

# CHAPTER 18-1

## CAVES – THE ENVIRONMENT

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# CHAPTER 18-1

## CAVES – THE ENVIRONMENT



Figure 1. Stalactite, stalagmite, and column formations in Avshalom Cave, Israel. Photo by Sir Joseph, through Creative Commons.

### Caves

Traditional definitions of caves note such characteristics as perpetual darkness, environmental stability, and oligotrophy, characters that apply to large cavities (**macrocaverns**) in rocks (Moseley 2009a). Moseley attempted to provide an ecological definition of a cave. But he did this from an animal perspective, and thus light mattered less than for bryophytes. By definition, macrocaverns, mesocaverns, and microcaverns differ from each other only in magnitude (*i.e.* scale). Because these caves differ in more characteristics than size, particularly in view of the habitat needs of the inhabitants, we should more properly refer to subterranean habitats.

Schuster (1958) noted that bryophytes are able to survive in small niches or "pockets" because of their small size, causing them to be limited by their microenvironment

rather than the macroenvironment. Thus, we can find unique communities in caves, no matter how small the cave may be (see Schade 1917; Clausen 1952).

### Terminology

Caves bring with them a set of terminology that is unfamiliar in other contexts. Some are necessary to understand the relevant literature.

Caves themselves, typically known as underground or subterranean habitats, have a number of other names, including **alcove**, **antre**, **cavern**, **cavity**, **chamber**, **den**, **dugout**, **gallery**, **grotto**, **hollow**, **pothole**, **recess**, **rock shelter**, **subterrane**, and **tunnel**. As a synonym of sinkhole (Figure 2), **doline** (Figure 3) or **dolina** refers to shallow, usually funnel-shaped depression of ground surface formed by solution in limestone regions.





Figure 2. Sinkhole with bryophytes in Wilson County, Tennessee, USA. Photo by Brian Stansberry, through Creative Commons.

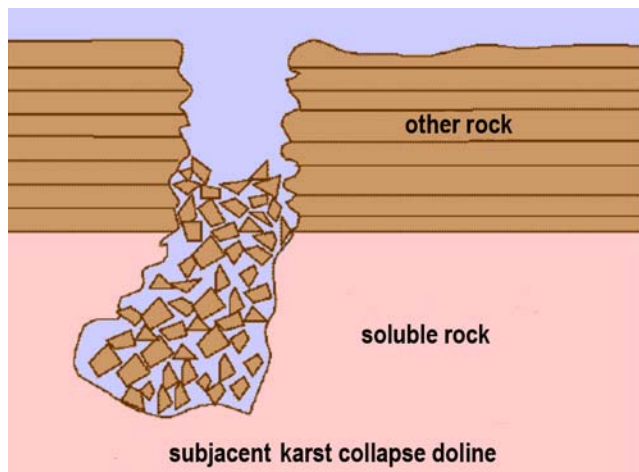


Figure 3. Doline diagram by B.Z. Saylor, MIT, <oeit.mit.edu>.

### Terms Used to Describe Caves

**algific:** cold producing

**algific cave:** subterranean cave that vents cold air; Figure 4



Figure 4. Algific talus slope with vent northeastern Iowa. Photo courtesy of Beth Lynch.

**column:** formed by union of stalagmite and stalactite; Figure 5, Figure 6



Figure 5. Travertine dripstone columns, San Salvador Island, Bahamas. Photo by James St. John, through Creative Commons.



Figure 6. Labelled speleothems. Photo by Dave Bunnell, through Creative Commons.

**flowstone:** rock deposited as thin sheet by precipitation from flowing water; Figure 6, Figure 7

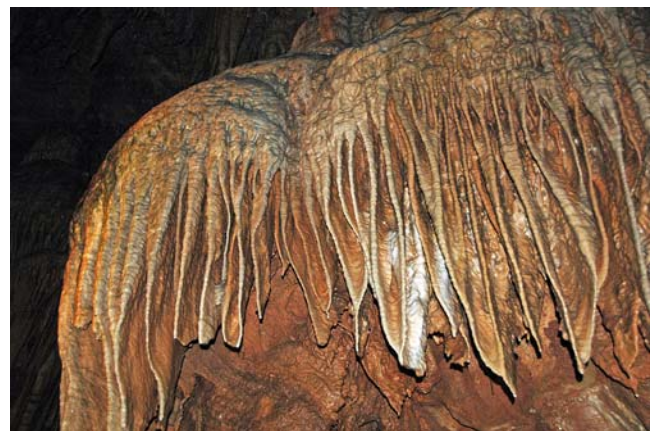


Figure 7. Travertine flowstone and draperies, Diamond Caverns, Kentucky. Photo by James St. John, through Creative Commons.



**helictite:** distorted form of stalactite, typically resembling twig; usually made of needle-form calcite and aragonite; Figure 8-Figure 9



Figure 8. Helictites at Treak Cavern, Derbyshire, UK. Photo by Bill Lion, through Creative Commons.



Figure 9. Helictites at Jenolan Caves, Australia. Photo by Jason 7825, through Creative Commons.

**soda straws:** speleothem in form of hollow mineral cylindrical tube; tubular stalactites; Figure 6, Figure 10

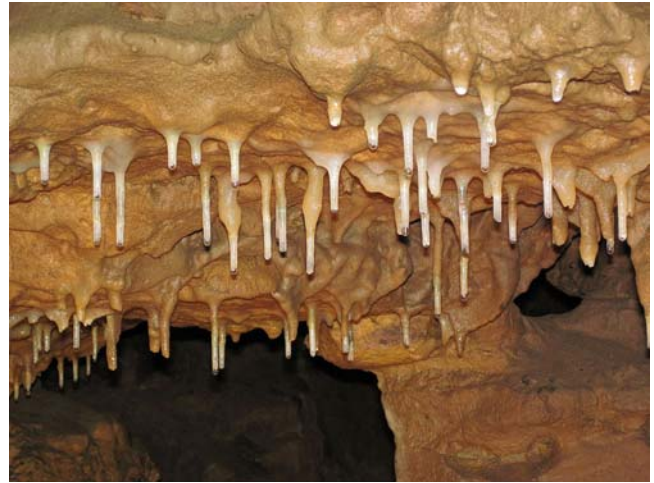


Figure 10. Travertine soda straw stalactites in dolostone, Crystal Cave, Wisconsin, USA. Photo by James St. John, through Creative Commons.

**speleothem:** structure formed in cave by deposition of minerals from water, *e.g.* stalactite or stalagmite; Figure 6

**stalactite:** type of cave structure, hanging from cave ceiling, formed by deposition of minerals from water (stalactites have to hang on tight; they form on the ceiling); Figure 1, Figure 6

**stalagmite:** type of cave structure, projecting from cave floor, formed by deposition of minerals from water dripping from ceiling (**stalagmites** are little mites; they form on the **ground**); Figure 1, Figure 6

**talus:** broken rock; Figure 11



Figure 11. **Talus slope** at Ruby Mountains. Photo from USGS, through public domain.

Moseley (2009a) defined cave dwellers, based on animals that live in caves. Various authors have used the same terms to describe bryophyte cave dwellers.

1. **Troglobites:** Obligate cavernicoles: species that can survive only in caves.
2. **Troglophiles:** Facultative cavernicoles: species which survive and are able to complete their life-cycle in caves, but also survive and complete their life-cycle in other habitats.

3. **Trogloxenes:** Species found in caves which cannot complete their life-cycles there:
  - a. **Habitual troglloxenes** – Species which habitually frequent caves and thus, whilst not completing their life-cycle there, form a part of the cave community (also called ‘regular troglloxenes’).
  - b. **Accidentals** – Surface (**epigean**) species introduced accidentally, *e.g.* by floods, or by straying in.

Moseley (2009a, b) contended that this grouping "lends support to the proposal, recently made elsewhere, that caves can be seen as transitional environments (ecotones) between adjacent hypogean, epigean and/or endogean communities. It also appears to eliminate a number of longstanding conceptual and terminological difficulties, and might offer a rich framework for new understanding of subterranean ecology."

### Ecotones

I have seen an analogy that **ecotones** are like a membrane, occupying relatively little space between two constituents. Cave openings have been compared to these ecotones, providing a rapid transition between environmental conditions, *i.e.* between hypogean, epigean, and endogean communities (Moseley 2009a).

Moseley (2009b) considers all caves to be ecotones because they have a "steep environmental gradient between adjacent ecological communities or ecosystems." Within the cave, the ecotonal changes include light levels (Figure 12), temperature (Figure 12), relative humidity (Figure 12), CO<sub>2</sub> concentration, and physical scale. These parameters apply well to large caves and caverns, but would not seem to apply as well to the very small caves between boulders or under ledges. Nevertheless, even these small spaces can have light and moisture gradients. Moseley argues that considering caves as ecotones can change the way we understand the communities we find there. He raises the question of what role "these transitional habitats play in the initial colonization of the subterranean milieu; and in persistence, adaptation and speciation of hypogean organisms." Although Prous *et al.* (2004) and Moseley examine the notion of caves as ecotones using an animal perspective, the ecotone perspective should apply to plant communities as well, particularly the bryophyte communities that respond to varying levels of light (*e.g.* Pentecost & Zhang 2001).

Prous *et al.* (2004) suggested a methodology using a similarity matrix. Prous *et al.* (2015) further elaborated on cave entrances as ecotones, noting that bryophytes were present as far as 30 m into the cave. The depth of light penetration is very much dependent on the size of the opening, the inclination, and the surrounding vegetation and rock formations that can block light entrance to the cave. Prous and coworkers reported "considerable light penetration even at 30 m."

### Cave Conditions

Caves typically serve as islands, providing habitats that are isolated from similar conditions outside the cave (Culver 1970). Hence, they can maintain isolated populations of bryophytes that continue to reproduce, mostly asexually. Under this isolation, bryophytes can

develop unique genotypes and even cryptic species, as noted already for animals (Moseley 2009a). In fact, Culver (1971) even considered caves to be like archipelagoes. But Culver (1970) pointed out that caves differ from islands by a lack of area effect. Nevertheless, both are subject to effects of time and stochastic processes.

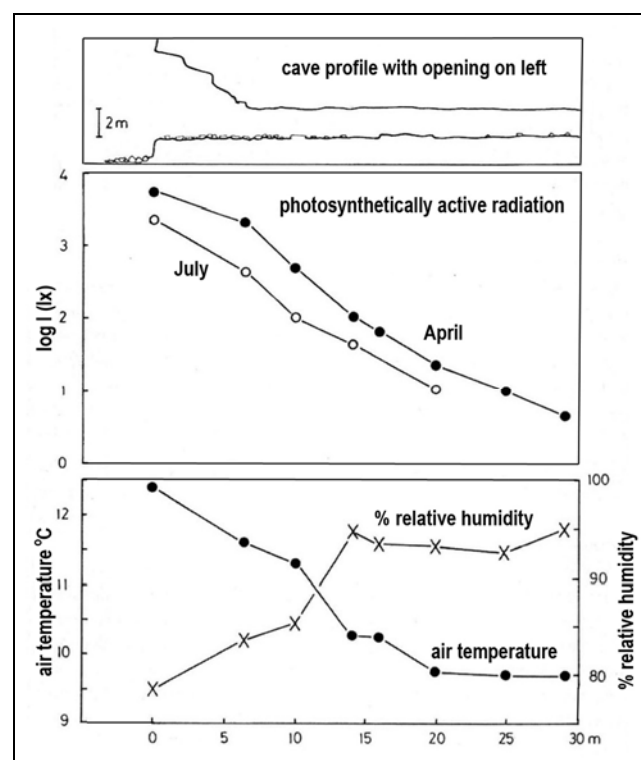


Figure 12. Cave parameters. Modified from Pentecost & Zhang 2001.

Caves provide natural laboratories for assessing the effects of gradients on species compositions (Poulson & White 1969). As islands, they can also help us to understand the effect of isolation on rate of genetic change and natural selection. And caves are simple systems with few tracheophytes to affect either competition or microclimate.

Tuttle and Stevenson (1978) have summarized the variation to be found in one cave environment and its impact on biological populations. They point out that many researchers have assumed a constancy in the cave environment, particularly that of temperature, assuming that it approximates the mean annual surface temperature. Researchers also often assume that humidity is near saturation and essentially unvarying. It is true that the cave environment varies less than that of the surrounding area, but it can indeed vary, at least in some caves, and this can impact the cave fauna (Jegla & Poulson 1970; Juberthie & Delay 1973; Delay 1974; Juberthie 1975; Poulson 1975; Tuttle 1975, 1976; Wilson 1975; Peck 1976), and presumably also the flora.

### Substrate

Working in Eastern Australia, Downing (1992) noted that bryophytes were more abundant, exhibiting greater percent cover and a greater number of species, on limestone substrates than on nonlimestone substrates. Such preference may contribute to the diversity found in caves.



Fraser *et al.* (2014) suggested that in glacial regions organisms could have survived in geothermal areas in sub-ice caves. Such refugia could have permitted bryophytes to survive in these glacial areas until the ice receded. However, the ice itself is not a very good substrate.

### Light

Like most studies, Mason-Williams and Benson-Evans (1967) identified two important ecological factors in Welsh caves: substrate and penetration of light. But they noted that aspect was also important, with north-facing walls having abundant growth and the south-facing walls having scanty, often atypical, growth. Bryophytes in higher light intensities had relatively typical life forms, but as light diminished the dendroid forms and smooth mats became less frequent and rough mats, thalloid mats, and wefts predominated. Spores of bryophytes were common throughout the sampled areas of the cave.

Similarly, Jedrejko and Ziober (1992) investigated bryophytes in caves on the Kracków-Wieluń Upland. They identified 10 liverworts, 59 mosses, and 3 unidentified mosses. Of these, 50% occur only where they get at least some time in full light. As expected, the number of species decreased with distance from light sources of cave inlets. Only 25% of the species occurred in continuously dry places.

Our constant attempts to classify things, even when they represent a continuum, have resulted in identification of the cave as the twilight zone **near** the entrance, a **middle** zone of complete darkness, and a zone of complete darkness and constant temperature **deep** in the cave (Poulson & White 1969). Among the fauna, the middle zone has several very common species which may go in and out of the cave.

### Temperature and Humidity

Light, moisture, and temperature are variables in the cave environment and are not as constant as once thought. Buecher (1999), in a study of Kartchner Caverns in Arizona, USA, found that the cave could become drier due to increased airflow. This was caused by air entering from a second entrance and also by climate change. The relative humidity in the cave was 99.4% (pretty damp!) but had the potential of dropping to only 98.7%. At this only slightly lower humidity, the moisture loss from the cave surfaces would double! This would initiate the drying of the cave interior. Outside moisture is always less than that in the cave except during rain events. But since movement of air into the cave in summer is reduced, this does little to replenish lost humidity.

De Freitas and Littlejohn (1987) illustrate the seasonal changes in Glowworm Cave in New Zealand. They found that the external air temperature and humidity can be determinants of the spatial and temporal distribution of air temperature and humidity within the cave. The external conditions are also important in determining direction of airflow. In winter, these forces result in strong drying and cooling of the cave interior. External air enters the cave and is warmed. In summer the humidity levels of the cave rise substantially, resulting in condensation throughout the cave as it warms.

Gamble *et al.* (2000) demonstrated that tropical flank margin caves in the Bahamas and Puerto Rico presented different temperature regimes from those in temperate

regions. These caves tend to be warmer than outside the cave in winter and cooler in summer. They also lacked diurnal temperature fluctuations. One cause for these differences is that these marginal caves tend to have a width greater than the length. Tidal water can also serve as a buffer to temperature conditions. These differences could be reflected in the bryophyte flora.

Cao and Yuan (1999) examined the water-holding capacity of the various groups of photosynthetic organisms and their effects on the carbon cycle on the rock surface. They found that the loss vs of absorption of water for algae was 18.8 and 1.6 times respectively, for lichens 2.9 and 19.1 times, and for mosses 81.2 and 8.1 times, compared to rocks with none of these growths. The organisms permit the rocks to hold onto water longer, increasing the rates of carbonate rock corrosion beneath them. Nutrients accumulate in these colonized areas and the biological cycle is accelerated.

### CO<sub>2</sub>

Asencio and Aboal (2011) noted that cave CO<sub>2</sub> concentrations were high (0.8% in cave compared to 0.45% in atmosphere). Oxygen was slightly lower (18.5%) than that of the atmosphere (~21%). The temperature ranged 27-43°C – much more variation than many people seem to expect in caves. The humidity (100%) is quite favorable for algal species.

Some caves have changing airflow patterns between summer and winter (Spotl *et al.* 2005). This results in changes in CO<sub>2</sub> levels within the cave. Spotl and coworkers document the predictable changes from high *p*CO<sub>2</sub> (partial pressure of dissolved CO<sub>2</sub>; gas phase pressure of carbon dioxide in air above waterway which would be in equilibrium with dissolved carbon dioxide) in summer and low *p*CO<sub>2</sub> in winter in the Obir Cave in Austria. Winter flushing by relatively CO<sub>2</sub>-poor air enhances degassing of CO<sub>2</sub> in the cave and leads to a high degree of supersaturation of calcite in dripwater (see also Whitaker *et al.* 2009).

Frisia *et al.* (2011) recorded a similar phenomenon in Grotta di Ernesto cave (NE Italy). Air advection causes the winter *p*CO<sub>2</sub> to drop in the cave air to ~500 ppm from a summer peak of ~1500 ppm, with a rate of air exchange between cave and free atmosphere of approximately 0.4 days. The process of cave ventilation forces degassing of CO<sub>2</sub> from dripwater before calcite precipitation onto stalagmites.

When investigating the Scoska Cave in the UK, Whitaker *et al.* (2009) suggested that bryophytes could act as CO<sub>2</sub> sinks, but that decomposition of bryophytes would release CO<sub>2</sub>. They concluded that most of the CO<sub>2</sub> in the photic zone of the cave came from advection and diffusion of air from deeper in the cave.

Mazina and Popkova (2020a) examined the effects of high CO<sub>2</sub> levels on the photosynthetic organisms in the photic zone of the Anyashka Cave in the Caucasus. The dominant photosynthesizers were **Cyanobacteria**. Nevertheless, the highest gross primary productivity (GPP) occurred in communities dominated by pteridophyte and bryophyte species on water-splashed clay. Such communities on limestone or clay on limestone exhibited lower GPP. The GPP of these various communities varied from -0.1503 g C m<sup>-2</sup> h<sup>-1</sup> to -0.0109 g C m<sup>-2</sup> h<sup>-1</sup>. They also

found that some of these communities served as CO<sub>2</sub> sinks, but others were actually CO<sub>2</sub> sources.

In the seven caves studied in Montenegro, Mazina *et al.* (2020) found that all communities on various substrates were carbon sinks, in both summer and winter. Maximal dry mass production occurred when acrocarpous mosses and case-forming **Cyanobacteria** dominated, both being maximal for both phototrophic respiration and gross primary production.

In the Balcarka Cave and adjacent soils in the Czech Republic, Faimon *et al.* (2012) determined that human visitors and **epikarstic** (uppermost weathered zone of carbonate rocks with substantially enhanced and more homogeneously distributed porosity and permeability) sources contribute to the CO<sub>2</sub> levels in the caves. The epikarstic source seems to control the dripwater chemistry and maximum CO<sub>2</sub> in the cave. In show caves such as this one, breathing by visitors and door openings create fluctuations in the levels.

In the Císařská Cave (Moravian Karst, Czech Republic), Faimon *et al.* (2006) compared the chamber CO<sub>2</sub> levels with that of the drip chemistry. They found that the peak levels of CO<sub>2</sub> during visitor presence did not reach the theoretical values at which the dripwater carbonates and air CO<sub>2</sub> would be at equilibrium. However, visitation only resulted in 2.85 hours of human contribution. Increasing that to 4 hours could exceed the dripwater contribution. Nevertheless, achieving the threshold values at which water would damage the calcite would require extreme conditions, *e.g.*, simultaneous presence of 100 persons in the cave chamber for 14 h.

Howarth and Stone (1990) found that in May and June the CO<sub>2</sub> levels in the deeper passages in Bayliss Cave, Australia, reached up to 200X the ambient CO<sub>2</sub> in the atmosphere. This environment supported the largest diversity of obligate cave fauna known in its bad air zone. Such levels should be beneficial for photosynthetic organisms, provided there is sufficient light, and can permit growth even in low light (Lovalo *et al.* 2010). Artificial illumination in such conditions should create an interesting environment for bryophytes and algae. Photosynthetic studies are needed across the CO<sub>2</sub> and light gradients, coupled with laboratory experiments to sort out the individual effects.

Liu *et al.* (2017) examined the **carbonic anhydrase** activity of six epilithic mosses on soil in the Puding karst area, Guizhou Province, China. Carbonic anhydrase **catalyzes** the bidirectional conversion of carbon dioxide (CO<sub>2</sub>) and water (H<sub>2</sub>O) into bicarbonate (HCO<sub>3</sub><sup>-</sup>) and protons (H<sup>+</sup>). These reactions are important in the photosynthetic pathway but are also important in the CO<sub>2</sub> equilibrium of the habitat.

Huang *et al.* (2015) found that external carbonic anhydrase activity differed among the bacteria, fungi, and **Actinomycota**. This activity in bacteria and fungi was promoted by Zn and Co, whereas it was promoted most by Ca in **Actinomycota**. See also Li *et al.* 2005 for more cation and anion effects. The role of these reactions in facilitating bryophyte photosynthesis remains unknown.

### Suitability for Flora and Fauna

Culver and Pipan (2009) note that the more superficial subterranean habitats such as small drainages that emerge

as seeps, small cavities in the uppermost part of karstified rock, talus slopes, and cracks and shallow tubes in lava share only two important characters with caves. They are **aphotic** (having too little light for photosynthesis) and they harbor fauna suited for subterranean life. For bryophytes, only the often very limited photic portion is of relevance. They consider that these aphotic habitats may have given rise to species of animals adapted for the deepest parts of caves. For bryophytes, the openings of such small "caves" could serve the same role, providing stepping stones between caves or serving as refugia where suitable cave habitats may have been destroyed by human activity.

### Radiation

Damaging radiation in caves can be much greater than outside. Buecher (1999) concluded that in Kartchner Caverns this was not enough to be of concern for cave visitors, but they could be for long-term employees. Measurements at the cave entrance are not representative of the deeper parts of the cave.

### Algific Caves

The **algific caves** (Figure 13-Figure 18) result from cold air drainage in places like the driftless area of northeastern Iowa and southwestern Wisconsin, USA. These serve as refugia for boreal bryophyte species (Andrews 2003; Dale Vitt, pers. comm. 4 August 2021).



Figure 13. Algific cave in Fillmore County, Minnesota, USA. Photo by S. C. Zager, MN DNR, through public domain.





Figure 14. Algific caves in Wisconsin, USA. Photo by Ryan O'Connor, Wisconsin DNR through public domain.



Figure 16. Algific talus slope with vent in northeastern Iowa with researcher collecting soil. Photo courtesy of Beth Lynch.



Figure 17. Algific talus slope with vents in northeastern Iowa. Photo courtesy of Beth Lynch.



Figure 15. Algific talus slope with mossy vent obscured by vegetation in northeastern Iowa. Photo courtesy of Beth Lynch.



Figure 18. Algific talus slope with mossy vent, northeastern Iowa. Photo courtesy of Beth Lynch.



Andrews (2003) described the windhole caves at Ice Mountain, West Virginia, USA (Figure 19). He concluded that bedrock benches in the subsurface of the slope provides surfaces where cooler air and water become trapped. This results in frost and ice accumulation. Surface benches at the bottom of the slope are continuously cooled by the heavier down-slope winds. Although the airflow cycles and structural makeup of the algific caves differs among North American locations, they typically sustain an unusually cold environment. These environments are able to support species that otherwise occur in more northern or higher altitude sites.

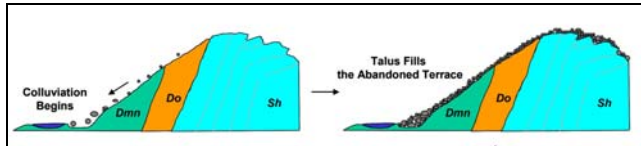


Figure 19. Algific slope cave formation, Ice Mountain, West Virginia, USA. The three colors are three different types of bedrock. Modified from Andrews 2003.

## Non-Bryophyte Flora

The changes in the flora of caves are very dependent on light intensity. Whereas the entrance of the cave may have tracheophytes, including seed plants, further in the cave the **Cyanobacteria**, algae, bryophytes, and ferns are the only photosynthetic organisms able to grow in the limited light (Gurnee 1994; Lamprinou *et al.* 2014; Turchinskaia *et al.* 2019). Less commonly they may have liverworts or lichens; fungi and bacteria comprise non-photosynthetic organisms (Czerwik-Marcinkowska *et al.* 2019).

Roldán and Hernández-Mariné (2009) summarized some of the important factors determining phototrophic biofilm communities in three caves in Spain. They found that these films consisted of **Cyanobacteria**, green microalgae, diatoms, mosses, and lichens, and that these communities differed among sampling sites. Light-related stress and low humidity both result in thinner biofilms and lower species diversity. Similarly, the duration of light exposure reduces both thickness and diversity.

## Microbes

In addition to photosynthetic organisms, caves provide suitable habitat for microbes and fungi (Laiz *et al.* 1999). Water communities are mainly composed of gram-negative rods and cocci (**Enterobacteriaceae** and **Vibrionaceae**), while those of ceiling rocks are mainly *Streptomyces* spp. (Figure 20). The conditions include high humidity, relatively low and stable temperature, water pH close to neutrality, and varying mixes of organic matter. These conditions seem to favor colonization and long-term growth of **Actinomycota** over other heterotrophic bacteria on ceiling rocks in the Altamira cave, Spain.

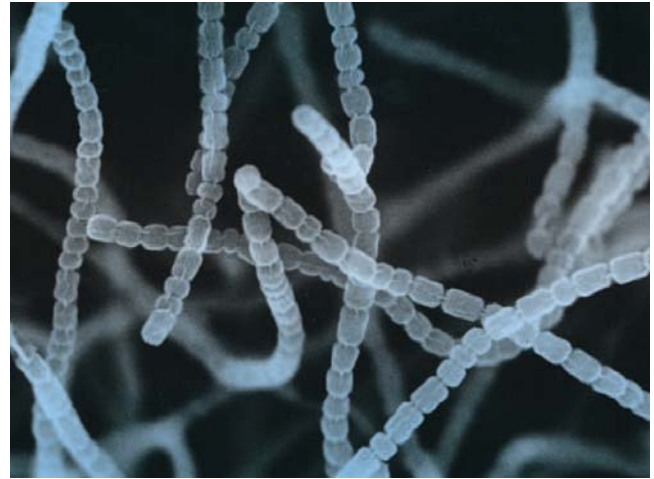


Figure 20. *Streptomyces* sp. Photo by Doc Warhol, through Creative Commons.

## Cyanobacteria and Algae

Algal and cyanobacterial communities have been described in a number of caves around the world. These communities typically form a zone dependent on the light intensity. For example, Selvi and Altuner (2007) have described the algal flora in Ballica Cave in Turkey. Buczkó and Rajczy (1989) reported 49 algal taxa, but only 17 bryophyte taxa in three caves in Hungary.

In caves of Bashkirskiy Ural Biosphere Reserve (southern Urals, Bashkortostan Republic, Russia), Gainutdinov *et al.* (2017) found 42 taxa of **Cyanobacteria** (42.9%), 31 taxa of **Bacillariophyta** (31.6%), 20 taxa of **Chlorophyta** (20.4%), 3 taxa of **Charophyta** (3.06%), and 2 taxa of **Ochrophyta** (2.04). *Leptolyngbya boryana* (**Cyanobacteria**; Figure 21-Figure 22), *Mychonastes homosphaera* (**Chlorophyta**; Figure 23), and *Eolimna minutissima* (**Bacillariophyta**; Figure 24) were present in all caves examined. The authors found that the diatoms *Humidophila contenta* (Figure 25), *Hantzschia amphioxys* (Figure 26), and *Orthoseira roeseana* (Figure 27), present in these caves, were those most commonly mentioned in other publications on caves. Others mentioned from other caves were *Pinnularia borealis* (**Bacillariophyta**; Figure 28), *Stichococcus bacillaris* (**Chlorophyta**; Figure 29), and *Klebsormidium flaccidum* (**Charophyta**; Figure 30-Figure 31). These species occurred in the highly illuminated areas on cave walls and on mosses at the cave entrance. Dominant algae in well-illuminated zones include the diatoms *Orthoseira roeseana*, *Humidophila contenta*, and *Hantzschia amphioxys*, and *Oscillatoria rupicola* (**Cyanobacteria**; Figure 32), using substrates of damp walls and mosses. They concluded that the similarity of algae on the wall surfaces and on mosses was because the moss samples were usually collected from the walls. The mosses at the cave entrances usually exist in moist conditions with adequate lighting, favoring the growth of algae.

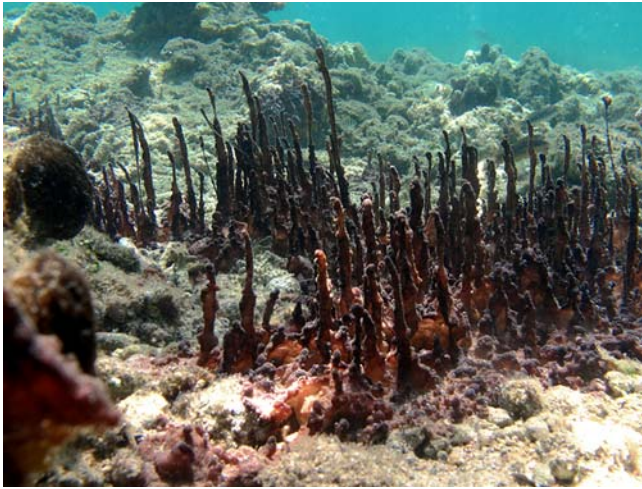


Figure 21. *Leptolyngbya* sp., a *Cyanobacteria* genus found in all caves examined by Gainutdinov *et al.* (2017) in the southern Urals. Photo by Philippe Bourjon, through Creative Commons.



Figure 22. *Leptolyngbya boryanum*, a *Cyanobacteria* species found in all caves examined by Gainutdinov *et al.* (2017) in the southern Urals. Photo from UTEX, through Creative Commons.

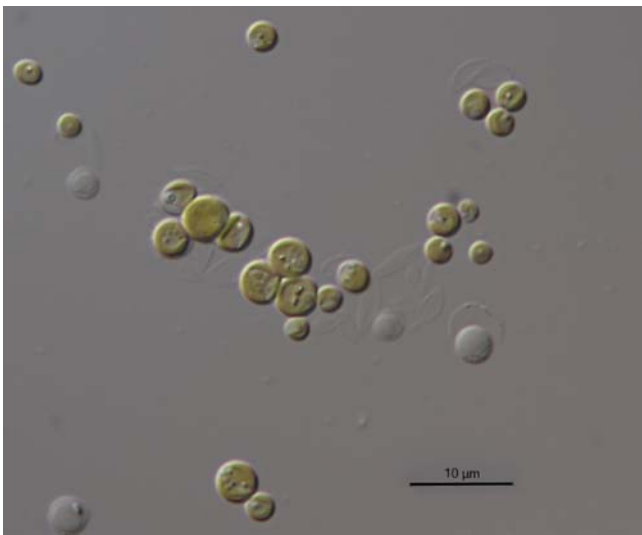


Figure 23. *Mychonastes homosphaera*, a *Chlorophyta* species found in all caves examined by Gainutdinov *et al.* (2017) in the southern Urals. Photo by T. Darienko, through Creative Commons.

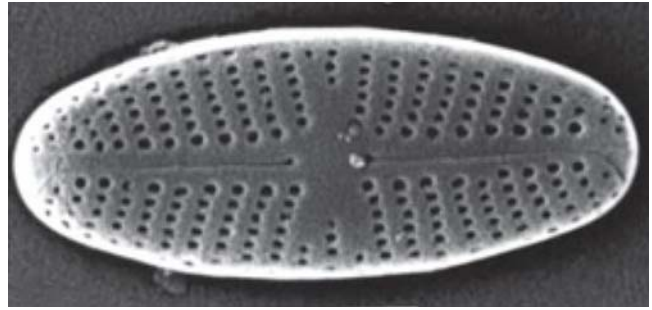


Figure 24. *Eolimna* sp. *Eolimna minutissima* is a diatom species found in all caves examined by Gainutdinov *et al.* (2017) in the southern Urals. Photo from Sala *et al.* 2003, through Creative Commons.

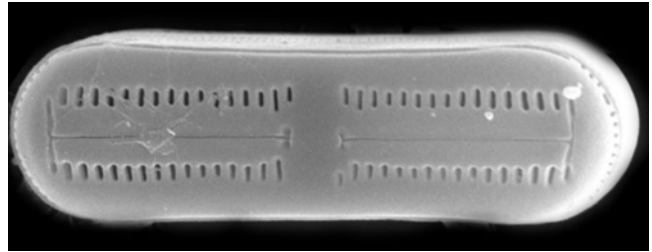


Figure 25. *Humidophila contenta*, a species of diatom that is among the most common in caves. Photo by Rex Lowe from <diatoms.org>, with permission.



Figure 26. *Hantzschia amphioxys*, a species of diatom that is among the most common in caves. Photo by Yuuji Tsukii, with permission.

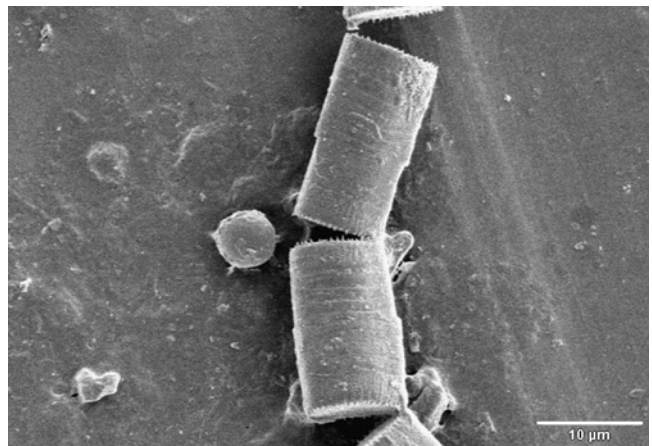


Figure 27. *Orthoseira roeseana*, a species of diatom that is among the most common in caves. Photo by Birger Skjelbred, Nordic Microalgae <www.nordicmicroalgae.org>, with online permission.



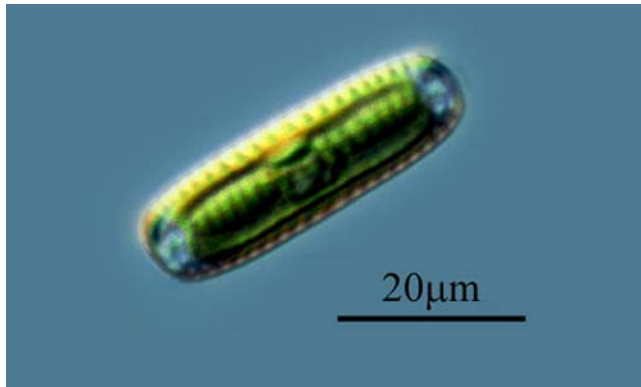


Figure 28. *Pinnularia borealis*, a diatom species that has been found in multiple cave studies. Photo from Proyecto Agua Water Project, through Creative Commons.

