CHAPTER 18-2
CAVES – OVERALL BRYOPHYTE FLORA

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Figure 1. Mammoth Cave entrance showing ferns and other plants at entrance and the rapid entrance into darkness. Photo through Creative Commons.

Bryophyte Flora

Overall

Lämmermayer (1912) described the bryophyte flora in 48 caves in Austria. He reported 72 bryophyte species. ***Eurhynchium*** *s.l.* was the most frequent genus and was represented by 6 species. ***Eurhynchium praelongum*** (Figure 2-Figure 3) occurred at only 200 lux. Thompson (1945) was among the early explorers of cave mosses. Rajczy (1978) explored the cave environment and its effect on mosses. Barr (1964) noted that the occurrence of numerous species of animal troglobites in any major limestone region is common and highly probable. But is that true of bryophytes?

Figure 2. ***Eurhynchium praelongum*** in England, member of the most common bryophyte genus in Austrian caves. Photo by Janice Glime.

Figure 3. ***Eurhynchium praelongum***, a species that occurred at 200 lux light intensity in an Austrian cave. Photo by Michael Lüth, with permission.

Hajdu (1977) opined that there are no true troglobites among the bryophytes because of their light limitations. Mosses (**Bryophyta**) form the bulk of the plant biomass in the caves studied in Hungary, and this seems to be the most likely case for most caves. Tracheophytes are more limited by light, and the algae and **Cyanobacteria** (Figure 4) form only thin crusts, thus contributing less to biomass.

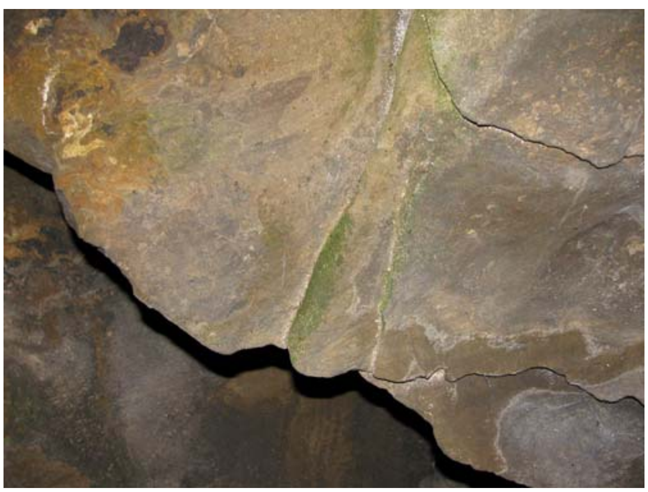

Figure 4. **Cyanobacteria** and algae on rock formations in Lost River Caverns, Pennsylvania, USA. Photo by Janice Glime.

Studied Caves

I was surprised when I began this chapter to find how many studies there have been on cave bryophytes. Studies included the Azores (Figure 5) and Canary Islands (González-Mancebo *et al*. 1989, 1991, 1992); Jennings (2009) wrote a Master's thesis on bryophyte diversity in Azorean caves. Other studies include Isle of May (Watson 1953), Jura Souabe, Swabian Alps, Germany (Dobat (1970), Saarland, Germany (Weber 1989), grottos in Italy, karst caves in the Ercole cave area, and Carso Triestino of Italy (Lo Giudice & Privitera 1984; Polli & Sguazzin 2002; Castello 2011), Polish caves (Ziober 1980, 1981), sea caves on the Isle of Capri in Italy (Sguazzin 2005), Cave Baradla (Figure 6) in Hungary (Hajdu & Orban 1981), other caves in Hungary (Rajczy 1982, 1989, 1990), Cave Perama in Greece (Rajczy 1979), caves in Romania (Stefureac 1985), moss and algal development in an urbanized cave in Bulgaria (Stoyneva *et al*. 2002), and karst caves in England (Zhang & Pentecost 2002).

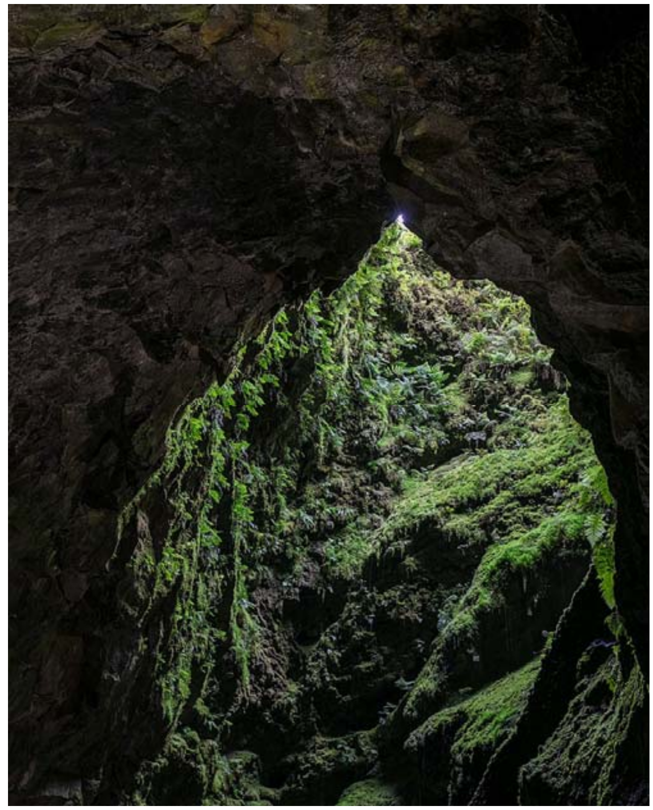

Figure 5. Cave in the Azores. Photo by Diego Delso, through Creative Commons.

Figure 6. Giant's Hall Baradla Cave, Hungary. Photo by Hanc Tomasz, through Creative Commons.

Cros and Rosselló (1984) relocated the mosses ***Palustriella commutata*** (Figure 7-Figure 8) and ***Eucladium verticillatum*** (Figure 9-Figure 10) reported by Maheu (1912) in caves of the Pityusic Islands in the Mediterranean Sea, but no bryophytes were mentioned in the early studies by Maheu (1912) in the coastal caves.

Figure 7. ***Palustriella commutata***, a long-time resident of caves in the Pityusic Islands, small islands in the Mediterranean Sea. Photo by Hermann Schachner, through Creative Commons.

