

CHAPTER 18-4

CAVES – BRYOPHYTE STRATEGIES

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CHAPTER 18-4

CAVES – BRYOPHYTE STRATEGIES



Figure 1. *Cyathodium cavernarum* on a dark ledge. Photo by Cédric de Foucault, through Creative Commons.

Rare Species and New Finds

I have tried throughout the book not to reveal the exact location of rare species. Bryologists and other collectors have been known to contribute to the disappearance of species from some locations through their collections.

Unique habitats always draw our attention in anticipation of finding something new, as already reported in Chapters 18-1 for the **Cyanobacteria** and algae in caves. Some of the rare bryophytes have been mentioned in Chapters 18-2 to 18-3. Likewise, the various caves and cave-like habitats often don't disappoint us for new bryophytes, particularly if they have not previously been explored by a bryologist. For example, Aziz (2011) reported 17 new species records for Iraq, and four of these were associated with caves. These included *Tortula viridifolia* (Figure 2) cited as *Pottia wilsonii* var. *crinata* and *Tortula truncata* (Figure 3-Figure 4).



Figure 2. *Tortula viridifolia* with capsules, a species Aziz found in caves as new to Iraq. Photo by Michael Lüth, with permission.



Figure 3. *Tortula truncata*, a species Aziz found in caves as new to Iraq. Photo from Botany Website, UBC, with permission.



Figure 4. *Tortula truncata* with capsules. Photo by Claire Halpin, with permission.

Vitt and Belland (1997) found that 25% of the mosses in Alberta, Canada, are rare. This study allows us to assess the characteristics of rare species. In their study, they found that pleurocarpous species, long-lived perennials, and competitive strategists were less likely to be among the rare species. Members of **Bryales**, **Dicranales**, and **Funariales** are more likely to be represented, whereas **Hypnales**, **Orthotrichales**, and **Sphagnales** are underrepresented. Of interest in cave bryology is that 42% of the rare species have boreal distributions, 57% occur on soil, and 34% occur on rock. These attributes make caves suitable places for finding disjunct and rare species.

Since caves create unique conditions within an ecosystem or region, it is not surprising to find that they harbor species that are rare for that area. In the Red River Gorge of Kentucky, USA, Studler and Snider (1989) found rare mosses and liverworts were "favored by the numerous caves and ravines." In the caves they found such rare species as *Bryoxiphium norvegicum* (Figure 5), *Hookeria acutifolia* (Figure 6), *Brothera leana* (Figure 7), *Diphyscium mucronifolium* (Figure 8), *Rhabdoweisia crispata* (Figure 9), *Syrrhopodon texanus* (Figure 10), *Trichostomum tenuirostre* (Figure 11-Figure 13), and *Plagiochila sullivantii* (Figure 14) representing relict or disjunctive taxa.



Figure 5. *Bryoxiphium norvegicum*, a rare taxon that can be abundant in caves. Photo by Amelia Merced, through Creative Commons.



Figure 6. *Hookeria acutifolia*, a rare taxon that can be abundant in caves. Photo by John Game, through Creative Commons.



Figure 7. *Brothera leana*, a rare taxon that can be abundant in caves. Photo by Wayne Lampa, through Creative Commons.



Figure 8. *Diphyscium mucronifolium*, a rare taxon that can be abundant in caves. Photo by Blanka Agüero, with permission.



Figure 11. *Trichostomum tenuirostre* sandstone cliff habitat in Ohio, USA. Photo by Bob Klips, with permission.



Figure 9. *Rhabdoweisia crispata* shaded at rock base, a rare taxon that can be abundant in caves. Photo by Tuomo Kuitunen <luopioistenkasvisto.fi>, with permission.



Figure 12. *Trichostomum tenuirostre* sandstone cliff habitat, a rare taxon that can be abundant in caves. Photo by Bob Klips, with permission.



Figure 10. *Syrrhopodon texanus* with gemmae, a rare taxon that can be abundant in caves. Photo by Bob Klips, through Creative Commons.



Figure 13. *Trichostomum tenuirostre*. Photo by Bob Klips, with permission.



Figure 14. *Plagiochila sullivantii*, a rare taxon that can be abundant in caves. Photo by probably Paul Davison, University of North Alabama.

Evans and Nichols (1935) reported that the original specimens of *Mesoptychia gillmanii* (as *Jungermannia gillmanii*; Figure 15) came from a cave in a cliff of Potsdam sandstone on an island in Lake Superior. This was collected in 1867 by Henry Gillman and seems to be the first liverwort collected in Michigan. However, Stephani concluded that it was in fact *Lophozia inflata*. Observations of the paroicous inflorescences later placed it in the genus *Leiocolea*, but its current status in Söderström *et al.* (2016) places it back in *Mesoptychia gillmanii*.

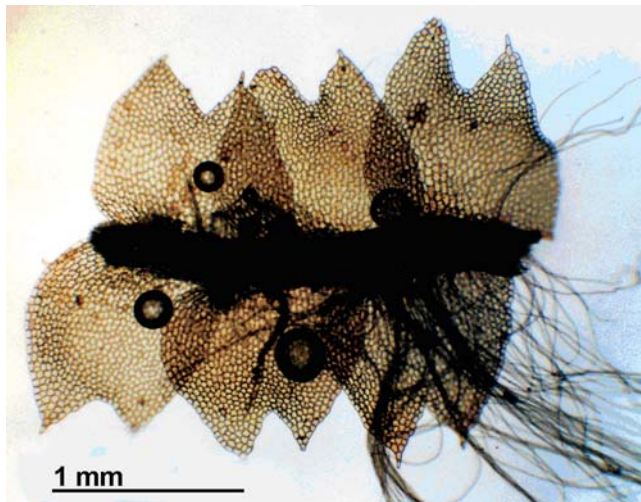


Figure 15. *Mesoptychia gillmanii*, a species first reported in Michigan, USA, from a cave in a cliff of Potsdam sandstone on an island in Lake Superior. Photo by David Wagner, with permission.

Hermann (1964) added *Aneura pinguis* (Figure 16) to the known flora of Mt. Katahdin, Maine, USA, from a collection on the peaty floor of a cave between huge boulders.

Sguazzin and Polli (2011) found *Ptychostomum moravicum* (= *B. laevipilum*; Figure 17-Figure 18) from a cave on Mount Saint Michael off the coast of Cornwall. Puglisi *et al.* (2019) found species that are rare in Sicily: *Brachytheciastrum collinum* (Figure 19), *Grimmia torquata* (Figure 20), *Ptychostomum cernuum* (Figure 21-Figure 22), *Rhabdoweisia fugax* (Figure 23), and *Tortula*

bolanderi (Figure 24) in Italian caves. Castello and Strazzaboschi (2013) reported the liverwort *Cololejeunea rossettiana* (Figure 25) from Della Grotta Dell'orso karst cave as new to the Friuli Venezia Giulia region of Italy.



Figure 16. *Aneura pinguis*, a species that added to the known Maine, USA, flora from a collection on the floor of a cave. Photo by Hermann Schachner, through Creative Commons.



Figure 17. *Ptychostomum moravicum*, a relatively rare species from a cave on Mount Saint Michael off the coast of Cornwall. Photo by Hugues Tinguy, with permission.



Figure 18. *Ptychostomum moravicum*, Photo by jonnyecology, through Creative Commons.



Figure 19. *Brachytheciastrum collinum* on rock, a rare species found in caves in Italy. Photo by Andy Hodgson, with permission.



Figure 22. *Ptychostomum cernuum*. Photo by Wayne Lampa, through Creative Commons.



Figure 20. *Grimmia torquata*, a rare species found in caves in Italy. Photo by Des Callaghan, with permission.



Figure 23. *Rhabdoweisia fugax* with capsules, on rock ledge, a rare species found in caves in Italy. Photo by Michael Lüth, with permission.



Figure 21. *Ptychostomum cernuum* with capsules, on rock, a rare species found in caves in Italy. Photo by Tom Neily, through Creative Commons.



Figure 24. *Tortula bolanderi* with capsules, a rare species found in caves in Italy. Photo by Randal, through Creative Commons.



Figure 25. *Cololejeunea rossettiana*, a rare species found in caves in Italy. Photo by George G., through Creative Commons.

In the Azores, Gabriel *et al.* (2006) found 119 bryophyte species in lava tubes and volcanic pits from Graciosa Island. However, there were no endemic plants from the Azores present. On the other hand, six European and four Macaronesian endemic species occurred in the entrances of these cave formations. One of these was a Vulnerable species and three were Rare. These cave entrances are important sites for harboring rare and endemic species.

Singh and Singh (2007) reported new records for Doon Valley, India, citing *Mesoptychia gillmanii* (Figure 15) in or near caves, *Asterella wallichiana* (Figure 26), *Plagiochasma appendiculatum* (Figure 27), *Marchantia paleacea* (Figure 28), and *Riccia cruciata* (see Figure 29) from a cave.

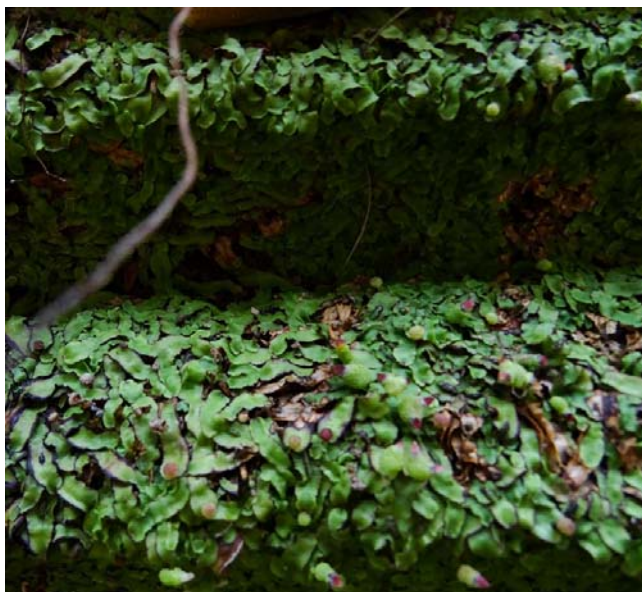


Figure 26. *Asterella wallichiana* on ledge, a species that was collected in or near a cave in India, adding to the known Indian bryophyte flora. Photo by Forest Owlet, through Creative Commons.



Figure 27. *Plagiochasma appendiculatum* in India, a species that was collected in or near a cave in India, adding to the known Indian bryophyte flora. Photo by Michael Lüth, with permission.



Figure 28. *Marchantia paleacea* with gemmae, a species that was collected in or near a cave in India, adding to the known Indian bryophyte flora. Photo by Earth.com, with permission.



