Ebook sponsored by Michigan Technological University and the International Association of Bryologists. Last updated 16 December 2021 and available at <http://digitalcommons.mtu.edu/bryophyte-ecology/>.

CHAPTER 18-1
CAVES – THE ENVIRONMENT

TABLE OF CONTENTS

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.

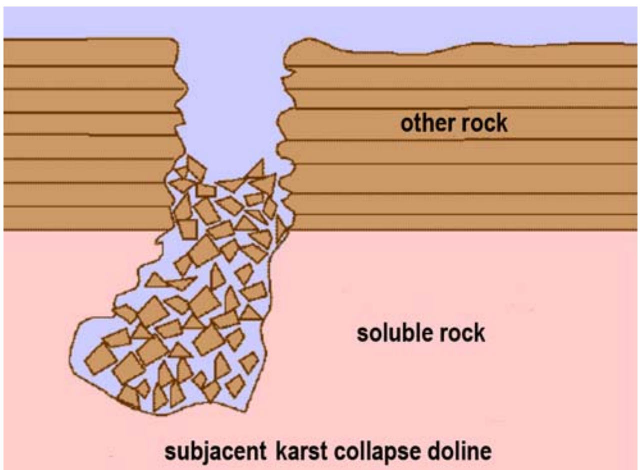

Figure 3. Doline diagram by B.Z. Saylor, MIT, <oeit.mit.edu>.

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.

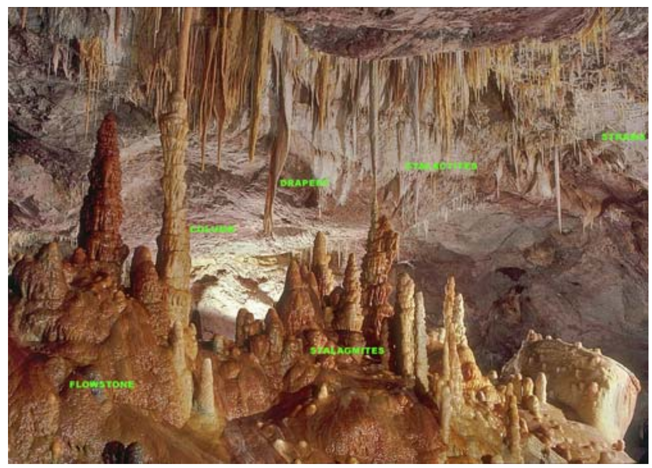

Figure 6. Labelled speleothems. Photo by Dave Bunnell, through Creative Commons.

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 **c**eiling, formed by deposition of minerals from water (stala**c**tites have to hang on tight; they form on the **c**eiling); 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 **g**round); 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 trogloxenes** – Species which habitually frequent caves and thus, whilst not completing their life-cycle there, form a part of the cave community (also called 'regular trogloxenes'). 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_2 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.

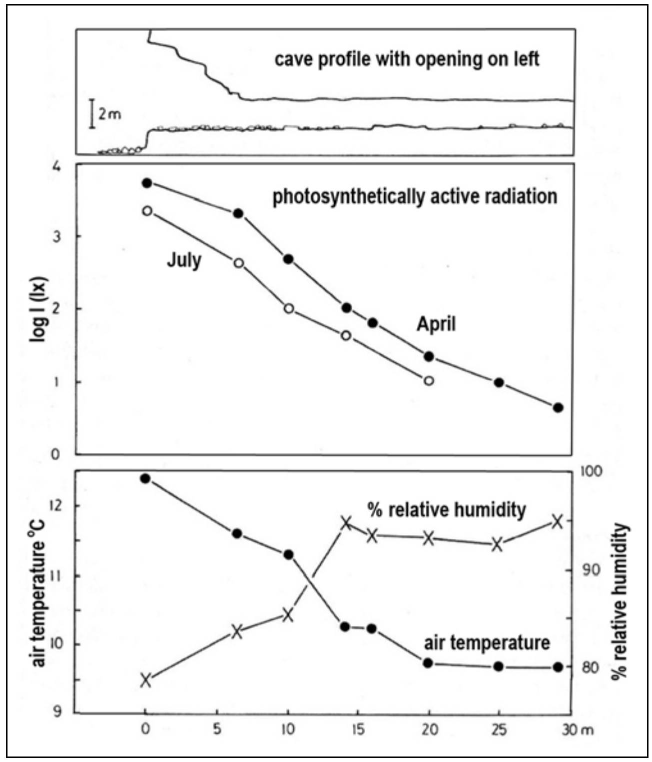

Figure 12. Cave parameters. Modified from Pentecost & Zhang 2001.

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 Krackòw-Wieluñ 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_2

Asencio and Aboal (2011) noted that cave CO_2 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 27-43ºC – 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_2 levels within the cave. Spotl and coworkers document the predictable changes from high ***p*CO_2** (partial pressure of dissolved CO_2; gas phase pressure of carbon dioxide in air above waterway which would be in equilibrium with dissolved carbon dioxide) in summer and low pCO_2 in winter in the Obir Cave in Austria. Winter flushing by relatively CO_2-poor air enhances degassing of CO_2 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 pCO_2 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_2 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_2 sinks, but that decomposition of bryophytes would release CO_2. They concluded that most of the CO_2 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_2 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^{-2} h^{-1} to -0.0109 g C m^{-2} h^{-1}. They also

found that some of these communities served as CO_2 sinks, but others were actually CO_2 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_2 levels in the caves. The epikarstic source seems to control the dripwater chemistry and maximum CO_2 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_2 levels with that of the drip chemistry. They found that the peak levels of CO_2 during visitor presence did not reach the theoretical values at which the dripwater carbonates and air CO_2 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_2 levels in the deeper passages in Bayliss Cave, Australia, reached up to 200X the ambient CO_2 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_2 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_2) and water (H_2O) into bicarbonate (HCO_3^-) and protons (H^+). These reactions are important in the photosynthetic pathway but are also important in the CO_2 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 15. Algific talus slope with mossy vent obscured by vegetation in northeastern Iowa. Photo courtesy of Beth Lynch.

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 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.

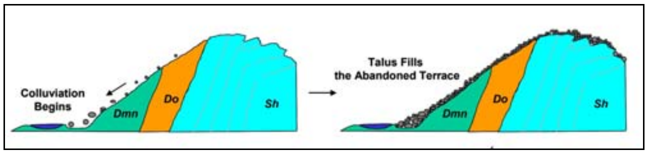

Figure 19. Algific slope cave formation, Ice Mountain, West Virginia, USA. The three colors are three different types of bedrock. Modified from Andrews 2003.

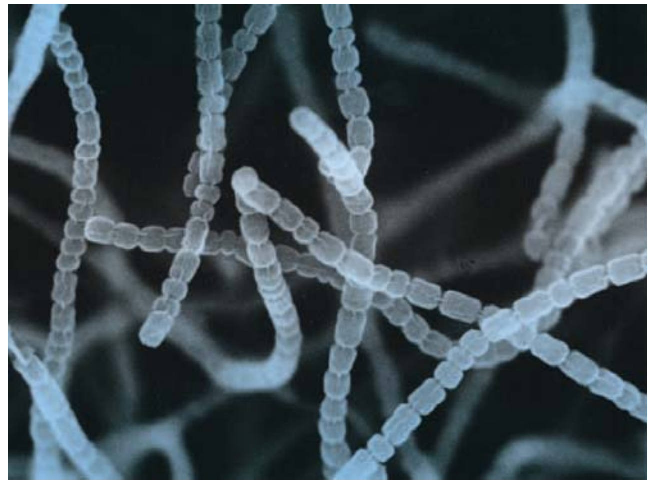

Figure 20. ***Streptomyces*** sp. Photo by Doc Warhol, through Creative Commons.

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 *p*H 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.

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 Bashkirskiyi 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.

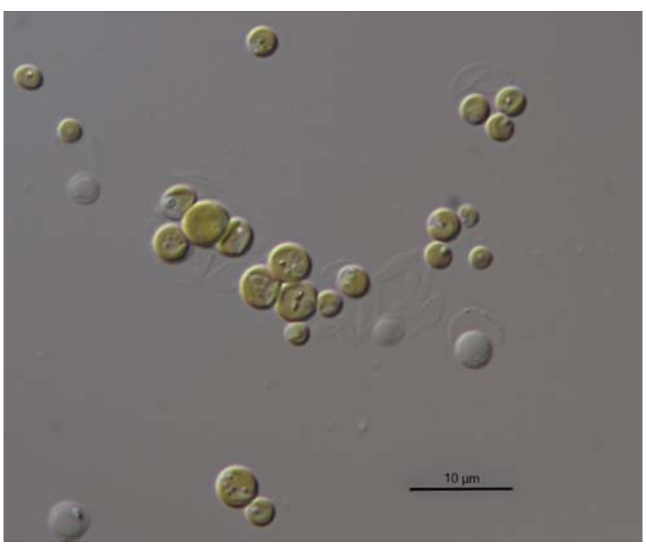

Figure 23. ***Mychonastes homosphaera***, a **Chlorophyta** species found in all caves examined by Gainutdinov *et al.* (2017) in the southern Urals**.** Photo by T. Darienko, through Creative Commons.

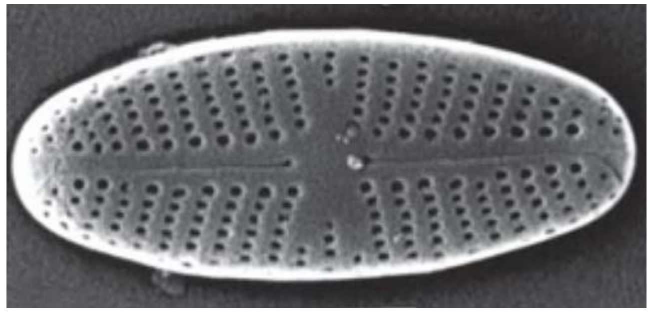

Figure 24. ***Eolimna*** sp. ***Eolimna minutissima*** is a diatom species found in all caves examined by Gainutdinov *et al.* (2017) in the southern Urals**.** Photo from Sala *et al*. 2003, through Creative Commons.