Downing (1992) compared substrate preferences of bryophytes at three locations in southeastern Australia, including the Jenolan Caves (Figure 11). Limestone substrates had more abundant bryophytes, exhibiting more species and greater percent ground cover, than did nonlimestone substrates. Many of the species from limestone sites were typical of arid and semiarid habitats in Australia. Downing *et al*. (1995) listed the bryophytes of Wombeyan Caves (Figure 12) in New South Wales. Downing *et al*. (1997) revisited the Yarrangobilly Caves (Figure 13) in New South Wales, Australia, and reported that most of the mosses collected by Watts in 1906 were still present. Martin (2003) reported on the flora of a volcanic collapse pit on the lower slopes of Onehunga, Auckland.

Figure 8. Early spring or low light growth form that one might find of ***Palustriella commutata*** or ***P. decipiens***. Photo by Michael Becker, through Creative Commons.

Figure 10. ***Eucladium verticillatum***, a common bryophyte in limestone caves. Photo by Christian Berg, through Creative Commons.

Figure 9. ***Eucladium verticillatum*** in lime seep, a bryophyte that prefers limestone substrate. Photo by Resso Taelspeus, through Creative Commons.

Figure 11. Interior of Jenolan Caves, Australia. Photo by Janice Glime.

Figure 12. Wombeyan karst cave, Fig Tree Cave Interior, New South Wales, Australia. Photo by XLerate, through Creative Commons.

Figure 13. Yarrangobilly Caves, Australia. Photo by Colin Henein, through Creative Commons.

In China, Zhang (1993) described moss communities of the Maolan karst caves. Zhang and Wang (2002) studied them at the Flying-Dragon Cave. Wang and Zhang (2002) explored the bryophytes in karst caves in Guangxi Province, China. Zhang *et al*. (2005) studied karst caves in the Guilin area (Figure 14). Li *et al*. (2015, 2019) studied the karstification processes and bryophyte diversity in various locations in China. Cong *et al*. (2017) studied epilithic mosses on rock in the Puding karst area.

Figure 14. Cave in Guilin area, China. Photo by Michael Gunther, through Creative Commons.

Shiomi (1991) described the ecological distribution of bryophytes and other plants based on cave effects on the Akiyoshi-dai Plateau in Japan.

Ren *et al*. (2021) characterized the cave bryophyte flora as having a poor but unique diversity. They found that it was related to the vegetation and microhabitat. When comparing six karst caves with varying degrees and types of disturbance in southern China (Figure 15), they found a total of 43 angiosperm species, 20 lycophyte and fern species, and 20 species of bryophytes. The highest disturbance coincided with the lowest species richness, number of individuals, and Shannon-Wiener diversity index, but had the highest Simpson's dominance index. Less disturbance was the opposite, corresponding with the highest species numbers, numbers of individuals, and Shannon-Wiener diversity index, and lowest Simpson's dominance index. Diversity also was affected by habitat heterogeneity, light intensity, water status, and nutrient availability. Liverworts were more common in low-light conditions; mosses were more common in strong light and were more drought tolerant. Diversity of bryophytes and tracheophytes diminished from the entrance to the intermediate plots to the distant plots (Figure 16). The bryophytes form crusts around the lights, facilitating colonization by other plants.

Figure 15. Furong Cave, a karst cave in southern China. Photo by Brookchi, through Creative Commons.

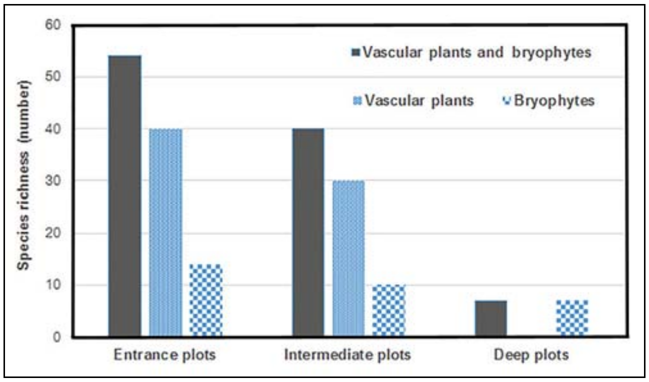

Figure 16. Cave species vs distance from entrance. Modified from Ren *et al*. 2021.

Pentecost (2010) found a total of 59 species, including 4 algae, 3 lichens, 47 bryophytes, 4 ferns, and only 1 angiosperm in Scoska Cave, UK (Figure 17). This is the most bryologically rich cave in Britain. Most (all but 9) of the species were recorded from other caves in Europe. Species richness declines rather irregularly from the entrance to 34 m depth, with relative irradiance decreasing from 12% of that in open sky to 0.004% at 34 m into the cave. Bryophytes occurred from 0-16 m into the cave, with relative irradiance decreasing to 0.2%. Only algae were able to grow at 34 m from the entrance. Whereas light decline represented a continuum, substratum characteristics and surface moisture were more irregular and accounted for various differences in the bryophyte flora.

Figure 17. Scoska Cave, UK. Photo by Bob Jenkins, through Creative Commons.

Moisture can also play a major role in determining the bryophyte flora. In one relatively dry cave on the Juan Fernandez Islands (Figure 18), Skottsberg (1935) found only the liverwort ***Balantiopsis purpurata*** (see Figure 19), although it was fairly well developed there. In another, ***Symphyogyna hochstetteri*** (see Figure 20) occurred in the illuminated edges of shallow pits, whereas ***Fissidens maschalanthus*** (see Figure 41-Figure 42) formed a closed carpet. In another cave Skottsberg found ***Balantiopsis purpurata***, ***Lepidozia*** sp. (Figure 21), ***Riccardia brevirarnosa*** (see Figure 98), ***Riccardia insularis*** (see Figure 98), and ***Symphyogyna hochstetteri***, and the mosses ***Distichophyllum subelimbatum*** (see Figure 22), ***Fissidens maschalanthus***, and several small areas of ***Philonotis krausei*** (see Figure 23). It is somewhat unusual to find more liverworts than mosses in a cave. On the Juan Fernandez Islands ***Riccardia insularis*** is not known outside the caves.

Figure 18. Juan Fernandez Islands, where dry caves have some unusual bryophyte species. Photo by Serpentus, through Creative Commons.

Figure 19. ***Balantiopsis*** sp.; ***Balantiopsis purpurata*** was the only liverwort found in a cave on the Juan Fernandez Islands off the coast of Chile. Photo by Felipe Osorio-Zúñiga, with permission.

Figure 20. ***Symphyogyna circinata***; ***Symphogyna hochstetteri*** occurs in the illuminated edges of shallow pits on the Juan Fernandez Islands. Photo by Jan-Peter Frahm, with permission.

