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CHAPTER 18-3
CAVES – ZONES OF BRYOPHYTE FLORA

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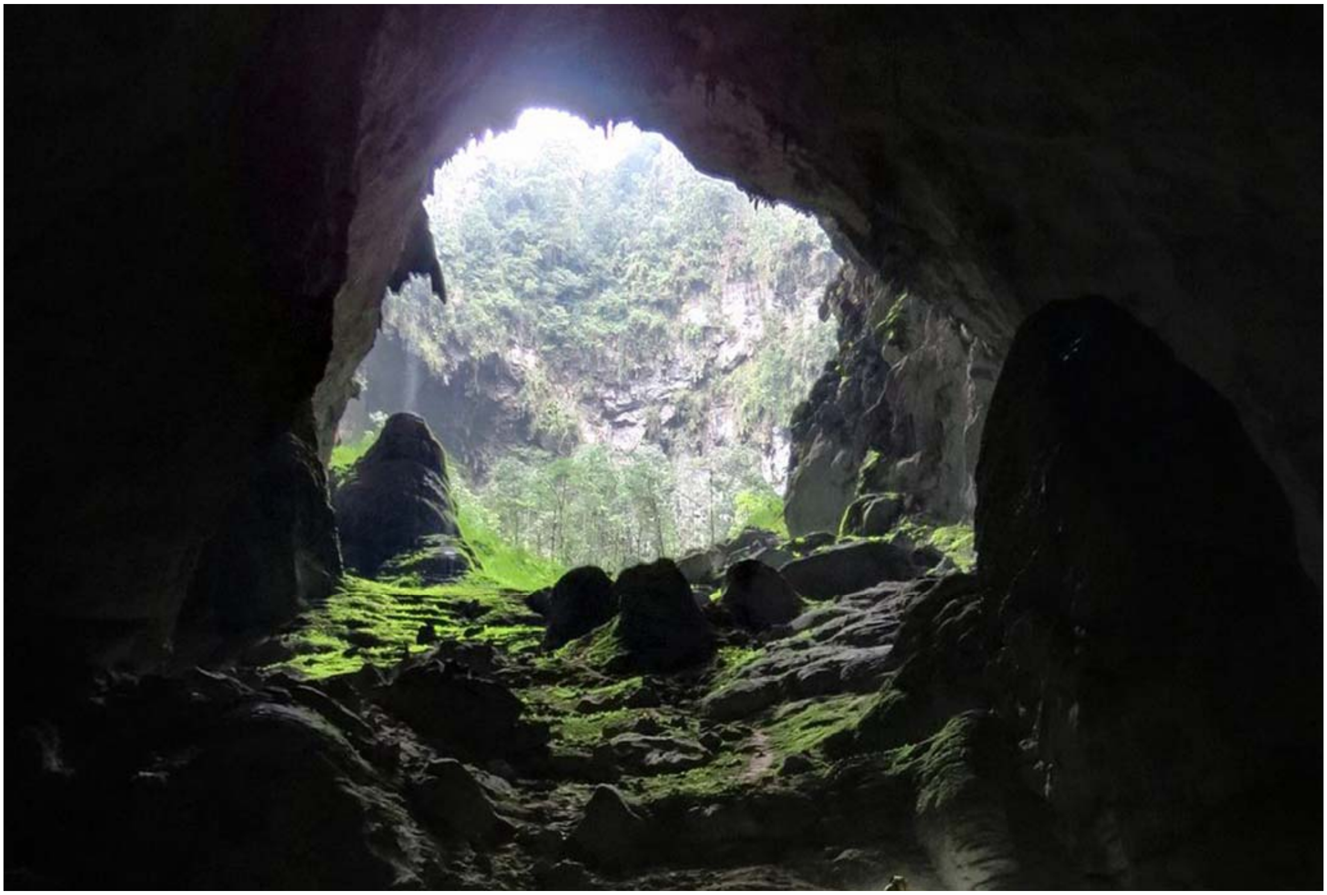

Figure 1. View of the twilight zone and entrance light at Son Doong Cave, Vietnam. Photo by Doug Knuth, through Creative Commons.

Habitat Differences

Cave Mouth Area

The area near the opening of the cave (Figure 1) can often have its own flora, different from the surrounding area and different from the cave entrance. These floral differences result from exposed rock of the cave, cool air emitted from the cave, and differing moisture conditions. Depending on the site, it might be drier due to exposure, but it can also be moister from air emitted by the cave. This is particularly true of caves with additional openings elsewhere among the rocks.

Conard (1938) found ***Pohlia elongata*** (Figure 2) with capsules and ***Pohlia proligera*** (Figure 3) with propagules around a cave mouth near Au Train, Michigan, USA. Capsules are typically uncommon within caves, but conditions of light and moisture, coupled with seasonal changes, can support the production of sporophytes near the entrance.

Figure 2. ***Pohlia elongata*** capsules, a species found with capsules around a cave mouth in Michigan, USA. Photo by David T. Holyoak, with permission.

Figure 3. ***Pohlia proligera*** with numerous propagules among the leaves, a species that occurs around a cave mouth in Michigan, USA. Photo by Hermann Schachner, through Creative Commons.

Areas near entrances can even support species unique in the area. For example, Aziz (2011) reported ***Tortula truncata*** (Figure 4) in rock fissures and at the mouth of Baston cave, a new species for Iraq.

Figure 4. ***Tortula truncata*** with numerous capsules, a species found for the first time in Iraq around a cave entrance. Photo from Botany Website, UBC, with permission.

Salamah *et al*. (2019) found six bryophyte species in the area near the Selarong Cave, Indonesia. These were ***Hyophila involuta*** (Figure 5-Figure 6), ***Barbula consanguinea*** (see Figure 7), ***Bryum erythropus*** (see Figure 123), ***Weissia controversa*** (Figure 8-Figure 9), ***Preissia*** sp. (Figure 10-Figure 11), and ***Vesicularia dubyana*** (Figure 12).

Figure 5. ***Hyophila involuta*** dry, a species that occurs in the area near a cave in Indonesia. Photo by Wayne Lampa, through Creative Commons.

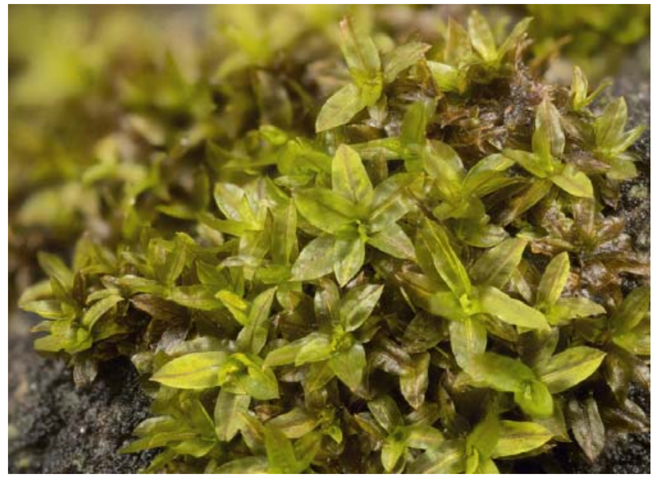

Figure 6. ***Hyophila involuta*** wet. Photo by Bob Klips, with permission.

Figure 7. ***Barbula unguiculata*** with capsules on wall, a species that occurs in the area near a cave in Indonesia. Photo by Susan Marley, through Creative Commons.

Figure 8. ***Weissia controversa*** on rock, a species that occurs in the area near a cave in Indonesia. Photo by Andrew Hodgson, with permission.

Figure 9. ***Weissia controversa*** with capsules. Photo by Hermann Schachner, through Commons.

Figure 10. ***Preissia quadrata***, in a genus that occurs in the area near a cave in Indonesia. Photo by Hermann Schachner, through Creative Commons.

Figure 11. ***Preissia quadrata*** with mature archegoniophores and dying thallus. Photo by Jiří Kameníček (BioLib, Obázek), with permission.

Figure 12. ***Vesicularia dubyana***, a species that occurs in the area near a cave in Indonesia. Photo by Tan Sze Wei, Aquamoss website <www.aquamoss.net>, with permission.

Castello and Strazzaboschi (2013) noted that the cave entrance of Grotta dell'Orso (Figure 13), a cave of the karst area of Trieste, Italy, is more bryologically rich than the area near the cave mouth despite the smooth, rocky walls and poor light in the entrance. Outside the cave most of the plants are concentrated in the first 50 cm above the ground where they experience higher humidity, particularly in small cornices, ravines, and rock irregularities. ***Conocephalum conicum*** (Figure 14) forms large colonies on the ground near the entrance.

Figure 13. Grotta dell'orso, Italy, cave mouth. Photo by Tiesse, through Creative Commons.

Figure 14. ***Conocephalum conicum*** males, a species that forms large colonies in the area near the entrance of Grotta dell'orso, Italy. Photo by Janice Glime.

Castello and Strazzaboschi (2013) described the exterior of the Della Grotta Dell'orso Cave (Figure 13). The exterior near the entrance had a northern exposure with intense dripping. They found that these conditions permitted growth of numerous bryophytes that are typical of the cave interiors, particularly from the shady, damp walls at the entrance. However, in the darker interior, few species are present, and only develop to about 10 m into the cave.

Puglisi *et al*. (2018) recognized a number of communities in the entrance and twilight area of Sicilian caves. In the lava caves, these included the liverwort species of ***Plagiochasma rupestre*** (Figure 15-Figure 16), ***Riccia glauca*** (Figure 17-Figure 18), and ***Targionia hypophylla*** (Figure 19); hornwort ***Anthoceros crispatus*** (see Figure 20); and moss species of ***Amphidium mougeotii*** (Figure 21-Figure 22), ***Bartramia ithyphylla*** (Figure 23), ***Brachythecium velutinum*** (Figure 24-Figure 25), ***Pohlia annotina*** (Figure 26-Figure 27), ***Pohlia cruda*** (Figure 28), ***Rhabdoweisia fugax*** (Figure 29), ***Rhynchostegiella tenella*** (Figure 30), and ***Timmia bavarica*** (Figure 31). In the karst caves they found ***Eucladium verticillatum*** (Figure 32-Figure 33), ***Thamnobryum alopecurum*** (Figure 34), ***Timmiella barbuloides*** (see Figure 35), and ***Weissia controversa*** (Figure 8-Figure 9).

