CHAPTER 18-5
CAVES – CAVERNS

TABLE OF CONTENTS

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Figure 1. Luray Cavern, Virginia, USA – a popular tourist cavern shown here illuminated with electric lights. Alejocrux, through public domain.

Caverns

Caverns are both natural and artificial. They are made by natural processes, but those places we typically call caverns are extensive networks of tunnels with interesting rock formations that attract the attention of tourists. To this end, enterprising companies installed lights that extend the distance into the cavern where the bryophytes, algae, and ferns are able to live.

Prior (1961) described the mosses in the well-known Luray Caverns, Virginia, USA (Figure 1). He found ***Amblystegium serpens*** (Figure 2) forming a loose mat with sporophytes in only one location on wet limestone. ***Amblystegium serpens*** is also common in European caves (*e.g.* Mulec & Kubešová 2010), but it is widespread and common outside caves, frequently presenting sporophytes. ***Anomodon rostratus*** (Figure 3) likewise occurred on moist limestone, along with ***Leptobryum pyriforme*** (Figure 4), but also occurred on silt of the cavern (Prior 1961). ***Bryum pseudotriquetrum*** (Figure 5) formed fairly "dense mats" on moist limestone, along with ***Leptobryum pyriforme***. ***Campylium hispidulum*** (Figure 6), sometimes with capsules, was scattered among 8 locations on moist limestone, either alone or with ***Leptobryum pyriforme*** and/or ***Eurhynchium hians*** (Figure 7). The latter species was abundant, occurring at 19 of the 33 study plots, either

in pure stands or mixed with other bryophytes. Only 3 populations of this species had sporophytes, but these were abundant. ***Tortula obtusifolia*** (Figure 8-Figure 9) formed a large, dense mat on wet limestone with just 2 sporophytes. ***Fissidens bryoides*** (Figure 10-Figure 11), a tiny rock-dwelling species, occurred only once, near the entrance. ***Funaria hygrometrica*** (Figure 12-Figure 13), a widespread species typically in exposed locations, occurred only once, with abundant sporophytes, contrasting sharply with ***Leptobryum pyriforme***, a species lacking sporophytes in the cavern despite being present at 18 locations. ***Leskea polycarpa*** (Figure 14) occurred only once, on wet limestone at the edge of an underground lake.

Figure 2. ***Amblystegium serpens***, a species common in European and some North American caves. Photo by Claire Halpin, with permission.

Figure 3. ***Anomodon rostratus***, a species that occurs on moist limestone and silt in Luray Caverns, Virginia, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 4. ***Leptobryum pyriforme***, a species that occurs on moist limestone in Luray Caverns, Virginia, USA. Photo by Robin Bovey, with permission through Dale Vitt.

Figure 5. ***Bryum pseudotriquetrum***, a species that grows in dense mats on moist limestone. Photo by J. C. Schou, with permission.

Figure 6. ***Campylium hispidulum***, a species found in 8 of the Luray Caverns, on moist limestone. Photo by Zihao Wang, through Creative Commons.

Figure 7. ***Eurhynchium hians***, a moss that occurs on moist limestone in the Luray Caverns, Virginia, USA. Photo by Wayne Lampa, through Creative Commons.

Figure 8. ***Tortula obtusifolia*** on rock, a species that forms large, dense mats on moist limestone in Luray Caverns. Photo by Bob Klips, with permission.

Figure 9. ***Tortula obtusifolia*** on rock, a species that can withstand drought. Photo by Bob Klips, with permission.

Figure 10. ***Fissidens bryoides*** on rock, a tiny moss that was found only once at the Luray Caverns, near the entrance. Photo by Zihao Wang, through Creative Commons.

Figure 11. ***Fissidens bryoides*** protonemata with new stems, a form that can be seen in some caverns. Photo by Bob Klips, with permission.

Figure 12. ***Funaria hygrometrica*** in rock crevice, a species that occurred only once in the Luray Caverns, but that had abundant sporophytes like the population shown here. Photo by Bob Klips, with permission.

Figure 13. ***Funaria hygrometrica*** showing basal leaves and young sporophytes before capsule development. Photo by Bob Klips, with permission.

Figure 14. ***Leskea polycarpa***, a species that occurred at the edge of an underground lake in the Luray Caverns. Photo by Hugues Tinguy, with permission.

Contrasting to the Northern Hemisphere Luray Caverns, de Lange and Stockley (1987) found only one of the same genera in the Lost World Cavern at Waitomo, New Zealand, where the light levels are low and the humidity is high. Documented species there include the liverworts ***Lobatiriccardia alterniloba*** (Figure 15), ***Heteroscyphus triacanthus*** (Figure 16), ***Frullania nicholsonii*** (Figure 17-Figure 18), ***Monoclea forsteri*** (Figure 19-Figure 20), ***Radula buccinifera*** (Figure 21-Figure 22), and ***Symphyogyna tenuinervis*** (Figure 23), and mosses ***Achrophyllum dentatum*** (Figure 24), ***Beeveria distichophylloides*** (Figure 25), ***Camptochaete arbuscula*** (Figure 26-Figure 27), ***Cyathophorum bulbosum*** (Figure 28), ***Distichophyllum microcarpon*** (see Figure 29), ***Echinodium hispidum*** (Figure 30), ***Fissidens leptocladus*** (Figure 31), ***Gymnostomum calcareum*** (Figure 32-Figure 33), ***Hypnodendron arcuatum*** (Figure 34-Figure 35) (Smart 1978), ***Hypopterygium filiculaeforme*** (Figure 36), ***Leucobryum candidum*** (Figure 37) (Smart 1978), ***Lopidium concinnum*** (Figure 38) (Smart 1978), ***Papillaria crocea*** (Figure 39-Figure 40), ***Pseudotaxiphyllum falcifolium*** (Figure 41), ***Racopilum convolutaceum*** (Figure 42), ***Thamnobryum pandum*** (Figure 43), ***Thuidium laeviusculum*** (Figure 44-Figure 45) (Smart 1978), and ***Weymouthia mollis*** (Figure 46), with ***Achrophyllum dentatum***, ***Echinodium hispidum***, and ***Thamnobryum pandum*** being the most important and common around the cave entrance. These species also occur in the low-light flora near the cave.

Figure 15. ***Lobatiriccardia alterniloba***, a liverwort in the Lost World Cavern at Waitomo, New Zealand. Photo by Joe Dillon, through Creative Commons.

Figure 16. ***Heteroscyphus triacanthus***, a leafy liverwort in the Lost World Cavern at Waitomo, New Zealand. Photo by John Steel, through Creative Commons.

Figure 17. ***Frullania nicholsonii***, a leafy liverwort in the Lost World Cavern at Waitomo, New Zealand. Photo by Shirley Kerr, with permission.

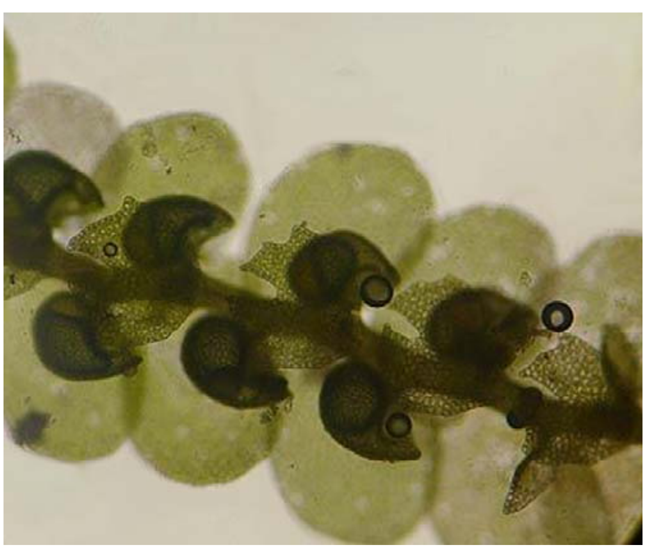

Figure 18. ***Frullania nicholsonii*** showing lobules and underleaves. Photo by Shirley Kerr, with permission.

Figure 19. ***Monoclea forsteri***, a thallose liverwort in the Lost World Cavern at Waitomo, New Zealand. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 20. ***Monoclea forsteri*** with sporophytes. Photo by John Braggins, with permission.

Figure 21. ***Radula buccinifera***, a leafy liverwort in the Lost World Cavern at Waitomo, New Zealand. Photo by John Walter, through Creative Commons.