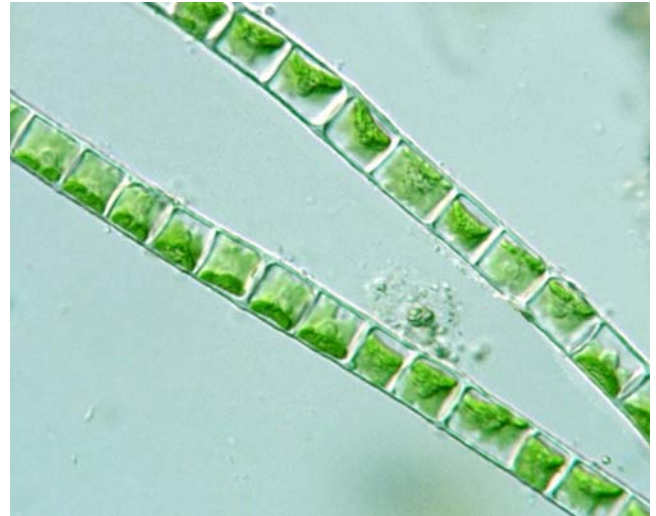


Figure 31. *Klebsormidium flaccidum*, a **Charophyta** species that has been found in multiple cave studies. Photo Yuuji Tsukii, with permission.

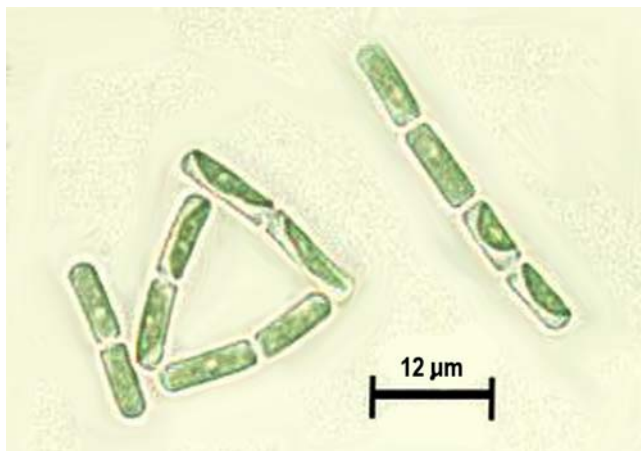


Figure 29. *Stichococcus bacillaris*, a **Chlorophyta** species that has been found in multiple cave studies. Photo from UTEX, through Creative Commons.



Figure 32. *Oscillatoria* filament; *O. rupicola* is a **Cyanobacteria** species that is common near cave lights in . Photo Yuuji Tsukii, with permission.



Figure 30. *Klebsormidium* sp. growing epiphytically. Photo by Des Callaghan, with permission.

Lowe *et al.* (2013) discovered two new species of diatoms in the genus *Orthoseira* (see Figure 27) from lava tubes in Hawai'i and Île Amsterdam (subAntarctic). The bottoms of these caves have a cover of mosses and liverworts surrounding a puddle.

Mulec and Kosi (2009) note the invasion of algae and **Cyanobacteria** deep into the caves where artificial illumination has been added so that visitors can see the cave interior. The caves are usually naturally humid, and the illumination makes them suitable for these growths. The authors consider the invading phototrophic organisms to be inappropriate aesthetically, but they note that the organisms also cause degradation of the cave substrata they colonize. These are especially problematic in caves with prehistoric art (Figure 33). It is advisable, for the preservation of the cave walls and art, to eliminate these **Cyanobacteria** and algae early because they play the most important role in early stages. Mosses and ferns typically colonize later. These photosynthetic organisms have acquired the name of **lampenflora**.





Figure 33. Rock art from 7000 BP, Cave of Beasts, Libyan desert; such paintings are easily damaged by algae and other growths and by methods used to remove those growths. Photo by Clemens Schmillen, through Creative Commons.

Distribution and species of **Cyanobacteria** and algae in caves are typically limited by the same parameters that influence bryophytes in cave habitats – reduced light intensity, low nutrients, and absence of seasonality (Dayner & Johansen 1991; Pedersen 2000; Popović *et al.* 2015). To these defining habitat characters, Mulec *et al.* (2008) added temperature, humidity, and flowing water as important in delimiting the aerial habitats.

Popović *et al.* (2015) noted that the biofilm on cave walls in Božana Cave (Serbia) included **Cyanobacteria**, algae, and microfungi. Popović *et al.* (2016) found a new coccoid member of the **Cyanobacteria**, *Nephrococcus serbicus*, from the Božana Cave, Serbia. Popović *et al.* (2015) found that chlorophyll content of the biofilm was not proportional to the light intensity, but was instead proportional to the biomass of the film. Coccoid **Cyanobacteria** were the most abundant at the lowest light intensities, whereas **Nostocales** occurred in the highest light. *Desmococcus olivaceus* (Figure 35-Figure 36) and *Trentepohlia aurea* (Figure 37-Figure 38) were the only green algae on the walls, whereas *Gloeocapsa* (Figure 39), *Scytonema* (Figure 40), *Aphanocapsa* (Figure 41), and *Chroococcus* (Figure 42) were the most common **Cyanobacteria**, with 21 taxa of *Chroococcus* alone.



Figure 34. *Nephrococcus* sp.; *Nephrococcus serbicus* (**Cyanobacteria**) was found as a new species in the Božana Cave, Serbia. Photo modified from Linda Amaral Zettler and David Patterson, through Creative Commons.



Figure 35. *Desmococcus olivaceus* growing on a log, a terrestrial member of **Chlorophyta** that also occurs on cave walls. Photo by Bob O'Kennon, through Creative Commons.

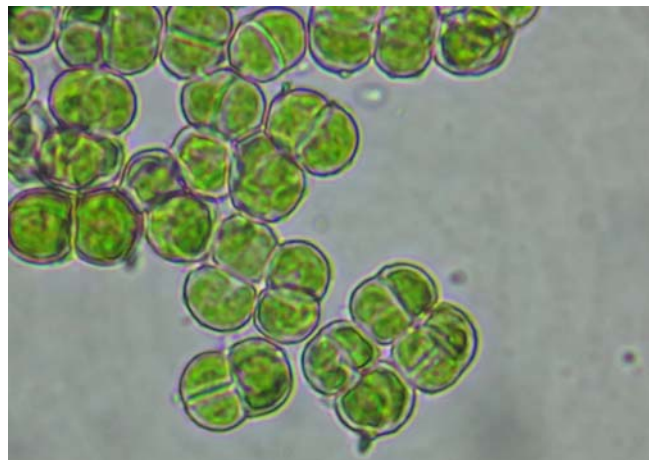


Figure 36. *Desmococcus olivaceus*, one of only two green algae found on cave walls in Božana Cave (Serbia). Photo by Alejandra Huereca, through Creative Commons.



Figure 37. *Trentepohlia aurea*, a terrestrial member of **Chlorophyta** that also occurs on cave walls. Photo by Malcolm Storey (DiscoverLife.com), with online permission.





Figure 38. *Trentepohlia aurea*, one of only two green algae found on cave walls in Božana Cave (Serbia). Photo by Alan J. Silverside, with permission.



Figure 41. *Aphanocapsa* sp., a genus common on cave walls in Serbia and elsewhere. Photo by Jason Oyadomari, with permission.

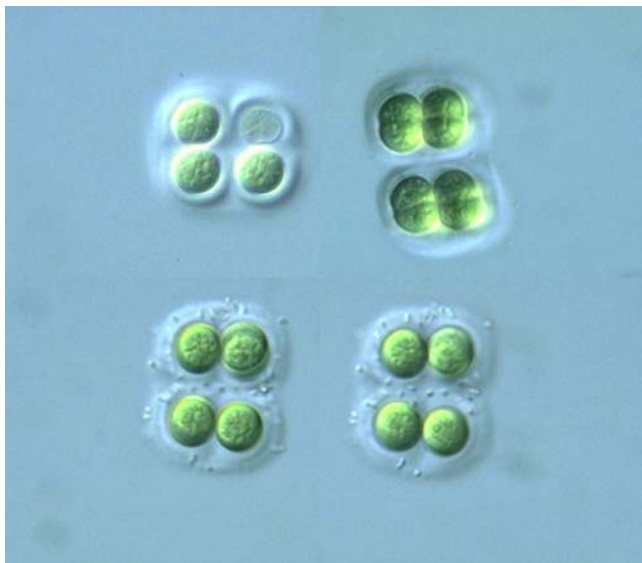


Figure 39. *Gloeocapsa*, a genus common on cave walls in Serbia and elsewhere. Photo by Yuuji Tsukii, with permission.

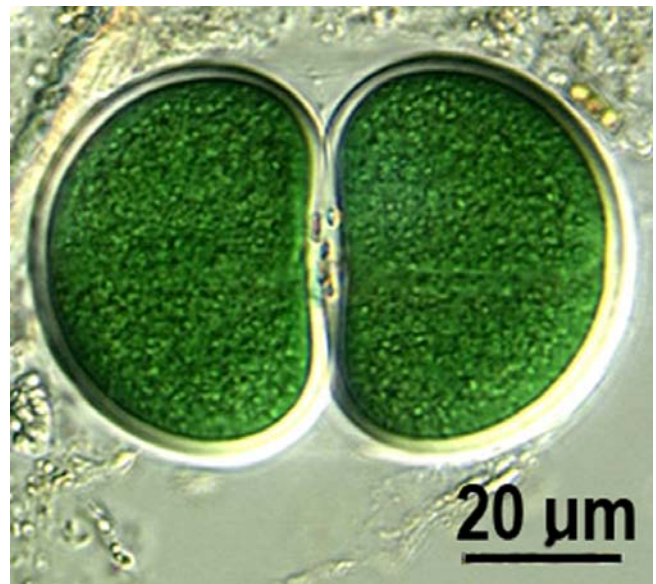


Figure 42. *Chroococcus* sp., a genus common on cave walls in Serbia and elsewhere. Photo by Jason Oyadomari, with permission.



Figure 40. *Scytonema* sp., a genus common on cave walls in Serbia and elsewhere. Photo from UTEX, through Creative Commons.

Mulec *et al.* (2008) reported on the **aerophytic** (designates living in air in terrestrial habitats, on rocks, stones, sediments, trees, needing water only from atmosphere) algal community from a cave entrance in contrast to the lampenflora. They found the entrance community to be almost entirely **Cyanobacteria**, whereas at the lights green algae (**Chlorophyta**) became more dominant. They concluded, based on lack of correlation of chlorophyll *a* concentration per surface unit with photon flux density, that microhabitat substrate characteristics were important in influencing algal growth. The chlorophyll *a* concentration is lower in algae at the cave entrance than it is among the lampenflora. The low temperatures of the cave result in a low light saturation point. At 9°C, the production of accessory photosynthetic pigments is elevated considerably in the **Cyanobacterium** *Chroococcus minutus* (Figure 43) and green alga *Chlorella* sp. (Figure 44).





Figure 43. *Chroococcus minutus*, a species for which accessory photosynthetic pigments increase when the temperature is lowered to 9°C. Photo from Nordic Microalgae <nordicmicroalgae.org>, through Creative Commons.

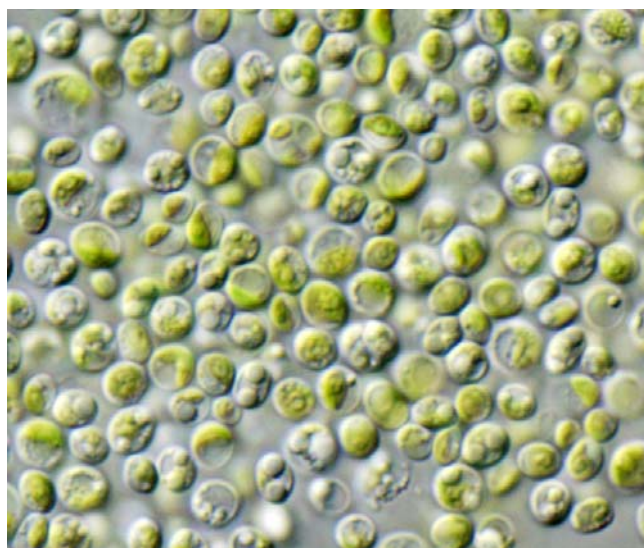


Figure 44. *Chlorella vulgaris*. A cave member of *Chlorella* increases its accessory photosynthetic pigments when the temperature is lowered to 9°C. Photo by Neon, through Creative Commons.

Popović *et al.* (2017) found that the greatest number of phototrophic microorganisms in three Siberian caves were **Cyanobacteria**, with *Gloeocapsa* (Figure 39, Figure 50, Figure 55, Figure 56) being the most diverse genus. They found that relative humidity is important in accounting for differences among the three microbial communities in the three caves. **Cyanobacteria** mostly occurred in locations with lower relative humidity, whereas **Chlorophyta** (green algae) and **Bacillariophyta** (diatoms) occurred where there was higher humidity.

Some of the biofilm taxa can be recognized by their colors (Popović *et al.* 2020). Coccoid cyanobacterial forms create gelatinous, olive to dark-green biofilms. *Gloeobacter* (Figure 45) appears purple; *Gloeocapsa* (Figure 46) is yellow, and *Chroococcidiopsis* (Figure 47) forms a black film. The heterocystic biofilms are primarily *Nostoc* (Figure 48-Figure 49) and are brown to dark in color.



Figure 45. *Gloeobacter* sp., a genus that appears purple in cave biofilms. Photo by Burn12121212, through Creative Commons.

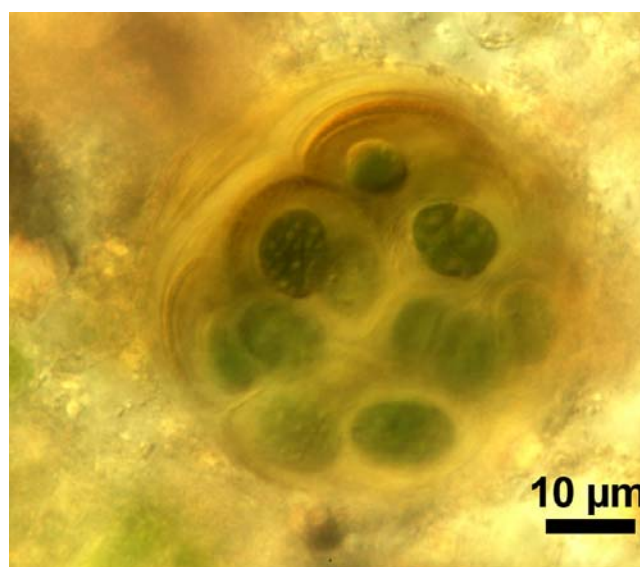


Figure 46. *Gloeocapsa rupestris* showing yellow color typical of its occurrence in cave biofilms. Photo by Cyanpro, through Creative Commons.

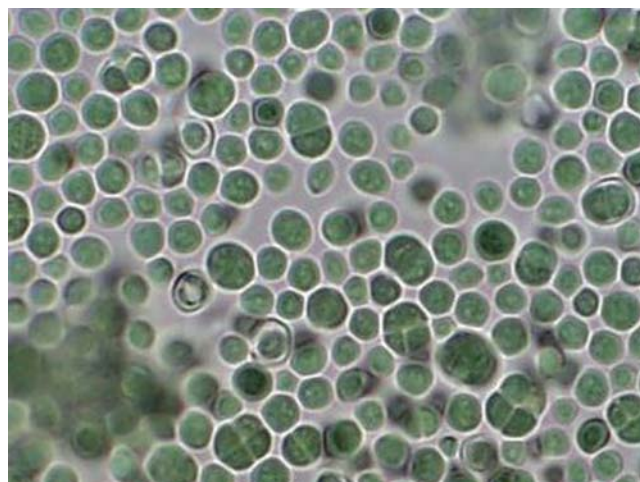


Figure 47. *Chroococcidiopsis* sp., a genus that appears black in cave biofilms. Photo by Burn12121212, through Creative Commons.





Figure 48. *Nostoc commune*, a common cave-dwelling member of **Cyanobacteria**, on soil with mosses. Photo by Yamamaya, through Creative Commons.

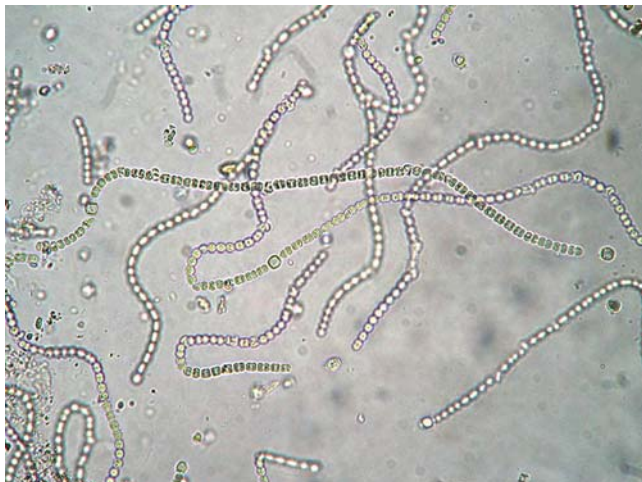


Figure 49. *Nostoc commune*, a common cave dweller. Photo by Kristian Peters, through Creative Commons.

Czerwik-Marcinkowska (2013) studied the **Cyanobacteria** and algae in ten caves in the Ojców National Park, Poland. The author identified 35 **Cyanobacteria**, 30 **Chlorophyta**, and 20 from other groups of algae. These were dominated by aerophytic **Cyanobacteria** (see also Komáromy *et al.* 1985). The **Cyanobacteria**/algae *Gloeocapsa alpina* (Figure 50), *Nostoc commune* (Figure 48-Figure 49), *Chlorella vulgaris* (Figure 44), *Dilabifilum arthropryeniae*, *Klebsormidium flaccidum* (Figure 51), *Muriella decolor*, *Neocystis subglobosa*, and *Orthoseira roseana* (Figure 27) were the most abundant taxa in all ten caves. The **Cyanobacteria** are typically the only phototrophs in the deepest parts of the caves, but around the entrance and electric lights they must compete for light with the other algae, bryophytes, and even ferns (Round 1981). Czerwik-Marcinkowska (2013) suggested that it was the nearly constant conditions that were so favorable to these algae.

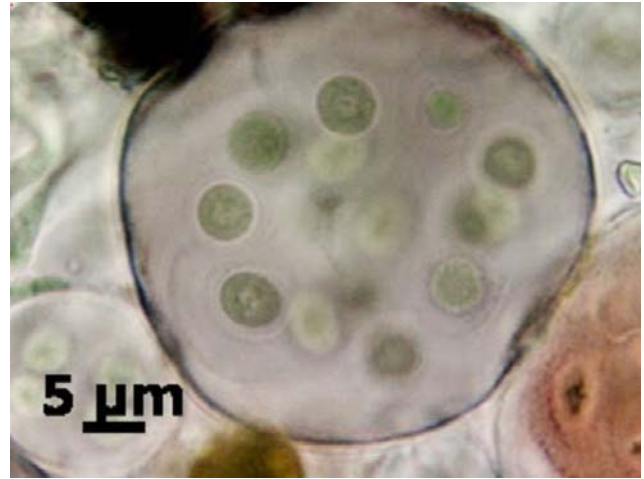


Figure 50. *Gloeocapsa alpina*, one of the most abundant **Cyanobacteria** in ten caves in the Ojców National Park, Poland. Photo from AlgaeBase, through Creative Commons.

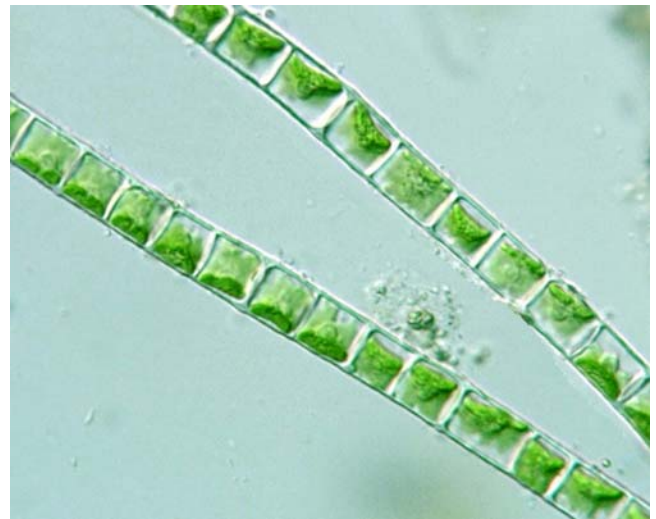


Figure 51. *Klebsormidium flaccidum*, a common green alga in ten caves in the Ojców National Park, Poland. Photo by Yuuji Tsukii, with permission.

In Seneca Cavern, Ohio, USA, Dayner and Johansen (1991) found 25 algal taxa in subaerial habitats. These were mostly aerophilic species, with the most abundant being *Chlorella miniata*, *Pleurochloris commutata* (**Ochrophyta**; see Figure 52), *Navicula tantula* (Figure 53), and *Navicula contenta* f. *biceps*. They considered the dim light in this earth crack cave and lack of running water to be the reason for the smaller than typical number of species.

Mazina and Popkova (2020b) found *Chroococcus minutus* (Figure 43) and *Chlorella vulgaris* (Figure 44) to be the most frequent phototrophs in all the studied caves in Ukraine, Italy, and Hungary.

When lights are present in caves, the phototrophs can penetrate to a much greater distance. Komáromy *et al.* (1985) used cluster analysis to clarify relationships of the photosynthetic organisms in the cave. These researchers found 42 algal taxa in a single Hungarian show cave. (This number apparently included the **Cyanobacteria** as they were considered by the authors to be blue-green algae). They noted that the **Cyanobacteria** were species with



small cell sizes and that both lichens and liverworts are extremely rare in the habitats surrounding lamps. They delineated the algae by using scrapings that were then cultured on liquid Bold medium.

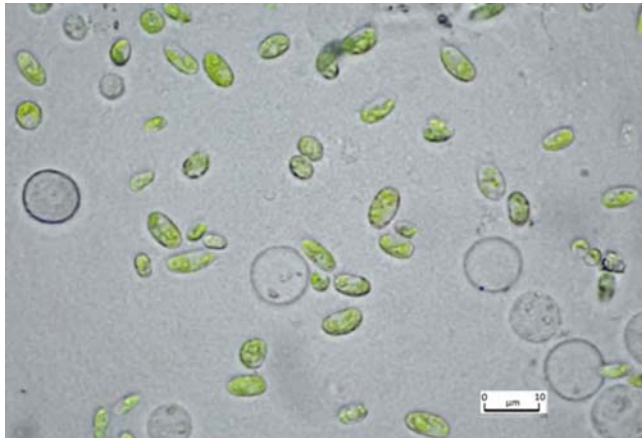


Figure 52. *Pleurochloris pyrenoidosa*; *P. commutata* is among the most abundant algae in Seneca Cavern, Ohio, USA. Photo by Pierre Noel, through Creative Commons.



Figure 53. *Navicula tantula*, a species that is among the most abundant algae in Seneca Cavern, Ohio, USA. Photo from UTEX, through Creative Commons.

Czerwik-Marcinkowska *et al.* (2019) similarly cultured scrapings of the algae and *Cyanobacteria* from walls of a cave in the Tatra Mountains of Poland. Ten of the species were *Cyanobacteria*; *Gloeocapsa* (Figure 39) was the most diverse genus. Four were diatom taxa. Diversity did not relate to temperature or humidity.

Czerwik-Marcinkowska *et al.* (2019) explored the relationship between brown bears (*Ursus arctos*; Figure 54) in caves and the diversity of airborne algae and *Cyanobacteria* in the Glowoniowa Nyża Cave, Tatra Mountains, Poland. Like Popović *et al.* (2017), they found the cyanobacterial genus *Gloeocapsa* (Figure 39, Figure 50, Figure 55, Figure 56) to be the most diverse. The highest number of species were in *Cyanobacteria* (10), but they also found 10 algae and four diatom species. The algal diversity did not correlate with temperature or humidity. The aerophytic organisms in the wall flora were apparently brought by wind, whereas the ones on twigs may have been brought by wind and bears. The bears in the cave use mosses, among other materials, to line their dens, creating another means of dispersal into the cave.



Figure 54. *Ursus arctos* (brown bear), a potential disperser of *Cyanobacteria* and algae into some caves. Photo by Magnus Johansson, through Creative Commons.

*Nostoc commune* (Figure 48-Figure 49) forms thick mats along with other airborne algae in the Glowoniowa Nyża Cave, Tatra Mountains, Poland (Czerwik-Marcinkowska *et al.* 2019). *Gloeocapsa atrata* (Figure 55) occurs in the cave and among mosses, especially on wet rocks (John *et al.* 2011). *Gloeotheca palea* (Figure 56) occasionally grows among mosses (Czerwik-Marcinkowska *et al.* 2019).

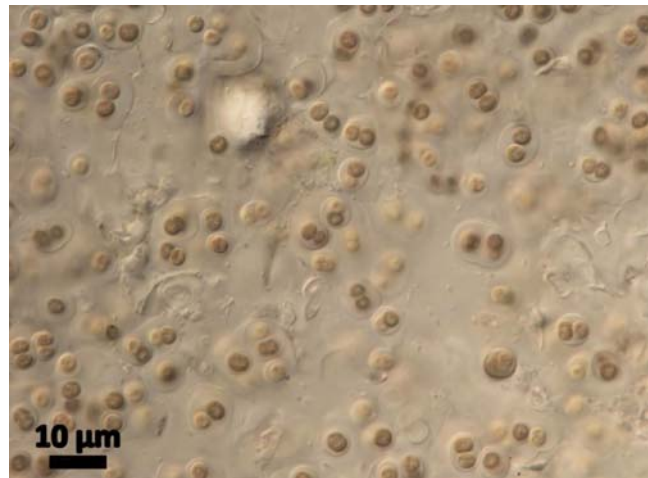


Figure 55. *Gloeocapsa atrata*, a species that occurs among mosses on wet cave rocks. Photo from AlgaeBase, through Creative Commons.



Figure 56. *Gloeotheca palea*, a species that occurs among mosses on wet cave rocks. Photo Davydov D., through Creative Commons.



Like many other researchers, Czerwik-Marcinkowska *et al.* (2015) found that aerophytic **Cyanobacteria** were the most important members of the cave photosynthetic microflora. The most frequent were *Aphanocapsa* (Figure 41), *Chroococcus* (Figure 42, Figure 43), *Gloeocapsa* (Figure 50, Figure 55-Figure 56), *Leptolyngbya* (Figure 21-Figure 22), and *Synechocystis* (Figure 57). The predominant green algae were *Apatococcus* (Figure 58), *Klebsormidium* (Figure 31), *Chlorella* (Figure 44), *Muriella*, and *Neocystis*. Diatoms were dominated by *Orthoseira* (Figure 27) and *Pinnularia* (Figure 28). The algae were mostly cosmopolitan and ubiquitous, with simple nutrient requirements and wide ecological tolerance.



Figure 57. *Synechocystis* sp., a member of **Cyanobacteria**, one of the most important members of the cave photosynthetic microflora. Photo by Yuuji Tsukii, with permission.



Figure 58. *Apatococcus* sp., a member of **Chlorophyta**, one of the most important members of the cave photosynthetic microflora. Photo by Yuuji Tsukii, with permission.

Popović *et al.* (2017) likewise found that most of the taxa in cave biofilms in Serbia belonged to the **Cyanobacteria**. **Chroococcales** were dominant, and *Gloeocapsa* (Figure 50, Figure 55-Figure 56) was the most diverse genus. They found that **Cyanobacteria** were able to dominate where humidity was lower; **Chlorophyta** and **Bacillariophyta** occurred in locations with higher humidity. The chlorophyll *a* content was highest on horizontal surfaces, corresponding with the highest content of organic and inorganic matter as well. The highest water content was maintained in biofilms that contained many **Cyanobacteria**.

Pouličková and Hašler (2007) reported aerophytic diatoms from caves in central Moravia in the Czech Republic. Rushforth *et al.* (1984) explored the subaerial diatom flora in the Thurston lava tube in Hawaii, USA. These occurred on wet mucilage and bryophytes on the walls. Falasco *et al.* (2015) described a new species of diatom (*Nupela troglaphila*) from the Bossea Cave in Italy. They also noted that Rushforth *et al.* (1984) had found *Nupela thurstonensis* on the wet walls and bryophytes of the Thurston lava tube in Hawai'i. Both species occurred near the entrance and the artificial lighting.

Falasco *et al.* (2014) reported that the cave flora produces polysaccharides, proteins, lipids, and nucleic acids. This matrix is anionic, and facilitates the adsorption of cations and dissolved organic molecules from the cave formations. These exchanges can contribute to the corrosion of the cave walls. Diatoms, in particular, typically colonize these areas when there is sufficient light. Falasco and coworkers reported 363 species of diatoms listed in the literature as occupying subterranean habitats. The most frequent cave diatom species, in order from most frequent, are *Hantzschia amphioxys* (Figure 26), *Humidophila contenta* (Figure 25), *Orthoseira roseana* (Figure 27), *Luticola nivalis* (see Figure 59), *Pinnularia borealis* (Figure 28), *Diademsis contenta* var. *biceps* (see Figure 60), and *Luticola mutica* (Figure 61). They also noted that it is not uncommon to find new species in these habitats.

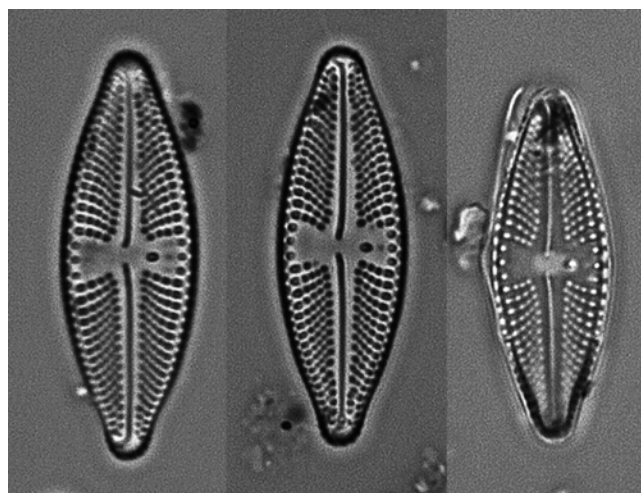


Figure 59. *Luticola* sp.; *Luticola nivalis* is one of the most frequent diatoms in caves. Photo by A. E. Drahos, through Creative Commons.

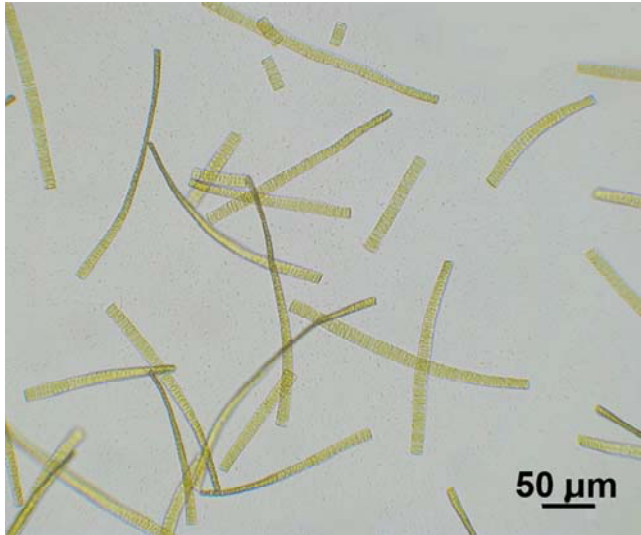


Figure 60. *Diadmesmis cf. gallica*; *Diadmesmis contenta* var. *biceps* is one of the frequent diatoms in caves. Photo modified from ©BELSPO, with online permission.

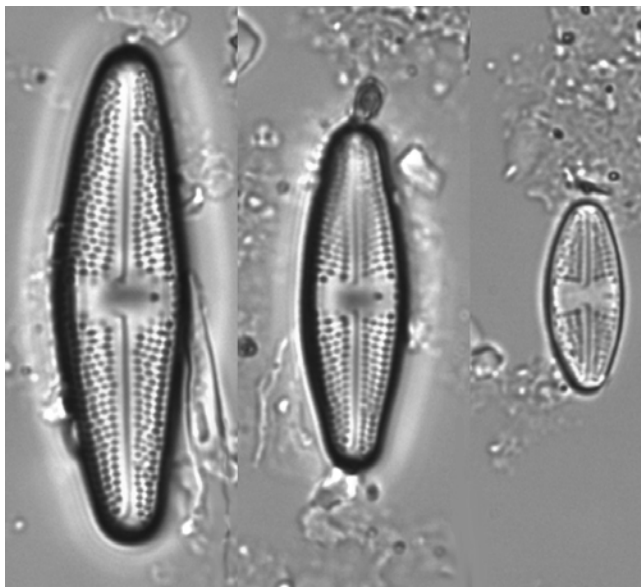


Figure 61. *Luticola mutica*, one of most common species of diatoms in caves. Photo by Lane Allen, through Creative Commons.

*Hantzschia amphioxys* (Figure 26) is aerophilous (Germain 1981) and one of the most frequently recorded taxa on submerged bryophytes (Reichardt 1985; van de Vijver & Beyens 1997). *Humidophila contenta* (Figure 25) occurs on both wet walls and on bryophytes (Rushforth *et al.* 1984; Roldán & Hernández-Maríné 2009). *Diadmesmis contenta* var. *biceps* (see Figure 60) occurs on wet walls and bryophytes (Dayner & Johansen 1991; Falasco *et al.* 2014). *Luticola mutica* (Figure 61) is one of the most frequent taxa on submerged bryophytes (Reichardt 1985; van de Vijver & Beyens 1997); it is resistant to moderately high conductivity levels (Pouličková & Hašler 2007). This tolerance seems to account for its common occurrence also in lowland rivers (van Dam *et al.* 1994; Czerwik-Marcinkowska & Mrozińska 2011).

*Pinnularia borealis* (Figure 28) is one of the most frequent diatoms on submerged bryophytes (Reichardt 1985; Van de Vijver & Beyens 1997; Falasco *et al.* 2014). Nevertheless, Vande Vijver and Beyens (1997) found it to be in an assemblage on very dry mosses in South Georgia. *Pinnularia borealis* (Figure 28), common in the Glowoniowa Nyża Cave, is aerophilous, but frequently occurs on submerged bryophytes and in wild caves near the main entrance on very wet walls (Garbacki *et al.* 1999). Van de Vijver and Beyens (1997) found that *Pinnularia borealis* size drops with the increasing dryness of the moss habitat.

Borrego-Ramos *et al.* (2018) reported on the diatoms from the Valporquero Cave in Spain. They found that moss-dwelling diatom associations differed from those in other parts of the cave. They found *Mayamaea cavernicola* (incorrectly identified as *Navicula seminulum* var. *hustedtii*; Figure 62), a species already known from a lava tube cave on the Hawai'ian Islands (Rushforth *et al.* 1984). A different sample from the Spanish cave was almost entirely made up of *Humidophila gallica* (see Figure 25).



Figure 62. *Mayamaea atomus*; *M. cavernicola* is a species known from lava tubes and caves. From Sarah Spaulding and Mark Edlund, <diatoms.org>, with permission.

Lauriol *et al.* (2006) found that 80% of the diatoms in ice caves (Figure 63) of the Yukon Territory were of local origin from subaerial habitats near the cave entrances. These include the sub-aerial diatoms *Orthoseira dendroteres* (a common bryophyte dweller; Figure 64) and *O. roseana* (Figure 27). Larger caves tended to have more species, presumably due to the greater air circulation in these caves. The **grus** (accumulation of angular, coarse-grained fragments resulting from granular disintegration of crystalline rocks), ice plugs, and ice stalagmites have the greatest relative abundance of diatoms, but the lowest diversity. Can these principles serve as models for bryophytes? It appears that they do.





Figure 63. Ice cave in natural glacier, often a home for diatom species in the genus *Orthoseira*. Photo by Serge J. F., through Creative Commons.

