10 Changing Perspectives on Subterranean Habitats

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In this chapter, we review the status of the hypothesis that the dichotomy between shallow and deep subterranean habitats is a fundamental one, updating the original book-length presentation of this hypothesis (Culver and Pipan 2014), and consider the status of dim light habitats, such as leaf litter and partially de-roofed caves (Mejía-Ortíz et al. 2018). We begin with a review of the habitats themselves and then look for generalities.

10.1 Historical Background

Humankind has been involved with caves for millennia. Caves were places of shelter for early humans in many parts of the world. They have served as places of worship for many societies in many times and places. Caves have been used as storehouses, as munitions factories, and as resting places for the dead. Caves play a prominent role in the myths and legends of many cultures throughout recorded history. Caves are secret places. Small children make "caves" by draping blankets over furniture. In contemporary society, caves frequently appear in movies and in cartoons. Show caves continue to draw thousands of visitors each year. Caves are also of great interest to scientists and explorers (White and Culver 2019).

Given this long connection with caves, it is not surprising the earliest discussions about the subterranean realm, in general, were about caves, and from the seventeenth century on, a number of theories of cave formation were put forward (Shaw 1992). The modern era of speleology began with the work of Cvijić (1893) on speleogenesis.

Study of the biology of the subterranean realm also began with cave animals, including the first description of an aquatic cave animal—the olm *Proteus anguinus* studied by Laurenti in 1768—and the first description of a terrestrial cave animal—the beetle *Leptodirus hochenwartii* by Schmidt in 1832. However, early on, Racoviţă (Racovitza) (1907), in his famous paper "Essai sur les problèmes biospéologiques", emphasized that the true habitat of many cave organisms was not the cave passage itself, but rather the cracks and crevices that occur in karst and other cave bearing rock. Although he did not further delineate this habitat, it was an impetus to lead European researchers to study non-cave habitats, such as the epikarst, hyporheic, and MSS (see below). Racovitza can be credited with showing the importance of habitat size (dimension) but not the position of these habitats in relationship to the surface. While it is difficult to overstate the importance of Racoviţă's work for the development of the study of subterranean biology in Europe (Sket 2006), it went largely unnoticed in North American until the last decade.

Racoviţă (1907) also established a convention that continues to the present—that of excluding the soil as a subterranean habitat (see Sket 2004). The reason given is primarily historical—the study of soils and soil fauna was well established as a separate discipline (pedology, pedobiology). Regardless of this, the soil has an obvious connection with other subterranean habitats, as do its inhabitants (Coiffait 1958). Sket (2004) further argues that organic matter is too abundant for the soil to be considered a subterranean habitat, but this exclusion leads to problems with other subterranean habitats, such as caves with extensive bat guano. We will make the contrary case, that soil should be included among subterranean habitats.

Perhaps the most obvious non-cave subterranean habitat, with the exception of soil, is the underflow of rivers and streams (Malard et al. 2000). The term hyporheic was originally coined by Orghidan (1959), and the hyporheic has

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M. Knez et al. (eds.), *Karstology in the Classical Karst*, Advances in Karst Science,
https://doi.org/10.1007/978-3-030-26827-5_10

become an important part, not only of the study of subterranean life but also of rivers and streams themselves (e.g. Buss et al. 2009). The study of the hyporheic as well as aquatic cave habitats was set forward as the separate discipline of groundwater ecology by Gibert et al. (1994). They also emphasized the importance of habitat (pore) size, as well as the nature and extent of surface/subsurface connections. The distinction between large pore and small pore aquatic habitats was further elaborated in a complex classification scheme by Botosaneanu (1986), but the basic division was between small (<1 cm) and large habitats.

In some ways, a conceptual equivalent of the hyporheic for terrestrial habitats is the "milieu souterraine superficiel" or MSS, which has come to mean any aphotic terrestrial subterranean habitat with intermediate habitat size. It was first coined by Juberthie et al. (1980) to describe covered scree slopes, these habitats were initially thought to be primarily dispersal corridors between karst areas and their associated caves. Since the initial description, it has been shown that the MSS is a habitat in its own right (Crouau-Roy et al. 1992) and that typically has an intimate connection with the soil and the soil fauna (Gers 1998). The term MSS has also been expanded to include a variety of habitats in volcanic rock, both covered and uncovered (Medina and Oromí 1990).

In recent years there have been extensive listings of subterranean habitats in general (Juberthie 2000), groundwater habitats (Hahn 2009), MSS habitats (Ortuño et al. 2013) and of different types of caves. The recent focus on types of caves hinges on the distinction between epigene and hypogene caves. Klimchouk (2017) defines hypogene speleogenesis as the formation of voids by upwelling liquids, independent of recharge from the overlying or adjacent surface. Eogenetic speleogenesis occurs exclusively in hydrologically open, near surface systems, in intimate contact with the landscape. Sendra et al. (2014) claimed that this dichotomy has profound effects on species richness, with hypogene caves being species poor.

Culver and Pipan (2008) introduced the concept of shallow subterranean habitats (SSHs) as a way of generalizing and grouping together of the array of subterranean habitats, an approach expanded and elaborated by Culver and Pipan (2011, 2014). They point out that all subterranean habitats less than 10 m from the surface share a number of features. First, they contain eyeless and depigmented individuals as well as eyed, pigmented individuals (Pipan and Culver 2012a; Culver and Pipan 2015). The eyeless, depigmented species have the convergent morphology typical of subterranean habitats, called troglomorphy by Christiansen (1962). Second, they are aphotic habitats (Culver and Pipan 2014). Third, with rare exceptions (calcrete aquifers) they have intimate connections with the surface, resulting in patterns of environmental variation that are intermediate between surface and deep subsurface habitats. Fourth, although variable, organic carbon tends to occur at higher levels than in deeper subterranean habitats. These ecological features (#2 to #4) present a contrasting selective environment to that of deep subterranean habitats that allows assessment of what is important in molding the inhabitants of all subterranean habitats.

10.2 Shallow Subterranean Habitats

From a landscape perspective, SSHs occur in a bewildering array of contexts and sizes. Furthermore, while some SSHs are well and carefully defined, such as the hyporheic (Malard et al. 2000) and epikarst (Jones et al. 2004), others, while more or less carefully defined initially, have come to have broader, ill-defined limits. This is especially true for the MSS, which has become a catch-all for aphotic environments in rocks and stones, in the absence of other terms. Vagueness of definition also holds for the hypotelminorheic, which has come to include nearly all small bodies of perched subsurface water that exit through seeps. We will not indulge in any further definitions or clarifications, of which there are perhaps already too many, but rather show the extent of SSHs.

10.2.1 Aquatic Habitats

10.2.1.1 Hypotelminorheic

The term "hypotelminorheic" was originally coined by Meštrov (1962) to describe a shallow subterranean habitat, no more than a few metres in depth that emerged at a small spring or seep. The original site of his studies was in Medvednica Mountain in Croatia (Fig. 10.1), and he later described similar sites in the foothills of the Pyrenees (Meštrov 1964). The Croatian site was not in karst and so it was somewhat unexpected that he found eyeless depigmented amphipods—*Niphargus tauri medvednicae* and *N. stygius licanus.* Meštrov (1962) also reported *Niphargus foreli* but this identification is probably in error (Culver et al. 2006). This troglomorphic morphology is characteristic of cave-dwelling species as well. The hypotelminorheic is a perched aquifer, and subsequent classification schemes of subterranean habitats place it in a separate category that seems to share few similarities with other subterranean habitats (Juberthie 2000). Culver et al. (2006) subsequently describe similar sites in Slovenia and the USA that also harboured eyeless depigmented amphipods. These habitats also had some differences with the Croatian site. In particular, the U.S. sites in the lower Potomac basin near Washington, DC, were not in mountainous or even hilly terrain.

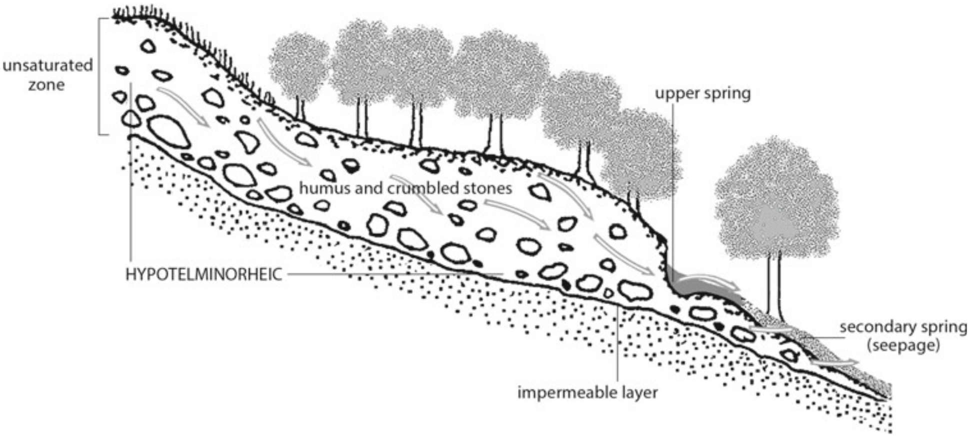


Fig. 10.1 Sketch of hypotelminorheic habitat, modified from Meštrov (1962) by Culver and Pipan (2014). Used with permission of Oxford University Press

Culver et al. (2006) list the following features of hypotelminorheic habitats:

- a persistent wet spot, a kind of perched aquifer;
- fed by subsurface water in a slight depression in an area of low to moderate slope;
- rich in organic matter;
- underlain by a clay layer, typically 5–50 cm beneath the surface;
- with a drainage area typically of less than 10,000 m^2;
- with a characteristic dark colour derived from the decayed leaves which are usually not skeletonized.

Most of the sites studied are in forested terrain, but Julian Lewis (pers. comm.) reports hypotelminorheic like sites in non-forested areas in the American Midwest and Rodrigues et al. (2012) reported a troglomorphic amphipod from perched aquifer in a wetland area, which has recently been deforested.