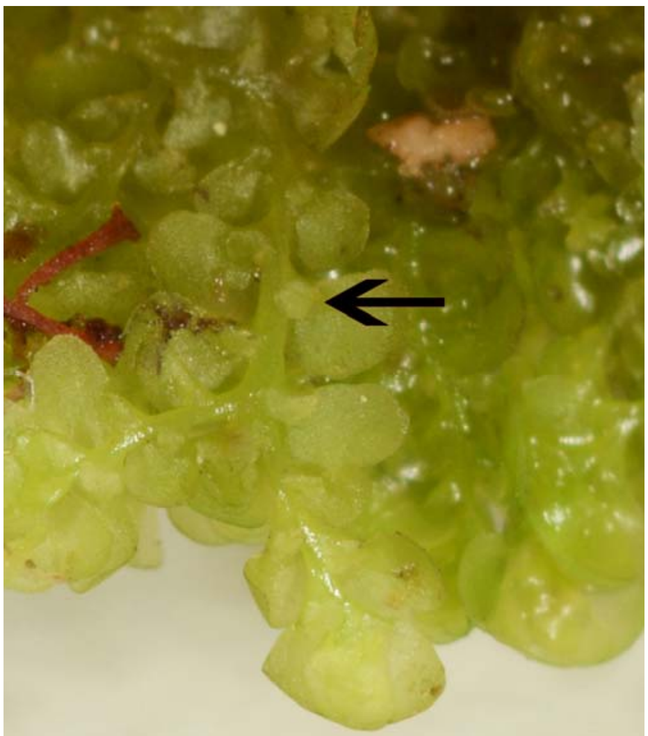

Figure 22. ***Radula buccinifera*** showing underleaf. Photo by John Walter, through Creative Commons.

Figure 23. ***Symphyogyna tenuinervis***, a liverwort in the Lost World Cavern at Waitomo, New Zealand. Photo by Shirley Kerr, with permission.

Figure 24. ***Achrophyllum dentatum***, a moss in the Lost World Cavern at Waitomo, New Zealand, where it is most common at the entrance. Photo by Des Callaghan, through Creative Commons.

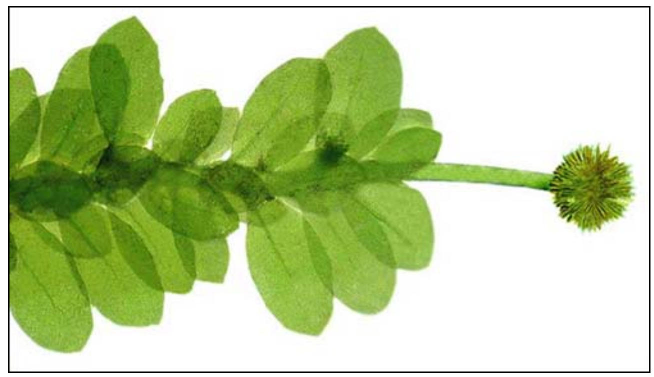

Figure 25. ***Beeveria distichophylloides***, a moss in the Lost World Cavern at Waitomo, New Zealand, where it is most common at the entrance. Photo by Bill and Nancy Malcolm, with permission.

Figure 26. ***Camptochaete arbuscula***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Peter de Lange, through Creative Commons.

Figure 27. ***Camptochaete arbuscula***. Photo by Alan Melville, through Creative Commons.

Figure 28. ***Cyathophorum bulbosum***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Peter Woodard, through Creative Commons.

Figure 29. ***Distichophyllum procumbens***; ***Distichophyllum microcarpon*** occurs in Lost World Cavern at Waitomo, New Zealand. Photo courtesy of Olubukunola O. Oyesiku.

Figure 30. ***Echinodium hispidum***, a moss in the Lost World Cavern at Waitomo, New Zealand, where it is most common at the entrance. Photo by John Steel, through Creative Commons.

Figure 31. ***Fissidens leptocladus***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Heino Lepp, Australian National Botanic Gardens, with online permission for educational use.

Figure 32. ***Gymnostomum calcareum***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Andy Hodgson, with permission.

Figure 33. ***Gymnostomum calcareum***. Photo by John Game, through Creative Commons.

Figure 34. ***Hypnodendron arcuatum*** with capsules, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo from Te Papa, through Creative Commons.

Figure 35. ***Hypnodendron arcuatum*** with capsules. Photo from Te Papa, through Creative Commons.

Figure 36. ***Hypopterygium filiculaeforme***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Sara Smerdon, through Creative Commons.

Figure 37. ***Leucobryum candidum***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by David Tng, with permission.

Figure 38. ***Lopidium concinnum*** with capsules, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Te Papa, through Creative Commons.

Figure 39. ***Papillaria crocea*** on a vertical wall, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Daniel Ohlsen, through Creative Commons.

Figure 40. ***Papillaria crocea***. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 41. ***Pseudotaxiphyllum falcifolium***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo from Te Papa, NZ, through Creative Commons.

Figure 42. ***Racopilum convolutaceum*** with capsules, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Figure 43. ***Thamnobryum pandum***, a moss in the Lost World Cavern at Waitomo, New Zealand, where it is most common at the entrance. Photo from Te Papa, through Creative Commons.

Figure 44. ***Thuidium laeviusculum***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Peter de Lange, through Creative Commons.

Figure 45. ***Thuidium laeviusculum***. Photo by Bill Malcolm, with permission.

Figure 46. ***Weymouthia mollis***, a moss in the Lost World Cavern at Waitomo, New Zealand. Photo by Clive Shirley, Hidden Forest <www.hiddenforest.co.nz>, with permission.

Visitors increase the exposure of the caverns to fluctuating temperatures, moisture fluctuations, drafts, propagules, light, exhaled CO_2, trampling, and other factors that alter the ability of bryophytes to reach and succeed in the interior of the caverns. Rakovec (2020) modelled the effect of visitor number and cave size on visitor impact. He found that the direct human sources of heat and CO_2 cause linear responses. But the exchange between the walls and the exterior have exponential consequences dependent on time. Thus, visitors have both direct and indirect effects on the flora in the display caverns.

Cave Lamp Communities (Lampenflora)

The flora associated with lights in caverns (**lampenflora**) has fascinated many researchers (*e.g.* Lundegårdh 1931; Maheu & Guérin 1935; Shiomi 1973; Rajczy 1979, 1989; Rajczy *et al*. 1985; Padisák *et al*. 1985; Végh 1985; Rajczy *et al*. 1986; Rajczy & Buczkó 1989; Olson 2002; Zhang & Wang 2002; Mazina & Maximov 2011; Cigna 2012; Mazina 2016a, b). Mulec (2012) noted that permanent electric lights are used in show caves to highlight cave formations for visitors. But these also create new ecological conditions that permit the colonization by lampenflora. Although the community is relatively complex, it is also limited in diversity, comprised usually of **Cyanobacteria** outermost from the light, to algae, bryophytes, and ferns (closest to the light) (Boros 1964; Castello 2014; D'Agostino *et al*. 2015; Mazina 2015; Kurniawan *et al*. 2018; Mulec 2018; Kozlova & Mazina 2020; Pfendler *et al*. 2021). Flowering plants are usually unable to live in these sites, although Mazina (2015) found two species of flowering plants near lamps in the Nomoafonskaya Cave, Abkhazia, in the South Caucasus.

Naturally illuminated caves provide sufficient light at the entrance and a short distance into the twilight zone (Figure 47) for some bryophytes to reach extensive development (Mulec 2018). Beyond that, in the dark zone, plants, including bryophytes, are only able to live near artificial lighting. Mazina (2016a) noted that the bryophyte diversity is higher in caves with artificial lighting. Popkova *et al*. (2019) noted that the lampenflora tends to be similar to that of the entrance zone. Thatcher (1949) found that the lampenflora extended 8-61 cm from the lamps, with light intensities ranging 250-800 lux. Verdoorn (1932) offers the opinion that the very dim light conditions may be offset by the higher carbon dioxide content of the limestone.

In New York, USA, Haring (1930) described the flora of the Howe Caverns. The lights were turned on and the caverns opened to the public in 1929. Within 2.5 months plant life began to appear. After 8 months, she identified 7 species of bryophytes from the two clumps given to her, although nearly 50 lights had bryophyte colonies. She listed the liverwort ***Marchantia polymorpha*** (Figure 48) and the mosses ***Amblystegium serpens*** (Figure 2), ***Amphidium mougeotii*** (Figure 49-Figure 50), ***Brachythecium rutabulum*** (Figure 51), ***Bryoerythrophyllum recurvirostrum*** (Figure 52), ***Bryum caespiticium*** (Figure 53-Figure 54), ***Leptobryum pyriforme*** (Figure 4), and ***Rosulabryum capillare*** (Figure 55).