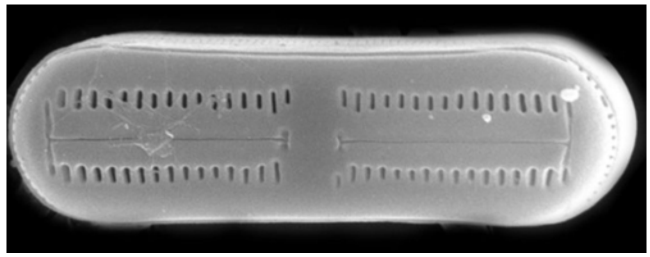

Figure 25. ***Humidophila contenta***, a species of diatom that is among the most common in caves. Photo by Rex Lowe from <diatoms.org>, with permission.

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

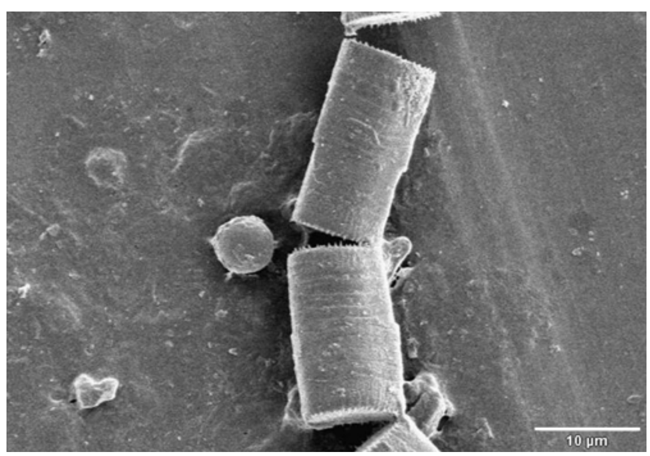

Figure 27. ***Orthoseira roeseana***, a species of diatom that is among the most common in caves. Photo by Birger Skjelbred, Nordic Microalgae <www.nordicmicroalgae.org>, with online permission.

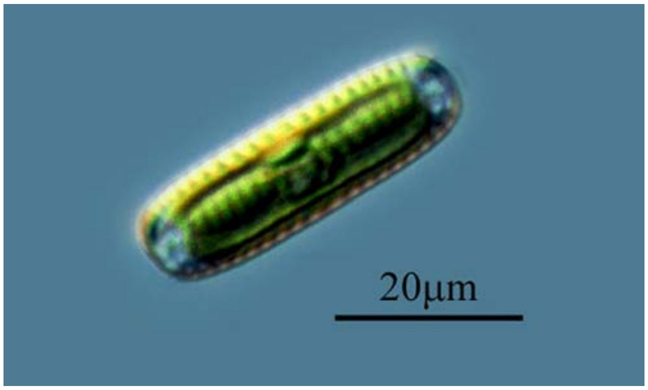

Figure 28. ***Pinnularia borealis***, a diatom species that has been found in multiple cave studies. Photo from Proyecto Agua Water Project, through Creative Commons.

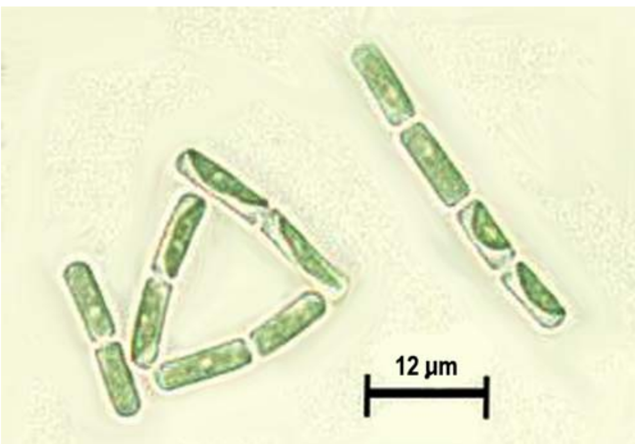

Figure 29. ***Stichococcus bacillaris***, a **Chlorophyta** species that has been found in multiple cave studies. Photo from UTEX, through Creative Commons.

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

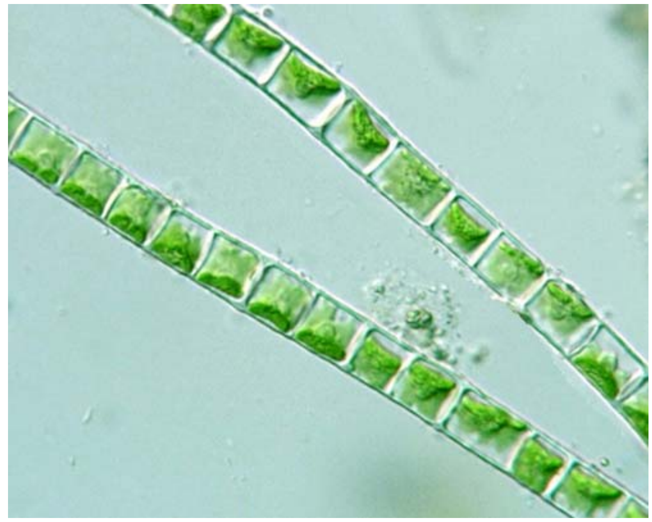

Figure 31. ***Klebsormidium flaccidum***, a **Charophyta** species that has been found in multiple cave studies. Photo Yuuji Tsukii, with permission.

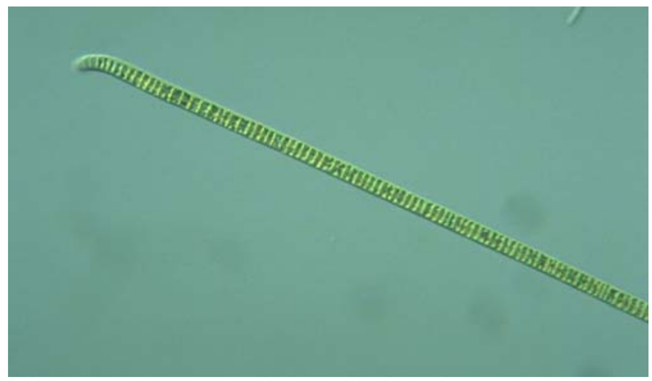

Figure 32. ***Oscillatoria*** filament; ***O. rupicola*** is a **Cyanobacteria** species that is common near cave lights in . Photo Yuuji Tsukii, with permission.

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.

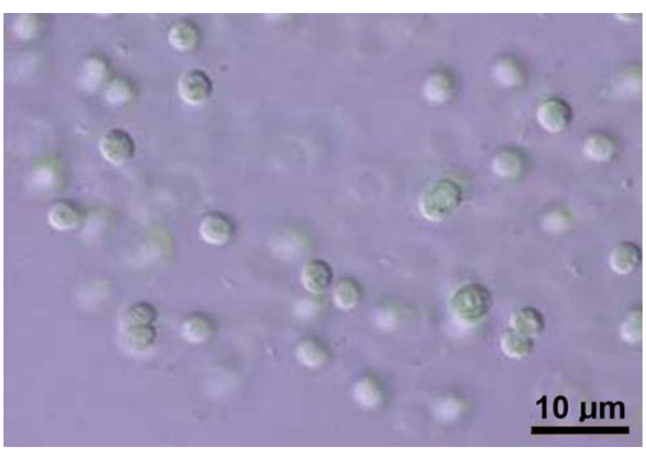

Figure 34. ***Nephrococcus*** sp.; ***Nephrococcus serbicus*** (**Cyanobacteria**) was found as a new species in the Božana Cave, Serbia. Photo modified from Linda Amaral Zettler and David Patterson, through Creative Commons.

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.

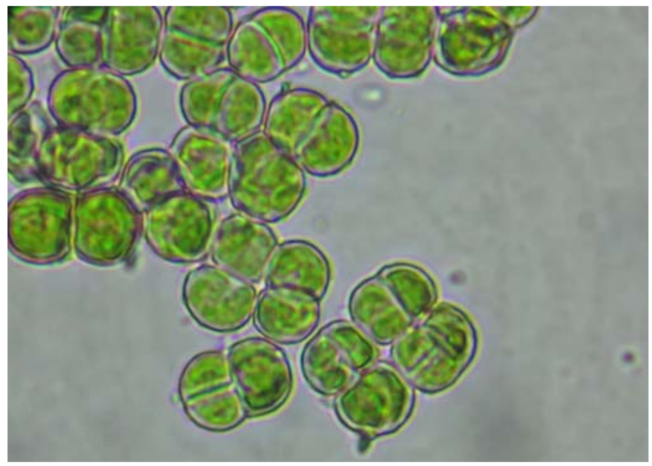

Figure 36. ***Desmococcus olivaceus***, one of only two green algae found on cave walls in Božana Cave (Serbia). Photo by Alejandra Huereca, through Creative Commons.

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

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

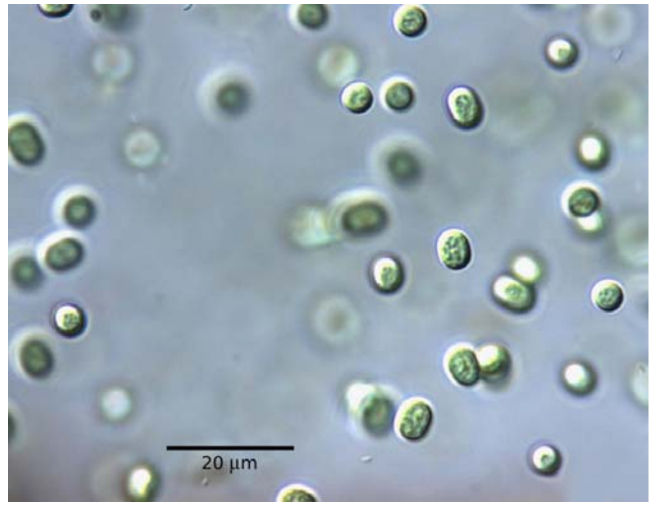

Figure 41. ***Aphanocapsa*** sp., a genus common on cave walls in Serbia and elsewhere. Photo by Jason Oyadomari, with permission.