Figure 29. *Riccia huebeneriana*; *Riccia cruciata* occurs in or near a cave in India, adding to the known Indian bryophyte flora. Photo by Show Ryu, through Creative Commons.

Puglisi and Privetera (2018) reported *Tortula bolanderi* (Figure 24) at the entrance of a grotto on Mt.

Etna in Sicily, a species that is rare in the Mediterranean area. Ursavaş and Çetin (2014) described the new species *Cinclidotus asumaniae* (see Figure 30) from a cave in southern Turkey, where it was on submerged and emergent rocks.

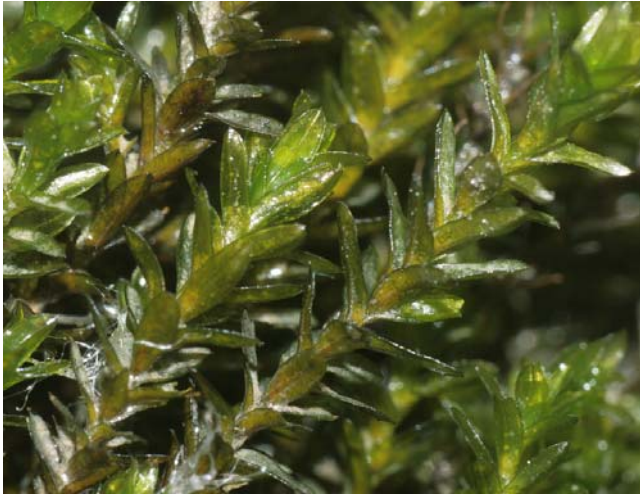


Figure 30. *Cinclidotus riparius*; *Cinclidotus asumaniae* was described as a new species from a cave in southern Turkey. Photo by Hermann Schachner, through Creative Commons.

In the Azores, Gabriel *et al.* (2006) reported interesting species in the lava tubes and volcanic pits. They were able to find six European and four Macaronesian endemic species in the entrances of these volcanic formations, including one vulnerable species and three rare species. Rare species at these entrances include *Fissidens coacervatus* (Figure 31), *Tetrastichium fontanum* (Figure 32), and *Tetrastichium virens* (Figure 33); the liverwort *Radula wichurae* (Figure 34) is considered vulnerable.



Figure 31. *Fissidens coacervatus* with capsules, endemic, Madeira, a rare species that occurs in the entrances of lava tubes and volcanic pits in the Azores. Photo by Michael Lüth, with permission.



Figure 32. *Tetrastichium fontanum*, a rare species that occurs in the entrances of lava tubes and volcanic pits in the Azores. Photo by Michael Lüth, with permission.



Figure 33. *Tetrastichium virens*, a rare species that occurs in the entrances of lava tubes and volcanic pits in the Azores. Photo by Michael Lüth, with permission.



Figure 34. *Radula kojana* branch; *Radula wichurae* is a vulnerable species that occurs at cave entrances. Photo by Kochibi, through Creative Commons.

In the Neotropics of Fernando de Noronha, Brazil, Vital *et al.* (1991) found *Fissidens cf. elegans* (Figure 35) to be common at the entrance of a small cave.



Figure 35. *Fissidens elegans* on rock, a species common at the entrance of a small cave in Brazil. Photo by Wayne Lampa, through Creative Commons.

On Isle Royale, in Lake Superior, Thorpe and Povah (1935) reported *Atrichum tenellum* (Figure 36) from a cave in Rock Harbor, but the misidentification of *Mnium thomsonii* (Figure 37) as *M. orthorrhynchum* in the USA (Crum 1983) means this could be in error, and now *M. orthorrhynchum* is considered a synonym of *Atrichum tenellum*.



Figure 36. *Atrichum tenellum*, a species known from a cave on Isle Royale, Michigan, USA. Photo by Hermann Schachner, through Creative Commons.



Figure 37. *Mnium thomsonii*, possibly the species found in a cave on Isle Royale. Photo by Hermann Schachner, through Creative Commons.

I cite several examples here, but there certainly must be more that were not immediately obvious to me.

Liverworts

Cyathodium cavernarum (Figure 1, Figure 38-Figure 39)

Cyathodium cavernarum (Figure 1, Figure 38-Figure 39) earned its name as a cave liverwort, but it is not restricted to caves. It has been described as **iridescent** (showing luminous colors that seem to change when seen from different angles; Figure 39) (Reeb *et al.* 2018) and **luminous** (Zhang *et al.* 2004b). Zhang *et al.* 2004b) attributed this to a "peculiar light-reflecting power which produces a kind of starry effect, so that the plants seem to flood the dark caves where they grow with a luminous, golden-green light."



Figure 38. *Cyathodium cavernarum* on rock. Photo by Hermann Schachner, through Creative Commons.

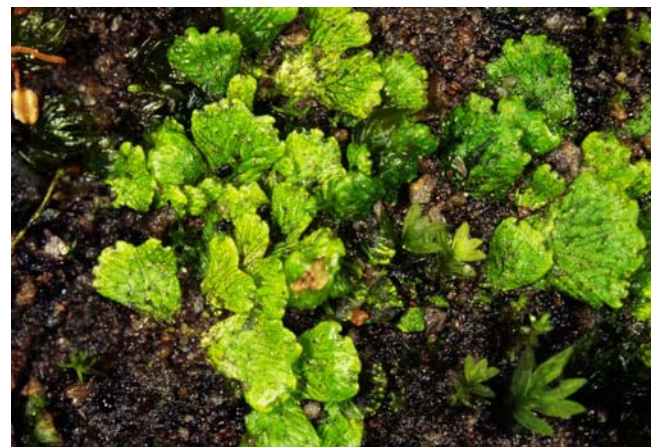


Figure 39. *Cyathodium cavernarum* on rock where it is dark enough for its iridescence to show. Photo by Jan-Peter Frahm, with permission.

Cyathodium cavernarum (Figure 1, Figure 38-Figure 39) is frequently found within 1-12 m into the karst caves of Guangxi province, P. R. China, whereas *C. smaragdinum* (Figure 40) occurs within 0.5-22 m (Zhang *et al.* 2004a). The latter species lacks luminescence. Zhang *et al.* (2004b) similarly reported *Cyathodium cavernarum* from karst caves in Yunnan Province, P. R. China, but there it was found at 6-24 m into the cave.

Differences in depth permissible for growth can result from greater light penetration into the cave, influenced by the size of the opening and shading outside the cave.



Figure 40. *Cyathodium smaragdinum* on rock. Photo through Creative Commons.

On Réunion Island, Ah-Peng *et al.* (2010) found *Cyathodium cavernarum* (Figure 1, Figure 38-Figure 39) on the walls of a lava cave. In Birds'-Nest Cave in Sarawak, Holttum (1938) found it with the fern *Tectaria dissecta* (Figure 41) in low light, forming an association at the furthest photosynthetic location from the mouth of the cave.



Figure 41. *Tectaria dissecta* on cave wall, one of the ferns living in low light in caves. Photo by Gildas Gâteblé, through Creative Commons.

Cyathodium cavernarum (Figure 1, Figure 38-Figure 39) is a widely distributed pantropical species (Duckett & Ligrone 2006), primarily of low altitudes (Nair *et al.* 2005). Duckett and Ligrone (2006) expanded its distribution with a find in southern Italy. Surprisingly, Glenny (2002) reported it from Australia. It is found in both urban areas and shaded disturbed areas. For example, Pócs and Arnstein Lye (1999) found it on overhanging, dripping or sprayed rocks as well as on temporarily inundated, muddy riverine forest floors. In Gujarat, India, it is one of the most widely distributed species of liverworts (Shah & Gujar 2016).

Scott *et al.* (1997) described *Cyathodium cavernarum* (Figure 1, Figure 38-Figure 39) from a collection in Australia: "The glistening golden-green plates of this very pretty thallose species, ~c. .5-1 cm across have an almost iridescent lustre accentuated by the darkness of the habitat. It seems to be confined to the floor of a single small cleft in south-facing cliffs of the Napier Range in the Kimberley

region of Western Australia." Glenny (2002) notes that the plants die off in late spring, regrowing from spores at the end of each wet season. This assumes that it is an annual with a very precarious survival in any location. One might expect this strategy to eventually be lost in cave populations that lack the usual seasonal fluctuations.

Mosses

Bartramia ithyphylla (Figure 42-Figure 43)

De Leeuw *et al.* (1998) describe the Antarctic *Bartramia ithyphylla* (Figure 42-Figure 43) from Cuverville Island, Antarctica. It grows in cushions in shallow caves and crevices, sometimes upright and sometimes upside down on the ceiling of the cave. It produced sporophytes in the crevices, but not elsewhere. Could it be that the caves and crevices, in this case, permit them to live in the otherwise hostile environment of Antarctica? Nevertheless, it is not restricted to these habitats elsewhere in the Antarctic region (Bergstrom *et al.* 2002; Matteri & Schiavone 2004). But on the South Sandwich Islands, this species occurs only on the heated soil of geothermal areas (Convey & Lewis Smith 2006).



Figure 42. *Bartramia ithyphylla* with capsules, on rock. Photo by Štěpán Koval, with permission.

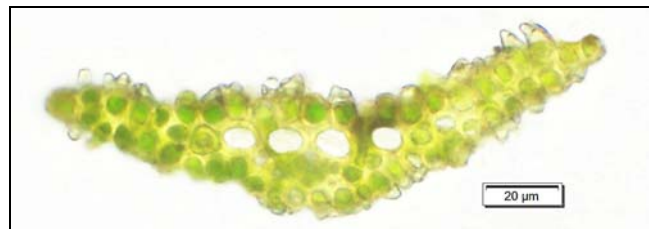


Figure 43. *Bartramia ithyphylla* leaf cs showing papillae and internal layering of leaf. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

***Cyclodictyon laetevirens* (Figure 44)**

Porley (2013) tells the story of the discovery of the moss *Cyclodictyon laetevirens* (Figure 44) in a Cornish sea cave. This resulted in its eradication by "a well-meaning but seriously misguided vicar keen to stop anyone else finding it." Porley was pleased to report that it was subsequently found in another cave nearby.



Figure 44. *Cyclodictyon laetevirens*, a moss that can live in sea caves. Sean Edwards, with permission.

Cyclodictyon laetevirens (Figure 44) is a rare moss in Britain and Ireland. It tolerates both acid and mildly basic substrata on deeply-shaded wet rocks in ravines, caves, and crevices near waterfalls (Smith 1978; Hill *et al.* 1994). *Cyclodictyon laetevirens* is unable to survive either dehydration or freezing (Burch 2003), perhaps explaining its existence in caves where the conditions are less variable.