Figure 21. ***Lepidozia reptans***; a species of ***Lepidozia*** occurs in at least one cave on the Juan Fernandez Islands. Photo by J. C. Schou, with permission.

Figure 22. ***Distichophyllum carinatum*** habitat in Allgau; ***Distihophyllum subelimbatum*** occurs in a cave on the Juan Fernandez Islands. Photo by Michael Lüth, with permission.

Figure 23. ***Philonotis fontana***; ***Philonotis krausei*** occurs in a cave on the Juan Fernandez Islands. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Bryophytes seem to be less diverse than algae in caves. Buczkó and Rajczy (1989) found 17 bryophyte taxa, compared to 49 algal taxa, in three caves in Hungary. The most characteristic moss was ***Amblystegium serpens*** (Figure 24-Figure 25).

Figure 24. ***Amblystegium serpens*** on rock ledge. Photo by Claire Halpin, with permission.

Figure 25. ***Amblystegium serpens*** leafy stem. Photo by Hermann Schachner, through Creative Commons.

Refugia

Caves often serve as refugia for rare species of more northern bryophytes, as observed in the Red River Gorge (Figure 26) of Kentucky, USA (Studlar & Snider 1989). Likewise, Christy and Meyer (1991) found that the **algific** (cold-producing) talus slopes in Wisconsin, USA, provided suitable microclimates for disjunct or relict plant and invertebrate populations. One third of the 39 species of bryophytes were restricted to the cold air vents there.

Figure 26. Red River Gorge, Kentucky, USA, showing caves in cliff. Photo by Jarek Tuszyński, through Creative Commons.

Puglisi *et al*. (2019) found boreo-arctic-montane species in some of the high mountain caves in Sicily; Fiol (1995) found that cavities in Mallorca (Figure 27) served as refugia. Alegro *et al*. (2015) found the circumpolar boreo-arctic montane ***Isopterygiopsis pulchella*** (Figure 28-Figure 29) and ***Platydictya jungermannioides*** (Figure 30-Figure 31) in rock crevices and caves as well as scattered in higher mountain areas of Croatia.

Figure 27. Cave at Porto Cristo, Mallorca. Photo by Lolagt, through Creative Commons.

Figure 28. ***Isopterygiopsis pulchella***, a species known from the low-light habitats of rock crevices and caves in Croatia. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Gabriel *et al.* (2006, 2011) considered the caves in the Azores (Figure 5) to serve as a refuge for bryophytes. Mulec (2018) likewise considered the dimly lit cave conditions to be refugia for some plants.

Figure 29. ***Isopterygiopsis pulchella***, a species of low-light locations. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

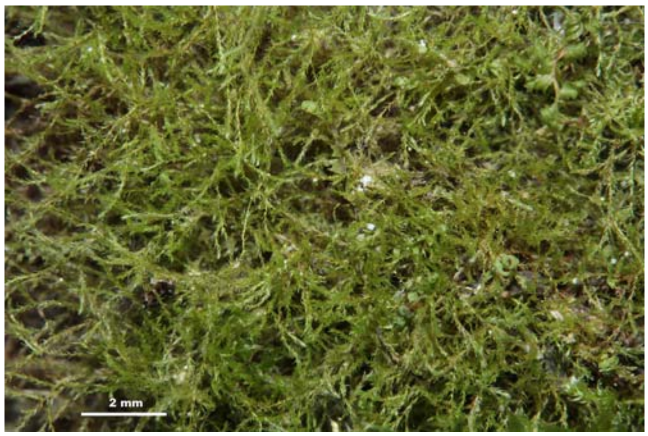

Figure 30. ***Platydictya jungermannioides***. Photo by Hermann Schachner, through Creative Commons.

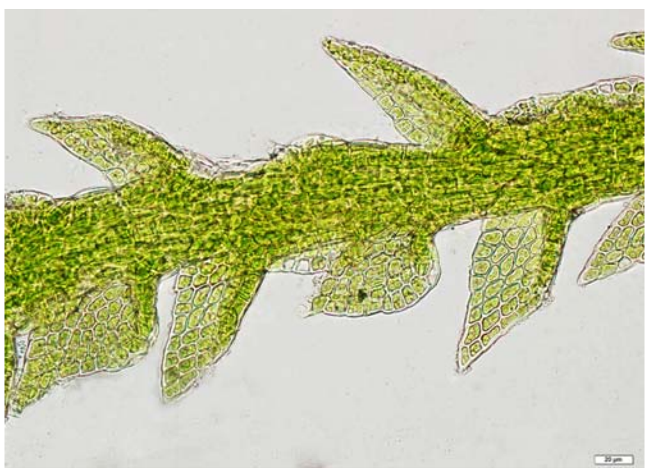

Figure 31. ***Platydictya jungermannioides*** branch. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

On the Socompa Volcano, Andes, Halloy (1991) found that at 6000 m asl communities of bryophytes, algae, fungi, lichens and animals formed at cave entrances where warm vapor (9-37ºC) was emitted. These warmer conditions at such high elevations permitted the development of communities, including bryophytes, up to 200 m².

Distance

In an artificial cave in the Iwato-jinjya area of Japan, Nakanishi (2002) found that bryophyte communities only extended 13 m into the cave, stopping 6 m short of the end of the cave (Table 1). The composition of the epigeous bryophyte communities changed more rapidly (ATR=5.97) (**ATR** = average turnover rate of species; Itow 1991) than did those of the other communities along the environmental gradients.

Table 1. Bryophytes on soil of Iwato-linjya, Minamitakaki, Nagasaki, Japan, showing position in the cave, up to 15 m. From Nakanishi 2002, with updated nomenclature.