Figure 15. ***Plagiochasma rupestre*** on rock, a species that occurs in lava caves. Photo by Rory Hodd, with permission.

Figure 16. ***Plagiochasma rupestre*** with archegoniophores. Photo by Valter Jacinto, through Creative Commons.

Figure 17. ***Riccia glauca*** on soil, a species that occurs in lava caves. Photo by Bernd Haynold, through Creative Commons.

Figure 18. ***Riccia glauca***. Photo by Štěpán Koval, with permission.

Figure 19. ***Targionia hypophylla***, a species that occurs in lava caves in Sicily. Photo by Luis Fernández García, through Creative Commons.

Figure 20. ***Anthoceros*** sp.; ***Anthoceros crispatus*** occurs in the entrance and twilight area of Sicilian lava caves. Photo from USFWS, through Creative Commons.

Figure 21. ***Amphidium mougeotii*** on rock wall with snow, a species that occurs in the entrance and twilight area of Sicilian lava caves. Photo by Tuomo Kuitunen <luopioistenkasvisto.fi.>, with permission.

Figure 22. ***Amphidium mougeotii***. Photo from Northern Forest Atlas, with permission through Jerry Jenkins.

Figure 23. ***Bartramia ithyphylla*** with capsules on rock, a species that occurs in lava caves. Photo by Štěpán Koval, with permission.

Figure 24. ***Brachythecium velutinum*** among rocks, a species that occurs in lava caves. Photo by Michael Lüth, with permission.

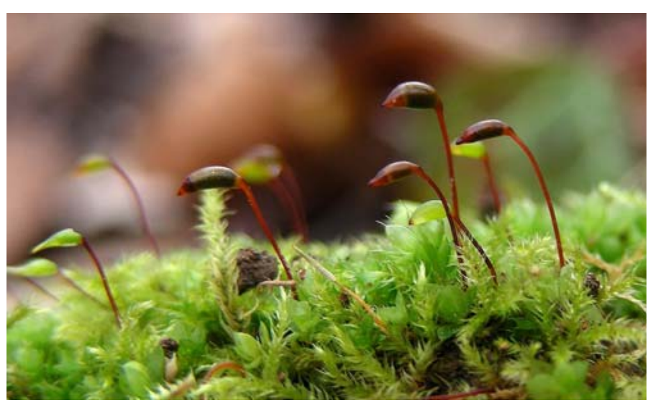

Figure 25. ***Brachythecium velutinum***. Photo by Michael Lüth, with permission.

Figure 26. ***Pohlia annotina*** among rocks, a species that occurs in lava caves. Photo by Hermann Schachner, through Creative Commons.

Figure 27. ***Pohlia annotina*** with bulbils, a common means of reproduction in caves. Photo by Hermann Schachner, through Creative Commons.

Figure 28. ***Pohlia cruda*** on rock, a species that occurs in lava caves. Photo by Štěpán Koval, with permission.

Figure 29. ***Rhabdoweisia crispata*** shaded at rock base, a species that occurs in lava caves. Photo by Tuomo Kuitunen <luopioistenkasvisto.fi.>, with permission.

Figure 30. ***Rhynchostegiella tenella*** with capsules, a species that occurs in the entrance and twilight area of Sicilian lava caves. Photo by Michael Lüth, with permission.

Figure 31. ***Timmia bavarica***, a species that occurs in lava caves. Photo by Štěpán Koval, with permission.

Figure 32. ***Eucladium verticillatum*** habitat or rock cliff face, a species that occurs in the karst caves of Sicily. Photo by Dick Haaksma, with permission.

Figure 33. ***Eucladium verticillatum*** with mite. Photo by Barry Stewart, with permission.

Figure 34. ***Thamnobryum alopecurum***, a species that occurs in the karst caves of Sicily. Photo by Michael Lüth, with permission.

Figure 35. ***Timmiella*** sp.; ***Timmiella barbuloides*** occurs in the karst caves of Sicily. Photo by Ken-Ichi Ueda, through Creative Commons.

The cave mouth can influence the vegetation near the entrance due to moist and cool air drafts emanating from the cave. Dalton (1995) found ***Seligeria cardotii*** (see Figure 36) as a new record for Tasmania on a moist calcareous rock face that was overhanging the entrance to a small cave. The moist conditions of the habitat were attributed to the limestone cave entrance and supported a lush bryophyte and fern flora there.

Figure 36. ***Seligeria*** sp.; ***Seligeria cardotii*** occurs in Tasmania on a moist calcareous rock face overhanging the entrance to a small cave. Photo by Bob Klips, with permission.

Gabriel *et al.* (2011) reported a number of bryophyte species that occurred both in the cave entrances and in the native forest in the Azores (Figure 37): ***Cyclodictyon laetevirens*** (Figure 38), ***Plagiochila longispina*** (Figure 39), ***Plagiothecium nemorale*** (Figure 40), ***Tetrastichium virens*** (Figure 41), and others.

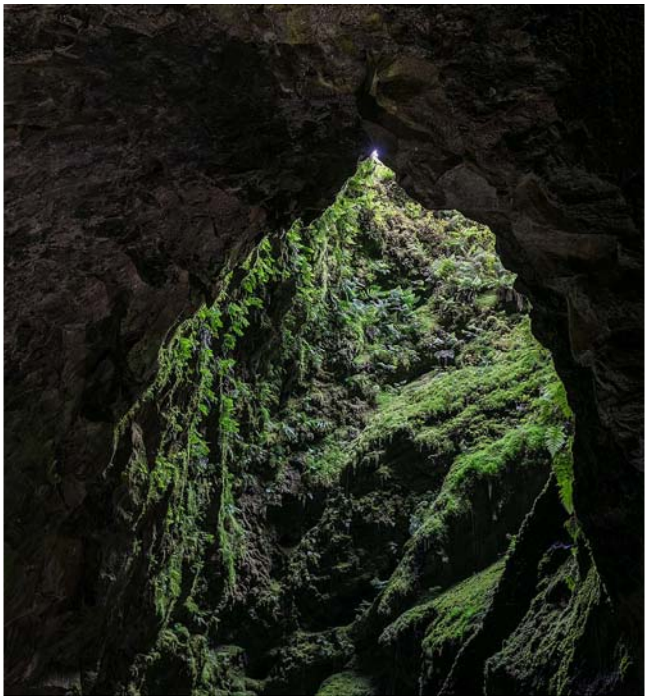

Figure 37. Cave entrance in the Azores. Photo by Diego Delso, through Creative Commons.

Figure 38. ***Cyclodictyon laetevirens***, a species that occurs in both cave entrances and in the native forest in the Azores. Photo by Sean Edwards, with permission.

Figure 39. ***Plagiochila longispina***, a species that occurs in both cave entrances and in the native forest in the Azores. Photo by Jan-Peter Frahm, with permission.

Figure 40. ***Plagiothecium nemorale***, a species that occurs in both cave entrances and in the native forest in the Azores. Photo by Hermann Schachner, through Creative Commons.

Figure 41. ***Tetrastichium virens*** with capsule, a species that occurs in both cave entrances and in the native forest in the Azores. Photo by Michael Lüth, with permission.

What seems to be lacking is a widespread comparison of abundance and frequency of each species of bryophyte within vs around the caves, particularly on similar substrata. Some studies imply that bryophyte cover is richer inside the cave due to the more constant conditions and available moisture. In other cases, the exterior is more favorable due to greater light intensity.

Entrance

"The entrance zone refers to the entry point of a cave, which usually receives adequate sunlight. This part of the cave opens to the outside environment and experiences varied temperatures, as it adjusts to the external environment and climate. The entrance zone can be either naturally formed or created by humans. Green plants grow in this zone because it has sunlight, which is needed for photosynthesis. The entrance zone of a cave can be inhabited by various forms of life, including beetles, small rodents, spiders, snakes, salamanders, earthworms, millipedes, owls, and snails. Additionally, certain terrestrial animals, such as raccoons and bears, may take refuge in the entrance zone to sleep, eat, and nest." (World Atlas 2021). These animals may influence the kinds of plants that arrive and survive there.

The cave entrance often provides protection not available further away. This can be shade and greater

moisture, thus protecting it from bright sun, high temperatures, and drought. For example, Aziz (2011) reported ***Tortula viridifolia*** (Figure 42) at the entrance of a cave as new for Iraq.

Figure 42. ***Tortula viridifolia*** with capsules, on rock, was reported as a new species for Iraq from a cave entrance. Photo by George G., through Creative Commons.

Grebe (1918) observed bryophytes from 5-10 meters from the mouths of several caves in Germany. The light was very dim and was reflected in from the cave surface. He reported thick mats of ***Amblystegium serpens*** (Figure 43-Figure 44) around electric lights in Dunkel der Deckenhohle at Iserlohn. Fiol (1995) explored the flora of cavity entrances of more than 40 cavities in Mallorca (Figure 45). He was able to report relict species and frequent species in the shafts. The moss ***Homalia lusitanica*** (Figure 46) occurs between 40 and 200 lux, whereas **Cyanobacteria** can survive 1/2000 of the surface light. The access region of the caves tend to support xerophytes, including the liverworts ***Plagiochila asplenioides*** (Figure 47) and ***Porella arboris-vitae*** (Figure 48), and mosses ***Anomodon viticulosus*** (Figure 49), ***Ctenidium molluscum*** (Figure 50-Figure 51), and ***Scorpiurium circinatum*** (Figure 52-Figure 53). In the entrance he found the liverworts ***Conocephalum conicum*** (Figure 14), ***Mesoptychia turbinata*** (Figure 54), and ***Pellia endiviifolia*** (Figure 55), and the mosses ***Neckera crispa*** (Figure 56) and ***Rhynchostegiella tenella*** (Figure 30), as well as a few of the access region species.

Figure 43. ***Amblystegium serpens*** with capsules on rocks, a species that occurs in thick mats around electric lights in Dunkel der Deckenhohle at Iserlohn, Germany.

Figure 44. ***Amblystegium serpens***. Photo by Michael Lüth, with permission.

Figure 45. Interior of cave at Porto Cristo, Mallorca. Photo by Lolagt, through Creative Commons.

Figure 46. ***Homalia lusitanica***, a species that can live at 40 and 200 lux in Mallorcan caves. Photo by Hugues Tinguy, with permission.

