halpin, with permission.

In 2022, the topic of fluorescence erupted on Bryonet again. Emmet Judziewicz and Virginia (Bryonet 13 March 2022) reported that on a casual one-hour walk in the Hawaiian rainforest, their UV flashlight revealed a "striking bright red fluorescence" in several leafy liverworts. These included **Cephaloziaceae**: ***Fuscocephaloziopsis connivens*** (Figure 125-Figure 126) **subsp.** ***sandvicensis***, ***Odontoschisma denudatum*** (Figure 127), and **Lepidoziaceae**: ***Lepidozia australis*** (Figure 128), ***Telaranea nematodes*** (Figure 129), but the common ***Bazzania praerupta*** (=***Bazzania cordistipula***; Figure 130-Figure 131) did not exhibit red florescence, nor did the other common leafy liverworts they examined.

Figure 123. ***Frullania dilatata*** demonstrating purple fluorescence under UV light from a special UV-emitting hand lens. Photo by Michael Lüth, with permission.

Figure 125. ***Fuscocephaloziopsis connivens***, a species that exhibits a bright red fluorescence in UV light. Photo by Hermann Schachner, through Creative Commons.

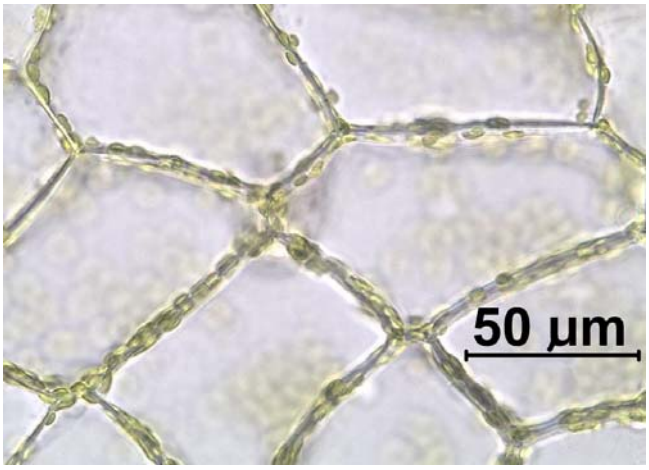

Figure 126. ***Fuscocephaloziopsis connivens*** cells showing chloroplasts clinging to cell walls. Photo by Hugues Tinguy, with permission.

Figure 127. ***Odontoschisma denudatum***, a species that exhibits a bright red fluorescence in UV light. Photo by Hermann Schachner, through Creative Commons.

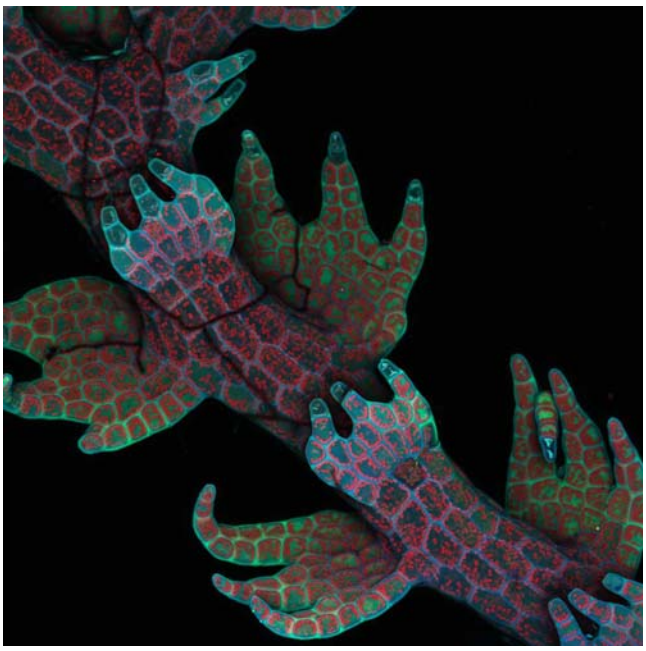

Figure 128. ***Lepidozia australis*** showing fluorescence. Photo by Robin Young, with permission through CC-BY-NC 4.0.

Figure 129. ***Telaranea nematodes***, a member of the **Lepidoziaceae** that exhibits fluorescence in UV light. Photo by Michael Lüth, with permission.

Figure 130. ***Bazzania praerupta***, a species in the **Lepidoziaceae** that does not fluoresce in UV light when viewed macroscopically. Photo by Lin Shanxiong, through Creative Commons.

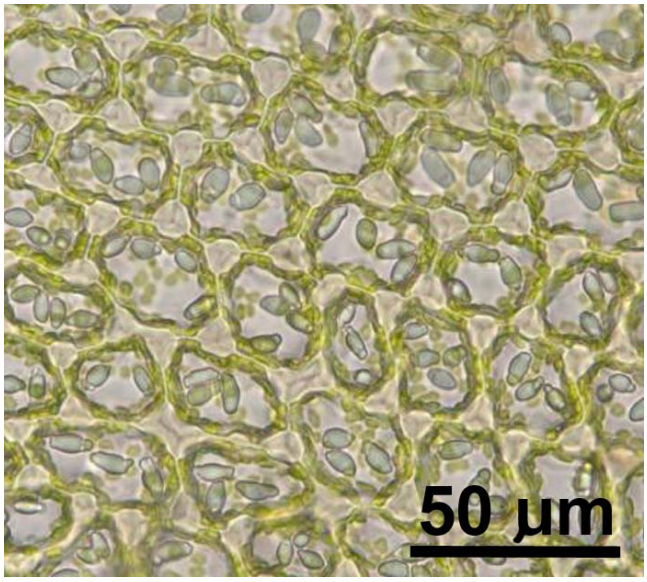

Figure 131. ***Bazzania praerupta*** leaf cells showing large trigones, but lacking papillae. Photo by Lin Shanxiong, through Creative Commons.

Andi Cairns (pers. comm. 27 March 2022) reported ***Bazzania vittata*** (Figure 132-Figure 134, Figure 174) fluorescing blue beside a ***Bazzania corbieri*** (Figure 132-Figure 134, Figure 135) that was not fluorescing. The adjacent mosses ***Leucobryum aduncum* var. *aduncum*** (Figure 132-Figure 133, Figure 136) and ***Pyrrhobryum paramattense*** (Figure 132-Figure 133, Figure 137) were likewise not fluorescing. Herbarium specimens of ***Bazzania vittata*** from Thornton Peak in North Queensland, Australia, also fluoresced blue even when **dry** (Andi Cairns, pers. comm. 29 March 2022). She explored an additional ~20 specimens of dried leafy liverworts from the Australian Wet Tropics and the only one that fluoresced blue under UV light was ***Bazzania vittata*** (Andi Cairns, pers. comm. 30 March 2022).

Figure 132. ***Bazzania vittata*** fluorescing blue in UV light with non-fluorescing ***Bazzania corbieri***, ***Leucobryum aduncum* var. *aduncum***, and ***Pyrrhobryum paramattense***. Photo by Will Cairns, courtesy of Andi Cairns.

Figure 133. ***Bazzania vittata*** fluorescing blue in UV light with non-fluorescing ***Leucobryum aduncum* var. *aduncum***, and ***Pyrrhobryum paramattense***. ***Bazzania corbieri*** appears to be fluorescing purple in some branches – perhaps dead ones with cells or structures no longer hiding the fluorescence? Photo by Will Cairns, courtesy of Andi Cairns.

Figure 134. ***Bazzania vittata*** fluorescing blue in UV light with non-fluorescing ***Bazzania corbieri***, ***Leucobryum aduncum* var. *aduncum***, and ***Pyrrhobryum paramattense***. Photo by Will Cairns, courtesy of Andi Cairns.

Figure 135. ***Bazzania corbieri***, a non-fluorescing species. Photo by Andrew Franks, with permission.

Figure 136. ***Leucobryum aduncum* var. *aduncum***, a species that lacks fluorescence. Photo by Niels Klazenga, with permission.

Figure 137. ***Pyrrhobryum paramattense*** with capsules, a species that lacks fluorescence. Photo by Peter Woodard, through Creative Commons.

David Glenny found fluorescence of ***Bazzania tayloriana*** (Figure 138) in New Zealand, reported again by John Braggins (Bryonet 18 April 2022) (Figure 139). This is true for specimens from both North and South Islands of New Zealand.

Figure 138. ***Bazzania tayloriana***, a species that exhibits blue fluorescence in UV light. Photo courtesy of John Braggins.

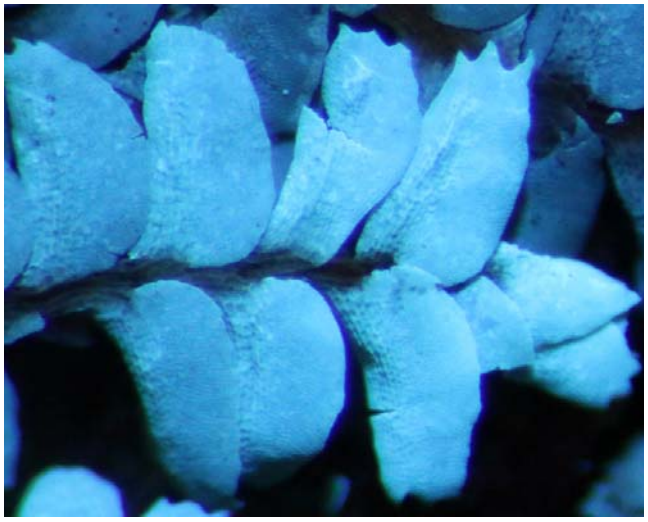

Figure 139. ***Bazzania tayloriana*** showing blue fluorescence. Photo courtesy of John Braggins.

In California, USA, when Ken Kellman (Bryonet 21 April 2022) discovered that the bark of the valley oak (***Quercus lobata***; Figure 140) was fluorescing dark red under the light of a uvBeast V3 MINI, he found that the fluorescence was coming from a tiny moss that proved to be ***Zygodon rupestris*** (Figure 59, Figure 141-Figure 142). But when he used UV light on the dry specimens, there was no fluorescence. Fluorescence appeared again when the moss was rewet. Both the leaves and the gemmae (Figure 143-Figure 144) were glowing red. The nearby mosses ***Antitrichia californica*** (Figure 145) and ***Homalothecium nuttallii*** (Figure 146) did not fluoresce, wet or dry.

Figure 140. ***Quercus lobata***, a species that can serve as substrate for fluorescent ***Zygodon rupestris***. Photo by JKehoe Photos, through Creative Commons.

Figure 141. ***Zygodon rupestris*** on a tree in the UK. Photo by Claire Halpin, with permission.

Figure 142. ***Zygodon rupestris***, a species known to exhibit fluorescence when hydrated but not when dry. Photo by Jonathan Sleath, with permission.

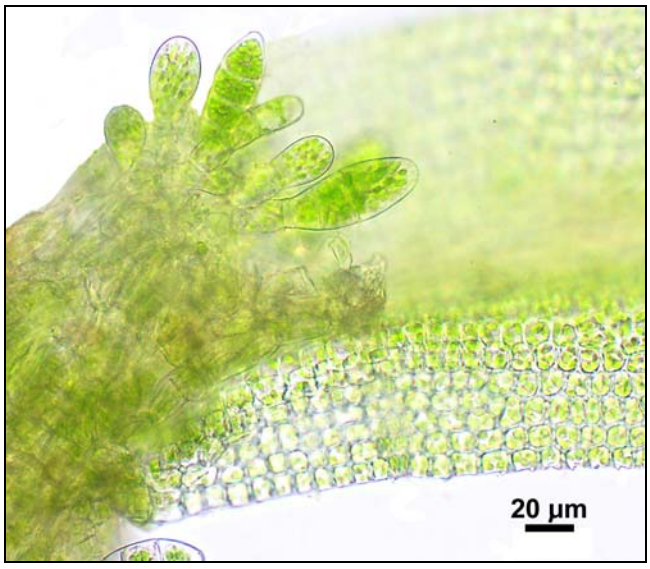

Figure 143. ***Zygodon rupestris*** leaf with gemmae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 144. ***Zygodon rupestris*** gemmae, a plant part that is able to fluoresce. Photo by Claire Halpin, with permission.

Figure 145. ***Antitrichia californica***, a pleurocarpous moss species that seems to lack macroscopic fluorescence capability. Photo by John Game, through Creative Commons.