***Didymodon glaucus* (Figure 45-Figure 46)**

Porley (2007) reported another threatened bryophyte, *Didymodon glaucus* (Figure 45-Figure 46), from caves in Europe. The species occurs deep in caves, near the entrance or surrounding artificial lights. Such localities are known in Hungary and Germany. In Luxembourg it occurs under rocky overhangs of calcareous sandstone, with similar habitats in Norway. Despite its somewhat wide occurrence in caves and shaded rock overhangs, it must reproduce completely by vegetative means; only female plants are known. Apparently *Didymodon verbanus*, a species with only males known, is actually the male of this species (Kučera 2002; TROPICOS 2021).



Figure 45. *Didymodon glaucus*, a threatened species that succeeds in caves in Europe. Photo by Tomas Hallingbäck, with permission.

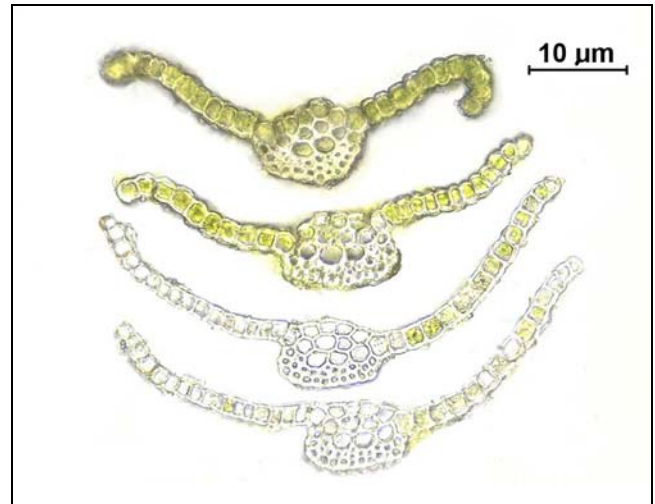


Figure 46. *Didymodon glaucus* leaf cells showing strong costa. Photo by Hugues Tinguy, with permission.

Didymodon glaucus (Figure 45-Figure 46) produces protonemal gemmae (Figure 47), both chains and single gemmae from modified axillary rhizoids (Porley 2004). In some locations, protonemal gemmae of *Eucladium verticillatum* (Figure 52-Figure 53) occur mixed with this species in the deep shade of clefts. On the other hand, *D. glaucus* does not tolerate excessive shading and the leafy plant disappears; however, the protonema often persists. *Amblystegium serpens* (Figure 48), when growing intermixed with *D. glaucus* (Figure 45-Figure 46), is able to increase as *D. glaucus* declines. Within 5 years, only a few moribund gemmae-bearing leafy shoots remain. Nevertheless, *D. glaucus* is able to penetrate deep into the cave, where it is able to grow in the light of the artificial cave lights.



Figure 47. *Didymodon glaucus* spores and tuber (protonemal gemmae). Photo by Hugues Tinguy and F. Bick, with permission.



Figure 48. *Amblystegium serpens* on rock ledge, a species that can outcompete *Didymodon glaucus* in low light. Photo by Claire Halpin, with permission.

Didymodon glaucus (Figure 45-Figure 46) is also known from calcareous walls of caves in the French Alps (Skrzypczak 2004) and inside cave entrances in Germany (Frahm 2005). In Sussex it grows in crevices and hollows.

The life strategy (During 1979, 1992) of *Didymodon glaucus* (Figure 45-Figure 46) has been considered a short-lived shuttle colonist by Hodgetts (1996) and a stress-tolerant perennial by Hallingbäck (1998). Despite its lack of spores, it is able to colonize quickly. Porley (2005) observed that it colonized a freshly exposed section of chalk between February 2003 and May 2004 at a location several meters from the nearest location. Dispersal outside of caves can be by rabbits that run along the cliff face ledges. In locations unsuitable for rabbits, it may benefit from snails such as *Trochulus striolatus* (Figure 49) and *Cochlodina laminata* (Figure 50) that have been observed crossing the moss.



Figure 49. *Trochulus striolatus*, a snail that might disperse *Didymodon glaucus* propagules. Photo by Roy Anderson, through Creative Commons.



Figure 50. *Cochlodina laminata* on rock with moss, a snail that might disperse *Didymodon glaucus* propagules. Photo by O. Gargominy, through Creative Commons.

***Epipterygium koelzii* (see Figure 51)**

Robinson (1968) found *Epipterygium koelzii* (see Figure 51) in a damp cave in the Himalayas. It remains an endemic there with apparently no further reports outside that area (Hanusch *et al.* 2020).



Figure 51. *Epipterygium tozeri*; *Epipterygium koelzii* occurs in a damp cave in the Himalayas. Photo by Ken-Ichi Ueda, through Creative Commons

***Eucladium verticillatum* (Figure 52-Figure 53)**

As I read the many studies on caves, I got the impression that *Eucladium verticillatum* (Figure 52-Figure 53) was perhaps the most likely bryophyte to find in a cave.



Figure 52. *Eucladium verticillatum*, a limestone species that builds tufa and statoliths in streams and caves, respectively. Photo by Christian Berg, through Creative Commons.

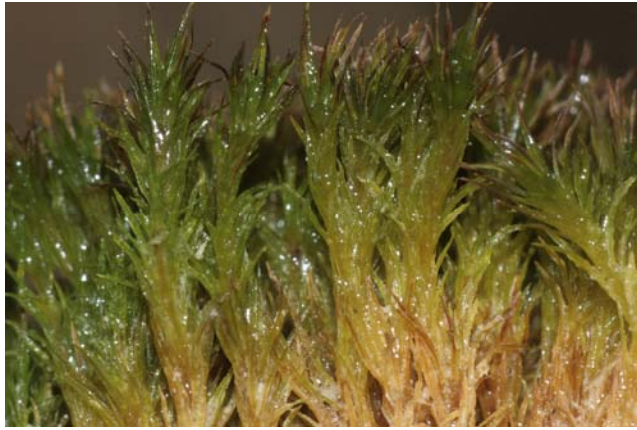


Figure 53. *Eucladium verticillatum*. Photo by Hermann Schachner, through Creative Commons.

Eucladium verticillatum (Figure 52-Figure 53) was found for the first time in Indiana, USA, in a wet, cave-like depression (Miller & Thomson 1959). Shirzadian and Gholami (2001) treated it as the first moss report from the Alisadr Cave in Iran. Aboutabl *et al.* (1999) widened the types of caves with their report of the species on exposed rocks or fragments in protected habitats, including "small" caves and wet crevices. Its growth formed carpets that covered wide areas on the vertical rock of a cave. It became inundated by rainwater and its surface exhibited a dense cover of the *Nostoc* (Cyanobacteria; Figure 54) balls. They found a higher concentration of metals in plants from a wadi-bed than from those in the cave.



Figure 54. *Nostoc commune* on soil with mosses. Photo by Yamamaya, through Creative Commons.

Popkova *et al.* (2019) found that *Eucladium verticillatum* (Figure 52-Figure 53) and several algae and Cyanobacteria (Figure 54) dominate the photosynthetic communities near the entrance and around lights in the Ahshtyrskaya Cave in Russia.

Osada (1958) described the habitats (Figure 55-Figure 63) of *Eucladium verticillatum* (Figure 52-Figure 53). It is

rare, despite being widespread geographically. Gradstein (1972) reported *Eucladium verticillatum* (Figure 52-Figure 53) from the entrance of a cave on the Maltese Islands, growing on moist limestone. It also had non-cave habitats on a moist perpendicular wall below an irrigation gully where it was whitish and lime-encrusted. A similar form is found in the Mediterranean area on constantly moist limestone rocks near springs and rivulets.



Figure 55. *Eucladium verticillatum* with accumulated minerals on the leaves. Photo by Martina Peoldt, through Creative Commons.



Figure 56. *Eucladium verticillatum* at cave entrance. Photo by Hermann Schachner, through Creative Commons.



Figure 57. *Eucladium verticillatum* in lime seep. Photo by Resso Taelseus, through Creative Commons.



Figure 58. *Eucladium verticillatum* on rock. Photo by Hermann Schachner, through Creative Commons.



Figure 59. *Eucladium verticillatum* on rock wall. Photo by Paul Bowyer, through Creative Commons.



Figure 60. *Eucladium verticillatum* on rock wall. Photo by Paul Wilson, with permission.



Figure 61. *Eucladium verticillatum* with calcium deposits. Photo by Christian Berg, through Creative Commons.



Figure 62. *Eucladium verticillatum* with mineral deposits. Photo by Martina Peoltl, through Creative Commons.



Figure 63. *Eucladium verticillatum* with mineral deposits on leaf tips. Photo by Armand Turpel, through Creative Commons.

Wigginton (2001) notes that *Eucladium verticillatum* (Figure 52-Figure 53) growing under an overhang in a deep gully was encrusted with tufa (Figure 61-Figure 63). The leaves were atypical, lacking the recurved, basal marginal teeth (Figure 64) and having sparse papillae, sometimes lacking the papillae entirely (Figure 65).



Figure 64. *Eucladium verticillatum* leaf. Photo by Armand Turpel, through Creative Commons.

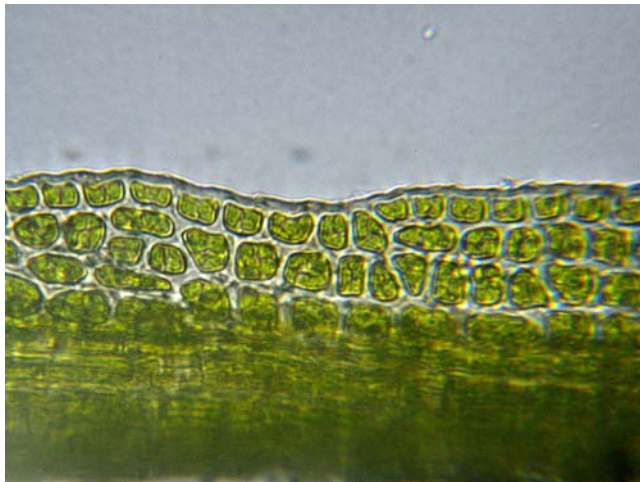


Figure 65. *Eucladium verticillatum* leaf margin showing sparse papillae, as one might find in a cave. Photo by Armand Turpel, through Creative Commons

Little is known of the reproduction of *Eucladium verticillatum* (Figure 52-Figure 53). It is **dioicous** and sporophytes seem to be rare in caves, although Dalby (1966a) reported seeing shrivelled archegonia. Instead, it appears that gemmae are the primary means of reproduction. These structures are attached to rhizoid branches among the lowermost leaves.