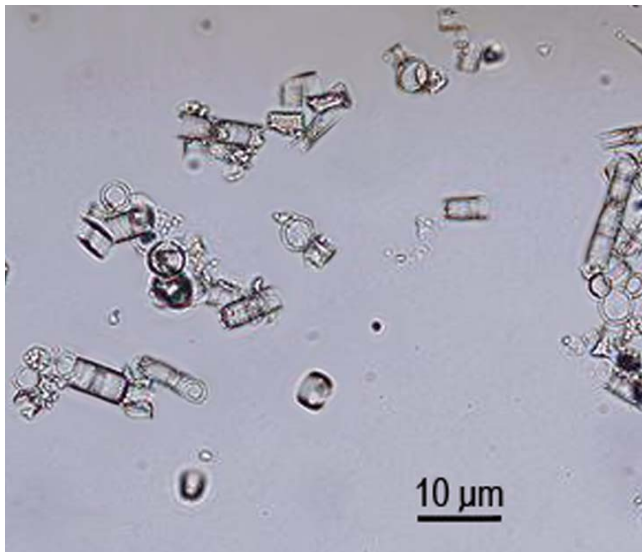


Figure 64. *Orthoseira dendroteres*, a subaerial diatom that occurs in ice caves in the Yukon Territory. Photo by UTEX, through Creative Commons.

When light enters the cave, particularly at the entrances, **Cyanobacteria** contribute to the growth of **stalactites** (tapering structures hanging like icicles from roof of cave, formed of calcium salts deposited by dripping water; "stalactites must hang on tight;" think **c** for ceiling; Figure 1, Figure 6) and **stalagmites** (mound or tapering columns rising from floor of cave, formed of calcium salts deposited by dripping water and often uniting with stalactite to form column; "stalagmites are little mites;" think **g** for ground; Figure 1, Figure 6) (Mulec *et al.* 2007).

The **Cyanobacteria** contribute to making the layers of stromatolitic stalagmites. Mulec *et al.* (2007) found 35 taxa associated with them at the cave entrance of Škocjanske jame, Slovenia. These had a low portion of coccoid **Cyanobacteria** and other **Cyanobacteria** such as *Calothrix* sp. (Figure 65), *Homeothrix* sp. (Figure 66), and *Schizothrix* sp. (Figure 67).



Figure 65. *Calothrix parietina*, a cave dweller in a genus that contributes to making layers of stalagmites. Photo from AlgaeBase, through Creative Commons.

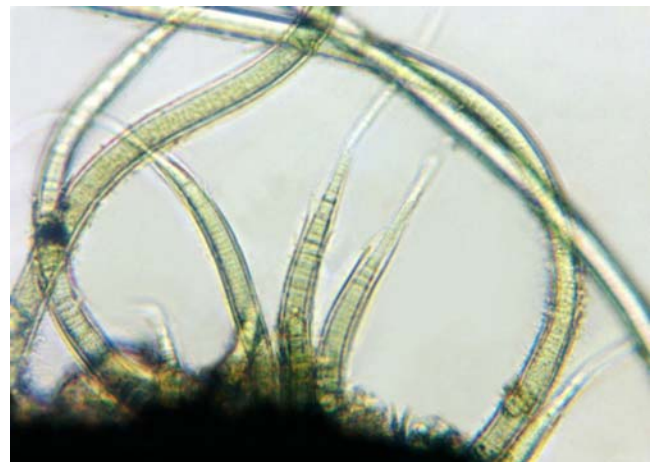


Figure 66. *Homeothrix* sp., in a genus that contributes to making layers of stalagmites. Photo from Manaaki Whenua – Landcare Research, with online permission.

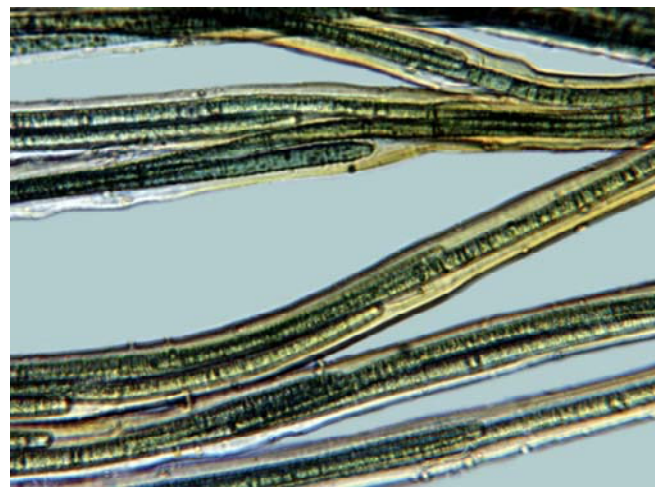


Figure 67. *Schizothrix* sp., in a genus that contributes to making layers of stalagmites. Photo from Manaaki Whenua – Landcare Research, with online permission.

One bryophyte that seems to occur in multiple caves is *Eucladium verticillatum* (Figure 68-Figure 69) (Dalby 1966a). It actually helps to build the stalactites by



collecting the dripping lime water. The stalactite surrounds the moss, and green leaves are visible only at the tips. It is notable that this species does not become etiolated even in the lowest illumination where it grows. Dalby found that it did not even become etiolated when kept in a polyethylene bag in total darkness for two months, but with no light I wouldn't have expected it to grow at all.



Figure 68. *Eucladium verticillatum* with mineral deposits on leaf tips. Photo by Armand Turpel, through Creative Commons.

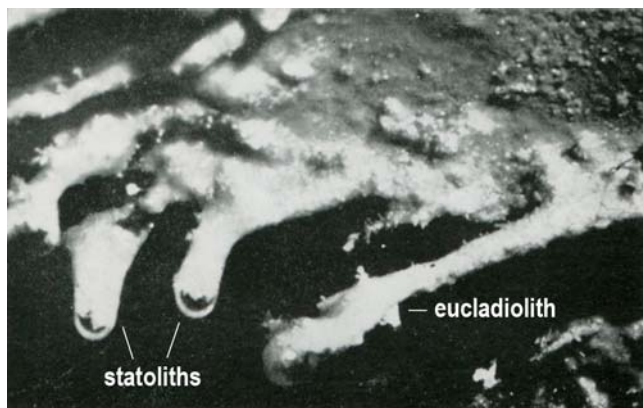


Figure 69. *Eucladium verticillatum* forming stalactite (eucladiolite) in mine in Dorset, UK. Note the nearly horizontal development of the eucladiolith. Photo from Dalby 1966b.

In the carbonate depositions on the lighted side of the stalactites, there were 14 species of **Cyanobacteria**, mainly coccoid forms (Mulec *et al.* 2007). Their growth and biolithogenic activity are especially associated with the moss *Eucladium verticillatum* (Figure 68-Figure 69). This results in formations known as **eucladioliths** (Figure 69) (Dalby 1966b).

Czerwik-Marcinkowska and Mrozińska (2011) reported 82 species of aerophytic **Cyanobacteria** and algae from 25 caves in the Polish Jura. Of these, 33 species were **Cyanobacteria** with the **Chlorophyta** represented by 30 species. There were even 2 species of **Dinophyta**. They found a number of rare species, some of them specific to these caves. **Cyanobacteria** at the entrance and around lights included predominantly *Calothrix parietina* (Figure 65), *Gloeocapsopsis magma* (Figure 70-Figure 71), *Nostoc commune* (Figure 48-Figure 49), *Oscillatoria brevis*

(Figure 72), and *Tolypothrix tenuis* (Figure 73). These **Cyanobacteria** competed with algae, especially the **Chlorophyta** *Chlamydomonas* sp. (Figure 74), *Muriella decolor*, and *Klebsormidium flaccidum* (Figure 31), as well as with mosses and pteridophytes. The moss *Cratoneuron* (Figure 75) was accompanied by aerophilic diatoms [*Humidophila contenta* (Figure 25), *Gomphonema italicum* (Figure 76-Figure 77)] and **Chlorophyta** [*Chlorella vulgaris* (Figure 44), *Trentepohlia aurea* (Figure 37-Figure 38), *Stichococcus bacillaris* (Figure 29)].



Figure 70. *Gloeocapsopsis magma* on rock, a common species at cave entrances and near lights. Photo by Randal, through Creative Commons.

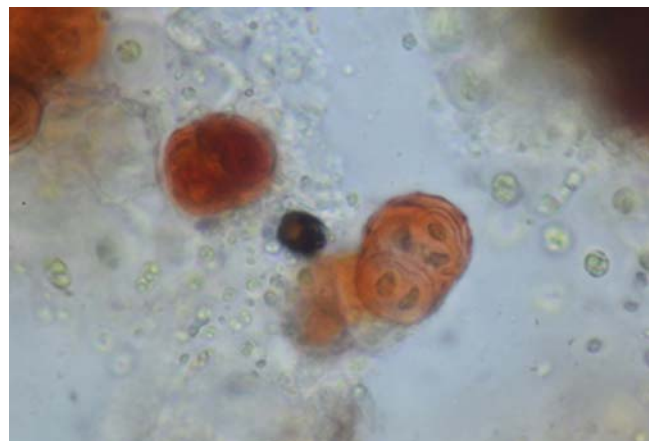


Figure 71. *Gloeocapsopsis magma*, a common cave species. Photo by Randal, through public domain.

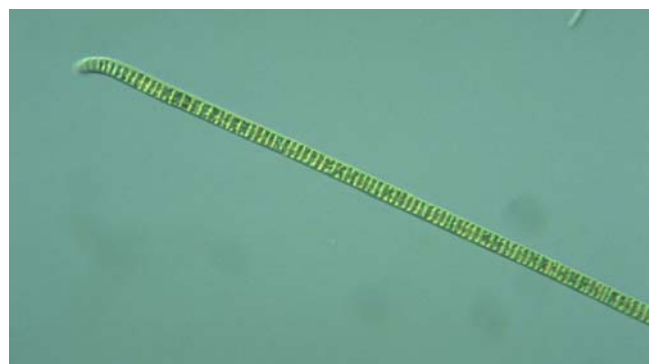


Figure 72. *Oscillatoria brevis*, a common cave entrance and lampenflora species. Photo by Yuuji Tsukii, with permission.





Figure 73. *Tolypothrix tenuis*, a common cave entrance and lampenflora species. Photo by Yuuji Tsukii, with permission.

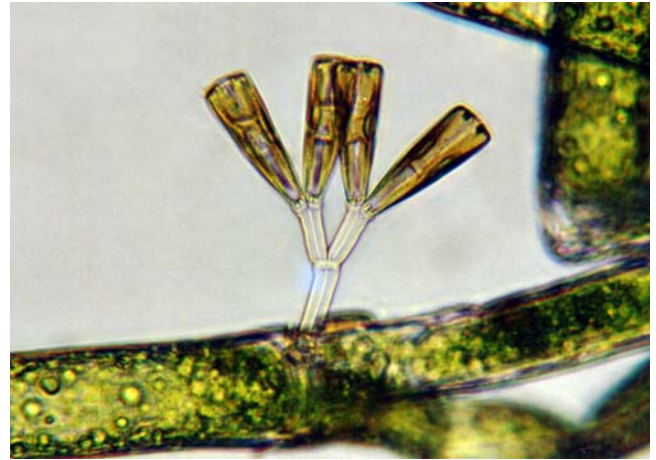


Figure 76. *Gomphonema* sp., member of a cave-dwelling diatom genus, attached to *Cladophora*. Photo from Manaaki Whenua – Landcare Research, with online permission.

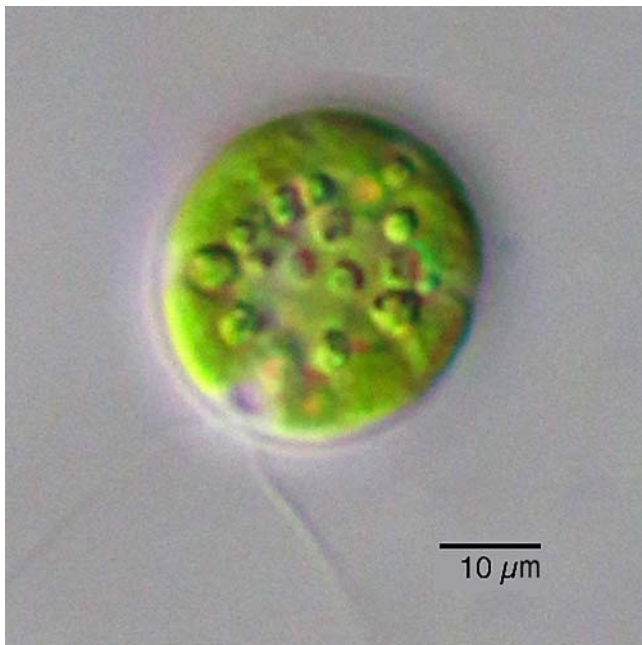


Figure 74. *Chlamydomonas globosa*, a common cave entrance and lampenflora species. Photo by Picturepest, through Creative Commons.

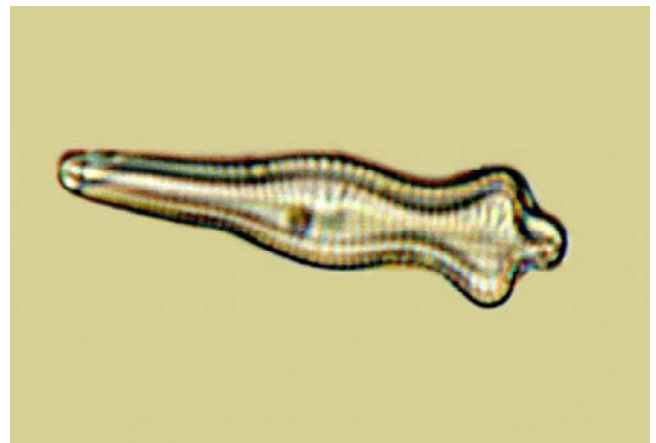


Figure 77. *Gomphonema* sp. Photo from Manaaki Whenua – Landcare Research, with online permission.

Sciuto *et al.* (2017) described the new genus *Timaviella* (Leptolyngbyaceae in Cyanobacteria) from the Giant Cave lampenflora in Italy. There were actually two species described for it in that cave (*Timaviella circinata* and *Timaviella karstica*).

Koch (1976) suggested that bryophytes create runoff that might affect the other organisms living with them. One such possibility is indicated between bryophytes and the green alga *Protococcus vestitus* (Figure 78). Data also suggested that bryophytes might be important in colonization by *Trochiscia ohioensis* (see Figure 79). It was closely associated with bryophytes at Ash Cave Cliff in Ohio, USA. But whereas *Trochiscia ohioensis* occurred in 51 collections, bryophytes occurred in only 6 of these. Nevertheless, both *Protococcus vestitus* and *Trochiscia ohioensis* had high correlations with bryophytes. They were present in 18 of the 20 stands in which *Trochiscia ohioensis* occurred. (Unfortunately, I was unable to match either of these algal species names to any in AlgaeBase; all records of the rare *Protococcus vestitus* other than this one are 19th century.) Koch suggested that the bryophytes, especially thallose liverworts, could retain enough moisture to make the habitat suitable for the algae. The frequently abundant chroococcalean Cyanobacteria are only present with the bryophytes when there is abundant moisture present.



Figure 75. *Cratoneuron filicinum*, a species that provides substrate for several species of diatoms in caves. Photo by Hermann Schachner, through Creative Commons.





Figure 78. *Apatococcus lobata* (syn. = *Protococcus viridis*); *Protococcus vestita* had a high correlation with bryophytes in Ash Cave Cliff in Ohio, USA. Photo by Yuuji Tsukii, with permission.



Figure 79. *Trochiscia aspera*; *T. ohioensis* has a high correlation with bryophytes on Ash Cave Cliff in Ohio, USA. Photo by Yuuji Tsukii, with permission.

**Cyanobacteria** with **heterocysts** (Figure 80) can fix atmospheric  $N_2$  into usable forms (Lamprinou *et al.* 2012) that prepare the environment for colonization of other **Cyanobacteria**, algae, and mosses (Ortega-Calvo *et al.* 1995). **Cyanobacteria** are important in many ecosystems for their ability to transform atmospheric nitrogen into usable forms. Asencio and Aboal (2011) found that *Scytonema julianum* (see Figure 40) contributed to this activity in Vapor Cave in Spain.

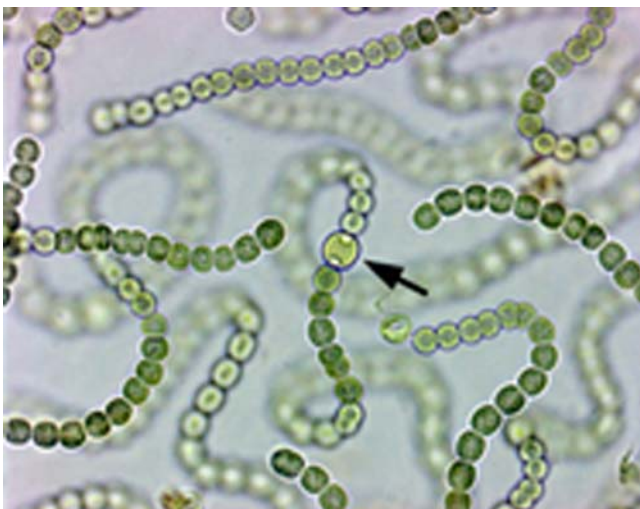


Figure 80. *Nostoc* sp. 1 showing heterocyst <vle.du.ac.in>, through Creative Commons.

## Fungi

Vanderwolf *et al.* (2013) documented 1029 species of fungi, slime molds, and yeasts, based on 225 publications on caves and mines. They found the **Ascomycota** to be the dominant group among these. The cave fungi communities are typically those requiring few nutrients (**oligotrophic**) and tolerating year-round low temperatures (**psychrotolerant**).

Fungi in three Serbian caves were primarily **Ascomycota** or **Zygomycota** (Popović *et al.* 2017). Popović *et al.* (2015, 2017) found that **Ascomycota** were common [e.g. *Alternaria* (Figure 81-Figure 82), *Aspergillus* (Figure 83), *Cladosporium* (Figure 84), *Epicoccum* (Figure 85-Figure 86), *Penicillium* (Figure 87-Figure 88), and *Trichoderma* (Figure 89-Figure 90)], while **Zygomycota** and **Oomycota** were less frequent in Božana Cave, Serbia. The only member of **Basidiomycota** was one of *Rhizoctonia s.l.* (Figure 91-Figure 92) (Popović *et al.* 2017).



Figure 81. *Alternaria alternata* on tobacco leaf. Photo from the Bugwood Network, through Creative Commons.



Figure 82. *Alternaria alternata*, a common **Ascomycota** fungus in three Serbian caves. Photo by Abdulghafour, through Creative Commons.





Figure 83. *Aspergillus oryzae*, a common *Ascomycota* fungus in three Serbian caves. Photo by Yulianna, through Creative Commons.

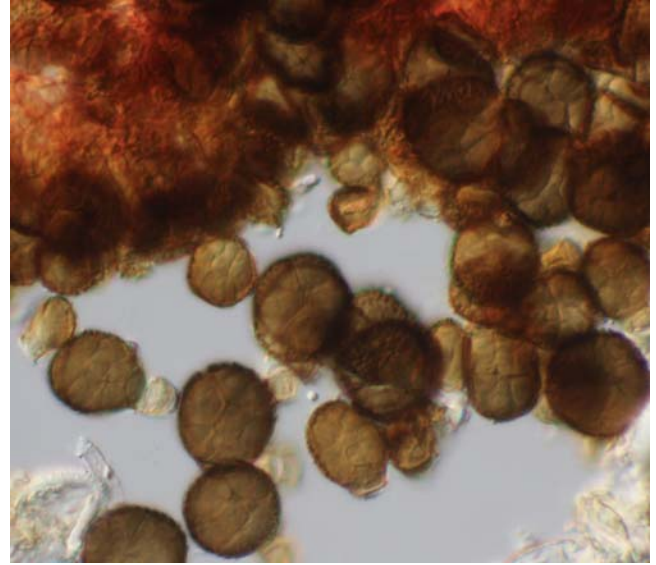


Figure 86. *Epicoccum nigrum*; the genus *Epicoccum* is a common *Ascomycota* fungus in three Serbian caves. Photo by Paul Cannon, through Creative Commons.

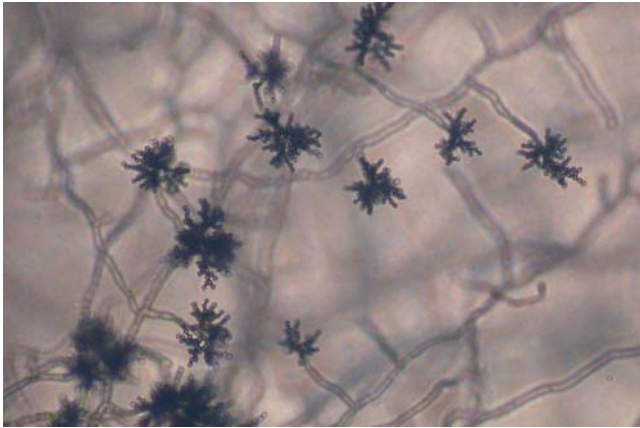


Figure 84. *Cladosporium* sp. conidia, a common *Ascomycota* fungus in three Serbian caves. Photo by Keisotyo, through Creative Commons.

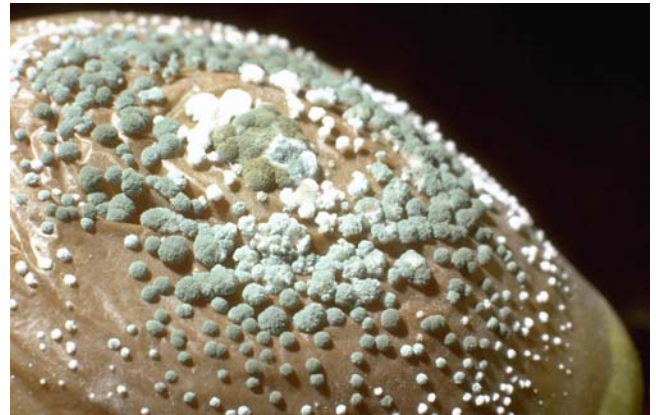


Figure 87. *Penicillium expansum* on pear. Photo by H. J. Larsen, through Creative Commons.



Figure 85. *Epicoccum nigrum* infection on mushroom. Photo by Walt Sturgeon, through Creative Commons.



Figure 88. *Penicillium spinulosum*; the genus *Penicillium* is a common *Ascomycota* fungus in three Serbian caves. Photo by Medmyco, through Creative Commons.





Figure 89. *Trichoderma* sp. on decaying wood in Japan. Photo by Keisotyo, through Creative Commons.

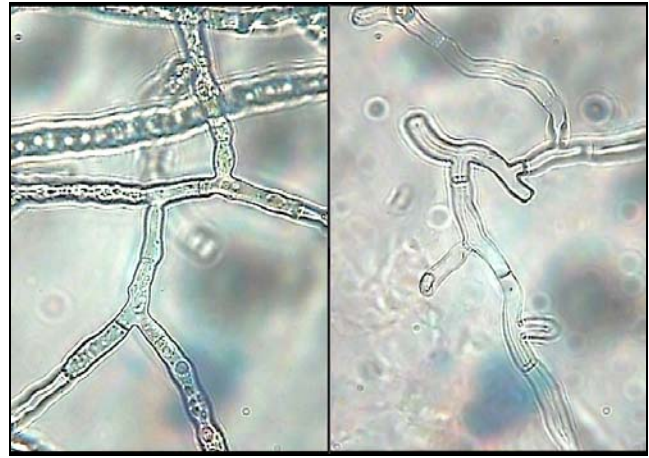


Figure 92. *Rhizoctonia solani*; *Rhizoctonia* s.l. is the only member of **Basidiomycota** found in three Serbian caves. Photo by Tashkoskip, through Creative Commons.



Figure 90. *Trichoderma fertile*; the genus *Trichoderma* is a common **Ascomycota** fungus in three Serbian caves. Photo through public domain.



Figure 91. *Rhizoctonia solani* on sugar beet root, a genus found in three Serbian caves. Photo through Creative Commons.

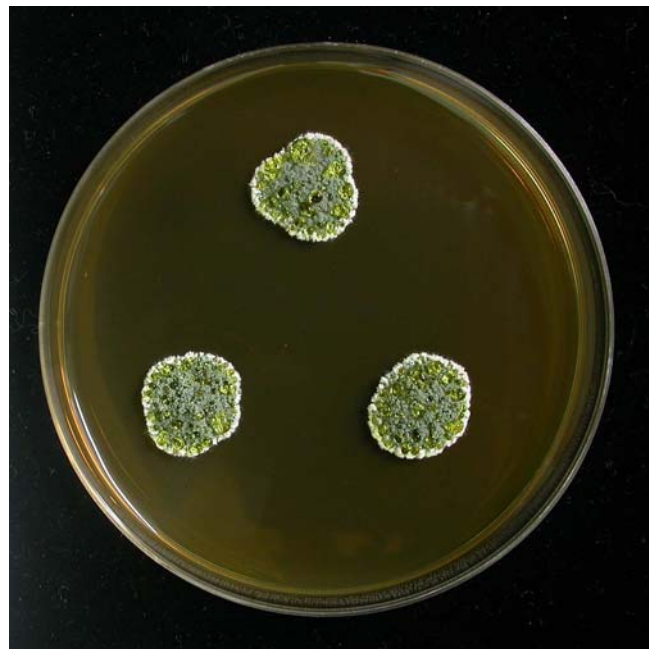


Figure 93. *Penicillium glandicola*, a frequent species in the Domica Cave system in Slovakia. Photo by Y. V. Sagar, through Creative Commons.

Air currents in the cave are likely to contribute to dispersal of fungal spores, but Jurado *et al.* (2009) suggested that insects within the cave might play a role in spore dispersal as well. This possibility is further supported by the fact that most of the fungi proved to be **entomopathogens** (micro-organisms capable of infecting insects). In European caves with rock-art paintings (Figure 33), a test area was sterilized and after two months the rock tablets placed there were heavily colonized by fungi.

Nováková (2009) reported on the microscopic fungi isolated from the Domica Cave system in Slovakia. The frequent species included *Penicillium glandicola* (Figure 93), *Trichoderma polysporum* (see Figure 89-Figure 90), *Oidiodendron cerealis*, *Mucor* spp. (Figure 94-Figure 95), *Talaromyces flavus* (Figure 96-Figure 97), and species of the genus *Doratomyces* (Figure 98).



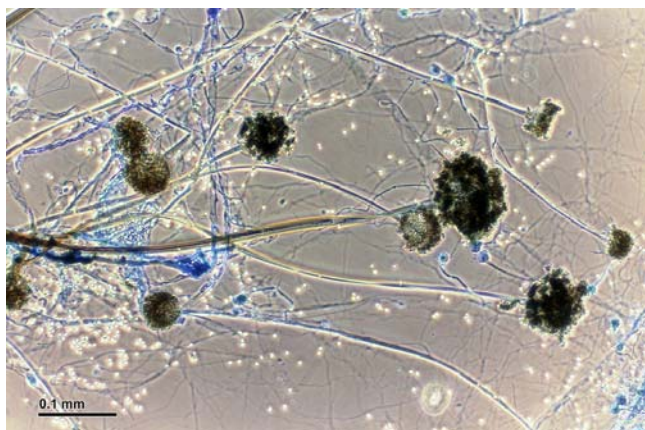


Figure 94. *Mucor* sp., a frequent genus in the Domica Cave system in Slovakia. Photo by Josef Reischig, through Creative Commons.



Figure 95. *Mucor* mature sporangium, a frequent genus in the Domica Cave system in Slovakia. Photo by Lucille K. Georg, CDC, through public domain.

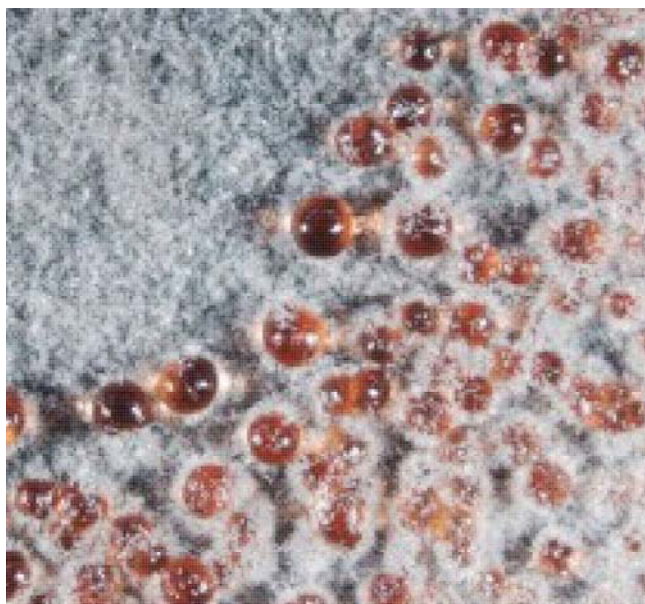


Figure 96. *Talaromyces atroseus* colony. Photo by Jens C. Frisvad, Neriman Yilmaz, Ulf Thrane, Kasper Bøwig Rasmussen, Jos Houbraken, and Robert A. Samson, through Creative Commons.

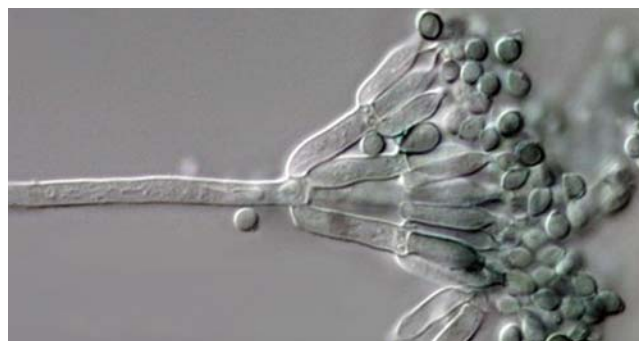


Figure 97. *Talaromyces atroseus*; *Talaromyces flavus* is frequent in the Domica Cave system in Slovakia. Photo by Jens C. Frisvad, Neriman Yilmaz, Ulf Thrane, Kasper Bøwig Rasmussen, Jos Houbraken, and Robert A. Samson, through Creative Commons.

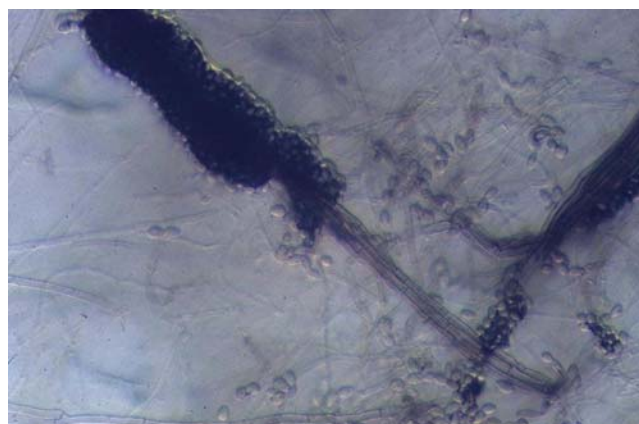


Figure 98. *Doratomyces stemonitis*; *Doratomyces* is a frequent genus in the Domica Cave system in Slovakia. Photo by Gerald Holmes, through Creative Commons.

## Summary

Caves are interesting ecotones of light and temperature gradients. They are further differentiated on type of substrate, pH, aspect, and air exchange. CO<sub>2</sub> levels can be higher than outside the cave, promoting greater photosynthesis in the limited light. Although conditions do fluctuate, they are more constant than outside the cave, being cooler in summer and warmer in winter. Because of these conditions, caves are often refugia, permitting the growth of species that do not grow elsewhere in the area.

A wide variety of caves exist, both large and small. Some are created in crevices, some among the rocks of talus slopes, and some in volcanic tubes, with a variety of other cave-like conditions as well. These can harbor rare species.

In addition to an array of bryophytes in the photic zone at the entrance of caves, others penetrate into the twilight zone. **Cyanobacteria**, algae, and fungi join the bryophytes, but usually penetrate farther into the darkness. *Streptomyces* (**Eubacteria**) species dominate the rock microbes. Among the **Cyanobacteria** *Gloeocapsa* often has the most species in a cave, but in others it is *Chroococcus* that has the most species.

Species like *Scytonema julianum* with heterocysts are able to fix atmospheric nitrogen gas into ammonia and ultimately amino acids.

*Humidophila contenta*, *Hantzschia amphioxys*, and *Orthoseira roeseana* are among the most frequent diatoms in caves, although *Pinnularia borealis* is common in some areas. Frequent **Chlorophyta** include *Stichococcus bacillaris* and *Klebsormidium flaccidum*. Fungi are most likely to be **Ascomycota** or **Zygomycota**, with **Basidiomycota** being relatively rare.

Rare and new species often occur in caves in the unusual conditions. Competition from tracheophytes is limited, further encouraging the growth algae and bryophytes.

## Acknowledgments

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# CHAPTER 18-2

## CAVES – OVERALL BRYOPHYTE FLORA

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# CHAPTER 18-2

## CAVES – OVERALL BRYOPHYTE FLORA



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.



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 9. *Eucladium verticillatum* in lime seep, a bryophyte that prefers limestone substrate. Photo by Resso Taelspeus, 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 10. *Eucladium verticillatum*, a common bryophyte in limestone caves. Photo by Christian Berg, 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.



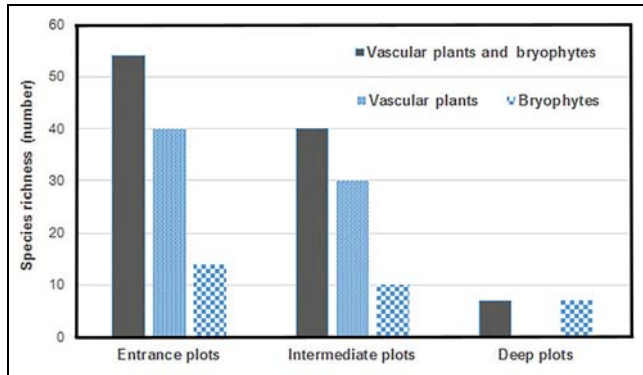


Figure 16. Cave species vs distance from entrance. Modified from Ren *et al.* 2021.

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*; *Symphyogyna 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; *Distichophyllum 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.

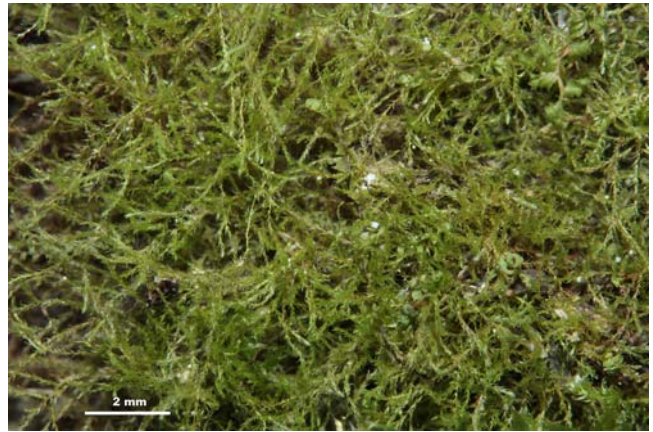


Figure 30. *Platydictya jungermannioides*. Photo by Hermann Schachner, through Creative Commons.