Some hypotelminorheic habitats harbour a rich fauna. The best studied area for hypotelminorheic fauna is the lower Potomac, where over 100 seeps have been sampled. The fauna includes five troglomorphic species of the amphipod *Stygobromus,* one *Caecidotea* isopod species, retaining pigment and small eyes but limited to seeps, and one *Fontigens* snail species, also with some pigment but limited to seeps and caves (Table 10.1). There are four species often found in seeps, but occurring in surface habitats as well.

Using direct current resistivity techniques, Staley (2016) found that drainage areas of hypotelminorheic sites in the Washington, DC, area ranged up to 2 ha in size, and that the clay beds could be up to 10 m in depth. It is not known if any species occupy the deeper clay beds. Pipan and Culver (2013) showed that hypotelminorheic sites were indeed richer in organic carbon relative to other subterranean habitats, but that rather than being uniformly higher, there were temporal spikes in organic content (Table 10.2). Unpublished studies by Daniel Fong show that the presence of troglomorphic amphipods in seeps is highly temperature dependent, indicating that they are actively foraging in the spring (Pipan et al. 2012). Current velocities in hypotelminorheic habitats and associated seeps are not great enough to dislodge the organisms. Gilbert et al. (2018) demonstrated that amphipods regularly found in seeps burrow into clay in the laboratory when open surface water is removed. We found amphipods in clay cores taken at hypotelminorheic sites in Nanos Mountain in Slovenia (unpublished).

In spite of the many environmental differences with caves (they really only share darkness as a commonality), there have been no demonstrations of morphological differences between cave and hypotelminorheic species. Culver et al. (2010) looked at body size, relative antennal length, and antennal segment number in *Stygobromus* amphipods found in caves and seeps, and found no differences between the two groups.

Although the definition of the hypotelminorheic given above is relatively clear, determining the location of hypotelminorheic sites in the field is not that straightforward. Small wet spots or puddles may be the result of seepage of groundwater, or simply the retention of rainwater in a spot of poor drainage. Keany et al. (2018) attempted to find a physico-chemical signature for small water bodies that contained hypotelminorheic species compared to sites that did not. Their study area was parklands in the Anacostia region of Washington, DC (Fig. 10.2). Seven environmental parameters—temperature, temperature deviation from average, radon, conductivity, DO, pH and depth of clay layer—could not distinguish between inhabited and uninhabited sites. Radon is an indirect measure of the age of the water. Sample size was relatively large (n = 130), suggesting that the lack of differences was not likely the result of small sample sizes. This is reinforced by the demonstration that the two main amphipod inhabitants—*Crangonyx shoemakeri* and *Stygobromus tenuis*—occurred in seeps with different physico-chemical characteristics. Based on stepwise logistic

Table 10.1 Species of amphipods, isopods and gastropods found in seeps in the lower Potomac River drainage and environs of Washington, DC. Modified from Culver and Pipan (2008). Ecological category refers to obligate subterranean dwellers (stygobionts) and facultative subterranean dwellers (stygophiles)

	Species	Ecological category	Hypotel-minorheic specialist	Troglomorphic
Amphipoda	*Stygobromus sextarius*	Stygobiont	Yes	Yes
	Stygobromus kenki	Stygobiont	Yes	Yes
	Stygobromus hayi	Stygobiont	Yes	Yes
	Stygobromus tenuis potomacus	Stygobiont	No	Yes
	Stygobromus pizzinnii	Stygobiont	No	Yes
	Crangonyx floridanus	Stygophile	No	No
	Crangonyx shoemakeri	Stygophile	No	No
	Gammarus minus	Stygophile	No	No
	Crangonyx palustris	Accidental	No	No
	Crangonyx serratus	Accidental	No	No
	Crangonyx stagnicolous	Accidental	No	No
	Gammarus fasciatus	Accidental	No	No
Isopoda	*Caecidotea kenki*	Stygobiont	Yes	Weakly
	Caecidotea nodulus	Stygophile	No	No
Gastropoda	*Fontigens bottimeri*	Stygobiont	Yes	Weakly

Table 10.2 Dissolved organic carbon (mg/L) for seeps, small springs, and hyporheic sites on Nanos Mountain, Slovenia. From Culver and Pipan (2014)

	Hyporheic	*Niphargus* seep	Other seeps	Small springs
Mean	2.77	4.52	1.63	2.72
Standard deviation	3.79	3.72	1.40	2.48
Minimum	0.41	0.83	0.4	0.13
Maximum	10.44	9.89	5.53	7.07
n	6	7	11	12

regression, *Stygobromus* preferred cooler water with lower conductivity and *Crangonyx* preferred warmer waters. Unoccupied sites may truly be unoccupied, or it may be that amphipods were present but not detected. A promising new way of sampling, one that should minimize false negatives, is to look for environmental DNA (eDNA) in water samples, a technique which does work in this habitat (Niemiller et al. 2017).

10.2.1.2 Epikarst

In 1973, Mangin used the term “epikarst” to describe the uppermost zone of karst, where there was enlargement of cavities and solution tubes, that greatly increases its secondary porosity, and was the active zone of transfer between karst and the overlying soil. Since that time, epikarst has become recognized as an important zone of water storage, of speleogenesis, and an important biological habitat (Williams 1983; Pipan 2005). It was the subject of an interdisciplinary symposium organized by the Karst Waters Institute (Jones et al. 2004) and review by Williams (2008a, b) provided a hydrogeological perspective on epikarst.

Wherever there is soil covering base rock, there is a zone of contact between the rock and the soil, typically consisting of an unconsolidated layer of rock mixed with soil—the regolith. This zone, given appropriate pH and water availability, is modified by the dissolution of rock into small cavities and channels. A commonly used definition is that agreed upon in the epikarst interdisciplinary symposium:

> Epikarst is located within the vadose zone and is defined as the heterogeneous interface between unconsolidated material, including soil, regolith, sediment, and vegetative debris, and solutionally altered carbonate rock that is partially saturated with water and capable of delaying or storing and locally rerouting vertical infiltration to the deeper, regional, phreatic zone of the underlying karst aquifer (Jones et al. 2004).

Epikarst is nearly universal in its occurrence (Gabrovšek 2004), although Kresic (2013) suggests it is not an aquifer in the sense of water available for human consumption, and questions the adequacy of empirical evidence. A sketch of epikarst and its connection to the underlying karst is shown in Fig. 10.3.

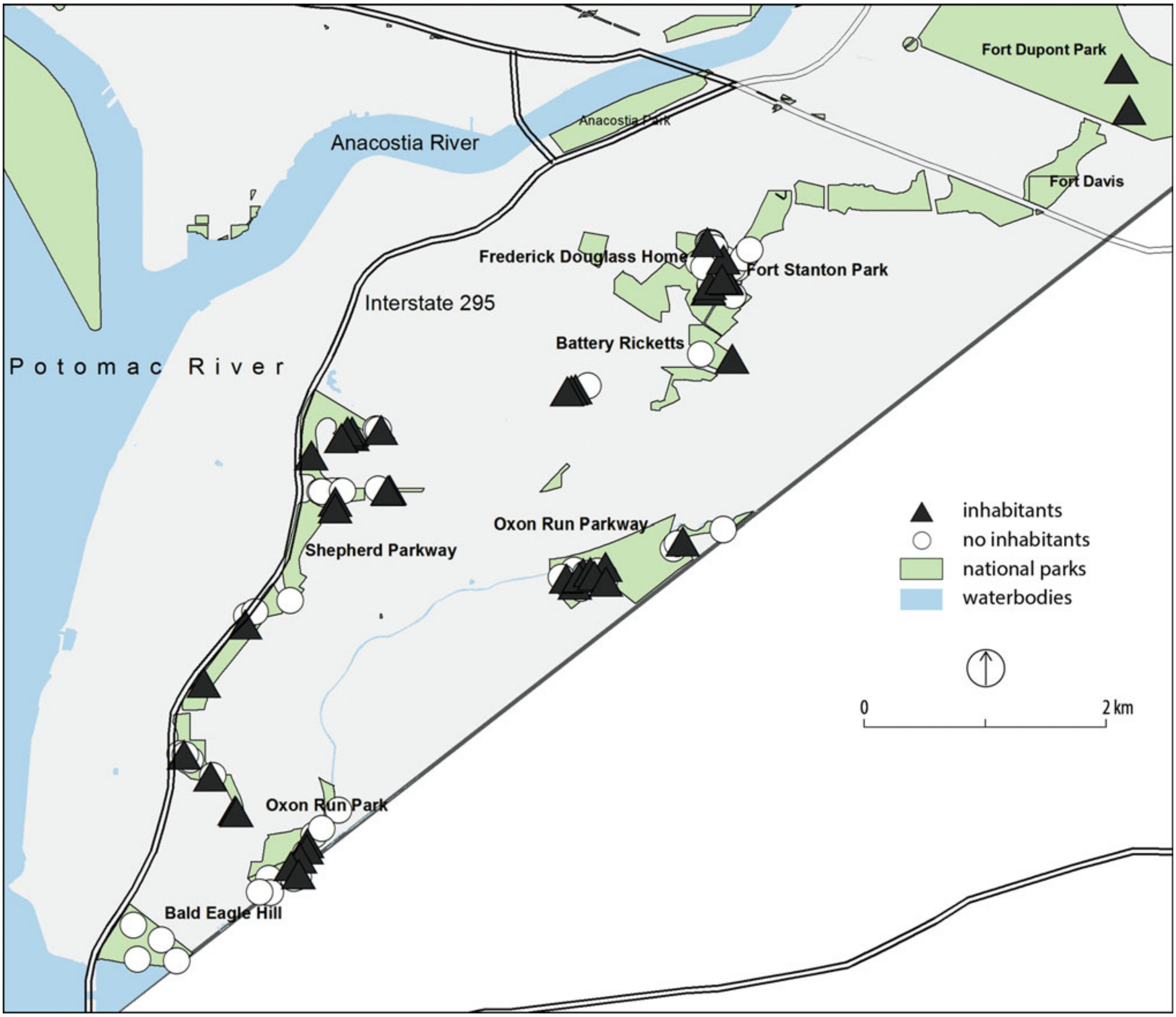


Fig. 10.2 Map of seeps in National Capital Parks East in Washington, D.C. Some sites are not visible because of overlap. From Keany et al. (2018)

Prior to Pipan's (2005) pioneering study of the epikarst fauna, information on the fauna was based entirely on sampling the inhabitants of drip pools, but this is a highly biased estimate of the epikarst fauna (Pipan et al. 2010). Pipan (2005) developed a device that continuously sampled water dripping from cave ceilings. The microcrustaceans (copepods but other groups as well) that are dislodged by the current are collected. This may be a biased sample as well because different species may be dislodged with differing probabilities, but it is unaffected by other sources of water. Her initial study, and several since then that are based on this sampling technique, found an astonishing array of species, especially in Slovenia (Table 10.3). The number of epikarst copepod species in some caves, e.g. Županova jama and Škocjanske jame in Slovenia, exceeds the number of stygobionts known from other aquatic habitats in the cave. Even in those caves where only two or three epikarst copepod species were found, these species represent a significant fraction of the total stygobiotic diversity known from the cave.