Dalby (1966a) provided a detailed description of the plants and the cave conditions where they occurred in a cave in Dorset, UK. The plants occurred in a mine cave of a sea cliff, where they occupied the floor, walls, and ceiling, penetrating to 14.6 m from the opening. Their light limit seemed to be at about 100 lux. Prior (1961) reported that growth stopped at about 400-500 lux in Luray Cavern. Mulec and Kubešová (2010), in Slovenian show caves, found that *Eucladium verticillatum* had the widest range of

acceptable light levels (1.4 to 530.0 $\mu\text{mol photons m}^{-2} \text{s}^{-2}$) for photosynthesis.

Dalby (1966a) reported that the plants remained alive in a polyethylene bag in total darkness for two months. It did not become etiolated, but Dalby did not indicate if it grew. Etiolation would require growth. It is possible that such long periods of darkness in the cave could be compensated by periods when the sun is low in the sky and light penetrates farther into the cave. These plants developed wider leaf laminae in poor light. *Eucladium verticillatum* (Figure 52-Figure 53) forms **eucladioliths** (Figure 66) by accretions around several stems. They ultimately leave the eucladiolith hollow. These structures are affected by growth of the moss toward light and downward pull of gravity. They are prone to breaking away from the ceiling, and when that happens, more *Eucladium verticillatum* will often colonize the bare spot.

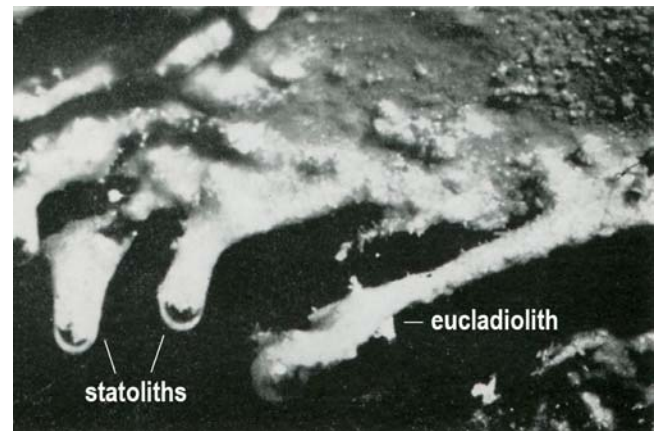


Figure 66. *Eucladium verticillatum* forming stalactite (eucladiotite; eucladiolith) in mine in Dorset, UK. Photo modified from Dalby 1966b.

Pentecost (1996) further described the formation of eucladioliths. The formation involves deposition of calcium carbonate through photosynthesis, evaporation, and CO_2 escape. Pentecost estimated that 6-12% of the carbonate was deposited through photosynthesis, 10-20% through evaporation, and the remaining 70-80% through gas escape.

Despite its rarity, El-Saadawi *et al.* (1997) were able to assess the variation in the chemical constituents of *Eucladium verticillatum* (Figure 52-Figure 53).

***Eurhynchium hians* (Figure 67-Figure 69)**

Reports on *Eurhynchium hians* (Figure 67-Figure 69) seem to be few. Papp *et al.* (2008) reported that it occurs on limestone rock in a cave in Montenegro. Prior (1961) reported it from the Luray Cavern in Virginia, USA. Achoual *et al.* (2021) found it associated with *Oxyrrhynchium speciosum* (Figure 70-Figure 71) stream under the waterfall of Pigeon Cave in Morocco. Wareham (1941) reported *Eurhynchium hians* from Hocking County, Ohio, USA, where many caves and canyons exist, but he did not mention its habitat there. It is also able to grow around lamps in show caves (Kubešová 2001), where it was frequent in the Moravian Karst of the Czech Republic.



Figure 67. *Eurhynchium hians*, a species that occurs in caves in limited locations in Europe, including around cave lamps. Photo by Bob Klips, with permission.



Figure 70. *Oxyrrhynchium speciosum*, a species that has been found in association with *Eurhynchium hians* in caves. Photo by Hugues Tinguy, with permission.



Figure 68. *Eurhynchium hians*. Photo by Bob Klips, with permission.



Figure 71. *Oxyrrhynchium speciosum*. Photo by George G., through Creative Commons.



Figure 69. *Eurhynchium hians* branch. Photo by Tuomo Kuitunen, with permission.

***Homalia webbiana* (see Figure 72-Figure 74)**

In the Azores, Gabriel *et al.* (2006) reported *Homalia webbiana* (see Figure 72-Figure 74) in the lava tubes and volcanic pits. *Homalia webbiana* is endemic to Europe and is known from only 10 localities in the Azorean archipelago. Sjögren (2003) found that it prefers pH above 5.5, permitting it to occur on lava boulders of stone fences and on cement. It can occur in strongly exposed habitats and is highly drought tolerant and is highly dominant on tree trunks, but it also occurs on cement and on coastal lava boulders in stone fences where it is greatly exposed.



Figure 72. *Homalia trichomanoides*; *Homalia webbiana* occurs in lava tubes and volcanic pits in the Azores. Photo by Janice Glime.



Figure 73. *Homalia trichomanoides*. Photo by Andrew Spink, with permission.



Figure 74. *Homalia trichomanoides*, on a canyon wall, Jacob's Creek, Keweenaw Co., Michigan, USA. Photo by Janice Glime.

There have been numerous taxonomic and systematic publications on *Homalia webbiana*, but ecological information is not very frequent. In part because of the confusion in the identity of the species, Ros *et al.* (2013) consider *Homalia webbiana* (see Figure 72-Figure 74) to be restricted to Macaronesia.

***Mittenia plumula* (Figure 75-Figure 77)**

Mittenia plumula (Figure 75-Figure 77) has lots of similarities to *Schistostega pennata* (Figure 75-Figure 77), including persistent, highly refractive protonemata, protonemal gemmae, and pennate leaves (Stone 1961a, b, 1986; Frahm 2012). It also seems to prefer similar habitats. Stone (1961a) describes the protonema (Figure 78-Figure 79) as highly refractive and lenticular.



Figure 75. *Mittenia plumula* growing on a vertical wall. Photo by David Tng, with permission.



Figure 76. *Mittenia plumula* mature gametophyte. Photo by David Tng, with permission.

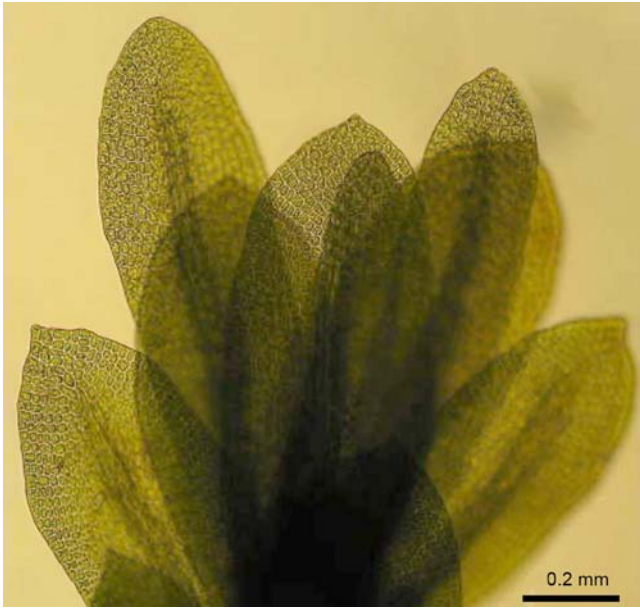


Figure 77. *Mittenia plumula* showing leaf structure. Photo by Tom Thekathyl, with permission.

I first learned about *Mittenia plumula* (Figure 75-Figure 77) in Australia when we found it at the entrance of a wombat hole (Figure 80-Figure 82). Fife and Shaw (1990) describe it as a species that grows only in microhabitats where it is deeply shaded. For example, it occurred 20 cm further beneath an overhang than did other bryophytes.



Figure 80. *Mittenia plumula* in wombat hole, showing iridescent look. Photo by Tony Markham; permission pending.



Figure 78. *Mittenia plumula* protonema in New Zealand. Photo courtesy of David Glenn.



Figure 81. *Mittenia plumula*, Mt Wilson, Blue Mountains, NSW, Australia, in opening of wombat hole. Photo by Janice Glime.

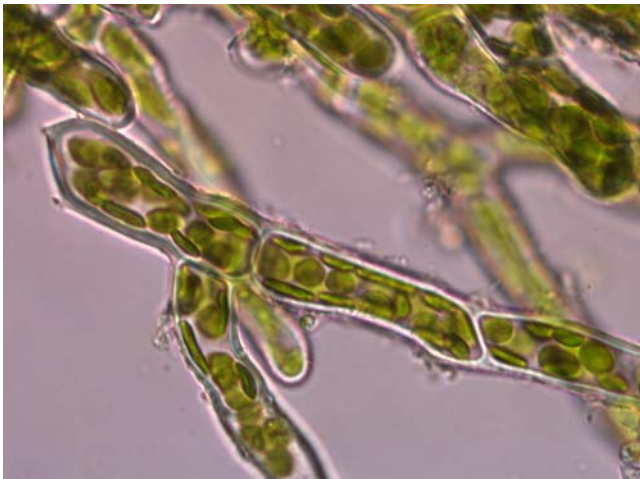


Figure 79. *Mittenia plumula* protonema from New Zealand. Photo courtesy of David Glenn.



Figure 82. *Mittenia plumula* growing on soil at wombat hole entrance, Mt. Wilson, NSW, Australia. Photo by Janice Glime.

Fife (1984) reported *Mittenia plumula* (Figure 75-Figure 77) from New Zealand. Its habitats include silt soil beneath a sandstone overhang in a roadcut, clay soil in a crevice beneath roots, and mesic humus beneath a granite boulder. It seems to prefer soil (Figure 83) to rock and occurs mostly in small cavities. Similarly, Beever and Brownsey (1993) found it under soil overhangs in New Zealand. But its habitats there also include rock walls of caves (Figure 84).



Figure 83. *Mittenia plumula* on soil in New Zealand. Photo by Janice Glime.



Figure 84. *Mittenia plumula* on cave wall, Okere Falls, NZ. Photo by Janice Glime.

***Schistostega pennata* (Figure 85-Figure 118)**

I first saw *Schistostega pennata* (Figure 85-Figure 118) on a field trip in New York, USA. It was in a small cave in a bank (Figure 87) where one had to look carefully to avoid shading it completely. It has earned its names of cave moss, goblin gold, or Dragon's gold (Berqvist 1991). In a cave in Alger County, Michigan (Figure 88-Figure 90), *Schistostega pennata* occurs on the ceiling of the cave, visible in the dim light due to its unique way of rotating its protonemal chloroplasts (Figure 91-Figure 102) to reflect (and absorb) maximum light intensity (Crum 1983). Conard (1938) refers to its presence in a tiny cave near Au Train, perhaps referring to the same location as that of Crum. He noted that *Schistostega pennata* "disappears" when you block the light so that it is unable to reflect (as in Figure 87).