Figure 47. Entrance light at Son Doong Cave, showing penetration of photosynthetic organisms. Photo by Doug Knuth, through Creative Commons.

Figure 48. ***Marchantia polymorpha*** with gemmae cups, a liverwort found in the lampenflora of Mammoth Cave, Kentucky, USA, and in Howe Caverns, New York, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 49. ***Amphidium mougeotii***, a moss found near lamps in Howe Caverns, New York, USA. Photo by Michael Lüth, with permission.

Figure 50. ***Amphidium mougeotii***. Photo by Hugues Tinguy, with permission.

Figure 51. ***Brachythecium rutabulum***, found in the lampenflora of Howe Caverns, New York, USA. Photo by Des Callaghan, with permission.

Figure 52. ***Bryoerythrophyllum recurvirostrum***, a species found in Crystal Cave, Wisconsin, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 53. ***Bryum caespiticium*** with capsules, a species found in Crystal Cave, Wisconsin, USA. Photo by Bob Klips, with permission.

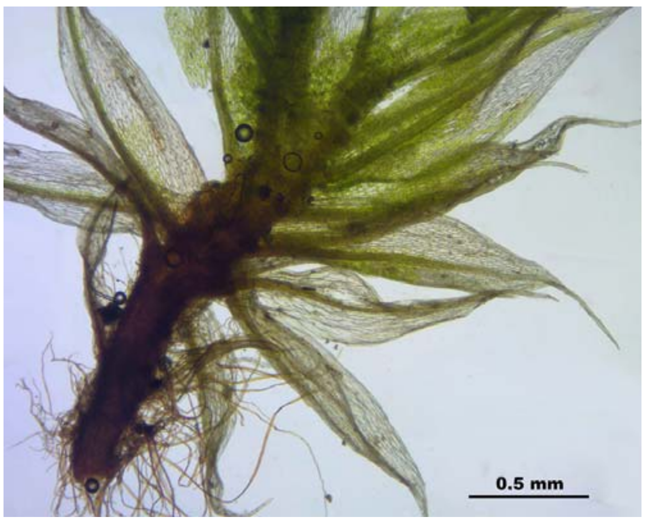

Figure 54. ***Bryum caespiticium*** showing numerous rhizoids. Photo by Hermann Schachner, through Creative Commons.

Figure 55. ***Rosulabryum capillare*** with capsules, on rock, found in the lampenflora of Howe Caverns, New York, USA. Photo through Creative Commons.

Kozlova and Mazina (2020) concluded that macrogroups dominated by bryophytes had well-defined boundaries, whereas the microgroups dominated by green algae were often located between these macrogroups, thus forming distinct but small communities and transitions.

Succession

Algae and **Cyanobacteria** typically are the first of the lampenflora to arrive (Hajdu 1977; Mulec & Kosi 2009; Cigna 2012). Following that are the bryophytes, ferns, and less frequently, seed plants. But Hajdu (1977) contends that the mosses will eventually outgrow and suppress the algae (presumably including the Cyanobacteria).

Hazslinsky (2002) noted that the lampenflora can spread "rather quickly." In Baradla Cave, Hungary, it doubled in seven years. Thomas (1897) reported that ***Rhynchostegiella tenella*** var. ***cavernarum*** (Figure 56) appeared around cave lights in about one year after their installation. The species ***Rhynchostegiella tenella*** has been found in underground rooms of the Roman Coliseum, suggesting that it is also a long-time stayer. Pfendler *et al*. (2021) conducted a quantitative study on bryophyte colonization on illuminated limestone blocks in caves. Some of the blocks similarly had dense colonization within a year.

Figure 56. ***Rhynchostegiella tenella***, a species that has appeared around cave lights within a year of their installation. Photo by Michael Lüth, with permission.

Popkova *et al*. (2019) found that the greatest similarity between the lampenflora and the entrance occurred under the greatest light intensity, supporting the role of light in determining the community structure. ***Eucladium verticillatum*** (Figure 57-Figure 58) was the predominant bryophyte in these photic zones, accompanied by the **Cyanobacteria** ***Microcystis pulverea*** (Figure 59) and ***Scytonema drilosiphon*** (see Figure 60) and the airborne and widespread green alga ***Chlorella vulgaris*** (Figure 61).

Figure 57. ***Eucladium verticillatum*** in lime seep, a common species around cavern lights. Photo by Resso Taelspeus, through Creative Commons.

Figure 58. ***Eucladium verticillatum***. Photo by Christian Berg, through Creative Commons.

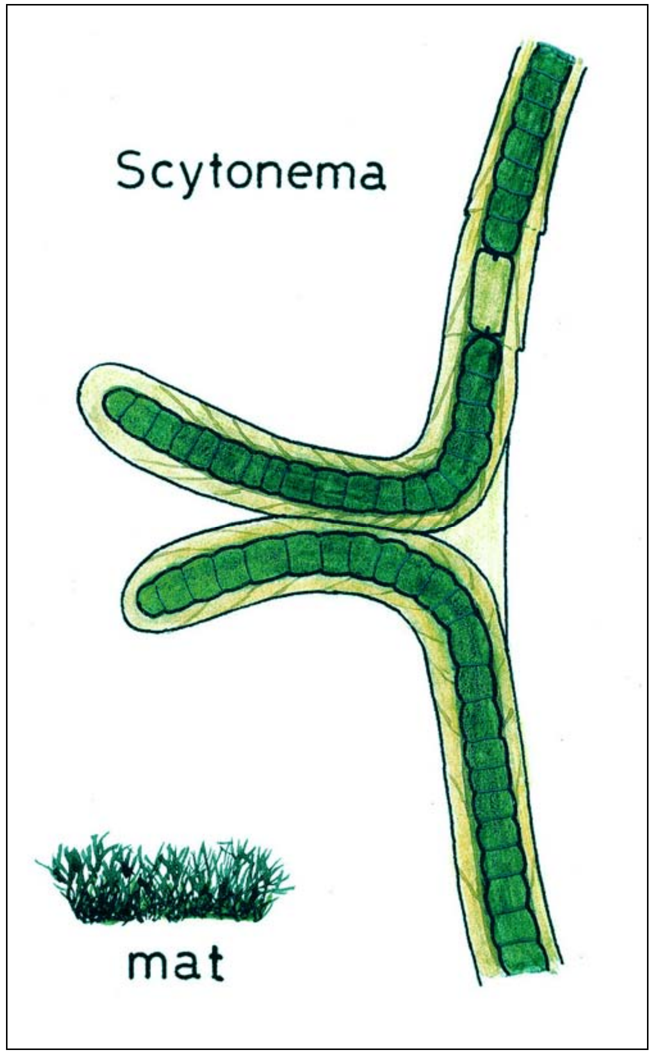

Figure 60. ***Scytonema***; ***Scytonema drilosiphon*** is one of the **Cyanobacteria** that grows near the lights in caverns. Drawing by Allen Pentecost, through Creative Commons.

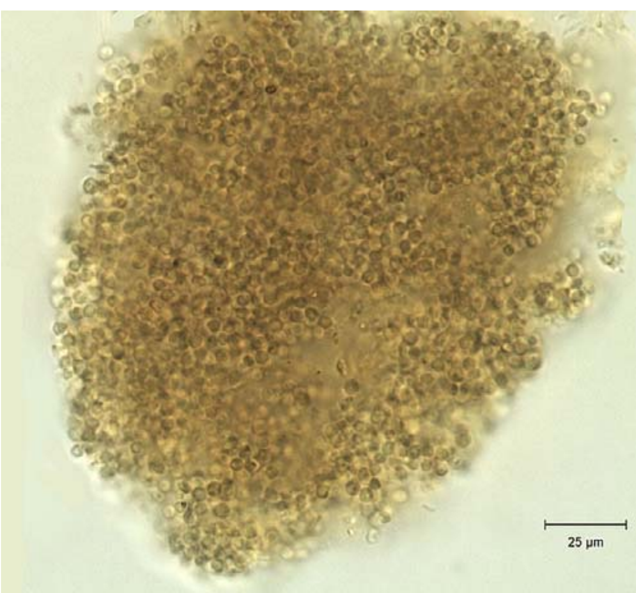

Figure 59. ***Microcystis pulverea***, a common member of **Cyanobacteria** found near lights in caverns. Photo by Chris Carter, with permission, AlgaeBase.