Other species are also found in epikarst drips. These include the little studied epikarst Ostracoda and Amphipoda. Culver et al. (2010) report that of 56 species of the subterranean amphipod genus *Stygobromus* known from the eastern United States, fully half (28) are limited to epikarst. Given the small diameter of epikarst habitats, it is not surprising that epikarst *Stygobromus* are smaller in size than species from other habitats. Overall, taxa small in size such

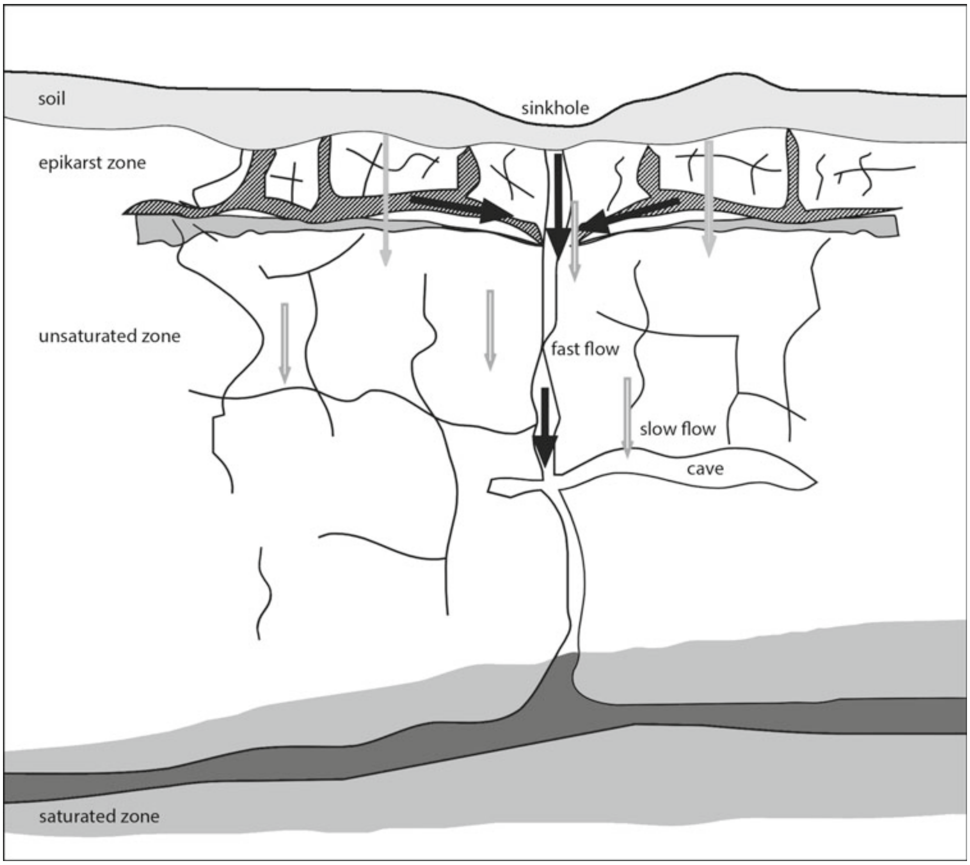


Fig. 10.3 Conceptual model of epikarst. Grey arrows indicate the direction of slow water flow and black arrows indicate faster flow paths. From Pipan (2005), used with permission of Založba ZRC, ZRC SAZU

as Copepoda are over-represented in epikarst relative to taxa with larger species, the largest of which, e.g. Decapoda, are entirely missing.

Since epikarst organisms are sampled either in drip pools or in dripping water itself, it may seem like a contradiction in terms to consider a terrestrial epikarst community. Since epikarst is well above the water table, and the amount of water storage in epikarst varies, then it follows that it includes some air-filled habitat. Very little is known about this habitat because the only terrestrial animals collected are those which are flushed out by moving epikarst water. Terrestrial species are usually much less common in epikarst habitats although all studies of the drip fauna have found terrestrial species (Culver and Pipan 2014). Only in the cave Huda luknja in Slovenia was the terrestrial fauna richer in species and more abundant than the aquatic epikarst fauna (Table 10.4). The reasons for the rich terrestrial epikarst found in this cave are not clear, but the geographic position of Huda luknja is such that overall, the subterranean terrestrial fauna is likely richer than the aquatic because the main climate factor forcing species in aquatic caves—the Messinian salinity crisis—was not at play in this cave. In contrast, Pleistocene effects, which often force the terrestrial fauna into caves (Culver and Pipan 2010), were likely to be strong.

Only for Slovenia are there sufficient data on epikarst species to attempt an explanation for the geographic patterns of epikarst species richness (see Table 10.3). To this end, Pipan et al. (2018) analyzed the geographic pattern of data from 81 drips in 13 caves. Overall, species richness was greatest in the Dinaric karst rather than the Alpine and isolated karst, a pattern repeated in other subterranean fauna. Within a cave, it was typically the case that one or sometimes drips had many more species than the other drips. For example, in Županova jama, one drip had ten of the 13 species known from the cave, and no other drip had more than five. Overall, most of the species richness was the result of differences between drips, caves and regions, rather within drip diversity. Overall, within drip diversity accounted for three species, different drips in a cave another three, different caves in a region six species, and different regions accounting for the remaining 18 species (Fig. 10.4). The

Table 10.3 Number of obligate subterranean dwelling copepod species found in epikarst drips. Data from Meleg et al. (2011), Pipan (2005), Pipan et al. (2006, 2018), Brancelj (2015) and Papi (2016)

Country	Cave	Number of epikarst stygobiotic copepod species
Italy	Grotta A del Ponte di Veja	4
	Covolo della Croce	3
	Grotta di Roverè Mille	2
Romania	Peştera Ciur Izbuc	4
	Peştera Ungurului	3
	Peştera Vadu Crişului	2
	Peştera cu Apă din Valea Leşului	2
	Peştera Doboş	2
Slovenia	Županova jama	13
	Škocjanske jame	8
	Pivka jama	8
	Dimnice	8
	Črna jama	8
	Velika pasica	7
	Zguba jama	6
	Postojnska jama	4
	Jama pod Babjim zobom	3
	Pološka jama	3
	Zadlaška jama	2
	Snežna jama	2
	Huda luknja	2
United States	Organ Cave	7

Table 10.4 Number of aquatic and terrestrial animals collected in dripping water, arranged by frequency of terrestrial species. Caves are in Slovenia unless otherwise indicated. From Culver and Pipan (2014)

	Terrestrial	Aquatic	Frequency of terrestrials
Huda luknja	78	46	0.63
Organ Cave, USA	176	212	0.45
Postojnska jama	11	27	0.29
Grotte du Cormoran, France	755	2391	0.24
Peştera Vadu-Crişului, Romania	2	11	0.15
Peştera Ungurului, Romania	29	326	0.08
Snežna jama na planini Arto	11	198	0.05
Peştera Vântului, Romania	3	55	0.05
Dimnice	8	158	0.05
Črna jama	16	348	0.04
Planinska jama	10	335	0.03
Škocjanske jame	8	525	0.02
Županova jama	7	462	0.01
Pivka jama	9	795	0.01

between site diversity (β-diversity) was largely due to replacement of species geographically, but nestedness (the occurrence of hotspots) was important as well. Besides the intrinsic interest in epikarst diversity patterns, it can also serve as a model for the study of subterranean biodiversity in general, because drip sampling at the level done by Pipan (2005 and subsequent studies) captures all or nearly all the species present, according to accumulation curves and other measures of sampling completeness (Pipan and Culver 2007; Pipan et al. 2018).

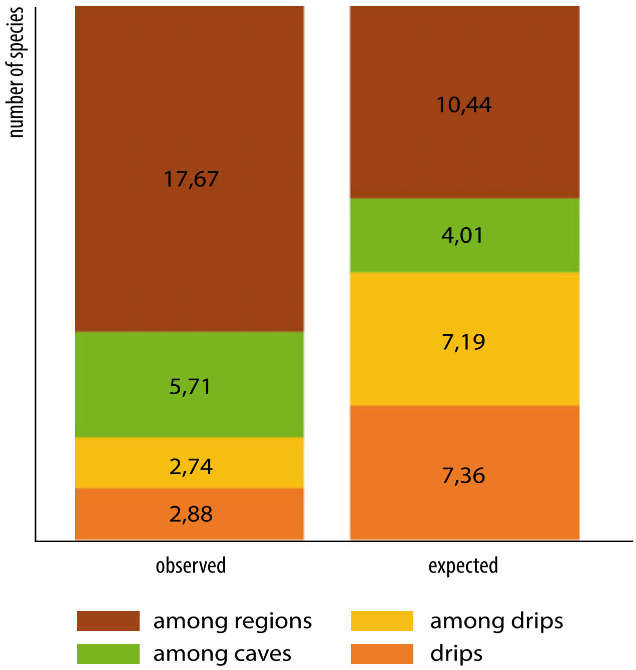


Fig. 10.4 Relative contribution of within drip (α-diversity), among drip, among cave and among region diversity (all β-diversity) to the overall diversity of 30 Slovenian epikarst copepod species, relative to random expectation. From Pipan et al. (2018)

10.2.1.3 Hyporheic

In common with soil, study and interest in the hyporheic are not limited to those researchers of subterranean life. In the case of the hyporheic, a term coined by Orghidan (1959), it is important in riverine ecology. The recognition of the importance of the hyporheic in the lotic biology originated with the discovery of Stanford and Gaufin (1974) that the enigmatic nymphal stage of the stonefly *Peraperla frontalis* was spent in sediments beneath and lateral to the streams from which the adults emerged. The hyporheic is an integral part of all riverine ecosystems, and Boulton and Hancock (2006) demonstrated that rivers and streams are groundwater-dependent ecosystems. Over the years, this has resulted in increased attention to the hyporheic as one of the keys to river and stream ecosystem health (e.g. Buss et al. 2009).