Stand No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Cover degree (%)	40	60	60	80	80	70	80	80	90	80	100	90	100	100
Number of species	6	8	10	9	8	12	14	13	15	13	14	15	17	15
Distance from St. 1. (m)	0	1	2	3	4	5	6	7	8	9	10	11	12	13
Plagiomnium maximoviczii	12	22	22	22	33	22	22	22	12	12	12	+	+	+
Heteroscyphys planus	22	22	22	22	22	12	12	12	12	12	12	+	+	+
Eurhynchium savatieri	12	12	12	22	22	22	22	+2	22	+	+	+	+	+
Thuidium cymbifolium	+2	+2	+2	12	22	+2	·	·	·	·	·	·	·	·
Lophocolea minor	+	+2	+2	+2	+2	+2	·	·	·	·	·	·	·	·
Pellia endiviifolia	+	22	22	·	·	·	·	·	·	·	·	·	·	·
Heteroscyphus coalitus	·	12	12	12	·	·	·	·	·	·	·	·	·	·
Dumortiera hirsuta	·	11	11	12	·	22	33	33	33	·	·	·	·	·
Makinoa crispata	·	·	12	12	22	12	12	12	·	·	·	·	·	·
Ctenidium capillifolium	·	·	·	·	·	+	12	+2	33	·	·	·	·	·
Marchantia emarginata subsp. *tosana*	·	·	·	·	·	+	+	·	·	·	·	·	·	·
Taxiphyllum taxirameum	·	·	·	·	·	+	+	+	+	·	·	·	·	·
Mnium laevinerve	·	·	·	·	·	·	+	12	12	·	·	·	·	·
Conocephallum japonicum	·	·	·	·	·	·	12	12	12	33	33	33	+	+
Fissidens tosaensis	·	·	·	·	·	·	+	+	+	+2	12	12	·	+
Radula japonica	·	·	·	·	·	·	·	·	+	+2	+2	+2	+2	·
Bryum capillare	·	·	·	·	·	·	·	·	+	22	22	22	+2	+2
Fissidens crispulus	·	·	·	·	·	·	·	·	+	12	12	·	·	·
Brachythecium plumosum	·	·	·	·	·	·	·	·	·	·	22	22	22	33
Haplocladium microphyllum	·	·	·	·	·	·	·	·	·	·	12	12	22	22
Thamnobryum · *subseriatum*	·	·	·	·	·	·	·	·	·	·	·	12	12	12
Isothecium subdiversiforme	·	·	·	·	·	·	·	·	·	·	·	12	12	+2
Thuidium pristocalyx	·	·	·	·	·	·	·	·	·	·	·	·	22	22
Bazzania tridens	·	·	·	·	·	·	·	·	·	·	·	·	+2	·

Lowe *et al*. (2013) found that the bottom of a lava tube cave (Figure 32) in Hawai'i was covered by bryophytes surrounding a puddle.

Prior (1961) provided a short review of cave bryophyte studies. He noted that the bryophytes from the Luray Caverns (Figure 33) in Virginia, USA, were all known from nearby areas in Virginia. Furthermore, the same genera were known from caves in Europe. These Luray Cavern species included ***Amblystegium serpens*** (Figure 24-Figure 25) (only 1 location, but with capsules), ***Anomodon rostratus*** (Figure 34), ***Ptychostomum pseudotriquetrum*** var. ***bimum*** (= ***Bryum pseudotriquetrum*** var. **bimum**; dense mats on moist limestone; see Figure 35-Figure 36), ***Campylium hispidulum*** (with sporophytes at 3 of 8 locations; on moist limestone and silt; Figure 37), ***Tortula obtusifolia*** (1 large mat on wet limestone with 2 capsules; Figure 38-Figure 39), ***Eurhynchium hians*** (on wet limestone, abundant, 3 of 19 collections with abundant sporophytes; Figure 40), ***Fissidens bryoides*** (moist limestone at cave entrance; Figure 41-Figure 42), ***Funaria hygrometrica*** (with numerous capsules; Figure 43), ***Leptobryum pyriforme*** (with numerous capsules at 10 of its 18 sites; Figure 44-Figure 45), ***Leskea polycarpa*** (on wet limestone, at edge of underground lake; Figure 46-Figure 47).

Figure 32. Lava tube, Maui, Hawai'i. Photo by Dronepicr, through Creative Commons.

Figure 33. Luray Cavern, Virginia, USA. Photo by Alejocrux, through public domain.

Figure 34. ***Anomodon rostratus*** dry, with capsules, a species known from caves in several locations, including Luray Caverns. Photo by Bob Klips, with permission.

Figure 35. ***Ptychostomum pseudotriquetrum***, a species forming dense mats on limestone in the Luray Cavern. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 36. ***Ptychostomum pseudotriquetrum*** stem showing rhizoids and decurrent leaf bases. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

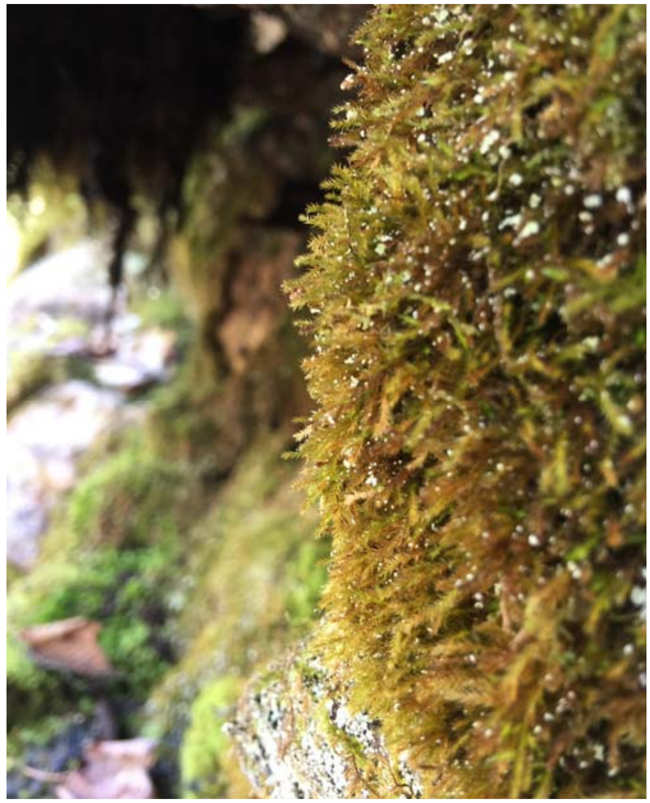

Figure 37. ***Campylium hispidulum*** on a vertical limestone wall, a species that occurs in Luray Caverns. Photo by Tom Neily, through Creative Commons.

Figure 38. ***Tortula obtusifolia*** on rock, a species that occurs in the Luray Caverns. Photo by Bob Klips, with permission.

Figure 39. ***Tortula obtusifolia*** on rock. Photo by Paul Wilson, with permission.

Figure 40. ***Eurhynchium hians***, a species that occurs in Luray Caverns. Photo by Bob Klips, with permission.

Figure 41. ***Fissidens bryoides*** with capsules, a species that occurs in the Luray Caverns. Photo courtesy of Donna Bennett.

Figure 42. ***Fissidens bryoides*** with retained protonemata. Photo by Dick Haaksma, with permission.

Figure 43. ***Funaria hygrometrica***, a species of low-competition habitats, usually exposed, that is known from Luray Caverns. Photo by Janice Glime.