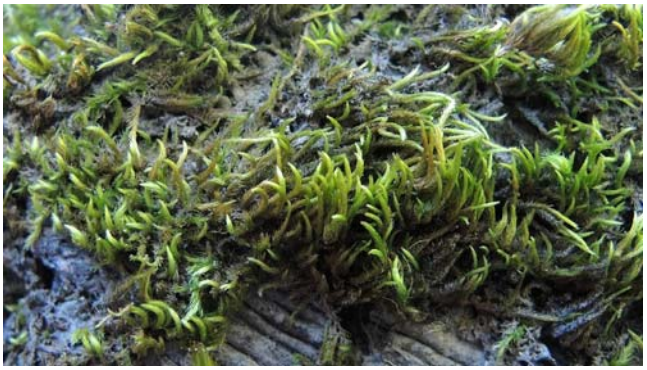

Figure 146. ***Homalothecium nuttallii***, a pleurocarpous species that seems to lack fluorescence capability. Photo by Michael Lüth, with permission.

Tom Ottley (Bryonet 23 April 2022) followed up on these observations with different collections of ***Zygodon rupestris*** (Figure 141-Figure 144). Although it seemed to be that the gemmae were fluorescing, after some difficulty he was able to determine with high power of the microscope that it was an alga that was fluorescing dark red. With the help of a UV microscope, Ottley (Bryonet 5 May 2022) was able to see two sorts of fluorescence in ***Z. rupestris*** (Figure 147). One was the bright whitish-blue from the contents of the gemmae (Figure 147) and the other was red from the chloroplasts of the associated algae (Figure 147). He found no detectable fluorescence in the laminal cells of the moss leaves.

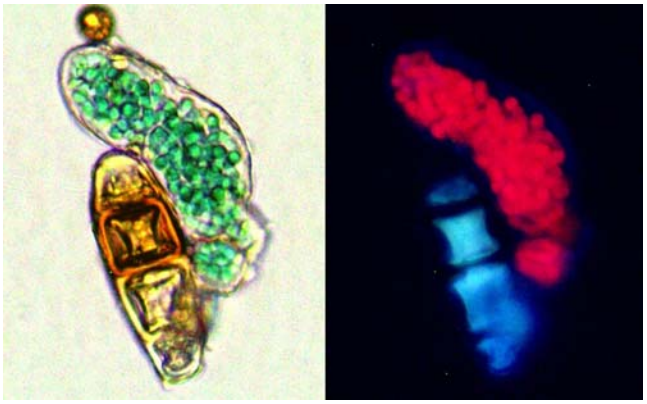

Figure 147. ***Zygodon rupestris*** fluorescence. **Left**: gemma and alga in LED white light. **Right**: gemma and alga fluorescing in UV light. Photo courtesy of Tom Ottley.

Eric Whiting (Bryonet 26 March 2022) was inspired by the Bryonet discussion to re-examine some of his ***Fossombronia*** (Figure 148) samples from semi-arid regions of Australia. Using a hand-held battery unit, he was able to see what appeared to be fluorescence in these, but not in other soil-crust bryophytes from New South Wales, Australia. However, with a stronger UV light he discovered that it was **reflectance** and not fluorescence (Eric Shiting, Bryonet 6 May 2022). He raised the question of whether reflectance could reduce the incoming light energy sufficiently to lower it to a tolerable level. He questioned whether UV light might be equally well reflected.

Figure 148. ***Fossombronia cf wondraczekii*** in Australia, in a genus that seems to lack macroscopic fluorescence. Photo by Bernd Haynold, through Creative Commons.

Magdalena Turzańska has documented the fluorescence of additional species with her photography. These include the liverworts ***Blasia pusilla*** (Figure 149-Figure 150), ***Barbilophozia*** (Figure 151), ***Cephalozia bicuspidata*** (Figure 152), ***Calypogeia*** sp. (Figure 153), ***Gymnocolea inflata*** (Figure 154), ***Lepidozia reptans*** (Figure 155), ***Lophocolea heterophylla*** (Figure 156-Figure 157), ***Marsupella sp***. (Figure 158), ***Metzgeria*** sp. (Figure 160), ***Plagiochila asplenioides*** (Figure 161), ***Radula complanata*** (Figure 162-Figure 163), and ***Trichocolea tomentella*** (Figure 164), and mosses ***Brachythecium*** sp. (Figure 165), ***Mnium hornum*** (Figure 166), ***Polytrichum piliferum*** (Figure 167-Figure 168), ***Tetraphis pellucida*** (), and ***Thuidium tamariscinum*** (Figure 169-Figure 171).

Figure 149. ***Blasia pusilla*** thallus section with **Cyanobacteria**. Photo by Magdalena Turzańska.

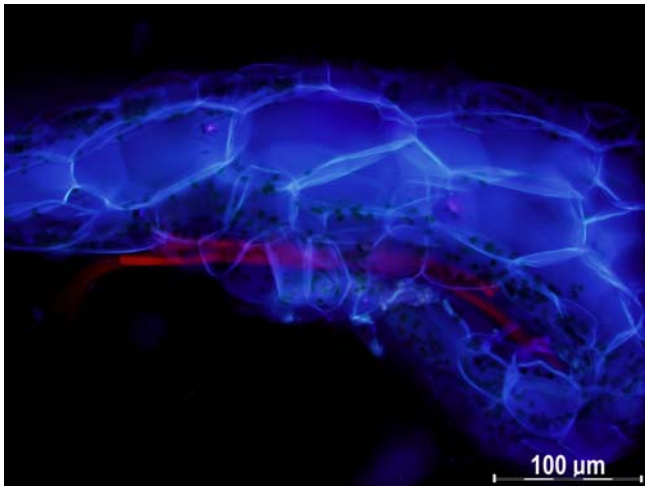

Figure 150. ***Blasia pusilla*** thallus section showing brilliant blue fluorescence. **Cyanobacteria** are fluorescing red. Photo by Magdalena Turzańska.

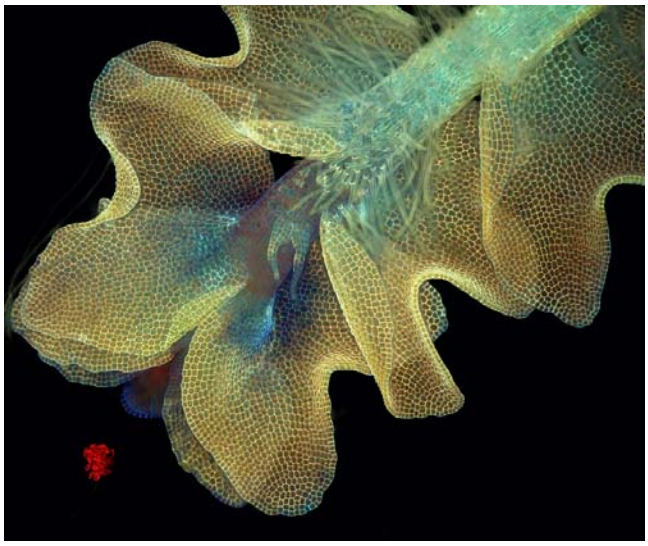

Figure 151. ***Barbilophozia*** sp. showing fluorescence in the leaf cell walls with the base of the leaf glowing blue. The stem has yet another shade of blue. The hair-like filaments are rhizoids. **Cyanobacteria** are fluorescing red in the lower left. Photo by Magdalena Turzańska.

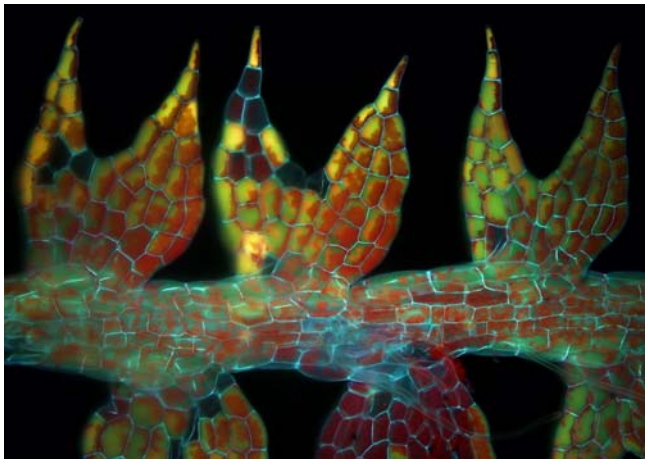

Figure 152. ***Cephalozia bicuspidata*** fluorescence, a tiny species that might be more easily located at night with a UV source. Photo by Magdalena Turzańska.

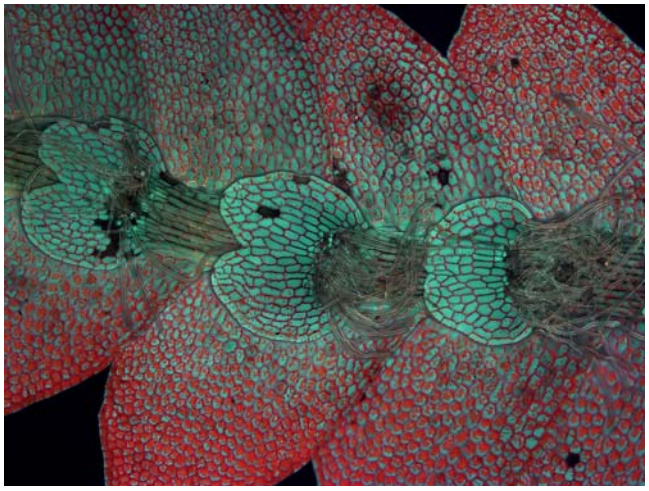

Figure 153. ***Calypogeia*** sp. with cell wall fluorescence; the fluorescence makes it easier to see the underleaves. Photo by Magdalena Turzańska.

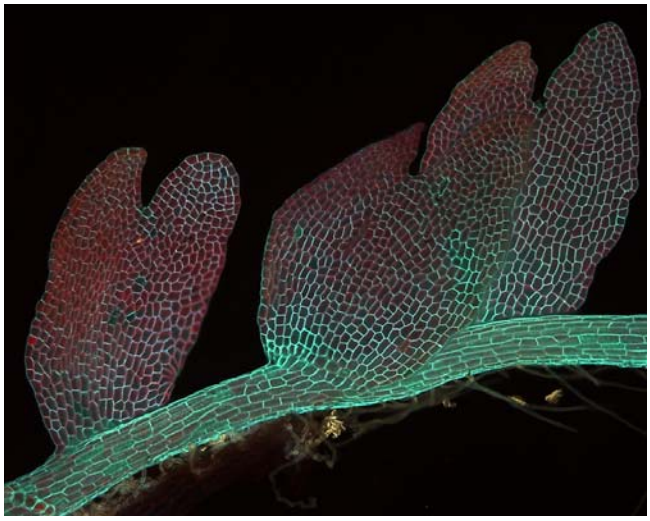

Figure 154. ***Gymnocolea inflata*** with green fluorescence of cell walls. Photo by Magdalena Turzańska.

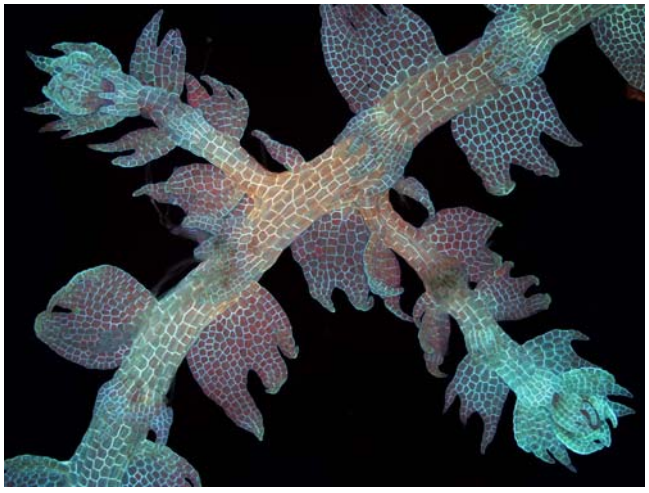

Figure 155. ***Lepidozia reptans*** ventral view showing blue cell wall fluorescence. Photo by Magdalena Turzańska.