There are other aquatic SSHs that share with the hyporheic not only proximity to the surface but also a small habitat diameter. These include the sediments of lake margins, and other water-saturated sand and gravel habitats close to the surface. Riverine biologists (e.g. Krause et al. 2011) emphasize the ecotonal nature of the hyporheic, between surface and groundwater, from a subterranean perspective, both the hyporheic and groundwater are aphotic habitats. Malard et al. (2002) provided a very useful diagram of the different ways the hyporheic and phreatic are connected (Fig. 10.5).

Gibert et al. (1990) and Vervier et al. (1992) also championed the ecotone perspective for the hyporheic, and the subterranean–surface contact in general. The hyporheic is what they call a lotic ecotone, where there are large-scale transfers of energy, materials and animals. The direction of transfer is two-way, and varies both spatially and temporally. In a typical stony-bottomed stream, there are areas of upwelling and downwelling (Fig. 10.6) that are the main areas of transfer. Water and nutrients thus spiral between surface and subsurface flows. The vertical distribution of some species is limited to the hyporheic, others to the phreatic, and yet others to both (Gibert et al. 1990).

Hyporheic habitats are widespread, occurring in the tropics and throughout the temperate zone (Culver and Pipan 2014). Stony-bottomed streams with a gravel hyporheic require a source of rocks, so flat areas tend to have sand or mud hyporheic zones, such as in much of the Midwest of the USA. The bulk of studies of the hyporheic, especially from a subterranean perspective, are of European rivers, especially the Rhône and its tributaries near Lyon, France, and the Danube wetlands near Vienna, Austria. Other well-studied sites include the Never Never River in Australia, Sycamore Creek in Arizona, USA, and the Flathead River in Montana, USA.

The invention of a pump that allows collection and filtration of hyporheic water, the Bou-Rouch pump (Bou and Rouch 1967), made possible the study of the hyporheic fauna. The fauna of the hyporheic includes troglomorphic species, other species known only from the hyporheic and phreatic but apparently unmodified morphologically, and yet other than that occurs seasonally (Malard et al. 2003).

The hyporheic can be remarkably diverse. Formed by a meander arm, the Lobau wetlands, an alluvial aquifer, are part of the flood plain of the Danube River near Vienna, Austria, and comprise the Danube Flood Plain National Park. A small 900 m^2 area of this flood plain, called Lobau C (Pospisil 1994), was monitored and sampled intensively. Loosely packed gravel, alternating with a thin layer of finer sediments, extends from 4 to 8 m beneath a thin soil cover. In Lobau C, 27 species were found, 11 of them troglomorphic.

Because of the small pore size of interstitial habitats, species have unique features of miniaturization, segment reduction, and fewer spines and bristles, that contrast with the morphology of cave animals. Coineau (2000) suggested that this is the result of progenesis, precocious sexual maturation. Miniaturization can be extreme, as in the case of the amphipod *Ingolfiella* which is less than 1 mm in length. Ingolfiellids from other habitats are often more than 10 mm in length. Oddly, a relatively large number of large-sized stygobiotic species occur in hyporheic habitats, especially amphipods. Some of these species are quite large. For example, *N. rhenorhodanensis* from hyporheic habitats is

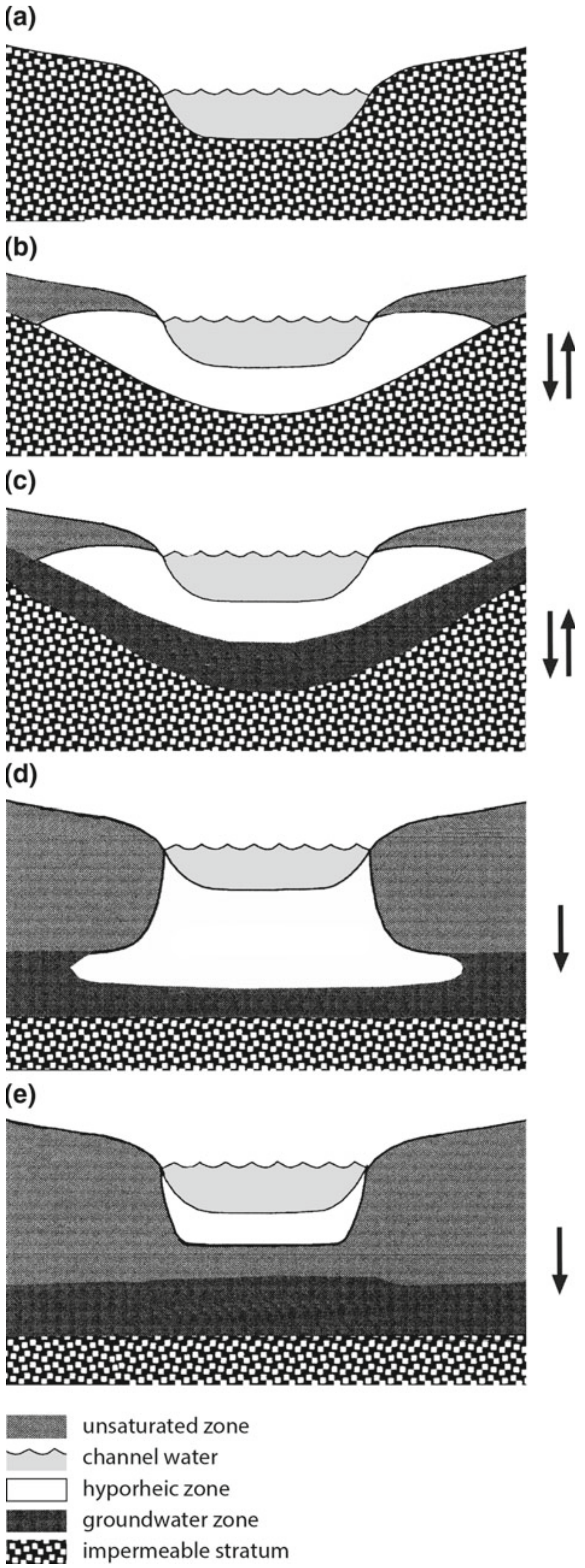


Fig. 10.5 Conceptual cross-sectional models of surface channels and beds showing relationships of channel to hyporheic, groundwater and impermeable zones. Thick arrows indicate direction of water fluxes between surface stream and underlying reservoirs. **a** No hyporheic zone, **b** hyporheic zone created only by advected channel water, **c** hyporheic zone created by advection by both channel water and groundwater, **d** hyporheic zone created only by infiltration of channel water beneath the stream bed (no parafluvial flow), **e** perched hyporheic zone created only by infiltration of channel water beneath the stream bed. From Malard et al. (2002), used with permission of John Wiley & Sons

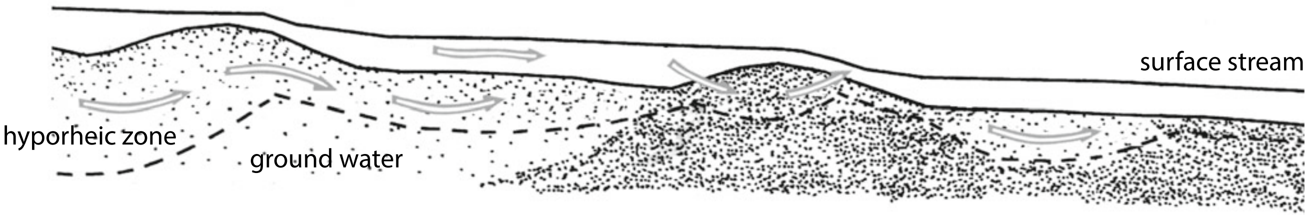


Fig. 10.6 Surface-subsurface hydrological exchanges in the hyporheic zone induced by spatial variation in stream-bed topography and sediment permeability. Dark areas represent fine sediments. Arrows indicate direction of flow and their width corresponds to flux rate of advected channel water with the sediments. Downwellings bring both organic matter and oxygen to the hyporheic zone. Modified from Malard et al. (2002), used with permission of John Wiley & Sons

greater than 10 mm but Ginet (1985) indicated that the body is thin and the appendages relatively short. Thinness and appendage shortening may actually be more important modifications for life in a small pore-size environment than body size itself.

10.2.1.4 Calcrete Aquifers

Calcrete aquifers are features of evaporite karst, and their fauna has been extensively studied in Western Australia. Depending on the geological context, calcrete aquifers may be very shallow (<5 m in the Yilgarn) but others may be tens of metres deep (in the Pilbara). There is a little surface manifestation of the calcrete aquifers although there typically is a playa (a dry lake that may periodically fill with water).

Development of calcrete aquifers depends on temperature and precipitation. Mann and Horwitz (1979) also suggested that periods of concentrated but rare rainfall lead to the development of bigger calcrete aquifers because of increased filtration of water. High evapotranspiration is also important for the direct chemical precipitation of calcium carbonate. Therefore, there are many actively precipitating calcrete systems that are very shallow, occurring at depths of less than 5 m below the surface. Overall, precipitation in calcrete-forming areas is less than 200 mm and potential evapotranspiration (PET) is greater than 3000 mm per year.

Near the entrance to the playa, a chemical delta forms where the calcrete unit broadens. Humphreys et al. (2009) described this system as an estuary with low salinity water near the intake (500–2000 mg/L TDS) that is alkaline and rich in bicarbonate. As it moves downstream, it becomes less alkaline and much more saline (20,000 to > 300,000 mg/L TDS). Morgan (1993) concluded that a separate geochemical system is associated with the formation of each salt lake along a palaeo-river. Each of these groundwater estuaries is connected to a separate calcrete and isolated from other calcrete aquifers, even those in close proximity, by strong salinity gradients.