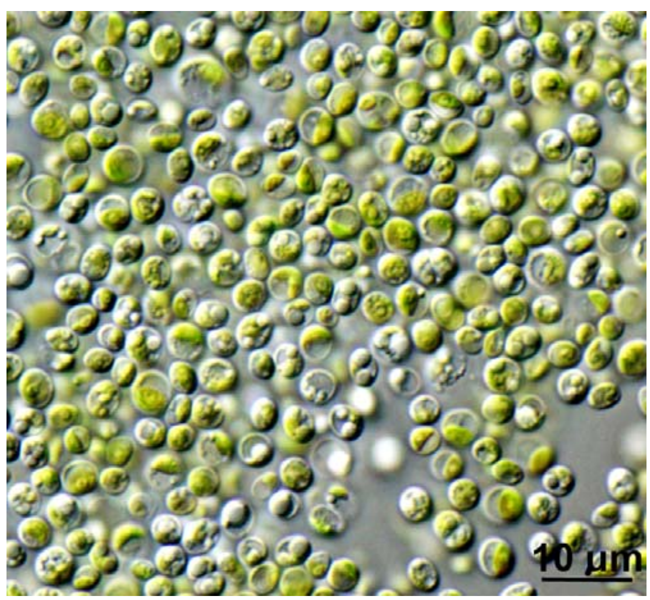

Figure 61. ***Chlorella vulgaris***, a widespread, airborne green alga that grows near lights in caverns. Photo by Neon, through Creative Commons.

Species Numbers

As an example of the distribution among photosynthetic groups near lamps, in addition to 2 flowering plants, Mazina (2015) found 34 species of **Cyanobacteria**, 5 **Chlorophyta**, 2 **Ochrophyta** (planktonic and benthic algae), 9 **Bacillariophyta** (diatoms), 22 **Bryophyta**, and 6 **Polypodiophyta** (ferns etc.) in Vorontsovskaya Cave, Russia. Komáromy *et al*. (1985) found 42 alga taxa (including **Cyanobacteria**), 10 moss taxa, and 1 fern taxon in the lamp-lit areas of the cave Anna-Barlang near Lillafuered, Hungary. In Italy, Castello (2012, 2014) found 16 moss species and 2 ferns (algae were not assessed) in the lampenflora. Castello found that some of the mosses were typical of cave entrances in the Italian Karst, but others were typical of disturbed and open habitats. Lundegårdh (1931) described the zonation as ferns nearest to the lamp, mosses farther away, and algae at the farthest locations from the light.

Mazina and Maximov (2011) reported 14 **Cyanobacteria**, 4 **Chlorophyta**, 4 **Bacillariophyta**, 11 **Bryophyta**, and 5 **Polypodiophyta** among the lampenflora of an excursion cave in Russia. The ferns were juveniles and the only moss with sporophytes was ***Isopterygiopsis pulchella*** (Figure 62). Moss protonemata (Figure 63) were subdominants on the limestone and **argillaceous veneers** (coverings containing clay).

Figure 62. ***Isopterygiopsis pulchella*** with capsule, the only species with a capsule in a Russian excursion cave. Photo by Michael Lüth, with permission.

Figure 63. Protonemata of the moss ***Physcomitrium pyriforme***, a typical sight in cave lampenflora Photo by Bob Klips, with permission.

In an exhibition cave in the Czech Republic, Faimon *et al*. (2003) found 12 taxa of algae and **Cyanobacteria** (Figure 59-Figure 60) and 19 moss taxa.

Dominant Species

Pentecost (2011) described the lampenflora of tourist caves in northern England. The **Cyanobacteria** (Figure 59-Figure 60) numbered 18 species, supporting the conclusion that it is the most species-rich group in the lamp communities. He also found 6 diatoms, 4 bryophytes, 1 coccoid green alga, and 1 fern species. The **Cyanobacteria** were the predominant organisms and grew at light levels of 0.06-2.08 µmol m^{-2} s^{-1}. ***Eucladium verticillatum*** (Figure 57-Figure 58) was the most common moss, surviving in light levels of 0.55-2.08 µmol m^{-2} s^{-1}

Mulec and Kubešová (2010) reported species from 8 Slovenian show caves. Once again, ***Eucladium verticillatum*** (Figure 57-Figure 58) was among the most frequent mosses, along with ***Amblystegium serpens*** (Figure 2), ***Brachythecium*** sp. (Figure 66), and ***Fissidens taxifolius*** (Figure 64). Bryophytes and ferns together comprised 37 taxa. Not surprisingly, ***Eucladium verticillatum*** had the widest range of photosynthetic photon flux density (1.4-530.0 µmol photons m^{-2} s^{-1}). ***Cratoneuron filicinum*** (Figure 65) even developed sporophytes at 2.1 and 2.4 µmol photons m^{-2} s^{-1}. ***Brachythecium salebrosum*** (Figure 66) developed sporophytes at 4.7 µmol photons m^{-2} s^{-1}.

Figure 64. ***Fissidens taxifolius*** with young capsules, a species known from Slovenian excursion caverns. Photo by Bob Klips, with permission.

Figure 65. ***Cratoneuron filicinum***, a species that can develop sporophytes at 2.1 and 2.4 µmol photons m^{-2} s^{-1}. Photo by J. C. Schou, with permission.

Figure 66. ***Brachythecium salebrosum***, a species that can develop sporophytes at 4.7 µmol photons m^{-2} s^{-1}. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Maheu (1926) recorded 6 moss species [***Anomodon attenuatus*** (Figure 67), ***A. rostratus*** (Figure 3), ***Brachythecium rivulare*** (Figure 68), ***Eurhynchium praelongum*** (Figure 69), ***Gymnostomum calcareum*** (Figure 32-Figure 33), and ***Plagiomnium rostratum*** (Figure 70)], and the liverwort ***Marchantia polymorpha*** (Figure 48) from the twilight zone, including lamp areas, of Mammoth Cave, Kentucky, USA. These bryophytes were etiolated and lacked sporophytes. Barr (1968) later reported 200 species of animals, 67 species of algae, 27 species of fungi, and 7 species of twilight-zone bryophytes in the Mammoth Cave system.

Figure 67. ***Anomodon attenuatus***, found in the lampenflora of Mammoth Cave, Kentucky, USA. Photo by Dendrofil, through Creative Commons.

Figure 68. ***Brachythecium rivulare***, found in the lampenflora of Mammoth Cave, Kentucky, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 69. ***Eurhynchium praelongum***, found in the lampenflora of Mammoth Cave, Kentucky, USA. Photo by Peter Woodard, through Creative Commons.

Figure 70. ***Plagiomnium rostratum***, found in the lampenflora of Mammoth Cave, Kentucky, USA. Photo by Hermann Schachner, through Creative Commons.

Like many other studies, D'Agostino *et al.* (2015) found that the bryophytes in the Zinzulusa Show Cave (South Italy) mainly consisted of unidentified protonemata Figure 63) and the mosses ***Rhynchostegiella tenella***

(Figure 56) and ***Eucladium verticillatum*** (Figure 57-Figure 58). The latter species is instrumental in the formation of concretions that grow from water that drips from the ceilings, but are oriented toward the outside of the cave due to the phototropic growth of the moss (Figure 117).

In a cave in Hungary, Komáromy *et al*. (1985) found the mosses ***Brachythecium velutinum*** (Figure 71), ***Campylium chrysophyllum*** (Figure 72), ***Eucladium verticillatum*** (Figure 57-Figure 58), ***Fissidens dubius*** (Figure 73), ***F. pusillus*** (Figure 74), ***Gymnostomum calcareum*** (Figure 32-Figure 33), ***Hypnum cupressiforme*** (Figure 75), ***Pseudoscleropodium purum*** (Figure 76), ***Rhynchostegium megapolitanum*** (Figure 77), and ***Tortella tortuosa*** (Figure 78) near lights. These were all common species outside the caves. Note the absence of liverworts.

Figure 71. ***Brachythecium velutinum***, a common moss species that is also frequent around lights in caverns in Hungary. Photo by James K. Lindsey, through Creative Commons.

Figure 72. ***Campylium chrysophyllum***, a common moss species that is also frequent around lights in caverns in Hungary. Photo by Hermann Schachner, through Creative Commons.

Figure 73. ***Fissidens dubius*** on vertical substrate, a moss species that is frequent around lights in caverns in Hungary. Photo by Hermann Schachner, through Creative Commons.

Figure 74. ***Fissidens pusillus*** with capsules on rock on vertical substrate, a moss species that is frequent around lights in caverns in Hungary. Photo by David T. Holyoak, with permission.

