# CHAPTER 9-5 LIGHT: CAVE MOSSES



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

# **Cave Mosses**

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 (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), 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.



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

This unusual jewel-like property (Figure 3) is the result of the protonema (Gistl 1926). The cells are lens-shaped (Figure 6) and their upper surface is curved in such a way as to focus the light on the interior of the cell (Figure 5; Figure 4). 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 6). If a change in the light direction occurs, as may happen seasonally, the chloroplasts can reposition themselves within one to three hours.



Figure 3. Protonemata of *Schistostega pennata* showing upright clumps. Photo by Misha Ignatov.



Figure 4. Protonema of *Schistostega pennata* showing lensshaped cells. Photo by Misha Ignatov.



Figure 5. The cave moss, *Schistostega pennata*, reprinted with permission from Zen Iwatsuki.



Figure 6. Lens-shaped cells of protonema of *Schistostega pennata* with chloroplasts arranged on one side of cell to focus light. Photo by 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 8]. 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 glowworm 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 7).



Figure 7. Luminous appearance of *Schistostega pennata* protonemata. Photo by Janice Glime.



Figure 8. A single plant of *Schistostega pennata* among its protonemata, the "small arched feather." Photo by Des Callaghan.

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 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 9), 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.



Figure 9. *Schistostega pennata* showing frond-like branches of leafy gametophyte. Photo with permission from <a href="http://www.botany.ubc.ca/bryophyte/LAB8.htm">http://www.botany.ubc.ca/bryophyte/LAB8.htm</a>>.

When I went to Germany, I was delighted to find *Schistostega pennata* 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).

#### Cyathodium

In the thallose liverwort genus *Cyathodium* (Figure 10), 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).

#### **Wombat Holes**

In Australia, a similar moss, *Mittenia plumula* (Figure 11) lives on dimly lit, clay-covered rock ledges and at the entrances to wombat holes, where the moss lives on soil. Stone (1961, 1986) concluded that *Mittenia* belongs in the order Schistostegales with *Schistostega*. Both have a pinnate leaf arrangement, protonemata with similar luminescent properties, similar pale color of the leafy plant, and similar habitats.



Figure 10. View through pore of *Cyathodium cavernarum*, a thallose cave liverwort that emits a yellowish luminescence in caves. Photo by Noris Salazar Allen.



Figure 11. *Mittenia plumula* growing in a wombat hole in Australia. Photos by Janice Glime.

#### **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. Even *Science* has accepted articles on mosses in Virginia (USA) caverns, including the famous Luray Cavern (Lang 1941, 1943), and Prior again studied Luray Cavern mosses, publishing in 1961 in *The Bryologist*.

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

The widespread *Fissidens taxifolius* 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.

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, Eucladium verticillatum (Figure 12), in a poorly lit cave, also occurring in caves in Hungary (Buczkó & Rajczy 1989). In Crystal Cave, Wisconsin, Thatcher (1949) found Barbula unguiculata, Brachythecium populeum, **Bryoerythrophyllum Brachythecium** salebrosum, recurvirostre, Bryum caespiticium, Bryum capillare, Ceratodon purpureus, Fissidens taxifolius, Leptodictyum Marchantia polymorpha, Plagiomnium riparium, cuspidatum, and Warnstorfia fluitans Like Conard, Thatcher observed the leaves to be more distant than is typical. Komáromy et al. (1985) likewise found Eucladium verticillatum, a Brachythecium (B. velutinum), and two species of Fissidens (F. cristatus, F. pusillus). Within only one year from its first illumination, Howe Cavern in New York, USA, already was adorned with Amblystegium serpens var. juratzkanum, Amphidium mougeotii, Brachythecium rutabulum, Bryum caespiticium, Bryum capillare, Leptobryum pyriforme, and Marchantia polymorpha encircling its new lights (Haring 1930). Buczkó and Rajczy (1989) found that Amblystegium serpens (=A. juratzkanum var. juratzkanum; Figure 13) 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.

It is perhaps not surprising that several **tufa formers** such as *Eucladium* (von der Dunk & von der Dunk 1980), *Barbula*, and *Didymodon* (Figure 14) 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 12. *Eucladium verticillatum*, a tufa-forming moss. Photo by Michael Lüth.



Figure 13. *Amblystegium serpens*, a common cave moss in Hungary. Photo by Michael Lüth.



Figure 14. Tufa-forming *Didymodon tophaceus*, a former of didymodontoliths. Note carbonates at base encrusted on older stems. Photo by Michael Lüth.

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* and *Pohlia nutans* (Figure 15). But then, these two mosses seem to do well in extremes, as long as it is not too hot.

Figure 15. *Pohlia nutans*, a widespread moss that frequents caves and mines. Photo by Michael Lüth.

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.

#### 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* and *Leptobryum pyriforme* (Figure 16) 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 17) and Plagiomnium ellipticum (Figure 18), 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 ±1°C 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<sub>2</sub> fixation that did the control samples from normal light (Table 1). One interesting event in Rajczy's experiment was that isopods (Mesoniscus graniger) consumed all the dead material of the plants. The mosses soon grew pale, then partly brown.



Figure 16. *Leptobryum pyriforme*, an invader of bare soil. Photo by Michael Lüth.

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

<sup>14</sup> CO <sub>2</sub> Incorporation				
	Net Activity (cmp/leaf)			Contrib dk
	total	dark	light	fix to total
	fix	fix	fix	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%

When *Atrichum undulatum* 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 19) were even thinner than in September, and only 1-2 stroma thylakoids were present. From 3 to 10 broad, low grana were present.



Figure 17. *Atrichum undulatum* leaves. Photo by Janice Glime.



Figure 18. Plagiomnium ellipticum. Photo by Michael Lüth.



Figure 19. 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* 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*, 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 1971).

And why did both species 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?

### 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.

# Acknowledgments

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