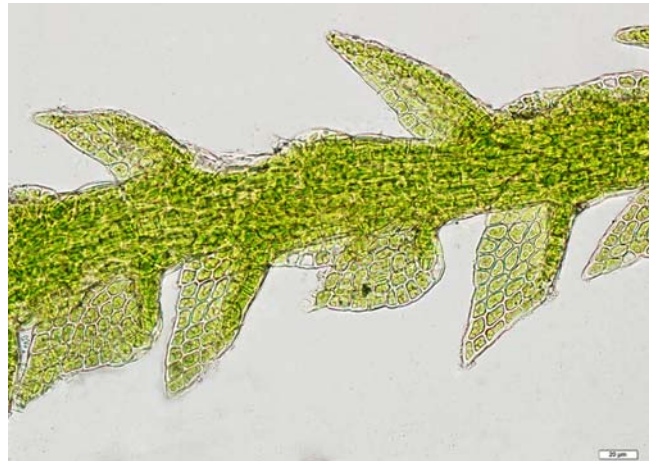


Figure 31. *Platydictya jungermannioides* branch. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

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 (9-37°C) was emitted. These warmer conditions at such high elevations permitted the development of communities, including bryophytes, up to 200 m<sup>2</sup>.



### Distance

In an artificial cave in the Iwato-jinja 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-jinja, 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
<i>Plagiommium maximoviczii</i>	12	22	22	22	33	22	22	22	12	12	12	+	+	+
<i>Heteroscyphus planus</i>	22	22	22	22	22	12	12	12	12	12	12	+	+	+
<i>Eurhynchium savatieri</i>	12	12	12	22	22	22	22	+2	22	+	+	+	+	+
<i>Thuidium cymbifolium</i>	+2	+2	+2	12	22	+2	-	-	-	-	-	-	-	-
<i>Lophocolea minor</i>	+	+2	+2	+2	+2	+2	-	-	-	-	-	-	-	-
<i>Pellia endiviifolia</i>	+	22	22	-	-	-	-	-	-	-	-	-	-	-
<i>Heteroscyphus coalitus</i>	-	12	12	12	-	-	-	-	-	-	-	-	-	-
<i>Dumortiera hirsuta</i>	-	11	11	12	-	22	33	33	33	-	-	-	-	-
<i>Makinoa crispata</i>	-	-	12	12	22	12	12	12	-	-	-	-	-	-
<i>Ctenidium capillifolium</i>	-	-	-	-	-	+	12	+2	33	-	-	-	-	-
<i>Marchantia emarginata</i> subsp. <i>tosana</i>	-	-	-	-	-	+	+	-	-	-	-	-	-	-
<i>Taxiphyllum taxirameum</i>	-	-	-	-	-	+	+	+	+	-	-	-	-	-
<i>Mnium laevinerve</i>	-	-	-	-	-	-	+	12	12	-	-	-	-	-
<i>Conocephallum japonicum</i>	-	-	-	-	-	-	12	12	12	33	33	33	+	+
<i>Fissidens tosaensis</i>	-	-	-	-	-	-	+	+	+	+2	12	12	-	+
<i>Radula japonica</i>	-	-	-	-	-	-	-	-	+	+2	+2	+2	+2	-
<i>Bryum capillare</i>	-	-	-	-	-	-	-	-	+	22	22	22	+2	+2
<i>Fissidens crispulus</i>	-	-	-	-	-	-	-	-	+	12	12	-	-	-
<i>Brachythecium plumosum</i>	-	-	-	-	-	-	-	-	-	-	22	22	22	33
<i>Haplocladum microphyllum</i>	-	-	-	-	-	-	-	-	-	-	12	12	22	22
<i>Thamnobryum subseriatum</i>	-	-	-	-	-	-	-	-	-	-	-	12	12	12
<i>Isoetium subdiversiforme</i>	-	-	-	-	-	-	-	-	-	-	-	12	12	+2
<i>Thuidium pristocalyx</i>	-	-	-	-	-	-	-	-	-	-	-	-	22	22
<i>Bazzania tridens</i>	-	-	-	-	-	-	-	-	-	-	-	-	+2	-



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

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 33. Luray Cavern, Virginia, USA. Photo by Alejocruz, 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.

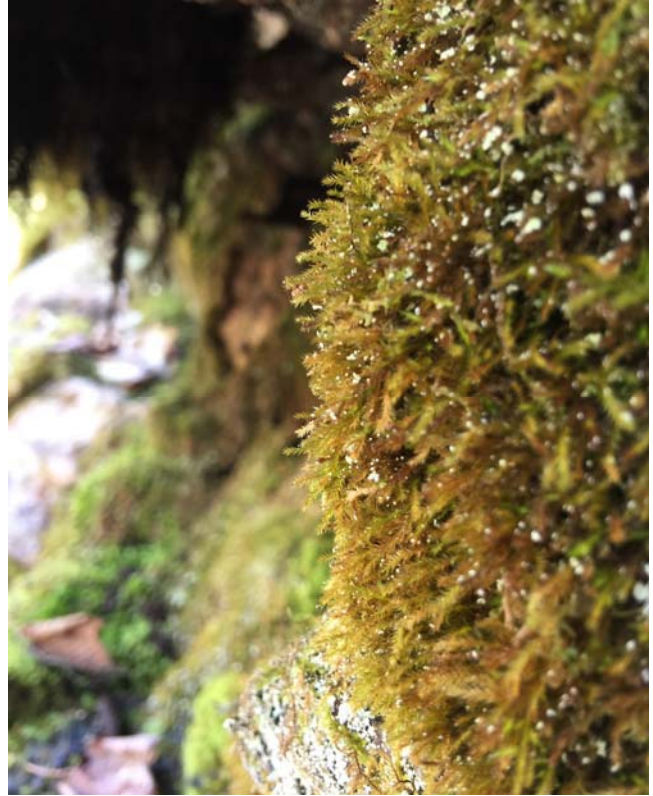


Figure 37. *Campylium hispidulum* on a vertical limestone wall, a species that occurs in Luray Caverns. Photo by Tom Neily, through Creative Commons.



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



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



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



Figure 42. *Fissidens bryoides* with retained protonemata. Photo by Dick Haaksma, 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 algae, 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 Kracków-Wieluń 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 pH 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 asplenoides* (Figure 72) were also present at most sites. Surprisingly, to me at least, *Pellia endiviifolia* (Figure 73) and *Conocepalum 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 58. *Ctenidium molluscum*, a mesophilous species from South Wales caves. Photo by Hermann Schachner, through Creative Commons.



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



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



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



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.

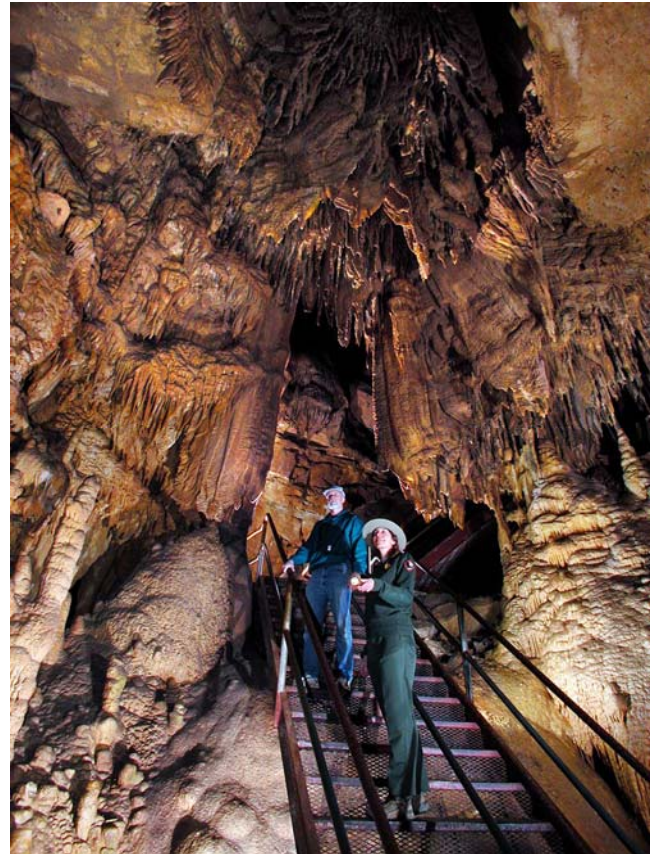


Figure 76. Mammoth Cave National Park. Photo through public domain.



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 arcegoniophores. 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 108. *Targionia hypophylla* showing purplish pouches beneath thallus. Photo by Ken Ichi Ueda, 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 109. *Anomodon rugelii* dry, a species of the cave twilight zone, but near the cave entrance. Photo by Hugues Tinguy, 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 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 120. *Hymenostylium recurvirostrum* with capsules. Photo by Paul Wilson, with permission.



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



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



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.



Figure 126. *Conocephalum japonicum*, a species that occurs at the bottom of caves of Guizhou Province, China. Photo by David Long, 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 127. *Dumortiera hirsuta*, a species that occurs at the bottom of caves of Guizhou Province, China. Photo by Michael Lüth, with permission.



Figure 125. *Riccia fluitans*, a species that occurs at a middle depth in caves of Guizhou Province, China. Photo by Ralf Wagner, 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 in a wide range of caves and locations. The Australian cave species tend to be species from arid and semiarid habitats.



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# CHAPTER 18-3

## CAVES – ZONES OF BRYOPHYTE FLORA

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# CHAPTER 18-3

## CAVES – ZONES OF BRYOPHYTE FLORA

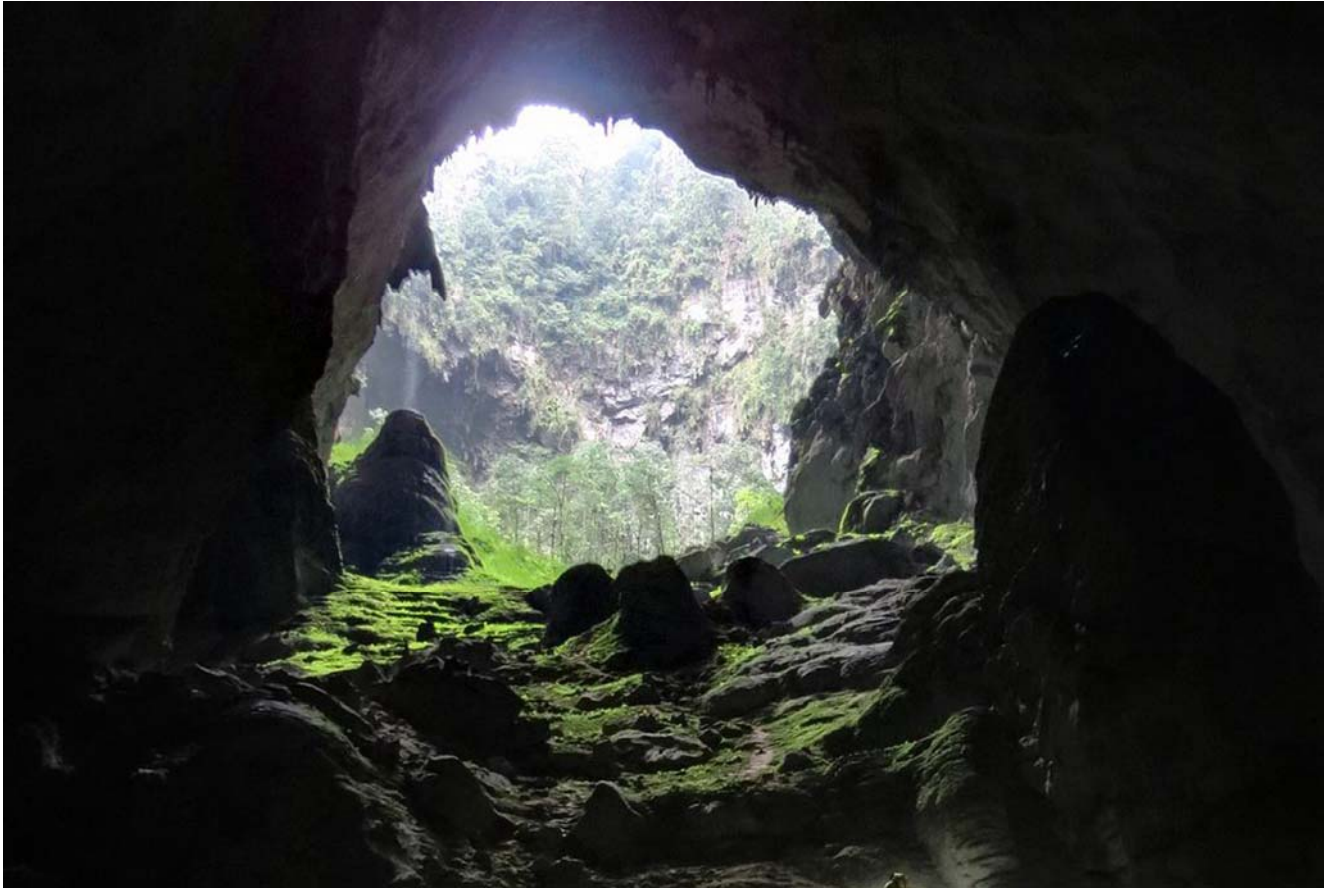


Figure 1. View of the twilight zone and entrance light at Son Doong Cave, Vietnam. Photo by Doug Knuth, through Creative Commons.

### 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 prolifera* (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 prolifera* 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 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](http://www.aquamoss.net)>, with permission.



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



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



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 28. *Pohlia cruda* on rock, a species that occurs in lava caves. Photo by Štěpán Koval, 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 barbuloidea* 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): *Cyclodietyon laetevirens* (Figure 38), *Plagiochila longispina* (Figure 39), *Plagiothecium nemorale* (Figure 40), *Tetrastichium virens* (Figure 41), and others.



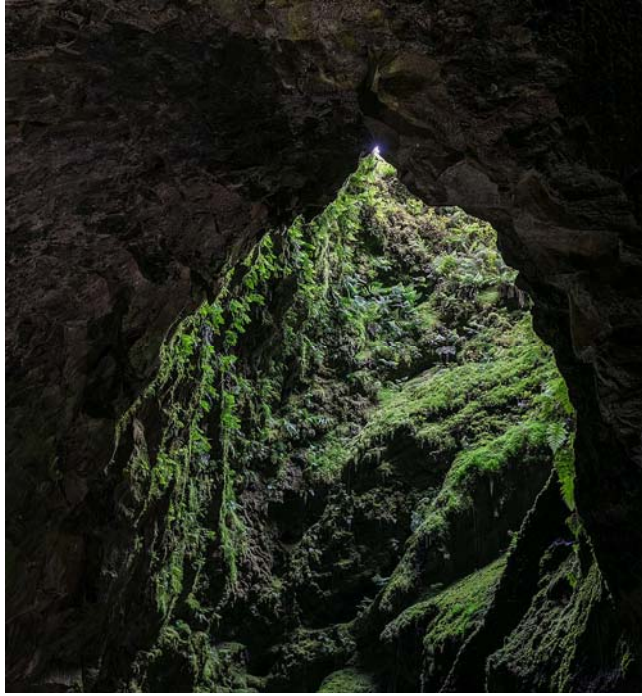


Figure 37. Cave entrance in the Azores. Photo by Diego Delso, through Creative Commons.



Figure 38. *Cyclocladon 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. *Tetracladus 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 Deckenhöhle 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 Deckenhöhle 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 50. *Ctenidium molluscum* in rock canyon, a species that occurs in the access region of Mallorcan caves. Photo by Michael Lüth, with permission.



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



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



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

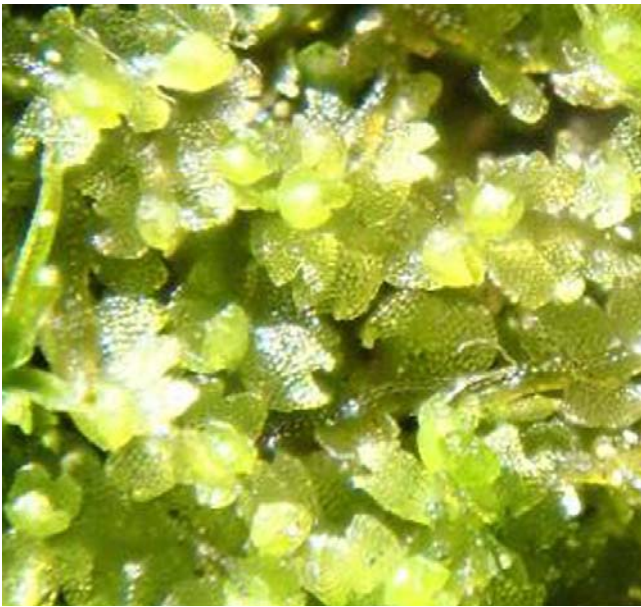


Figure 54. *Mesoptychia turbinata*, a species of the entrance zone in Mallorcan caves. Photo by Hugues Tinguy, with permission.



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.

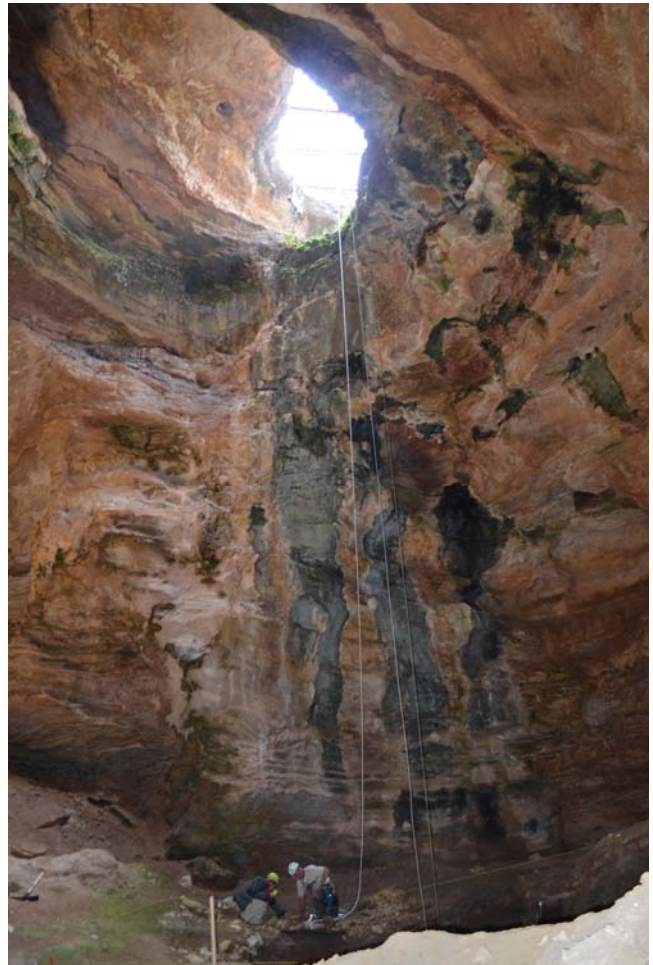


Figure 57. Natural Trap Cave, Wyoming. Photo from Bureau of Land Management, through public domain.



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 humid, 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 Montenegro. Photo through Creative Commons.

Buczko and Rajczy (1989) reported the troglophile *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. *Plagiommium vesicatum*, a species that is unable to penetrate beyond the entrances of karst caves in China. Photo from Digital Museum, Hiroshima University, with permission.

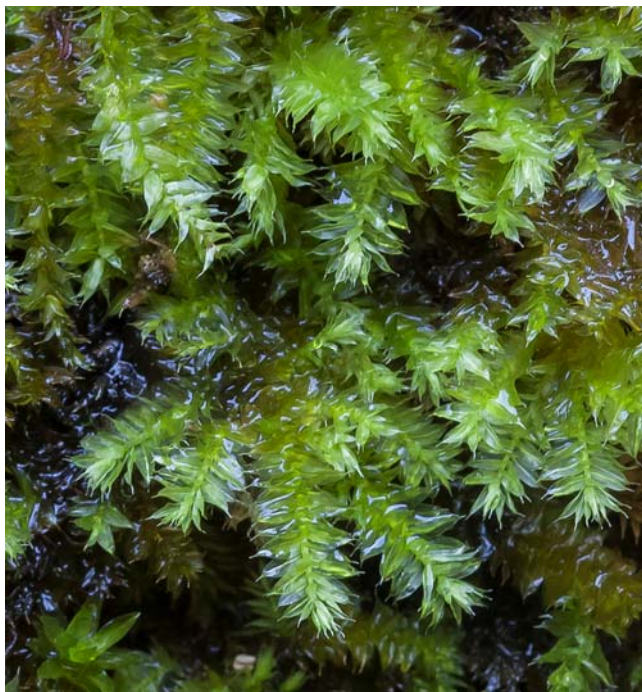


Figure 70. *Racopilum cuspidigerum*, a species that is unable to penetrate beyond the entrances of karst caves in China. Photo by John Game, through Creative Commons.



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.



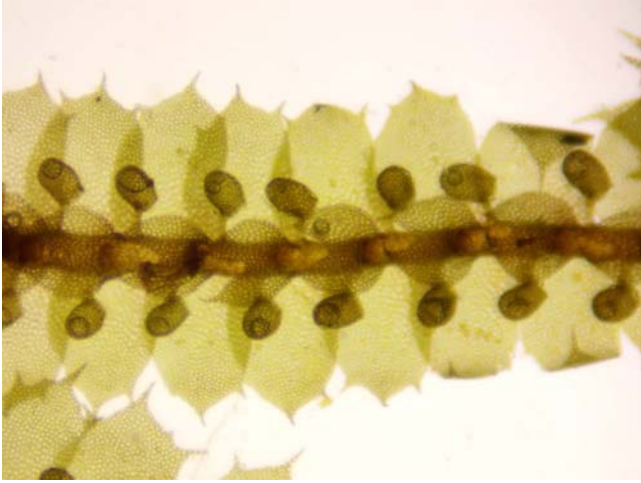


Figure 74. *Jubula hutchinsiae* branch. Photo by Rory Hodd, with permission.



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



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



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



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.

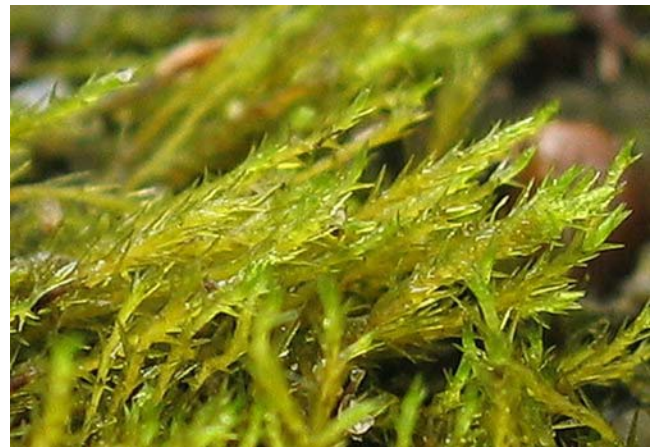


Figure 84. *Archidium alternifolium*. Photo by Andrew Spink, with permission.



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



Figure 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.



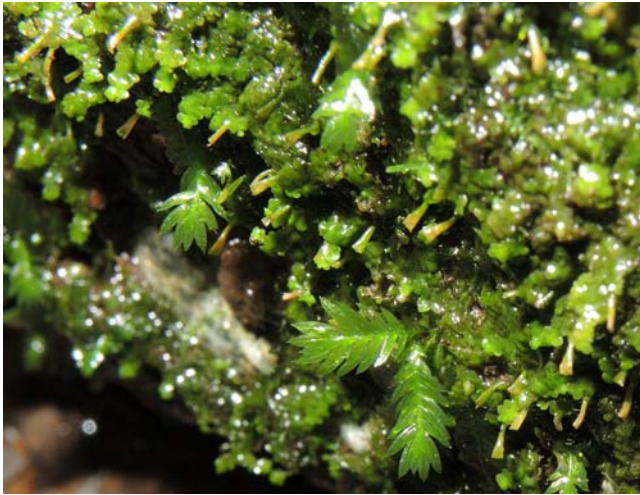


Figure 86. *Radula holtii* with perianths, a species in the Azores that occurs at cave entrances, but that could disappear due to climate change. Photo by Rory Hodd, with permission.

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 asplenoides* (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), *Isoetecium myosuroides* (Figure 102), and *Dichodontium pellucidum* (Figure 103). Note that only *Pellia endiviifolia*, *Plagiochila asplenoides*, 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 94. *Plagiomnium undulatum*, a species that occurs at the entrance of a cave in Ireland. Photo by Hermann Schachner, through Creative Commons.



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



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



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



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



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



Figure 102. *Isoetecium 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 luisei* (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), *Fossombronina casepitiiformis* (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.

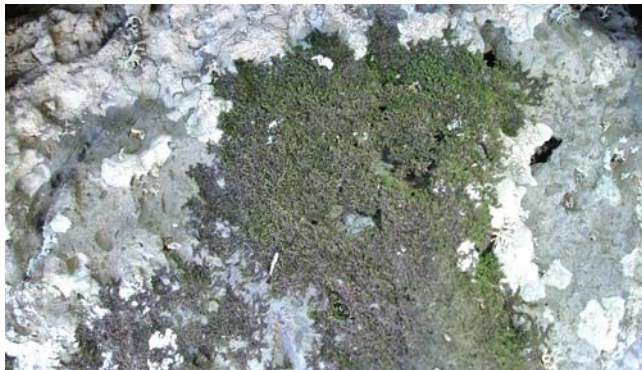


Figure 104. *Frullania azorica* on rock, a relatively rare species that occurs at cave entrances in the Azores. Photo by Rosalina Gabriel, with permission.

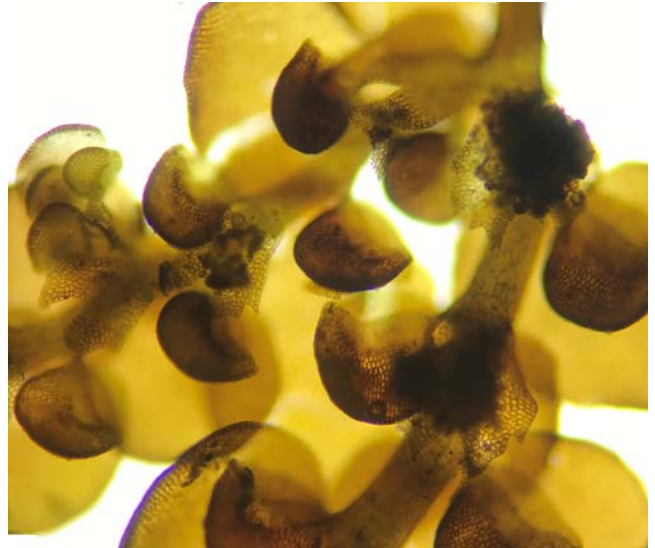


Figure 105. *Frullania azorica*. Photo courtesy of Tatiana Oliveira da Silva.



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 117. *Frullania tamarisci*, a more common species that occurs at cave entrances in the Azores. Photo by David T. Holyoak, 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 118. *Lunularia cruciata*, a more common species that occurs at cave entrances in the Azores. Photo by Hermann Schachner, through Creative Commons.



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



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



Figure 127. *Heterocladium wulfsbergii*. Photo by Claire Halpin, 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 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 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).

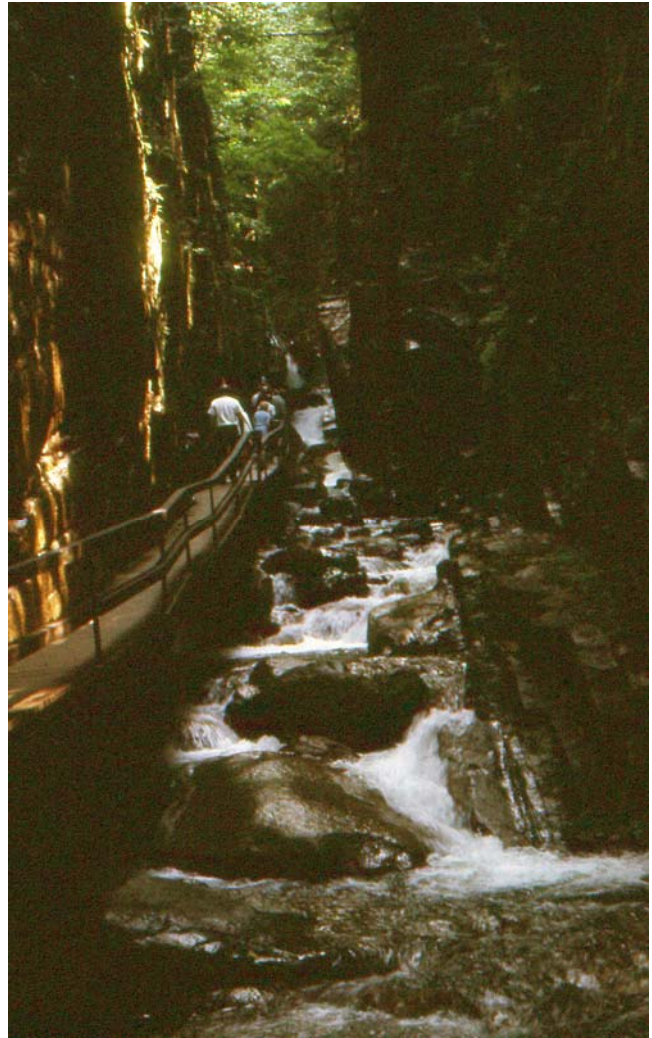


Figure 135. Flume, Franconia Notch, New Hampshire, USA, where small caves can have *Campylium chrysophyllum*. Photo by Janice Glime.



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 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 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 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.

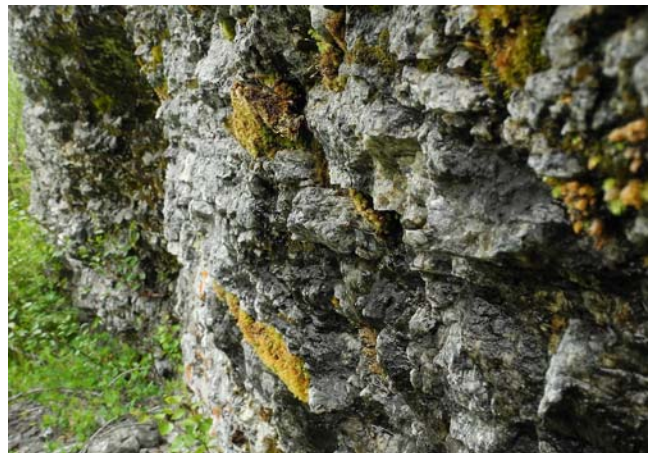


Figure 150. *Isopterygiopsis pulchella*, a species of the twilight zone in the Della Grotta Dell'orso, Italy. Photo by Michael Lüth, with permission.



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) (15.9 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.

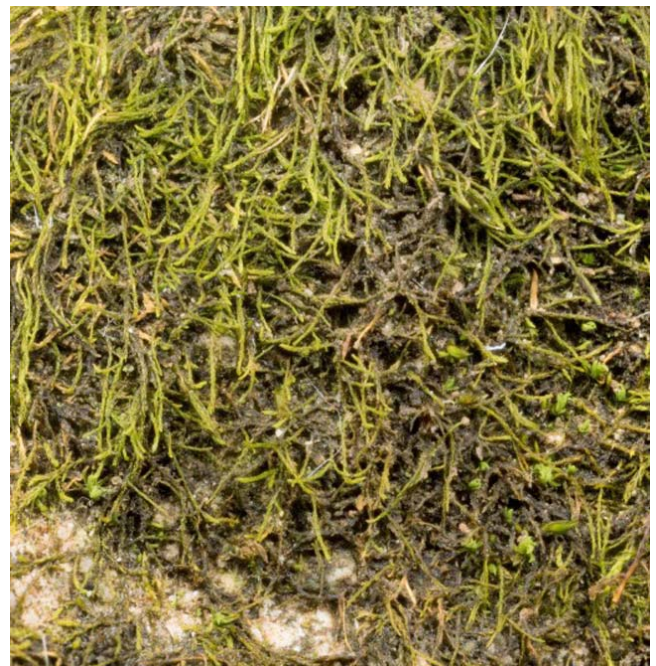


Figure 161. *Platydictya confervoides*. Photo by Bob Klips, with permission.

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

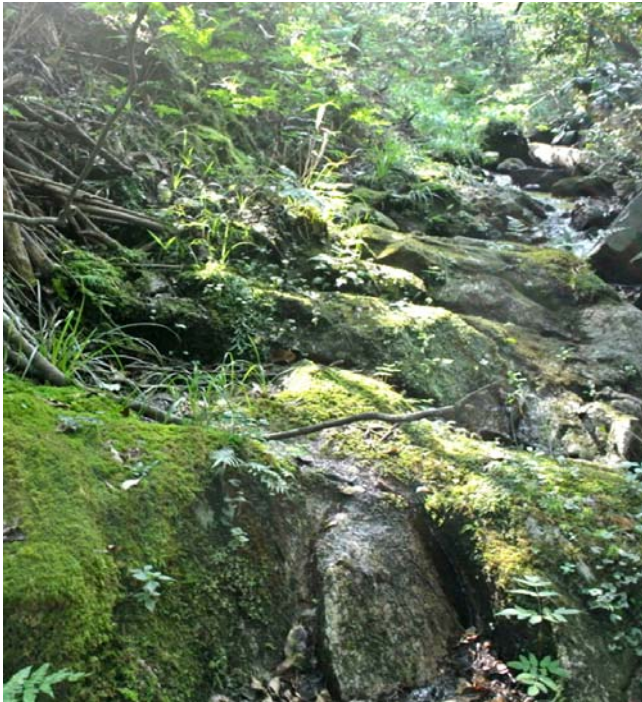


Figure 163. *Radula kojana* habitat on rock, a species that occurs only in deep locations in karst caves in southern China. Photo by Kochibi, through Creative Commons.

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 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.

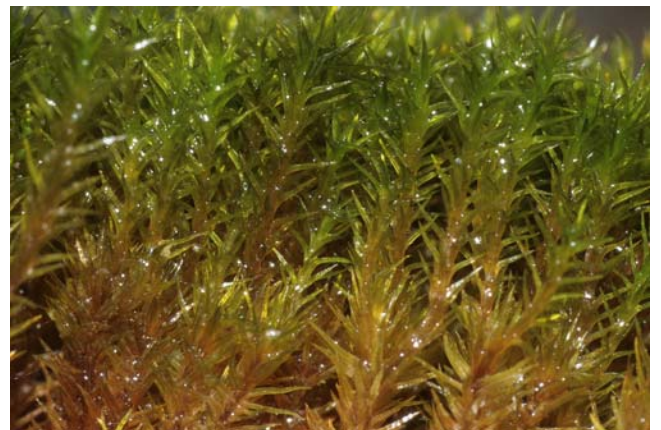


Figure 172. *Hymenostylium recurvirostrum*. Photo by Hermann Schachner, through Creative Commons.





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

As always, I am indebted to the many people who have given me permission to use their images. And I thank those foray leaders who have included caves and cave-like environments in the field trips.

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# CHAPTER 18-4

## CAVES – BRYOPHYTE STRATEGIES

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# CHAPTER 18-4

## CAVES – BRYOPHYTE STRATEGIES



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

### Rare Species and New Finds

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

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



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





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



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

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

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



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



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



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





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



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



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



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



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



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



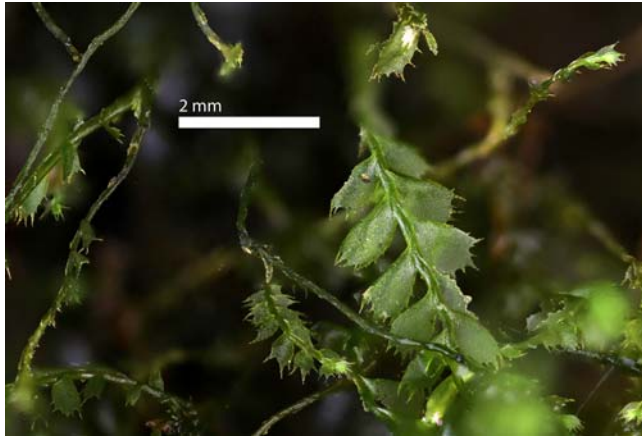


Figure 14. *Plagiochila sullivantii*, a rare taxon that can be abundant in caves. Photo by probably Paul Davison, University of North Alabama.