Figure 75. ***Hypnum cupressiforme***, a moss species that is frequent around lights in caverns in Hungary. Photo by Fabio Cianferoni, through Creative Commons.

Figure 76. ***Pseudoscleropodium purum***, a common moss species that is also frequent around lights in caverns in Hungary. Photo by Emilie Bernard, through Creative Commons.

Figure 77. ***Rhynchostegium megapolitanum***, a moss species that is also frequent around lights in caverns in Hungary. Photo by David T. Holyoak, with permission.

Figure 78. ***Tortella tortuosa*** on rock, a common moss species that is also frequent around lights in caverns in Hungary. Photo by Bernd Haynold, through Creative Commons.

Verdoorn (1927) reported ***Brachythecium velutinum*** (Figure 71), ***Rhynchostegium murale*** (Figure 79), and ***Rosulabryum capillare*** (Figure 80) around the dim lights of 2 German caves. These exhibited small, etiolated, and crumpled leaves.

Figure 79. ***Rhynchostegium murale*** with capsules on rock – a species that occurs around dim lights in some German caves. Photo by Hugues Tinguy, with permission.

Figure 80. ***Rosulabryum capillare*** with capsules, on rock, a species that occurs around dim lights in some German caves. Photo by 3 through Creative Commons.

Kubešová (2001) reported 46 species of bryophytes in the lampenflora in public caves in the Moravian Karst (Czech Republic) in the 1960s to 1970s, but only 34 were located in 1999-2000. Of these, 2 liverworts and 10 moss species could not be relocated, but 2 new moss species were found. The bryophytes present all occur on the soil and rocks outside the caves (Rajczy 1989; Šmarda 1970). The mosses ***Amblystegium serpens*** (Figure 2), ***Eurhynchium hians*** (Figure 7), ***Leptobryum pyriforme*** (Figure 4), and ***Rhynchostegium murale*** (Figure 79) were frequent in the 1970s and in the later study (Kubešová 2001). The liverworts ***Fossombronia wondraczekii*** (Figure 81) and ***Pellia epiphylla*** (Figure 82) and the mosses ***Aulacomnium androgynum*** (Figure 83), ***Dichodontium pellucidum*** (Figure 84), ***Eurhynchium angustirete*** (Figure 85), ***Mnium marginatum*** (Figure 86), ***Plagiomnium affine*** (Figure 87), ***Plagiomnium rostratum*** (Figure 88), ***Rhizomnium punctatum*** (Figure 89), ***Timmia bavarica***

(Figure 90), ***Tortella tortuosa*** (Figure 78), and ***Trichostomum tenuirostre*** (Figure 91-Figure 92), were not relocated. The mosses ***Ditrichum flexicaule*** (Figure 93-Figure 94), ***Rhodobryum ontariense*** (Figure 95), and ***Thamnobryum alopecurum*** (Figure 96) were new in the present study. The mosses ***Brachythecium velutinum*** (Figure 71), ***Ceratodon purpureus*** (Figure 97-Figure 98), ***Dichodontium pellucidum*** (Figure 84), ***Funaria hygrometrica*** (Figure 12-Figure 13), ***Leptobryum pyriforme*** (Figure 4), ***Physcomitrium pyriforme*** (Figure 63, Figure 99), ***Rhynchostegium murale*** (Figure 79), and ***Tortula subulata*** (Figure 100-Figure 101) had at least some fertile populations in the 1970s, but only ***Funaria hygrometrica*** (Figure 12-Figure 13) was fertile in the later study. Hajdu (1977) noted that sporophytes were rare in cave bryophyte populations. Were these changes due to competition by later arrivals, or to changing conditions due to human presence?

Figure 81. ***Fossombronia wondraczekii*** with capsules, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Michael Lüth, with permission.

Figure 82. ***Pellia epiphylla*** with capsules, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hermann Schachner, through Creative Commons.

Figure 83. ***Aulacomnium androgynum*** with gemmae, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hugues Tinguy, with permission.

Figure 84. ***Dichodontium pellucidum***, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Claire Halpin, with permission.

Figure 85. ***Eurhynchium angustirete***, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hermann Schachner, through Creative Commons.

Figure 86. ***Mnium marginatum***, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hermann Schachner, through Creative Commons.

Figure 87. ***Plagiomnium affine*** branches, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hermann Schachner, through Creative Commons.

Figure 88. ***Plagiomnium rostratum***, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hermann Schachner, through Creative Commons.

Figure 89. ***Rhizomnium punctatum***, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Jean Faubert, with permission.

Figure 90. ***Timmia bavarica***, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Hugues Tinguy, through Creative Commons.

Figure 91. ***Trichostomum tenuirostre*** habitat, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Bob Klips, with permission.

Figure 92. ***Trichostomum tenuirostre***. Photo by Bob Klips, with permission.

Figure 93. ***Ditrichum flexicaule***, a species found in Moravian Karst (Czech Republic) in 1999-2000, but not in the 1960s to 1970s. Photo by Hermann Schachner, through Creative Commons.

Figure 94. ***Ditrichum flexicaule*** among rocks. Photo by Hermann Schachner, through Creative Commons.

Figure 95. ***Rhodobryum ontariense***, a species found in Moravian Karst (Czech Republic) in 1999-2000, but not in the 1960s to 1970s. Photo by Hugues Tinguy, with permission.

Figure 96. ***Thamnobryum alopecurum*** on vertical surface, a species found in Moravian Karst (Czech Republic) in 1999-2000, but not in the 1960s to 1970s. Photo by Hugues Tinguy, with permission.

Figure 97. ***Ceratodon purpureus*** on rock, a species that was fertile in the 1970's, but not in 1999-2000 in the Moravian Karst. Photo by Aleksandr Levon, through Creative Commons.

Figure 98. ***Ceratodon purpureus*** with capsules. Photo by Bob Klips, with permission.

Figure 99. ***Physcomitrium pyriforme*** with capsules, a species that has capsules in early lampenflora, but not 30 years later, in the Moravian Karst. Photo by Lee Elliot, through Creative Commons.

Figure 100. ***Tortula subulata***, a species that was fertile in the 1970's, but not in 1999-2000 in the Moravian Karst. Photo by Hermann Schachner, through Creative Commons.

Figure 101. ***Tortula subulata*** with immature capsules, on rock. Photo by Hugues Tinguy, with permission.

Kubešová (2013) reported ***Amblystegium serpens*** (Figure 2), ***Brachytheciastrum velutinum*** (Figure 102), ***Cratoneuron*** spp. (Figure 65), and ***Fissidens taxifolius*** (Figure 64) as frequent species around lights in 14 caves in the Czech Republic, all common outside caves as well. In total, he found 62 moss species, but no liverworts, with 0-24 species in a single cave. Overall, 45% of the bryophyte flora remains the same as in the past (1960s-70s). In the 1988-1990 period, 26% of the species were newly recorded. Only nine of the 1960-70's species of mosses were relocated in 1988-1990.

Figure 102. ***Brachytheciastrum velutinum***, a frequent species around lights in 14 caves in the Czech Republic. Photo by Claire Halpin, with permission.

When Kubešová (2005, 2006) reviewed the bryophytes in public caves in the Czech Republic, he found that the mosses ***Amblystegium serpens*** (Figure 2), ***Brachythecium velutinum*** (Figure 71), ***Fissidens taxifolius*** (Figure 64) and ***Leptobryum pyriforme*** (Figure 4) were the ones most frequently present in both early studies in the 1960s-70s and in 2004.

But in North America, the composition differs. Thatcher (1949) noted the absence of both ***Reboulia*** (Figure 103) and ***Eucladium*** (Figure 57-Figure 58) in Crystal Cave in Wisconsin, USA, a tourist cavern. Only ***Ceratodon purpureus*** (Figure 97-Figure 98), ***Fissidens***

taxifolius (Figure 64), ***Leptobryum pyriforme*** (Figure 4), and ***Rosulabryum capillare*** (Figure 80) were found in both the Crystal Cave, Wisconsin, and the Czech caverns. Instead, Thatcher reported the thallose liverwort ***Marchantia polymorpha*** (Figure 48) and the mosses ***Barbula unguiculata*** (Figure 104), ***Brachythecium populeum*** (Figure 105-Figure 106), ***Brachythecium salebrosum*** (Figure 66), ***Bryoerythrophyllum recurvirostrum*** (Figure 52), ***Bryum caespiticium*** (Figure 53-Figure 54), ***Leptodictyum riparium*** (Figure 107-Figure 108), ***Plagiomnium cuspidatum*** (Figure 109), and ***Warnstorfia fluitans*** (Figure 110) from Crystal Cave. A small amount of the fern ***Cryptogramma stelleri*** (Figure 111) was the only fern present, and in only a small amount, but with prothalli, growing among moss protonemata (Figure 63). ***Bryum caespiticium*** was the only moss to display a sporophyte – a single sporophyte for the entire study.