Figure 47. ***Plagiochila asplenioides***, a species found in the cave access region of Mallorcan caves. Photo by Malcolm Storey, <DiscoverLife.com>, with online permission.

Figure 48. ***Porella arboris-vitae***, a species that occurs in the access region of Mallorcan caves. Photo by Abalg, through Creative Commons.

Figure 49. ***Anomodon viticulosus***, a xerophytic species that occurs in the access region of Mallorcan caves. Photo by Aimon Niklasson, with permission.

Figure 50. ***Ctenidium molluscum*** in rock canyon, a species that occurs in the access region of Mallorcan caves. Photo by Michael Lüth, with permission.

Figure 51. ***Ctenidium molluscum***. Photo by Michael Lüth, with permission.

Figure 52. ***Scorpiurium circinatum*** habitat on a rock wall, a xerophytic species that occurs in the access region of Mallorcan caves. Photo by Hugues Tinguy, with permission.

Figure 53. ***Scorpiurium circinatum*** dry. Photo by David T. Holyoak, with permission.

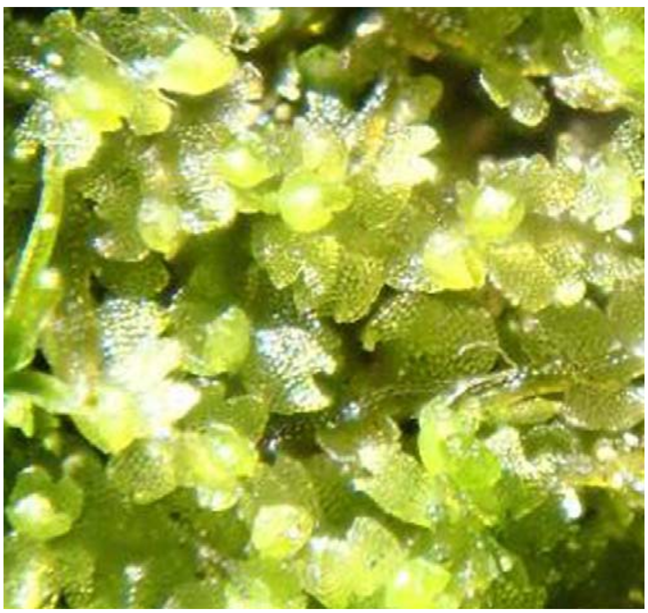

Figure 54. ***Mesoptychia turbinata***, a species of the entrance zone in Mallorcan caves. Photo by Hugues Tinguy, with permission.

Figure 55. ***Pellia endiviifolia*** with red antheridia, a species of the entrance zone in Mallorcan caves. Photo by Hermann Schachner, through Creative Commons.

Figure 56. ***Neckera crispa***, a species of the entrance zone in Mallorcan caves. Photo by Hermann Schachner, through Creative Commons.

Rushin (1973) reported that mostly bryophytes grow on the upper ledges near the cave entrance and where light reaches the floor of the Natural Trap Cave (Figure 57) in the Bighorn Mountains of Wyoming, USA. The cool, moist environment is ideal for the bryophytes. But farther into the cave where it is dark, only bacteria and fungi survive.

Figure 57. Natural Trap Cave, Wyoming. Photo from Bureau of Land Management, through public domain.

Borges *et al*. (2008) indicated a twofold importance of cave entrances for both bryophytes and arthropods in the Azores (Figure 37). They are sheltered and humic, supporting good diversity of bryophytes representing 25% of the Azorean bryophyte flora; many of the species found there are rare or endemic. They argued that these serve as hotspots for species that permit us to answer ecological questions.

In Montenegro, Kozlova *et al*. (2019) found 64 species of algae and Cyanobacteria and 21 species of bryophytes in the entrance zone of 7 caves (Figure 58). They found that the morphology of the cave entrance was more important than the proximity to the opening in determining the composition of the phototrophic community.

Figure 58. Cave entrance in Montenegra. Photo through Creative Commons.

Buczkó and Rajczy (1989) reported the troglophil ***Eucladium verticillatum*** (Figure 32-Figure 33) "in great mass" on rock at the entrance of a Hungarian cave.

Natcheva (2008) reported ***Conocephalum conicum*** (Figure 14, Figure 59-Figure 61) from the Zandana (Biserna) cave in Bulgaria. My own experience supports this as a suitable habitat for the species. I have seen it on canyon walls at Hocking Hills, Ohio, USA (Figure 59-Figure 60), behind Hungarian Falls (Figure 61) in Houghton County, Michigan, USA, and near the entrance in a cave in Wales.

Figure 59. ***Conocephalum conicum*** on canyon walls, Hocking Hills, Ohio, USA. Photo by Janice Glime.

Figure 60. Ash Cave at Hocking Hills, Ohio, USA. Photo courtesy of Kim Barton.

Figure 61. Crest of Hungarian Falls, Tamarack City, Michigan, USA. ***Conocephalum conicum*** grows behind the waterfall on the rock. Photo by Janice Glime.

Pentecost and Zhang (2006) found ***Eucladium verticillatum*** (Figure 32-Figure 33), ***Gymnostomum aeruginosum*** (Figure 62-Figure 63), and ***Palustriella commutata*** (Figure 64-Figure 65) at cave entrances in European travertines, but these species failed to penetrate into the twilight zone. Pentecost and Zhang (2001) found that these three species were common at 0-4 m from the entrance with 10% relative irradiation (RI) in Scoska Cave (Figure 66) in the UK.

Figure 62. ***Gymnostomum aeruginosum***, a species that occurs at cave entrances in European travertines, but it fails to penetrate into the twilight zone. Photo by Michael Lüth, with permission.

Figure 63. ***Gymnostomum aeruginosum*** with capsules. Photo by Michael Lüth, with permission.

Figure 64. ***Palustriella commutata*** habitat in Scotland, a species that occurs at cave entrances in European travertines, but it fails to penetrate into the twilight zone. Photo by Michael Lüth, with permission.

Figure 65. ***Palustriella commutata***. Photo by Michael Lüth, with permission.

Figure 66. Entrance of Scoska Cave, Littondale, UK. Photo by Bob Jenkins, through Creative Commons.

Zhang *et al*. (2004a) studied the bryophytes in the entrance zone of a karst cave in Kunming, China. Ren *et al*. (2021) found a similar restriction to that in the UK found by Pentecost and Zhang (2001, 2006) for the mosses ***Ectropothecium zollingeri*** (Figure 67), ***Hypopterygium tamarisci*** (Figure 68), ***Plagiomnium vesicatum*** (Figure 69), and ***Racopilum cuspidigerum*** (Figure 70-Figure 71), and the liverwort ***Lejeunea sordida*** (see Figure 75-Figure 76) to the entrance area of karst caves in southern China.

Figure 67. ***Ectropothecium zollingeri***, a species that is unable to penetrate beyond the entrances of karst caves in China. Photo by Jan-Peter Frahm, with permission.

Figure 68. ***Hypopterygium tamarisci*** with capsules, a species that is unable to penetrate beyond the entrances of karst caves in China. Photo by George Shepherd, through Creative Commons.

Figure 69. ***Plagiomnium vesicatum***, a species that is unable to penetrate beyond the entrances of karst caves in China. Photo from Digital Museum, Hiroshima University, with permission.

Figure 70. ***Racopilum cuspidigerum***, a species that is unable to penetrate beyond the entrances of karst caves in China. Photo by John Game, through Creative Commons.

Figure 71. ***Racopilum cuspidigerum*** branch. Photo by Peter Woodward, through Creative Commons.

Gabriel *et al*. (2008) noted that cave entrances in the Azores (Figure 37) were particularly humid. Gabriel (2006) found that ~25% of the Azorean bryoflora can be found in this habitat. He noted that 19 vulnerable and 13 rare bryophytes on the European Red List can be found there. Gabriel *et al*. (2008) used both published records and their own field sampling to evaluate the species diversity and rarity of bryophytes at the entrances of all known Azorean lava tubes and volcanic pits (Gabriel *et al*. 2008). They found the frequent liverworts to include ***Calypogeia arguta*** (Figure 72), ***Jubula hutchinsiae*** (Figure 73-Figure 74), and ***Lejeunea lamacerina*** (Figure 75-Figure 76). Frequent mosses included ***Epipterygium tozeri*** (Figure 77-Figure 78), ***Eurhynchium praelongum*** (Figure 79), ***Fissidens serrulatus*** (Figure 80), ***Pseudotaxiphyllum elegans*** (Figure 81), ***Tetrastichium virens*** (Figure 41), and ***Tetrastichium fontanum*** (Figure 82). Even some rare Azorean species appeared at the entrances: ***Archidium alternifolium*** (Figure 83-Figure 84), ***Asterella africana*** (Figure 85), and ***Plagiochila longispina*** (Figure 39). Gabriel *et al*. (2018) found ***Radula holtii*** (Figure 86) at cave entrances in the Azores (Figure 37) and expressed concern that climate change and other factors of anthropogenic origin could threaten it. Gabriel *et al*. (2011) consider ***Asterella africana*** to be a specialist of cave entrances.

Figure 72. ***Calypogeia arguta***, a species that occurs at the entrances of all known Azorean lava tubes and volcanic pits. Photo by Claire Halpin, with permission.

Figure 73. ***Jubula hutchinsiae*** beside a waterfall, a species that occurs at the entrances of all known Azorean lava tubes and volcanic pits. Photo by Michael Lüth, with permission.

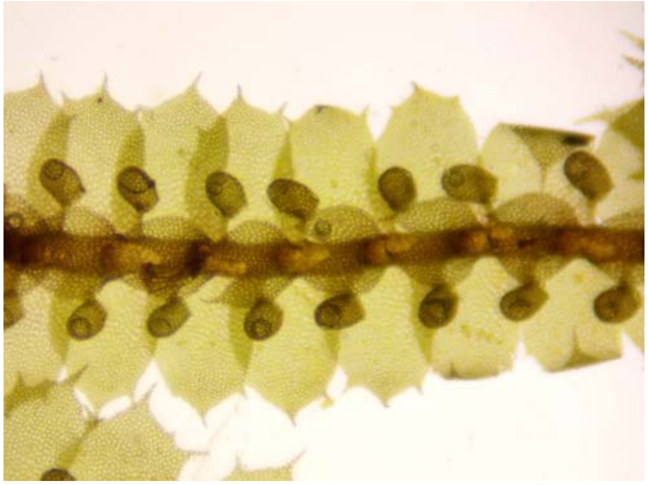

Figure 74. ***Jubula hutchinsiae*** branch. Photo by Rory Hodd, with permission.