Figure 85. *Schistostega pennata* leafy gametophytes on rock, a moss of low light such as that in caves. Photo by Hermann Schachner, through Creative Commons.



Figure 86. *Schistostega pennata* leafy gametophytes. Photo from Northern Forest Atlas, with permission through Jerry Jenkins.



Figure 87. Nancy Slack exploring a small cave with *Schistostega pennata*, my first view of the species. Photo by Janice Glime.



Figure 88. Cave entrance, Alger County, Michigan, home of *Schistostega pennata*. Photo by Janice Glime.



Figure 91. *Schistostega pennata* leafy plant with protonema. Photo by Des Callaghan, with permission.

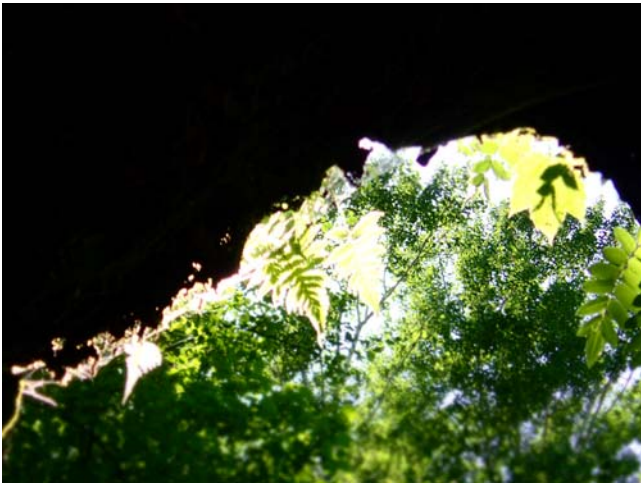


Figure 89. View from entrance of cave in Alger County, Michigan. There are protonemata overhead, but the lighting is wrong to see the luminescence. Photo by Janice Glime.



Figure 92. *Schistostega pennata* showing luminescence. Photo Courtesy of John Christy.

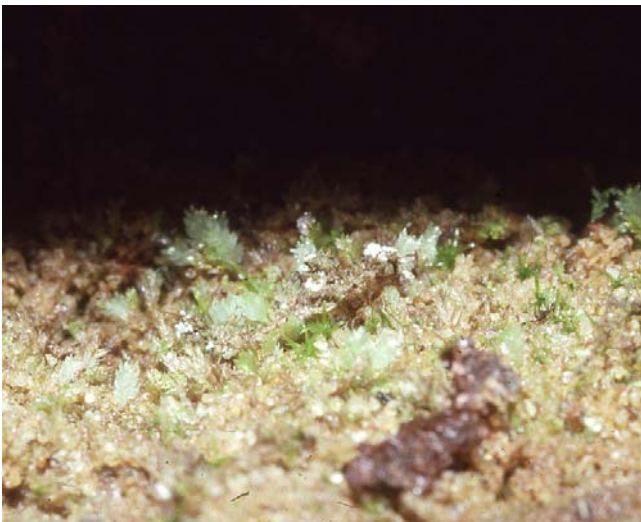


Figure 90. *Schistostega pennata*, on a ledge near Scott's Cave, Munising, MI. Photo by Janice Glime.



Figure 93. *Schistostega pennata* luminescent protonemata. Photo courtesy of Martine Lapointe.

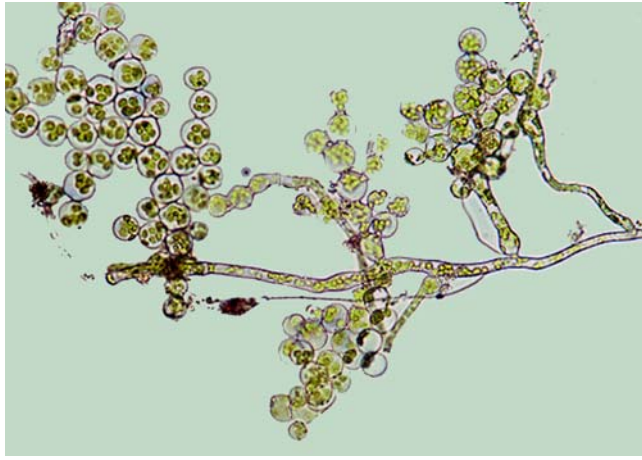


Figure 94. *Schistostega pennata* protonema with gemmae. Photo courtesy of Irene Bisang.



Figure 97. *Schistostega pennata* carpet with both leafy gametophytes and luminescent protonemata. Photo by Alpsdake, through Creative Commons.



Figure 95. *Schistostega pennata* with protonemata and leafy gametophytes on soil. Photo courtesy of Martine Lapointe.

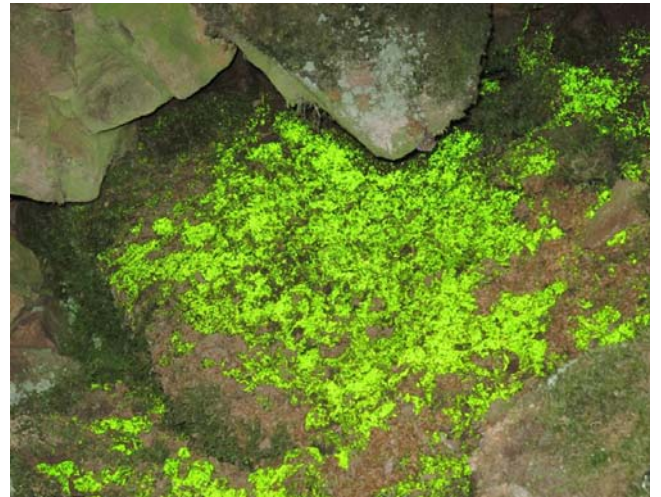


Figure 98. *Schistostega pennata* protonemata showing luminescence in cave. Photo by Hugues Tinguy, with permission.



Figure 96. *Schistostega pennata* leafy plant with protonemata at base. Exposure to light suppresses the luminescence. Photo by Bob Klips, with permission.



Figure 99. *Schistostega pennata* showing luminescent protonemata and a few leafy plants. Photo by Bob Klips, with permission.

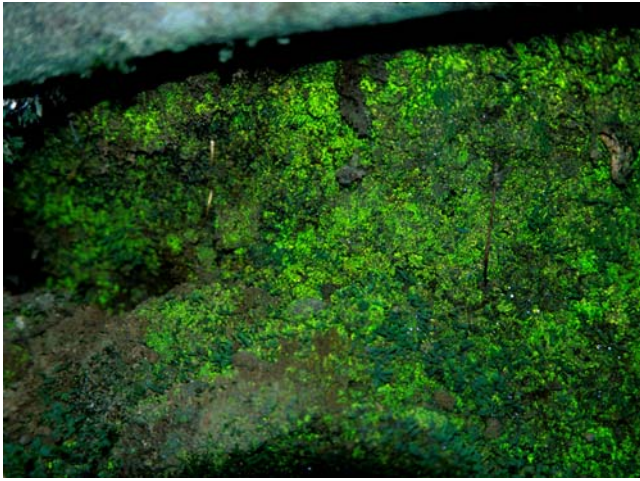


Figure 100. *Schistostega pennata* luminescence. Photo by Martin Hutten, with permission.

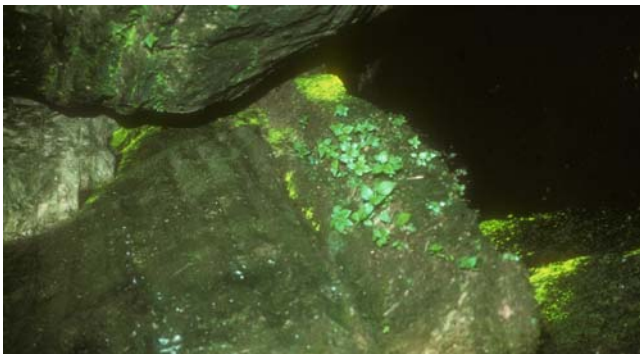


Figure 101. *Schistostega pennata* protonemata. Photo by courtesy of John Christy.



Figure 102. *Schistostega pennata* showing lens-shaped protonema cells. Photo by Misha Ignatov, with permission.

In Japan, there is a national monument (Figure 103-Figure 104) to the cave where *Schistostega pennata* (Figure 85-Figure 118) grows (Glime & Iwatsuki 1987). It inspired an opera that told the lore of a group of stranded sailors who spent the winter in the cave. They had no source of food and no way to travel in the dead of winter, so they resorted to cannibalism. When the last two men remained, one of these sailors was saved from death because his would-be killer saw the glow of the moss behind the poor sailor's head and changed his mind about murdering his companion for food. Kanda (1988) reviewed the status of the colony in the cave.



Figure 103. *Schistostega pennata* Monument in Japan. Photo by Janice Glime.



Figure 104. *Schistostega pennata* monument, Japan, with view into cave where the moss grows. Photo by Janice Glime.

Schistostega pennata (Figure 85-Figure 118) grows in a variety of low-light habitats (Figure 105-Figure 110). I have seen *Schistostega pennata* in Germany at the base of a boulder on soil that was protected by the overhang of the boulder. The most prolific growth I have seen was on the roof of a cave behind a waterfall in the Upper Peninsula of Michigan, USA (Figure 88). In Iraq, Aziz (2011) reported it from a Shanadar cave (also spelled Shanidar; Figure 111), noting its rarity in Iraq.



Figure 105. *Schistostega pennata* protonemata showing luminescence in cave. Photo by César Garcia, with permission.



Figure 106. *Schistostega pennata* on rock in a crevice, showing protonemal luminescence. Photo courtesy of Martine Lapointe.



Figure 107. *Schistostega pennata* in a rock crevice with luminescent protonemata showing deeper in. Photo by Michael Lüth, with permission.



Figure 108. *Schistostega pennata* protonemata in cave. Photo by Hugues Tinguy, with permission.



Figure 109. *Schistostega pennata* habitat. Photo courtesy of Martine Lapointe.



Figure 110. *Schistostega pennata* growing on a darkened soil bank. Photo courtesy of Martine Lapointe.



Figure 111. Shanadar cave, Iraqi Kurdistan, a cave where one can find *Schistostega pennata*, a rare species in Iraq. Photo by Osama Shukir Muhammed Amin, through Creative Commons.

Kanda (1971) described cave localities for *Schistostega pennata* (Figure 85-Figure 118) in Hokkaido, Japan. Its substrate rocks included granite, andesite, and the base of a fallen tree. The mean pH of its substrates was 4.7, but it was found once at 6.8. Matsuda (1963) noted that it also occurs in artificial caves.