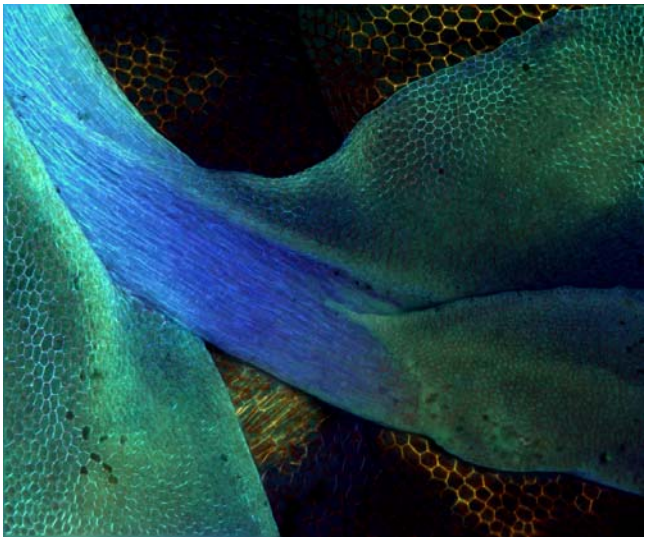

Figure 156. ***Lophocolea heterophylla*** fluorescence showing blue stem cells and greenish leaf cell walls. Photo by Magdalena Turzańska.

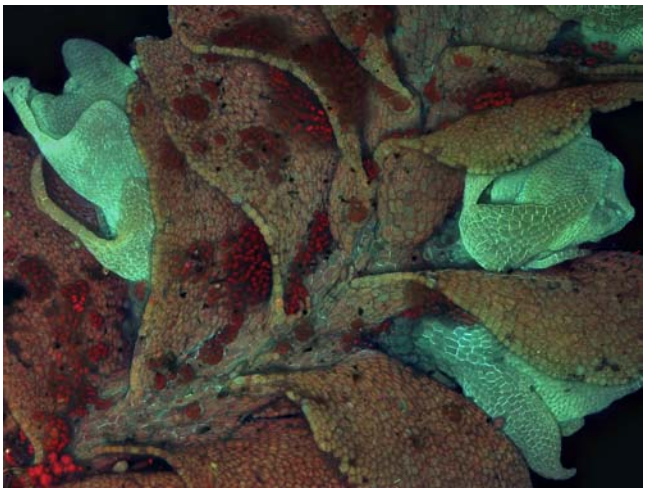

Figure 157. ***Lophocolea heterophylla*** with red patches of **Chlorophyta** fluorescing on leaves that are apparently dead or at a different stage of maturity from the branches with greenish cell wall fluorescence. Photo by Magdalena Turzańska.

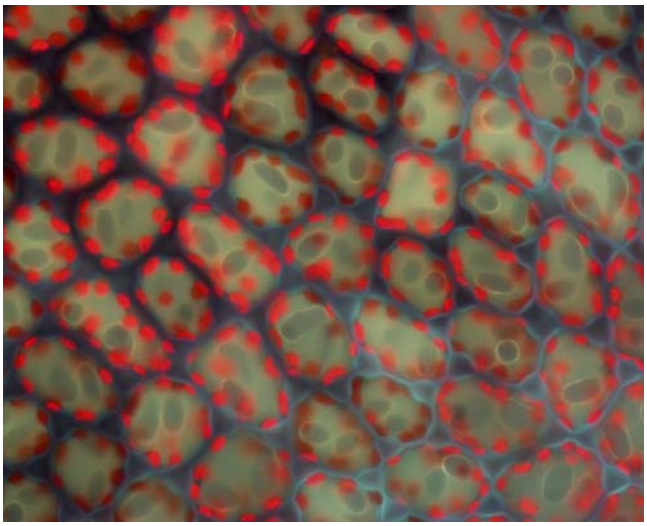

Figure 158. ***Marsupella*** sp. leaf cells fluorescing blue. Photo by Magdalena Turzańska.

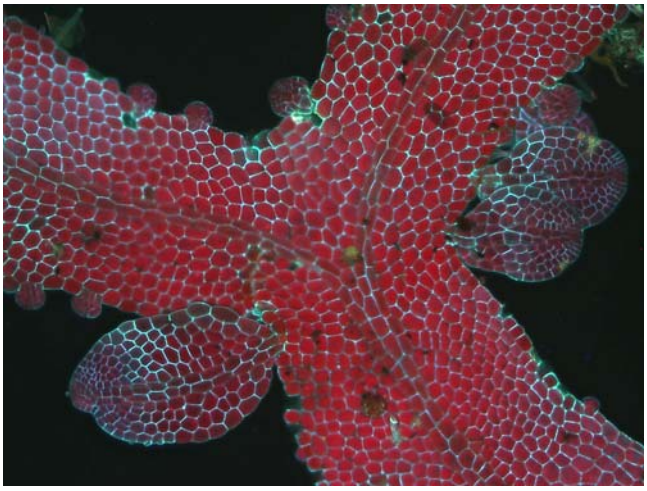

Figure 159. ***Metzgeria*** sp. blue-green fluorescence of cell walls. Photo by Magdalena Turzańska.

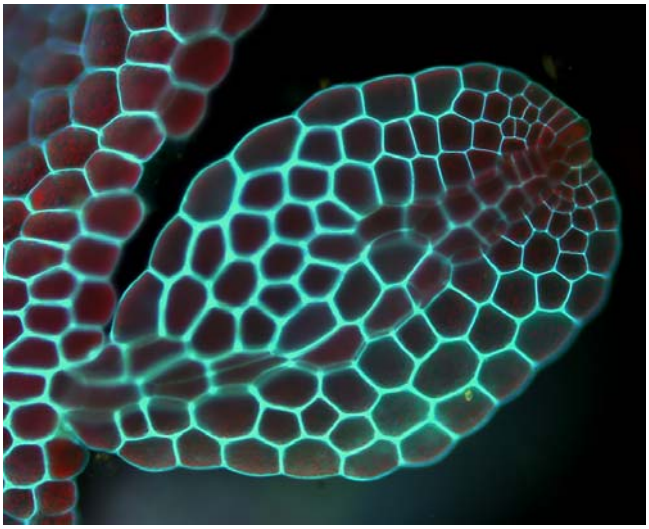

Figure 160. ***Metzgeria*** sp. showing blue-green cell wall fluorescence. Photo by Magdalena Turzańska.

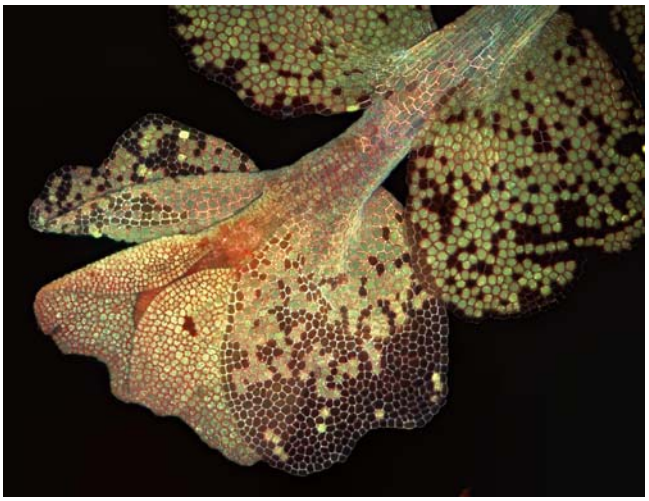

Figure 161. ***Plagiochila asplenioides*** exhibiting golden leaf cell wall fluorescence. Stem cell walls have a more pinkish cast. Photo by Magdalena Turzańska.

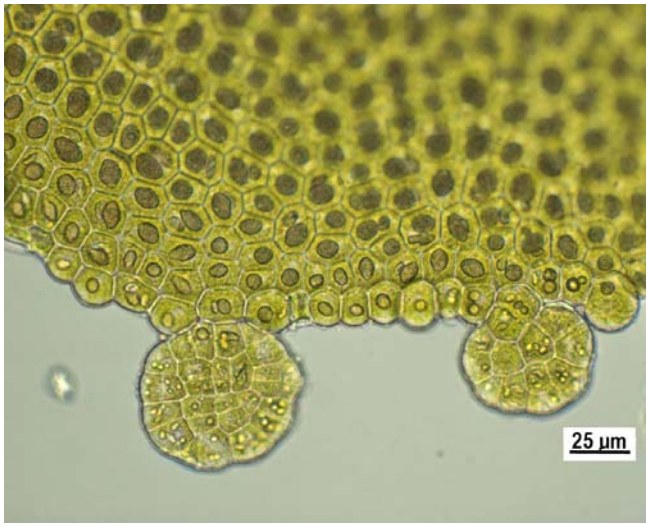

Figure 162. ***Radula complanata*** with gemmae, shown in white light. Photo by Blanka Aguero, with permission.

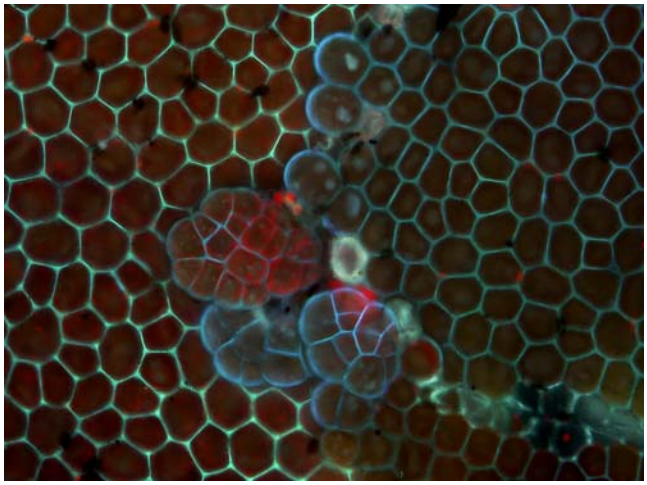

Figure 163. ***Radula complanata*** leaf cell wall and gemmae cell wall fluorescence. Note the difference in color between the blue gemmae cell walls and greenish walls of lamina cells. Photo by Magdalena Turzańska.

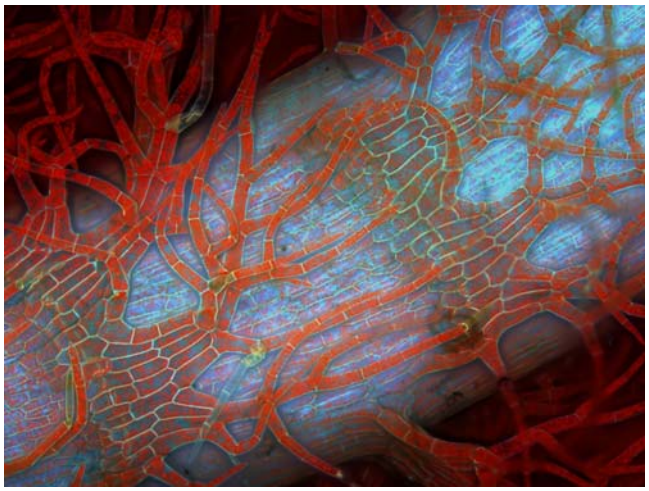

Figure 164. ***Trichocolea tomentella*** with blue cell wall fluorescence. Photo by Magdalena Turzańska.

Figure 165. ***Brachythecium*** fluorescence with leaf cell walls fluorescing aqua and the stems fluorescing bright red. This view makes the leaf bases easy to see. Photo by Magdalena Turzańska.

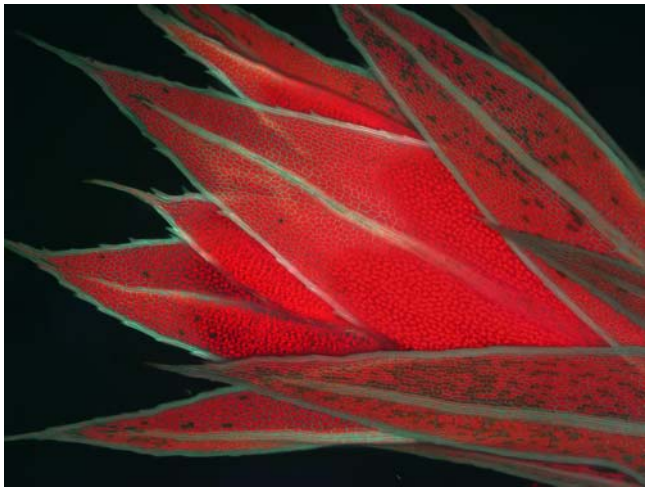

Figure 166. ***Mnium hornum*** leaf border and costa fluorescence with brilliant chlorophyll fluorescence in the leaf cells. Photo by Magdalena Turzańska.