Figure 44. ***Leptobryum pyriforme*** with capsules on rock, a species that occurs in Luray Caverns. Photo by Michael Lüth, with permission.

Figure 45. ***Leptobryum pyriforme*** stems. Photo by Štěpán Koval, with permission.

Figure 46. ***Leskea polycarpa*** in Denmark, a species that is known from Luray Caverns. Photo by Weblar, through Creative Commons.

Figure 47. ***Leskea polycarpa***. Photo from Snappy Goat, through public domain.

Numbers of Species

Sguazzin and Polli (2011) reported 7 liverworts and 25 mosses from a cave on Mount Saint Michael off the coast of Cornwall. Zhang and Pentecost (2002) found 65 bryophyte taxa in 41 genera and 20 families in various karst caves in England (from 1998 to 2000) and Pentecost and Zhang (2001) found 4 algae, 3 lichens, 47 bryophytes, 4 ferns, and 1 angiosperm in just the Scoska Cave (Figure 17), North Yorkshire, UK, the most species-rich cave known in Britain to date. All but nine of these species were known from other European caves. Castello and Strazzaboschi (2013) reported 9 liverworts and 33 mosses from Della Grotta Dell'orso (Figure 48) in Italy. In Sicily, Puglisi *et al*. (2019) identified 20 liverworts, 3 hornworts, and 113 mosses in 28 caves. Rajczy (1979) found only 2 liverworts and 14 mosses at the upper entrance of Cave Perama (Figure 49) in Greece, but only 7 mosses were found within the cave. Rajczy *et al*. (1986) reported 11 algae and 7 bryophyte taxa in one cave and 38 alga, 12 moss, 1 fern, and 1 angiosperm in another in the Bükk Mountains of Hungary (Figure 50).

Figure 48. Cave Grotta Dell'orso, Italy, a karst cave. Photo by Tiesse, through Creative Commons.

Figure 49. Cave interior, Perama Cave, Greece. Photo from <7toucans.com>, through Creative Commons.

Figure 50. Cave entrance, Balla-barlang Cave, Bükk Mountains, Hungary. Photo by Czina Tivadar, through Creative Commons.

Jedrejko and Ziober (1992) found 72 bryophyte species, including 10 liverworts, 59 mosses, and 3 mosses that remained unidentified in the Krackòw-Wieluñ Upland caves of Poland. Of these, 50% developed only in full access of light, with numbers of species diminishing with distance from the entrance.

In China, Zhang *et al*. (1996a, b) reported 59 bryophyte species in 43 genera from the karst caves of Huangguoshu. Zhang *et al*. (2005) found 28 species in only 18 genera in karst caves of the Guilin area, China (Figure 14).

Ammons (1933) found 46 moss and 44 liverwort species at the entrance of McKinney's Cave, West Virginia, USA. She noted the absence of ***Reboulia*** (Figure 51) and ***Eucladium*** (Figure 9-Figure 10). Within the cave she reported 31 liverwort species and 34 moss species, including 3 ***Sphagnum*** (Figure 69) species.

Figure 51. ***Reboulia hemispherica***, a cave dweller that was absent in McKinney's Cave, West Virginia, USA. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission from Russ Kleinman and Karen Blisard.

Species

Mason-Williams and Benson-Evans (1967) described some of the ecological requirements of cave bryophytes in South Wales. Most of the caves visited had mesophilous forms with a *p*H tolerance of 4.8-7.0. These included ***Amblystegium serpens*** (Figure 24-Figure 25), ***Bryoerythrophyllum recurvirostrum*** (Figure 52-Figure 53), ***Thamnobryum alopecurum*** (Figure 54-Figure 55), ***Fissidens bryoides*** (Figure 41-Figure 42), ***F. taxifolius*** (Figure 56-Figure 57), ***Ctenidium molluscum*** (Figure 58), ***Rhizomnium punctatum*** (Figure 59). Few acid-tolerant forms occurred: ***Polytrichum juniperinum*** (Figure 60-Figure 61), ***Pseudotaxiphyllum elegans*** (Figure 62-Figure 64), ***Hypnum cupressiforme*** (Figure 65-Figure 66), ***Blindia acuta*** (Figure 67-Figure 68), ***Sphagnum subnitens*** (Figure 69). The mesophilic liverworts ***Pellia epiphylla*** (Figure 70-Figure 71) and ***Plagiochila asplenioides*** (Figure 72) were also present at most sites. Surprisingly, to me at least, ***Pellia endiviifolia*** (Figure 73) and ***Conocephalum conicum*** (Figure 74-Figure 75) were found less frequently. Mason-Williams and Benson-Evans (1958) considered ***Pseudotaxiphyllum elegans*** to be one of the most shade-tolerant mosses in acid sites.

Figure 52. ***Bryoerythrophyllum recurvirostrum*** on rock wall. Photo by Calum McLennan, through Creative Commons.

Figure 53. ***Bryoerythrophyllum recurvirostrum*** showing red bases. Photo by Christian Berg, through Creative Commons.

Figure 54. ***Thamnobryum alopecurum*** in limestone cave at Traeth Glaslyn Nature Reserve, Wales. Photo by Janice Glime.

Figure 55. ***Thamnobryum alopecurum***. Photo by David T. Holyoak, with permission.

Figure 56. ***Fissidens taxifolius***, a species that occurs in caves in South Wales. Photo by David T. Holyoak, with permission.

Figure 57. ***Fissidens taxifolius***. Photo by Hermann Schachner, through Creative Commons.

Figure 58. ***Ctenidium molluscum***, a mesophilous species from South Wales caves. Photo by Hermann Schachner, through Creative Commons.

Figure 59. ***Rhizomnium punctatum***, a mesophilous species from South Wales caves. Photo by Bob Klips, with permission.

Figure 60. ***Polytrichum juniperinum*** on rock, a mesophilous species in South Wales caves. Photo by Robbie Hannawacker, through public domain.

Figure 61. ***Polytrichum juniperinum*** showing leaves with edges rolled over (**arrow**) and calyptra over young sporophyte. Photo from Botany Website, UBC, with permission.

Figure 62. ***Pseudotaxiphyllum elegans*** on wall, a species that grows in South Wales caves. Photo by Hermann Schachner, through Creative Commons.

Figure 63. ***Pseudotaxiphyllum elegans*** showing growth form. Photo from Botany Website, UBC, with permission.

Figure 64. ***Pseudotaxiphyllum elegans*** asexual propagules produced in winter, a typical means of propagation in caves. Photo from Botany Website, UBC, with permission.