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

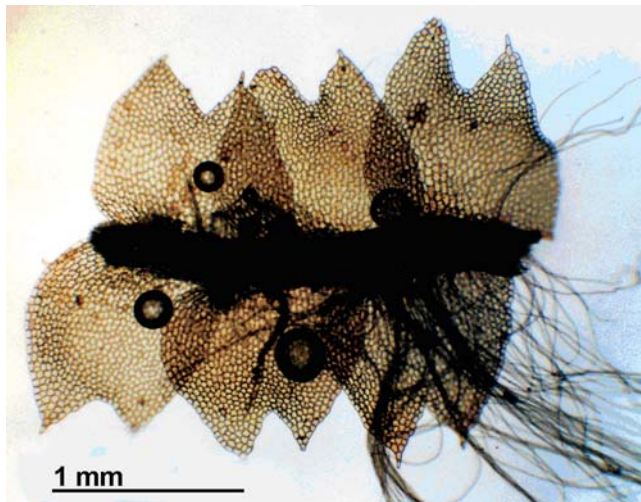


Figure 15. *Mesoptychia gillmanii*, a species first reported in Michigan, USA, from a cave in a cliff of Potsdam sandstone on an island in Lake Superior. Photo by David Wagner, with permission.

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

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

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



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



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



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





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



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



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



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



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



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





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

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

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

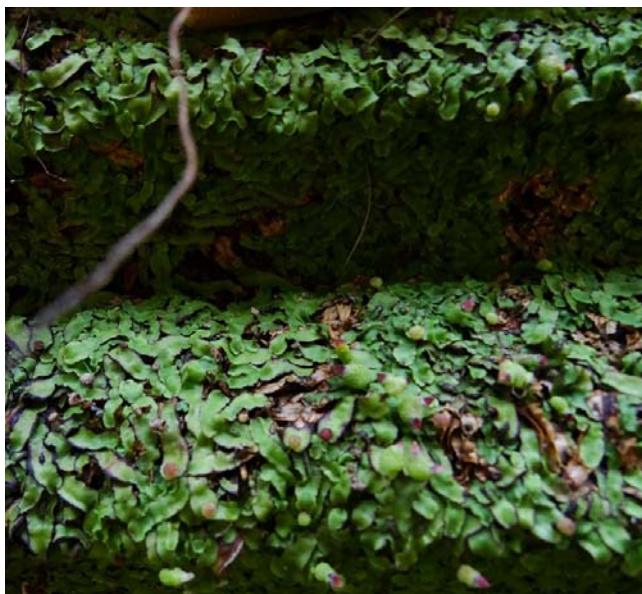


Figure 26. *Asterella wallichiana* on ledge, a species that was collected in or near a cave in India, adding to the known Indian bryophyte flora. Photo by Forest Owlet, through Creative Commons.



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



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



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

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



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

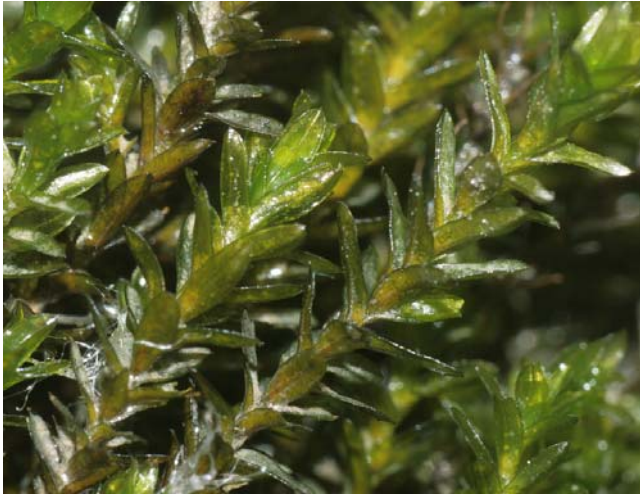


Figure 30. *Cinclidotus riparius*; *Cinclidotus asumaniae* was described as a new species from a cave in southern Turkey. Photo by Hermann Schachner, through Creative Commons.

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



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



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



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



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

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





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

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



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



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

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

## Liverworts

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

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



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

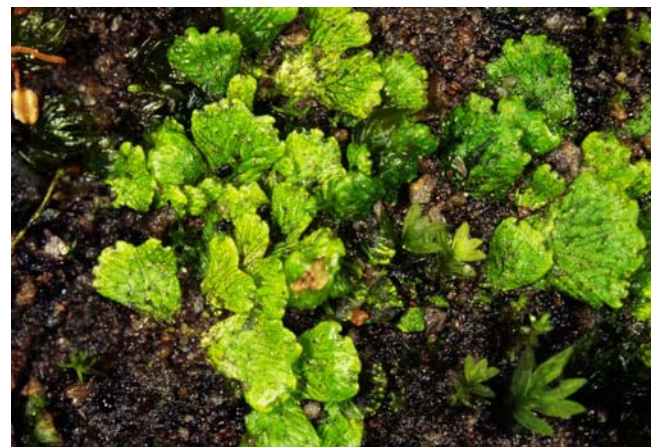


Figure 39. *Cyathodium cavernarum* on rock where it is dark enough for its iridescence to show. Photo by Jan-Peter Frahm, with permission.

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



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



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

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



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

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

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

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

## Mosses

### *Bartramia ithyphylla* (Figure 42-Figure 43)

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



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

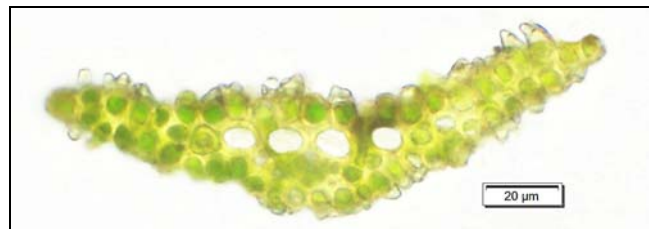


Figure 43. *Bartramia ithyphylla* leaf cs showing papillae and internal layering of leaf. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



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

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



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

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

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

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



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

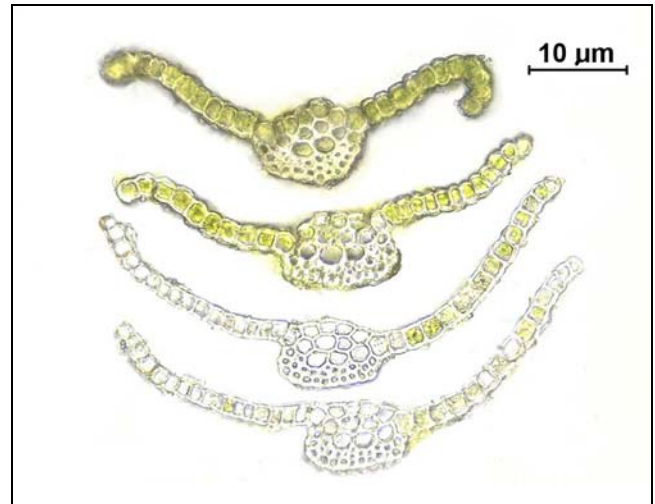


Figure 46. *Didymodon glaucus* leaf cells showing strong costa. Photo by Hugues Tinguy, with permission.

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



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





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

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

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



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



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

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

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



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

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

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



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



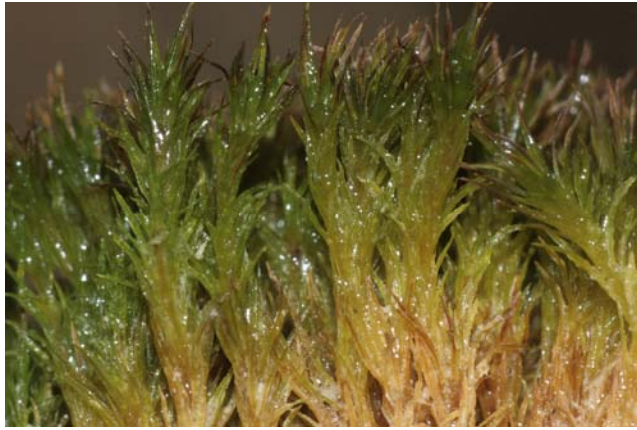


Figure 53. *Eucladium verticillatum*. Photo by Hermann Schachner, through Creative Commons.

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



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

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

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

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



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



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



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





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



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



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



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



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



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



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



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

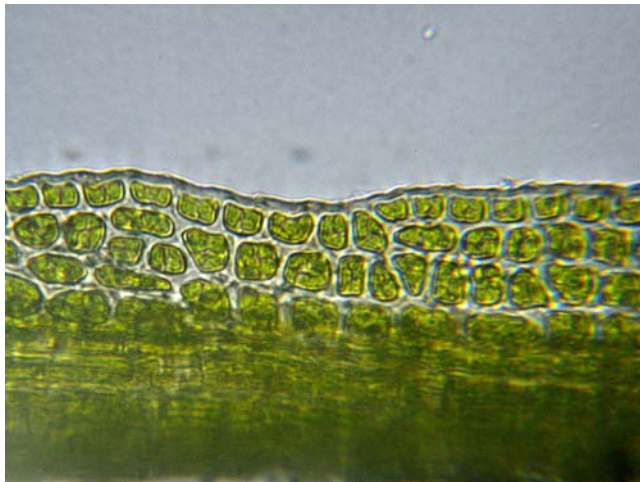


Figure 65. *Eucladium verticillatum* leaf margin showing sparse papillae, as one might find in a cave. Photo by Armand Turpel, through Creative Commons

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

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

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

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

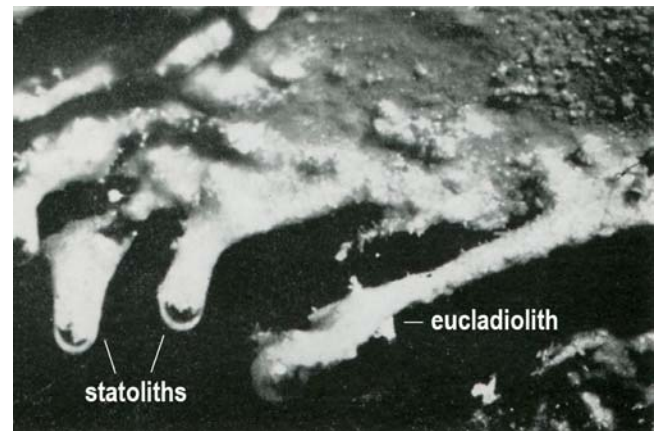


Figure 66. *Eucladium verticillatum* forming stalactite (eucladiotite; eucladiolith) in mine in Dorset, UK. Photo modified from Dalby 1966b.

Pentecost (1996) further described the formation of eucladioliths. The formation involves deposition of calcium carbonate through photosynthesis, evaporation, and  $\text{CO}_2$  escape. Pentecost estimated that 6-12% of the carbonate was deposited through photosynthesis, 10-20% through evaporation, and the remaining 70-80% through gas escape.

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

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

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





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



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



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



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



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

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

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





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



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



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

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

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

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



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



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



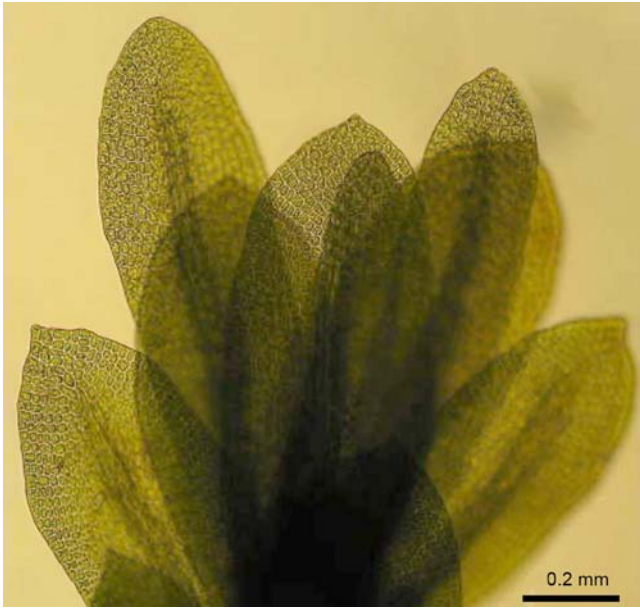


Figure 77. *Mittenia plumula* showing leaf structure. Photo by Tom Thekathyl, with permission.



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



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



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



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



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



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



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



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

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

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



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



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



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





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



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

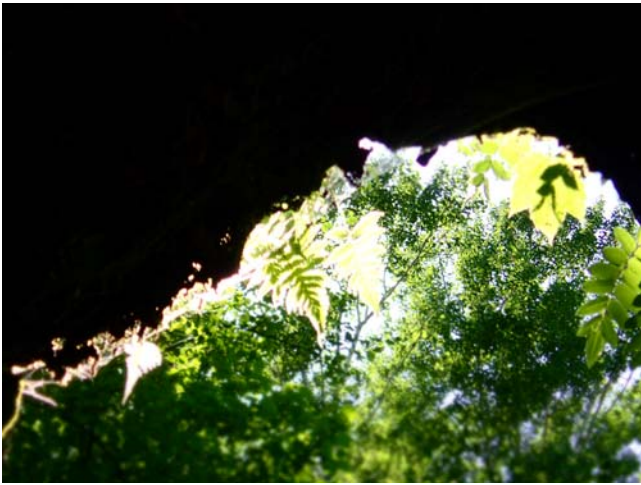


Figure 89. View from entrance of cave in Alger County, Michigan. There are protonemata overhead, but the lighting is wrong to see the luminescence. Photo by Janice Glime.



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



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



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



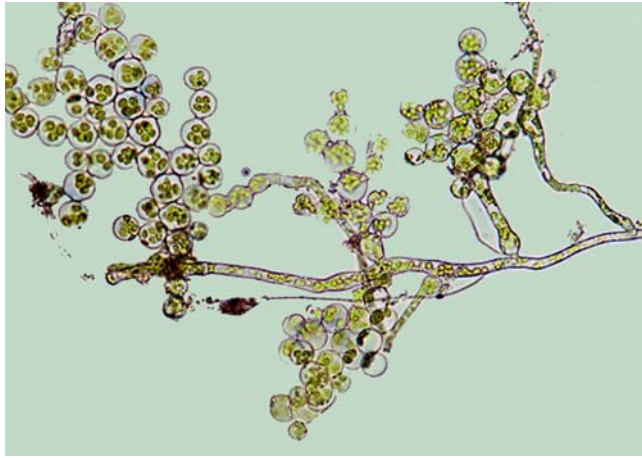


Figure 94. *Schistostega pennata* protonema with gemmae. Photo courtesy of Irene Bisang.



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



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

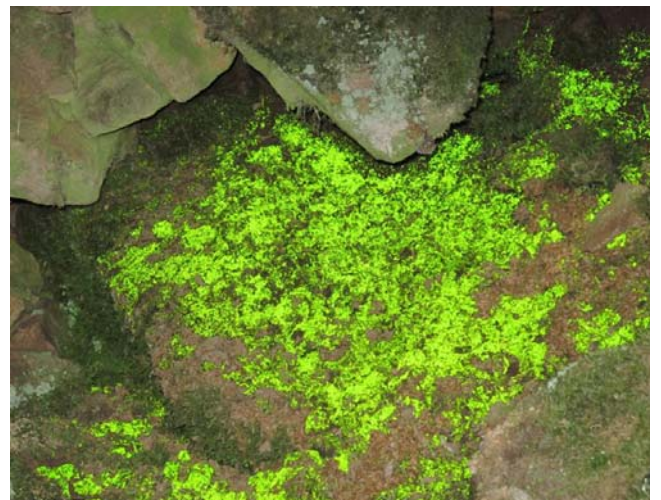


Figure 98. *Schistostega pennata* protonemata showing luminescence in cave. Photo by Hugues Tinguy, with permission.



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



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



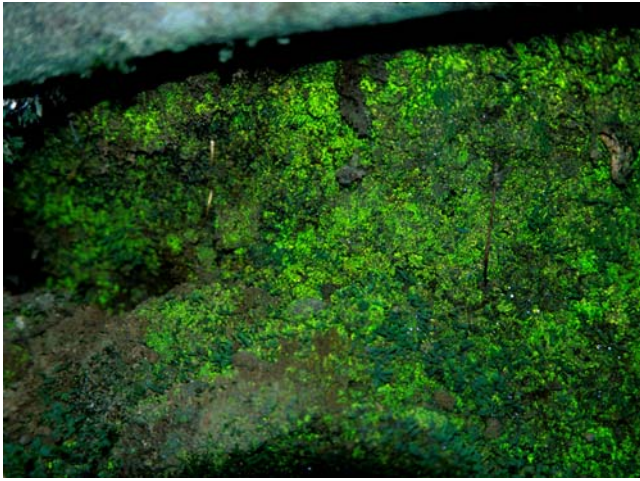


Figure 100. *Schistostega pennata* luminescence. Photo by Martin Hutten, with permission.

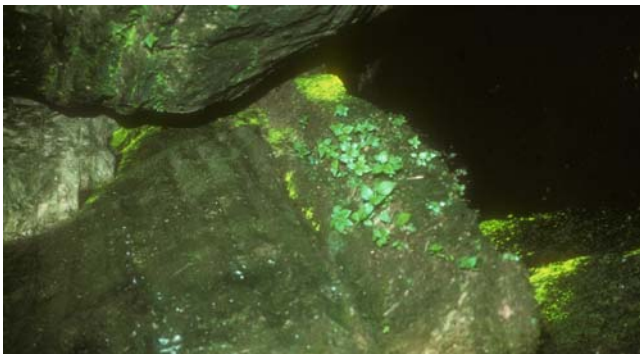


Figure 101. *Schistostega pennata* protonemata. Photo by courtesy of John Christy.



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

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



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



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

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



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





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



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



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



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



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



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

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



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

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



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

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



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



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



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



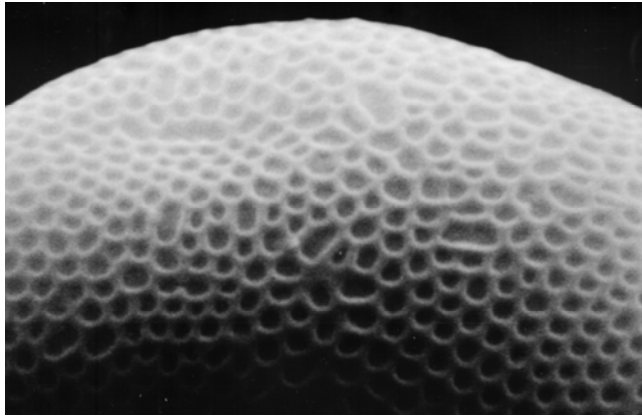


Figure 116. *Schistostega pennata* SEM of spore surface. Photo by Misha Ignatov.

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



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

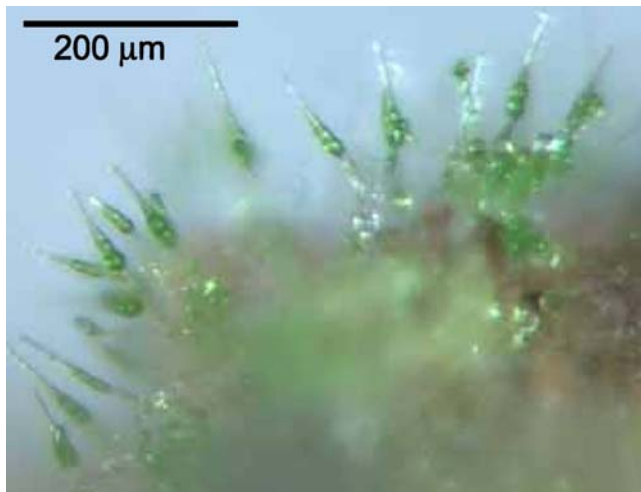


Figure 118. *Schistostega pennata* protonemal gemmae. Photo modified from Ignatov *et al.* 2012, with permission.

### *Takakia lepidozoides* (Figure 119-Figure 122)

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

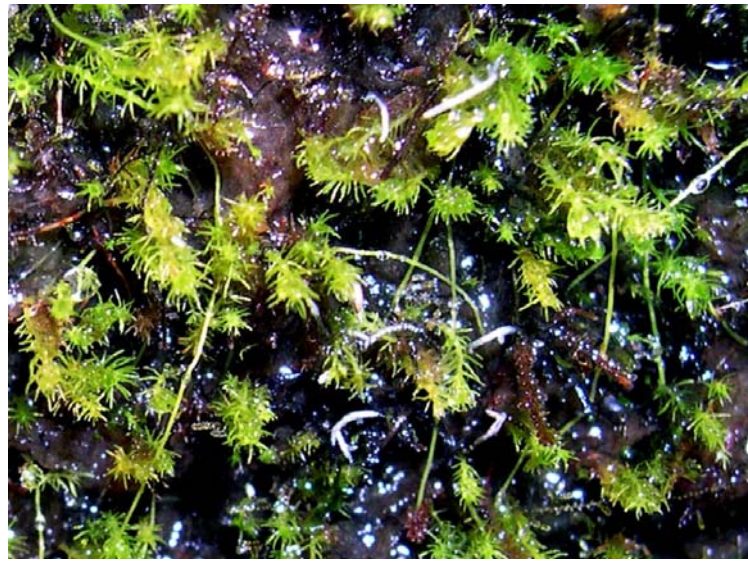


Figure 119. *Takakia lepidozoides*, a species sometimes found in caves or cave-like situations. Photo by Quentin Cronk, through Creative Commons.



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





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



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



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



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

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

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

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

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





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



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



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

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



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



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

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





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

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

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

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

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

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



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



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

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



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

## Bryophyte Adaptations

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

The pH seems to matter. Mason-Williams and Benson-Evans (1958) found that there is a richer bryophyte flora on limestone than on acid rocks. In water, high pH prevents most bryophytes from getting enough CO<sub>2</sub> for photosynthesis. So what is the value of the high pH to bryophytes in many caves?

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



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

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



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

## Responses to Low Light

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

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

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

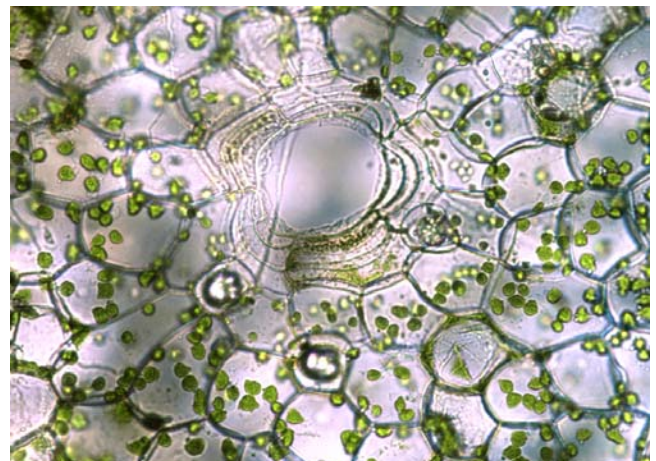


Figure 135. *Cyathodium cavarnarum* thallus pore and photosynthetic epidermis. Photo courtesy of Noris Salazar Allen.



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



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



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

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



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

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

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





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



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

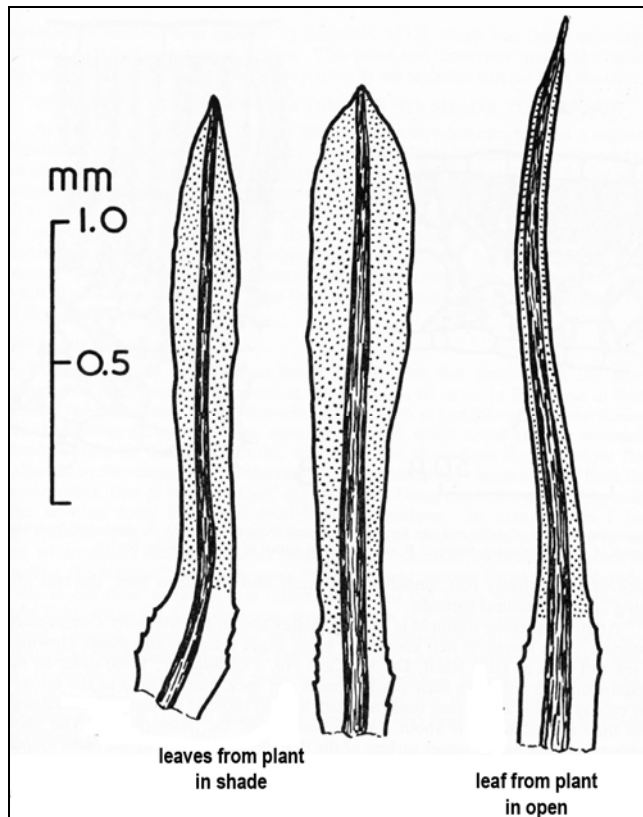


Figure 141. *Eucladium verticillatum* deep shade and open leaves. Diagram modified from Dalby 1966b.



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



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

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

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



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



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

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



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

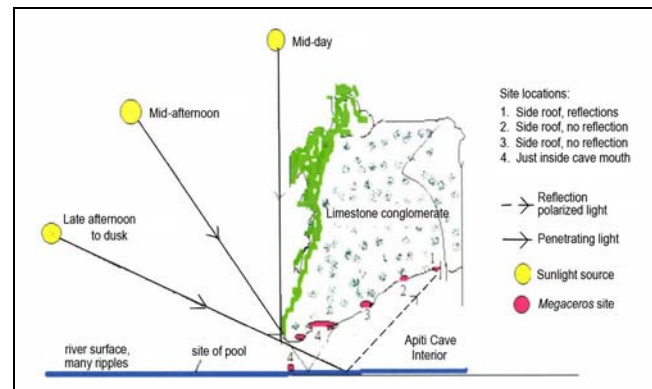


Figure 146. Sunlight paths at various times of the day in a cave at Apiti. Note the reflections onto the cave roof from 14:00–17:00 hours, thus illuminating colonies of *Megaceros pellucidus* for part of the day. Modified from Watkins 2002.

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





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



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



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

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

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



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

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



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



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

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

## Reproduction

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



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



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

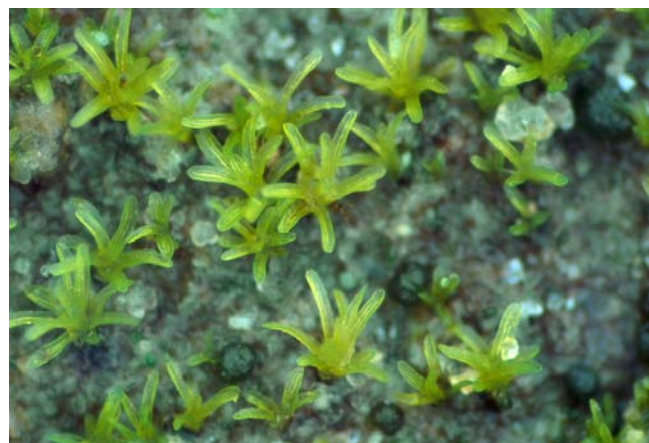


Figure 154. *Gyroweisia tenuis*. Photo by Tomas Hallingbäck, with permission.

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



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

## Summary

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

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

Rhizoids are important for "cementing" bryophytes to the cave ceilings. pH can be important in creating a favorable CO<sub>2</sub> environment.

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

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

## Acknowledgments

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# CHAPTER 18-5

## CAVES – CAVERNS

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# CHAPTER 18-5

## CAVES – CAVERNS



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

### Caverns

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

Prior (1961) described the mosses in the well-known Luray Caverns, Virginia, USA (Figure 1). He found *Amblystegium serpens* (Figure 2) forming a loose mat with sporophytes in only one location on wet limestone.

*Amblystegium serpens* is also common in European caves (e.g. Mulec & Kubešová 2010), but it is widespread and common outside caves, frequently presenting sporophytes. *Anomodon rostratus* (Figure 3) likewise occurred on moist limestone, along with *Leptobryum pyriforme* (Figure 4), but also occurred on silt of the cavern (Prior 1961). *Bryum pseudotriquetrum* (Figure 5) formed fairly "dense mats" on moist limestone, along with *Leptobryum pyriforme*. *Campylium hispidulum* (Figure 6), sometimes with capsules, was scattered among 8 locations on moist limestone, either alone or with *Leptobryum pyriforme* and/or *Eurhynchium hians* (Figure 7). The latter species was abundant, occurring at 19 of the 33 study plots, either



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



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



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



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



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





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



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



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



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



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



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





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



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



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

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



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





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



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



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

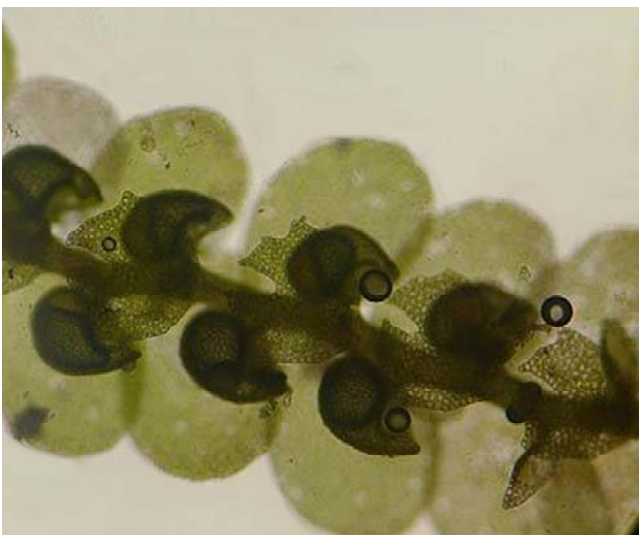


Figure 18. *Frullania nicholsonii* showing lobules and underleaves. Photo by Shirley Kerr, with permission.



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





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



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



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



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



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



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





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



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



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



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



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



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





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



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



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



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



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



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





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



Figure 40. *Papillaria crocea*. Photo by Clive Shirley, Hidden Forest <[www.hiddenforest.co.nz](http://www.hiddenforest.co.nz)>, with permission.



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



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

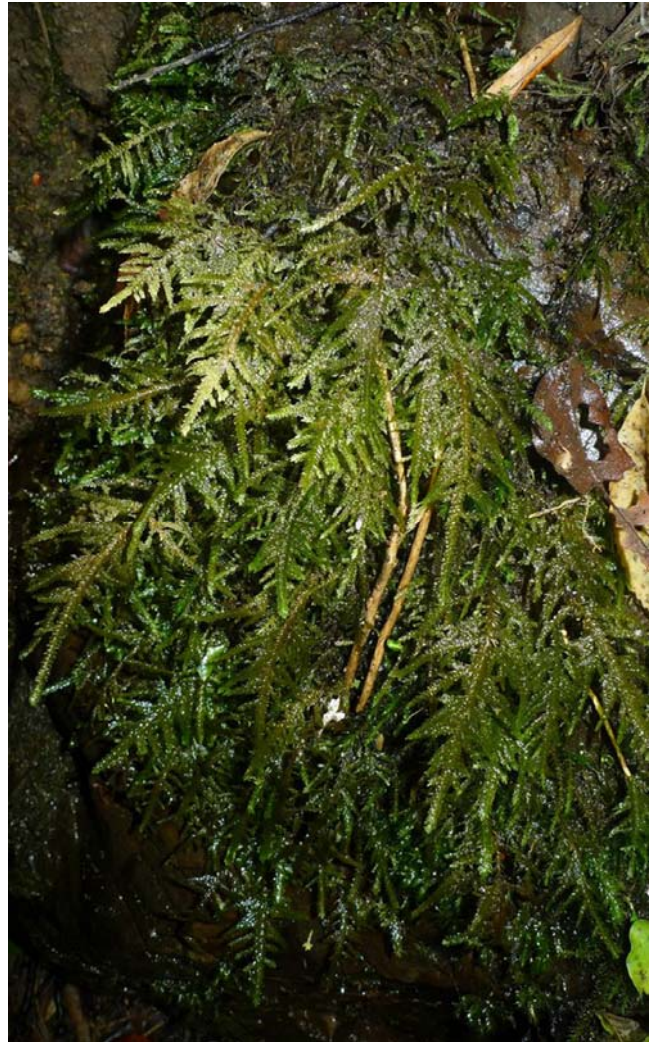


Figure 43. *Thamnobryum pandum*, a moss in the Lost World Cavern at Waitomo, New Zealand, where it is most common at the entrance. Photo from Te Papa, through Creative Commons.





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



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



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

Visitors increase the exposure of the caverns to fluctuating temperatures, moisture fluctuations, drafts, propagules, light, exhaled CO<sub>2</sub>, trampling, and other factors

that alter the ability of bryophytes to reach and succeed in the interior of the caverns. Rakovec (2020) modelled the effect of visitor number and cave size on visitor impact. He found that the direct human sources of heat and CO<sub>2</sub> cause linear responses. But the exchange between the walls and the exterior have exponential consequences dependent on time. Thus, visitors have both direct and indirect effects on the flora in the display caverns.

### Cave Lamp Communities (Lampenflora)

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

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

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





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



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

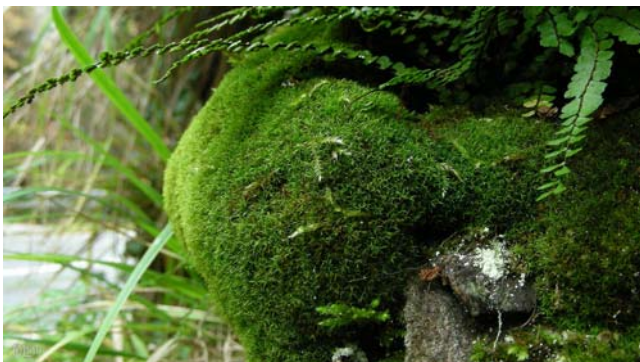


Figure 49. *Amphidium mougeotii*, a moss found near lamps in Howe Caverns, New York, USA. Photo by Michael Lüth, with permission.



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



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



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





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



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



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

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

### Succession

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

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



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

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





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



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

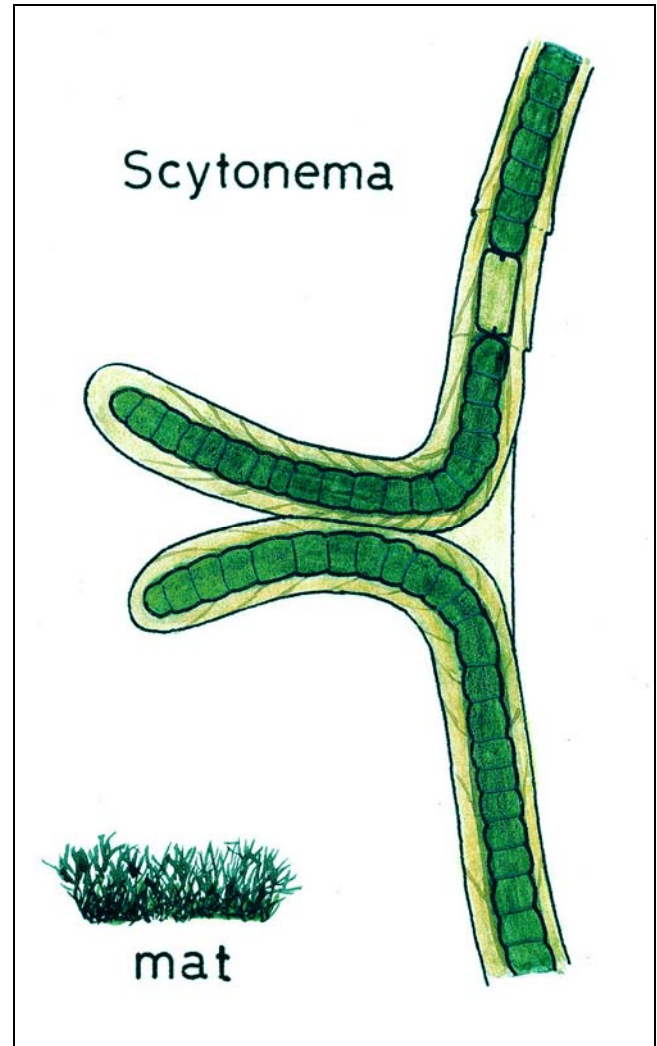


Figure 60. *Scytonema*; *Scytonema drilosiphon* is one of the **Cyanobacteria** that grows near the lights in caverns. Drawing by Allen Pentecost, through Creative Commons.