Reinoso Franco *et al.* (1994) reported on its ecology in the Iberian Peninsula. The cave was very humid, only 50 m above the sea, and the substrate had a pH of 5.7. Werner (2011) reported it as occurring in caves in Luxembourg.

Schistostega pennata (Figure 85-Figure 118) is listed as rare in Latvia, with only 21 published records from 1924 until 2010 (Mežaka *et al.* 2011). Of these, 18 records were from protected areas. Its most common habitat there is on *Picea abies* (Figure 112) root mass rather than on sandstone. This demonstrates that even small "caves" such as those created by roots provide suitable habitat. It also occurs in the minicaves made by roots in calcareous areas (Crum 1983).



Figure 112. *Picea abies* that can form a habitat for *Schistostega pennata* among exposed roots. Photo from European Environment Agency, through Creative Commons.

Schistostega pennata (Figure 85-Figure 118) has sticky spores (Figure 113-Figure 116) much like those of the *Splachnaceae* (Ignatov & Ignatova 2001). This suggests that it may be dispersed by animals, perhaps insects. Its rapid expansion upon arrival at a new location in Russia supports this, and Ignatov and Ignatova suggest it could be dispersed by birds, mammals, insects, or spiders.



Figure 113. *Schistostega pennata* leafy plants with sporophytes. Photo courtesy of Martine Lapointe.



Figure 114. *Schistostega pennata*, with capsules. Photo by Martin Hutten, with permission.



Figure 115. *Schistostega pennata* capsule with sticky spores. Photo by Misha Ignatov.

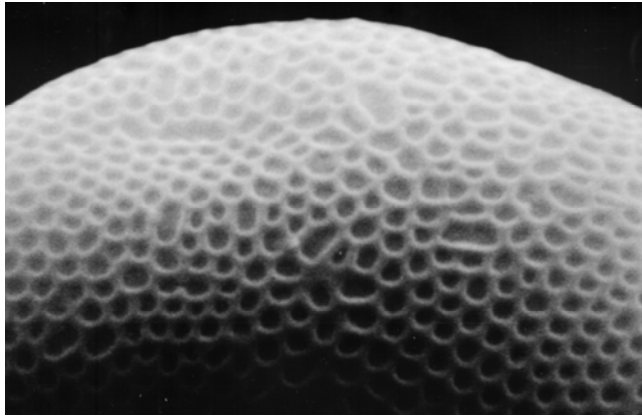


Figure 116. *Schistostega pennata* SEM of spore surface. Photo by Misha Ignatov.

Edwards (1978) described protonemal gemmae (Figure 117-Figure 118) from a British *Schistostega pennata* (Figure 85-Figure 118). In particular, he noted the similarity to those of *Mittenia plumula* (Figure 75-Figure 77). This is a common means of propagation in cave bryophytes.



Figure 117. *Schistostega pennata* protonemata with gemmae branches. Photo courtesy of Misha Ignatov.

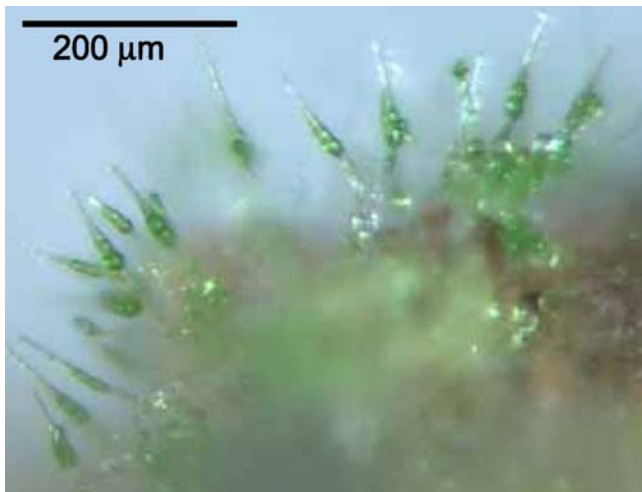


Figure 118. *Schistostega pennata* protonemal gemmae. Photo modified from Ignatov *et al.* 2012, with permission.

Takakia lepidozoides (Figure 119-Figure 122)

Takakia (Figure 119-Figure 122) has been reported from distant places around the world. It is so unusual that for a long time bryologists were unable to put it into a phylum with certainty. Phycologists wouldn't claim it as an alga. In the absence of sporangia or antheridia, it was originally classified as a liverwort, but Mizutani (1967) considered the stalked archegonia to be a moss character. Finally, sporophytes were found in *Takakia ceratophylloides* (Figure 123) and it has capsules with spiral sutures that split much like those of *Andreaeobryum* (Figure 124). It is now classified as a moss (Murray 1988; Smith & Davison 1993).



Figure 119. *Takakia lepidozoides*, a species sometimes found in caves or cave-like situations. Photo by Quentin Cronk, through Creative Commons.



Figure 120. *Takakia lepidozoides*. Photo by Rafael Medina, with permission.



Figure 121. *Takakia lepidozoides*. Photo by Rafael Medina, with permission.



Figure 122. *Takakia lepidozoides*. Photo by Stu Crawford, through Creative Commons.



Figure 123. *Takakia ceratophylla* with dehiscent capsules. Photo by Karen Renzaglia, with permission.



Figure 124. *Andreaebryum macrosporum* with capsules. Photo by Botany Website, UBC, with permission.

In the Kinabalu National Park, Sabah, Malaysia, Akiyama *et al.* (2001) found *Takakia lepidozoides* (Figure 119-Figure 122) at Paca Cave. Unfortunately, it is unclear if it is inside or near the cave. Caves are certainly not its typical habitat. Persson (1958) found it on soil partly covering non-calcareous rocks. Higuchi and Lin (2005) reported it from Taiwan. Other records from the Himalayas likewise are in cool locations, but not caves. It seems to prefer places that are constantly moist.

***Tetrodontium brownianum* (Figure 125-Figure 130)**

In Michigan, USA, *Tetrodontium brownianum* (Figure 125-Figure 130) occurs under over-hanging ledges of calcareous sandstone near Munising (Steere 1942). These ledges are associated with waterfalls. Sporophytes were present only on plants attached to the ceiling of an open cave, but not on plants adhering to vertical rock walls.

A number of the rare bryophytes that are known from caves seem to have unusual protonemata. *Tetrodontium brownianum* (Figure 125-Figure 130) instead has a rather unusual stem (Hodgetts 1915). It is nearly stemless with the vegetative part consisting of a tuft of narrowly clavate frondiform leaves (Figure 125). These may even be somewhat palmately branched at the apex where the capsule (Figure 126) is produced.



Figure 125. *Tetrodontium brownianum* plant showing the short stem and branching. Photo by Hugues Tinguy, with permission.



Figure 126. *Tetrodontium brownianum* with capsules. Photo by Andy Hodgson, with permission.



Figure 127. *Tetrodontium brownianum* with capsules. Photo by Hugues Tinguy, with permission.

Slack and Horton (2010) explored the bryophytes of the Bering Glacier Region. There one can find small caves formed by the rocks of the tundra. They found the rare *Tetrodontium brownianum* (Figure 125-Figure 130) in such a small cave there. Other records indicate that it lives on the underside of overhanging rock. Müller (2004) found it inverted on a sandstone overhang in Saxony. Grout (1899) reported it from stones in Devil's Den in New Hampshire, USA, where it grew upright on moist stones near the top of the cave.



Figure 128. *Tetrodontium brownianum* upside down on boulder, showing setae and capsules. Photo by Stefan Gey, through Creative Commons.



Figure 129. *Tetrodontium brownianum* upside down on boulder. Photo by Stefan Gey, through Creative Commons.

Gauthier (2011) described the genus *Tetradontium* from Québec, Canada, to grow exclusively in the shade on both acidic and limestone rocks. It occurs suspended from the ceiling of rock shelters (caves?), in rock wall crevices (Figure 130), and even at the bottom of caves in constant high humidity but not oozing rocks. Williams (1968) reported it as new to Ontario, Canada, occurring in moist crevices of shaded granite cliffs.



Figure 130. *Tetrodontium brownianum* habitat in rock wall crevices. Photo by Stefan Gey, through Creative Commons.

Pentecost and Rose (1985) reported *Tetrodontium brownianum* (Figure 125-Figure 130) as common under rock overhangs at the Wealden sandrocks in the UK. Pursell (2006) found it in a similar Saxon habitat on the underside of a sandstone overhang.

In North America, Lawton and Ireland (1963) reported it from under a rock ledge in Washington state. Taylor (1967) found it British Columbia on a boulder face in the forest, presumably receiving enough shade from the forest. Snider and He (1992) referred to *Tetrodontium brownianum* (Figure 125-Figure 130) as a rare cave moss in Ohio, USA.

***Timmia norvegica*/*Timmia sibirica* (Figure 131-Figure 132)**

Vitt and Horton (1979) found what they considered might be *Timmia norvegica* (Figure 131-Figure 132) on rock in the spray zone in a small limestone cave in Banff National Park in Alberta, Canada. Although the species is somewhat common in more northern locations, it is critically imperiled in Alberta and represented a new record for the province at the time. The authors suggested that it

might actually be a previously undescribed species. However, later investigations caused Horton (1981) to place it in *T. sibirica*, a species that is also critically endangered in Alberta, having a predominantly High Arctic distribution. The typical habitat of *T. sibirica* is on strongly calcareous substrates adjacent to waterfalls, along streams, or in low-lying tundra (Horton 1981). Based on nuclear and chloroplast sequence data, Budke and Goffinet (2006) considered this to be a morphotype of *T. norvegica* with the presence of multipapillose cells in *T. sibirica* being a homoplastic trait. Hedenäs (2011) further evaluated the *norvegica* group and concluded, based on the 26S differences and morphological evidence, that *T. sibirica* is a valid separate species.



Figure 131. *Timmia norvegica*, a species that sometimes grows in small caves in limestone areas. Photo by Hermann Schachner, through Creative Commons.



Figure 132. *Timmia norvegica*, a species that sometimes grows in small caves in limestone areas. Photo by Hermann Schachner, through Creative Commons.

Timmia sibirica is a relatively rare species, occurring mostly on wet or moist calcareous sites (FNA 2021). It is often near small streams or on seepage slopes, near snowmelt areas, or in open tundra depressions. Its distribution is throughout the Arctic tundra, but at low elevations. Fedosov *et al.* (2018) reported *T. sibirica* on a gentle foothill slope and moist hollow on gravelly ground on the Russian Arctic Severny Island, demonstrating its lack of necessity for a cave-like environment.

Brassard (1979) noted the rarity of sporophytes in the genus *Timmia*, with only three populations known with sporophytes for *T. norvegica* (Figure 131-Figure 132) and only immature spores known from *T. sibirica*.