Figure 65. ***Hypnum cupressiforme*** on rock in a minicave. Photo by Fabio Clanferoni, through Creative Commons.

Figure 66. ***Hypnum cupressiforme*** with capsules. Photo by Aconcagua, through Creative Commons.

Figure 67. ***Blindia acuta*** on rock, a species that occurs in caves in South Wales. Photo by David T. Holyoak, with permission.

Figure 68. ***Blindia acuta*** with capsules, on rock. Photo by David T. Holyoak, with permission.

Figure 69. ***Sphagnum subnitens*** with capsules, a species that can occur in caves in South Wales. Photo by David T. Holyoak, with permission.

Figure 70. ***Pellia epiphylla***, a species that occurs in caves in South Wales. Photo by Frank Vincentz, through Creative Commons.

Figure 71. ***Pellia epiphylla*** with capsules. Photo by Hermann Schachner, through Creative Commons.

Figure 72. ***Plagiochila asplenioides***, a species that occurs in caves in South Wales. Photo by J. C. Schou, with permission.

Figure 73. ***Pellia endiviifolia*** with capsules, a species that occurs in caves in South Wales. Photo by Hermann Schachner, through Creative Commons.

Figure 74. ***Conocephalum conicum*** on cave roof. Photo by Allen Norcross, with permission.

Figure 75. ***Conocephalum conicum***, a species that occurs in caves in South Wales. Photo by Lairich Rig, through Creative Commons.

In North America, Maheu (1926) explored Mammoth Cave (Figure 76) and two others in Kentucky, USA. The bryophytes in all three caves were identical: the mosses ***Anomodon attenuatus*** (Figure 77-Figure 78), ***A. rostratus*** (Figure 34), ***Brachythecium rivulare*** (Figure 79), ***Eurhynchium praelongum*** (Figure 2-Figure 3), ***Gymnostomum calcareum*** (Figure 80-Figure 81), and ***Plagiomnium rostratum*** (Figure 82), and the thallose liverwort ***Marchantia polymorpha*** (Figure 83). Maheu described the plants as etiolated, and lacking sporophytes. ***Marchantia polymorpha*** occurred in the least light but did not exhibit the morphological changes seen in the other species.

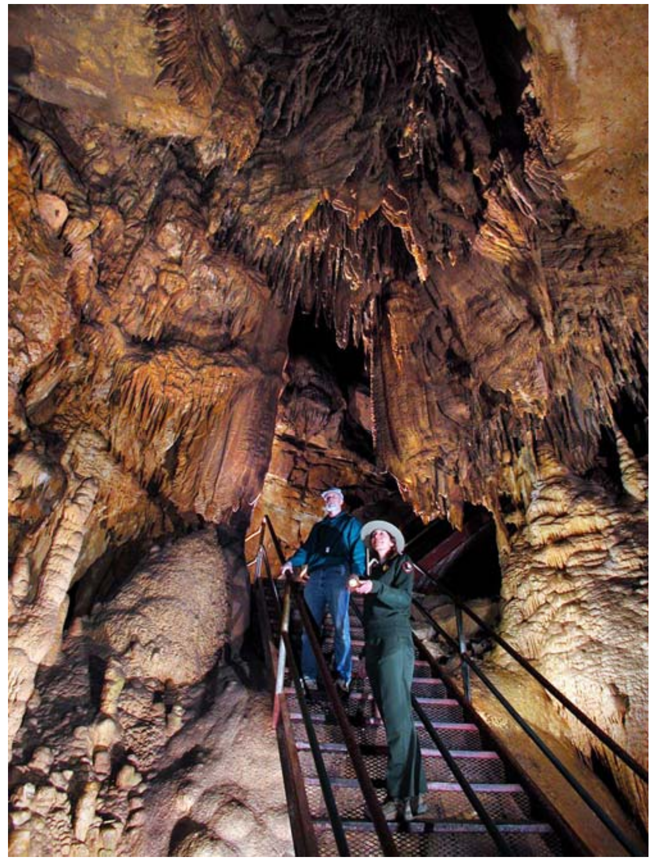

Figure 76. Mammoth Cave National Park. Photo through public domain.

Figure 77. ***Anomodon attenuatus***, a species that occurs in Mammoth Cave. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 78. ***Anomodon attenuatus*** wet. Photo by Hermann Schachner, through Creative Commons.

Figure 79. ***Brachythecium rivulare***, a species that occurs in Mammoth Cave, Kentucky. Photo by Hugues Tinguy, with permission.

Figure 80. ***Gymnostomum calcareum*** on rock, a species that occurs in Mammoth Cave. Photo by L. Jensen, University of Auckland, with online permission.

Figure 81. ***Gymnostomum calcareum***. Photo by L. Jensen, University of Auckland, with online permission.

Figure 82. ***Plagiomnium rostratum***, a species that occurs in Mammoth Cave. Photo by Hermann Schachner, through Creative Commons.

Figure 83. ***Marchantia polymorpha***, a species that occurs in Mammoth Cave. The cups contain gemmae that are a primary means of dispersal in caves. Photo by Jan-Peter Frahm, with permission.

Puglisi *et al*. (2019) found the mosses ***Amphidium mougeotii*** (Figure 84-Figure 85), ***Isopterygiopsis pulchella*** (Figure 28), ***Rhynchostegiella tenella*** (Figure 86-Figure 87), and ***Thamnobryum alopecurum*** (Figure 54-Figure 55), to be well adapted to the cave environment.

Figure 84. ***Amphidium mougeotii*** on rock, a species that is well adapted to cave life.. Photo by Hugues Tinguy, with permission.

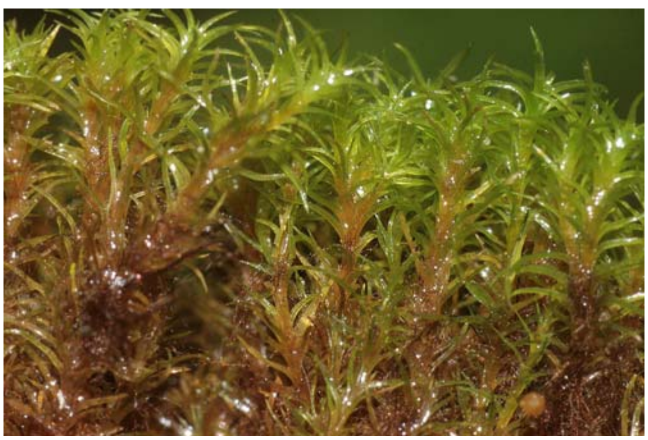

Figure 85. ***Amphidium mougeotii***, Photo by Hermann Schachner, through Creative Commons.