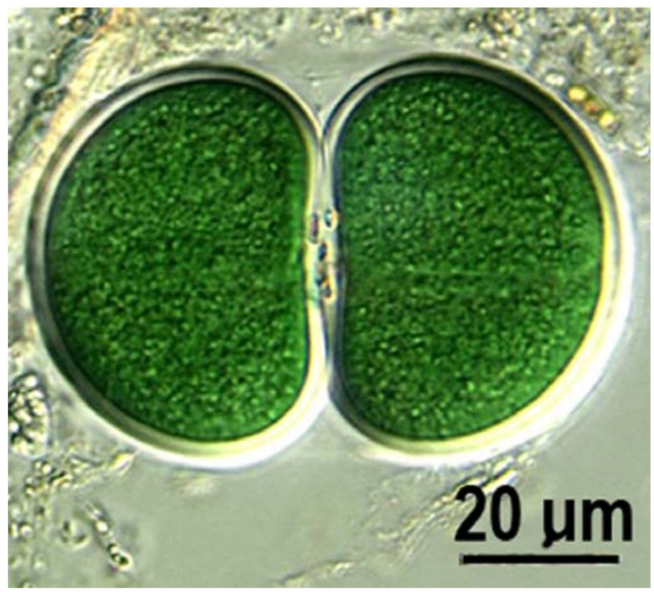

Figure 42. ***Chroococcus*** sp., a genus common on cave walls in Serbia and elsewhere. Photo by Jason Oyadomari, with permission.

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 9ºC, 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 9ºC. Photo from Nordic Microalgae <nordicmicroalgae.org>, through Creative Commons.

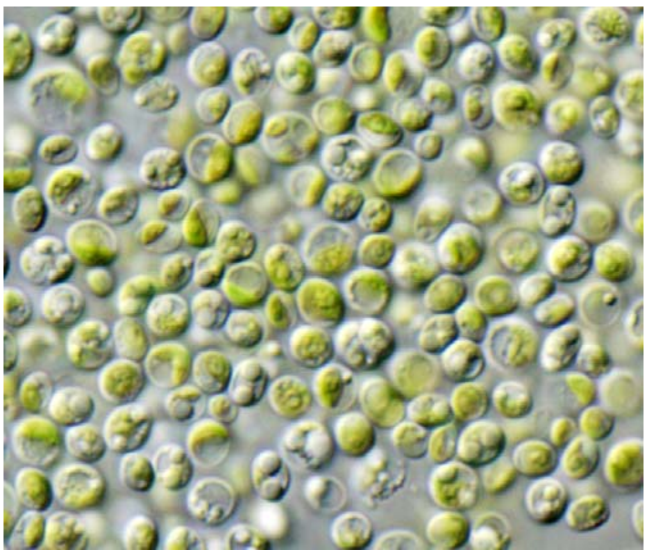

Figure 44. ***Chlorella vulgaris***. A cave member of ***Chlorella*** increases its accessory photosynthetic pigments when the temperature is lowered to 9ºC. Photo by Neon, through Creative Commons.

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.

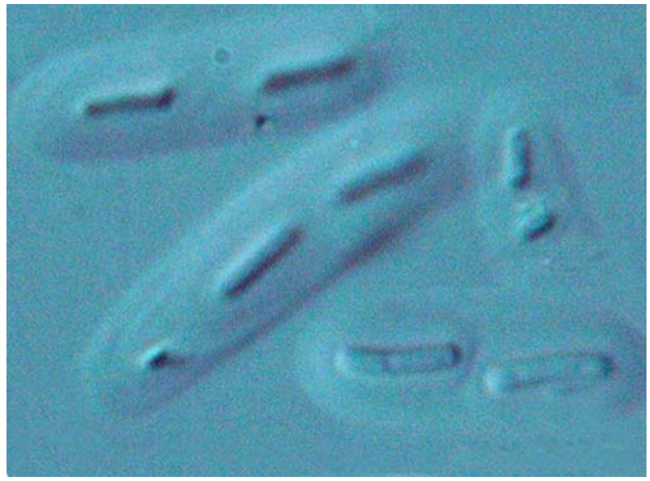

Figure 45. ***Gloeobacter*** sp., a genus that appears purple in cave biofilms. Photo by Burn12121212, through Creative Commons.

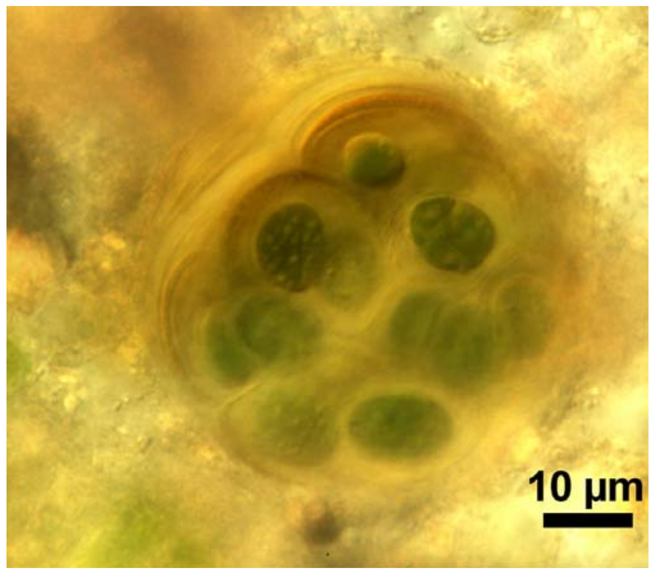

Figure 46. ***Gloeocapsa rupestris*** showing yellow color typical of its occurrence in cave biofilms. Photo by Cyanpro, through Creative Commons.

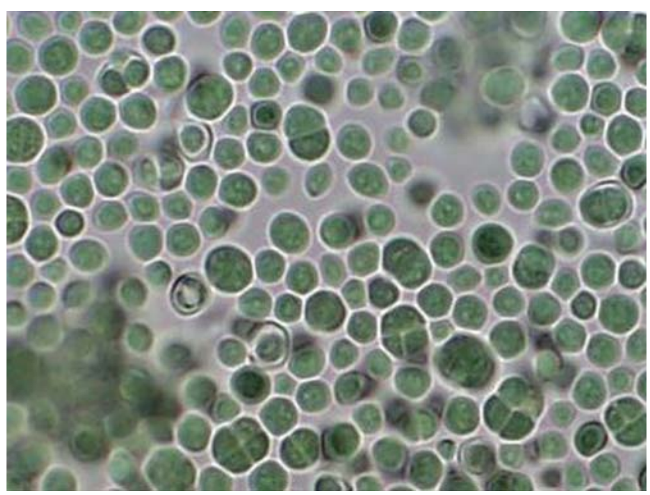

Figure 47. ***Chroococcidiopsis*** sp., a genus that appears black in cave biofilms. Photo by Burn12121212, through Creative Commons.

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

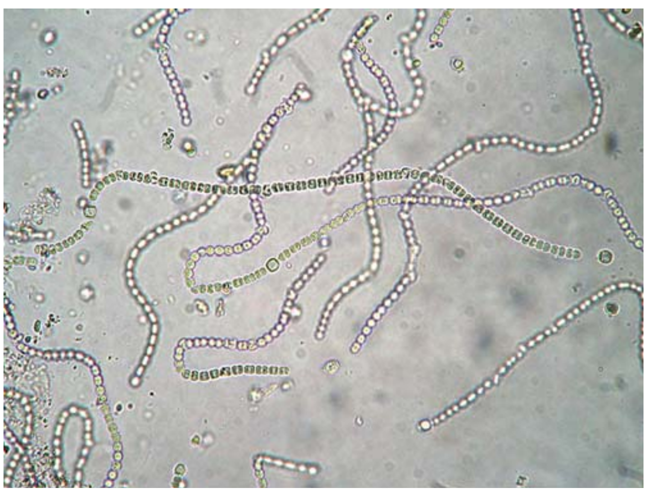

Figure 49. ***Nostoc commune***, a common cave dweller. Photo by Kristian Peters, through Creative Commons.

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 arthropyreniae***, ***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.

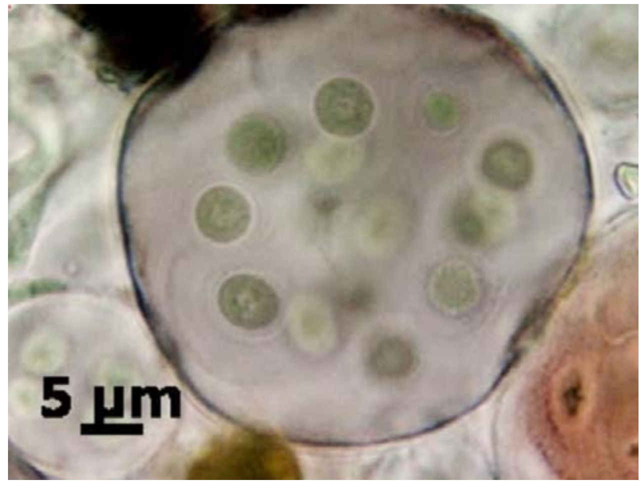

Figure 50. ***Gloeocapsa alpina***, one of the most abundant **Cyanobacteria** in ten caves in the Ojców National Park, Poland. Photo from AlgaeBase, through Creative Commons.