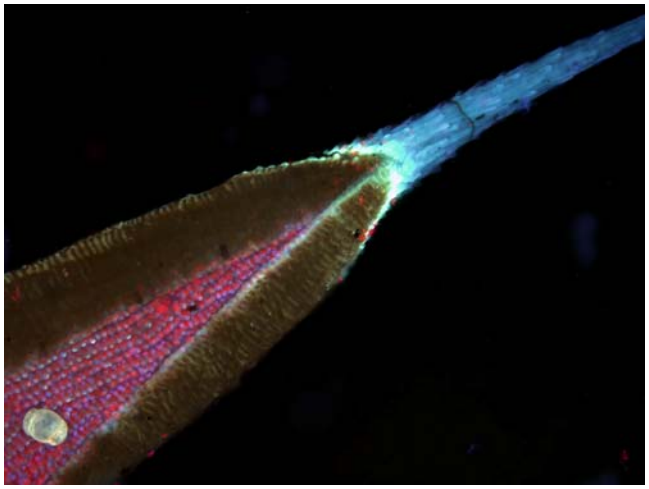

Figure 167. ***Polytrichum piliferum*** leaf fluorescence showing red chlorophyll and blue leaf hair tip. The cell walls of the lamellae can barely be seen fluorescing blue. Photo by Magdalena Turzańska.

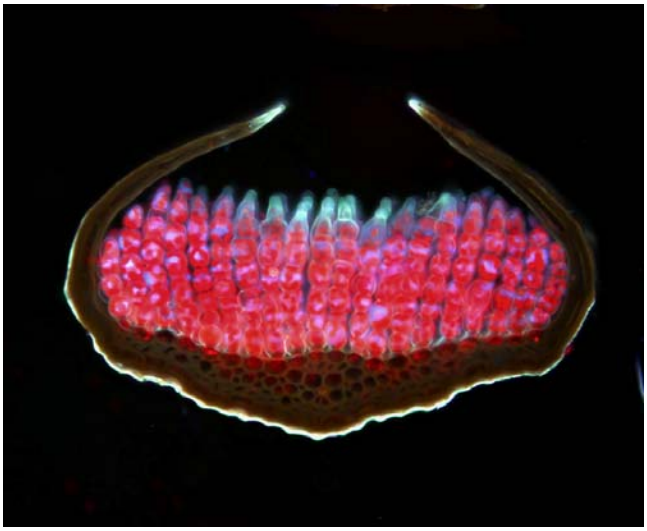

Figure 168. ***Polytrichum piliferum*** leaf cs showing blue fluorescence of the outer cells of lamellae and pale yellow of leaf surface. The lamellae cell walls are fluorescing throughout, but the fluorescence is barely visible due to the strong fluorescence of the chlorophyll. Photo by Magdalena Turzańska.

Figure 169. ***Thuidium tamariscinum*** in sunlight, a species with fluorescent leaf cell walls and contrasting costa fluorescence when illuminated with UV light. Photo by Hermann Schachner, through Creative Commons.

Figure 170. ***Thuidium tamariscinum*** fluorescence in UV light. Photo by Magdalena Turzańska.

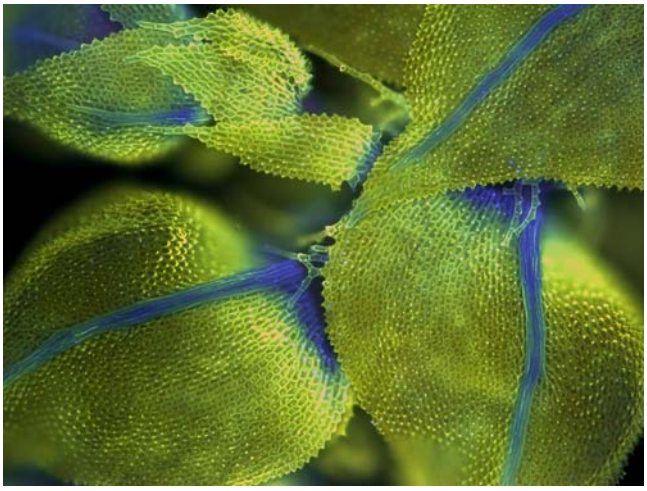

Figure 171. ***Thuidium tamariscinum*** showing a blue fluorescence in the costa and yellow fluorescence in the leaf cell walls, indicating that they have different compounds. These colors have been created by adding berberine to cause the fluorescence. Note the striking difference between the natural fluorescence in Figure 170 and that with berberine stain in this image. Photo by Magdalena Turzańska.

A search of internet images turned up some additional species. One such discovery was a beautiful image of two ***Sphagnum*** species growing together with one (possibly ***Sphagnum divinum***) fluorescing a deep blue-purple and the other lacking fluorescence (Figure 172).

Figure 172. ***Sphagnum*** spp. in white (**upper**) and UV (**lower**) light. The fluorescing moss (**lower**) appears to be ***Sphagnum divinum***, based on its reddish tint (**upper**) and larger, fleshy appearance. Photo ©Damon Noe, with permission.

Sources of Fluorescence

These examples raise the question of the compound(s) causing the fluorescence in bryophytes and why do some have it and others do not. For example, Tamás Pócs (Bryonet 24 March 2022) recalled that ***Bazzania vittata*** (Figure 173-Figure 174) was the only liverwort with fluorescence among those present on the summit of Bellenden Ker in Queensland, Australia.

The two best-known molecules exhibiting fluorescence are chlorophyll and lignin (Donaldson 2020). However, numerous others also exist. These elicit a variety of colors and some (ferulates – one of phenolic compounds) change color with a change in *p*H or chemicals such as Naturstoff reagent (flavonoids). Use of glutaraldehyde as a fixing agent can also induce autofluorescence and permit the imaging of proteins in organelles in the cell protoplast.

It is unclear which structures in bryophytes are responsible for the fluorescence. Andi Cairns (pers. comm. 30 March 2022) suggested that the fluorescence might be due to surface quality. To support this idea, she cited the glaucous surface with minute papillae on both ***Bazzania vittata*** (Figure 173-Figure 174) and ***B. tayloriana*** (Figure 175-Figure 176) (Meagher 2019). ***Zygodon rupestris*** (Figure 59) also has multiple papillae per cell (Figure 177).

Figure 173. ***Bazzania vittata*** in LED light, a species that exhibits fluorescence Photo by Will Cairns, courtesy of Andi Cairns.

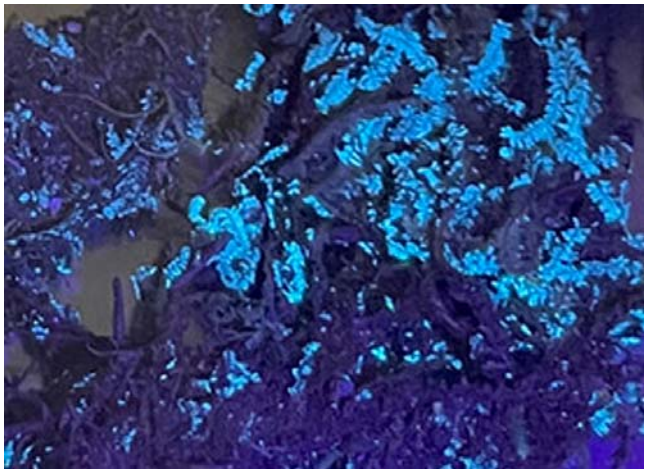

Figure 174. ***Bazzania vittata*** fluorescing. Photo courtesy of Andi Cairns.

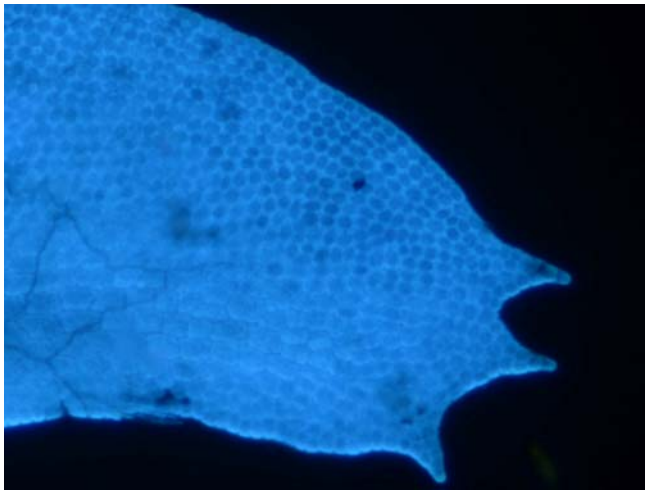

Figure 175. ***Bazzania tayloriana*** leaf showing minute papillae visible on the margins and blue fluorescence. Photo courtesy of David Glenny.

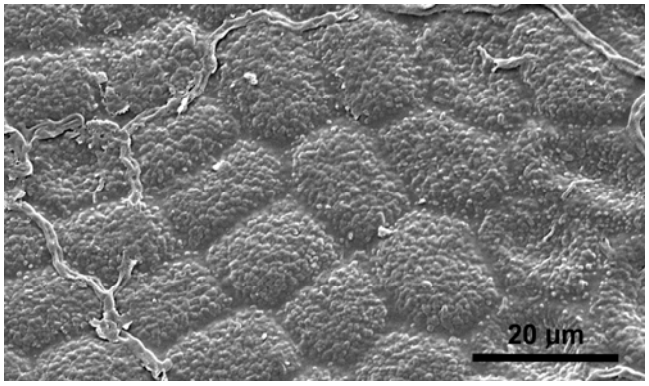

Figure 176. ***Bazzania tayloriana*** dorsal surface cells showing minute papillae. Photo courtesy of John Braggins.

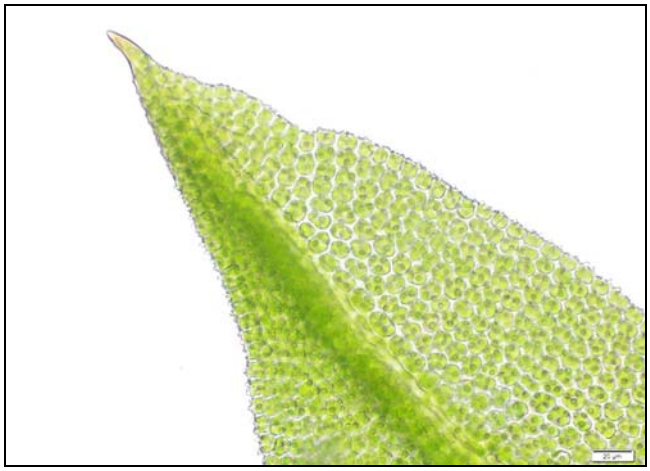

Figure 177. ***Zygodon rupestris*** leaf cells showing papillae. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

It is interesting that McClure and Miller (1967) explored the flavonoids causing fluorescence at such an early date without precipitating more studies on this property in a wider range of bryophytes. They found that most of the fluorescence came from flavonoids and some phenolics, as reported by Dave Kofranek (Bryonet 23 April 2022). It is further interesting that none of the pleurocarpous mosses tested exhibited fluorescence, an observation consistent with that of Ken Kellman (Bryonet 21 April 2022) for ***Antitrichia*** (Figure 145) and ***Homalothecium*** (Figure 146). The study only listed blue and purple reactions, so perhaps there was no testing for those that fluoresce red, yellow, or other colors. There is so much remaining for us to understand.

Magdelena Turzańska has found only weak fluorescence in pleurocarpous mosses, ass seen here in ***Hypnum*** sp. (Figure 178).

Figure 178. ***Hypnum*** sp., a pleurocarpous moss showing a golden cell wall fluorescence. Photo by Magdalena Turzańska.

Role

Fluorescence can help to attract pollinators in flowering plants and thus aid in dispersal, but its role in bryophytes is unknown and unexplored. Andi Cairns speculated on the function of fluorescence in bryophytes as agents of antiherbivory (Andi Cairns, pers. comm. 2 June 2022), and J. K. Oliver suggested that they might just be **spandrels** (phenotypic trait that is byproduct of evolution of some other characteristic, rather than direct product of adaptive selection) – a term introduced by Gould and Lewontin (1979) (Andi Cairns, pers. comm., 24 March 2022).