The fauna of calcrete aquifers is accessible only by sampling the water from wells that have been drilled as a result of water and mineral prospecting. The connection with the surface is one-way, via infiltrating water. There are no exits. The source of organic carbon is unknown but may be from infiltrating water (which is itself low in organic carbon) or perhaps from chemoautotrophy (Culver and Pipan 2014).

Species richness in calcrete aquifers is very high. For example, there are a total of 28 stygobionts in three calcrete aquifers associated with Lake Way, and all within 20 km of each other. Fourteen are known from a single aquifer and the number in each aquifer ranges from 9 to 17 (Humphreys et al. 2009). Since there are hundreds of such aquifers, the total Australian calcrete aquifer fauna may number in the thousands. Calcrete aquifers have served as important evolutionary models of colonization and speciation as a result of climate forcing (in this case drying during the Pliocene; Leys et al. 2003), allopatric and micro-allopatric speciation (Guzik et al. 2009; Leijs et al. 2012), and the evolution of limiting similarity as a result of competition (Vergnon et al. 2013).

10.2.1.5 Other Aquatic SSHs

There are other aquatic subterranean habitats where organisms modified for subterranean life may occur. Pentecost (2005) reported a specialized subterranean fauna in travertine, and there are habitats associated with wetlands that have never been investigated in terms of subterranean organisms, or at least we are unaware of any such reports. Likewise, it is possible that such organisms may be found in vernal pools, and of course, some vernal pools may turn out to have connections with shallow groundwater. Leijs et al. (2009) report on a device designed to sample groundwater upwellings in wetlands, but it appears to have been little used.

Springs are ecotones between groundwater and surface water, and typically have their own characteristic fauna (Botosaneanu 1998). There are many reports of stygobionts collected from springs in karst areas in Europe (but curiously, not in the United States). It is generally assumed that these organisms are washed out of aphotic, subterranean habitats, but it may well be that they live in the dimly lit springs themselves. Mejía-Ortíz et al. (2018) report a

Table 10.5 Species list for erosional MSS site in laurel forest in Teno, Tenerife, Canary Islands. Data from Pipan et al. (2011)

Taxa	Troglomorphic	Edaphobionts	Generalists
Arachnida			
Acari		4	
Araneae	3		4
Opiliones			1
Pseudoscorpionida	1	1	2
Hexapoda			
Collembola		7	
Diplura		1	
Insecta			
Blattaria	2		
Coleoptera	3	5	21
Hemiptera			2
Diptera			3
Hymenoptera			6
Chilopoda		1	
Diplopoda	1	3	1
Crustacea: Isopoda			1
Total	10	22	41

number of terrestrial organisms without eyes or pigment living in an extensive twilight zone cave.

10.2.2 Terrestrial Habitats

10.2.2.1 Epikarst

Epikarst is best known as an aquatic habitat because it was first described in relation to its storage capacity of water (Mangin 1973) and because the only way to sample the fauna is by filtering dripping water. Nevertheless, since it is only a partially filled aquifer whose water volume varies over time, there is terrestrial habitat in the epikarst. All samplings of drips have yielded terrestrial species (Table 10.3). Among sampled caves, only in the cave Huda luknja in Slovenia is the terrestrial fauna richer in species and more abundant than the aquatic epikarst fauna (Pipan et al. 2008). At least one subterranean specialist species was noted in two studies—a Collembola in the genus *Arrhopalites* in Grotte du Cormoran in France (Gibert 1986) and the beetle *Otiorhynchus anophthalmus* in Huda luknja in Slovenia (Pipan et al. 2008). Nothing more is known about the terrestrial epikarst fauna beyond the fact that it is present, because of our inability to sample it directly.

10.2.2.2 MSS

The term “milieu souterrain superficiel” (mesovoid shallow substratum in English) was coined by Juberthie et al. (1980) for what they believed to be dispersal corridors for troglobionts that were found in isolated karst areas (see also Ueno 1977). It was originally described as moss and soil covered talus slopes with intermediate-sized spaces among the rocks. The early work of Crouau-Roy (1987) showed that it was more than a dispersal corridor, and a habitat, in the sense of containing source populations, particularly of beetles in the genus *Speonomus*. Gers (1998) showed that the MSS fauna in the Pyrenees Mountains sites that he, Juberthie, and Crouau-Roy studied, was closely connected to the soil fauna, because many soil specialists were also found in the MSS. It is interesting to note that the original impetus for studying the MSS, i.e. the search for a dispersal corridor, would in a contemporary context probably be resolved by looking cryptic speciation (Trontelj et al. 2009) in the different karst massifs.

The term MSS proved to be a very useful one, and it was expanded to cover other terrestrial habitats of intermediate pore size. These include a variety of volcanic MSS habitats, included clinker. Volcanic MSS has proven to be very rich in species in the Canary Islands (Medina and Oromí 1990; Oromí and Martín 1992; Pipan et al. 2011). An example of species composition and richness in a Canary Island MSS site is shown in Table 10.5. In this forested MSS site, there were 10 troglomorphic species, 22 soil specialists and 41 other species, demonstrating not only the richness of the specialized subterranean fauna but also the importance of the soil fauna in MSS sites. The MSS remains unstudied for Hawaii, which has a rich lava tube fauna (Howarth 1972). However, Howarth (1983) mentions the importance of

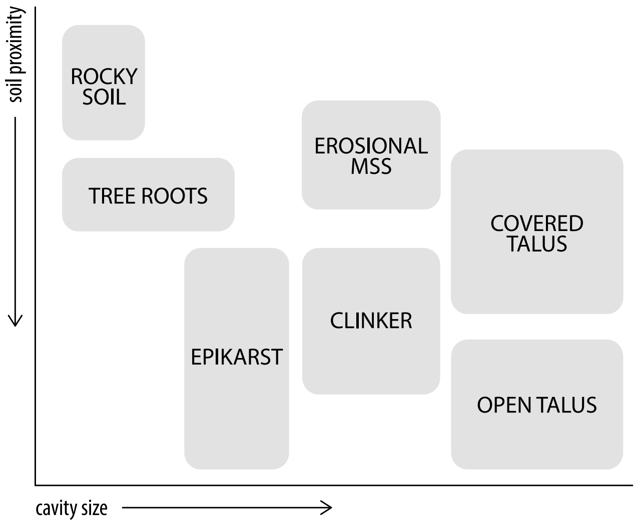


Fig. 10.7 Conceptual diagram of different terrestrial shallow subterranean habitats. The position of the rectangles indicates the typical range of pore sizes and connectivity to the soil. From Culver and Pipan (2014), used with permission of Oxford University Press

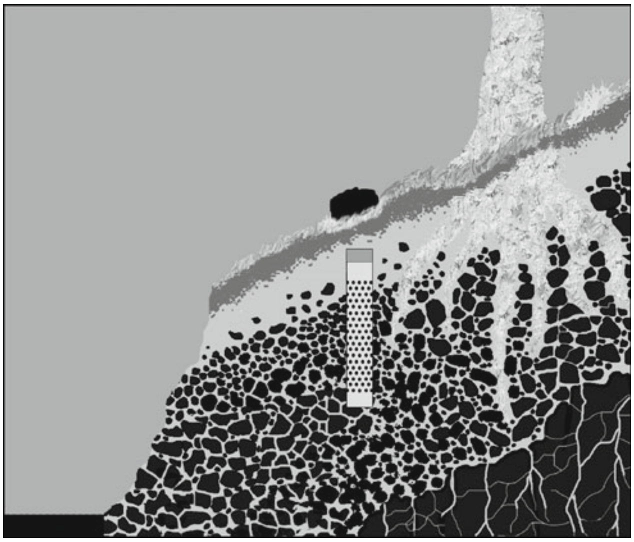


Fig. 10.8 An MSS trap installed in the MSS close to a road cut. From López and Oromí (2010)

"mesocaverns," roughly the equivalent of MSS, in the evolution of the lava tube fauna. Růžička (1990) demonstrated the uncovered scree and talus slopes also contain species with troglomorphic features that are unique to such habitats. There are undoubtedly other such subterranean terrestrial habitats with reduced eyed, specialized species. Epikarst is in fact such a habitat—it just has a prior name. Culver and Pipan (2014) placed some of these MSS like habitats along the axes of soil proximity and pore size (Fig. 10.7).

Ortuño et al. (2013) suggested a classification of MSS habitats into four categories:

- bedrock MSS,
- colluvial (slope) MSS,
- alluvial MSS,
- volcanic MSS.

While the first three categories are straight forward and reflect the origin and topographic setting of the MSS, the last term actually combines three for volcanic sites, and so perhaps the fourth category should be subsumed under the other three. The most extensive study of the MSS fauna to date is that of Giachino and Vailati (2010) on Italian MSS sites, and they provide numerous case studies. Mammola et al. (2016) provide an extensive summary of the more than 200 MSS studies to date.

Sampling the MSS is a challenge. The simplest sampling technique is some version of "dig and search" (Mammola et al. 2016), especially turning over large boulders. Buried pitfall traps have been extensively used since the first studies of Crouau-Roy et al. (1992) and Gers (1998). This involves habitat destruction and reconstruction in order to position the trap. López and Oromí (2010) describe a trap that once inserted can be sampled multiple times (Fig. 10.8). According to Mammola et al. (2016), this has become the standard.

Open scree slopes are a particularly difficult habitat to sample because the slopes are unstable and it is difficult to create a hole in which to put a pitfall trap. Růžička (1982, 1988) designed a trap to be left for extended periods by drilling a hole in small board and then placing the pitfall trap in the board. To counter the problem of instability of the rocks, he uses a set of nested rings that allow the making of an initial hole in the talus slopes.

10.2.2.3 Soil

In spite of the tradition of not including as a subterranean habitat (see above), we include it for several reasons (Culver and Pipan 2014). First, and most obvious, it is an aphotic habitat, at least below a few cm in depth. For example, Ciani et al. (2005) reported that 99% of the light at a wavelength of 700 nm disappeared at depth of between 120 and 300 µm. Second, the soil and by implication its fauna is closely connected to other subterranean habitats, especially the MSS (see Table 10.5). Coiffait (1958), a pioneer in the study of the soil fauna as a subterranean fauna, viewed soil as the central subterranean habitat (Fig. 10.9). The soil may be a staging habitat for colonization of larger diameter subterranean sites, especially the MSS.