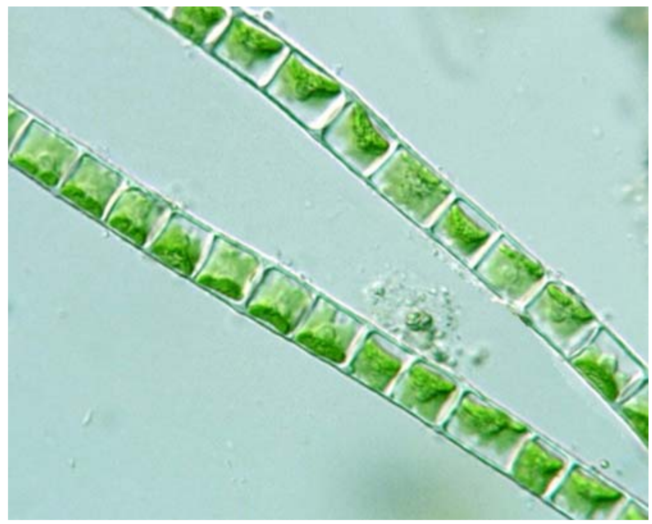

Figure 51. ***Klebsormidium flaccidum***, a common green alga in ten caves in the Ojców National Park, Poland. Photo by Yuuji Tsukii, with permission.

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.

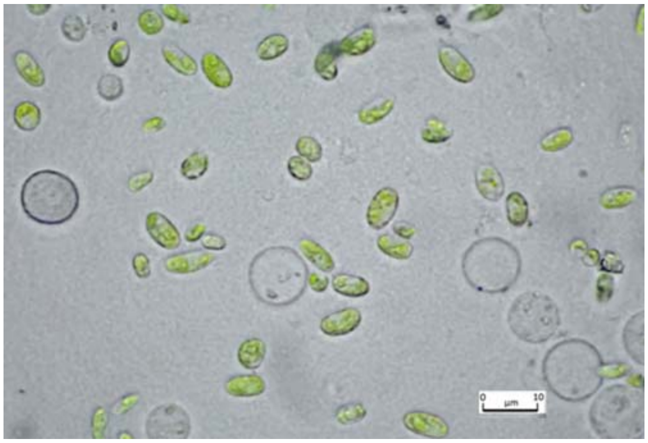

Figure 52. ***Pleurochloris pyrenoidosa***; ***P. commutata*** is among the most abundant algae in Seneca Cavern, Ohio, USA. Photo by Pierre Noel, through Creative Commons.

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, Tartra 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). ***Gloeothece palea*** (Figure 56) occasionally grows among mosses (Czerwik-Marcinkowska *et al*. 2019).

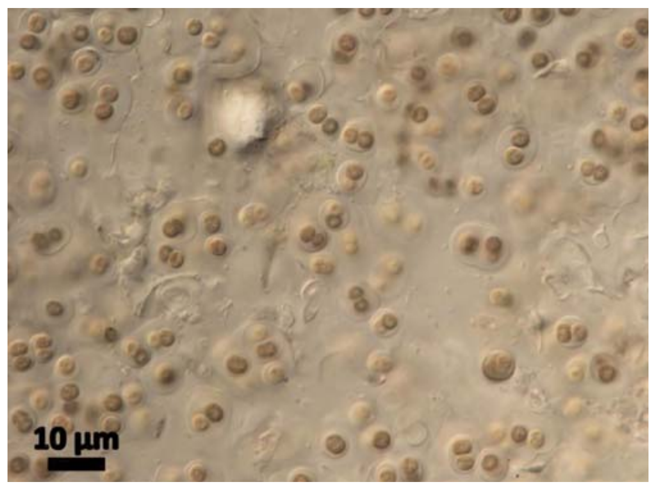

Figure 55. ***Gloeocapsa atrata***, a species that occurs among mosses on wet cave rocks. Photo from AlgaeBase, through Creative Commons.

Figure 56. ***Gloeothece 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**.

Poulíčková 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 troglophila***) 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), ***Diadesmis 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.

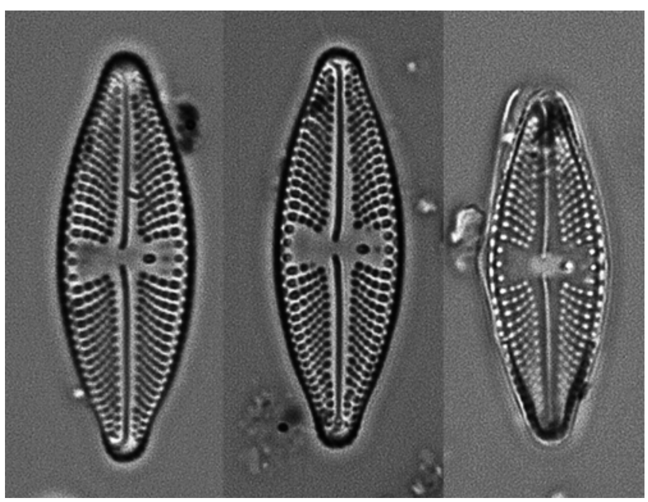

Figure 59. ***Luticola*** sp.; ***Luticola nivalis*** is one of the most frequent diatoms in caves. Photo by A. E. Drahos, through Creative Commons.

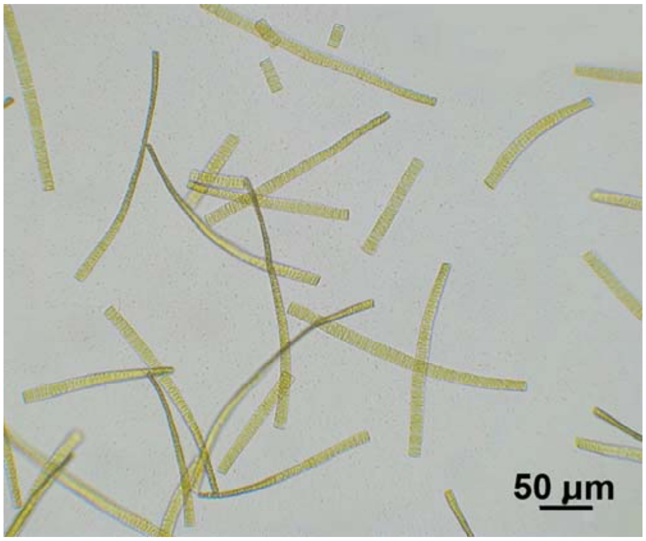

Figure 60. ***Diadesmis*** *cf.* ***gallica***; ***Diadesmis contenta*** var. ***biceps*** is one of the frequent diatoms in caves. Photo modified from ©BELSPO, with online permission.

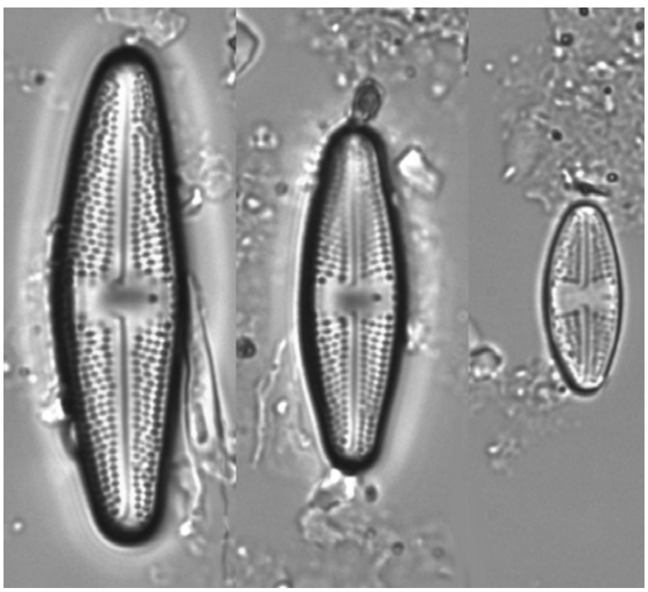

Figure 61. ***Luticola mutica***, one of most common species of diatoms in caves. Photo by Lane Allen, through Creative Commons.

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-Mariné 2009). ***Diadesmis 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 (Poulíčková & 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.

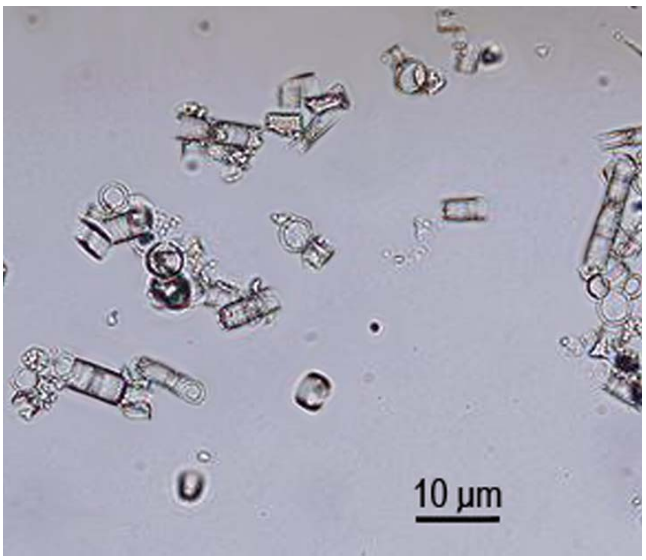

Figure 64. ***Orthoseira dendroteres***, a subaerial diatom that occurs in ice caves in the Yukon Territory. Photo by UTEX, through Creative Commons.

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; "stala**g**mites 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.

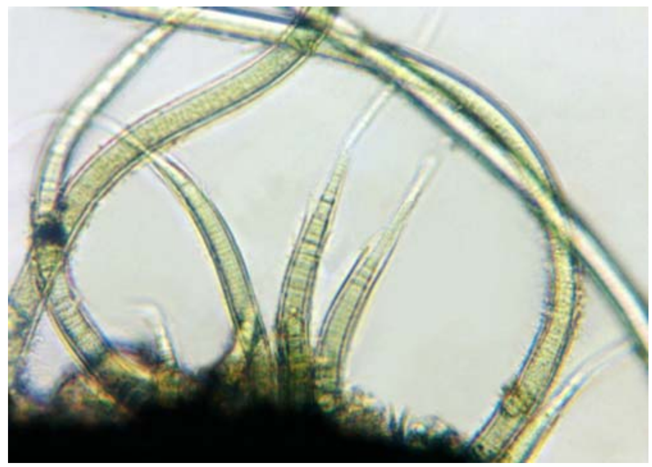

Figure 66. ***Homeothrix*** sp., in a genus that contributes to making layers of stalagmites. Photo from Manaaki Whenua – Landcare Research, with online permission.