Bryophyte Adaptations

Zhang *et al.* (1996a, b) reported that of eight bryophyte life forms found in the karst caves of Huangguoshu, Guizhou, China, the predominate forms were **mats**, **short turfs**, **tall turfs**, and **wefts**. In the karst caves in England, Zhang and Pentecost (2002) found **fans** (4.08%), **mats** (4.08%), **short turfs** (20%), **tall turfs** (9.22%), and **wefts** (61.5%)

The pH seems to matter. Mason-Williams and Benson-Evans (1958) found that there is a richer bryophyte flora on limestone than on acid rocks. In water, high pH prevents most bryophytes from getting enough CO₂ for photosynthesis. So what is the value of the high pH to bryophytes in many caves?

Many of the cave bryophytes grow on the ceiling of the cave. This means adherence is important, particularly where the ceiling is dripping. Hughes (1982) found that the rhizoids of *Tortula muralis* (Figure 133) become well cemented in the oolitic limestone. We might expect similar attachment in cave bryophytes.



Figure 133. *Tortula muralis* on rock, a species that produces protonemal gemmae in caves. Photo by Bjorn S., through Creative Commons.

Rajczyk (1978; 1978-1979) found that *Atrichum undulatum* (Figure 134) could live more than two years in cave conditions. The humidity ranged 95-100%.



Figure 134. *Atrichum undulatum*, a species that can live more than two years in cave conditions. Photo by Hermann Schachner, through Creative Commons.

Responses to Low Light

Puglisi *et al.* (2018) demonstrated a relationship between lighting conditions and bryophyte life form in Sicilian caves. Davison *et al.* (1995) reported "interesting" morphotypes in two liverworts from Cave Spring, Mississippi, USA.

Marschall and Proctor (2004) reported that bryophytes, especially liverworts, typically grow in light conditions at <10% relative illumination. But in a single limestone cave, Pentecost and Zhang (2001) reported that 14 species of mosses and liverworts grew at light levels below 0.5% relative illumination. *Fissidens dubius* and *Thamnobryum alopecurum* occurred at levels as low as 0.2% relative illumination. For the cave moss *Schistostegia pennata*, survival at even lower levels (0.005-0.2% relative illumination) is possible (Toda 1918).

Lang (1905) described the morphology of *Cyathodium* (Figure 1, Figure 38-Figure 39). It has retained the layer of air chambers with pores (Figure 135), but the basal portion of the thallus is mostly only a single layer of cells. It lacks assimilation filaments in the air chambers and instead assimilation occurs in the epidermis (Figure 135). This could be a photosynthetic advantage by reducing light blockage by the plant itself.

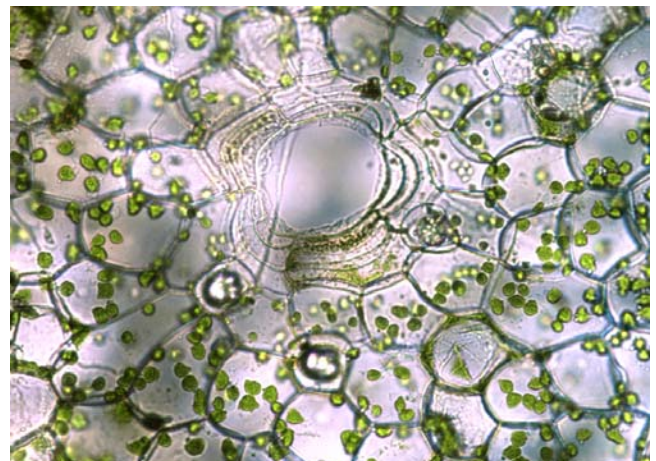


Figure 135. *Cyathodium cavarnarum* thallus pore and photosynthetic epidermis. Photo courtesy of Noris Salazar Allen.

Dunham and Lowe (1927) described the unusual growth of bryophytes in such habitats as caves. He discovered early in his career that bryophytes, like tracheophytes, "reach out" to the light, at times exceeding their normal height in low light conditions. He describes the leaves of *Leptobryum pyriforme* (Figure 136) from a specimen that had grown in the basement of an old iron foundry – the stems were 5 cm long compared to 1 cm in the light. A similar elongated growth occurred in *Ceratodon purpureus* (Figure 137) from the dark pocket of a ledge. I have experienced the same etiolated appearance of mosses growing in my terrarium, making the habitus unrecognizable.



Figure 136. *Leptobryum pyriforme* showing internodal areas that elongate in low light. Photo by Štěpán Koval, with permission.



Figure 137. *Ceratodon purpureus* with capsules, a species that responds to low light by stem elongation. Photo by Štěpán Koval, with permission.

Etiolation is a common response of mosses to low light (Mulec 2018). Dalby (1966b) reported that *Pohlia nutans* (Figure 138) becomes etiolated when buried under leaves. In a cave, *Eurhynchium* sp. (see Figure 67-Figure 69) has elongated branches with small, widely spaced leaves. I have found that mosses in plastic bags continue to grow in the lower light of the lab, becoming very etiolated.



Figure 138. *Pohlia nutans* with capsules, on rock, a species that elongates when buried by leaves. Photo by J. C. Schou, with permission.

In caves of South Wales, Mason-Williams and Benson-Evans (1967) found that dominant bryophyte growth forms changed with light intensity. As the light decreased, **dendroids** and **smooth mats** decreased in abundance, whereas **rough** or **thalloid mats** and **wefts** increased.

Dalby (1966b) reported on various responses to reduced light in caves. In *Rhizomnium punctatum* (Figure 139) and *Cyrtomnium* (Figure 140), the leaves grew perpendicular to the light, which in a cave comes from a low position that would normally strike the side of any plant growing away from gravity. In *Eurhynchium hians* (Figure 67-Figure 69), it is the flattened branches that grow perpendicular to light. *Eucladium verticillatum* (Figure 52-Figure 53) leaves become broader in shade (Figure 141) and Dalby noted that this response is uncommon in mosses. The liverwort *Conocephalum conicum* (Figure 142-Figure 143), on the other hand, is smaller in the shade; even the areolae are 1/3 as wide. By contrast, *Eucladium verticillatum* growing near a lamp died when the lamp was replaced with a brighter bulb. I have seen the same thing happen to house plants that are placed outside when the weather gets warm. But in this case, Dalby considered the heat and resulting desiccation to be the cause of the *E. verticillatum* death.



Figure 139. *Rhizomnium punctatum*, a species whose leaves can change positions to become perpendicular to the light. Photo by Hermann Schachner, through Creative Commons.



Figure 140. *Cyrtomnium hymenophylloides*, a species whose leaves can change positions to become perpendicular to the light. Photo by Hermann Schachner, through Creative Commons.

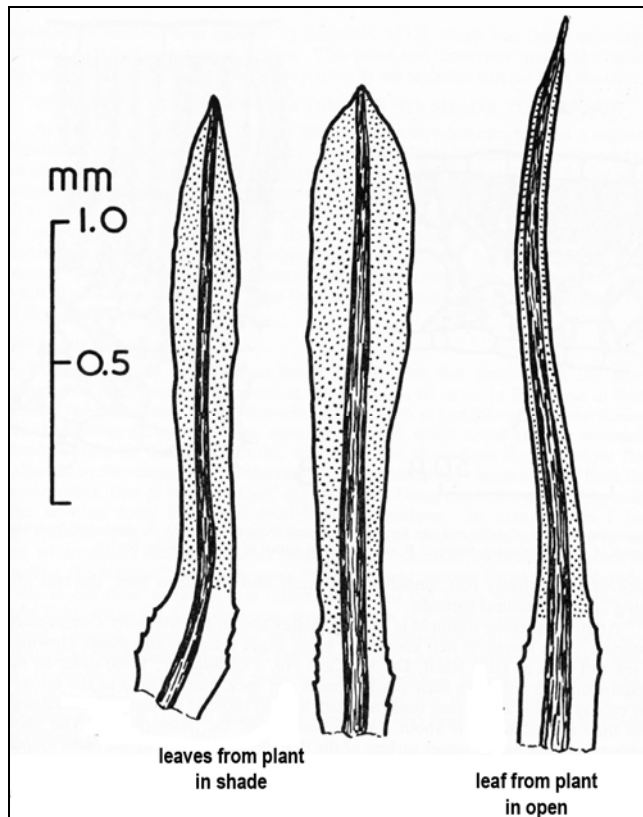


Figure 141. *Eucladium verticillatum* deep shade and open leaves. Diagram modified from Dalby 1966b.



Figure 142. *Conocephalum conicum* showing pores and areolae. Both the thallus and areolae are smaller in the shade. Photo by Hermann Schachner, through Creative Commons.



Figure 143. *Conocephalum conicum* cs of thallus where photosynthesis occurs. Photo by Ralf Wagner, with permission.

Richards (1932) found that *Isopterygiopsis muellerianum* (Figure 144) in complete darkness in a cave had numerous small chloroplasts. Richards assumed it was growing saprophytically, but it is also possible that in some seasons, probably winter, it received enough light to grow. At other times it could be dormant. Even protonemata can remain dormant for an inordinate period of time. Bristol (1916) found that protonemata that had remained sealed for 50 years began to grow when given water and light, demonstrating the incredible dormancy capability of some bryophytes.

Uniyal *et al.* (2007) noted that bryophytes are able to acclimate to low light. Watkins (2002) examined the adaptations of *Megaceros pellucidus* (Figure 145) to extremely low light conditions. The light conditions of $0.5\text{--}7\ \mu\text{mol photons m}^{-2}\text{ s}^{-1}$ where it grows in the wet, cool temperate rainforest are similar. Unlike cave bryophytes, this species has the opportunity to use the burst of light in sunflecks. But its ability to use reflected light from water (or rocks in caves) could be similar to opportunities for cave bryophytes. The chloroplast position of this hornwort in its rainforest habitat is an expanded form that is situated on the periclinal cell wall closest to the light source. Thallus sections revealed that when the thallus is irradiated with blue light of more than $3\ \mu\text{mol photons m}^{-2}\text{ s}^{-1}$ the

chloroplasts shrank "dramatically" and moved to a position on anticlinal walls. Red (662 nm) light of $<130 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ or darkness did not elicit any response in the chloroplast position except in those cells that had been exposed to blue light. In the latter case, the chloroplast expanded and resumed the position closest to the light source. Specimens were obtained from the Apiti Glow Worm Caves where sunlight is reflected off the river surface, reaching considerable distance into the cave. As seen in Figure 146, the light penetration changes as the sun arches across the sky during the day.



Figure 144. *Isopterygiopsis muellerianum* branch, a species that develops many small chloroplasts when in complete darkness. Photo by Wayne Lampa, through Creative Commons.