Of course, it is true, as is the case of the hyporheic, that much of the interest and study of the habitat is unconnected to its being a subterranean habitat. These studies include understanding soil fertility, as an example Sket's argument

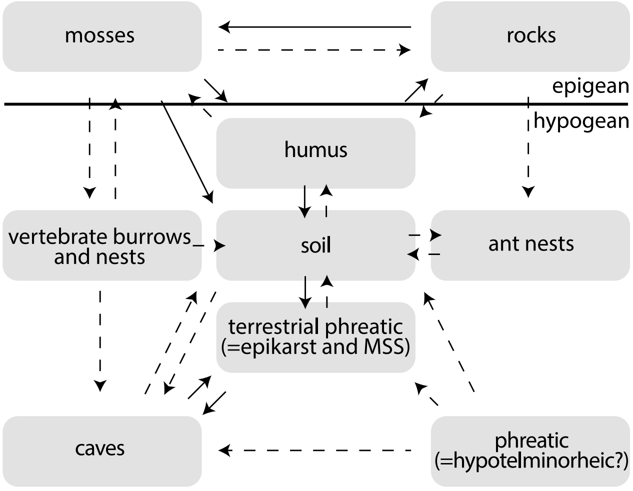


Fig. 10.9 Relationships between various shallow subterranean habitats and surface habitats, with a focus on the soil. Modified from Coiffait (1958) by Culver and Pipan (2014), and used with permission of Oxford University Press

(2004) that soil is too rich in organic nutrients to be a subterranean habitat is unconvincing, especially in light of the fact other subterranean habitats can be rich in organic carbon.

The morphology of soil-dwelling invertebrates is quite different from that of cave-dwelling invertebrates (Culver and Pipan 2014). While they share eye and pigment loss and reduction, soil specialists (edaphobionts) tend to be miniaturized and/or elongated, with reduced appendage lengths (Culver and Pipan 2014). Many speleobiologists, especially those studying Collembola and other groups that inhabit both soil and caves, recognize this fundamental morphological distinction. However, some (e.g. Halse and Pearson 2014) lump all subterranean fauna into troglofauna, with differentiating the components.

In his extensive study of the soil fauna of the Pyrenees, Coiffait (1958) found a rich invertebrate fauna—nearly 21,000 individuals from a total 0.8 m^3 of soil taken from 100 sites. The faunal composition is shown in Fig. 10.10. Among the 194 species of beetle that he found, 78 were edaphobionts, soil specialists found nowhere else. These species showed eye and pigment reduction, as well as appendage reduction. None of the species he found were cave-dwelling species, and they were likely too large and too non-compact to occur in soil. However, the reverse was not true. Edaphobionts were common in MSS sites in the same region (Crouau-Roy 1987) and in an MSS site in the Canary Islands (Table 10.5). In these habitats, both morphotypes can occur. The soil fauna does show a sharp decline with depth (Coiffait 1958; Culver and Pipan 2014), presumably as a result of reduced organic carbon and perhaps, soil compaction.

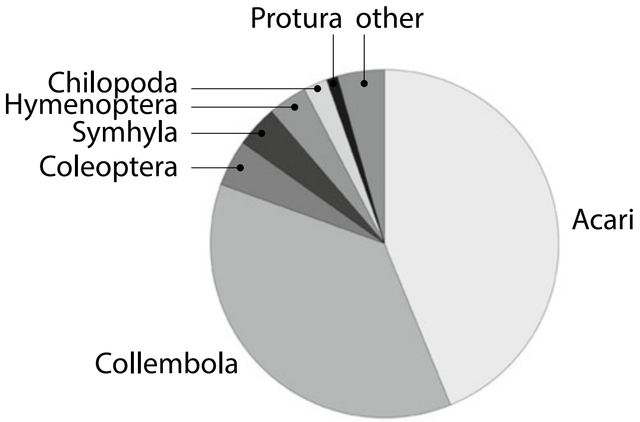


Fig. 10.10 Pie diagram of species composition of soil samples from 100 sites in the Pyrenees Mountains. Compiled from Coiffait (1958) by Culver and Pipan (2014). Used with permission of Oxford University Press

10.2.2.4 Lava Tubes

Typically, lava tubes form very close to the surface, and are long tubes of more or less constant diameter. Kazumura Cave in Hawaii, is the longest known lava tube, with 65 km of passage and 101 entrances, and rarely if ever is more than 10 m below the surface, even though its total depth is greater than 1000 m (www.caverbob.com). Lava tube densities, at least in Hawaii, are very high, up to 14 caves/km^2 in the Kiholo Bay (Medville 2009). La Cueva del Viento in the Canary Islands, one of the world most diverse caves with respect to terrestrial troglobionts (Culver and Pipan 2013), is over 20 km long but is at a depth of 2.5–7 m from the surface. The shallowness of lava tubes is a result of the way that they form. Basically, lava flows cool on the surface, and the lava below keeps flowing, creating a void. Often, these lava flows are sequential with younger flows going beneath older flows (Hon et al. 1994). There are some lava tubes that are deeper than 10 m, and some features of volcanic landscapes, including pit craters and open volcanic conduits are very deep, sometimes greater than 100 m (Palmer 2007), but most of what we know about subterranean habitats in lava is from shallow lava tubes and the MSS habitats associated with lava flows. Hence, we include them as shallow subterranean habitats, although as is the case with calcrete aquifers, there are deeper components.

In both the Hawaiian Islands and the Canary Islands, where the fauna has been best studied, roots of trees break through the roof of the lava tubes, and at least in Hawaii, they are a primary source of food, although this has not been confirmed by stable isotope studies. Whether this is the cause of the high species richness in lava tubes is unclear. Canarian lava tubes have fewer roots, shallower ceiling, older age and a much richer fauna (Fig. 10.11). While the two areas are similar regarding the major taxa present,

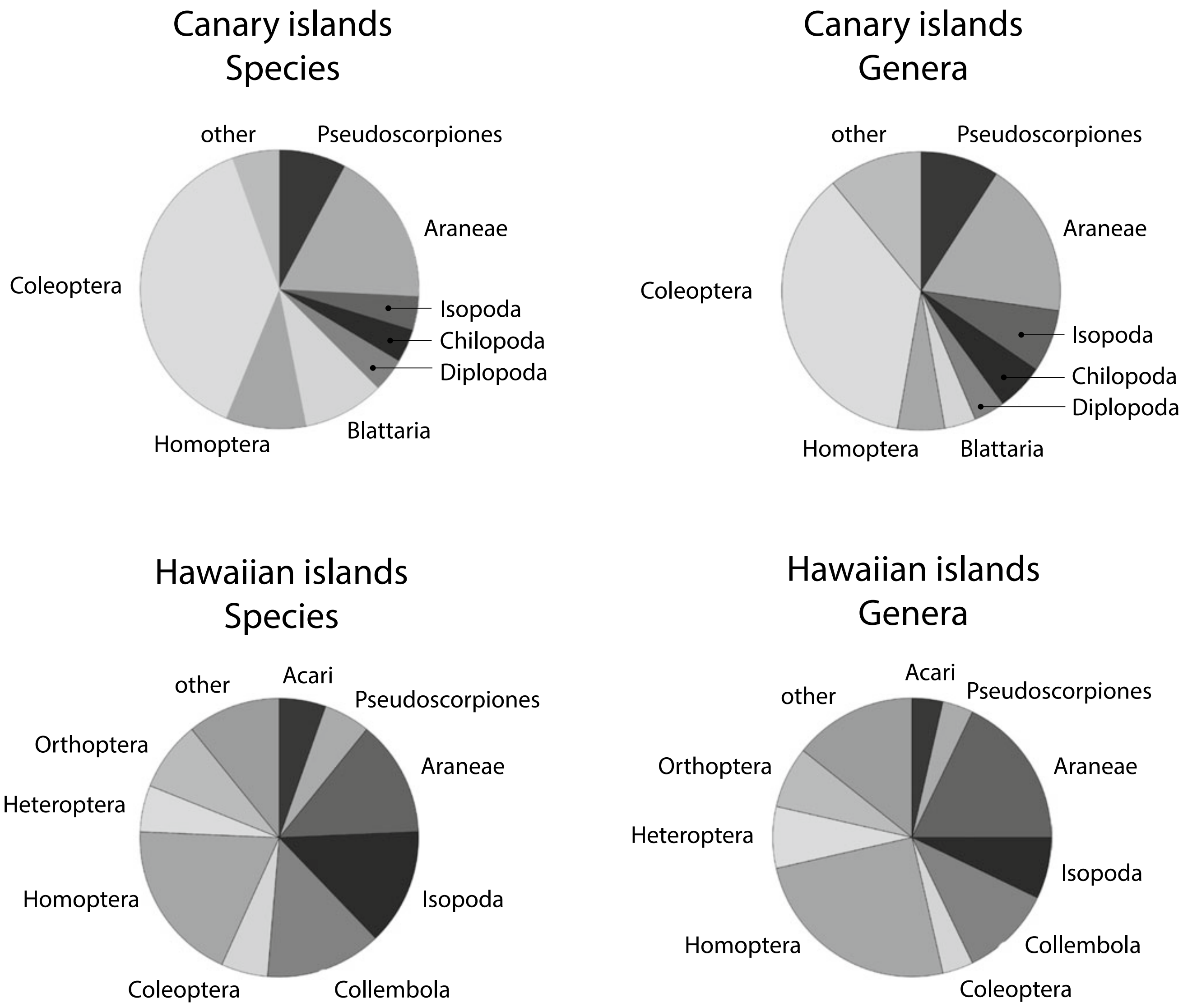


Fig. 10.11 Pie charts of species and generic richness of troglobionts from the Canary Islands and Hawaiian Islands. There were 128 species and 55 genera from the Canary Islands, and groups listed as "other" were Opiliones, Amphipoda, Collembola, Zygentoma, Dermaptera and Heteroptera. There were 37 species and 27 genera from the Hawaiian Islands, and groups listed as "other" were Amphipoda, Diplopoda, Dermaptera and Lepidoptera. Data for the Canary Islands are from Oromí and Izquierdo (unpublished), and data for Hawaii from Howarth (1987) and Hobbs and Culver (unpublished). Used with permission of Oxford University Press

Coleoptera and Araneae dominate the Canarian fauna with respect to number of species, Homoptera, Collembola and Araneae dominate the Hawaiian fauna with respect to number of species. A point of distinction of the lava tube fauna compared to other subterranean faunas is that it is likely that they actively invaded lava tubes, rather than were trapped by the vicissitudes of environmental change, a process Howarth (1987) called "adaptive shift." Since the Hawaiian Islands are quite young geologically, the island of Hawaii is 430,000 years old, and the resulting minimum speciation rates are among the fastest known (Wessel et al. 2013).