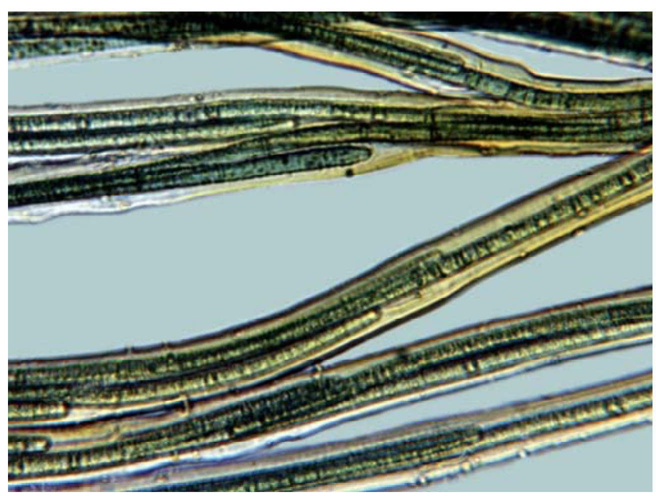

Figure 67. ***Schizothrix*** sp., in a genus that contributes to making layers of stalagmites. Photo from Manaaki Whenua – Landcare Research, with online permission.

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.

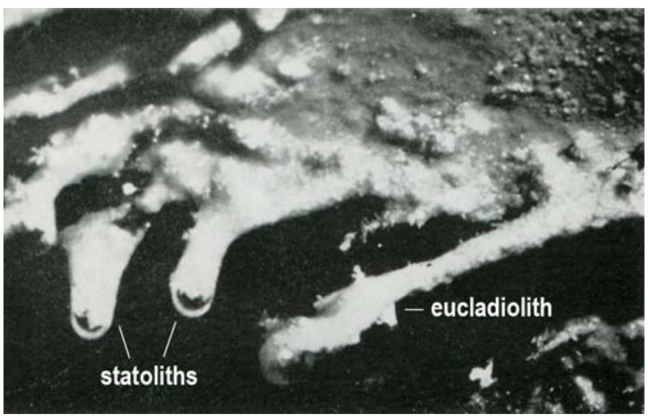

Figure 69. ***Eucladium verticillatum*** forming stalactite (eucladiotite) in mine in Dorset, UK. Note the nearly horizontal development of the eucladiolith. Photo from Dalby 1966b.

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.

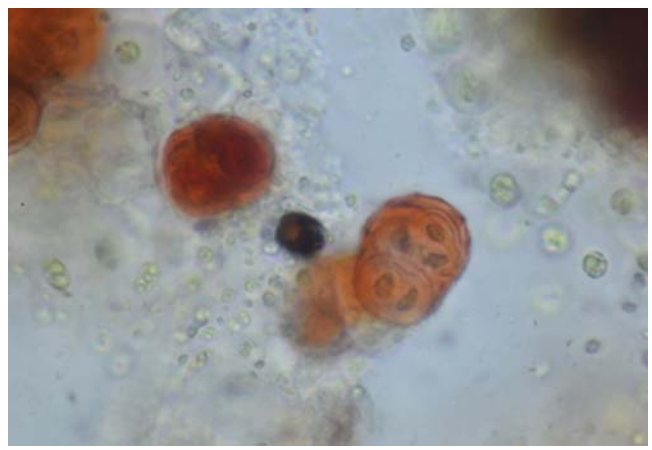

Figure 71. ***Gloeocapsopsis magma***, a common cave species. Photo by Randal, through public domain.

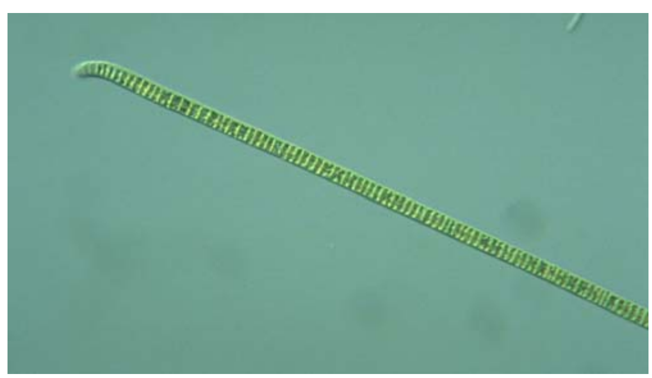

Figure 72. ***Oscillatoria brevis***, a common cave entrance and lampenflora species. Photo by Yuuji Tsukii, with permission.

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

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

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

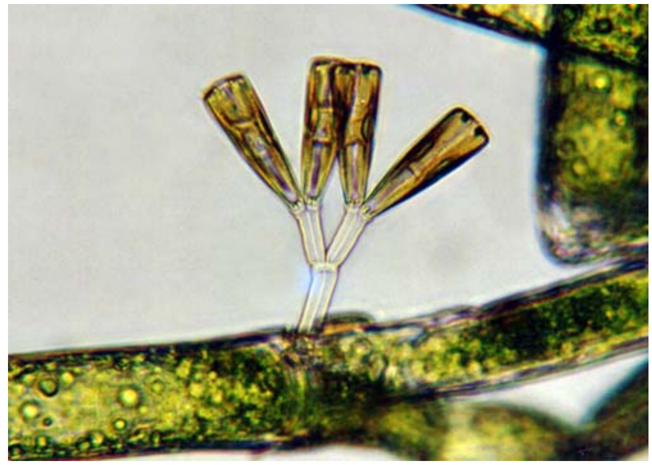

Figure 76. ***Gomphonema*** sp., member of a cave-dwelling diatom genus, attached to ***Cladophora***. Photo from Manaaki Whenua – Landcare Research, with online permission.

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 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.

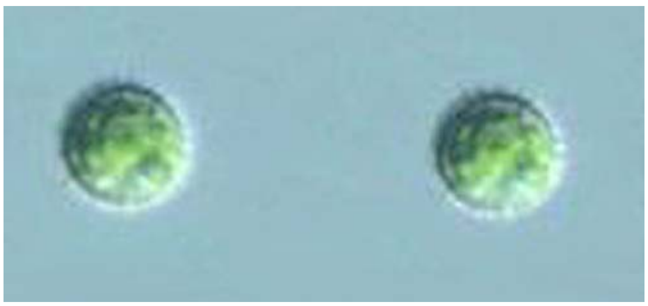

Figure 79. ***Trochiscia aspera***; ***T. ohioensis*** has a high correlation with bryophytes on Ash Cave Cliff in Ohio, USA. Photo by Yuuji Tsukii, with permission.

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.

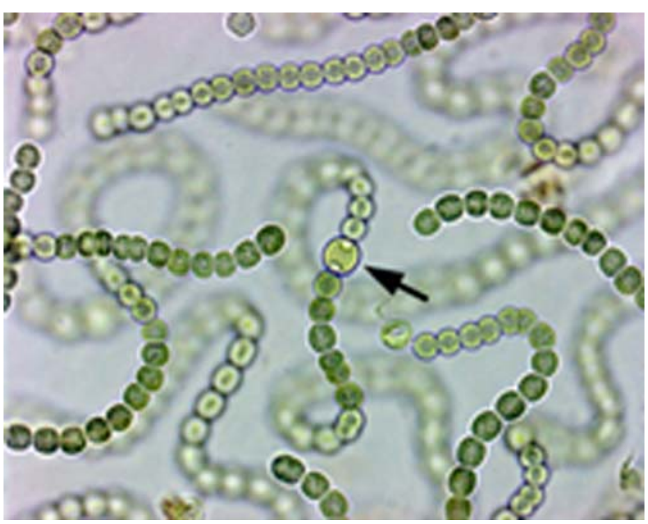

Figure 80. ***Nostoc*** sp. 1 showing heterocyst <vle.du.ac.in>, through Creative Commons.

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.

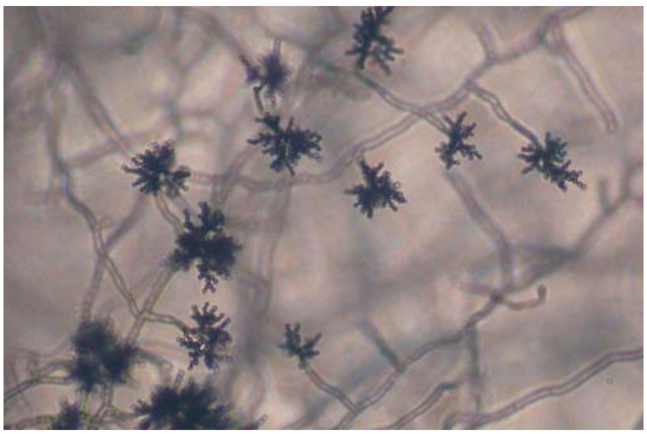

Figure 84. ***Cladosporium*** sp. conidia, a common **Ascomycota** fungus in three Serbian caves. Photo by Keisotyo, through Creative Commons.