Figure 75. ***Lejeunea lamacerina*** habitat, a species that occurs at the entrances of all known Azorean lava tubes and volcanic pits. Photo by Michael Lüth, with permission.

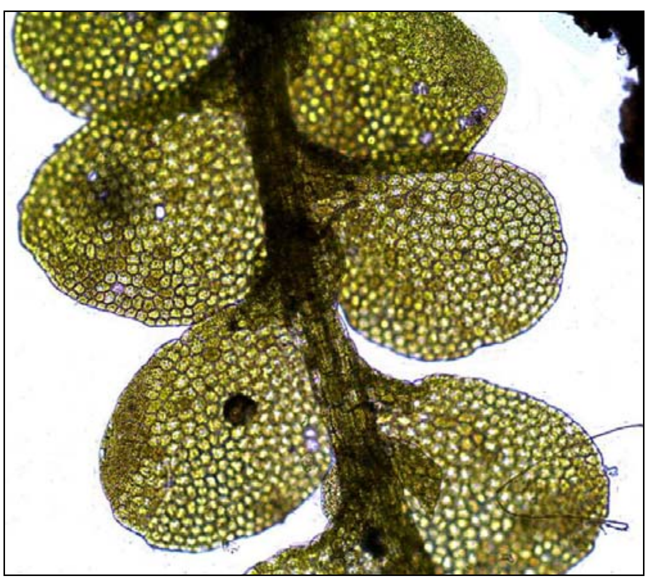

Figure 76. ***Lejeunea lamacerina*** branch. Photo by Hugues Tinguy, with permission.

Figure 77. ***Epipterygium tozeri*** showing water on waxy surface; this species is frequent in Azorean lava tubes and volcanic pits. Photo by Michael Lüth, with permission.

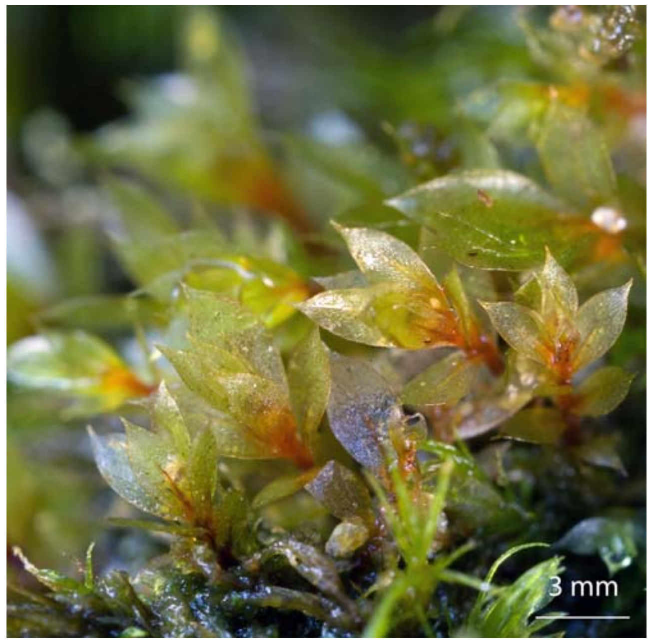

Figure 78. ***Epipterygium tozeri***. Photo by Felipe Gutiérrez Pérez, through Creative Commons.

Figure 79. ***Eurhynchium praelongum***, a frequent moss at entrances of Azorean lava tubes and volcanic pits. Photo by David T. Holyoak, with permission.

Figure 80. ***Fissidens serrulatus***, a species that occurs at the entrances of all known Azorean lava tubes and volcanic pits. Photo by Artdivcan, with permission.

Figure 81. ***Pseudotaxiphyllum elegans*** with capsule, a species that occurs at the entrances of all known Azorean lava tubes and volcanic pits. Photo by Matt Goff, with permission.

Figure 82. ***Tetrastichium fontanum***, a species that is frequent in Azorean lava tubes and volcanic pits. Photo by Michael Lüth, with permission.

Figure 83. ***Archidium alternifolium***, a rare species in the Azores, but that occurs at cave entrances. Photo by George G., through Creative Commons.

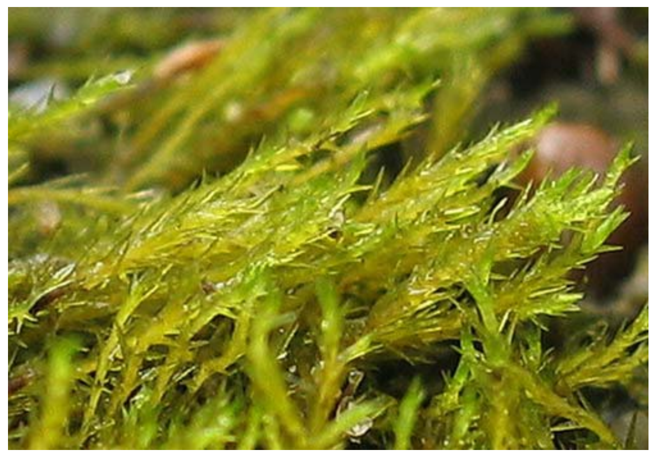

Figure 84. ***Archidium alternifolium***. Photo by Andrew Spink, with permission.

Figure 85. ***Asterella africana*** with archegoniophores, a rare species in the Azores, but that occurs at cave entrances. Photo by Paulo A. V. Borges, with permission.

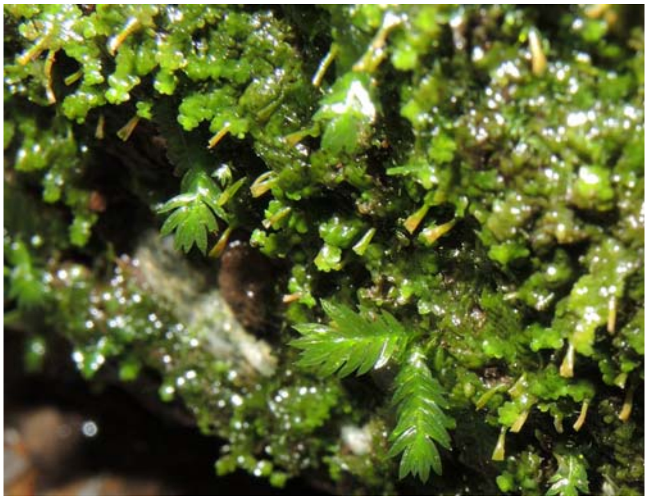

Figure 86. ***Radula holtii*** with perianths, a species in the Azores that occurs at cave entrances, but that could disappear due to climate change. Photo by Rory Hodd, with permission.

Ros *et al*. (2000) found ***Schistidium cinclidodonteum*** (Figure 87) on rocks with soil in a protected and dark cave in Morocco (Figure 88). Its more typical habitat is on acid rocks that are periodically flooded or in stream beds.

Figure 87. ***Schistidium cinclidodonteum***, a species that occurs on rocks with soil in a dark cave in Morocco. Photo by Scot Loring, through Creative Commons.

Figure 88. Interior of Morocco cave. Photo by Diego Delso, through Creative Commons.

Pilkington (2003) found the flora of the cave entrance of a cave in Ireland (Figure 89) to contrast sharply with that of the nearby surface vegetation. The entrance had 23 species of tracheophytes and 17 species of bryophytes in 20 quadrats: ***Ctenidium molluscum*** (Figure 50-Figure 51), ***Eurhynchium praelongum*** (freq=14; Figure 79), ***Fissidens taxifolius*** (Figure 90), ***Thuidium tamariscinum*** (Figure 91-Figure 92), ***Palustriella commutata*** (wet places; Figure 64-Figure 65), ***Rhizomnium punctatum*** (Figure 93), ***Pellia endiviifolia*** (Figure 55), ***Thamnobryum alopecurum*** (freq=20; Figure 34), ***Plagiochila asplenioides*** (Figure 47), ***Plagiomnium undulatum*** (freq=15; Figure 94-Figure 95), ***Plagiomnium affine*** (Figure 96), ***Calliergonella cuspidata*** (Figure 97), ***Plagiochila spinulosa*** (Figure 98-Figure 99), ***Brachythecium rutabulum*** (Figure 100), ***Hookeria lucens*** (wet places; Figure 101), ***Isothecium myosuroides*** (Figure 102), and ***Dichodontium pellucidum*** (Figure 103). Note that only ***Pellia endiviifolia***, ***Plagiochila asplenioides***, and ***Plagiochila spinulosa*** are liverworts.

Figure 89. Entrance of a Keshcorran Cave, Ireland. Photo by Jon Sullivan, through public domain.

Figure 90. ***Fissidens taxifolius***, a species that occurs at the cave entrance of a cave in Ireland. Photo by David Holyoak, with permission.

Figure 91. ***Thuidium tamariscinum***, a species to be found at a cave entrance in Ireland. Photo by Hermann Schachner, through Creative Commons.

Figure 92. ***Thuidium tamariscinum*** branch. Photo by Hugues Tinguy, with permission.

Figure 93. ***Rhizomnium punctatum*** on canyon wall, a species to be found at a cave entrance in Ireland. Photo by Janice Glime.

Figure 94. ***Plagiomnium undulatum***, a species that occurs at the entrance of a cave in Ireland. Photo by Hermann Schachner, through Creative Commons.

Figure 95. ***Plagiomnium undulatum*** branch showing undulations. Photo by James K. Lindsey, through Creative Commons.

Figure 96. ***Plagiomnium affine***, a species that occurs at the entrance of a cave in Ireland. Photo by Michael Becker, through Creative Commons.

Figure 97. ***Calliergonella cuspidata***, a common wetland species that occurs at the entrance of a cave in Ireland. Photo by Hermann Schachner, through Creative Commons.

Figure 98. ***Plagiochila spinulosa***, a species that occurs at the entrance of a cave in Ireland. Photo by David T. Holyoak, with permission.

Figure 99. ***Plagiochila spinulosa***. Photo by David Rycroft, with permission.

Figure 100. ***Brachythecium rutabulum*** with capsules, a species that occurs at the entrance of a cave in Ireland. Photo by J. C. Schou, through Creative Commons.

Figure 101. ***Hookeria lucens***, a species that occurs at the entrance of a cave in Ireland. Photo by Malcolm Storey, <DiscoverLife.com>, with online permission.