10.2.2.5 Iron-Ore Caves

Over 3000 caves have been reported from iron-ore deposits in Brazil (Auler et al. 2014). They tend to be very short and superficial, some so short they lack a dark zone. They are embedded in a matrix of fractured porous rock. While the caves are convenient collecting sites, the primary habitat for the highly endemic fauna (see Souza-Silva et al. 2011) is likely the cracks, pores and fissures of the canga and the banded iron formation. The primary agent for formation of the caves involves bioreduction of Fe(III) by iron-reducing bacteria that convert insoluble solid Fe(III) into aqueous Fe(II), allowing for the mobilization of iron and generation of voids (Parker et al. 2013). The fauna reviewed by Ferreira et al. (2018) is much richer in species than limestone caves of the same length (Souza-Silva et al. 2011). Ferreira et al. (2018) suggested that because the caves are close to the surface and have higher resource levels, they may be more diverse.

10.3 Deep Subterranean Habitats

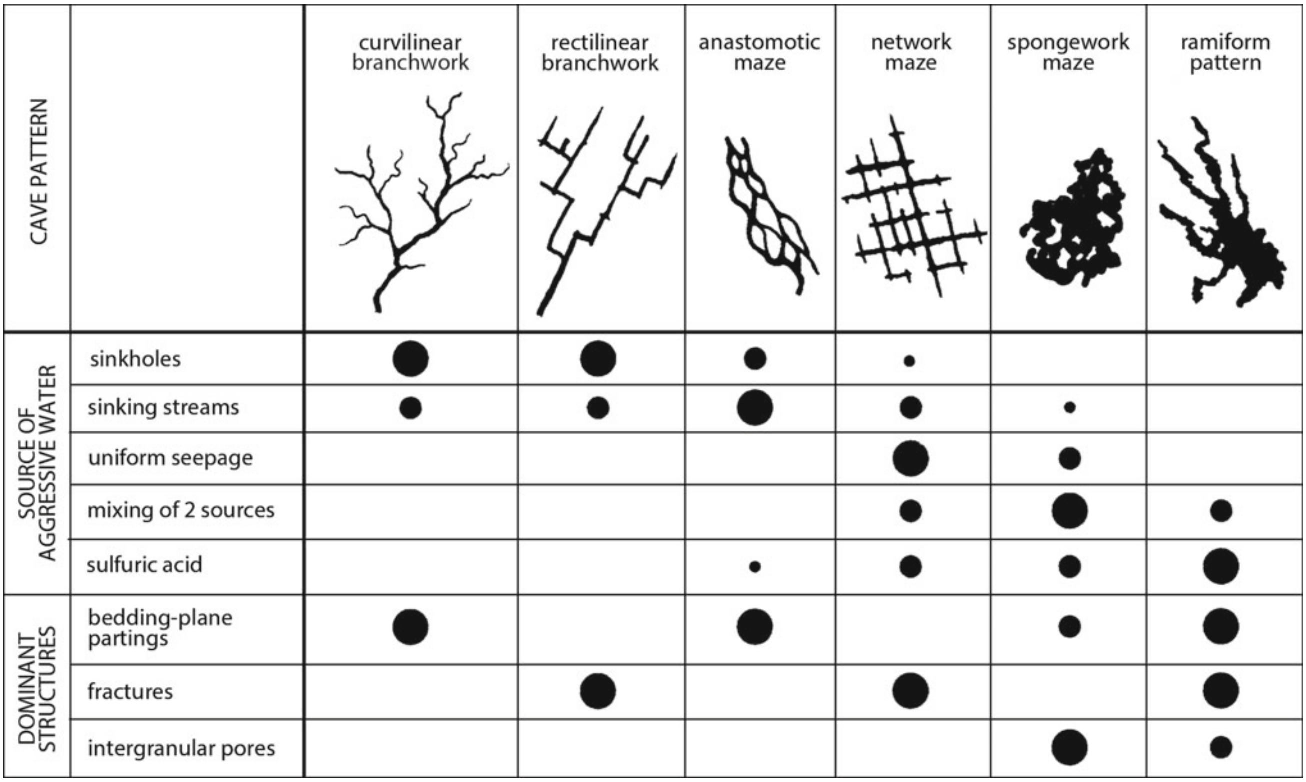
10.3.1 Caves

The incredible diversity of size, shape and geometry of caves has held the fascination of geoscientists for generations. The very diversity of caves has made generalization difficult, and a strong tradition of idiopathic description of caves persists. Nonetheless, some very insightful generalizations about caves have been put forward. The first, and one that has been known for centuries, is that caves are typically found in water-soluble rocks, especially limestone, dolomite and gypsum. This is of course because caves typically form by the action of water-borne acids, especially carbonic acid and to a lesser extent sulfuric acid. Second, the source of aggressive water, e.g. sinking streams, has a major impact on passage geometry (Fig. 10.12) (Palmer 2012). Third, much of the variety of cave passages can be generated by computer modelling infiltrating water under a hydrostatic head (Dreybrodt and Gabrovšek 2002). Fourth, under some circumstances, caves can form in almost any kind of rock, including quartzite, lava (discussed above), sandstone and even granite (White et al. 2019).

Recently, Audra and Palmer (2015) propose a general model for speleogenesis in soluble rocks, incorporating earlier models such as Ford and Ewers' (1978) three-stage model that seems to account for much if not all of the observed variability in cave development. Audra and Palmer identify four major cave types:

- juvenile, where they are perched above underlying aquicludes;
- looping, where recharge varies greatly with time, to produce epiphreatic loops;
- water-table caves, where flow is regulated by a semi-pervious cover; and
- caves in the equilibrium stage, where flow is transmitted without significant flooding.

What is much less clear, with one exception, is the connection between cave size and shape, and species



		curvilinear branchwork	rectilinear branchwork	anastomotic maze	network maze	spongework maze	ramiform pattern
SOURCE OF AGGRESSIVE WATER	sinkholes	⬤	⬤	●	•		
	sinking streams	●	●	⬤	●	•	
	uniform seepage				⬤	●	
	mixing of 2 sources				●	⬤	●
	sulfuric acid			•	●	●	⬤
DOMINANT STRUCTURES	bedding-plane partings	⬤		⬤		●	⬤
	fractures		⬤		⬤		⬤
	intergranular pores					⬤	●

Fig. 10.12 Relation of cave patterns to mode of source of water and geologic structure. Dot sizes show the relative abundance of each pattern within the various categories. Categories across the top of the figure are the different geometries of cave passages. From Palmer (2012). Used with permission of Elsevier Ltd

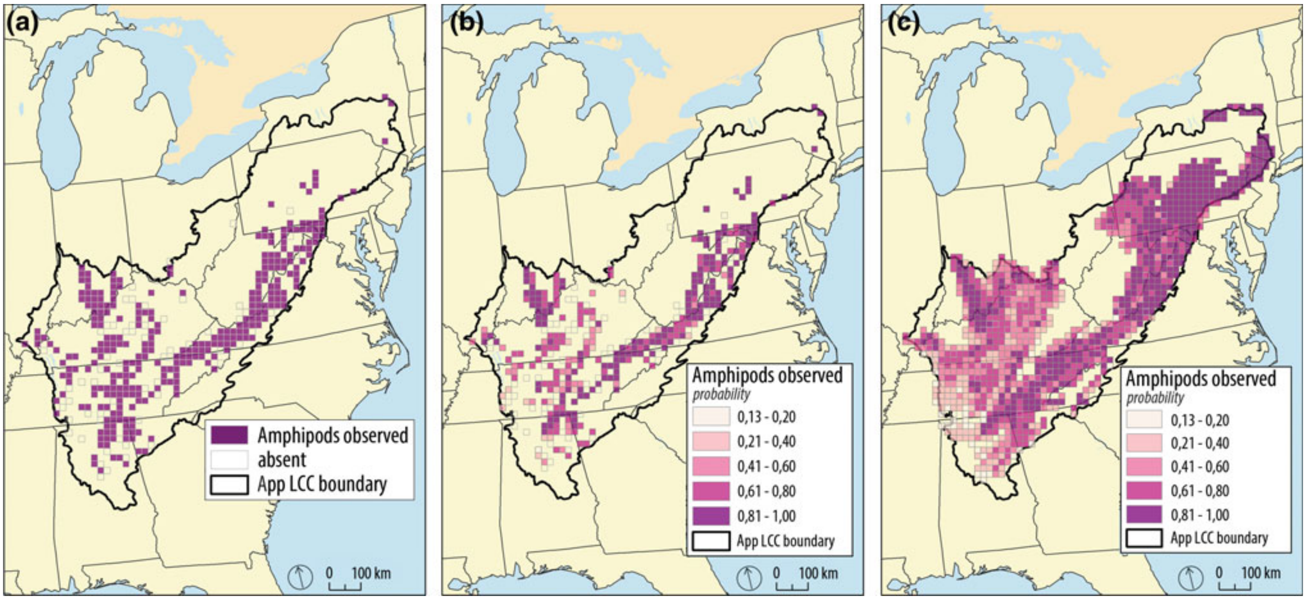


Fig. 10.13 Maps of observed and predicted distribution of troglobitic amphipods (largely the genera *Stygobromus* and *Crangonyx*) in the Appalachian and Interior Low Plateau provinces in eastern United States. **a** observed distribution of troglobiotic amphipods in 20 × 20 km grid, **b** predicted probabilities of occurrence of troglobitic amphipods in those grid cells that have observed troglobionts, **c** predicted probabilities of occurrence of troglobiotic amphipods in all grid cells with karst. From Christman et al. (2016)

composition and richness. Even cave length, presumably a measure of available habitat, is an inconsistent predictor at best (but see Simões et al. 2015 and Ferreira et al. 2018). On the other hand, Christman et al. (2016) showed that landscape features, especially latitude, percent karst in a quadrat, and rugosity, were good predictors of the presence or absence of major troglomorphic groups, e.g. amphipods, for the cave fauna of the eastern United States (Fig. 10.13). However, different landscape features were important for different groups, and understanding the patterns is difficult at best.