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

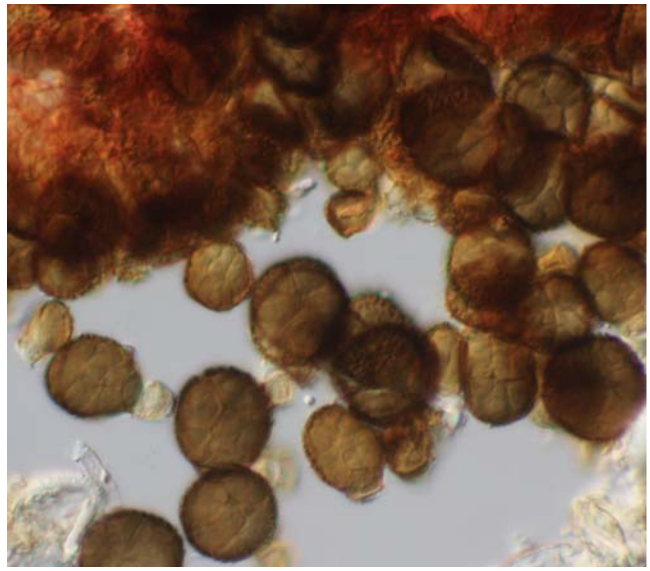

Figure 86. ***Epicoccum nigrum***; the genus ***Epicoccum*** is a common **Ascomycota** fungus in three Serbian caves. Photo by Paul Cannon, through Creative Commons.

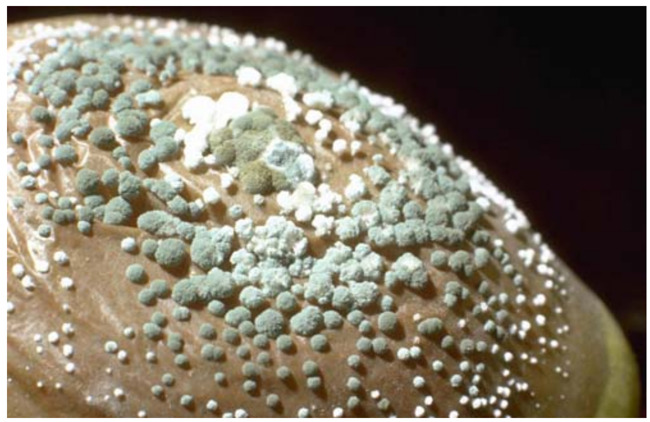

Figure 87. ***Penicillium expansum*** on pear. Photo by H. J. Larsen, through Creative Commons.

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.

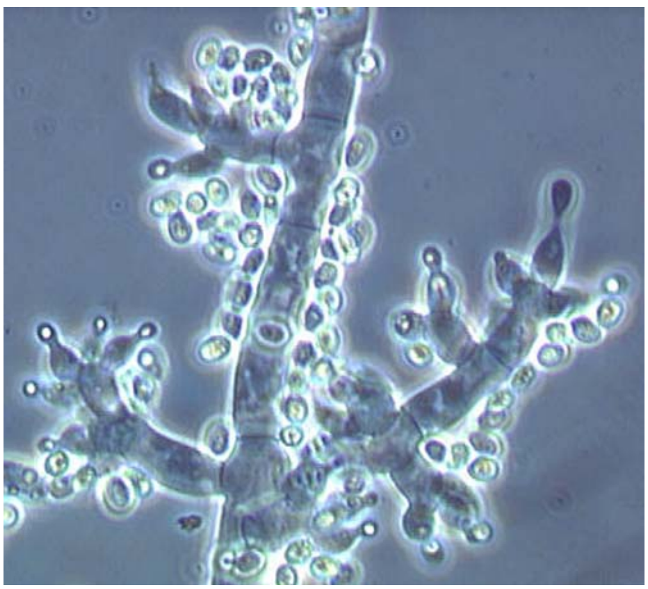

Figure 90. ***Trichoderma fertile***; the genus ***Trichoderma*** is a common **Ascomycota** fungus in three Serbian caves. Photo through public domain.

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

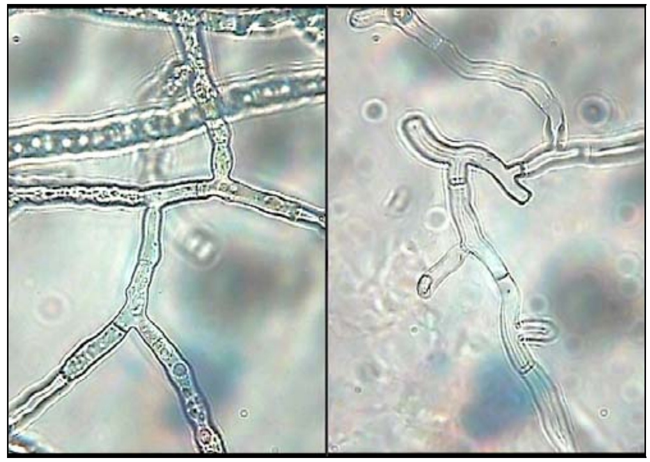

Figure 92. ***Rhizoctonia solani***; ***Rhizoctonia*** *s.1*. is the only member of **Basidiomycota** found in three Serbian caves. Photo by Tashkoskip, through Creative Commons.

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

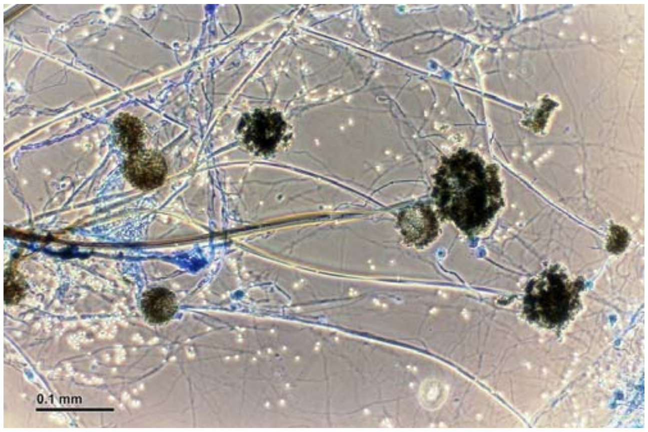

Figure 94. ***Mucor*** sp., a frequent genus in the Domica Cave system in Slovakia. Photo by Josef Reischig, through Creative Commons.

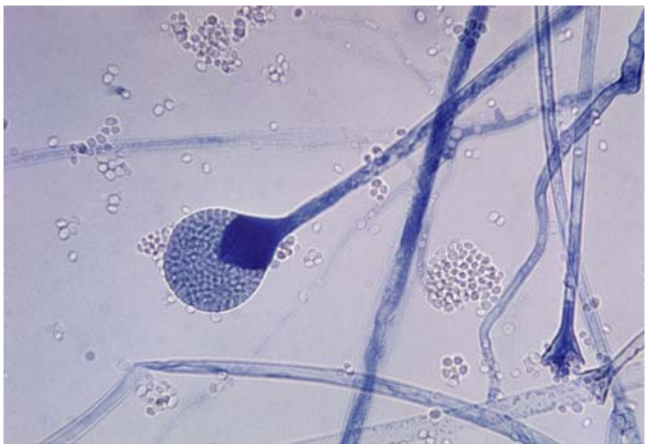

Figure 95. ***Mucor*** mature sporangium, a frequent genus in the Domica Cave system in Slovakia. Photo by Lucille K. Georg, CDC, through public domain.

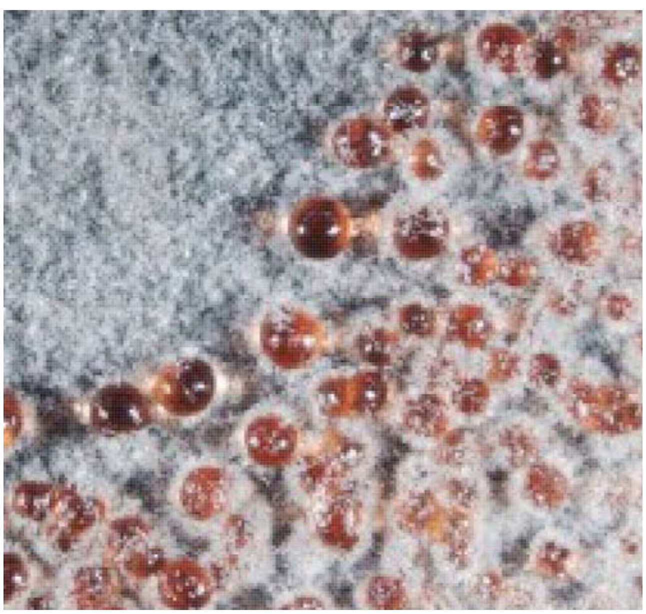

Figure 96. ***Talaromyces atroroseus*** colony. Photo by Jens C. Frisvad, Neriman Yilmaz, Ulf Thrane, Kasper Bøwig Rasmussen, Jos Houbraken, and Robert A. Samson, through Creative Commons.

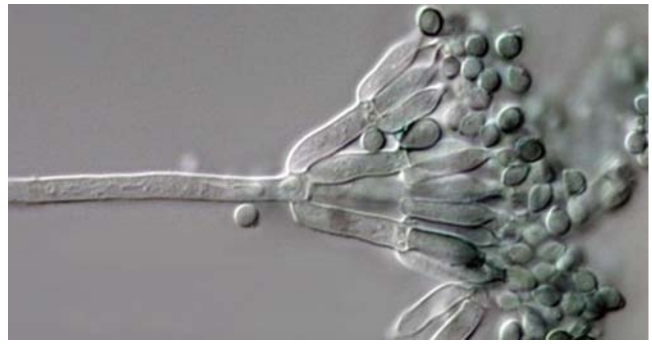

Figure 97. ***Talaromyces atroroseus***; ***Talaromyces flavus*** is frequent in the Domica Cave system in Slovakia. Photo by Jens C. Frisvad, Neriman Yilmaz, Ulf Thrane, Kasper Bøwig Rasmussen, Jos Houbraken, and Robert A. Samson, through Creative Commons.