In tracheophytes, Body *et al*. (2019) found that the yellow fluorescent protein that causes yellow fluorescence was produced in response to **jasmonic acid**, a compound produced in response to herbivory. But we thus far have no evidence that this, or any other fluorescence in bryophytes, is a response to herbivory.

But it is always fun to speculate. It is the start of hypotheses that can be tested. Tom Ottley (pers. comm. 5 May 2022) speculated about the potential role in dispersal of gemmae. Musing that the bryophytes could just make blue pigments instead, he realized that bryophytes are not known to make blue pigments. He suggested that perhaps the compound responsible is able to convert UV light to blue. On the other hand, insects are able to see reflected UV light itself (Turpin 2012). This might be a way of making gemmae and other propagules visible amid the maze of non-emitting leaves, just as it helped Gisela Nordhorn-Richter to locate them for her taxonomic studies. For leafy liverworts, the gemmae are more easily

discernable because of their locations at leaf margins. So far, I have found no information to indicate widespread presence of fluorescence in leafy liverwort gemmae. Perhaps the leaf fluorescence helps the insects to find the plants themselves, with contact with gemmae being almost inevitable.

Lloyd (1924) suggested that the taxonomist could use fluorescent color differences to identify **Cyanobacteria**, especially between closely related species. This seems to be possible with some bryophytes, often being a presence-absence difference. But we need many more UV views of bryophytes to really understand the color variation and its potential use in identification.

Perhaps a more important question needs to be answered. Which of these fluorescent colors can other organisms see? Are the colors we see with UV light under the microscope visible to organisms in nature?

For example, in cross section, a species of ***Leucobryum*** (Figure 179) demonstrated cell wall fluorescence. On the other hand, when viewed in the field with a UV light source, ***Leucobryum aduncum* var. *aduncum*** (Figure 132-Figure 133, Figure 136) exhibited no fluorescence.

Figure 179. ***Leucobryum glaucum*** leaf cs showing fluorescence of the cell walls. Photo by Magdalena Turzańska.

As I saw the color of fluorescence in more and more species of bryophytes, I was inclined to think that these are indeed spandrels. The compounds that produce them are often secondary compounds that serve in functions of structure, antiherbivory, and antibiotics. The fact that they fluoresce is likely just a product of the class of compounds that have these functions. At the same time, there is no evolutionary rule that a compound cannot have more than one adaptive quality. It would be interesting to see if the various colors have any correlation with habitat conditions and if they are inducible or always present.

Methodology

For most of our purposes, the field equipment can be simple and relatively inexpensive. Andi Cairns and colleagues used an LED white light head torch (ASD $3.00) and a small UV torch (ASD $14.99, no name, made in China). For their photography they used a combination of the two lights to obtain both fluorescence of one species while showing lack of fluorescence in the other species present. The photos were taken with an iPhone.

For microscopic work, Magdalena Turzańska uses UV light and an Olympus BX50 fluorescence microscope with an Olympus DP 71 camera.

Staining bryophytes can help to make fluorescence visible in some weakly fluorescing structures. Magdalena Turzańska uses berberine (extracted from *Chelidonium majus* roots) for cell wall staining. These are shown below in ***Diplophyllum albicans*** (Figure 180) and ***Nowellia curvifolia*** (Figure 181). Other stains can be used for special purposes.

Bryophytes have been used to develop methods for detecting fluorescent compounds present in small quantities (Delépée & Pouliquen 2002; Zhao *et al*. 2007). Delépée and Pouliquen (2002) used ***Fontinalis antipyretica*** (Figure 65, Figure 70-Figure 71) to develop a method for detecting oxolinic acid. Cerovic *et al*. (1999) reviewed the potential of using fluorescence signals for remote sensing of vegetation. Can this application be used for bryophytes?

Figure 180. ***Diplophyllum albicans*** female shoot showing fluorescence of the dye berberine in the leaf and perianth cell walls. This is not natural fluorescence. The fluorescence is too weak to be visible without the dye. Photo by Magdalena Turzańska.

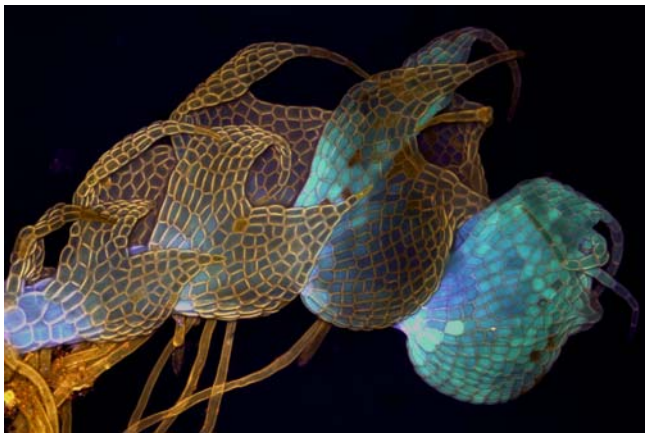

Figure 181. ***Nowellia curvifolia*** showing golden cell wall fluorescence in the leaves after staining with berberine. Photo by Magdalena Turzańska.

Prospects

It appears that fluorescence in bryophytes is a field wide open for study. So many evolutionary questions remain unanswered. How widespread is it among bryophytes? Are the compounds involved the same as those in tracheophytes? Which structures fluoresce? Does this location differ among species or habitats? Which compounds predominate in the bryophytes, and are there phylogenetic patterns to their presence? Can the colors of fluorescence be used to help in identification? Can it help us find some of the tiny species growing among larger species? Does the fluorescence attract arthropods, especially would-be dispersal agents? If so, to what degree does it improve dispersal chances? Does the phenomenon have any adaptive value in particular habitats? Does the fluorescence change with seasons? with temperature? [we know that chlorophyll fluorescence can change with temperature (Deltoro *et al*. 1999)], with drying? Is fluorescence lost over time in herbarium specimens?

Pigments

As in the algae, one can use the chlorophyll-to-phaeophytin ratio to assess physiological stress in bryophytes (Lopez *et al*. 1997). This ratio proved to be a better indicator of environmental stress than presence-absence data for species in 188 stretches of river in northwest Spain. Organic pollution was indicated most strongly, with *p*H also strongly correlated.

As discussed in other chapters, pigments can respond to changes in light intensity. Dark-colored wall or cytoplasmic pigments are present in genera like ***Frullania*** (Figure 123) that are able live high in the canopy or at high elevations (Li *et al*. 1989; Glime *et al*. 1990). Aquatic bryophytes that grow in cold water and full sunlight likewise may produce red cytoplasmic pigments, as seen in ***Fontinalis*** (Figure 182).

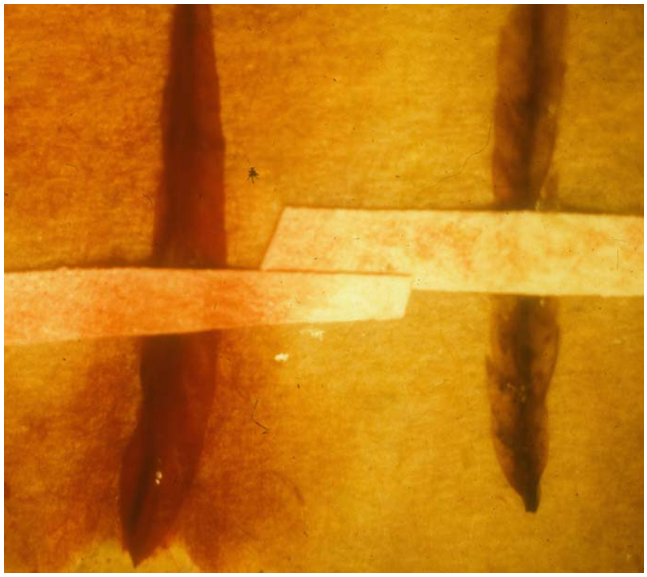

Figure 182. ***Fontinalis antipyretica*** producing red cytoplasmic pigments under water stress in high light. Photo by Janice Glime.

One can only speculate about the advantages of color. Red pigments can be a bit of an enigma. They can respond to both high light and low light. In bright light they are protectors, being positioned between the light source and chlorophyll, often in cell walls where they can protect the entire cell. In low light they seem to work best on the lower surface, or the side away from the light source.

In tropical forests some of the flowering plants have purplish-red coloration on the undersides of leaves. Botanists have considered this to be an adaptation to the low light there. Red algae live in the ocean depths and absorb green light using red pigments (Ritz *et al*. 2000), with most of the red light absorbed by the water itself. These deep water algae are able to activate the red pigments and transfer the energy to the chlorophyll antenna system (photosynthetic light-harvesting antennae) where it activates the chlorophyll electrons (Bag 2021). The chlorophyll antenna system works in bryophytes as well. In bryophytes, thee most frequent of the antenna pigments are α- and β-carotene, lutein, zeaxanthin, violaxanthin, and neoxanthin (Taylor *et al*. 1972). See Chapter 11-1 of this volume for a more thorough discussion of the role of antenna pigments in bryophytes.

Deep forest plants such as bryophytes are able to absorb the green light that filters through the canopy (Neill & Gould 2000; Ruberti *et al*. 2012) and reflect it, presumably to the chlorophyll. In the red alga *Rhodella violacea*, the genes for the production of the red and blue-green pigments phycoerythrin and phycocyanin, respectively, are down-regulated in bright light (Ritz *et al*. 2000). Since chlorophyll is most active in the red end of the spectrum (Wang & Folta 2013), such red reflectance could offer a light enhancement under a green canopy. In ***Arabidopsis thaliana***, when both green and blue light are present, the anthocyanin (red) level is lower than when only blue light is present (Bouly *et al*. 2007; Zhang & Folta 2012) and the degree of reduction of the anthocyanin depends on the rate at which the green light is delivered with the blue light (Zhang & Folta 2012). Melati *et al*. (2019) demonstrated that shaded plants of the Luja plant (*Peristhrophe bivalvis*) has a higher red pigment concentration in shade plants than in full light intensity.

More relevant to the purplish liverwort scales is the red coloration on the undersurfaces of rainforest extreme shade plants. Increased anthocyanin coloration on tracheophyte leaf undersurfaces correlates with the increased absorption of light at the upper (violet) end of the photosynthetic action spectrum (Lee & Graham 1986). Whereas increased red pigments can be a stress response to shade plants exposed to high light intensity, it appears that red pigments on the lower surfaces of photosynthetic organs might have a different function in light capture.

Since anthocyanin is often the pigment responsible for a purplish color, it is possible this mechanism is at work in the liverworts as well, reflecting the limited light that manages to penetrate that far and thus increase that which activates the chlorophyll. It is not an antenna pigment because it is not near the chlorophyll. Such a potential advantage has not, to my knowledge, been explored in the liverworts.

Coloration can also be used as a diagnostic tool. In tracheophytes, pigment variations are indicators for several nutrient deficiencies, toxicities, or antagonisms (Martínez-Abaigar & Núñez-Olivera 1998). Little has been done with color as a nutrient status indicator in bryophytes.

We know that the flavonoid pathway is a specialized metabolic pathway in plants (Davies *et al*. 2020). In flowering plants, flavonoids signal pollinators and dispersal organisms, but they also assist in tolerance to abiotic stresses. We have presumed that this pathway arose during the colonization of land, suggesting that it may have arisen in bryophytes as a defense against UV and drought. It is, nevertheless, absent in hornworts. The bryophyte pathway and its regulation are similar in some ways and differ in others when compared to that seen in flowering plants. One proposal is that flavonoids helped early land plants cope with increased exposure to UVB. But they also helped overcome the dangers imposed by desiccation and extreme temperatures (Markham 1988; Jorgensen 1994; Kenrick & Crane 1997; Cockell & Knowland 1999; Rozema *et al*. 2002; Ligrone *et al*. 2012; Mouradov & Spangenberg 2014; Demarsy *et al*. 2017; Davies *et al*. 2018; de Vries & Archibald 2018; Rensing 2018). Alternatively, Stafford (1991) proposed that these compounds regulated auxin action as well as signalling to mycorrhizal and symbiotic fungi, *i.e.*, serving in communication between complementary organisms. Stafford argued against the UVB-screening role because early concentrations would probably have been low, thus limiting their efficiency at a time when UV-B was particularly high.