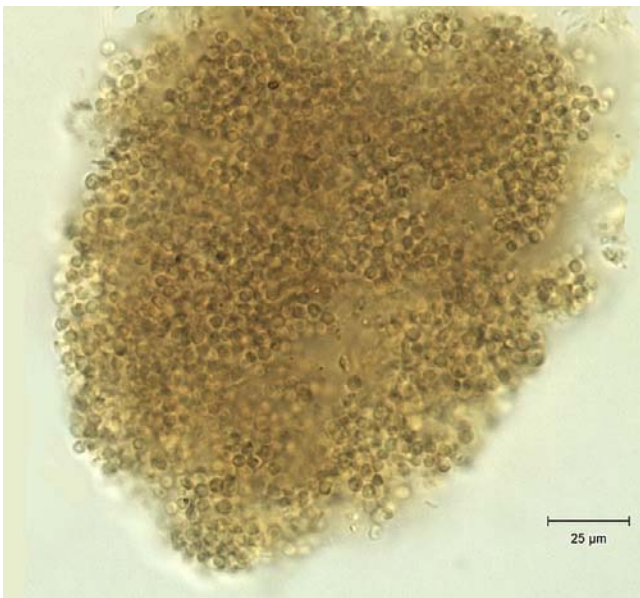


Figure 59. *Microcystis pulverea*, a common member of **Cyanobacteria** found near lights in caverns. Photo by Chris Carter, with permission, AlgaeBase.

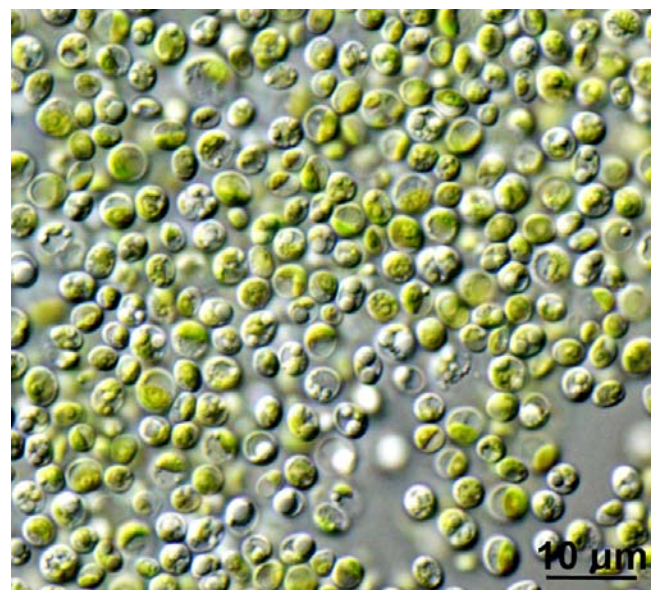


Figure 61. *Chlorella vulgaris*, a widespread, airborne green alga that grows near lights in caverns. Photo by Neon, through Creative Commons.



### Species Numbers

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

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



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



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

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

### Dominant Species

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

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



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



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





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

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



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



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



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



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

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



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

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



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



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



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



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



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





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



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



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

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



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



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

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



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



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



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



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

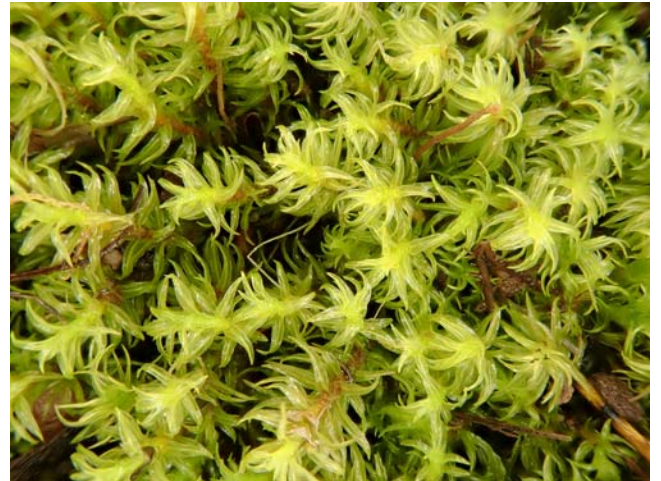


Figure 84. *Dichodontium pellucidum*, a species found in Moravian Karst (Czech Republic) in the 1960s to 1970s, but not relocated in 1999-2000. Photo by Claire Halpin, with permission.



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





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



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



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



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



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



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





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



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



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



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



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

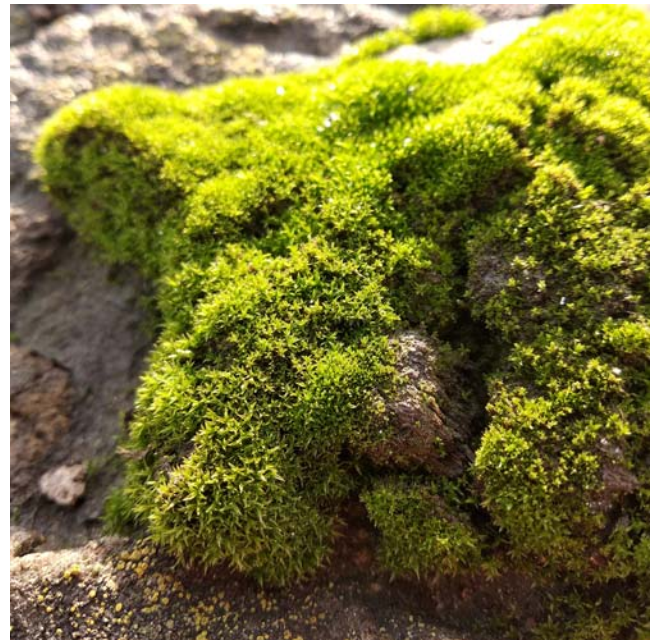


Figure 97. *Ceratodon purpureus* on rock, a species that was fertile in the 1970's, but not in 1999-2000 in the Moravian Karst. Photo by Aleksandr Levon, through Creative Commons.





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



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



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



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

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



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

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

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



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



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

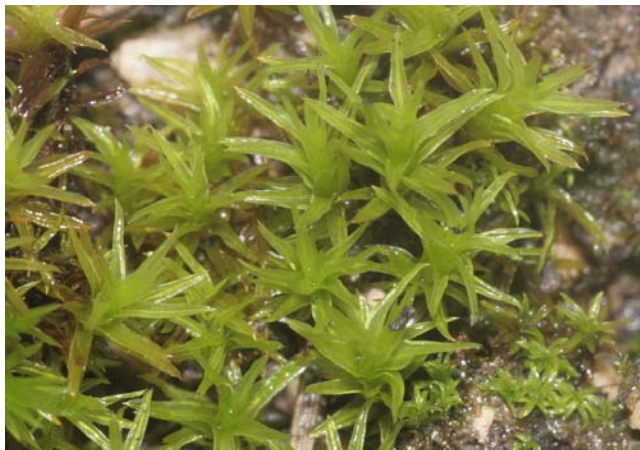


Figure 104. *Barbula unguiculata*, a species found in Crystal Cave, Wisconsin, USA – a tourist cavern. Photo by Hermann Schachner, through Creative Commons.



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



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



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





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



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



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

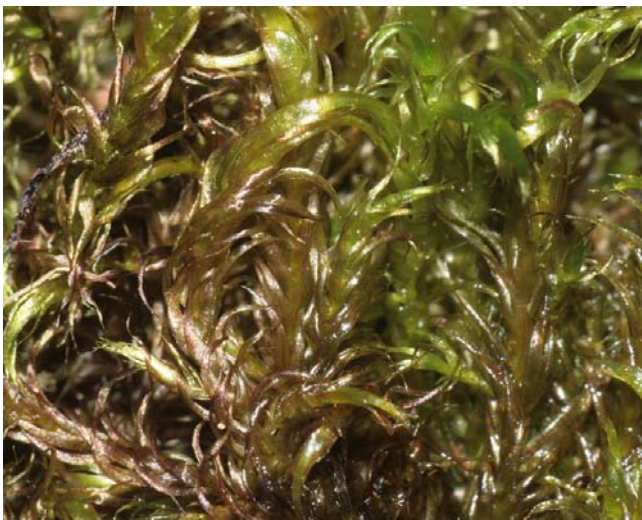


Figure 110. *Warnstorfia fluitans*, a species found in Crystal Cave, Wisconsin, USA. Photo by Hermann Schachner, through Creative Commons.



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

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





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



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

### Modifications of Cave Dwellers

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



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

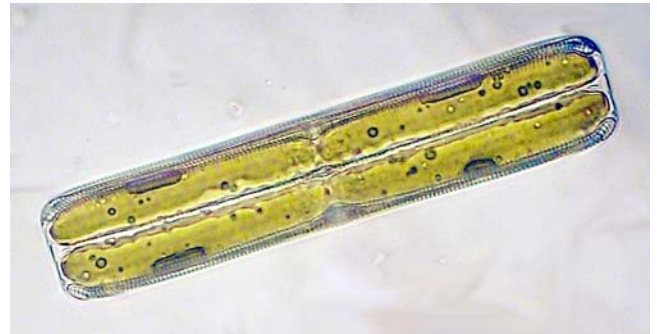


Figure 116. *Pinnularia* sp. a diatom in a genus that occurs on cave bryophytes. Photo by Denis Barthel, through Creative Commons.

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

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



modification, despite penetrating the greatest distance into the cave.

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

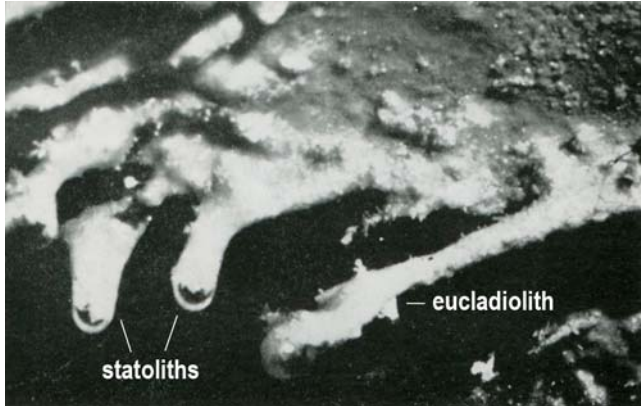


Figure 117. *Eucladium verticillatum* forming stalactite (eucladiotite) in mine in Dorset, showing horizontal growth of the statolith (eucladiolith in this case). Photo from Dalby 1966b.

### Life Strategies

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

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

### Propagation and Survival

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

lampenflora communities, while *Entodon schleicheri* (Figure 120) and *Tortella* sp. (Figure 78) had the highest abundance in the natural entrance zone.



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



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



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

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



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

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

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

### Conservation and Control Measures

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

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

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

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

### Human Impacts

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

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

Russell and MacLean (2008) also noted the addition of concrete and steel structures, change in the air movement regime, and alteration of temperature through the movement of warm bodies through the cave. Human presence in the cave can also alter the available CO<sub>2</sub> (Russell & MacLean 2008; Lamprinou *et al.* 2014). This becomes more apparent when ventilation is limited (Russell & MacLean 2008; Lang *et al.* 2015). And the addition of entrances or blockage of entrances changes airflow patterns within the cave, with the entrance of visitors disturbing the relatively limited variation in temperature and humidity.

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

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

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

### Treatments - Chemical

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





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

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

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

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

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

Sea caves (Figure 122) require special management (Gurnee 1994) that involves innovative techniques to

protect them from the intrusion of visitors and exposure to the destructive sea air. These are sometimes protected by glass enclosures, use of boats and vehicles that keep visitors from especially sensitive areas, and lighting and cleaning techniques that minimize lampenflora.



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

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

### Treatments – Alternative Lighting Regimes

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

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

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



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

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

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



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

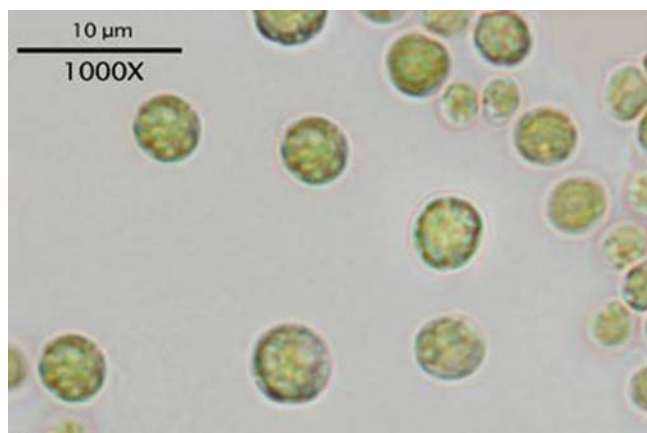


Figure 124. *Chlorella sorokiniana*, a member of **Chlorophyta** in which growth is prevented by green light. Photo by UTEX, through Creative Commons.

### Pollution and Role of Bryophytes

In the Zhijin Cave in China, heavy metal pollution was introduced by the development of the karst caves for show

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



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

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

### Summary

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

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



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

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

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

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

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# CHAPTER 18-6

## CAVES – SIMILAR SECLUDED HABITATS

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# CHAPTER 18-6

## CAVES – SIMILAR SECLUDED HABITATS



Figure 1. Zen Iwatsuki photographing fissure in lava, with bryophytes, Grjotagja, Myvatn, Iceland, 1985. Photo by Janice Glime.

### Artificial "Caves"

#### Mine Shafts

Mines and mine shafts, in many ways, act like caves. Their cold air typically comes from lower levels rather than through channels above. They are dark, and they are usually damp. These habitats can have their own unique bryophyte flora, often influenced by the types of minerals being mined. Strip mines can in some cases resemble sink holes, but often have a much shorter history and much less moisture. But I have to wonder why I was unable to find many studies on these human-made habitats.

In Ireland, Holyoak and Lockhart (2009) found *Cephaloziella massalongi* (Figure 2) at the top of a copper

mine shaft on rock where it was lightly shaded (Figure 3). Although it seems to always be associated with copper in Britain, *Cephaloziella massalongi* only occurs on acidic sites (Figure 4), and is not known from limestone sites. Cornish sites typically have pH levels of 5.1-5.4 and are often associated with moderate levels of both lead and zinc as well as copper. Callaghan (2011) studied the ecology of this species and found that it typically grows in shaded conditions (Figure 4) with less than 10% relative light, a level that characterizes many of the liverworts (Marschall & Proctor 2004). In an old mine adit of Wales, it grew at 2.5 lux (0.2% relative light). Callaghan suggested that *Cephaloziella massalongi* may be confined to such shaded conditions because of its need for moisture and inability to successfully compete elsewhere.





Figure 2. *Cephaloziella massalongi*, a copper-tolerant liverwort. Photo by Des Callaghan, with permission.



Figure 3. *Cephaloziella massalongi* habitat in old metal mine. Photo by Des Callaghan, with permission.



Figure 4. *Cephaloziella massalongi* in Hermon Copper Bog under overhanging sod that provides it with shade. Photo by Des Callaghan, with permission.

The number of taxa in the Tongshankou Copper Mine in China is much greater than in many caves (Pen & Zhang 2005). So far 29 moss taxa, representing 7 families and 20 genera, have been identified. Pan *et al.* (2011) found a similar number of species (30 taxa) in four abandoned mercury mines in China. Bryophytes occurred within the first 10 m into the mine. The life forms were 60% short turfs, 33% wefts, and 7% mats. Among these was the luminous thallose liverwort *Cyathodium smaragdinum* (Figure 5).



Figure 5. *Cyathodium smaragdinum*, a luminous thallose liverwort that is known from a copper mine in China. Photo by 楊玉鳳, through Creative Commons.

Koponen (1977) reported the mosses *Pohlia nutans* (Figure 6) and *Ceratodon purpureus* (Figure 7-Figure 10) at a depth of 176 m in a mine in Finland. But this mine was continuously illuminated by electric lights. The mosses covered an area of ~0.5 m<sup>2</sup> in this mine under a constant ~8°C and high humidity. The mine was rich in zinc, lead, and copper. *Ceratodon purpureus* is a moss of a wide range of habitats, from dry roadsides to submerged in Antarctic ditches and resplendent on its boulders (Figure 9). It is not unusual to see it growing on stone ledges (Figure 10).



Figure 6. *Pohlia nutans* with capsules on rock, a widespread species that occurs at a depth of 176 m in a mine in Finland. Photo by J. C. Schou, with permission.





Figure 7. *Ceratodon purpureus*, a moss that can grow at 176 m depth in a continuously illuminated mine. Photo by Michael Lüth, with permission.



Figure 8. *Ceratodon purpureus* with immature capsules, showing how abundant the capsules can be. Photo courtesy of Dale Sievert.



Figure 9. *Ceratodon purpureus* on boulders in the Antarctic. Photo courtesy of Rod Seppelt.



Figure 10. *Ceratodon purpureus* on a shaded ledge in Dollar Bay, Michigan, USA. Photo by Janice Glime.

Mine entrances seem to be overlooked habitats where one might find unusual species in areas where similar cave habitats are absent. On the other hand, the surface around mines is typically rich in ore and often has rare species (*e.g.* Callaghan 2018), but these areas are not similar to caves and will be discussed elsewhere.

### Subways

Subways are manmade caves, but are typically illuminated and are open at both ends. They are likely to suffer from the pollution created by trains.

The granitic subway in Stockholm has lighting throughout. Established in 1970, the tunnel has a flora including *Cyanobacteria*, fungi, bacteria, diatoms, and the moss *Eucladium verticillatum* (Figure 11), a species not known elsewhere in Stockholm. Its occurrence on granite is unusual – it usually occurs on limestone. The subway also is home to a spider that is unknown elsewhere in Sweden.

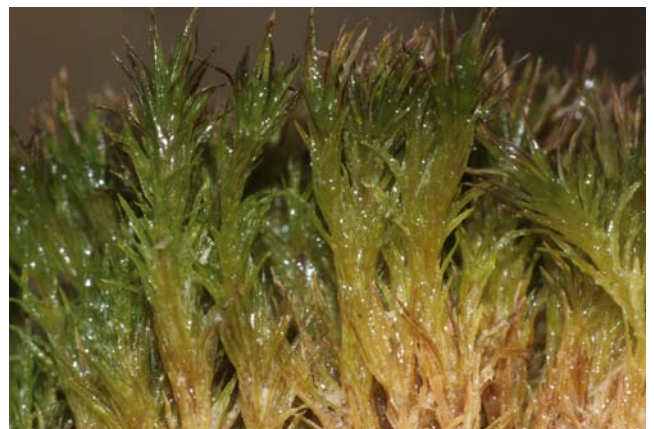


Figure 11. *Eucladium verticillatum*, a moss that grows in a granitic subway in Stockholm. Photo by Hermann Schachner, through Creative Commons.

### Small Caves and Fissures

Various fissures and cracks in rocks (Figure 1, Figure 12-Figure 13), including lava, make tiny caves and cave-like habitats that are suitable refuges for bryophytes. While



in Iceland, Yojiro Iwatsuki uncovered *Saelania glaucescens* (Figure 14) growing completely hidden under cracked rocks in a lava field (Figure 15-Figure 17).



Figure 12. Fissures in hard lava rock, Myvatn, Iceland, making cave-like environments. Photo by Janice Glime.



Figure 13. Fissures with hot springs at bottom and bryophytes growing on the warm, humid rocks, Myvatn, Iceland. Photo by Janice Glime.



Figure 14. *Saelania glaucescens*, a species that grows in protected areas on cliffs or even completely under rocks in volcanic areas. Photo by Janice Glime.



Figure 15. Cracked lava that hides *Saelania glaucescens* north of Reykjahlid, Iceland. Photo by Janice Glime.



Figure 16. *Saelania glaucescens* revealed as layers of rock are removed, north of Reykjahlid, Iceland. Photo by Janice Glime.



Figure 17. *Saelania glaucescens* with capsules revealed from under lava crack N of Reykjahlid, Iceland. Photo by Janice Glime.

Krukowski and Świerkosz (2005) found the fern *Vandenboschia radicans* (Figure 18) in its easternmost locality in Europe. Its gametophytes grew in horizontal rock fissures with sparse growths of the mosses *Schistostega pennata* (Figure 19) and *Distichium inclinatum* (Figure 20). I observed the same phenomenon with *Asplenium scolopendrium* gametophytes growing among mosses on the vertical sides of boulders in the Upper Peninsula of Michigan, USA.





Figure 18. *Vandenboschia radicans*, a fern species whose prothalli grow in rock crevices with mosses in Europe. Photo through Creative Commons.



Figure 19. *Schistostega pennata* carpet; dark green plants are upright gametophytes; yellow-green color indicates presence of the protonemata; this mat of mosses can provide suitable habitat in crevices for the fern *Vandenboschia radicans* in Europe. Photo by Alpsdake, through Creative Commons.



Figure 20. *Distichium inclinatum*; this mat of mosses can provide suitable habitat in crevices for the fern *Vandenboschia radicans* in Europe. Photo by Hermann Schachner, through Creative Commons.

## Scree

**Scree** (slopes covered with small loose stones; **talus**; Figure 21-Figure 22) create numerous minicaves that can act as refugia for more northern boreal and Arctic

bryophyte, pteridophyte, and arthropod species (Růžička *et al.* 2012). These can even have year-round ice.



Figure 21. Scree in Switzerland, creating tiny darkened caves where bryophytes enjoy protection. Photo by Urs Kormann, through Creative Commons.



Figure 22. Talus slope at Ruby Mountains, Nevada, USA. Photo from USGS, through public domain.

In the Czech Republic, 92 bryophyte and 10 pteridophyte species were encountered among the scree. The liverworts *Sphenolobus saxicola* (Figure 23), *Diplophyllum taxifolium* (Figure 24), *Gymnomitrium*



*concinnum* (Figure 25), *Gymnomitrium corallioides* (Figure 26-Figure 27), and *Barbilophozia sudetica* (Figure 28), and mosses *Andreaea rupestris* (Figure 29), *Polytrichastrum alpinum* (Figure 30), *Racomitrium fasciculare* (Figure 31) and *Racomitrium lanuginosum* (Figure 32) have isolated populations in the Kamenec Hill of the Czech Republic, and the populations of the fern *Cryptogramma crista* (Figure 33) and liverworts *Gymnomitrium* spp. (Figure 25-Figure 27) represent the lowest known elevational limits for the Czech Republic and Central Europe. Some species occur only near ice plots, including the liverworts *Diplophyllum taxifolium*, *Gymnomitrium corallioides*, and *Lophozia sudetica* and the mosses *Andreaea rupestris* and *Polytrichastrum alpinum*. On the other hand, the liverworts *Sphenolobus saxicola* and *Gymnomitrium concinnum* and mosses *Racomitrium fasciculare* and *Racomitrium lanuginosum* never occurred near ice.



Figure 25. *Gymnomitrium concinnum*, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Štěpán Koval, with permission.



Figure 23. *Sphenolobus saxicola*, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo through Creative Commons.



Figure 26. *Gymnomitrium corallioides*, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Rory Hodd, with permission.



Figure 24. *Diplophyllum taxifolium*, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Hermann Schachner, through Creative Commons.



Figure 27. *Gymnomitrium corallioides*. Photo by Hermann Schachner, through Creative Commons.





Figure 28. *Barbilophozia sudetica*, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Hugues Tinguy, with permission.

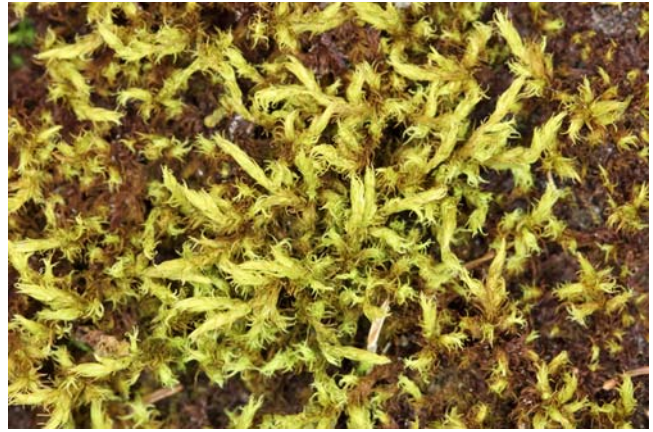


Figure 31. *Racomitrium fasciculare*, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Jean Faubert, with permission.



Figure 29. *Andreaea rupestris*, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by J. C. Schou, with permission.



Figure 32. *Racomitrium lanuginosum*, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Hermann Schachner, through Creative Commons.



Figure 30. *Polytrichastrum alpinum*, a species that is found in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by David T. Holyoak, with permission.



Figure 33. *Cryptogramma crispa*, a species that reaches its lowest elevation in cavities among the scree of Kamenec Hill of the Czech Republic. Photo by Joan Simon, through Creative Commons.



These scree habits likewise provide a deep labyrinth where arthropods and other organisms find refuge (Růžicka *et al.* 2010). In NE Bohemia, Czech Republic, deep vertical spaces among the scree provide microhabitats for montane bryophyte species such as the liverwort *Diplophyllum taxifolium* (Figure 24), and the mosses *Dicranum elongatum* (Figure 34) and *Pohlia drummondii* (Figure 35) occur. Living among these are numerous arthropods, with spiders and beetles being the most numerous. A total of 304 species of arthropods were identified in the study.



Figure 34. *Dicranum elongatum* with capsules, a species that lives in deep cavities among the scree in NE Bohemia, Czech Republic. Photo by Jean Faubert, with permission.



Figure 35. *Pohlia drummondii*, a species that lives in deep cavities among the scree in NE Bohemia, Czech Republic. Photo by David T. Holyoak, with permission.

In Iceland, the mosses *Distichium capillaceum* (Figure 36-Figure 37), *Mnium marginatum* (Figure 38), and *Pohlia cruda* (Figure 39), and the fern *Cystopteris fragilis* (Figure 40), grow over the **loess** (silt-sized sediment formed by accumulation of wind-blown dust) deposits inside the scree cavities, surviving with reduced light but buffered microclimate (Blažková 1973). Similar associations also occur in crevices on loess in the Czech Republic (Hesselbo 1918; Šmarda 1947).



Figure 36. *Distichium capillaceum* with capsules, under grass cave; this species grows over the loess deposits inside in karst cavities and at the bottom of the deep karstic Macocha Chasm in the Czech Republic. Notice the lines of reddish brown capsules. Photo by Michael Lüth, with permission.



Figure 37. *Distichium capillaceum*. Photo by Hermann Schachner, through Creative Commons.



Figure 38. *Mnium marginatum*, a species that grows over the loess deposits in karst cavities. Photo by Hermann Schachner, through Creative Commons.





Figure 39. *Pohlia cruda*, a species that grows over the loess deposits in karst cavities. Photo by Hermann Schachner, through Creative Commons.



Figure 40. *Cystopteris fragilis* among mosses on rock, a species that grows over the loess deposits in karst cavities. Photo by Bryant Olson, through Creative Commons.

Similar cavities occur in lava fields (Figure 41). Blažková (1973) described these from northern Iceland. Aeolian sediments accumulate on the bottom of these cavities. Light intensity is greatly reduced and the microclimate is buffered from the extremes at the surface. Blažková reported 12 bryophyte species from these. In very dark parts of the cavities mainly liverworts occur, including *Blepharostoma trichophyllum* (Figure 42), *Mesoptychia collaris* (Figure 43-Figure 44), and *Sauteria alpina* (Figure 45-Figure 46). Close to the openings where it is well illuminated, one can find *Polytrichum juniperinum* (Figure 47-Figure 48) and especially *Timmia austriaca* (Figure 49).



Figure 41. Sheep near lava rock at Myvatn, northern Iceland, showing the tumbled arrangement of rocks that creates minicaves. Photo by Janice Glime.



Figure 42. *Blepharostoma trichophyllum*, a species that can occur in dark cavities of lava fields in northern Iceland. Photo by Hermann Schachner, through Creative Commons.



Figure 43. *Mesoptychia collaris*, a species that can occur in dark cavities of lava fields in northern Iceland. Photo by Hermann Schachner, through Creative Commons.





Figure 44. *Mesoptychia collaris* with capsules. Photo by Hermann Schachner, through Creative Commons.

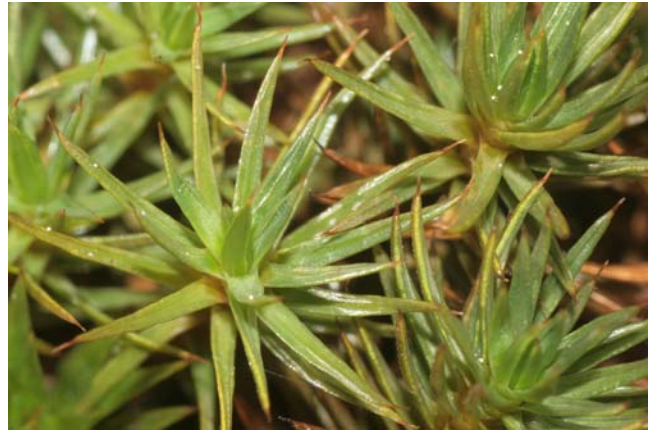


Figure 47. *Polytrichum juniperinum*, a species that grows close to the openings of cavities among lava stones where it is well illuminated. Photo by Hermann Schachner, through Creative Commons.



Figure 45. *Sauteria alpina*, a species that can occur in dark cavities of lava fields in northern Iceland. Photo by Michael Lüth, with permission.



Figure 48. *Polytrichum juniperinum* with male splash cups. Photo by Ian Sutton, through Creative Commons.



Figure 46. *Sauteria alpina* with archegoniophores. Photo by Hermann Schachner, through Creative Commons.



Figure 49. *Timmia austriaca*, a species that grows close to the openings of cavities among lava stones where it is well illuminated. Photo by Jean Faubert, with permission.

Bjarnason (1991) considered every cavity around a boulder at Hekla (Figure 50), southern Iceland, to be



different, thus making all the holes different in ecological character. The moss *Racomitrium lanuginosum* (Figure 32) frequently grows on these rocks and covers the cavity (Figure 51-Figure 52), making the area somewhat dangerous for walking. The very deep, narrow lava clefts (Figure 53-Figure 54) support vegetation similar to that of the holes, with *Conostomum tetragonum* (Figure 55), *Pohlia drummondii* (Figure 35), *Pohlia wahlenbergii* (Figure 56), and *Polytrichastrum sexangulare* (Figure 57-Figure 58). The vegetation in these narrow lava cavities at Hekla has a very different flora from those in northern Iceland (Figure 41). Some species prefer the holes in the Hekla area, but are not restricted to them: the liverworts *Blepharostoma trichophyllum* (Figure 42) and *Nardia geoscyphus* (Figure 59) and the mosses *Isopterygiopsis pulchella* (Figure 60), *Mnium stellare* (Figure 61), *Oligotrichum hercynicum* (Figure 62), and *Pohlia cruda* (Figure 39). Many species also occupy the crags, including the liverworts *Diplophyllum albicans* (Figure 63) and *Mesoptrychia gillmanii* (Figure 64) and the mosses *Encalypta ciliata* (Figure 65) and *Plagiothecium cavifolium* (Figure 66-Figure 67). Others occur in small ruptures in the main surface (Figure 54), including the liverwort *Cephaloziella divaricata* (Figure 68-Figure 69) and mosses *Dicranoweisia crispula* (Figure 70), *Diphyscium foliosum* (Figure 71), and *Pohlia drummondii*. As in northern Iceland, *Racomitrium lanuginosum* (Figure 32, Figure 51-Figure 52) is common near the openings of the holes, infrequently accompanied by *Andreaea rupestris* (Figure 29) and *Schistidium apocarpum* (Figure 72) (Bjarnason 1991). As in northern Iceland, the moist, sandy bottom (40-60 cm) supports small patches of liverworts; mixed with larger bryophytes such as the moss *Bartramia ithyphylla* (Figure 73) and liverwort *Plagiochila porelloides* (Figure 74). In wide, shallow holes the number of species is greater at this sandy bottom, including *Brachythecium albicans* (Figure 75), *Polytrichum juniperinum* (Figure 47-Figure 48), *Rhytidiadelphus squarrosus* (Figure 76), and *Timmia austriaca* (Figure 49).



Figure 50. Hekla, Iceland, cairns and various rock sizes. Photo by cogdogblog, through Creative Commons.



Figure 51. *Racomitrium* mounds, Iceland. Photo by Janice Glime.



Figure 52. Lava beds of Nass Valley, British Columbia, with *Racomitrium*, illustrating the cavities and multiple formations created. Photo by Darren Kirby, through Creative Commons.



Figure 53. Fissure in hard lava rock, with the lichen *Cetraria* and bryophytes, Myvatn, Iceland. Photo by Janice Glime.





Figure 54. Fissure with mosses in its small rupture, N. Myvatn, Iceland. Photo by Janice Glime.



Figure 57. *Polytrichastrum sexangulare*, a species that occurs in very deep, narrow lava clefts in Iceland. Photo by Tomas Hallingbäck, with permission.



Figure 55. *Conostomum tetragonum* with capsules, a species that occurs in very deep, narrow lava clefts in Iceland. Photo by Hermann Schachner, through Creative Commons.



Figure 58. *Polytrichastrum sexangulare*. Photo by Hermann Schachner, through Creative Commons.



Figure 56. *Pohlia wahlenbergii*, a species that occurs in very deep, narrow lava clefts in Iceland. Photo by Hermann Schachner, through Creative Commons.



Figure 59. *Nardia geoscyphus*, a species that prefers the holes in the Hekla area of Iceland, but is not restricted to them. Photo by Rayna Natcheva, with permission.





Figure 60. *Isopterygiopsis pulchella* with capsule, a species that prefers the holes in the Hekla area of Iceland, but is not restricted to them. Photo by Michael Lüth, with permission.



Figure 63. *Diplophyllum albicans*, a species that occupies the crags in the Hekla area of Iceland. Photo by David T. Holyoak, with permission.



Figure 61. *Mnium stellare*, a species that prefers the holes in the Hekla area of Iceland, but is not restricted to them. Photo by Hermann Schachner, through Creative Commons.



Figure 64. *Mesoptychia gillmanii*, a species that occupies the crags in the Hekla area of Iceland. Photo by Tomas Hallingbäck, with permission.



Figure 62. *Oligotrichum hercynicum*, a species that prefers the holes in the Hekla area of Iceland, but is not restricted to them. Photo by Štěpán Koval, with permission.



Figure 65. *Encalypta ciliata* with capsules, among rocks, a species that occupies the crags in the Hekla area of Iceland. Photo by Tony Frates, through Creative Commons.





Figure 66. *Plagiothecium cavifolium* on shale, a species that occupies the crags in the Hekla area of Iceland. Photo by Bob Klips, with permission.



Figure 67. *Plagiothecium cavifolium*. Photo by Christian Berg, through Creative Commons.