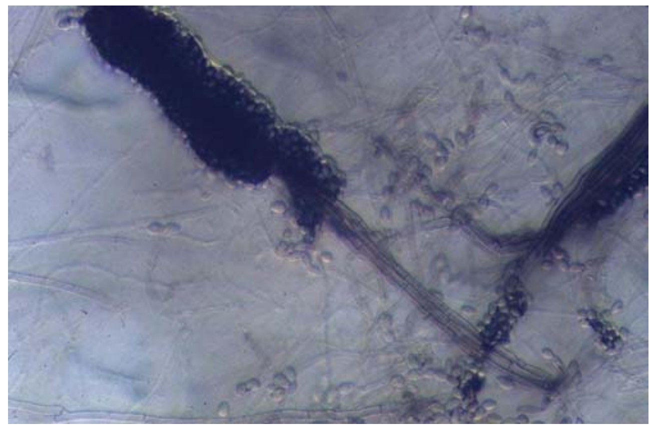

Figure 98. ***Doratomyces stemonitis***; ***Doratomyces*** is a frequent genus in the Domica Cave system in Slovakia. Photo by Gerald Holmes, through Creative Commons.

Summary

Caves are interesting ecotones of light and temperature gradients. They are further differentiated on type of substrate, *p*H, aspect, and air exchange. CO_2 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

Many Bryonetters responded to my call for images for this chapter. Wolfgang Hofbauer provided me with a paper that gave me a good list of current references on wind holes. Thank you to our Chinese colleagues (Wen Ye, Xinlei Guo, Yang Liu, Xiaoming Shao, and Wang Zhe) who responded to my request for the English translation of the abstract of a Chinese study.

Literature Cited

Andrews, K. M. 2003. A Geological and Geophysical Investigation of Ice Mountain Talus, Hampshire County, West Virginia. MS thesis, Department of Geology and Geography, West Virginia University, Morgantown, WV, 77 pp.

Asencio, A. D. and Aboal, M. 2011. *In situ* acetylene reduction activity of *Scytonema julianum* in Vapor cave (Spain). Internat. J. Speleol. 40: 17-21.

Borrego-Ramos, M., Blanco, S., and Olenici, A. 2018. Diatoms from the Valporquero Cave (León, NW Spain), with the description of *Germainiella legionensis sp. nov*. J. Cave Karst Stud. 80(4): 181-189.

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

Buecher, R. H. 1999. Microclimate study of Kartchner Caverns, Ariz. J. Cave Karst Stud. 61(2): 108-120.

Cao, J. H. and Yuan, D. X. 1999. Relationship between water-holding of carbonate rock and saxicolous algae, lichen and moss and its ecological significance. Geochimica 28: 248-256.

Clausen, E. 1952. Hepatics and humidity, a study on the occurrence of hepatics in a Danish tract and the influence of relative humidity on their distribution. Dansk. Bot. Ark. 15: 1-80.

Culver, D. C. 1970. Analysis of simple cave communities. I. Caves as islands. Evolution 24: 463-474.

Culver, D. C. 1971. Caves as archipelagoes. Bull. Natl. Speleol. Soc. 33: 97-100.

Culver, D. C. and Pipan, T. 2009. Superficial subterranean habitats – gateway to the subterranean realm? Cave Karst Sci. 35: 5-12.

Czerwik-Marcinkowska, J. 2013. Observations on aerophytic Cyanobacteria and algae from ten caves in the Ojców National Park. Acta Agrobot. 66(1): 39-51.

Czerwik-Marcinkowska, J. and Mrozińska, T. 2011. Algae and Cyanobacteria in caves of the Polish Jura. Polish Bot. J. 56: 203-243.

Czerwik-Marcinkowska, J., Wojciechowska, A., and Massalski, A. 2015. Biodiversity of limestone caves: Aggregations of aerophytic algae and Cyanobacteria in relation to site factors. Polish J. Ecol. 63: 481-499.

Czerwik-Marcinkowska, J., Zwijacz-Kozica, T., Pusz, W., and Wojciechowska, A. 2019. The relationship between presence of brown bear (*Ursus arctos*) and diversity of airborne algae and Cyanobacteria in the Glowoniowa Nyża Cave, Tartra Mountains, Poland. J. Cave Karst Stud. 81(1): 57-67.

Dalby, D. H. 1966a. The growth of *Eucladium verticillatum* in a poorly illuminated cave. Rev. Bryol. Lichenol. 34: 288-301.

Dalby, D. H. 1966b. The growth of plants under reduced light. Stud. Speleol. 1: 193-203.

Dam, H. van, Mertens, A., and Sinkeldam, J. 1994. A coded checklist and ecological indicator values of freshwater diatoms from The Netherlands. Netherlands J. Aquat. Ecol. 28: 117-133.

Dayner, D. M. and Johansen, J. R. 1991. Observations on the algal flora of Seneca Cavern, Seneca County, Ohio. Ohio J. Sci. 91: 118-121.

Delay, B. 1974. Les conditions thermiques des mileux terrestres dans la zone d'heterothermie des massifs calaires et leurs influences sur le developpement de *Speonomus longicornis* (Coleoptere, Bathysciinae). Ann. Speleol. 29: 121-136.

Downing, A. J. 1992. Distribution of bryophytes on limestones in Eastern Australia. Bryologist 95: 5-14.

Faimon, J., Stelcl, J., and Sas, D. 2006. Anthropogenic CO_2-flux into cave atmosphere and its environmental impact: A case study in the Císařská Cave (Moravian Karst, Czech Republic). Sci. Tot. Environ. 369: 231-245.

Faimon, J., Ličbinská, M., and Zajíček, P. 2012. Relationship between carbon dioxide in Balcarka Cave and adjacent soils in the Moravian Karst region of the Czech Republic. Internat. J. Speleol. 41: 17-28.

Falasco, E., Ector, L., Isaia, M., Wetzel, C. E., Hoffmann, L., and Bona, F. 2014. Diatom flora in subterranean ecosystems: A review. Internat. J. Speleol. 43: 231-251.

Falasco, E., Bona, F., Isaia, M., Piano, E., Wetzel, C. E., Hoffmann, L., and Ector, L. 2015. *Nuphela troglophila sp. nov.*, an aerophilous diatom (Bacillariophyta) from the Bossea cave (NW Italy), with notes on its ecology. Fottea, Olomouc 15(1): 1-9.

Fraser, C. I., Terauds, A., Smellie, J., Convey, P., and Chown, S. L. 2014. Geothermal activity helps life survive glacial cycles. Proc. Natl. Acad. Sci. 111: 5634-5639.

Freitas, C. R. de and Littlejohn, R. N. 1987. Cave climate: Assessment of heat and moisture exchange. J. Climatol. 7: 553-569.

Frisia, S., Fairchild, I. J., Fohlmeister, J., Miorandi, R., Spötl, C., and Borsato, A. 2011. Carbon mass-balance modeling and carbon isotope exchange processes in dynamic caves. Geochim. Cosmochim. Acta 75: 380-400.

Gainutdinov, I. A., Abdullin, Sh. R., Sharipova, M. Yu, and Dubovik, I. E. 2017. Cyanobacteria and algae in some caves of Bashkirskiyi Ural Biosphere Reserve (southern Urals, Bashkortostan Republic, Russia). Cave Karst Sci. 44(3): 119-126.

Gamble, D. W., Dogwiler, J. T., and Mylroie, J. 2000. Field assessment of the microclimatology of tropical flank margin caves: Climate Res. 16: 37-50. doi:10.3354/cr016037.

Germain, H. 1981. Flore des diatomées Diatomophycées eaux douces et saumâtres du Massif Armoricain et des contrées voisines d'Europe occidentale. Soc. Nouv. Éd. Boubée, Paris, 444 pp.

Gurnee, J. 1994. Management of some unusual features in the show caves in the United States. Internat. J. Speleol. 23: 13-17.

Howarth, F. G. and Stone, F. D. 1990. Elevated carbon dioxide levels in Bayliss Cave, Australia: Implications for the evolution of obligate cave species. Pacific Sci. 44: 207-218.

Huang, F., Huang, Y. M., Gao, X., and Cao, J. H. 2015. Effects of karst environmental factors on activity of soil microorganic extracellular carbonic anhydrase of karst area in Maocun village, Guilin. J. South. Agric. 46: 1792-1797.

Jedrejko, K. and Ziober, A. 1992. The bryophytes of chosen caves on the Krackòw-Wieluñ Upland and its relation to microclimate conditions and ecological differentiation of habitats. Ziemia Czestochowska 18: 107-151.

Jegla, T. C. and Poulson, T. C. 1970. Circannian rhythms-I. Reproduction in the cave crayfish, *Orconectes pellucidus inermis*. Comp. Biochem. Physiol. 33: 347-355.

John, D. M., Whitton, B. A., and Brook, A. J. 2011. The Freshwater Algal Flora of the British Isles. An Identification Guide to Freshwater and Terrestrial Algae. 2nd Ed. Cambridge University Press, pp. 1-878.

Juberthie, C. 1975. Vie southerraine et reproduction. Bull. Soc. Zool. France 100: 177-201.

Juberthie, C. and Delay, B. 1973. Influence des facteurs abiotiques, temperature et nature du substrat, sur le developpement embryonnaire du Coleoptere Bathysciinae trogobie *Speonomus longicornis*. Ann. Speleol. 4: 689-696.

Jurado, V., Fernandez-Cortes, A., Cuezva, S., Laiz, L., Cañaveras, J. C., Sanchez-Moral, S., and Saiz-Jimenez, C. 2009. The fungal colonisation of rock-art caves: Experimental evidence. Naturwissenschaften 96: 1027-1034.

Koch, A. R. Jr. 1976. Floristics and ecology of algae on sandstone cliffs in east-central and southeastern Ohio. Ph. D. Dissertation. The Ohio State University, Columbus, 186 pp.

Komáromy, Z. P., Padisak, J., and Rajczy, M. 1985. Flora in the lamp-lit areas of the cave "Anna-Barlang" near Lillafuered (Hungary). Ann. Hist. Nat. Mus. Natl. Hung. 77: 103-112.

Laiz, L., Groth, I., Gonzalez, I., and Saiz-Jimenez, C. 1999. Microbiological study of the dripping waters in Altamira cave (Santillana del Mar Spain). J. Microbiol. Meth. 36: 129-138.

Lamprinou, V., Danielidis, D. B., Economou-Amilli, A., and Pantazidou, A. 2012. Distribution survey of Cyanobacteria in three Greek caves of Peloponnese. Internat. J. Speleol. 41: 267-272.