I have long been confounded by the one-purpose approach of so many biologists, especially ecologists. It seems to me that these compounds could very well have been as Stafford proposed, serving to signal both auxins and fungi, but at the same time contributing to protection from UV-B. As time proceeded, those individuals that produced more flavonoids would have greater survival rates in the face of extreme temperatures, drought, and UV-B, permitting them to occupy habitats not available to those individuals that produced lesser concentrations of flavonoids. Most likely starting as primitive anthocyanins in the liverworts, the flavonoids have kept adding roles and become more effective at them (Berland *et al*. 2019).

Jumping to the 21st Century, researchers have discovered **auronidins** in ***Marchantia polymorpha*** (Berland *et al*. 2019). But Berland and coworkers discovered that the red pigments in the liverwort ***Marchantia*** (Figure 102, Figure 110, Figure 183-Figure 184) are not anthocyanins, but rather are phenylpropanoids that they have named **auronidins**, a previously unknown and distinct flavonoid class. Liverworts produce red cell-wall-bound pigments called **riccionidins** (now known to be auronidins) as a response to stresses, including UV-B, drought, and nutrient deficiency. Berland and coworkers suggest that these may have been the first anthocyanidins formed in the early land plants and distinct from the anthocyanins. They provide red coloration similar to that of anthocyanins, but they also have a strong fluorescence. Their antioxidant properties could be important in several pathways, but they seem to restricted to cell walls.

This suggests that we should look at fluorescence in our consideration of early evolutionary relationships among bryophytes. Martínez-Abaigar and Núñez-Olivera (2022) have reviewed UV effects on bryophytes, noting that these effects depend on species and evolutionary lineage. Mosses are more UV-tolerant than are liverworts. It should be enlightening to discover where fluorescence exists and how it relates to current habitats and that of the ancestors.

The discovery of auronidins raises so many questions for me. What organs have them? What are the adaptive values, if any, in these organs? Can they tell us an evolutionary story? How do they relate to habitats? Does their fluorescence give the plants any advantage, or is it simply a consequence of having the compound be useful for other characteristics? Are the colors seasonal?

Figure 183. ***Marchantia polymorpha*** with gemmae, showing distribution of red pigmentation, presumably auronidins. Photo by Dick Haaksma, with permission.

Figure 184. ***Marchantia polymorpha*** with red archegoniophores, but green thalli, Laxarbakki, Myvatn, Iceland, 26 July 1987. These red pigments are most likely auronidins. Photo by Janice Glime.

Yet another advantage of the auronidins is their ability to enhance resistance to the fungus ***Phytophthora palmivora*** (Carella *et al*. 2019). Hyphae are unable to penetrate in highly pigmented regions of these plants.

Leaf Canopy

It is well known that chlorophyll concentration increases in response to reduced light availability (Niinemets & Tobias 2014). But within the bryophyte canopy, older tissues are lower on the plant and thus receive less light. In this case, the chlorophyll

concentration decreases with not only age, but also with decreasing light availability (Davey & Ellis-Evans 1996; Niinemets & Tobias 2014). Furthermore, in lower light, the plants are less dense and the leaves are usually farther apart, decreasing the density (Niinemets & Tobias 2014). This reduction in density increases the light interception per leaf area. Pleurocarpous mosses are able to acclimate structurally to light levels by adjusting the density of leaves and branches, whereas non-branching acrocarpous mosses lack the ability to change branching density. In addition, mosses under low water conditions have a greater degree of aggregation, thus further reducing light penetration. But as mosses desiccate they have greater light penetration further down the stem than the same mosses when hydrated, increasing productivity in older parts (Davey & Ellis-Evans 1996).

Absorption is not equal throughout the spectrum. Davey and Ellis-Evans (1996) observed that the greatest attenuation occurred at wavelengths corresponding to the peaks of chlorophyll absorption (675 nm and below 450 nm). Other factors that affect absorption include stem orientation, stem density, leaf size and orientation, and pigment content.

Leaf Angle

Angle of incidence (Figure 185) is the angle formed between the direction of light and the vertical (difference from straight on), so a low sun has a higher angle of incidence. **Leaf angle** (Figure 186) is the angle made by the axil of the leaf and the axis. It affects the reflectance of light in plants. Therefore, a small leaf angle (approaching vertical) creates the effect of a large angle of incidence.

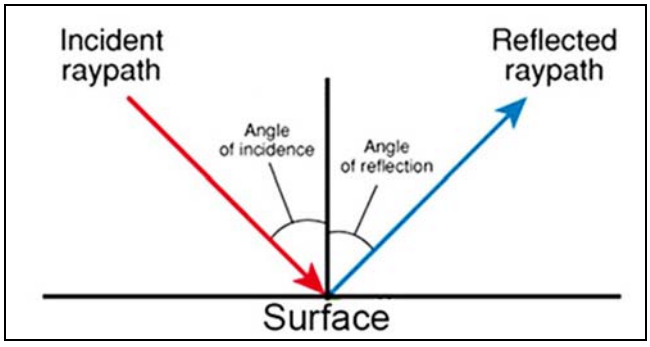

Figure 185. Angle of incidence and reflection pathway. Drawing modified from Clive Dexter at <http://ezbackgrounds.com/blog/ezlighting-guide-angle-incidence.php>.

Howard (1967) demonstrated that leaf angles in four tracheophyte species of 0-30° (=90-60° angle of incidence) made little difference in reflectance, but when the angle of incidence was smaller, the reflectance increased rapidly, consequently rapidly reducing photosynthesis. In the tree leaves of *Eucalyptus regnans*, photosynthesis begins to decrease at ~72° leaf angle, and at 45°, photosynthesis drops to 70% of values of horizontal leaves. At 5° leaf angles it approaches 0% (Kriedmann *et al*. 1964).

In bryophytes, many moss species raise their leaves and wrap them around the stem as they dry, effectively providing greater protection to the chlorophyll by greater overlapping of leaves. In the desert moss ***Syntrichia caninervis*** (Figure 187), leaf angle changes (Figure 188) are an important means of protecting against the effects of high light intensity during long periods of desiccation (Wu *et al*. 2014). First, the leaf movement helps to slow drying, permitting the plant to adjust physiologically in preparation for desiccation (see Chapters 7-5 and 7-6 in Water Relations). Second, the acute leaf angle of only 30° of a dry plant protect the photosynthetic cells. And third, when the leaf rehydrates, it returns in 7 seconds to an angle of 69-84°, with the first leaves reaching normal position in only 1 second. The hyaline cells at the leaf base are thin-walled and facilitate rapid uptake of water, swell, and push the leaf away from the stem. The leaf hair also play a role in reflecting light and reducing its impact on the chlorophyll. But the leaf hairs (**awns**) play another role that thus far has not been explained. They somehow are important in adjusting the leaf angle. When these awns are removed, the angle adjustment is retarded.

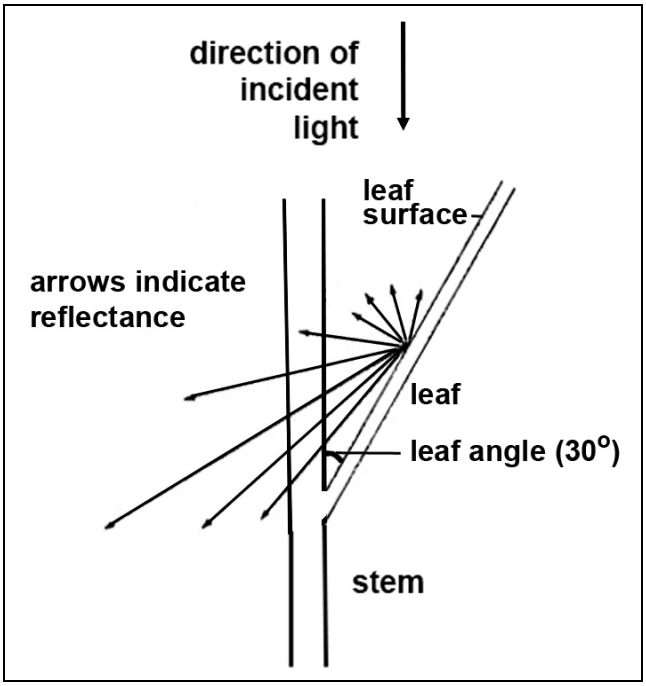

Figure 186. Incidence light and reflectance on a leaf at an acute angle. In this case, the incident light strikes the leaf at an angle of 60° from the straight up light that would strike the leaf from a perpendicular direction. Redrawn from Howard 1967.

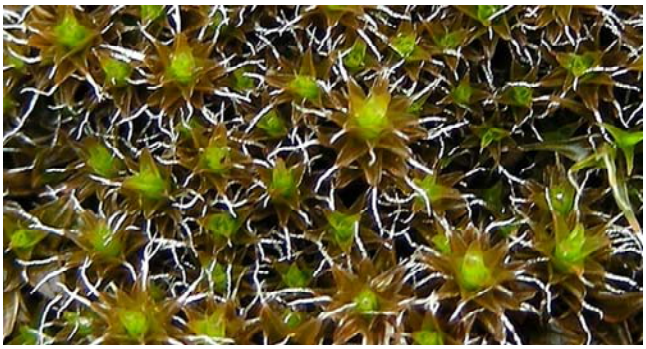

Figure 187. ***Syntrichia caninervis***, a species that changes leaf angles in response to drying. Photo by Michael Lüth, with permission.

Figure 188. ***Syntrichia caninervis*** dry exhibiting twisted leaves with a small leaf angle. Photo by Sheri Hagwood, through public domain.

Xerophytic mosses like ***Syntrichia ruralis*** (Figure 53) can look much darker and expose less surface area to the atmosphere, whereas the wet cells change the optical properties, making the cell walls more translucent (Glime & Church, unpubl.).

Summary

Protonemata of some mosses, such as ***Schistostega pennata***, are able to position their chloroplasts to receive maximum available light and the lens-shaped cells help to focus the light. Their high reflectance provides a luminescence in caves. Similar reflective abilities are present in ***Mittenia plumula*** that lives in wombat holes. ***Cyathodium*** species that live in caves have a similar reflective ability in their thalli.

Some bryophytes are able to live in the dim light surrounding light bulbs in visitor caves, exceeded in their low-light survival only by the algae. Many of the cave bryophytes are also typical of other habitats of greater light intensity, including high-light tolerators like ***Ceratodon purpureus*** and ***Pohlia nutans***. Some are the **tufa formers** that often are so encrusted with limestone that only their tips are able to get sufficient light for photosynthesis. ***Amblystegium serpens*** seems able to live in the lowest light at only 232 lux.

One response to bryophytes in deep caves is **etiolation**, which spaces leaves further apart, thus exposing more surface area to the little light available. In some species, the number of chloroplasts and size of grana can increase and growth can occur even in the dark. Long, thin "exploratory" branches may form. In ***Atrichum undulatum*** the starch disappeared in winter but reappeared in spring, in the dark! When placed in the light, photosynthesis began without delay.

Various plant parts may exhibit fluorescence. So far this ability is known from leaf cell walls, stems, spores, antheridia, archegonia, paraphyses, capsules, peristomes, elaters, gemmae, and bulbils, in addition to the chlorophyll fluorescence known from all photosynthetic organisms. Fluorescence under the microscope has been exhibited in many bryophyte species, but few seem to have been documented in the field. Fluorescence may be caused by a number of compounds, including flavonoids, fatty acids, and lignin-like compounds. Its colors vary widely, but are not visible to the human eye when bright sunlight is present. Nevertheless, many kinds of insects are able to see these colors even in daylight. Its role remains unknown, and it may simply be a property of the cell wall components and antibiotic compounds, but its value in attracting dispersal agents should be explored.

Some mosses develop pigments in response to increased light intensity, although chlorophyll concentrations usually decrease. Others change the leaf angles, decreasing the damage to chlorophyll. Antenna pigments help to transfer light energy to the chlorophyll in low light and pigments on the lower surface may help by reflecting red light back to the chlorophyll.

The light intensity diminishes as it penetrates the bryophyte canopy, but when the leaves dry, more light may reach older portions.