Figure 86. ***Rhynchostegiella tenella*** on a rock ceiling. Photo by Andy Hodgson, with permission.

Figure 87. ***Rhynchostegiella tenella*** with many sporophytes, on rock. Photo by Michael Lüth, with permission.

Among the 17 bryophyte species in three Hungarian caves (*e.g.* Figure 6), the most common included ***Pellia endiviifolia*** (Figure 73), ***Amblystegium serpens*** (Figure 24-Figure 25), ***Bryum*** sp. (see Figure 88), ***Encalypta vulgaris*** (Figure 89), ***Eucladium verticillatum*** (Figure 9-Figure 10), ***Eurhynchium schleicheri*** (Figure 90), ***Fissidens taxifolius*** (Figure 56-Figure 57), ***Plagiomnium cuspidatum*** (Figure 91), ***Rhynchostegiella tenella*** (Figure 86-Figure 87), and ***Rhynchostegium murale*** (Figure 92) (Buczkó & Rajczy 1989).

Figure 88. ***Bryum capillare***; a species of ***Bryum*** is common in some Hungarian caves. Photo by Andy Hodgson, with permission.

Figure 89. ***Encalypta vulgaris*** with capsules, on rock, a species known from Hungarian caves. Photo by Kai Vellak, through Creative Commons.

Figure 90. ***Eurhynchium schleicheri***, a species known from Hungarian caves. Photo by Hugues Tinguy, with permission.

Figure 91. ***Plagiomnium cuspidatum***, a species known from Hungarian caves. Photo by Bob Klips, with permission.

Figure 92. ***Rhynchostegium murale***, a species known from Hungarian caves. Photo by Michael Lüth, with permission.

The flora of a very wet rock cave in Corsica, France, however, had a different array of species (Sotiaux *et al*. 2007). These included ***Aneura maxima*** (Figure 93-Figure 95), ***Lophocolea fragrans*** (Figure 96-Figure 97), and ***Riccardia multifida*** (Figure 98) near a stream in the cave; ***Plagiothecium cavifolium*** (Figure 99) occurred in a rock cave along a stream. ***Neckera menziesii*** (Figure 100) occurred in microcaves in schist rocks. ***Gymnostomum aeruginosum*** (Figure 101-Figure 102) was more typical of caves, occurring in a rock cave.

Figure 93. ***Aneura maxima*** habitat in ravine in Norway, a habitat shaded by a deep cut in the rock. Photo by Jan-Peter Frahm, with permission.

Figure 94. ***Aneura maxima***, a species known from near a stream in a rock cave in Corsica. Photo by Jan-Peter Frahm, with permission.

Figure 95. ***Aneura maxima*** branch of thallus. Photo by Hugues Tinguy, with permission.

Figure 96. ***Lophocolea fragrans***, a species known from near a stream in a rock cave in Corsica. Photo by David T. Holyoak, with permission.

Figure 97. ***Lophocolea fragrans*** branch. Photo by George G., through Creative Commons.

Figure 98. ***Riccardia multifida***, a species known from near a stream in a rock cave in Corsica. Photo by Hermann Schachner, through Creative Commons.

Figure 99. ***Plagiothecium cavifolium***, a species that occurs in a rock cave along a stream in Corsica. Photo by Hermann Schachner, through Creative Commons.

Figure 100. ***Neckera menziesii***, a species that occurs in a rock cave along a stream in Corsica. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Figure 101. ***Gymnostomum aeruginosum*** on limestone rock. Photo by Bob Klips, with permission.

Figure 102. ***Gymnostomum aeruginosum*** with capsules and ***Nostoc***, a species that occurs in a rock cave along a stream in Corsica. Photo by Hermann Schachner, through Creative Commons.

Rajczy *et al*. (1986) were unable to relocate four cave species in a Hungarian cave. One of these was a typical cave dweller, ***Eucladium verticillatum*** (Figure 9-Figure 10), which may have been destroyed by excavations. ***Rhynchostegiella tenella*** (Figure 86-Figure 87), a typical cave moss, was found as new.

Tanaka *et al*. (2001) discussed the mosses of a limestone cave in Kyushi, Japan.

Zonation

The steepest and most evident zonation pattern in caves is related to light intensity. Pentecost and Zhang (2001) found that species richness exhibited an irregular decline from the entrance (12% relative irradiance compared to open sky) to 0.004% relative irradiance at 34 m depth. Bryophytes occurred at 0-16 m in light that declined to 0.2% relative irradiance. Differences in substrate characters and surface moisture caused the irregularities in bryophyte decline with distance.

Zhang *et al*. (1996b) identified 68 communities of bryophytes in 7 karst caves in the Huangguoshu area of China. They classified the ecological distribution of the bryophytes as limestone and dolomite, limestone soil, and cave tufa.

Hajdu (1977) considered the zones to be cave entrances, area around lights, and darkness. Hajdu considered the cave-dwelling plants to have extremely low ecological requirements. Nevertheless, there seems to be no species that is restricted to cave environments.

More commonly, caves are divided into three major zones based on light intensity. These are **entrance** (Figure 1), **twilight**, and **dark** zone (World Atlas 2021). But perhaps this is not the most appropriate classification for photosynthetic organisms since they are unable to occupy the third zone.

Hajdu (1977) described the vegetation changes within the cave from the most harsh habitat to the most favorable. In that order, they progressed from blue-green bacteria to green algae and diatoms to mosses and finally in the best conditions to ferns. But he noted that the larger plants will eventually outgrow the smaller ones, thus causing mosses to replace the algae. Fiol (1995) examined bryophytes at cavity entrances in Mallorca (Figure 27) and described different regions, especially in shafts.

Uniyal *et al*. (2007) described the zonation seen in an array of caves as a result of decreasing light. They found that the liverworts ***Plagiochasma appendiculatum*** (Figure 103-Figure 104), ***Plagiochasma pterospermum***, ***Plagiochila chinensis*** (Figure 105), ***Porella densifolia*** (see Figure 106), and ***Targionia hypophylla*** (Figure 107-Figure 108), and mosses ***Anomodon rugelii*** (Figure 109-Figure 110), ***Plagiothecium neckeroideum*** (Figure 111-Figure 112), and ***Pelekium versicolor*** (Figure 113) occur at the twilight zone near the cave entrance. ***Funaria*** (Figure 43) and ***Cyathodium*** (Figure 115) invade the bare substrate further into the cave. ***Cryptomitrium himalayense*** (see Figure 114), ***Cyathodium tuberosum*** (Figure 115), ***Lejeunea*** (Figure 116), ***Fissidens*** (Figure 56-Figure 57), ***Isopterygium albescens*** (see Figure 117), and ***Plagiothecium neckeroideum*** occur on rock ledges in the cave interior. Even further from the entrance light one might find ***Cryptomitrium***. ***Stephensoniella brevipedunculata*** (Figure 118) and ***Hymenostylium recurvirostrum*** (Figure 119-Figure 120) may grow together in deep-shaded caves (Tewari *et al*. 1994).