Figure 102. ***Isothecium myosuroides***, a species that occurs at the entrance of a cave in Ireland. Photo by Claire Halpin, with permission.

Figure 103. ***Dichodontium pellucidum*** on rock ledge, but restricted to clay soil in Scoska Cave, North Yorkshire, UK. Photo by Claire Halpin, with permission.

Gabriel *et al*. (2006) found relatively rare species at cave entrances in the Azores (Figure 37), including the non-threatened ***Frullania azorica*** (Figure 104-Figure 105), ***Frullania microphylla*** (Figure 106), ***Homalia webbiana*** (Figure 107), ***Marchesinia mackaii*** (Figure 108-Figure 109), ***Myurium hochstetteri*** (Figure 110), ***Fissidens luiserii*** (name of unknown status; Figure 111), and the rare ***Tetrastichium fontanum*** (Figure 82), ***Fissidens coacervatus*** (Figure 112), and ***Tetrastichium virens*** (Figure 41). ***Radula wichurae*** (see Figure 86) is vulnerable. Other more common species were also present at cave entrances: the hornwort ***Anthoceros punctatus*** (Figure 113); liverworts ***Calypogeia arguta*** (Figure 114), ***Lophocolea coadunata*** (Figure 115), ***Conocephalum conicum*** (Figure 14, Figure 59-Figure 61), ***Fossombronia casepitiformis*** (Figure 116), ***Frullania tamarisci*** (Figure 117), ***Lejeunea lamacerina*** (Figure 76), ***Lunularia cruciata*** (Figure 118), ***Plagiochila bifaria*** (Figure 119), ***Porella obtusata*** (Figure 120), ***Radula lindenbergiana*** (Figure 121), ***Riccardia latifrons*** (Figure 122); mosses ***Bryum canariense*** (Figure 123), ***Campylopus pilifer*** (Figure 124-Figure 125), ***Epipterygium tozeri*** (Figure 77-Figure 78), ***Heterocladium wulfsbergii*** (Figure 126-Figure 127), ***Hypnum cupressiforme*** (Figure 128-Figure 129), ***Leucobryum juniperoideum*** (Figure 130), ***Plagiothecium nemorale*** (Figure 40), ***Perigonium gracile*** (Figure 131), ***Scorpiurium circinatum*** (Figure 132-Figure 133), ***Thamnobryum maderense*** (Figure 134). This is an unusually large number of liverworts for cave habitats.

Figure 104. ***Frullania azorica*** on rock, a relatively rare species that occurs at cave entrances in the Azores. Photo by Rosalina Gabriel, with permission.

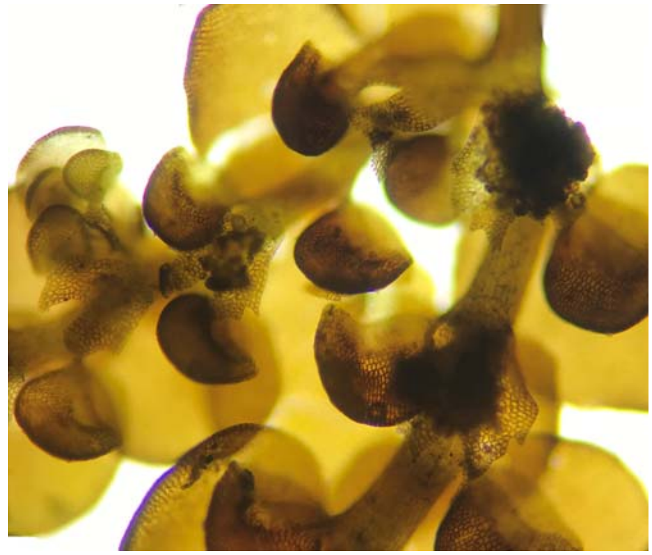

Figure 105. ***Frullania azorica***. Photo courtesy of Tatiana Oliveira da Silva.

Figure 106. ***Frullania microphylla*** on rock, with enlarged inset. This is a relatively rare species that occurs at cave entrances in the Azores. Photo by Michael Lüth, with permission.

Figure 107. ***Homalia webbiana***, a relatively rare species that occurs at cave entrances in the Azores. Photo from <Earth.com>, with permission.

Figure 108. ***Marchesinia mackaii*** habitat on limestone boulder, England; this is a relatively rare species that occurs at cave entrances in the Azores. Photo by Richtid, through Creative Commons.

Figure 109. ***Marchesinia mackaii***. Photo by Malcolm Storey <DiscoverLife.com>, with online permission.

Figure 110. ***Myurium hochstetteri***, a relatively rare species that occurs at cave entrances in the Azores. Photo by Michael Lüth, with permission.

Figure 111. ***Fissidens luisieri*** with capsules, from Madeira off Africa, a relatively rare species that occurs at cave entrances in the Azores. Photo by Michael Lüth, with permission.

Figure 112. ***Fissidens coacervatus*** with capsules, Madeira, a relatively rare species that occurs at cave entrances in the Azores. Photo by Michael Lüth, with permission.

Figure 113. ***Anthoceros punctatus***, a more common species that occurs at cave entrances in the Azores. Photo by Malcolm Storey <DiscoverLife.com>, with online permission.

Figure 114. ***Calypogeia arguta***, a more common species that occurs at cave entrances in the Azores. Photo by Claire Halpin, with permission.

Figure 115. ***Lophocolea coadunata***, a more common species that occurs at cave entrances in the Azores. Photo by J. C. Schou, with permission.

Figure 116. ***Fossombronia casepitiformis*** with capsules, a more common species that occurs at cave entrances in the Azores. Photo by Michael Lüth, with permission.

Figure 117. ***Frullania tamarisci***, a more common species that occurs at cave entrances in the Azores. Photo by David T. Holyoak, with permission.

Figure 118. ***Lunularia cruciata***, a more common species that occurs at cave entrances in the Azores. Photo by Hermann Schachner, through Creative Commons.

Figure 119. ***Plagiochila bifaria***, a more common species that occurs at cave entrances in the Azores. Photo by Paulo Borges, with permission.

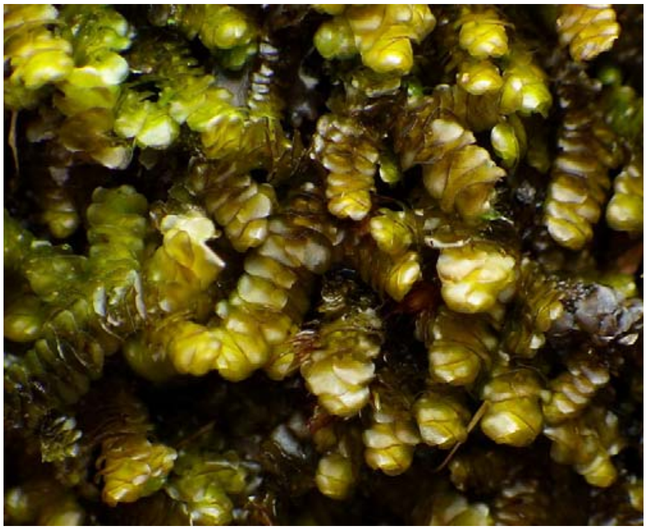

Figure 120. ***Porella obtusata***, a more common species that occurs at cave entrances in the Azores. Photo by Kristian Hassel, through Creative Commons.

Figure 121. ***Radula lindenbergiana***, a more common species that occurs at cave entrances in the Azores. Photo by Hermann Schachner, through Creative Commons.

Figure 122. ***Riccardia latifrons***, a more common species that occurs at cave entrances in the Azores. Photo from Botany Website, UBC, with permission.

Figure 123. ***Bryum canariense***, a more common species that occurs at cave entrances in the Azores. Photo by Claire Halpin, with permission.

Figure 124. ***Campylopus pilifer***, a more common species that occurs at cave entrances in the Azores. Photo by Blanka Aguero, with permission.

Figure 125. ***Campylopus pilifer***. Photo by Des Callaghan, with permission.

Figure 126. ***Heterocladium wulfsbergii*** on vertical rock, a more common species that occurs at cave entrances in the Azores. Photo by Claire Halpin, with permission.

Figure 127. ***Heterocladium wulfsbergii***. Photo by Claire Halpin, with permission.

Figure 128. ***Hypnum cupressiforme*** on rock wall, a more common species that occurs at cave entrances in the Azores. Photo by Allen Norcross, with permission.

Figure 129. ***Hypnum cupressiforme***. Photo by Michael Lüth, with permission.

Figure 130. ***Leucobryum juniperoideum***, a more common species that occurs at cave entrances in the Azores. Photo by David T. Holyoak, with permission.

Figure 131. ***Pterogonium gracile*** wet, a more common species that occurs at cave entrances in the Azores. Photo by David T. Holyoak, with permission.

Figure 132. ***Scorpiurium circinatum***, a more common species that occurs at cave entrances in the Azores. Photo by Hugues Tinguy, with permission.

Figure 133. ***Scorpiurium circinatum*** dry. Photo by David T. Holyoak, with permission.

Figure 134. ***Thamnobryum maderense***, a more common species that occurs at cave entrances in the Azores. Photo by Kristian Peters, with permission.

Even small caves can provide unique local habitats. In the Flume (Figure 135) at Franconia Notch, New Hampshire, USA, ***Campylium chrysophyllum*** (Figure 136) was only found on the floor of a small cave above the falls (Glime 1982).