Acknowledgments

Thank you to Misha Ignatov for providing me with a prepublication copy of Ignatov *et al.* (2012) and providing me with numerous images of ***Schistostega***. And thank you to Martin Hutten for offering his *Schistostega* images. Noris Salazar Allen introduced me to *Cyathodium cavernarum* and provided me with images. Michael Lüth has been especially generous in granting permission for me to use any of his images. I appreciate David Kofranek for his effort to take a picture of *Caltha palustris* with UV light. And I certainly thank all the photographers who posted their images on the web, and later granted me permission to use them in this chapter. I especially appreciate help from Magdalena Turzańska for her wonderful images of structures not illustrated elsewhere and for telling me her staining method. Thank you to Scott Zona for helping me to get in contact with Tony Markham to get his permission to use images from his wombat hole video, and to Tony for giving me permission to use his images. Thank you to Andi Cairns for reviewing an earlier draft of the fluorescence section, for several email discussions on the topic, and for several references. Bryonetters provided me with several enlightening discussions, images, and observations on fluorescence in bryophytes, as noted herein.

Literature Cited

Arróniz-Crespo, M., Leake, J. R., Horton, P., and Phoenix, G. K. 2008. Bryophyte physiological responses to, and recovery from, long-term deposition and phosphorus fertilisation in acidic grassland. New Phytol. 180: 864-874.

Bag, P. 2021. Light harvesting in fluctuating environments: Evolution and function of antenna proteins across photosynthetic lineage. Plants 10(6): 1184.

Berland, H., Albert, N. W., Stavland, A., Jordheim, M., McGhie, T. K., Zhou, Y., Zhang, H., Deroles, S. C., Schwinn, K. E., Jordan, B. R., Davies, M., and Andersen, Ø. M. 2019. Auronidins are a previously unreported class of flavonoid

pigments that challenges when anthocyanin biosynthesis evolved in plants. Proc. Natl. Acad. Sci. 116: 20232-20239. <https://www.pnas.org/doi/abs/10.1073/pnas.1912741116>.

Berqvist, K. 1991. Dragon's gold (*Schistostega pennata*). Sver. Nat. 4: 42-43.

Body, M. J., Dave, D. F., Coffman, C. M., Paret, T. Y., Koo, A. J., Cocroft, R. B., and Appel, H. M. 2019. Use of yellow fluorescent protein fluorescence to track OPR3 expression in Arabidopsis thaliana responses to insect herbivory. Front Plant Sci 10: 1586.

Boros, A. 1964. Uber die Moose, die unter dem Einfluss der elektrischen Beleuchtung in des innere der hohlen in Ungarn und in der Tschechoslowakei Eindringen. Internat. J. Speleol. 1: 45-46.

Bouly, J.-P., Schleicher, E., Dionisio-Sese, M., Vandenbussche, F., Straeten, D. Van Der, Bakrim, N., Meier, S., Batschauer, A., Galland, P., Bittl, R., and Ahmad, M. 2007. Cryptochrome blue light photoreceptors are activated through interconversion of flavin redox states. J. Biol. Chem. 282: 9383-9391.

Bowers, M. C. 1968. New localities for mosses rarely found in Michigan's Upper Peninsula. Mich. Bot. 7: 93-94.

Bowley, D. R. 1973. The environment of *Schistostega pennata* (Hedw.) Hook. and Tayl.: New Vermont stations. Rhodora 75: 149-153.

Brandes, H. 1967. Fluorescenzmikroskopische Analyse der Knospenanlagen von Moosprotonemen nach Anfarbung mit Acridinorange. Planta 74: 45-54.

Buczkó, K. and Rajczy, M. 1989. Contributions to the flora of Hungarian caves II. Flora of three caves near Beremend, Hungary. Stud. Bot. Hung. 21: 13-25.

Carella, P., Gogleva, A., Hoey, D. J., Bridgen, A. J., Stolze, S. C., Nakagami, H., and Schornack, S. 2019. Conserved biochemical defenses underpin host responses to oomycete infection in an early divergent land plant lineage. Curr. Biol. 29: 1-13.

Case, J. W. 1975. New data on the distribution of the moss *Schistostega pennata* in Alberta. Can. Field-Nat. 89: 456-457.

Cerovic, Z. G., Samson, G., Morales, F., Tremblay, N., and Moya, I. 1999. Ultraviolet-induced fluorescence for plant monitoring: present state and prospects. Agronomie 19: 543-578.

Champlin, R. L. 1969. A Rhode Island station for luminous moss. Rhodora 71: 305.

Chorvatova, A. M., Uherek, M, and Chorvat, D. 2021. Biosensing the presence of metal nanoparticles by spectrally- and time-resolved endogenous fluorescence in water moss *Fontinalis antipyretica*. Front. Phys. 9: 634324.

Christy, J. A. and Meyer, T. A. 1991. Bryophytes of algific talus slopes in Wisconsin's driftless area. Rhodora 93: 242-247.

Cockell, M. M. and Knowland, J. 1999. Ultraviolet radiation screening compounds. Biol. Rev. 74: 311-345.

Conard, H. S. 1932. Cave mosses. Bryologist 35: 13.

Conard, H. S. 1938. The foray in Upper Michigan, 1937. Bryologist 41: 18-22.

Crum, H. 1973. Mosses of the Great Lakes Forest. Contrib. Univ. Mich. Herb. 10: 1-404.

Csintalan, Z., Proctor, M. C. F., and Tuba, Z. 1999. Chlorophyll fluorescence during drying and rehydration in the mosses *Rhytidiadelphus loreus* (Hedw.) Warnst., *Anomodon viticulosus* (Hedw.) Hook. & Tayl. and *Grimmia pulvinata* (Hedw.) Sm. Ann. Bot. 84: 235-244.

Dalby, D. H. 1966a. The growth of *Eucladium verticillatum* in a poorly illuminated cave. Rev. Bryol. Lichénol. 34: 929-930.

Dalby, D. H. 1966b. The growth of plants under reduced light. Stud. Speleol. 1: 193-203.

Davey, M. C. and Ellis-Evans, J. C. 1996. The influence of water content on the light climate within Antarctic mosses characterized using an optical microprobe. J. Bryol. 19: 235-242.

Davies, K., Albert, N., Zhou, Y., and Schwinn, K. 2018. Functions of flavonoid and betalain pigments in abiotic stress tolerance in plants. Ann. Plant Rev. Online 1: 1-41.

Davies, K., Jibran, R., Zhou, Y., Albert, N. W., Brummell, D. A., Jordan, B. R., Bowman, J. L., and Schwinn, K. E. 2020. The evolution of flavonoid biosynthesis: A bryophyte perspective. Front. Plant Sci. 11: 7-21. <https://www.frontiersin.org/articles/10.3389/fpls.2020.00007/full>.

Delépée, R. and Pouliquen, H. 2002. Determination of oxolinic acid in the bryophyte *Fontinalis antipyretica* by liquid chromatography with fluorescence detection. J. Chromatog. B 775(1): 89-95.

Deltoro, V. I., Calatayud, Á., Morales, F., Abadía, A., and Barreno, E. 1999. Changes in net photosynthesis, chlorophyll fluorescence, and xanthophyll cycle interconversions during freeze-thaw cycles in the Mediterranean moss *Leucodon sciuroides*. Oecologia 120: 499-505.

Demarsy, E., Goldschmidt-Clermont, M., and Ulm, R. 2017. Coping with 'Dark Sides of the Sun' through photoreceptor signaling. Trends Plant Sci. 23: 260-271.

Donaldson, L. 2020. Autofluorescence in plants. Molecules 25(10): 2393.

Dunham, E. M. and Lowe, R. L. 1927. Mosses of unusual growth or unusual habitat. Bryologist 30: 62-65.

Dunk, K. von der and Dunk, K. von der. 1980. Algen und Moose bauen einen Aquadukt aus Tuff. Mikrokosmos 69: 50-55.

Edwards, S. R. 1978. Protonemal gemmae in *Schistostega pennata* (Hedw.) Web. & Mohr. J. Bryol. 10: 69-72.

Faimon, J., Stelcl, J., Kubešová, S., and Zimak, J. 2003. Environmentally acceptable effect of hydrogen peroxide on cave 'lamp-flora', calcite speleothems and limestones. Environ. Pollut. 122: 417-422.

Farrar, D. R. 1998. The tropical flora of rockhouse cliff formations in the eastern United States. J. Torrey Bot. Soc. 125(2): 91-108.

Fries, N. 1945. Some experiments with mosses cultured in the dark. Botanisches Not. 417-424.

Gistl, R. 1926. Relation of light to the protonema of *Schistostega*. (Beziehung zwischen Licht und *Schistostega*-Vorkeim). Ber. Deutsch. Bot. Gesell. 44: 483-492.

Glenny, David. 2020 (27 May). Blog-Goblins' gold at Ōparara River basin.docx. <https://nzbiota.nz/archives/1182>.

Glime, J. M. and Iwatsuki, Z. 1987. Bryophytes in opera. Bryol. Times 41: 7.

Glime, J. M., Hudy, P. S., and Hattori, S. 1990. Diversity and altitudinal niche width characteristics for 35 taxa of the Papua New Guinea *Frullania* flora with consideration of sibling pairs. Tropical Bryology 2: 103-117.

Gould, S. J. and Lewontin, R. 1979. The spandrels of San Marco and the Panglossian Paradigm: A critique of the adaptationist programme. Proc. Roy. Soc. Lond. B 205(1161): 581-598.

Hadju, L. 1979. Die heutige Lage der Algenforschung in den Höhlen und deren Probleme in Ungarn. Karszt és Barlangkutatás 6: 103-116.

Hale, M. E. 1956. Fluorescence of lichen depsides and depsidones as a taxonomic criterion. Castanea 21: 30-32.

Hamerlynck, E. P., Tuba, Z., Csintalan, Z., Nagy, Z., Henebry, G., and Goodin, D. 2000. Diurnal variation in photochemical dynamics and surface reflectance of the desiccation-tolerant moss, *Tortula ruralis*. Plant Ecol. 151: 55-63.

Hanley, S. 1982. A technique for surveying aquatic plant populations using an echo-sounder. Proc., EWRS 6th Symp. Aquatic Weeds. Novi Sad, Yugoslavia, pp. 171-176.

Haring, I. M. 1930. Plant growth under electric light. Bryologist 33: 89-91.

Howard, J. A. 1967. Spectral energy relations of isobilateral leaves. Austral. J. Biol. Sci. 19: 757-766.

Ignatov, M., Ignatova, E., Belousova, A., Filatova, T., and Sigaeva, A. 2012. An additional observation on protonema of *Schistostega pennata* (Bryophyta). Arctoa 21: 1-20.

Iwatsuki, Z. 1977. *Schistostega pennata* and moss balls – mosses designated as natural monuments in Japan. Shizenkagaku Hakubutsukan 44: 64-67.

Jedrzejko, K. and Ziober, A. 1992. The bryophytes of chosen caves on the Krackòw-Wieluñ Upland and its relation to microclimate conditions and ecological differentiation of habitats. Ziemia Czestochowska 18: 107-151.

Jorgensen, R. 1994. The genetic origins of biosynthesis and light-responsive control of the chemical UV screen of land plants. In: Ellis, B. E., Kuroki, G. W., and Stafford, H. A. (eds.). Recent Advances in Phytochemistry, vol. 28. Springer, Boston, USA, pp. 179-192.

Kanda, H. 1971. *Schistostega pennata* Hedw. in Hokkaido: Its ecology and germination. Hikobia 6: 60-75.

Kanda, H. 1988. The present situation of the colony of *Schistostega pennata* Hedw. in the Makkausa Cave, Rausa, Hokkaido. Proc. Bryol. Soc. Japan 52: 165-166.

Kenrick, P. and Crane, P. R. 1997. The origin and early evolution of plants on land. Nature 389: 33-39.

Koike, Y. 1989. Culture of *Schistostega pennata* in empty bottles in urban areas. Proc. Bryol. Soc. Japan 5: 27-28.

Kol, E. 1966. The effect of algae on germination and growth of rice I. Adv. Front. Plant Sci. 15: 51-69.

Komáromy, Z. P., Padisak, J., and Rajczy, M. 1985. Flora in the lamp-lit areas of the cave "Anna-Barlang" near Lillafuered (Hungary). Ann. Hist. Nat. Mus. Natl. Hung. 77: 103-112.