Figure 103. ***Plagiochasma appendiculatum***, a species of the twilight zone, but near the cave entrance. Photo by Michael Lüth, with permission.

Figure 104. ***Plagiochasma appendiculatum*** with archegoniophores. Photo by Michael Lüth, with permission.

Figure 105. ***Plagiochila chinensis***, a species of the twilight zone, but near the cave entrance. Photo by Yang Jia-Dong, through Creative Commons.

Figure 106. ***Porella obtusata***; ***Porella densifolia*** is a species of the twilight zone, but near the cave entrance. Photo by Michael Lüth, with permission.

Figure 107. ***Targionia hypophylla*** on rock, a species of the twilight zone, but near the cave entrance. Photo by Malcolm Storey, DiscoverLife.com, with online permission.

Figure 108. ***Targionia hypophylla*** showing purplish pouches beneath thallus. Photo by Ken Ichi Ueda, through Creative Commons.

Figure 109. ***Anomodon rugelii*** dry, a species of the cave twilight zone, but near the cave entrance. Photo by Hugues Tinguy, with permission.

Figure 110. ***Anomodon rugelii*** wet. Photo by Hermann Schachner, through Creative Commons.

Figure 111. ***Plagiothecium neckeroideum***, a species of rock ledges in the cave interior. Photo by Taiwan Life Encyclopedia, through Creative Commons.

Figure 112. ***Plagiothecium neckeroideum***. Photo by David Long, with permission.

Figure 113. ***Pelekium versicolor***, a species able to live in the twilight zone. Photo by John C. Brinda, through Creative Commons.

Figure 114. ***Cryptomitrium tenerum***; ***Cryptomitrium teneriffae*** is a species able to live in the twilight zone of caves. Photo by Sachacari, through Creative Commons.

Figure 115. ***Cyathodium tuberosum***, a species of the twilight zone, but near the cave entrance. Photo by Silvia Pressel and Jeff Duckett, with permission.

Figure 116. ***Lejeunea lamacerina***; a species of ***Lejeunea*** occurs on rock ledges in the cave interior. Photo by Andrew Hodgson, with permission.

Figure 117. ***Isopterygium tenerum***, a species of rock ledges in the cave interior. Photo from Biopix, through Creative Commons.

Figure 118. ***Stephensoniella brevipedunculata***, a species able to grow in the deeper shade of caves. Photo by Anil Sharma, permission pending.

Figure 119. ***Hymenostylium recurvirostrum*** on cliff face, a species able to grow in the deeper shade of caves. Photo by Bob Klips, with permission.

Figure 120. ***Hymenostylium recurvirostrum*** with capsules. Photo by Paul Wilson, with permission.

Some mosses don't seem to be as sensitive to the diminishing light. Ren *et al*. (2021) reported that among 20 bryophyte species in six karst caves in southern China, ***Eurhynchium hians*** (Figure 40), ***Fissidens teysmannianus*** (Figure 121), and ***Taxiphyllum taxirameum*** (Figure 122-Figure 123) occur in entrance plots, intermediate plots, and deep plots, the latter two having different degrees of light in the twilight zone.

Figure 121. ***Fissidens teysmannianus*** on rock ledge, a species that occurs in entrance, intermediate, and deep locations in Chinese caves. Photo by Wuchan Kwan, permission pending.

Figure 122. ***Taxiphyllum taxirameum*** in Ohio, a species that occurs in entrance, intermediate, and deep locations in Chinese caves. Photo by Bob Klips, with permission.

Figure 123. ***Taxiphyllum taxirameum*** with capsule. Photo by Bob Klips, with permission.

Li *et al.* (2019) identified three zones for liverworts in four caves in the Guizhou Province, China: middle-depth cave, mainly of ***Cyathodium smaragdinum*** (Figure 124) + ***Pellia endiviifolia*** (Figure 73) + ***Riccia fluitans*** (Figure 125); lower-middle-depth cave, mainly of ***Cyathodium smaragdinum*** + ***Riccia fluitans***; bottom cave, mainly including ***Pellia endiviifolia*** + ***Conocephalum japonicum*** (Figure 126) + ***Dumortiera hirsuta*** (Figure 127). These caves tended to have 1-2 dominant liverwort species. The diversity in both vertical and horizontal distances from the entrance were affected by the gradient variation of temperature, humidity, and illumination.

Figure 124. ***Cyathodium smaragdinum*** on rock, a species that occurs at a middle depth in caves of Guizhou Province, China. Photo through Creative Commons.

Figure 125. ***Riccia fluitans***, a species that occurs at a middle depth in caves of Guizhou Province, China. Photo by Ralf Wagner, with permission.

Figure 126. ***Conocephalum japonicum***, a species that occurs at the bottom of caves of Guizhou Province, China. Photo by David Long, with permission.

Figure 127. ***Dumortiera hirsuta***, a species that occurs at the bottom of caves of Guizhou Province, China. Photo by Michael Lüth, with permission.

Summary

Among the cave bryophyte flora, ***Eurhynchium*** often is represented by the most species, often occurring in very low light (200 lux). But light limitation limits the number of bryophyte species able to grow at any distance into the cave, creating zones known as **entrance**, **twilight**, and **dark**. Algae and **Cyanobacteria** typically comprise more species than do bryophytes; liverworts are usually few in species number. Light conditions create a zonation pattern of ferns in the best conditions, to moss, to algae, and in the most distant photic zone, the **Cyanobacteria**. Disturbance further limits the species richness. And as one might expect, richness decreases with distance from the cave entrance. Nevertheless, the cave bryophyte flora tends to be unique, with some species known only from caves in some regions. Caves serve as refugia in many geographic regions.

There are many studies on the cave flora in Europe and Asia, but studies occur on all the continents. ***Eucladium verticillatum*** occurs frequently on both sides of the Atlantic and may contribute to the formation of stalactites in limestone caves. Likewise, ***Amblystegium serpens*** is common is a wide range of caves and locations. The Australian cave species tend to be species from arid and semiarid habitats.

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