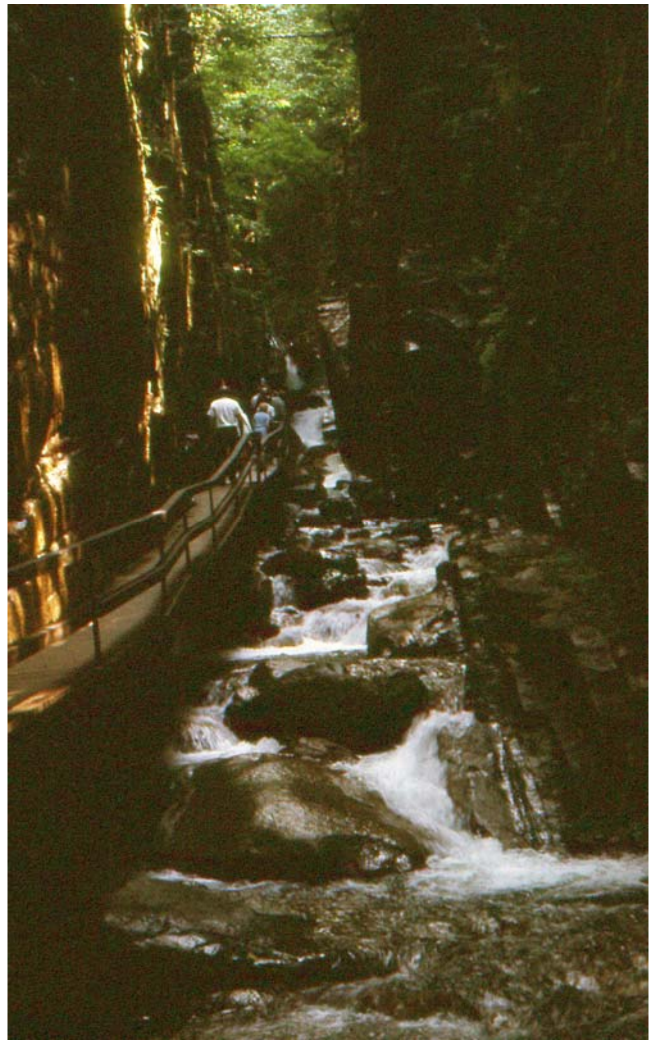

Figure 135. Flume, Franconia Notch, New Hampshire, USA, where small caves can have ***Campylium chrysophyllum***. Photo by Janice Glime.

Figure 136. ***Campylium chrysophyllum***, a species that occurs in a very shallow cave in the Flume at Franconia Notch, New Hampshire, USA. Photo by Bob Klips, with permission.

Twilight Zone

The **twilight zone** (Figure 137) is the part of a cave that receives a small amount of sunlight since it is not too far from the entrance. This seems to coincide with the **threshold** part of the cave, where light penetrates to some degree. This zone is cool and damp, and its temperature is usually relatively constant. The twilight zone is shared by both outside organisms and cave dwellers.

Figure 137. Twilight zone of Rawhiti Cave, South Island, New Zealand. Photo by Pseudopanax, through public domain.

Pleurocarpous mosses such as ***Amblystegium serpens*** var. ***juratzkanum*** (Figure 138) predominate among bryophytes in areas with less light (down to 232 lux) in the three Hungarian caves studied by Buczkó and Rajczy (1989), although the acrocarpous moss ***Bryoerythrophyllum recurvirostrum*** (Figure 139) also occurs in deeper parts.

Figure 139. ***Bryoerythrophyllum recurvirostrum*** showing red base, an acrocarpous moss that grows in deep parts of caves. Photo by Janice Glime.

In Mallorcan caves (Figure 45), Fiol (1995) described the "transition zone," which presumably corresponds with the **twilight zone**. The bryophytes in this zone seem to include the most cavernicolous of the entrance species, including ***Eucladium verticillatum*** (Figure 32-Figure 33), ***Fissidens dubius*** (Figure 140), ***Homalia lusitanica*** (Figure 46), ***Mnium*** sp. (Figure 152-Figure 153), and ***Thamnobryum alopecurum*** (Figure 34). ***Thamnobryum alopecurum*** and ***Homalia lusitanica*** mark the light extinction limit of bryophytes into the next zone. Relicts include the liverwort ***Jungermannia atrovirens*** (Figure 141), and the mosses ***Taxiphyllum wissgrillii*** (Figure 142), ***Orthothecium intricatum*** (Figure 143), and ***Rhizomnium punctatum*** (Figure 62), all of which were known in Mallorca only from these caves.

Figure 138. ***Amblystegium serpens*** var. ***juratzkanum*** with capsules, on rock. Pleurocarpous mosses such as this one predominate in areas with less light. Photo by Štěpán Koval, with permission.

Figure 140. ***Fissidens dubius*** on rock ledge, a species that occurred deepest within Scoska Cave, North Yorkshire, UK. Photo by Hermann Schachner, through Creative Commons.

Figure 141. ***Jungermannia atrovirens*** with perianths, a relict species known in Mallorca only from caves. Photo by Hugues Tinguy, with permission.

Figure 142. ***Taxiphyllum wissgrillii***, a species that occurs on a boulder at the deepest position of bryophyte presence in the Della Grotta Dell'orso, Italy. It is a relict species known in Mallorca only from caves. Photo by Hugues Tinguy, with permission.

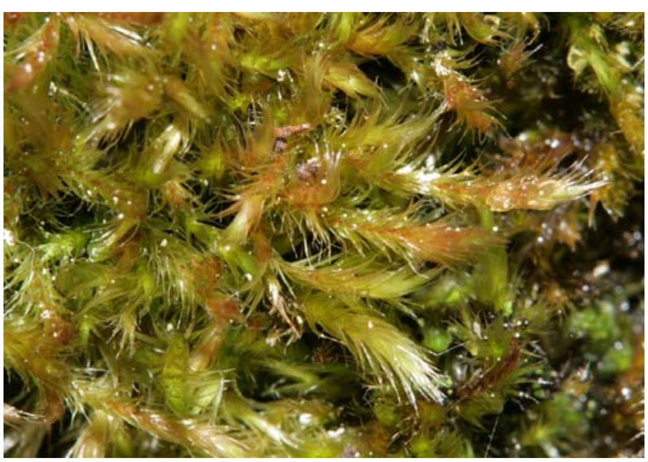

Figure 143. ***Orthothecium intricatum***, a relict species known in Mallorca only from caves. Photo by Hermann Schachner, through Creative Commons.

In the Azores (Figure 37), Frahm (2005) found bryophytes in a small crater with a cave at the bottom. Ferns are common where there is enough light, but bryophytes extend farther into the dark interior. These are primarily ***Riccardia chamedryfolia*** (Figure 144-Figure 145) and ***Thamnobryum*** sp. (Figure 34), with smaller quantities of ***Cyclodictyon laetevirens*** (Figure 38) and ***Fissidens serrulatus*** (Figure 80). He describes the ***Thamnobryum*** as conspicuous because of its large, lax plants with long, flagelliform branches.

Figure 144. ***Riccardia chamedryfolia***, a species that occurs in a cave at the bottom of a crater in the Azores. Photo by Bernd Haynard, through Creative Commons.

Figure 145. ***Riccardia chamedryfolia***. Photo by Hugues Tinguy, with permission.

In the Della Grotta Dell'orso, Italy (Figure 146-Figure 147), Castello and Strazzaboschi (2013) found ***Oxyrrhynchium speciosum*** (Figure 148) and ***Taxiphyllum wissgrillii*** (Figure 142) on a large boulder 10 m from the entrance, marking the deepest position of bryophytes in the cave. Bryophyte growth in the twilight zone was more reduced than at the entrance, with species exhibiting stunted growth in small patches. Other species in the twilight zone included ***Fissidens crispus*** (Figure 149), ***Isopterygiopsis pulchella*** (Figure 150-Figure 151), ***Mnium stellare*** (Figure 152-Figure 153), ***Neckera complanata*** (Figure 154-Figure 155), and ***Rhynchostegiella tenella*** (Figure 30).

Figure 146. Outside of entrance to Grotta dell'orso, Italy. Photo by Tiesse, through Creative Commons.

Figure 149. ***Fissidens crispus***, a species of the twilight zone in the Della Grotta Dell'orso, Italy. Photo by D. B. Tucker, through Creative Commons.

Figure 147. Grotta dell'orso, Italy, inside entrance, entering the twilight zone. Photo by Tiesse, through Creative Commons.

Figure 150. ***Isopterygiopsis pulchella***, a species of the twilight zone in the Della Grotta Dell'orso, Italy. Photo by Michael Lüth, with permission.

Figure 148. ***Oxyrrhynchium speciosum***, a species that occurs on a boulder at the deepest position of bryophyte presence in the Della Grotta Dell'orso, Italy. Photo by Hugues Tinguy, with permission.

Figure 151. ***Isopterygiopsis pulchella*** on a rock wall. Photo by Michael Lüth, with permission.

Figure 152. ***Mnium stellare*** with capsules, on rock, a species of the twilight zone in the Della Grotta Dell'orso, Italy. Photo by Michael Lüth, with permission.

Figure 153. ***Mnium stellare***. Photo by Hermann Schachner, through Creative Commons.

Figure 154. ***Neckera complanata*** on a vertical substrate, a species of the twilight zone in the Della Grotta Dell'orso, Italy. Photo by Gerd Höhenberger, through Creative Commons.

Figure 155. ***Neckera complanata*** on rock. Photo by Andy Hodgson, with permission.

Pentecost and Zhang (2001, 2006) found that ***Eurhynchium pumilum*** (Figure 156), ***Fissidens adianthoides*** (Figure 157-Figure 158), and ***Pseudotaxiphyllum elegans*** (Figure 81) were frequent bryophytes in the region 6-10 m with relative illumination (RI) 1-2% in Scoska Cave (Figure 66), North Yorkshire, UK. ***Amblystegium serpens*** (Figure 44), ***Fissidens dubius*** (Figure 140), and ***Thamnobryum alopecurum*** (Figure 34) penetrated the furthest. ***Thamnobryum alopecurum*** was the most frequently encountered bryophyte in the cave. Further into the cave they found ***Orthothecium intricatum*** (Figure 143), ***Pseudotaxiphyllum elegans***, ***Rhynchostegiella teneriffae*** (Figure 159), and ***Platydictya confervoides*** (Figure 160-Figure 161) (l5.9 m, RI 0.23%). ***Dichodontium pellucidum*** (Figure 103) was restricted by substrate to clay soil.