Koponen, T. 1977. Kulosammal (*Ceratodon purpureus*) ja varstasammal (*Pohlia nutans*) 176 m syvyydessa Vihannin Kaivoksessa. [*Ceratodon purpureus* and *Pohlia nutans* found at a depth of 176 m in the mine at Vihanti, Finland.]. Luonnon Tutkija 81: 59.

Kriedemann, P. E., Neales, T. F., and Ashton, D. H. 1964. Photosynthesis in relation to leaf orientation and light interception. Austral. J. Biol. Sci. 17: 591-600.

Kubešová, S. 2009. [Poster] Bryophytes at lamps in selected public caves in the Czech Republic – past and present situation. Nowellia Bryologica numéro spécial, p. 158.

Lang, W. B. 1941. Mosses in the Virginia caverns. Science 94: 414.

Lang, W. B. 1943. The mosses of Luray Cavern, Virginia. Science 98: 173, 174.

Lee, D. W. and Graham, R. 1986. Leaf optical properties of rainforest sun and extreme shade plants. Amer. J. Bot. 73: 1100-1108.

Li, X., Glime, J. M., and Hattori, S. 1989. Ecological gradient analysis of the genus *Frullania* on Mt. Albert Edward, Papua New Guinea. J. Hattori Bot. Lab. 66: 359-369.

Ligrone, R., Duckett, J. G., and Renzaglia, K. S. 2012. Major transitions in the evolution of early land plants: A bryological perspective. Ann. Bot. 109: 851-871.

Lloyd, F. E. 1924. The fluorescent colors of plants. Science 59: 241-248.

Lo Giudice, R. and Privitera, M. 1984. Sulla brioflora di alcune grotte etnee (Grotta Forcato, Grotta delle Palombo, Grotta dei Ladri). Arch. Bot. Biogeogr. Ital. 59(3-4): 137-157.

Lopez, J., Retuerto, R., and Carballeira, A. 1997. D665/D665a index versus frequencies as indicators of bryophyte response to physicochemical gradients. Ecology 78: 261-271.

Lovelock, C. E. and Robinson, S. A. 2002. Surface reflectance properties of Antarctic moss and their relationship to plant species, pigment composition and photosynthetic function. Plant Cell Environ. 25: 1239-1250.

Maheu, J. and Guerin, H. P. 1935. Influence de la lumiere electrique sur la flore cavernicole. Bull. Soc. Bot. France 82: 477-494.

Markham, K. R. 1988. Distribution of flavonoids in the lower plants and its evolutionary significance. In: Harborne, J. B. (ed.). Flavonoids. Chapman and Hall, London, UK, pp. 427-468.

Martínez-Abaigar, J. and Núñez-Olivera, E. 2022. Bryophyte ultraviolet-omics: From genes to the environment. J. Exper. Bot. 73: 4412-4426. <https://doi.org/10.1093/jxb/erac090>.

Matsuda, Y. 1963. *Schistostega pennata* Hook. et Tayl. occurs in artificial caves. Misc. Bryol. Lichenol. 3(3): 41.

McClure, J. W. and Miller, H. A. 1967. Moss chemotaxonomy. A survey for flavonoids and the taxonomic implications. Nova Hedw. 14: 2-4.

Meagher, D. A. 2019. A synopsis of the genus *Bazzania* (Marchantiophyta: Lepidoziaceae) in Australia. Austral. Syst. Bot. 32: 310-362.

Melati, R., Sugito, Y., Aini, N., and Nihayati, E. 2019. Quality optimization of Luja plant (*Peristrophe bivalvis* Merrill) by means of light intensity manipulation and identification of substance with pigment potential. Biosci. Res. 16(2): 1660-1667.

Merced, A. and Renzaglia, K. S. 2017. Structure, function and evolution of stomata from a bryological perspective. Bryo. Div. Evol. 39: 7-20.

Mouradov, A. and Spangenberg, G. 2014. Flavonoids: A metabolic network mediating plants adaptation to their real estate. Front. Plant Sci. 5: 620.

Neill, S. and Gould, K. S. 2000. Optical properties of leaves in relation to anthocyanin concentration and distribution, Can. J. Bot. 77: 1777-1782.

Niinemets, Ü. and Tobias, M. 2014. Scaling light harvesting from moss "leaves" to canopies. In: Hanson, D. T. and Rice, S. K. (eds.). Photosynthesis in Bryophytes and Early Land Plants. Springer, Dordrecht, pp. 151-171.

Nordhorn-Richter, G. 1984a. Bryophytes with asexual forms of propagation under the fluorescence microscope. In: Vana, J. (ed.), Proceedings of the Third Meeting of Bryologists from Central and East Europe, Univerzita Karlova, Praha, pp. 93-98.

Nordhorn-Richter, G. 1984b. Primare Fluoreszenz bei Moosen. Leitz-Mitt. Wiss. U. Techn. 8(6): 167-170.

Nordhorn-Richter, G. 1984c. Primary fluorescence of mosses. Leitz-Mitt. Wiss. Tech. 8: 167-170.

Nordhorn-Richter, G. 1985a. Investigation of bryophytes with the fluorescence microscope. Bryol. Times 31: 4.

Nordhorn-Richter, G. 1985b. New results from fluorescence microscopy of bryophytes. Abstr. Bot. 9(Suppl. 2): 119-121.

Nordhorn-Richter, G. 1988. Fluorescence microscopy in bryology. In: Glime, J. M. (ed.): Methods in bryology, Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan, pp. 193-197.

Pringsheim, E. G. and Pringsheim, O. 1935. Physiologische Studien am Moosen. III. Die Züchtung von Laubmoosprotonemen im Dunkeln. Jahrb. Wiss. Bot. 82: 311-332.

Prior, P. V. 1961. Studies on the mosses of Luray Cavern. Bryologist 64: 215-222.

Proctor, M. C. F. 2003. Experiments on the effect of different intensities of desiccation on bryophyte survival, using chlorophyll fluorescence as an index of recovery. J. Bryol. 25: 201-210.

Proctor, M. C. F. and Smirnoff, N. 2011. Ecophysiology of photosynthesis in bryophytes: Major roles for oxygen photoreduction and non-photochemical quenching? Physiol. Plant. 141: 130-140.

Rajczy, M. 1978-1979. Effect of the cave environment on some mosses. Ann. Univ. Sci. Budapest. Rolando Eötvös Nom. Sec. Biol. 20-21: 125-136.

Rajczy, M. 1979. Contributions to the bryoflora of Greece. I. The bryophytes of the Cave Perama near Joannina. Stud. Bot. Hung. 13: 3-5.

Rajczy, M., Buczkó, K., and Komáromy, Z. 1986. Contributions to the flora of the Hungarian caves. I. Flora of the entrances of the caves Loek-voelgyi-barlang and Szeleta-barlang. Stud. Bot. Hung. 19: 79-88.

Reinoso Franco, J., Rodriguez Oubiña, J., and Viera Benitez, M. C. 1994. Precisions on the ecology and chorology of *Schistostega pennata* (Hedw.) Webb & Mohr. in the Iberian Peninsula. Lazaroa 14: 13-19.

Rensing, S. A. 2018. Great moments in evolution: The conquest of land by plants. Curr. Opin. Plant Biol. 42: 49-54.

Ridgway, J. E. and Larson, D. A. 1966. Sporogenesis in the bryophyte *Anthocerosis* (*sic*): Features shown by fluorescence microscopy. Letters to Nature. Nature 209: 1154.

Ritz, M., Thomas, J. C., Spilar, A., and Etienne, A. L. 2000. Kinetics of photoacclimation in response to a shift to high light of the red alga *Rhodella violacea* adapted to low irradiance. Plant Physiol. 123: 1415-1426.

Rozema, J., Björn, L. O., Bornman, J. F., Gaberščik, A., Häder, D. P., Trošt, T., Germ, M., Klisch, M., Gröniger, A., Sinha, R. P., Lebert, M., He, Y.-Y., Buffoni-Hall, R., Bakker, N. V. J. de, Staaig, J. van de, and Meijkamp, B. B. 2002. The role of UV-B radiation in aquatic and terrestrial ecosystems – an experimental and functional analysis of the evolution of UV-absorbing compounds. J. Photochem. Photobiol. B Biol. 66: 2-12.

Ruberti, I., Sessa, G., Ciolfi, A., Possenti, M., Carabelli, M., and Morelli, G. J. B. A. 2012. Plant adaptation to dynamically changing environment: The shade avoidance response. Biotech. Adv. 30: 1047-1058.

Sarafis, V. 1971. Modern methods in the investigation of bryophyte morphology. N. Z. J. Bot. 9: 725-738.

Servettaz, C. 1913. Recherches experimentelles sur le développement et la nutrition des mousses en milieux stérilisées. Ann. Sci. Nat., Bot. Sér. IX. 17: 111-224.

Shi, D.-J., Wu, P.-C., Qiu, Y.-Y., and Wang, M.-Z. 1992. Comparative studies on photosynthetic fluorescence spectra and fluorescence kinetics of bryophytes. Acta Phytotax. Sinica 30: 320-330.

Shiomi, T. 1973. Bryophytes growing around the illumination in the Akiyoshi-do cave, Yamaguchi Prefecture. Proc. Bryol. Soc. Japan 4: 45.

Stafford, H. A. 1991. Flavonoid evolution: An enzymic approach. Plant Physiol. 96: 680-685.

Stefureac, T. I. 1985. Recherches bryospeliologiques sur certaines grottes de Roumanie. Rev. Roumaine Biol., Ser. Biol. Vég. 30: 109-116.

Stone, I. G. 1961. The highly refractive protonema of *Mittenia plumula* (Mitt.) Lindb. (Mitteniaceae). Proc. Roy. Soc. Victoria 74: 119-124.

Stone, I. G. 1986. The relationship between *Mittenia plumula* (Mitt.) Lindb. and *Schistostega pennata* (Hedw.) Web. & Mohr. J. Bryol. 14: 301-314.

Talamond, P., Verdeil, J. L., and Conéjéro, G. 2015. Secondary metabolite localization by autofluorescence in living plant cells. Molecules 20: 5024-5037.

Taylor, A. O., Jesper, N. M., and Christeller, J. T. 1972. Plants under climatic stress. III. Low temperature, high light effects on photosynthetic products. Plant Physiol. 47: 798-802.

Thatcher, E. P. 1949. Bryophytes of an artificially illuminated cave. Bryologist 52: 212-214.

Vries, J. de and Archibald, J. M. 2018. Plant evolution: Landmarks on the path to terrestrial life. New Phytol. 217: 1428-1434.

Wang, Y. and Folta, K. M. 2013. Contributions of green light to plant growth and development. Amer. J. Bot. 100: 70-78.

Weber, D. 1989. Die Höhlenfauna und -flora des Hölenkatastergebietes Rheinland-Pfalz/Saarland, 2. Abh. Karst-Höhlenkunde 23: 1-250.

Wilson, T. and Hastings, J. W. 2013. Bioluminescence. Harvard University Press, Cambridge, MA.

Wolfbeis, O. S. 1985. The fluorescence of organic natural products. In: Schulman, S. G. (ed.). Molecular Luminescence Spectroscopy. Methods and Applications. Part 1. John Wiley & Sons, New York, pp. 167-370.

Wu, N., Zhang, Y.-M., Downing, A., Aanderud, Z. T., Tao, Y., and Williams, S. 2014. Rapid adjustment of leaf angle explains how the desert moss, *Syntrichia caninervis*, copes with multiple resource limitations during rehydration. Funct. Plant Biol. 41: 168-177.

Zhang, C., Li, X., and Chao, C. 2004. New records of luminous liverworts from the Karst Caves of Guangxi Province, PR China: *Cyathodium cavernarum* Kunze sent *C. smaragdium* Schiffin ex Keissler (Cyathodiaceae, Hepaticae). Carsologica Sinica 2: 154-157.

Zhang, T. and Folta, K. M. 2012. Green light signaling and adaptive response. Plant Signal. Behav. 7: 75-78.

Zhao, X., Wang, H., You, J., and Suo, Y. 2007. Determination of free fatty acids in bryophyte plants and soil by HPLC with fluorescence detection and identification by online MS. Chromatographia 66(3): 197-206.

Ziober, A. 1981. Ecological characteristic of the cave bryoflora of the Krakow-Wielun Upland. In: Szweykowski, J. (ed.). New Perspectives in Bryotaxonomy and Bryogeography, Adam Mickiewicz University, Poznan, pp. 135-140.