Figure 103. ***Reboulia hemispherica*** with archegoniophores; ***Reboulia*** is found in some European caverns, but was absent in Crystal Cave, Wisconsin, USA. Photo by Bob Klips, with permission.

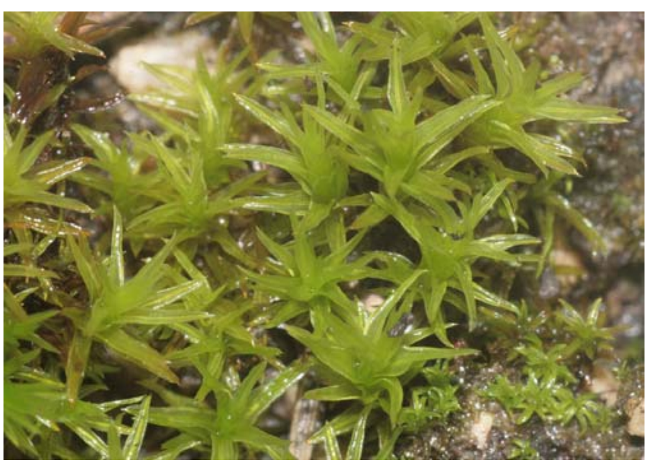

Figure 104. ***Barbula unguiculata***, a species found in Crystal Cave, Wisconsin, USA – a tourist cavern. Photo by Hermann Schachner, through Creative Commons.

Figure 105. ***Brachythecium populeum*** on rock, a species that occurs in Crystal Cave, Wisconsin, USA. Photo by Michael Lüth, with permission.

Figure 106. ***Brachythecium populeum*** with capsules. Photo by Hermann Schachner, through Creative Commons.

Figure 107. ***Leptodictyum riparium*** on rock at edge of stream, a species found in Crystal Cave, Wisconsin, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 108. ***Leptodictyum riparium***. Photo by J. C. Schou, with permission.

Figure 109. ***Plagiomnium cuspidatum*** branches, a species found in Crystal Cave, Wisconsin, USA. Photo by Hermann Schachner, through Creative Commons.

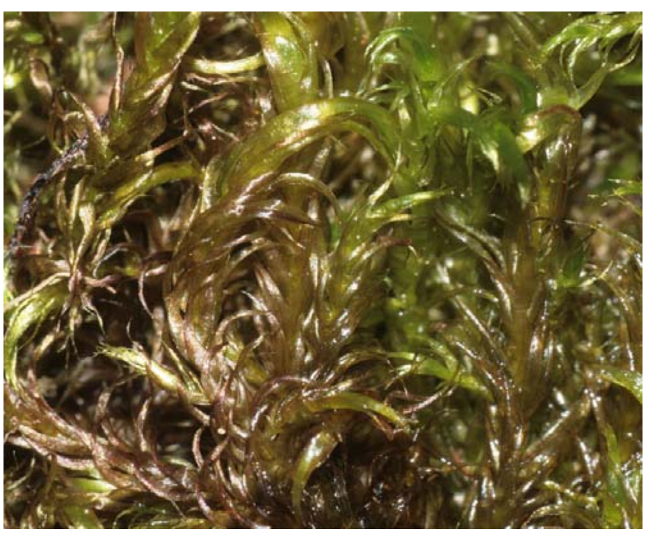

Figure 110. ***Warnstorfia fluitans***, a species found in Crystal Cave, Wisconsin, USA. Photo by Hermann Schachner, through Creative Commons.

Figure 111. ***Cryptogramma stelleri*** in rock crevice, a species found in Crystal Cave, Wisconsin, USA. Photo by Rob Routledge, through Creative Commons.

Castello (2014) found 16 moss species and 2 ferns in 26 sites near artificial lights of various kinds in the Trieste Karst in NE Italy. The most common of these were the mosses ***Eucladium verticillatum*** (Figure 57-Figure 58), ***Fissidens bryoides*** (Figure 10-Figure 11), ***Oxyrrhynchium schleicheri*** (Figure 112-Figure 113), and ***Rhynchostegiella tenella*** (Figure 56) and the fern ***Asplenium trichomanes*** (Figure 114-Figure 115). Of these, ***Eucladium verticillatum*** was the most common, exhibiting a wide amplitude for light intensity and substrate type (see also Dalby 1966a; Popkova *et al*. 2019). The most important factors determining the species present were light intensity, water availability, type of substrate, morphological features of surfaces, and presence of clay. To these factors, Mazina (2016a) added the connection of the location with the surface.

Figure 112. ***Oxyrrhynchium schleicheri***, one of the most common mosses near cavern lights at the Trieste Karst in NE Italy. Photo by Hugues Tinguy, with permission.

Figure 113. ***Oxyrrhynchium schleicheri*** branch. Photo by Hermann Schachner, through Creative Commons.

Figure 114. ***Asplenium trichomanes*** on rock wall, one of the most common plants near cavern lights at the Trieste Karst in NE Italy. Photo by Egon Krogsgaard, through Creative Commons.

Figure 115. ***Asplenium trichomanes*** on rock wall. Photo by Ori Fragman-Sapir, through Creative Commons.

Modifications of Cave Dwellers

Piano *et al*. (2015) found that increased illumination was the primary factor influencing both increased presence and increased productivity of **Cyanobacteria** (Figure 59-Figure 60), **diatoms** (Figure 116), and **green algae** (Figure 61). The presence of seeping water on the substrate and the distance from the cave entrance are important in determining patterns of colonization. Differences in light likewise influences the bryophyte flora, its appearance, its physiological acclimation, and its productivity.

Figure 116. ***Pinnularia*** sp. a diatom in a genus that occurs on cave bryophytes. Photo by Denis Barthel, through Creative Commons.

The lampenflora organisms are usually ubiquitous in nature, having the ability to survive in new conditions through a wide ecological tolerance (Mulec 2012; Mazina 2016a). Nevertheless, lampenflora bryophytes are often etiolated (Mulec 2018). Conard (1932) remarked on the ***Fissidens taxifolius*** (Figure 64) that he found within 20 cm of a light in Crystal Cave, Virginia, USA. The leaves were more widely spaced than in typical specimens outside caves. Prior (1961) found that the leaves of cave-dwelling mosses are often much more crisp than those outside the cave. Prior also found that the number of chloroplasts seems to be unaffected by the light intensities; nevertheless, the mosses are typically pale, resulting from a reduction in chlorophyll content.

Maheu (1926) summarized the reported modifications of cave and sink hole bryophytes. These included sterility, elongation of leaves, increased spacing of leaves along the stem, elongation of cells, and disappearance or attenuation of the costa or rib. The liverworts present the least

modification, despite penetrating the greatest distance into the cave.

The phototropic response is quite evident among acrocarpous mosses, with some inclined as much as 75º from vertical at the deepest location of mosses in the cave (Prior 1961). When the nearest lamp is on the ground, this response is evident throughout the growth; such responses cause some statoliths to develop horizontally (Figure 117). For example, sporophytes on ***Leptobryum pyriforme*** (Figure 4) are inclined in the same way as the stem of the gametophyte.

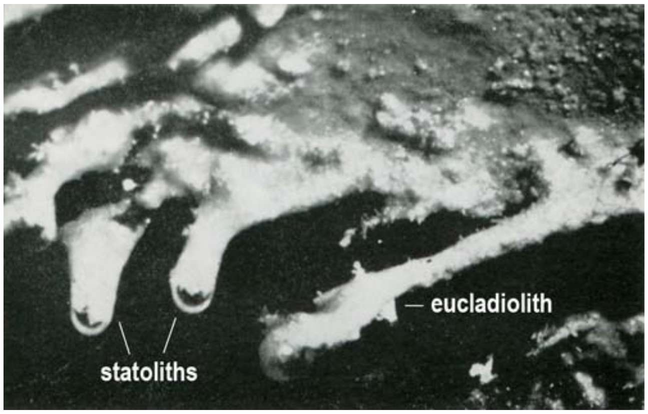

Figure 117. ***Eucladium verticillatum*** forming stalactite (eucladiotite) in mine in Dorset, showing horizontal growth of the statolith (eucladiolith in this case). Photo from Dalby 1966b.