Lamprinou, V., Danielidis, D. B., Pantazidou, A., Oikonomou, A., and Economou-Amilli, A. 2014. The show cave of Diros vs. wild caves of Peloponnese, Greece-distribution patterns of Cyanobacteria. Internat. J. Speleol.43: 335-342.

Lauriol, B., Prévost, C., and Lacelle, D. 2006. The distribution of diatom flora in ice caves of the northern Yukon Territory, Canada: Relationship to air circulation and freezing. Internat. J. Speleol. 35: 83-92.

Li, W., Yu, L.-J., Yu, J.-F., Jia, L.-P., and Wu, Y. 2005. Effects of karst environmental factors on expression and activity of bacterial extracellular carbonic anhydrase. Microbiol. China 5: 35-39.

Liu, T. L., Cong, C. L., Hu, D., Wang, S. J., and Zhang, X. Q. 2017. Carbonic anhydrase activity of six epilithic mosses and their underlying soil in the Puding karst area, Guizhou Province. Carsol. Sinica 36: 187-192.

Lovalvo, D., Clingenpeel, S. R., McGinnis, S., Macur, R. E., Varley, J. D., Inskeep, W. P., Glime, J., Nealson, T., and McDermott, T. R. 2010. A geothermal-linked biological oasis in Yellowstone Lake, Yellowstone National Park, Wyoming. Geobiology 8: 327-336.

Lowe, R. L., Kociolek, J. P., and Vijver, B. van de. 2013. Two new *Orthoseira* species (Bacillariophyceae) from lava tubes on Île Amsterdam and Big Island (Hawai'i). Phytotaxa 111: 39-52.

Mason-Williams, A. and Benson-Evans, K. 1967. Summary of results obtained during a preliminary investigation of the bacterial and botanical flora of caves in South Wales. Internat. J. Speleol. 2: 397-402.

Mazina, S. E. and Popkova, A. V. 2020a. Biodiversity and productivity of phototrophic communities from the illuminated cave zone with high content of CO_2. Cave Karst Sci. 47: 131-137.

Mazina, S. E. and Popkova, A. V. 2020b. Distribution of photosynthetic species in grotto type caves of different regions. RUDN J. Ecol. Life Safety 28: 275-284.

Mazina, S. E., Kozlova, E. V., Turchinskaya, S. M., Pichugina, E. K., Yuzbekov, A. K., and Pešić, V. 2020. Carbon fluxes intensity from substrates and phototrophic consortiums of the photic zones in Montenegro caves. Ecol. Monteneg. 34: 20-33.

Moseley, M. 2009a. Size matters: Scalar phenomena and a proposal for an ecological definition of 'cave.' Cave Karst Sci. 35(3): 89-94.

Moseley, M. 2009b. Are all caves ecotones. Cave Karst Sci. 36(2): 53-58.

Mulec, J. and Kosi, G. 2009. Lampenflora algae and methods of growth control. J. Cave Karst Stud. 71(2): 109-115.

Mulec, J., Kosi, G., and Vrhovšek, D., 2007. Algae promote growth of stalagmites and stalactites in karst caves (Škocjanske jame Slovenia). Carbonates Evaporites 22(1): 6-9.

Mulec, J., Kosi, G., and Vrhovšek, D. 2008. Characterization of cave aerophytic algal communities and effects of irradiance levels on production of pigment. J. Cave Karst Stud. 70(1): 3-12.

Nováková, A. 2009. Microscopic fungi isolated from the Domica Cave system (Slovak Karst National Park, Slovakia). A review. Internat. J. Speleol. 38: 71-82.

Ortega-Calvo, J. J., Ariño, X., Hernandez-Marine M., and SaizJimenez C. 1995. Factors affecting the weathering and colonization of monuments by phototrophic microorganisms. Sci. Tot. Environ. 167: 329-341.

Peck, S. B. 1976. The effect of cave entrances on the distribution of cave-inhabiting terrestrial arthropods. Internat. J. Speleol. 8: 309-321.

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

Popović, S., Subakov Simić, G., Stupar, M., Unković, N., Predojević, D., Jovanović, J., and Ljaljević Grbić, M. 2015. Cyanobacteria, algae and microfungi present in biofilm from Božana Cave (Serbia). Internat. J. Speleol. 44: 141-149.

Popović, S., Simić, G. S., Korać, A., Golić, I., and Komárek, J. 2016. *Nephrococcus serbicus*, a new coccoid cyanobacterial

species from Božana Cave, Serbia. Phytotaxa 289(2): 135-146.

Popović, S., Subakov, S. G, Stupar, M., Unković, N., Krunić, O., Savić, N., and Ljaljević Grbić, M. 2017. Cave biofilms: Characterization of phototrophic Cyanobacteria and algae and chemotrophic fungi from three caves in Serbia. J. Cave Karst Stud. 79(1): 10-23.

Popović, S., Krizmanić, J., Vidaković, D., Karadžić, V., Milovanović, Ž., Pećić, M., and Simić, G. S. 2020. Biofilms in caves: Easy method for the assessment of dominant phototrophic groups/taxa *in situ*. Environ. Monitor. Assess. 192(11): 1-17.

Poulíčková, A. and Hašler, P. 2007. Aerophytic diatoms from caves in central Moravia (Czech Republic). Preslia 79: 185-204.

Poulson, T. L. 1975. Symposium of life histories of cave beetles: An introduction. Internat. J. Speleol. 7: 1-5.

Poulson, T. L. and White, W. B. 1969. The cave environment. Science 165: 971-981.

Prous, X., Ferreira, R. L., and Martins, R. P. 2004. Ecotone delimitation. Epigean-hypogean transition in cave ecosystems. Austral Ecol. 24: 374-382.

Prous, X., Ferreira, R. L., and Jacobi, C. M. 2015. The entrance as a complex ecotone in a Neotropical cave. Internat. J. Speleol. 44: 177-189.

Puglisi, M. and Privitera, M. 2018. New and noteworthy records of mosses from Italian national and regional Parks. Plant Biosyst. 152: 604-607.

Reichardt, E. 1985. Diatomeen an feuchten Felsen des Südlichen Frankenjuras. Ber. Bayer. Bot. Gesell. 56: 167-187.

Roldán, M. and Hernández-Mariné, M. 2009. Exploring the secrets of the three-dimensional architecture of phototrophic biofilms in caves. Internat. J. Speleol. 38: 41-53.

Round, F. E. 1981. The Ecology of Algae. Cambridge University Press, Cambridge, London, New York, New Rochelle, Melbourne, Sydney, 653 pp.

Rushforth, S. R., Kaczmarska, I., and Johansen, J. R. 1984. The subaerial diatom flora of Thurston lava tube, Hawaii. Bacillaria 7: 135-157.

Sala, S. E., Ramírez, J. J., and Plata, Y. 2008. Diatoms from lentic and lotic systems in Antioquia, Chocó and Santander Departments in Colombia. Rev. Biol. Trop. 56: 1159-1178.

Schade, F. A. 1917. Ueber den mittleren jahrl. Warmegenuss bei *Webera nutans* und *Leptoscyphus taylori* im Elbsandsteingebirge. Ber. Deutsch. Bot. Ges. 35: 490-505.

Schuster, R. M. 1958. Boreal Hepaticae, a Manual of the Liverworts of Minnesota and Adjacent Regions III. Phytogeography. Amer. Midl. Nat. 59: 257-332.

Sciuto, K., Moschin, E., and Moro, I. 2017. Cryptic cyanobacterial diversity in the Giant Cave (Trieste, Italy): The new genus *Timaviella* (Leptolyngbyaceae). Cryptog. Algol. 38: 285-323.

Selvi, B. and Altuner, Z. 2007. Algae of Ballica Cave (Tokat-Turkey). Internat. J. Nat. Eng. Sci. 1: 99-103.

Spotl, C., Fairchild, I. J., and Tooth, A. F. 2005. Cave air control on drip water geochemistry, Obir Caves (Austria): Implications for speleothem deposition in dynamically ventilated caves. Geochim. Cosmochim. Acta 69: 2451-2468.

Turchinskaia, S., Mazina, S., and Semikolennykh, A. 2019. Phototroph biocrusts in karst caves: Biodiversity, spatial organization and ecological functions. Source of life - 30th Congress of Soil Science Society of Poland SOIL.

Tuttle, M. D. 1975. Population ecology of the gray bat (*Myotis grisescens*): Factors influencing early growth and development. Occ. Pap. Mus. Nat. Hist., Univ. Kans. 36: 1-24.

Tuttle, M. D. 1976. Population ecology of the gray bat (*Myotis grisescens*): Philopatry, timing and patterns of movement, weight loss during migration, and seasonal adaptive strategies. Occ. Pap. Mus. Nat. Hist., Univ. Kans. 54: 1-38.

Tuttle, M. D. and Stevenson, D. E. 1978. Variation in the cave environment and its biological implications. In: Zuber, R., Chester, J., Gilbert, S., and Rhodes, G. (eds.). Proceedings of the National Cave Management Symposium, Albuquerque, N. M., pp. 108-121.

Vanderwolf, K., Malloch, D., McAlpine, D. F., and Forbes, G. J. 2013. A world review on fungi, yeasts, and slime molds in caves. Internat. J. Speleol. 42: 77-96.

Vijver, B. Van de and Beyens, L. 1997. The epiphytic diatom flora of mosses from Strømness Bay area, South Georgia. Polar Biol. 17: 492-501.

Whitaker, T., Jones, D., Baldini, J. U. L., and Baker, A. J. 2009. A high-resolution spatial survey of cave air carbon dioxide concentrations in Scoska Cave (North Yorkshire, UK): Implications for calcite deposition and re-dissolution. Cave Karst Sci. 36(3): 85-92.

Wilson, J. 1975. The effect of low humidity on the distribution of *Heteromurus nitidus* (Collembola) in Radford Cave, Devon. Trans. Brit. Cave Res. Assoc. 2: 123-126.