Uniyal *et al.* (2007) noted that bryophytes are able to acclimate to low light. Watkins (2002) examined the adaptations of *Megaceros pellucidus* (Figure 145) to extremely low light conditions. The light conditions of $0.5\text{--}7 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ where it grows in the wet, cool temperate rainforest are similar. Unlike cave bryophytes, this species has the opportunity to use the burst of light in sunflecks. But its ability to use reflected light from water (or rocks in caves) could be similar to opportunities for cave bryophytes. The chloroplast position of this hornwort in its rainforest habitat is an expanded form that is situated on the periclinal cell wall closest to the light source. Thallus sections revealed that when the thallus is irradiated with blue light of more than $3 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ the chloroplasts shrank "dramatically" and moved to a position on anticlinal walls. Red (662 nm) light of $<130 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ or darkness did not elicit any response in the chloroplast position except in those cells that had been exposed to blue light. In the latter case, the chloroplast expanded and resumed the position closest to the light source. Specimens were obtained from the Apiti Glow Worm Caves where sunlight is reflected off the river surface, reaching considerable distance into the cave. As seen in Figure 146, the light penetration changes as the sun arches across the sky during the day.



Figure 145. *Megaceros pellucidus*, a species whose chloroplasts are next to the walls closest to the light source in low light. Photo by Ashley M. Bradford, through Creative Commons.

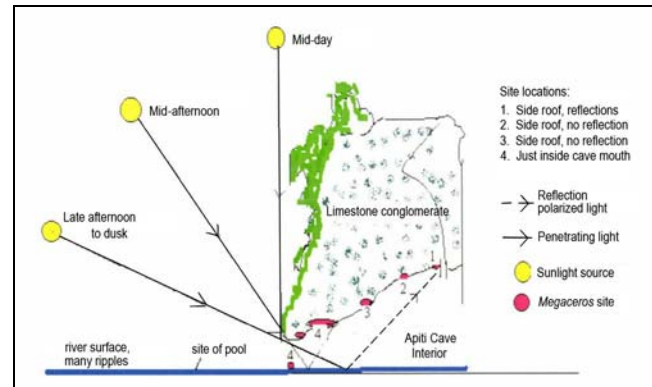


Figure 146. Sunlight paths at various times of the day in a cave at Apiti. Note the reflections onto the cave roof from 14:00–17:00 hours, thus illuminating colonies of *Megaceros pellucidus* for part of the day. Modified from Watkins 2002.

Gabriel and Bates (2003) studied the photosynthetic responses of bryophytes and the effects of light intensity on these responses of bryophytes from the Azores. They found photosynthetic saturation at $30 \mu\text{mol m}^{-2} \text{s}^{-1}$. The lowest rate was in *Andoa berthelotiana* (Figure 147) ($20 \mu\text{mol m}^{-2} \text{s}^{-1}$) and the highest in *Myurium hochstetteri* (Figure 148) ($68 \mu\text{mol m}^{-2} \text{s}^{-1}$). The dark respiration rate is critical for tolerating shade; it was highest in the species with the highest P_{max} . The extremely low light compensation point of $7 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ in *Fissidens serrulatus* (Figure 149) is adaptive in its deep shade and cave habitats. *Myurium hochstetteri*, on the other hand, is restricted to habitats with good illumination; it has the highest light compensation point.



Figure 147. *Andoa berthelotiana*, a species with a low light saturation point for photosynthesis. Photo by Pedro Cardoso, with permission through Azoresbioportal.



Figure 148. *Myurium hochstetteri* on exposed rock, a species with a high light saturation point for photosynthesis, and thus restricted to high light sites. Photo by Michael Lüth, with permission.



Figure 149. *Fissidens serrulatus*, a species with an extremely low compensation point that permits it to live in such dark places as caves. Photo by David T. Holyoak, with permission.

One adaptation that may be helpful to cave bryophytes is the ability to synthesize chlorophyll in the dark. The data on this topic is scant indeed, and it seems to be

assumed to be a bryophyte character even though it appears that it has only been demonstrated in *Marchantia* (Figure 150-Figure 151) (Takio *et al.* 1988; Ueda *et al.* 2014). Takio and coworkers demonstrated that cultured cells of *Marchantia paleacea* subsp. *diptera* (Figure 150) had a doubling time of 1.2 days when grown in the light and 1.5 days when grown in the dark. Chlorophyll concentrations were high ($6-15 \mu\text{g mg}^{-1}$ dry weight) in both types of cultures. But this is not conclusive evidence that whole plants growing deep in caves are able to sustain such ability. The cultures were maintained at least 16 days before these measurements, but they had glucose in the medium, so we need evidence that the glucose did not provide the energy needed for the dark production of chlorophyll.



Figure 150. *Marchantia paleacea* subsp. *diptera* females with capsules, a subspecies whose cultured cells produce chlorophyll in the dark. Photo by Janice Glime.

Another study on *Marchantia polymorpha* (Figure 151) indicates that it has the genes for light-independent Pchlide reductase (Ueda *et al.* 2014). But in flowering plants, these genes (for DPOR) that occur in the chloroplast seem to be lost. This means that *M. polymorpha* has the enzyme needed to produce chlorophyll in the dark.



Figure 151. *Marchantia polymorpha* gemmae cups, growing among rocks. This species has genes for producing chlorophyll in the dark. Photo by Rudolf Macek, with permission.

But what about other bryophytes? Ueda and coworkers noted that we do not understand why the DPOR genes have been lost from the chloroplast in some land plants, while persisting in others. Nor do we understand what environmental factors might have played a role in this loss in some and not in others. I cannot accept one record of these genes in a single liverwort as proof of their general presence in bryophytes. Nevertheless, their presence in *Marchantia polymorpha* (Figure 151), and their implied presence in *Marchantia paleacea* var. *diptera* (Figure 150), suggest that at least some cave bryophytes might be able to produce chlorophyll in the dark. This would make living in the limited light of caves, and particularly near the artificial lighting, an opportunity to take advantage of these genes for DPOR.

Jack Brunkard (Bryonet 17 August 2021) explained the two enzymes (LPOR and DPOR) that can catalyze the same reaction of reducing protochlorophyllide to chlorophyllide *a* (the immediate precursor of chlorophyll). LPOR is light dependent and DPOR is not. DPOR is strongly and irreversibly inhibited by oxygen. Brunkard suggested that many bryophytes that live in low light and moist environments that become hypoxic could gain an advantage from having DPOR in these environments. On the other hand, for plants that live in well-oxygenated habitats, DPOR would be inhibited by the oxygen. Furthermore, red light is most effective in production of LPOR, but many bryophytes live in forests that transmit predominantly green light through the canopy. This means that bryophytes with DPOR (that does not need red light) would have an advantage in these conditions. In some caves green light transmission predominates through the surrounding canopy and into the cave. But for the lampenflora, in most cases the light source emits predominantly red waves. Clearly we need further studies on the presence of DPOR throughout bryophytes and how it relates to their habitats.

Reproduction

Komáromy *et al.* (1985) found that the mosses occupying lamp-lit areas in the Anna-Barlang cave of Hungary were mostly **colonists** and **perennials**, each represented by five species. Colonists were the most frequent, most likely as a function of good dispersal ability. The cave bryophytes must be able to establish quickly or remain for a long time. Mason-Williams and Benson-Evans (1967) reported that spores were common and widespread in caves in South Wales, were commonly found around the threshold areas, and were widespread in soil samples throughout the caves. Nevertheless, protonemal gemmae seem to be important in the reproduction of cave mosses. Whitehouse (1980) found these on *Didymodon luridus* (Figure 47, Figure 152), *Gyroweisia tenuis* (Figure 153-Figure 154), *Eucladium verticillatum* (Figure 52-Figure 53), and *Schistostega pennata* (Figure 85-Figure 118). He considered them to be an adaptation for survival and propagation at low light intensities.



Figure 152. *Didymodon luridus*, a cave moss that produces protonemal gemmae. Photo by Hermann Schachner, through Creative Commons.



Figure 153. *Gyroweisia tenuis* on rock, a cave-dwelling species that produces protonemal gemmae. Photo by Michael Lüth, with permission.

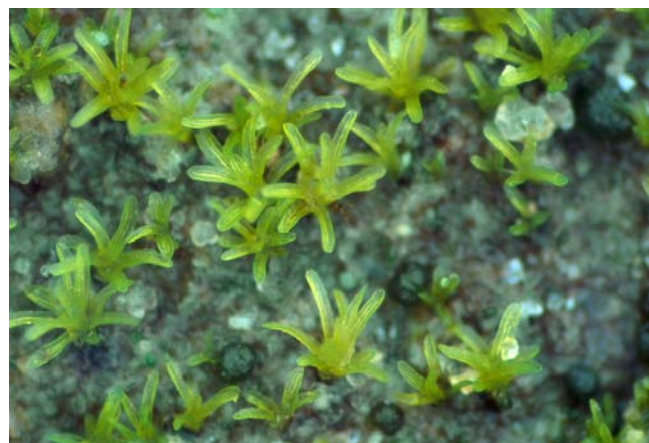


Figure 154. *Gyroweisia tenuis*. Photo by Tomas Hallingbäck, with permission.

Allen and Korpelainen (2006) found *Cyathodium* (Figure 1, Figure 38-Figure 39) species to be **r-selected** (have high reproductive capacity). The **dioicous** species

that produce abundant sporophytes also produce tubers. As already noted, *Cyathodium cavernarum* (Figure 1, Figure 38-Figure 39) dies off in late spring and regrows from spores at the end of the wet season (Glenny 2002).

Summary

Caves are among those environments that often have rare, relict, or even unique species. Some of these are specialized cave or low light species, not to be found outside such habitats. Others are widespread species with a broad ecological range.

Cyclodictyon cavernarum is the only liverwort that is primarily a cave dweller, exhibiting a "luminescence" similar to that seen in *Schistostega pennata*. A number of mosses are either rare or occur predominantly in low light.

Rhizoids are important for "cementing" bryophytes to the cave ceilings. pH can be important in creating a favorable CO₂ environment.

Thallose liverworts such as *Cyathodium* compensate for low light by reducing plant interference, in this case by having photosynthesis in the epidermis. **Etiolation** is common in mosses in low light. Dominant growth forms change from **dendroids** and **smooth mats** to **rough** or **thalloid mats** and **wefts** as light decreases. Growth tends to form perpendicular to light. Chloroplasts can be more numerous in low light. *Marchantia* can synthesize chlorophyll in the dark, but this has not been explored in other taxa; DPOR may facilitate this when oxygen levels are low, *i.e.*, light is too low for photosynthesis. Both protonemata and gametophores can remain dormant for long periods of time.

Colonists and **perennials** seem to be most successful. Spores can be common throughout the caves, but protonemal gemmae are more common than in species assemblages in most other habitats. The **r-selected** species may have an advantage, but this needs to be explored for cave species.

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