Life Strategies

In a Hungarian cave, Komáromy *et al*. (1985) found that moss species in lamp-lit areas were **colonists** and **perennials** (5 species each). Similarly, in the Czech Republic Kubešová (2006, 2013) found the most frequent life strategies to be **colonists** and **perennials**, but also included fugitives, with the most common growth forms being **short turf** and **rough mat**.

Sporophytes are generally scarce among bryophytes in caves. Prior (1961) seems to have found more than most bryologists, with 50% of the moss species in Luray Cavern Kentucky, USA, having sporophytes. As noted earlier, he found ***Amblystegium serpens*** (Figure 2), ***Campylium hispidulum*** (Figure 6), ***Tortula obtusifolia*** (Figure 8-Figure 9), ***Eurhynchium hians*** (Figure 7), ***Funaria hygrometrica*** (numerous; Figure 12-Figure 13), and ***Leptobryum pyriforme*** (Figure 4) with sporophytes in at least some locations. He noted that plants farthest from the lights often did not have capsules, but conceded that these could simply be too young.

Propagation and Survival

Mazina and Kozlova (2018) attempted to determine dominant propagation means occurring in the Lipska Cave in Montenegro. They used soil and water samples from the unlighted zone and cultured them to understand the propagules that were able to enter through airflows. Among these, they identified 17 species of algae and **Cyanobacteria**, and 12 bryophyte species. The mosses ***Fissidens taxifolius*** (Figure 64) and ***Brachythecium tommasinii*** (Figure 118-Figure 119) dominated the lampenflora communities, while ***Entodon schleicheri*** (Figure 120) and ***Tortella*** sp. (Figure 78) had the highest abundance in the natural entrance zone.

Figure 118. ***Brachythecium tommasinii***, a species that occurs in Lipska Cave in Montenegro. Photo by Hermann Schachner, through Creative Commons.

Figure 119. ***Brachythecium tommasinii***. Photo by Hermann Schachner, through Creative Commons.

Figure 120. ***Entodon schleicheri*** with capsules. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

In Russia and the Crimea, Mazina (2016a) found the highest species diversity of bryophytes and ferns in caves where the lampenflora had not been removed. In seeming

contrast, Burgoyne *et al*. (2021), using DNA identification, found that bacterial communities of unlit nearby caves had a greater diversity than did the excursion caves with lights (Lehman Caves, Great Basin National Park, Nevada, USA). There was little overlap among the communities of the Lehman Caves. Could it be that the lampenflora out-competed the bacteria? But this would not be true away from the lights.

In Virginia, USA, caves, Lang (1941) found the colors of the lampenflora to add a "pleasing variation" to the natural colors of the rock formations. These same organisms are absent within the caves where there are no lights. Lang noted that during the tourist season, the organisms may experience a lighted period as long as that in nature outside the cave. However, in winter they are seldom illuminated and usually turn yellowish or brown and die. On the other hand, many such caves around the world continue to serve the public throughout the year, permitting the continued growth of the lampenflora.

Lang (1943) collected mosses from the Luray Caverns, Virginia, USA, and kept them between blotters, dry and dark for one year. Under these conditions, the mosses remained as green as when first collected. This is consistent with their ability to dry in nature and remain alive, whereas those that were kept moist by the cave, but without light, most likely used up their energy through respiration and were therefore unable to manufacture new chlorophyll while remaining physiologically active.

Conservation and Control Measures

Although the lampenflora is considered by some to be unsightly, the greater concern is its ability to deteriorate the substratum. **Cyanobacteria** (Figure 59-Figure 60), in particular, are common in these dimly lit conditions (Mulec 2012).

Conservation in the caves can have conflicting goals. On the one hand, to maintain the original conditions of the natural cave, it is desirable to prevent or remove the growth around cave lights needed to provide safety to tourists (Kim 2008). On the other hand, these can be points of interest to both scientists and tourists, illustrating the differences in light requirements among the algae, bryophytes, and ferns. Furthermore, lights are necessary for safety in show caves.

In Pacitan, Indonesia, the extensive karst topography creates a large number of caves, several of which serve as show caves (Kurniawan *et al*. 2017). The show caves provide many jobs in the area, both in the caves and in the community through tourism, and they are of essential economic importance to the local area. This use is more sustainable of the caves than is mining, but the tourism creates problems that are often in conflict with management for profit.

Many impacts of cave visitation are more subtle, noticed only by those conducting intensive study on the cave. This is particularly true for the non-photosynthetic cave dwellers. Elliott (2006) noted that typical cave dwellers such as some insects, salamanders, bats, and other animals have long life spans, slow rates of reproduction, and ability to survive in low food conditions. Some of the cave dwellers (*e.g.* moths, raccoons, bears) are seasonal, surviving there in winter and other unfavorable weather conditions. These organisms often avoid humans and can disappear without the average visitor ever noticing.

Human Impacts

Kurniawan and coworkers (2017) cited various dangers to the natural beauty of the caves: cement walkways, lights of various colors, big fans, added perfumes, weak regulation of visitor numbers, breakage and other damage of the rock formations, and application of dangerous substances to lessen the odor of guano and repel the cave fauna. Not only do the lights permit growth of lampenflora, but visitors introduce dust that covers the formations and alters their colors, leave garbage, vandalize, alter the microclimate, and cause decline in the numbers of biota. Similar impacts have been documented in other studies (Gillieson 2011; Mulec 2019).

Most cave formations of interest for tourists occur in limestone formations. The presence of lampenflora introduces organic acids that can corrode the limestone substrate (Aley 2004; Cigna 2012).

Russell and MacLean (2008) also noted the addition of concrete and steel structures, change in the air movement regime, and alteration of temperature through the movement of warm bodies through the cave. Human presence in the cave can also alter the available CO_2 (Russell & MacLean 2008; Lamprinou *et al*. 2014). This becomes more apparent when ventilation is limited (Russell & MacLean 2008; Lang *et al*. 2015). And the addition of entrances or blockage of entrances changes airflow patterns within the cave, with the entrance of visitors disturbing the relatively limited variation in temperature and humidity.

Visitors to caves can be a major source of propagules, especially on shoes and boots (Mulec 2014). Mulec estimated that more than 10,000 colony-forming units arrive per 100 cm^2 in such caves.

Many researchers have pointed out the destructive nature of cave lamps and human presence to the natural formations (Rajczy *et al*. 1997; Kubešová 2001; Cigna 2011; Gillieson 2011; Parise 2011; Mulec 2012; Šebela & Turk 2014; Mazina 2015; Piano *et al*. 2015; Meyer *et al*. 2017; Mulec 2019; Pfendler *et al*. 2021). Mulec (2012) considered the lampenflora to be unsightly, as well as having detrimental effects on the underlying substrata. But, unfortunately, the chemicals available to remove the lampenflora are not specifically targeted to these organisms, but can also be detrimental to the cave fauna. Furthermore, they can corrode the very substrate that is in need of protection. New lighting technology and better practices seem to be a better means of control.

In public caves in the Czech Republic, Kubešová (2006) found that the species richness was highest in the caves where the visitors' tour was long and the caves experienced the highest number of visitors. Hence, it is likely that humans are strong dispersal agents.

Treatments - Chemical

In Crystal Cave, Sequoia National Park, California, USA, Meyer *et al*. (2017) found that 1.0 and 0.5% sodium hypochlorite (Clorox) effectively eliminate lampenflora in 11 and 21 days, respectively, greatly outperforming 15.0% hydrogen peroxide. The springtail ***Tomocerus celsus*** (see Figure 121) had a similar diet both when living among the lampenflora and away from it. Nevertheless, ***T. celsus*** experiences a negative response to 1.0% sodium hypochlorite, and its presence was inversely related to the effectiveness of each treatment.

Figure 121. *Tomocerus vulgaris*; ***Tomocerus celsus*** lives among the lampenflora in Crystal Cave, Sequoia National Park, California, USA. Photo by Andy Murray, through Creative Commons.

Because chlorine and other compounds used to remove lampenflora are deleterious to the cave substrate, Faimon *et al*. (2003) tested hydrogen peroxide as an alternative in a cave in the Moravian Karst, Czech Republic. They found that a 15% by volume solution was an adequate strength to destroy the lampenflora. But limestone and speleothem dissolution rates were 1 order of magnitude higher than that by the karst water. To alleviate this problem, they found that there was little damage if a few limestone fragments were added to the solution at least 10 hours prior to application.

Mulec (2018) elaborated on the types of changes that lampenflora can make in caves. Plant thalli can calcify, and tuffaceous stalactites and stromatolitic stalagmites add variety to the cave formations. But these are natural processes, at times increased by access of the phototrophs deeper into the cave by the presence of artificial light.