Figure 68. *Cephaloziella divaricata*, a species that occupies the crags in the Hekla area of Iceland. Photo by Hermann Schachner, through Creative Commons.

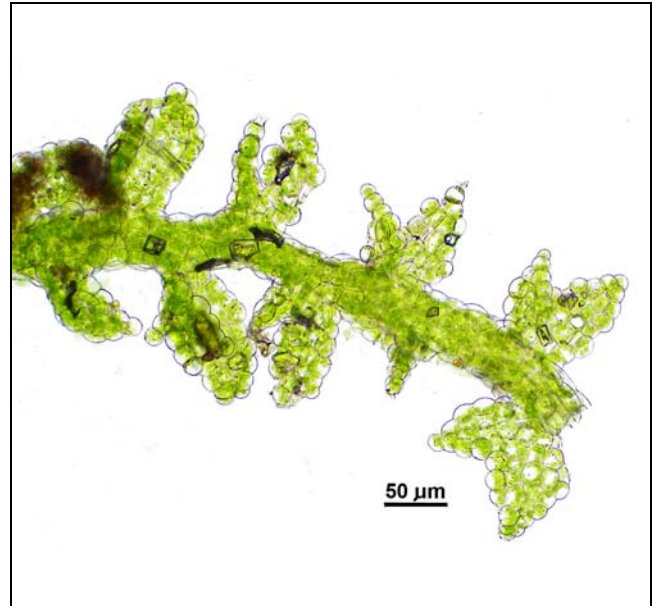


Figure 69. *Cephaloziella divaricata* branch. Photo from Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 70. *Dicranoweisia crispula* with capsules, on rock, a species that occupies the crags in the Hekla area of Iceland. Photo by Hermann Schachner, through Creative Commons.



Figure 71. *Diphyscium foliosum* capsules, a species that occupies the crags in the Hekla area of Iceland. Photo by Hermann Schachner, through Creative Commons.





Figure 72. *Schistidium apocarpum* with capsules, a species that occurs near the opening of an ice cave in Iceland. Photo by Hermann Schachner, through Creative Commons.



Figure 74. *Plagiochila porelloides* on vertical bank, a species that occurs on the moist, sandy bottoms (40-60 cm) of small caves in Iceland. Photo from Botany Website, UBC, with permission.



Figure 73. *Bartramia ithyphylla* with capsules on vertical rock, a species that occurs on the moist, sandy bottoms (40-60 cm) of small caves in Iceland. Photo by Štěpán Koval, with permission.



Figure 75. *Brachythecium albicans*, a species that occurs in the shallow bottom of wide, sandy holes in Iceland. Photo by Kristian Peters, through Creative Commons.



Figure 76. *Rhytidiadelphus squarrosus*, a species that occurs in the shallow bottom of wide, sandy holes in Iceland. Photo by Johan N, through Creative Commons.



## Ice Caves

Bryophytes in ice caves (Figure 77) are much more uncommon. Jakab (2000) found *Heterocladium heteropterum* (Figure 78-Figure 79) and *Cyrtomnium hymenophylloides* (Figure 80) in ice caves in Romania. But outside, the caves can cause a **temperature inversion** (reversal of normal decrease of air temperature with altitude). Other bryophytes seem to benefit from the conditions emanating from these caves, permitting more Arctic species to survive here.



Figure 77. Ice cave in natural glacier. Photo by Serge J. F., through Creative Commons.



Figure 78. *Heterocladium heteropterum* on rock, a species that occurs in an ice cave in Romania. Photo by Štěpán Koval, with permission.



Figure 79. *Heterocladium heteropterum* branch showing large stem leaves and smaller branch leaves. Photo by Štěpán Koval, with permission.



Figure 80. *Cyrtomnium hymenophylloides*, a species that occurs in an ice cave in Romania. Photo by Michael Lüth, with permission.

## Windholes

**Windholes** (Figure 81-Figure 83, Figure 88) are also known as **Kaltluftlöcher**, **Kondenswassermoore**, and **ventaroles** (Wolfgang Karl Hofbauer, pers. comm. 26 July 2021). Natural windholes are made by the wind in sandstone formations as a result of centuries of wind and weather, making the rock formations pock-marked with windholes and caves. In summer, these cool the surrounding area with cool air that blows out, but during winter the air from the windholes is milder than that of the surrounding area (Kong *et al* 2011). These can be categorized as talus (Figure 84), cave (Figure 81-Figure 83), and sink types of windholes. Like caves, these can provide refugia for plants that normally occur at higher elevations or closer to the poles (Kong *et al*. 2012).





Figure 81. Algific talus slope with windholes in northeastern Iowa, USA. photo courtesy of Beth Lynch.



Figure 83. Algific cave opening (windhole) in Fillmore County, Minnesota, USA. Photo by S. C. Zager, MN DNR, through public domain.

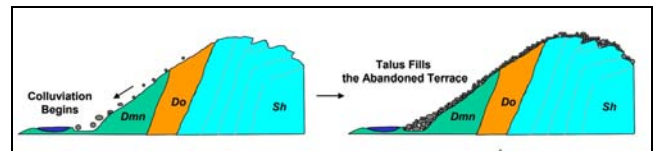


Figure 84. Algific slope cave formation, Ice Mountain, West Virginia, USA. Modified from Kevin M. Andrews, MS thesis 2003.



Figure 82. Algific talus slope with windholes obscured by mosses and other vegetation, northeastern Iowa, USA. Photo courtesy of Beth Lynch.



Figure 85. *Protochilopsis grandiretis*, an Arctic species that grows in windholes in Austria. Photo by Vadim Bakalin, with permission.





Figure 86. *Odontoschisma macounii*, an Arctic species that grows in windholes in Austria. Photo from Earth.com, with permission.



Figure 87. *Tritomaria scitula*, an Arctic species that grows in windholes in Austria. Photo by Tomas Hallingbäck, with permission.

Bakalin *et al.* (2017) describe these as formations in East Manchuria of Russia as places where the wind enters large holes tens of meters above, then goes underground, where it passes among wet stones and cliffs in areas with much lower temperatures due to evaporation of water from the stones. Therefore, at the exit hole, the air temperature may be about 10°C below that of the surrounding environment.

In the Wisconsin Driftless Area, USA, Christy and Meyer (1991) similarly reported disjunct species that are restricted to the "refrigerated" windholes (Figure 88). Among these, the tiny moss *Seligeria donniana* (Figure 89) was new to Wisconsin. Among the 39 species of bryophytes identified from four of the largest algific slopes, one third were restricted to these cold air vents. These included the liverworts *Marchantia polymorpha* (Figure 90), *Porella platyphylla* (Figure 91), and *Preissia quadrata* (Figure 92), and the mosses *Abietinella abietinum* (Figure 93), *Anomodon attenuatus* (Figure 94), *Anomodon rostratus* (Figure 95), *Bartramia pomiformis* (Figure 96), *Brachythecium oxycladon* (Figure 97), *Koponeniella*

*graminicolor* (Figure 98), *Bryoerythrophyllum recurvirostrum* (Figure 99), *Campylium chrysophyllum* (Figure 100), *Ceratodon purpureus* (Figure 7-Figure 10), *Climacium americanum* (Figure 101), *Didymodon fallax* (Figure 102), *Entodon seductrix* (Figure 103), *Eurhynchium hians* (Figure 104), *Hylocomiadelphus triquetrus* (Figure 105), *Mnium marginatum* (Figure 38), *Mnium stellare* (Figure 61), *Plagiomnium cuspidatum* (Figure 106), *Plagiomnium medium* (Figure 107), *Pohlia wahlenbergii* (Figure 56), *Rhodobryum ontariense* (as *Rhodobryum roseum*; Figure 108), *Seligeria campylopoda* (Figure 109), *Seligeria donniana*, *Thuidium delicatulum* (Figure 110), and *Thuidium recognitum* (Figure 111).



Figure 88. Algific caves (windholes) in Wisconsin, USA. Photo by Ryan O'Connor, Wisconsin DNR, through public domain.



Figure 89. *Seligeria donniana* with capsules, a species that occurs in windholes in the algific slopes of the Driftless Area of Wisconsin, USA. Photo by Tom Neily, with permission.





Figure 90. *Marchantia polymorpha*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Brenda Dobbs, through Creative Commons.



Figure 91. *Porella platyphylla*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.



Figure 92. *Preissia quadrata*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.



Figure 93. *Abietinella abietinum* on rock, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.



Figure 94. *Anomodon attenuatus*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Dendrofil, through Creative Commons.



Figure 95. *Anomodon rostratus*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.





Figure 96. *Bartramia pomiformis* with capsules, on rock ledge, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by David T. Holyoak with permission.



Figure 99. *Bryoerythrophyllum recurvirostrum* with capsules, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.



Figure 97. *Brachythecium oxycladon*, on rock ledge, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.



Figure 100. *Campylium chrysophyllum*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.



Figure 98. *Koponeniella graminicolor*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.



Figure 101. *Climacium americanum*, a common species in moist habitats, occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Rafael Medina, through Creative Commons.





Figure 102. *Didymodon fallax*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Jean Faubert, with permission.



Figure 103. *Entodon seductrix*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.



Figure 104. *Eurhynchium hians*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Wayne Lampa, through Creative Commons.



Figure 105. *Hylocomiadelphus triquetrus*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by J. C. Schou, with permission.



Figure 106. *Plagiomnium cuspidatum* branch, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.



Figure 107. *Plagiomnium medium* with capsules, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Bob Klips, with permission.





Figure 108. *Rhodobryum ontariense*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.



Figure 111. *Thuidium recognitum*, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Sture Hermansson, with online permission.



Figure 109. *Seligeria campylopoda* with capsules showing tropism, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo from Earth.com, with permission.



Figure 110. *Thuidium delicatulum* with capsules, a species that occurs on algific slopes in the Driftless Area of Wisconsin, USA, but only in windholes. Photo by Hermann Schachner, through Creative Commons.



Figure 112. *Hylocomium splendens*, a northern species that can be found around windhole vents in Iowa, USA. Photo by Hugues Tinguy, with permission.

Beth Lynch (pers. comm. 29 July 2021) finds a few bryophyte species that are common around the windhole vents of northeastern Iowa, USA (Figure 81-Figure 82), but are very infrequent or absent in the surrounding areas. Presumably due to these microclimatic conditions, *Hylocomium splendens* (Figure 112) and *Hylocomiadelphus triquetrus* (Figure 105) can be relatively common on the algific slopes, but are absent in other cool, moist microsites in the area. It is interesting that, like most caverns, these areas seem to be devoid of leafy liverworts.



Higuchi (1991) reported that the montane mosses *Dicranum elongatum* (Figure 34) and *Pohlia drummondii* (Figure 35) and liverwort *Diplophyllum taxifolium* (Figure 24) occur in windhole areas of the Senpoku-gun in Japan.

The unusual microclimate near the windholes can bring surprises for curious bryologists (Choi *et al.* 2020). Choi *et al.* (2020) found *Mannia fragrans* (Figure 113) and *Mannia androgyna* (Figure 114) in windholes near the Donggang River, the first find of these species in Korea. Borovichev and Bakalin (2016) similarly reported *Mannia triandra* (Figure 115) from the windhole area of Magadan Province and the Korean Peninsula.



Figure 113. *Mannia fragrans*, a species that occurs in windholes in Korea. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.



Figure 114. *Mannia androgyna*, a species that occurs in windholes in Korea. Photo from Earth.com, with permission.



Figure 115. *Mannia triandra* with archegoniophores among rocks, a species that occurs in windholes in Korea. Photo by Oliver Dürhammer, through Creative Commons.

Shirasaki (1990) investigated the ecological distribution of bryophytes in the windhole areas of Mt. Naeba, Niigata and Nagano Prefectures, Japan. Shirasaki (1998) found that the moss *Trachycystis flagellaris* (Figure 116) sometimes grows on the ground under shrubs where there are cool sites maintained by windholes that provide a temperature below 10°C and a high air humidity in warmer seasons.



Figure 116. *Trachycystis flagellaris*, a species that grows on the ground under shrubs where there are cool sites maintained by windholes in Japan. Photo by Misha Ignatov, with permission.

Hitoshi and Masaji (2003) found that in the windhole area of Niigata Prefecture, Japan, one could find *Pogonatum urnigerum* (Figure 117) and *Polytrichastrum formosum* (Figure 118) growing together. Elsewhere, *Pogonatum urnigerum* is able to grow at higher elevations than those of *Polytrichastrum formosum*, whereas their distribution on a flat map is similar. *Pogonatum urnigerum* often has caducous leaves, as known in the Arctic (Long 1988) and in northern New York, USA (McDaniel & Miller 2000).





Figure 117. *Pogonatum urnigerum* with capsules, among rocks, a species that grows in windhole areas of Japan. Photo by Claire Halpin, with permission.



Figure 118. *Polytrichastrum formosum*, a species that grows in windhole areas of Japan. Photo by Leonhard Lenz, through Creative Commons.

At the Bixby State Park and Preserve in Iowa, USA, Kleinman and Blisard (2018) reported 68 bryophyte species from the algific talus slopes near cold air vents. Of these, 16 moss species and 1 liverwort species are uncommon elsewhere in the Bixby park.

## Sinkholes

**Sinkholes** (cenote, sink, sink-hole, sink hole, swallow, swallow hole, or doline; Figure 119-Figure 121) are large depressions in the ground due to collapse of the underlying substrate. This collapse is often caused by karstic processes that dissolve underlying carbonate rocks.



Figure 119. Sinkhole along Rio Camuy, Puerto Rico, aerial view. Photo from US Geological Survey, through Creative Commons.



Figure 120. Looking out of deep sinkhole at Gouffre-v-hdr in France, showing vegetation at the bottom. Photo through Creative Commons.





Figure 121. Sinkhole with bryophytes in Wilson County, Tennessee, USA. Photo by Brian Stansberry, through Creative Commons.

Linares *et al.* (2017) demonstrated the correlation between drought and the formation of sinkholes. This has occurred repeatedly in the karst of the fluvial valley of northeastern Spain (Figure 122), and it has been widely visible in Florida, USA (Figure 123), due to the emptying of aquifers by water usage and periods of drought.



Figure 122. Sinkhole Chinchón dolina c, collapse sinkhole in Spain. Photo through Creative Commons.



Figure 123. Sinkhole, Dover, Florida, USA, collapsed during a winter freeze event. Photo by Ann Tihansky, USGS, through public domain.

Sinkholes encompass some of the same characteristics as caves, especially high humidity and reduced light intensity (Maheu 1926). Because they are sunken, they tend to be more moist than the surrounding forest, with humidity increasing toward the base (Maheu 1926; Li *et al.* 2020b). The additional moisture is at least a contributor to lower temperatures. Maheu noted that the same dominant genera of mosses occurred in the sinkholes as in caves: *Anomodon* (Figure 94-Figure 95), *Eurhynchium* (Figure 104), *Mnium* (Figure 38, Figure 61). Perhaps this is in part due to their ease of starting protonemata from stems and leaves of these mosses. Maheu also considered that the protonemata of the mosses could enter in symbiosis with fungi. The modifications in these conditions are likewise similar to those of cave bryophytes: sterility, leaf elongation, longer internodes, elongation of cells, and disappearance or attenuation of the rib or costa.

The sinkhole often has greater bryophyte diversity than does the surrounding surface forest, but it also can increase the diversity of the adjoining forest. Li *et al.* (2020a) reported 71 taxa of bryophytes from a sinkhole forest in southeastern China, whereas the forest at the surface had only 29, and farther from the sinkhole only 22 taxa were present (Figure 124). Furthermore, the sinkholes were more favorable to liverworts, with 22 taxa compared to only 2 in the adjoining surface forest. In this study, 93% of the sinkhole bryophytes were absent from the surface forest. Li and coworkers found that in the sinkholes the dominant families were **Brachytheciaceae** (Figure 75, Figure 104), **Fissidentaceae** (Figure 128), **Plagiocladiaceae** (Figure 74), and **Hypopterygiaceae** (Figure 125). The sinkhole bryophytes, by importance, were *Conocephalum conicum* (Figure 126), *Homaliodendron montagneanum* (see Figure 127), *Fissidens cristatus* (Figure 128), *Leucobryum glaucum* (Figure 129-Figure 130), *Makinoa crispata* (Figure 131), *Plagiomnium rhynchophorum* (Figure 132), *Claopodium aciculium* (see Figure 133), *Eurhynchium laxirete* (see Figure 104), *Claopodium gracillimum* (see Figure 133), and *Fissidens hyalinus* (Figure 134). The surface families were completely different, with the exception of **Brachytheciaceae**.

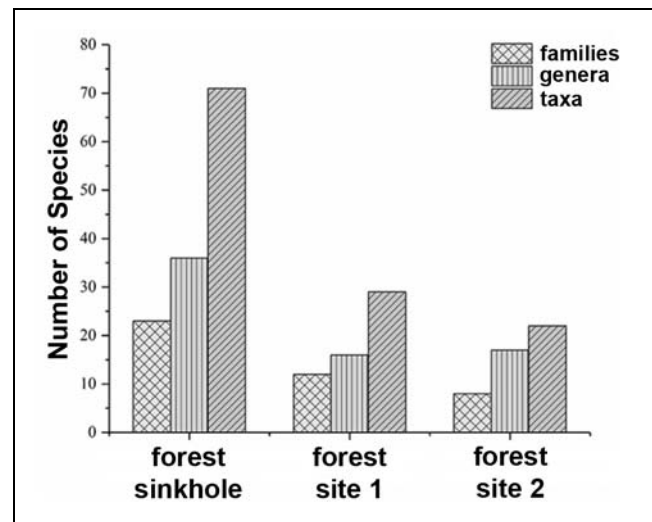


Figure 124. Sinkhole diversity vs forest diversity at 2 distances from sinkhole. Modified from Li *et al.* 2020a.





Figure 125. *Hypopterygium filiculaeforme*, a member of the family **Hypopterygiaceae**, a family that is among the dominant families occurring in sinkholes in China. Photo by Sara Smerdon, through Creative Commons.



Figure 128. *Fissidens cristatus*, one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by Brad von Blon, through Creative Commons.



Figure 126. *Conocephalum conicum* with archegoniophores, most important bryophyte associated with sinkholes in sinkhole forest in southeastern China. Photo by Claire Halpin, with permission.



Figure 129. *Leucobryum glaucum* habitat on cliff, Canyon Falls, Michigan, USA, one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by Janice Glime.



Figure 127. *Homaliodendron flabellatum*; *Homaliodendron montagneanum* is among most important bryophytes associated with sinkholes in forest in southeastern China. Photo by Chris Alice Kratzer, through Creative Commons.



Figure 130. *Leucobryum glaucum*. Photo by Janice Glime.





Figure 131. *Makinoa crispata* with capsules, one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by 楊玉鳳, through Creative Commons.



Figure 132. *Plagiomnium rhynchophorum*, one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by Paul Davison, with permission.



Figure 133. *Claopodium* sp.; *Claopodium aciculum* and *C. gracillimum*, both among the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by John Game, with permission.



Figure 134. *Fissidens hyalinus* (whitish green), one of the most important bryophytes associated with sinkholes in a sinkhole forest in southeastern China. Photo by Ivanov, with permission.

In the Guda Sinkhole in China, Li *et al.* (2020b) found 75 species of bryophytes. They recorded the highest bryophyte diversity and abundance in the middle and upper sections, with the lowest in the top section and in the base. Furthermore, the most rapid turnover of species occurred in the two middle sections, presumably in response to a rapidly changing gradient of conditions of light and moisture. On the other hand, Vána *et al.* (2014) found the liverworts *Riccardia insularis* (see Figure 135) and *Calypogeia fissa* (Figure 136) on both the floor and wall of a sink-hole cave on Ile Amsterdam in the South Indian Ocean.



Figure 135. *Riccardia multifida*; *Riccardia insularis* occurs in a sink-hole cave on Ile Amsterdam in the South Indian Ocean. Photo by Hermann Schachner, through Creative Commons.





Figure 136. *Calypogeia fissa*, a liverwort that occurs on both the floor and walls of a sink-hole cave on Ile Amsterdam in the South Indian Ocean. Photo by Claire Halpin, with permission.

In the large (280 m deep, 300 m diameter) Monkey-Ear sinkhole in China, Li *et al.* (2018) found 71 species of bryophytes. The greatest diversity was on tree trunks (41 species), followed by forest land > stone surfaces > carrion > leaf surfaces. There are 10 different life forms, 88% of which are typical of dark, humid habitats, whereas only 12% are adapted to bright light and dry conditions. The dissimilarity with surface bryophyte communities is high. Light, humidity, and temperature all influence the distribution of species, but light had the most influence.

In their study of Karst Mountain Sinkhole of Southeastern China, Li *et al.* (2020a) found that the number of life forms diminished from the sink hole to the first forest site and diminished more to the second (farthest) forest site (Figure 137).

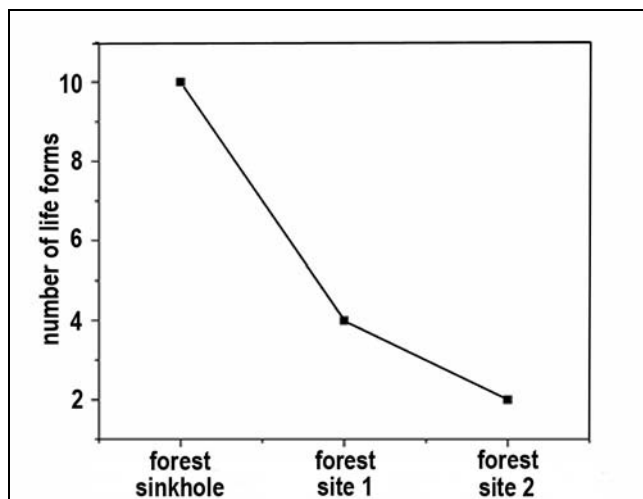


Figure 137. Sinkhole vs forest life forms in Karst Mountain Sinkhole of Southeastern China. Modified from Li *et al.* 2020a.

Thus, like caves, sinkholes provide refugia for species that are unable to live in that geographic region outside the sinkhole (Li *et al.* 2020a). Enclosing cliffs reduce the rate of water loss, thus increasing the humidity within the sinkhole. And these same cliffs can contribute to shading that reduces the temperature as well as the light levels. Furthermore, at least in the sinkhole studies in southeastern

China, the nutrients are in greater supply in the sinks (Figure 138), although one would think this would be more beneficial to tracheophytes than to bryophytes.

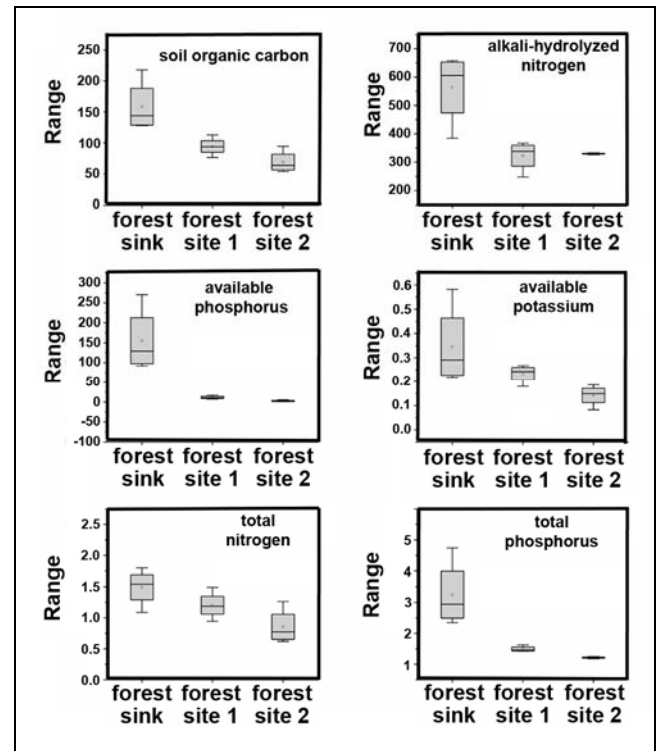


Figure 138. Soil nutrients in sinkhole forest and two surface forests. Bottom and top sections of the box plots indicate the inner quartile ranges. Horizontal bar within the box represents median. Whiskers indicate spread. Modified from Li *et al.* 2020a.

Rosseló and Ginés (1980), referring to them as potholes, reported 36 species of bryophytes in 23 sinkholes of Mallorca. They considered *Eucladium verticillatum* (Figure 11), *Fissidens cristatus* (Figure 128), *Homalia lusitanica* (Figure 139), *Mnium* sp. (Figure 38, Figure 61), and *Thamnobryum alopecurum* (Figure 140) to be "regular inhabitants." These species are likewise known from caves.



Figure 139. *Homalia lusitanica*, a common species in sinkholes of Mallorca. Photo by Hugues Tinguy, with permission.





Figure 140. *Thamnobryum alopecurum* with capsules, a common species of sinkholes of Mallorca. Photo by David T. Holyoak, with permission.

Ferguson and Knobloch (1998) likewise found a high plant diversity in the Pliocene sinkhole of Willerhausen, Germany. Herrero-Borgonon and Puche (1987) found 26 moss species in the sinkholes of the Valencia region, Spain. In the Apuseni Mountains of Romania, Sass-Gyarmati *et al.* (2009) identified 21 liverwort and 59 moss species in sinkholes, compared to 43 species of *Cyanobacteria* and 50 of lichens.

Sinkholes can often present interesting species that are not found in other habitats of the area and, like caves, may provide conditions suitable for species of more polar or higher elevation habitats (Luo & Zhang 2017). Li *et al.* (2020c) explored the third largest sinkhole in the world – Haolong sinkhole in China. They identified 183 species, of which 26 are endemic to China.

Reyes-Colón and Sastre-D.J. (2000) reported 50 bryophyte species two sinkholes in the north-central karst region of Puerto Rico. They found that the bryophyte flora of the sinkholes was very different from that of the Puerto Rican forests and considered them to be centers for diversity in the area. Pérez and Jesús (2009) reported new bryophyte species from sinkholes in old-growth forest fragments in Puerto Rico. Allred (1998) rediscovered the tiny moss *Fissidens littlei* (Figure 141) in a sinkhole in New Mexico, USA.



Figure 141. *Fissidens littlei*, a rare, tiny moss found in a sinkhole in New Mexico, USA. Photo by Dale A. Zimmerman Herbarium, Western New Mexico University, with permission.

Other rare surprises may delight the explorer. In the Alpena, Michigan, USA, limestone sinks, Robinson and Wells (1956) found *Mannia sibirica* (see Figure 113-Figure 115), *Seligeria calcarea* (Figure 142-Figure 143), and *Tritomaria scitula* (Figure 87), all new for Michigan. In all, there were 110 species of bryophytes in six sinks. Later Miller and Vitt (1970) found *Orthotrichum pallens* (Figure 144) in sinkholes in Alpena County – a new species for the eastern part of North America. Priwer (1979) reported that bryophytes were dominant in number of species in these sinks, and that she did not find rare species of tracheophytes.

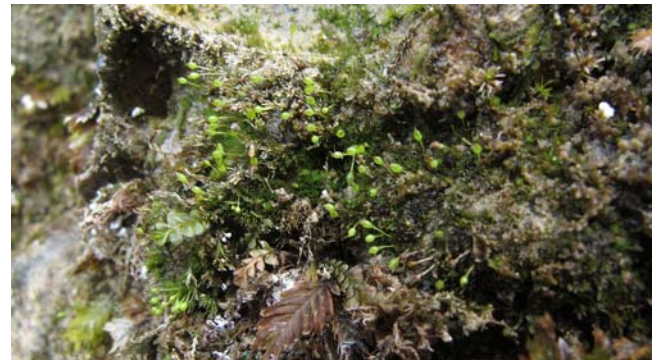


Figure 142. *Seligeria calcarea* with capsules, a species that occurs in the Alpena limestone sinks, Michigan, USA. Photo by Michael Lüth, with permission.



Figure 143. *Seligeria calcarea* with capsules, on stone. Photo by Brian Eversham, with permission.



Figure 144. *Orthotrichum pallens* with capsules; its occurrence in sinkholes in Alpena County, Michigan, USA, represented a new species for the eastern part of North America. Photo by Hermann Schachner, through Creative Commons.



In New Zealand, *Timmia norvegica* (Figure 145) occupies sinkholes on rock where there is seepage and calcareous detritus over marble (Horton & Bartlett 1983). This species is one of the bipolar species whose distributions are hard to explain.



Figure 145. *Timmia norvegica*, a species that occurs on seepage rocks in calcareous sinkholes in New Zealand. Photo by Hermann Schachner, through Creative Commons.

Cao *et al.* (2020) described the relationship of the bryophytes to the microbial communities of sinks in the Guizhou Province, China. They found 145 species of bryophytes in the sinks, five of which were highly drought tolerant, including *Eurohypnum leptothallum*, *Hyophila involuta* (Figure 146-Figure 147), and *Racopilum cuspidigerum* (Figure 148). They found that both moss species and the karst rocky desertification types affect the microbial communities, but that the moss species had the much stronger effect on the microbial diversity. Bacteria species composition changed strongly between mosses and drought resistance factors. Hence, bryophytes play a strong role in these communities.



Figure 146. *Hyophila involuta* wet, a highly drought-tolerant moss found in karst sinks in Guizhou Province, China. Photo by Bob Klips, with permission.



Figure 147. *Hyophila involuta* dry, a drought-tolerant species that survives on dry vertical rock surfaces. Photo by Bob Klips, with permission.



Figure 148. *Racopilum cuspidigerum*, a highly drought-tolerant moss found in karst sinks in Guizhou Province, China. Photo by Andrew Thornhill, through Creative Commons.

Like so many of the richest bryophyte sites, sinkholes are subject to human disturbance (Liu *et al.* 2019). As refugia, the sinkholes play a crucial role in retaining many rare species, at least at the local level. As you might expect, the number of species in undisturbed sinkholes was considerably higher than in those affected by tourism or farming. Others, sadly, are used as garbage dumps.

## Karstification

**Karst** (type of topography formed from dissolution of soluble rocks such as limestone, dolomite, and gypsum; characterized by underground drainage systems with sinkholes and caves) topography provides a variety of cave-like small and large spaces where bryophyte can live.

Šmarda (1947) recorded the presence of *Distichium capillaceum* (Figure 36-Figure 37) and *Timmia bavarica* (Figure 149) at the bottom of the deep karstic Macocha Chasm in the Czech Republic, thriving in little light but a moist environment with basic soil.





Figure 149. *Timmia bavarica*, a species that grows at the bottom of the deep karstic Macocha Chasm in the Czech Republic. Photo by Hugues Tinguy, through Creative Commons.

Jia *et al.* (2014) explored the role of karst bryophytes and their local occupancy. They found 33 bryophytes in their study area in a Guizhou mountain area of China. In

particular, they found that bryophytes were important in storing water, becoming saturated at 849-1474% of dry weight. Soil absorption ranged 464-1025%. Furthermore, they absorbed the heavy metals Pb, Zn, and Cd, with concentrations 2.25, 3.98, and 2.49 times that in their substrates, respectively. The concentrations in the bryophytes were not significantly correlated with that in their substrate. The researchers concluded that bryophytes had an important role both in providing a water reserve and in absorbing heavy metals from automotive exhaust. The water absorption helps to stabilize the road slopes in the karst area. Wu *et al.* (2019) described the vertical distribution of the **Hypopterygiaceae** and the environmental factors influencing that distribution in a karst sinkhole in China.

### Bryokarst

That's right. Bryophytes contribute to karstification (Meng *et al.* 2019). Meng and coworkers explained that bryophytes can act as physical forces, including expansion, curling, freezing, and thawing (Figure 150-Figure 151). These are most evident under alternating wet and dry conditions and can destroy rock. They also can destroy rocks through metabolic secretions and the  $H_2CO_3$  formed using the  $CO_2$  expelled in respiration.

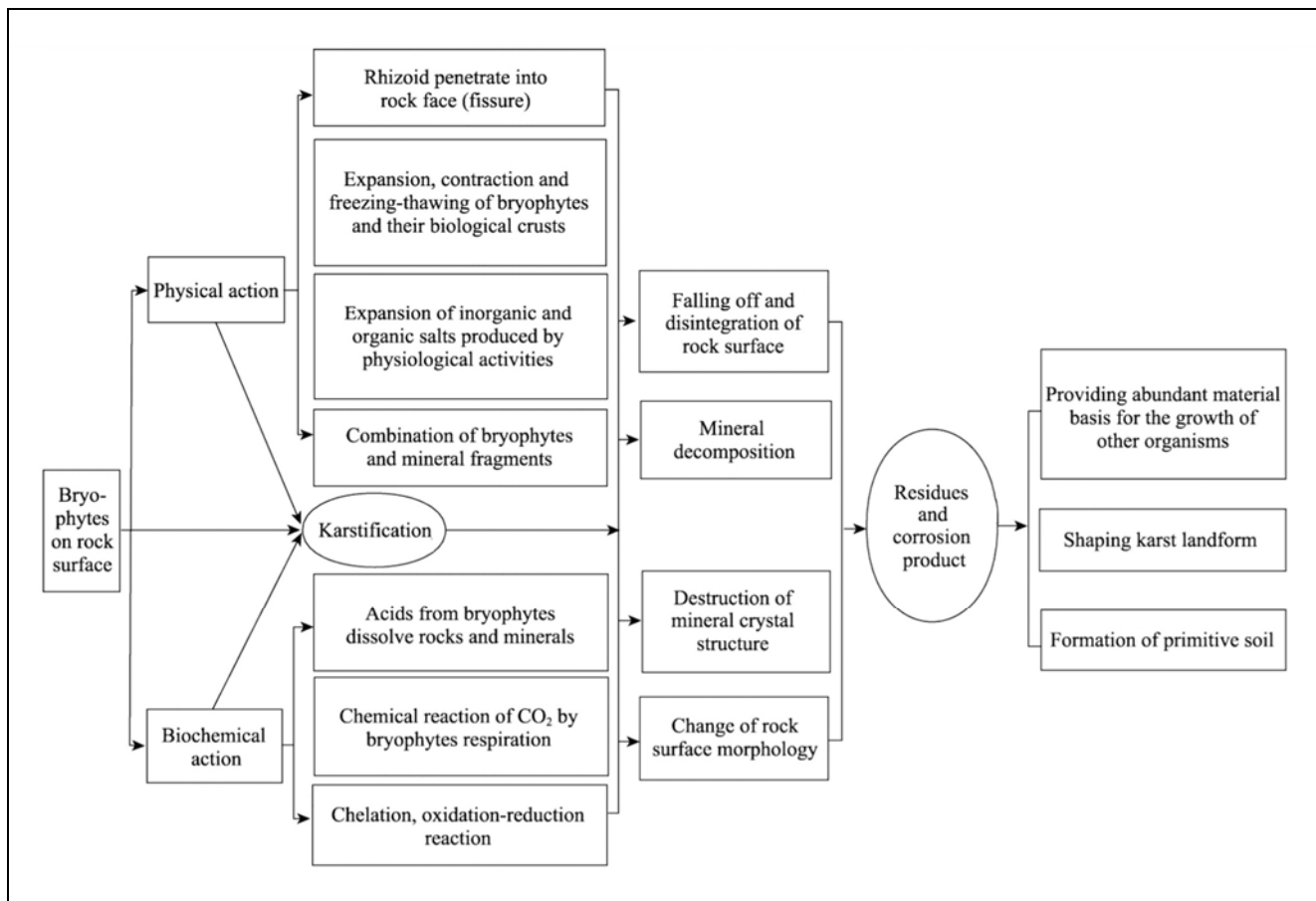


Figure 150. Flowchart showing bryophyte role in karstification. Mosses on the rock surface use physical and biochemical action to destroy and corrode the rock, change the rock surface morphology, and form the karst microtopography. The dissolved products are deposited to form the original soil. Modified from Meng *et al.* 2019.