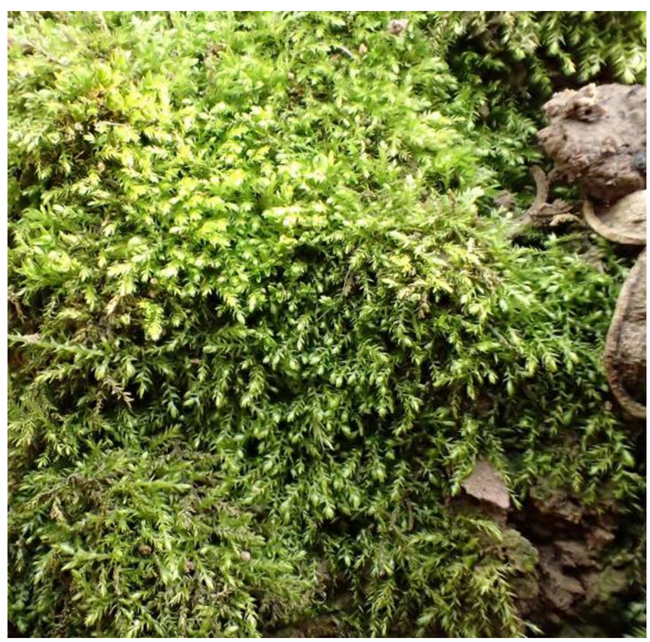

Figure 156. ***Eurhynchium pumilum***, a species frequent in the region 6-10 m with RI of 1-2% in Scoska Cave, North Yorkshire, UK. Photo by Hugues Tinguy, with permission.

Figure 157. ***Fissidens adianthoides*** with capsules on rock, a species frequent in the region 6-10 m with RI of 1-2% in Scoska Cave, North Yorkshire, UK. Photo by Michael Lüth, with permission.

Figure 158. ***Fissidens adianthoides***. Photo by Hermann Schachner, through Creative Commons.

Figure 159. ***Rhynchostegiella teneriffae***, among the species that occurred deepest within Scoska Cave, North Yorkshire, UK. Photo by Hermann Schachner, through Creative Commons.

Figure 160. ***Platydictya confervoides*** habitat on boulder, a species that occurs deepest within Scoska Cave, North Yorkshire, UK. Photo by Bob Klips, with permission.

Figure 161. ***Platydictya confervoides***. Photo by Bob Klips, with permission.

Ren *et al.* (2021) found that some species were restricted to the twilight zone of six karst caves in southern China. ***Fissidens taxifolius*** (Figure 90) and ***Hyophila javanica*** (see Figure 162) occurred only in intermediate light. ***Radula kojana*** (Figure 163-Figure 164) was found only in deep plots. This led them to conclude that liverworts were better adapted to low light conditions, but this needs a much wider sampling effort in a wide range of caves. Furthermore, they found that the mosses were in locations that indicate they are more drought tolerant, which could account for the absence of liverworts in areas closer to the opening.

Figure 162. ***Hyophila involuta*** with capsules among rocks; ***Hyophila javanica*** occurs only in intermediate light in karst caves in southern China. Photo by Wayne Lampa, through Creative Commons.

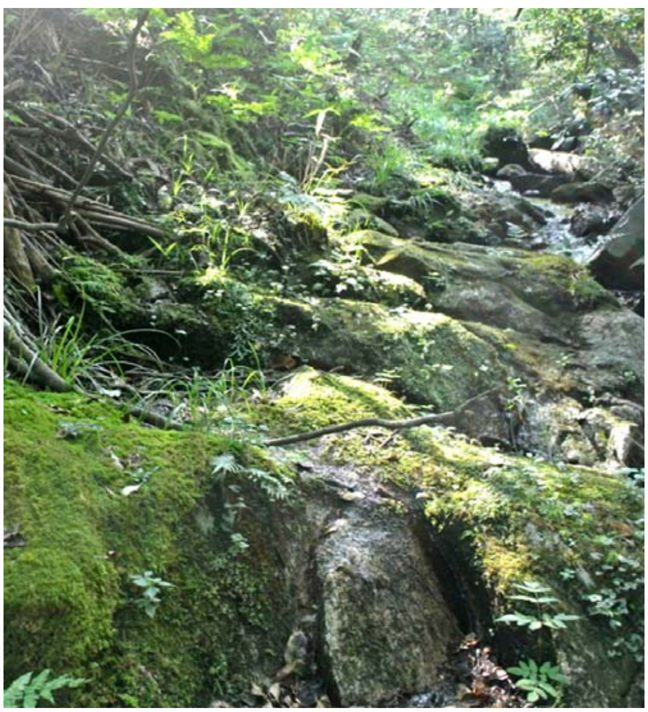

Figure 163. ***Radula kojana*** habitat on rock, a species that occurs only in deep locations in karst caves in southern China. Photo by Kochibi, through Creative Commons.

Pentecost and Zhang (2001) found that in Scoska Cave (Figure 66), UK, ***Hypnum resupinatum*** (Figure 165), ***Orthothecium intricatum*** (Figure 143), and ***Weissia*** cf. ***perssonii*** (Figure 166) penetrated the farthest, to regions where the RI fell to about 0.4%. Liverworts were unable to penetrate very far, an absence that the researchers attributed to the dry conditions of the cave. Only ***Conocephalum conicum*** (Figure 14, Figure 59-Figure 61) and ***Metzgeria conjugata*** (Figure 167) were able to penetrate to 12 m.

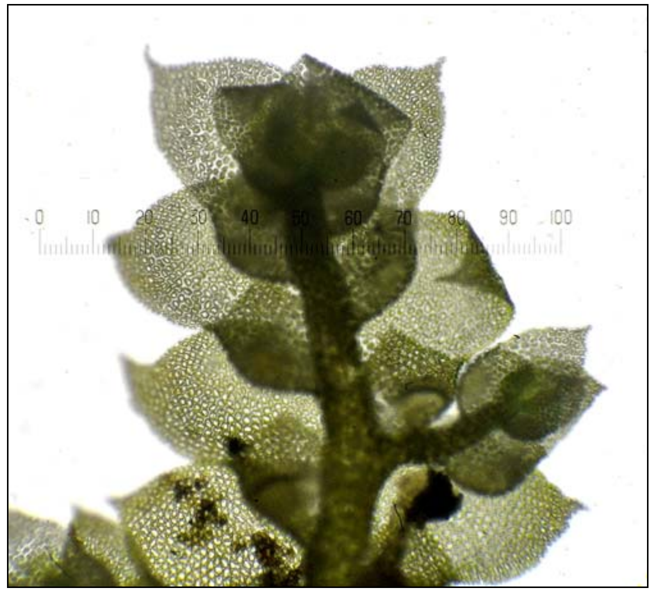

Figure 164. ***Radula kojana*** branch. Photo by Kochibi, through Creative Commons.

Figure 165. ***Hypnum resupinatum*** on rock, among the species that penetrate the farthest into the Scoska Cave, UK. Photo by George G., through Creative Commons.

Figure 166. ***Weissia perssonii*** with capsules, among the species that penetrate the farthest into the Scoska Cave, UK. Photo by Barry Stewart, with permission.

Figure 167. ***Metzgeria conjugata*** on rock, the species that penetrated the farthest (12 m) into Scoska Cave, UK. Photo by Barry Stewart, with permission.

Wang *et al*. (1998) examined the biokarst formations in the twilight zone of Chinese caves.

In a study of 17 Guilin caves (*e.g.* Figure 168), Zhang *et al*. (2005) found ***Gymnostomum calcareum*** (Figure 169-Figure 170), ***Hymenostylium recurvirostrum*** (Figure 171-Figure 172), and ***Philonotis turneriana*** (Figure 173) associated with travertine deposits in the twilight zone of karst caves in the Guilin area of China. Guo *et al*. (2018) examined the communities of dolomite cave twilight zones in Shuidong Cave in Guizhou Province, China.

Figure 168. Cave at Guilin (Li River), Crown Cave, China. Photo by Dan Lundberg, through Creative Commons.

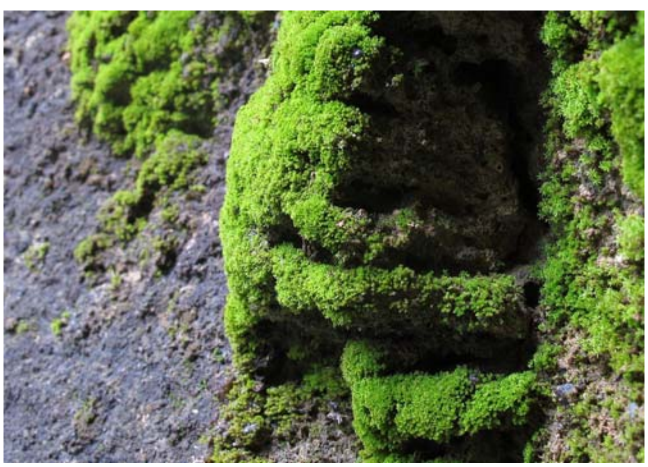

Figure 169. ***Gymnostomum calcareum*** on vertical rock, a species associated with travertine deposits in the twilight zone of karst caves in the Guilin area of China. Photo by Michael Lüth, with permission.

Figure 170. ***Gymnostomum calcareum***. Photo by Larry Jensen, with permission.

Figure 171. ***Hymenostylium recurvirostrum*** on shaded wall in India, a species associated with travertine deposits in the twilight zone of karst caves in the Guilin area of China. Photo by Michael Lüth, with permission.

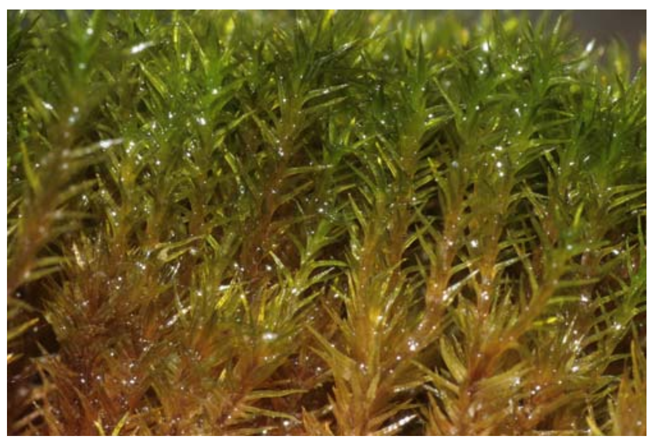

Figure 172. ***Hymenostylium recurvirostrum***. Photo by Hermann Schachner, through Creative Commons.

Figure 173. ***Philonotis turneriana***, a species associated with travertine deposits in the twilight zone of karst caves in the Guilin area of China. Photo by Kochibi, through Creative Commons.

Stalactites and Stalagmites

In addition to growing on cave walls, some bryophytes are able to grow in the stalactite or stalagmites where there is enough moisture dripping down. In Yunnan Province, P. R. China, Zhang *et al*. (2004b) found ***Gymnostomum aurantiacum*** (see Figure 169-Figure 170) and ***Hymenostylium recurvirostrum*** (Figure 171-Figure 172). These can contribute to the formation of the stalactites. ***Eucladium verticillatum*** (Figure 32-Figure 33) and ***Didymodon*** (Figure 174) are also important in forming stalactites. For a description of this process, see Chapter 18-1 of this volume. Bryophytes seem to be rare on the surfaces of these formations, perhaps in part due to the changing nature of the formations.