In prehistoric caves, serious damage may occur to wall paintings, as observed in the Lascaux cave in France (Ruspoli 1986). In historic caves where cave art is of interest, alteration of the artwork is of concern (Mulec 2018). The hygroscopic nature of the **Cyanobacteria** (Figure 59-Figure 60) and algae (Figure 61) and can make them especially harmful to artwork (Roldán *et al.* 2006). The lampenflora creates a greenish cast to the artwork and the photosynthetic organisms promote the growth of bacteria and fungi that "weather" the underlying art. Mulec (2018) contended that altering the spectra of the lights did not help in preventing lampenflora. Instead, he recommended removing the lampenflora and restricting the use of the lamps.

Kim (2008) noted that even though the lights may be shut down for periods of time, these **Chlorophyta** (Figure 61) and **Bryophyta** that have disappeared grow again "immediately" when suitable growth conditions return. Kim (2008) recommended the "necessity" of keeping the illumination distance over 2 m and using indirect light. This researcher warned against unintentional dispersal by moist pieces of cloth or sponge when removing the lampenflora and noted the importance of removing them at an early stage of development. Heat created by the lighting can also be a problem.

Sea caves (Figure 122) require special management (Gurnee 1994) that involves innovative techniques to protect them from the intrusion of visitors and exposure to the destructive sea air. These are sometimes protected by glass enclosures, use of boats and vehicles that keep visitors from especially sensitive areas, and lighting and cleaning techniques that minimize lampenflora.

Figure 122. View from inside of sea cave at Cape Greco National Park, Cyprus. Photo by Kallerno, through Creative Commons.

De Freitas (2010) emphasized the importance of managing the microclimate in the caves. These are easily altered by changes in entrance conditions, changing both spatial and temporal patterns of the climates within the cave. And changing air patterns will necessarily change patterns of dispersal of propagules. This means that management techniques must be appropriate to a particular cave condition or needed environmental condition.

Treatments – Alternative Lighting Regimes

Kim (2008) reported that the cave green algae and bryophytes disappeared by shutting down the lights and maintaining the natural low temperatures in caves. But this is not an option in show caves.

Whereas daylight spectrum lighting and red-enriched tungsten lighting promote the growth of **Cyanobacteria**, algae, and plants, UV light has antibiotic properties and is even used in hospitals and microbiology labs to control pathogens and contaminants. UV lights have been used to control the lampenflora in some caves (Mulec & Kosi 2009). In Grotta Gigante, Trieste, Italy, new germicidal lamps earned the cave the 2008 Green certificate (Fabbricatore 2009). These were considered environmentally friendly and kept the lampenflora under control. For safety purposes, these are on timers that turn them on when no other lights are on in the cave. They can be detrimental to human eyes and skin, so their use should be avoided when humans are in the cave. But what about the fauna of the cave?

Pfendler *et al*. (2021) experimented with the growth of bryophytes on block samples with several pigments such as one might find in the prehistoric art. Several blocks in the study sustained dense bryophyte propagation. Nevertheless, the success of growth rate correlated with the chemical composition of the pigments. Such elements as As, Cr, Ti, and Co reduced bryophyte growth. UV-C light proved to be highly efficient *in situ*, although in the laboratory such treatments experienced fast recolonization. The researchers suggested that the recolonization was due

to the high density of the bryophyte growth that protected the lower parts from the UV-C light penetration.

Perhaps a better solution is the use of green light (Roldán *et al*. 2006). Changes is the light spectrum can include pigment changes in the **Cyanobacteria** and algae. In fact, green light affects pigment composition (Tandeau de Marsac *et al*. 1988; Albertano 1991). But it also retards growth (Hauschild *et al*. 1991) and causes vacuolation in the chlorophyll thylakoid system (Albertano 1991). An added bonus is that it provides the maximum absorbance in human vision.

Using the cyanobacterian ***Gloeothece membranacea*** (Figure 123) and chlorophytan ***Chlorella sorokiniana*** (Figure 124), Roldán *et al*. were able to demonstrate that green light could prevent the growth of photosynthetic organisms, except for those capable of modifying accessory pigments. Even so, the very light-adaptable ***Gloeothece membranacea*** exhibited lower photosynthetic pigment biovolume, smaller thylakoid regions, and a weaker mean fluorescence intensity.

Figure 123. ***Gloeothece membranacea***, a member of **Cyanobacteria** that is damaged by green light. Photo by Chris Carter, with permission.

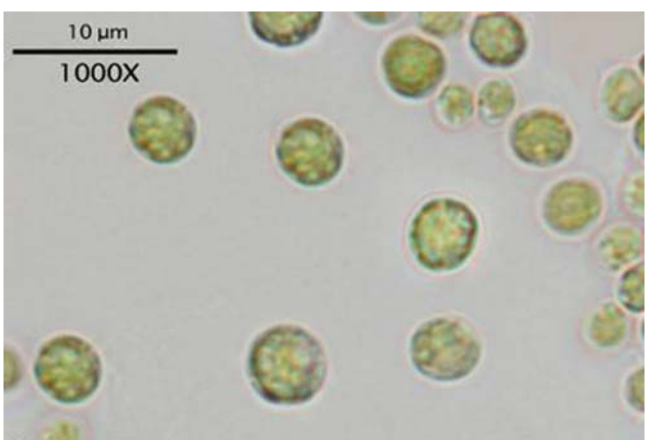

Figure 124. ***Chlorella sorokiniana***, a member of **Chlorophyta** in which growth is prevented by green light. Photo by UTEX, through Creative Commons.

Pollution and Role of Bryophytes

In the Zhijin Cave in China, heavy metal pollution was introduced by the development of the karst caves for show purposes. Liu *et al*. (2018) sought to determine the effect of the bryophytes on the cave pollution. The cave had 12 liverwort and 37 moss taxa, dominated by **Pottiaceae**, **Fissidentaceae**, and **Mniaceae**. Mercury levels were especially elevated and represented the most serious pollutant in the cave. The bryophyte community diminished as the heavy metal levels increased. Furthermore, the bryophytes served as accumulators that could be used to indicate the level of pollution in the cave. The liverwort ***Conocephalum conicum*** (Figure 125), in particular, is affected by substrate Hg content and can be used as a biomonitor in caves.

Figure 125. ***Conocephalum conicum***, a species that can be used to monitor mercury in caves. Photo by Claire Halpin, with permission.

One consequence of the lampenflora is the production of **aragonite** (mineral consisting of calcium carbonate, typically occurring in white seashells, including pearls, and as colorless prisms in deposits in hot springs) instead of **calcite** (more common form of calcium carbonate in limestone caves) (Forti 1980). This is accomplished by the different arrangement of atoms. Such modifications can be minimized by use of special lamps that do not support the range of maximum absorption for photosynthesis (Gurnee 1994; Olson 2002; Roldán *et al.* 2006; Mulec & Kosi 2009; Lamprinou *et al*. 2014).

Summary

Succession of **lampenflora** usually begins with **Cyanobacteria**, then algae, then bryophytes, and finally ferns (and possibly flowering plants). The **Cyanobacteria** and algae are forced farther and farther from the light by the increasingly larger bryophytes and ferns. The caves with lamps typically have greater species diversity of bryophytes and other cave flora.

Dominant bryophyte species, and those with widespread occurrence, include ***Amblystegium serpens***, ***Eucladium verticillatum***, ***Fissidens bryoides***, and ***Fissidens taxifolius***, but dominant species differ regionally. Liverworts are few or absent. ***Rhynchostegiella tenella*** can arrive and establish within one year.

Bryophytes in the low light of caves, whether in the twilight zone or around lights, frequently have diminished chlorophyll content (pale), leaves more widely spaced, leaves elongated, cell elongation, reduction of costa, and reduction or lack of sexual structures. They are often positively phototropic.

The lampenflora are typically **colonists** and **perennials** with a **rough mat** or **short turf** life form. The sporophyte generation is poorly represented, and the plants seem to rely on asexual propagules and fragmentation for spreading within the cave. Those with sporophytes typically produce them frequently outside the caves, but the converse is less likely.

The lampenflora is typically considered a nuisance in caverns. It changes the colors, increases the decomposition of the cave, and can damage prehistoric artwork. Efforts to remove or prevent the lampenflora include peroxide, scraping, and reducing the time lights are on. But new treatments with green light or use of UV light when humans are not present offer promise.

Although bryophytes are susceptible to damage by pollutants, they can also be accumulators that help to remove heavy metals and other pollutants introduced by human activity.

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