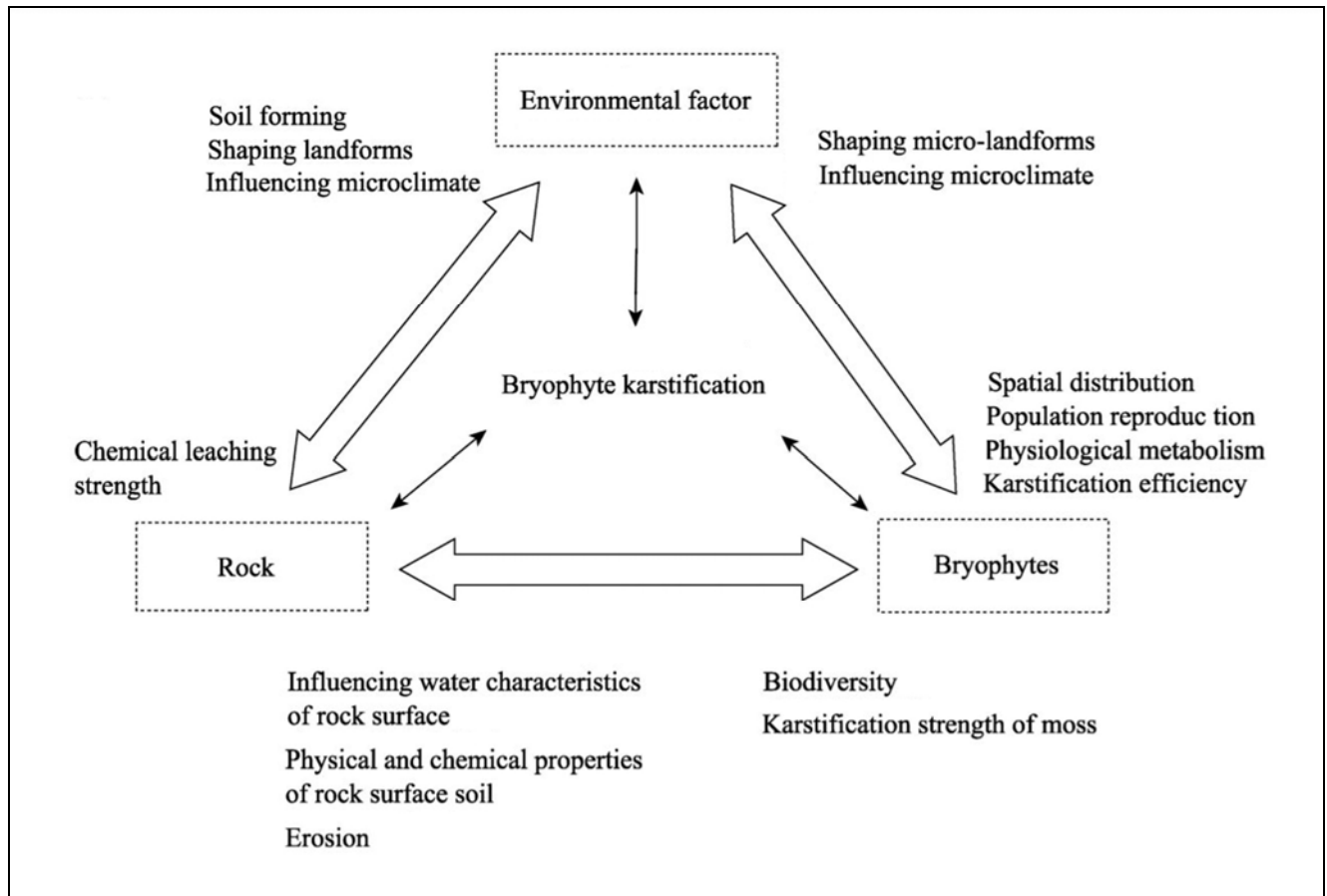


Figure 151. Three-way circulation interaction modified from Meng *et al.* (2019). The bryophytes, environmental factors, and rock promote and restrain each other in the karstification process. The environmental factors and rock affect the karstification process and its efficiency by controlling the community characteristics, morphology, physiological processes, genes, and other bryophyte factors. The resulting lithology, composition, occurrence of rock, and the improvement of the bryophytes on the rock surface microhabitat (temperature, humidity, light, soil fertility, microbes) are closely related to the rate of karstification.

Zhang *et al.* (1996) described four types of **bryokarst** deposition from caves (drop bryophytes-tufa, waterfall bryophyte-tufa, seasonal river bryophyte-tufa, and phototropism bryophytes-scale) in the Huangguoshu area of China, based on light, water availability, and bryophyte growth. They also identified four forms of bryophyte corruptions: corrosional hole, corrosional spot, corrosional block, and corrosional filament. These caves had 59 species of bryophytes in 43 genera.

Pentecost (1987) enumerated the annual growth rates of some mosses associated with tufa formation: *Palustriella commutata* (Figure 152), 1-4 mm; *Eucladium verticillatum* (Figure 11), 2-3 mm; *Hymenostylium recurvirostrum* (Figure 153-Figure 155), 1-3 mm; *Platyhypnidium riparioides* (Figure 156), *ca.* 30 mm. Pentecost (1996) followed this study with one on the role of photosynthesis vs other factors in the karstification process. *Palustriella commutata* and *Eucladium verticillatum* both deposited 6-12% of the carbonate through photosynthesis. In addition, 10-20% was deposited through evaporation and 70-80% through gas evasion.



Figure 152. *Palustriella commutata*, a moss that grows 1-4 mm per year in tufa formation. Photo by J. C. Schou, with permission.





Figure 153. *Hymenostylium recurvirostrum* habit, a moss associated with tufa formation. Photo by Hermann Schachner, through Creative Commons.



Figure 156. *Platyhypnidium riparioides*, a moss that grows ~30 mm per year in tufa formation. Photo by Hermann Schachner, through Creative Commons.



Figure 154. *Hymenostylium recurvirostrum* on side of cliff, with icicles. Photo by Bob Klips, with permission.



Figure 155. *Hymenostylium recurvirostrum* showing color of lower portions and three growth regions distinguishable by color changes. This species grows 1-3 mm per year in tufa formations. Photo by Hermann Schachner, through Creative Commons.



Figure 157. *Didymodon tophaceus* habitat at cliff base. Photo by Jean Faubert, with permission.

Lyons and Kelly (2020) pointed out the paucity of knowledge regarding deposition rate of tufa or the growth rates of involved bryophytes living in petrifying springs. Using fixed bar markers, they measured the heights of bryophytes at six petrifying springs in Ireland. They found that tufa deposits increased  $20.5 \pm 1.1 \text{ mm yr}^{-1}$ . The moss *Palustriella commutata* (Figure 152) worked together with the surface water to increase the annual deposition of tufa by  $5.7 \pm 1.9 \text{ mm}$ . Unvegetated tufa achieved a growth of only  $16.5 \pm 3.0 \text{ mm yr}^{-1}$ . Thus, with an annual growth of  $27.6 \pm 1.9 \text{ mm}$ , *Palustriella commutata* outgrows the unvegetated tufa growth. The smaller mosses *Didymodon tophaceus* (Figure 157-Figure 158) and *Eucladium verticillatum* (Figure 11) grew only  $9.1 \pm 1.6 \text{ mm yr}^{-1}$  and  $9.5 \pm 1.3 \text{ mm yr}^{-1}$ , respectively, thus being less important in tufa formation; they were typically displaced by *Palustriella commutata* through competition.





Figure 158. *Didymodon tophaceus*, a tufa moss that grows at a mean of  $9.1 \pm 1.6 \text{ mm yr}^{-1}$ . Photo by David T. Holyoak, with permission.



Figure 160. *Conocephalum salebrosum* under overhanging rocks, a common liverwort in rock canyons and behind waterfalls. Photo by Claire Halpin, with permission.

## Waterfall Caves

Waterfalls often fall over ledges, creating a curtain in front of shallow caves. These caves are typically shaded and moist, with rock surfaces (Figure 159).

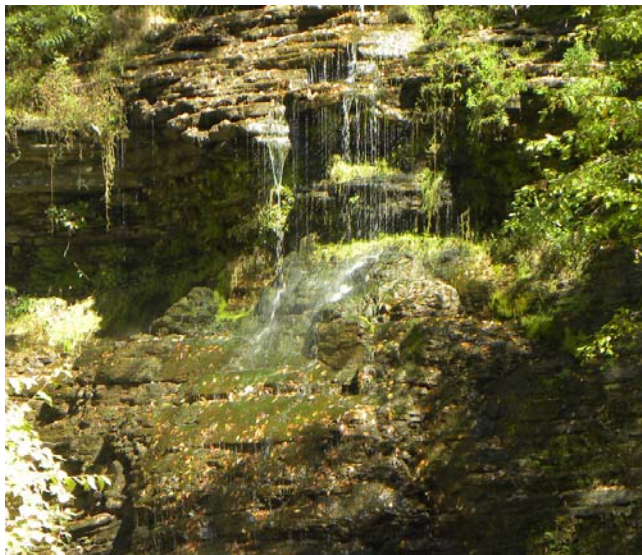


Figure 159. Waterfall in West Virginia, USA, with bryophytes and ferns growing on the ledges behind the water. Photo by Eileen Dumire, with permission.



Figure 161. *Conocephalum salebrosum*, a common species in cool, shaded, damp places in the US. Photo by Claire Halpin, with permission.

I have seen *Conocephalum* (Figure 126, Figure 160-Figure 161) species several times in the shallow caves behind waterfalls (Figure 162). Although these were usually named as *Conocephalum conicum* (Figure 126) in North America, we have recently realized that these are really *Conocephalum salebrosum* (Figure 160-Figure 161), a species with much larger thalli than those of the former. This habitat occurs in the Keweenaw Peninsula of Michigan, USA, and at Hocking Hills, Ohio, USA. The latter also has a number of small caves where the species is abundant.



Figure 162. Scot Falls, Michigan, USA, with cave behind waterfalls. Bryophytes occur on the ceiling of the cave. Photo by Janice Glime.



Higuchi *et al.* (2020) reported *Fissidens geminiflorus*, *F. nobilis* (Figure 163), and *Timmiella anomala* (Figure 164) on wet stones in a cave behind a waterfall in Cambodia.



Figure 163. *Fissidens nobilis*, a moss that lives on wet stones behind a waterfall in Cambodia. Photo by Janice Glime.



Figure 164. *Timmiella anomala*, a moss that lives on wet stones behind a waterfall in Cambodia. Photo from Earth.com, with permission.

Natalie Cleavitt found *Haplodontium macrocarpum* (Figure 165) in Mountain Park, Alberta, Canada, where it occurs on the underside of overhangs associated with ephemeral waterfalls (Dale Vitt, pers. comm. 4 August 2021).



Figure 165. *Haplodontium macrocarpum* on cave wall, a species that also occurs under overhangs of ephemeral waterfalls. Photo by René J. Belland, with permission.

Townsend (2006) reported *Epipterygium tozeri* (Figure 166) from Kenya in a cave behind a waterfall.



Figure 166. *Epipterygium tozeri*, a species that grows in a cave behind a waterfall in Kenya. Photo by Hugues Tinguy, with permission.

## Other Bryophyte Roles

Building and destroying cave formations are not the only roles of bryophytes in caves. They increase the diversity of stalactites and stalagmites (Mulec 2018). They can be diversity hotspots. Bryophytes increase the loss of water by 81.2 times and absorption by 8.1 times, the highest compared to the algae (18.8 and 1.6) and lichens 2.9 and 19.1) (Cao & Yuan 1999). Bryophytes also prolong the period of water loss by 610%, but do not extend the period of absorption. This improves the water holding by 57.2 times! This increases the activity of the carbon cycle on the rock surface, affection rates of corrosion under the growths.

Pentecost (1999) notes the importance of bryophytes, along with algae, in stabilizing ephemeral sand ripples on steep rock surfaces in the UK. Fu and Zhang (2010) identified four types of bryophyte erosions on limestone: erosional fusion, erosional plaques, erosional bands, and erosional blocks.

Ren *et al.* (2010) found that the rare and endangered flowering plant *Primulina tabacum* (Figure 167) is found



only at cave entrances of a small number of karst caves in southern China. The researchers transplanted small plants of this species to several new cave entrances. The only seedlings that survived were associated with the moss *Gymnostomiella longinervis* (Figure 168), performing well under the cover of the moss. It appears that the moss nurse plant is necessary for the success of *P. tabacum*.



Figure 167. *Primulina linearifolia* × *Primulina tabacum*; *Primula tabacum* seems to require the moss *Gymnostomiella longinervis* to be successful in karst cave entrances. Photo by Kenpei, through Creative Commons.



Figure 168. *Gymnostomiella longinervis* on bark, a moss that helps *Primulina tabacum* succeed in entrances of karst caves in southern China. Photo through Creative Commons.

Submerged cave bryophytes can serve as substrate for the diatom *Pinnularia borealis* (Figure 169) (Czerwik-Marcinkowska *et al.* 2019). The cyanobacterial *Gloeocapsa atrata* (Figure 170) occurs frequently on

mosses on wet cave wall rocks in the Glowoniowa Nyża Cave. The latter species can contribute to nitrogen fixation, thus increasing the levels of usable nitrogen in the cave.



Figure 169. *Pinnularia borealis*, a diatom that often uses bryophytes as a substrate in caves. Photo from BELSPO, with online permission.

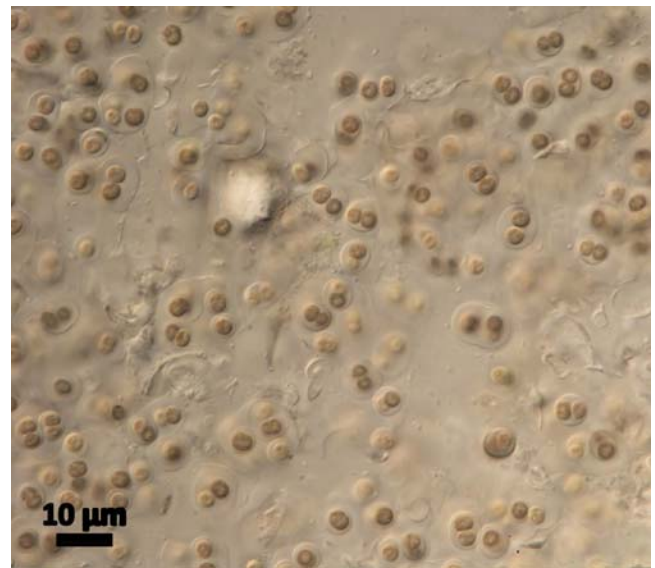


Figure 170. *Gloeocapsa atrata*, a member of **Cyanobacteria** that fixes nitrogen and can occur on mosses in caves. Photo by Sergei Shalygin, through Creative Commons.

## Cave Fauna Interactions with Bryophytes

Galas *et al.* (1996) found that the decay rates of two seed plants and of moss were all slow in a mountain cave in the Tatra Mts., Poland. They attributed this slowness to the absence of large shredders in the cave. The energy released through respiration by microorganisms on the moss was higher than that released from microorganisms on sorb and alder litter.

Cao and Yuan (1999) reported that the water holding by evaporation of carbonate rock increases 81.3 times and water absorption by 8.1 times for mosses compared to relative fresh rock samples. The amount of water holding by the rock improves 57.2 times with mosses on them.



## Copepods

In Japan, Iwatsuki and Ueno (1959) found the fern *Cyrtomium fortunei* (Figure 171) and moss *Fissidens geminiflorus* (see Figure 128, Figure 134, Figure 141, Figure 163) to be dominant, sometimes obtaining a "full growth." They also found cave fauna that associated with the mosses, including the harpacticoid copepod *Bryocamptus zschokkei* (Figure 172), the latter occurring in a carpet of *Fissidens geminiflorus*.



Figure 171. *Cyrtomium fortunei*, a dominant fern in some Japanese caves. Photo by Bing Liu, Kew Plants of the World, through Creative Commons.



Figure 172. *Bryocamptus zschokkei*, a harpacticoid copepod associated with mosses in caves in Japan. Photo by Joe Connolly, through Creative Commons.

Stoch (2000) reviewed the aquatic fauna of caves in northern Italy, including some that are part of the bryophyte fauna. Watiroyram *et al.* (2012) found 11 species of the copepod *Bryocyclops* (Figure 173) from wet mosses in caves.

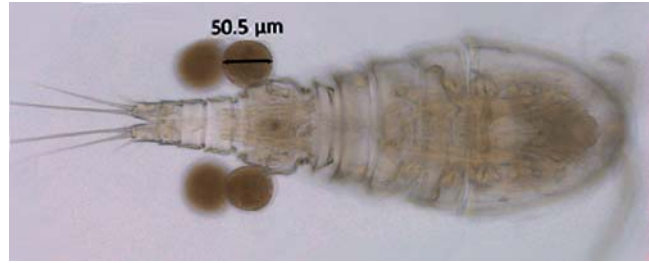


Figure 173. *Bryocyclops* sp.; 11 species in this genus occur among mosses caves in Italy. Photo by Watiroyram, S., through Creative Commons.

## Tardigrades

One of the best places to look for tardigrades is nestled among the leaves of bryophytes. Cave-dwelling tardigrades are no exception to that (Bartels & Nelson 2007). This affinity for bryophytes, particularly mosses, includes a special adaptation for feeding on the mosses [Tardigrada (Water Bears) 2005]. Members of *Echiniscidae* are adapted to this mode of living by having a long stylet that can penetrate the moss cell wall and suck out the cell contents. In addition to eating moss cell contents, the bryophyte dwellers might eat epiphytic diatoms and bacteria from the moss surface.

## Insects

In addition to the copepod, Iwatsuki and Ueno (1959) found the troglophilous fly *Exechia* sp. (fungus fly; Figure 174) associated with the mosses in a cave in Japan.



Figure 174. *Exechia fusca* adult, a fungus fly similar to those that occur with mosses in a Japanese cave. Photo by Jostein Kjaerandsen, through Creative Commons.

Even in Death Valley, California, USA, caves can serve as a refuge for insects. Hungerford (1917) reported the true bug *Mesovelia mulsanti* (Figure 175) from among mosses in a hot spring cave. Later, Polhemus and



Chapman (1979) reported *Mesovelia amoena* (Figure 176) on moss-covered rocks in hot spring caves, also in Death Valley. This species is parthenogenetic in Hawaii, a trait that might make reproduction easier in caves. Kamp (1970) reported cave grasshoppers that were associated with bryophytes in caves in the western United States.



Figure 175. *Mesovelia mulsanti*, a true bug that occurs among mosses in a hot spring cave in Death Valley, California, USA. Photo by Matt Bertone, through Creative Commons.



Figure 176. *Mesovelia amoena* wingless female, a species that lives on moss-covered rocks in hot spring caves in Death Valley, California, USA. Photo by Claudia Moreno-R., Wendy Molina-J., Juliana Barbosa, and Filipe Moreira, through Creative Commons.

In icefields, ice bugs (*Grylloblattodea*) lay their eggs in the soil or mosses (Ramel 2015). They hide under stones during the day and prefer low temperatures. These insects also occur in caves in Korea. These insects are extremophiles. In the Oregon Caves in the Klamath Mountains of Oregon and California, USA, Schoville (2012) found three new species of *Grylloblattodea*: *Grylloblatta oregonensis* (Figure 177), *G. siskiyouensis*, and *G. marmoreus*. This species occupies the dark zone and twilight zone of caves. Their relationships to the bryophytes in the caves is not known, but they may have the same uses for egg laying as members of the genus found in Korea.



Figure 177. *Grylloblatta oregonensis*, a new species discovered in Oregon caves in the twilight and dark zones. Other members of the genus use mosses for egg laying, but egg laying has not been described in this species. Photo through Creative Commons.

There are two tiphiid wasp species (*Tiphia andersoni* and *T. nona* – see Figure 178) that are able to hibernate beneath rocks surrounded by mosses in caves (Wynne 2013). Moss gardens in lava tubes have the most developed bryophyte communities (Lindsey 1951) and present a biologically unique bryophyte community (Lightfoot *et al.* 1994; Wynne 2013). This includes a high arthropod biological diversity (Wynne 2013).



Figure 178. *Tiphia* sp. Several species in the genus hibernate beneath rocks surrounded by mosses in caves. Photo by XPDA, through Creative Commons.

### Other Arthropods

Importantly, this habitat has been identified as supporting at least two presumed relict species (Lightfoot *et al.* 1994, this paper) and high arthropod biological diversity (Wynne 2013).

Benedict (1979) found that the pseudoscorpion *Apochthonius forbesi* (see Figure 179) benefits from the mossy litter layer in sinks in Oregon, USA. This species was described as a new species based on populations in a lava tube sink where it lived at the cold air trap that



retained permanent ice but a mossy litter layer. *Syarinus* (Figure 180) was an accompanying species in this habitat.



Figure 179. *Apochthonius diabolus*; *Apochthonius forbesi* lives in lava tube sinks with permanent ice and a mossy litter layer. Photo by Steve Taylor and Mike Slay, through Creative Commons.



Figure 180. *Syarinus* sp.; a species in this genus of pseudoscorpion accompanies *Apochthonius forbesi* in lava tube sinks with permanent ice and a mossy litter layer. Photo by P. M. Brousseau, through Creative Commons.

Wynne and Shear (2016) found a new millipede species, *Austrotyla awishoshola* in "cave moss gardens" in New Mexico, USA. The millipedes need mesic conditions, and these are limited in these caves to locations with mosses. As is the case for mosses, the caves serve as refugia for insects and other fauna that found refuge here following the end of the more moist Pleistocene. Such refugia are known in other parts of the world where mosses have become the restricted environment for relict species (Benedict 1979; Wynne *et al.* 2014).

For the invertebrate cave fauna, the bryophytes provide opportunities for a high diversity. They are also home to the relict spider *Lepthyphantes turbatrix* (Figure 181) (Wynne 2013).



Figure 181. *Lepthyphantes turbatrix*, a spider that uses cave mosses as a home. Photo by Tom Murray, through Creative Commons.

## Salamanders

Some salamanders are especially adapted to cave living. Others benefit from the cooler, more moist conditions. Gorman and Camp (1953) found the new species *Hydromantes shastae* (Figure 182-Figure 183) under a mossy log at a cave entrance in California, USA. The salamander *Aneides aeneus* (Figure 184) is known to eat mosses (Lee & Norden 1973), although it may just be the result of foraging there for ants and spiders. This salamander has occurred in Bat Cave in Rutherford County, North Carolina, USA, and is also known from Cooper's Rock, West Virginia, where small caves or cave-like habitats can occur among the rocks.



Figure 182. *Hydromantes shastae*, a species that includes mossy logs at a cave entrance as a hiding place. Photo by James Bettaso, USFWS, through public domain.





Figure 183. *Hydromantes shastae* showing a color form that is well adapted to a mossy habitat. Photo by John Clare, through Creative Commons.



Figure 184. *Aneides aeneus*, a species known to eat mosses and hangs out among boulders and in caves. Photo by Alan Cressler, through public domain.

## Frogs

In the borderland between Venezuela and Brazil, Myers and Donnelly (1997) found the frog *Eleutherodactylus cavernibardus* (*cavernibardus* means cave singer; see Figure 185) calling during the day in local caves formed by granite boulders or on mosses. It is likely that the frogs use both of these habitats.



Figure 185. *Eleutherodactylus planirostris*; *Eleutherodactylus cavernibardus* calls from mosses in caves. Photo by Todd Pierson <[www.discoverlife.org](http://www.discoverlife.org)>, with permission.

Angulo *et al.* (2003) reported *Stefania riae* in a sinkhole at Sarisariñama tepui in Peru. The habitat lacked either flowing or standing water, but the walls of rocks, crevices, and caves were moist and mossy, presumably providing moisture for the frogs, as suggested by Barrio-Amorós and Fuentes (2003).

## Reptiles

Little seems to be known about the role of bryophytes for cave reptiles. Storey (2006) reported that reptiles seek refuge in winter in locations such as caves, burrows, grass, or moss hummocks. It might be worthwhile to look for some of the smaller reptiles among the cave mosses in winter. If nothing else, the mosses might be a source of invertebrate food. I wonder if lizards and snakes find the older sinkholes in Florida suitable.

## Birds

Even birds can benefit from bryophytes in caves. In Brazil the White-collared Swift [*Streptoprocne zonaris* (Figure 186)] typically breeds in wet caves next to waterfalls (Figure 187) (Biancalana 2014). Nests are made mostly of bryophytes (Figure 188). The birds returned to the same nest sites in subsequent years.



Figure 186. *Streptoprocne zonaris* on rock wall. Photo by Amesac, through Creative Commons.





Figure 187. *Streptoprocne zonaris* behind waterfall, where it typically builds nests mostly of mosses. Photo by Donald Hobern, through Creative Commons.



Figure 188. *Streptoprocne zonaris* on nest made of mosses. Photo by Sesernam, through Creative Commons.

On the young island of Surtsey, Iceland, a Herring Gull-Glaucous Gull hybrid pair [*Larus argentatus* (Figure 189) - *Larus hyperboreus* (Figure 190)] nested in a small collapsed cave, using primarily the moss *Racomitrium* (Figure 31-Figure 32) as nesting material (Olafsson 1982). When a Berlese funnel was used to search the nest for arthropods, only a single specimen, that of an **acarid** (mites & ticks) was revealed.



Figure 189. *Larus argentatus*; a hybrid of this species uses *Racomitrium* as nesting material in the volcanic island of Surtsey, Iceland, in a collapsed cave. Photo by Kulac, through Creative Commons.



Figure 190. *Larus hyperboreus* and offspring; a hybrid of this species uses *Racomitrium* as nesting material in the volcanic island of Surtsey, Iceland, in a collapsed cave. Photo by A. Weith, through Creative Commons.

The Biscutate Swift (*Streptoprocne biscutata*; Figure 191) has been studied at its home in a cave in the Paraná State, southern Brazil (Pichorim 2002). The birds use bryophytes, among other plants and lichens, to build its nests. When the birds are nesting in the cave, the cave floor has abundant moss and lichen fragments. The birds collect these materials for nesting and at times even pull pieces of bryophytes from the vertical wall. The unusual observation was that they appeared to chew the fragments soon afterwards. Observations of a viscous substance in the moss fragments in the nests suggest that the chewing was practiced to add the saliva. Fragments in the nests included the liverworts *Frullania brasiliensis* (Figure 192) (most common – 14 of 23 nests), *Herbertus* sp. (Figure 193), *Lejeunea flava* (Figure 194), *Omphalanthus filiformis* (Figure 195), *Plagiochila* sp. (see Figure 74), and *Plagiochila rutilans* (see Figure 74), and the mosses *Campylopus* sp. (see Figure 196), *Campylopus aemulans* (Figure 196), *Leucobryum crispum* (Figure 197), *Leucoloma* sp. (Figure 198), *Macromitrium punctatum* (Figure 199), *Phyllogonium viride* (Figure 200), *Polytrichum juniperinum* (Figure 47-Figure 48), *Porotrichum longirostre* (see Figure 201), *Rhacocarpus* sp. (Figure 202), *Schlotheimia rugifolia* (Figure 203), *Schlotheimia tecta* (Figure 204), *Sematophyllum subpinnatum* (see Figure 205), *Squamidium leucotrichum* (Figure 206), *Syrrophodon prolifer* (Figure 207), and *Zelometeorium recurvifolium* (Figure 208).





Figure 191. *Streptoprocne biscutata*; when this species nests in caves in Brazil, it uses mosses available from the cave floor as nesting material. Image by Joseph Wolf and J. W. Wood, through public domain.



Figure 192. *Frullania brasiliensis*, a liverwort used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Jan-Peter Frahm, with permission.



Figure 193. *Herbertus aduncus* subsp. *hutchinsiae*; a species of *Herbertus* is used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by J. Barry Stewart, with permission.



Figure 194. *Lejeunea flava*, a liverwort used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Rory Hodd, with permission.



Figure 195. *Omphalanthus filiformis*, a liverwort used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Michael Lüth, with permission.



Figure 196. *Campylopus aemulans*, a moss species used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Michael Lüth, with permission.





Figure 197. *Leucobryum crispum*, a moss species used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Claudio Delgadillo-Moya, with permission.



Figure 198. *Leucoloma* sp., a moss species used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Shyamal L., through Creative Commons.



Figure 199. *Macromitrium punctatum*, a moss species used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Maarta Luz Uribe, through Creative Commons.



Figure 200. *Phyllogonium viride* with capsules, a moss species used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by George Shepherd, with online permission.



Figure 201. *Porotrichum bigelowii* branch; *Porotrichum longirostre* is a moss species used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Brian Starzomski, through Creative Commons.



Figure 202. *Rhacocarpus purpurascens*; a species of *Rhacocarpus* is used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Jan-Peter Frahm, with permission.





Figure 203. *Schlotheimia rugifolia*, a moss species used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Juan David Parra, through Creative Commons.



Figure 204. *Schlotheimia tecta*, a moss species used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Michael Lüth, with permission.



Figure 205. *Sematophyllum* sp.; *Sematophyllum subpinnaatum* is used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Michael Lüth, with permission.



Figure 206. *Squamidium leucotrichum*, a moss species used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Michael Lüth, with permission.

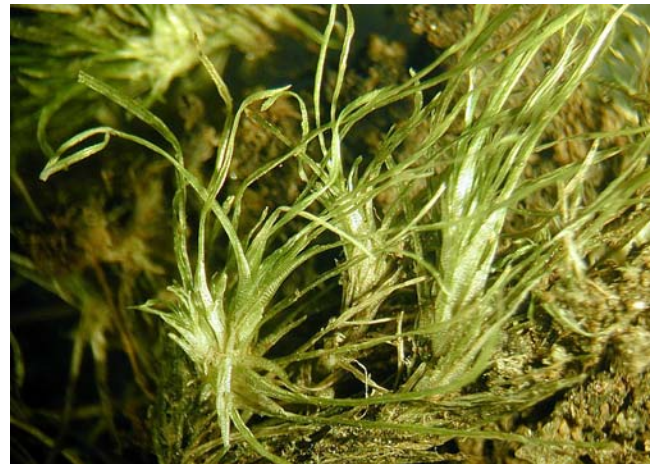


Figure 207. *Syrrhopodon prolifer* var. *scaber*, a moss species used in the nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Michael Lüth, with permission.



Figure 208. *Zelometeorium patulum*; *Zelometeorium recurvifolium* is used in nests of the Biscutate Swift (*Streptoprocne biscutata*) in Brazilian caves. Photo by Michael Lüth, with permission.



## Mammals

Several mammals use caves as their dens. The bear has perhaps the most influence on the bryophytes. The brown bear (*Ursus arctos*; Figure 209) includes mosses to line its den (Czerwik-Marcinkowska *et al.* 2019). This can bring moss spores and fragments into the cave for possible establishment and growth there.



Figure 209. *Ursus arctos* (brown bear) running, a species that uses mosses to line its den in caves. Photo by Malene Thyssen, through Creative Commons.

## Sampling Methods

Bryophyte sampling methods have varied among researchers. Many researchers sought only to document the flora, with no attempt to quantify species. Li *et al.* (2020a) used 8 plots, 10 x 10 m, in each section of a sinkhole, totalling 80 plots. In addition to assessing the bryophyte flora, they measured depth, pH, light level, humidity, temperature, and slope, making it possible to find correlations.

Although caves have more constant conditions than those found outside the cave, conditions nevertheless vary between caves and within the caves. Poulson and Culver (1969) measured evaporative rate, substrate moisture, substrate organic content, predictability and stability of food and microclimate, substrate diversity, and intensity of flooding in Mammoth Cave, Kentucky, USA. They found that arthropod diversity exhibited significant correlations with substrate diversity, substrate organic content, and intensity of flooding. To this list, light intensity must be added for photosynthetic organisms, and even for some cave animals. Thus it is instructive to measure these conditions.

Nakanishi (2002) established 14 quadrats in a light intensity gradient. The quadrats were 20 x 20 cm and restricted to clayey soils; they assessed the bryophytes using the Braun-Blanquet method.

Pakeman *et al.* (2019) used Attribute values based on the Ellenberg values (see Schaffers & Sýkora 2000) to describe the nitrogen, light, and moisture in bryophyte habitats in Scotland. These have been used in some cave studies for similar purposes.

## Summary

Cave-like conditions are present in a variety of landforms. Among these are mine shafts, subways, fissures, minicaves among rocks and at the base of boulders, among scree, ice caves, windholes, sinkholes, behind water falls, and in animal burrows. These differ in available light, substrate, moisture, nutrients, pH, and toxic substances such as pollutants.

Mine shafts are often vertical structures with light diminishing with depth. The exposure of the substrate to the ore being mined can be a toxic factor. There are few published records of bryophytes in mines, but the presence of the ubiquitous *Ceratodon purpureus* is a not surprising find.

Subways are typically well lit and may have some of the same species as caves. Because the subway age is known, it can provide a suitable laboratory for studying colonization rates.

Small fissures often support surface bryophytes due to their collection of nutrients and soil and a greater moisture-holding ability than the rock surface. Larger fissures as found in lava fields, geothermal areas, and some large rock formations may support bryophytes for a short distance into the fissure, again dependent on light, moisture, and substrate type. Such fissures offer protection from direct sun, reducing sun bleaching, photoinhibition, and drying.

Among the lava rocks and fissures one can find *Saelania glaucescens*, *Distichium inclinatum*, and *Schistostega pennata*, but much more study is needed to relate the bryophyte species to the cave-like locations vs the surface locations. The scree presents a similar problem, although there are more studies that list species found there. Despite the shallowness of its caves, they can provide cool refugia in otherwise hot, dry, exposed fields of rock.

Ice caves typically do not support bryophytes, but *Heterocladium heteropterum* and *Cyrtomnium hymenophylloides* are known in ice caves. On the other hand, the cool air from these caves, especially in summer, can alter the climate and bryophyte composition outside the cave. Windholes have similar effects, providing a cool cave, but also cooling the area near the cave. These cool refugia permit Arctic species to live at much lower latitudes, occurring there as disjuncts.

Sinkholes have much in common with caves, including low light and usually greater moisture. However, they experience seasonal changes much like the surrounding forest. They have many species on their walls that coincide with those in caves. Their responses to these conditions are similar to those of bryophytes in caves: sterility, leaf elongation, longer internodes, elongation of cells, and disappearance or attenuation of the rib or costa. The protection provided by the sinkhole can result in a greater species diversity than that found in the surrounding forest.

**Karstification** is a process of dissolution of soluble rocks, characterized by underground drainage systems with sinkholes and caves. Bryophytes can play a role in the process, creating stalactites and stalagmites by the accumulation of CaCO<sub>3</sub> around some bryophyte



species, particularly accomplished by *Eucladium verticillatum*. The bryophytes can also destroy rock formations by exuding organic acids or holding water that makes breakdown of the rock easier.

Waterfall caves maintain a moist habitat while reducing light intensity. They seem to be an especially suitable habitat for some *Conocephalum* species. There are probably many records for this habitat, but they are often embedded in studies of the larger area without specific separation of the cave area.

Bryophytes in caves can serve various roles for the cave fauna. For copepods, tardigrades, insects, and other arthropods, they provide cover and moisture and sometimes food. Salamanders may forage there or sometimes use the bryophytes for cover and moisture conservation. Frogs can use them as calling locations and sources of moisture. Reptiles can occasionally be found there. Birds use them for nesting material, as do some mammals, especially bears.

Cave sampling is useful to determine gradient effects on species composition. This sampling typically uses quadrats (plots) of 10 x 10 cm or larger. A distance transect is useful for assessing gradient effects. It is useful to measure both physical and chemical parameters along these transects.

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