Figure 174. ***Didymodon brachyphyllus*** on rock; ***Didymodon*** is an important genus for forming stalactites. Photo by Michael Lüth, with permission.

Vertical Shafts

Not all cave inclines progress slowly away from the entrance. Moseley *et al*. (2013) describe a cave in Nova Scotia, Canada, that has vertical shafts as entrances (Figure 175). The fern zone is missing, and three pleurocarpous mosses are dominant: ***Loeskeobryum brevirostre*** (Figure 176), ***Isopterygiopsis muellerianum*** (Figure 177-Figure 178) (1st dominant), and ***Heterocladium dimorphum*** (Figure 179), along with two liverwort species: ***Calypogeia*** (Figure 72; Figure 114) and ***Lophocolea*** (Figure 115). The crustose lichen ***Lepraria*** sp. also occurs on the shaft walls. ***Isopterygiopsis muellerianum*** is the most prominent bryophyte and extends to the deepest location of photosynthetic organisms. ***Loeskeobryum brevirostre*** is present only in the uppermost part of the shaft where it is able to receive sufficient light.

Figure 175. Wisqoq Cave from surface, showing shaft entrance, Nova Scotia, Canada. Photo modified from Moseley 2017, through Creative Commons.

Figure 176. ***Loeskeobryum brevirostre***, one of the dominant bryophytes in a cave in Nova Scotia, Canada. Photo by Bob Klips, with permission.

Figure 177. ***Isopterygiopsis muellerianum*** on rock, one of the dominant bryophytes in a cave in Nova Scotia, Canada. Photo from <Earth.com>, with permission.

Figure 178. ***Isopterygiopsis muellerianum*** branch. Photo by Wayne Lampa, through Creative Commons.

Figure 179. ***Heterocladium dimorphum***, one of the dominant bryophytes in a cave in Nova Scotia, Canada. Photo by Štěpán Koval, with permission.

Summary

The cave bryophyte flora is generally divided into that of the **entrance**, **twilight zone**, and **dark zone**. A further zone of note is the cave mouth area on the outside of the cave. The penetration of light suitable for photosynthesis is the limiting factor for these bryophyte distributions.

Because of the influence of cave temperatures on the **mouth** area, this area can have species that are unique within the region. There tend to be more liverworts there, and mosses such as propaguliferous ***Pohlia*** spp. and ***Tortula truncata*** may be present.

The **entrance** provides only a short distance with sufficient light for a number of species, with morphology of the opening being more important than distance in determining light penetration. One of the most common bryophytes here is ***Amblystegium serpens***. The cave moss ***Eucladium verticillatum*** is often in this zone, especially on the eastern side of the Atlantic. This area can harbor rare species, and species composition often contrasts sharply with that outside the cave.

The **twilight zone** has a more buffered climate than the entrance, but due to low light it has fewer species. Both ***Amblystegium serpens*** and ***Eucladium verticillatum*** extend into this zone, often being abundant. Its often moist conditions and suitable substrate can create refugia for bryophytes not occurring elsewhere in the region. Several species of ***Fissidens*** are among those surviving in this low light.

Stalactites and stalagmites are seldom colonized by bryophytes, but ***Eucladium verticillatum*** and several other bryophytes can contribute to their formation. **Vertical shafts** differ in flora and light intensity from horizontal cave entrances.

Acknowledgments

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Literature Cited

Aziz, F. H. 2011. Seventeen spp. new records for the moss flora of Iraq. Phyton 80: 35-46.

Borges, P. A., Gabriel, R., Pereira, F. E., Mendonça, E., and Sousa, E. 2008. Use of ATLANTIS TIERRA 2.0 in mapping the biodiversity (invertebrates and bryophytes) of caves in the Azorean archipelago. In: Espinasa-Pereña, R. and John Pint, J. (eds.). XII International Symposium on Vulcanospeleology, Tepoztlan, Morelos, Mexico, 2-7 July 2006, pp. 253-259.

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

Castello, M. and Strazzaboschi, L. 2013. Le briofite Della Grotta Dell'orso (33-7vg, Carso Triestino, Ne Italia). [Bryophytes of the Grotta Dell'Orso karst cave (33-7VG, Trieste Karst,

Ne Italy)]. Atti e Memorie della Commissione Grotte "E. Boegan." 44: 55-71.

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

Dalton, P. J. 1995. *Seligeria cardotii* R. Br., a new moss record for Tasmania. N. Z. J. Bot. 33: 143-145.

Fiol, L. 1995. Flora de les Entrades de les Cavitats de Mallorca. [Flora at the cavity entrances in Mallorca.]. Endins 20: 145-153.

Frahm, J. P. 2005. New or interesting records of bryophytes from the Azores. Trop. Bryol. 26: 45-48.

Gabriel, R. 2006. Use of ATLANTIS Tierra 2.0 in mapping the biodiversity (invertebrates and bryophytes) of caves in the Azorean Archipelago. AMCS Bull. 19 / SMES Bol. 7: 253-259.

Gabriel, R., Pereira, F., Câmara, S., Homem, N., Sousa, E., and Henriques, M. I. 2006. Bryophytes of lava tubes and volcanic pits from Graciosa Island (Azores, Portugal). Proceedings of the XI International Symposium on Vulcanospeleology (Tepóztlan, Morelos, Mexico, July 2006). Association for Mexican Cave Studies 119: 260-263.

Gabriel, R., Pereira, F., Borges, P.A.V., and Constância, J. P. 2008. Indicators of conservation value of Azorean caves based on its bryophyte flora at cave entrances. Proceedings of the X, XI and XII International Symposia on Vulcanospeleology: 114-118.

Gabriel, R., Homem, N., Couto, A. B., Aranda, S. C., and Borges, P. A. 2011. Azorean bryophytes: A preliminary review of rarity patterns. Açoreana: Rev Estud. Açor. suppl. 7: 149-206.

Gabriel, R., Sim-Sim, M., González-Mancebo, J. 2018. Conservation concern' bryophytes find refuge on cave entrances in the Azores. ARPHA Conference Abstracts 1: e29395. <https://doi.org/10.3897/aca.1.e29395>.

Glime, J. M. 1982. Bryophytes of the Flume, Franconia Notch State Park, N. H. Rhodora 84: 149-152.

Grebe, C. 1918. Studien zur Biologie und Geographie der Laubmoose. Hedwigia 59: 99.

Guo, Y, Wang, Z. H., and Zhang, Z. H. 2018. Study on community characteristics of bryophytes in dolomite cave twilight zones: An example of the Shuidong Cave in Suiyang County, Guizhou Province. Carsologica Sinica 37: 388-399.

Kozlova, E. V., Mazina, S. E., and Pešić, V. 2019. Biodiversity of phototrophs in illuminated entrance zones of seven caves in Montenegro. Ecol. Montenegrina 20: 24-39.

Moseley, M. 2017. Genesis of schlottenkarren on the Avon Peninsula of Nova Scotia (Canada) with implications for the geochronology of evaporite karsts and caves of Atlantic Canada. Internat. J. Speleol. 46: 267-276.

Moseley, M., Smith, M., Broders, H., and Burns, L. 2013. Biology of Wisqoq Cave, a raccoon-inhabited cave in Nova Scotia. Speleobiol. Notes 5: 66-73.

Natcheva, R. 2008. *Conocephalum salebrosum*: A new liverwort to the bryophyte flora of Bulgaria. Phytologia Balcan. 14: 323-326.

Pentecost, A. and Zhang, Z. 2001. The distribution of plants in Scoska Cave, North Yorkshire, and their relationship to light intensity. Internat. J. Speleol. 30: 27-37.

Pentecost, A. and Zhang, Z. 2006. Response of bryophytes to exposure and water availability on some European travertines. J. Bryol. 28: 21-26.

Pilkington, S. 2003. The flora of Poulnagollum Pot, Co. Clare, Ireland. Proc. Univ. Bristol Spelaeol. Soc. 23(1): 27-34.

Puglisi, M., Kürschner, H., and Privitera, M. 2018. Phytosociology and life syndromes of bryophyte communities from Sicilian caves, a clear example of relationship between bryophytes and environment. Plant Sociol. 55: 3-20.

Ren, H., Wang, F., Ye, W., Zhang, Q., Han, T., Huang, Y., Chua, G., Hui, D., and Guo, Q. 2021. Bryophyte diversity is related to vascular plant diversity and microhabitat under disturbance in karst caves. Ecol. Indic. 120: 106947.

Rushin, C. J. 1973. Interpretive and paleontologic values of Natural Trap Cave Bighorn Mountains Wyoming. M. S. thesis, Resource Conservation, University of Montana, Missoula, 97 pp.

Salamah, Z., Sasongko, H., and Zulianti, E. 2019. Diversity of Bryophyte in the Selarong Cave Area, Bantul, Yogyakarta. Indonesian J. Biol. Ed. 2(1): 35-39.

Wang, F. X., Cao, J. H., and Huang, J. F. 1998. Biokarst in the cave twilight zones. Carsologica Sinica 17: 42-48.

World Atlas. 2021. What Are the Different Zones of a Cave? Accessed 29 August 2021 at <https://www.worldatlas.com/articles/what-are-the-different-zones-of-a-cave.html>.

Zhang, Z., Li, X.-N., Peng, T., and Xhao, C.-H. 2004a. New records of luminous liverworts from the karst caves of Guangxi province, P. R. China: *Cyathodium cavernarum* Kuntze and *C. smaragdium* [sic!] Schiffn. [sic!] ex Kessler (Cyathodiaceae, Hepaticae). Acarologia Sinica 23: 154-157.

Zhang, Z.-H., Peng, T., Li, X.-N., and Zhao, C.-H. 2004b. A study on the bryophytes of karst cave threshold at Kunming Area in Yunnan Province, PR China. Carsologica Sinica 23: 229-233.

Zhang, Z.-H., Zhao, C.-H., Li, X.-N., Peng, T., Huang, W.-H., and Jiang, H. 2005. Bryophytes of karst caves in Guilin area, China. Guihaia 25: 107-111.