The one aspect of speleogenesis that seems to have a clear impact on species richness is the distinction between epigene and hypogene caves. Hypogene caves are formed from deep upflow independent of adjacent recharge areas (Klimchouk 2017), and epigene caves are formed with water from adjacent recharge areas. Sendra et al. (2014) found that hypogene caves in the Iberian Peninsula were less biologically diverse than epigene caves presumably because they are more isolated from surface waters. Gypsum caves appear to be generally less diverse, probably because they form quickly and decay quickly. On the other hand, some hypogenic caves are chemoautotrophic and, because of this energy source, harbour a very diverse fauna. Such caves include Peştera Movile in Romania, one of the richest caves in the world (Culver and Pipan 2013) and Ayallon Cave in Israel (Por et al. 2013).

Thousands of species, both terrestrial and aquatic, have become isolated in caves and evolved a characteristic morphology of reduced eyes and pigment, along with elaborated extra-optic sensory structures. The causes of isolation in caves, the timing of isolation and the factors involved in the evolution of the specialized morphology are all topics of intensive research and disagreement. A sense of the richness of the cave fauna can be gleaned from Table 10.6, where caves with either 25 aquatic troglomorphic species or 25 terrestrial troglomorphic species are listed. Most caves have less than 10 specialized species, and globally there are thousands of such species (Culver and Pipan 2019).

10.3.2 Deep Aquifers

Many water-filled cavities occur at depths of hundreds of metres and are important water sources for many areas. The fauna is difficult to study because animals typically get destroyed in the process of pumping water to the surface. However, Malard et al. (1994) devised a pump that allowed collection of invertebrates from wells up to 50 m in depth. The Triadou wells in the Lez aquifer in France yielded 34 stygobionts, making it one of the richest subterranean fauna site known. Sampling from deep artesian aquifers is much easier since water rises to the surface on its own accord. The Edwards Aquifer in Texas resurges at a number of springs and artesian wells. One of these, a well in San Marcos, Texas, has been sampled extensively (Longley 1981). At present, 44 species of obligate subterranean invertebrates have been collected from this well (B. Hutchins, pers. comm.).

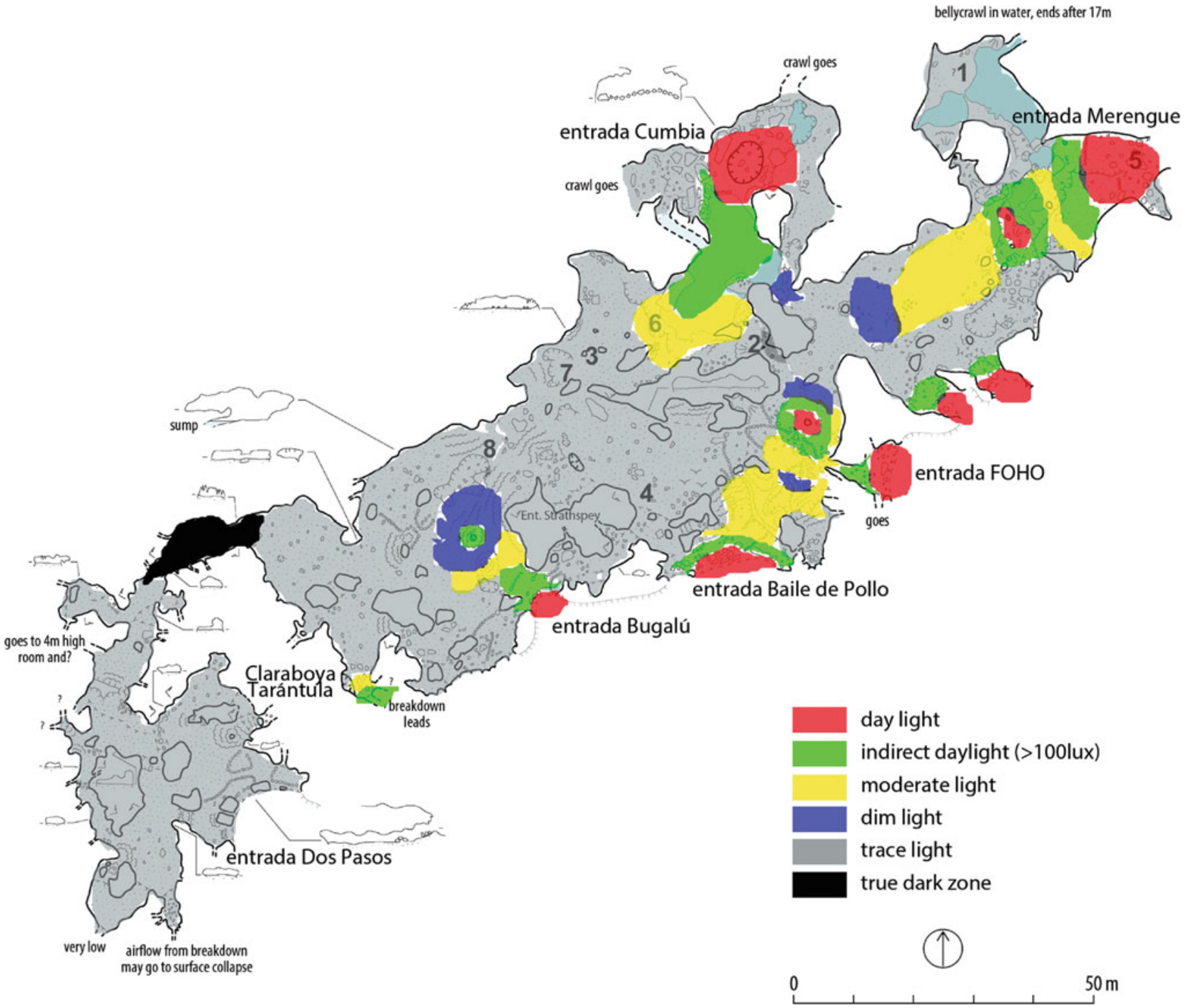


Fig. 10.14 Map of zones of incident light in Sistema Muévelo Rico. Red color is day light; green color is indirect daylight (>100 lux); yellow color is moderate light; blue color is dim light; grey color is trace light; and black color is the true dark zone. From Mejía-Ortíz et al. (2018)

The reasons for deep sites being species rich are somewhat perplexing, because organic carbon and nutrients decline with depth. However, there is chemolithoautotrophic activity in the Edwards Aquifer (Hutchins et al. 2016), and chemolithoautotrophy may be quite common in deep aquifers.

10.4 Comparison Between Various SSHs

10.4.1 What Unites SSHs?

Our working definition of shallow subterranean habitats (Culver and Pipan 2008, 2011, 2014; Pipan and Culver 2012b) is very simple—aphotic habitats less than 10 m from the surface. The 10 m limit is arbitrary, but was designed to include those habitats above caves, in areas where caves are present, as well as subterranean habitats in areas where there are no caves. SSHs we discussed included the hypotelminorheic, epikarst (terrestrial and aquatic), intermediate-sized terrestrial habitats, calcrete aquifers, hyporheic, soil, iron-ore caves and lava tubes. As Ribera et al. (2018) point out, there are often components of SSHs in deeper habitats, and this includes lava tubes, MSS and calcrete aquifers. It is also true that almost all caves, except with artificial entrances, have a component in the shallow subterranean zone. Nonetheless, the distinction between the shallow and deep subterranean habitats is useful, as we argue below.

All of SSHs are likely to be aphotic, although there have been very few direct measurements of light in these habitats.

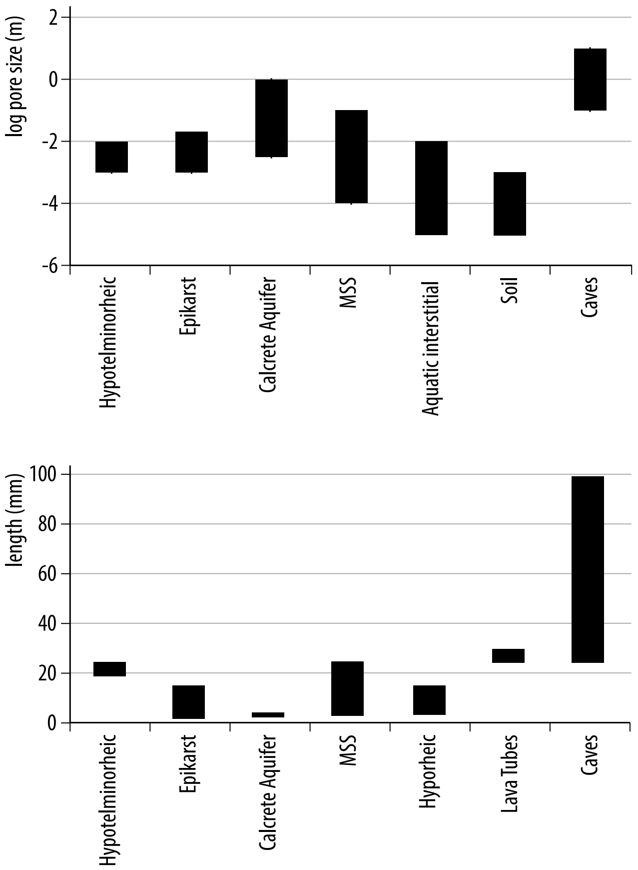


Fig. 10.15 Generalized size of shallow subterranean habitats compared to caves for diameter (top panel) and size of organisms living the habitats (bottom panel)

The absence of light is not necessarily an obvious feature of all of these habitats, although for some cases it is, such as even a few cm deep in the soil. Our measurements of that most superficial of SSHs, the hypotelminorheic, indicated that even at five cm in depth, this was an aphotic habitat. There are other habitats that are little studied that may also be aphotic. These include the spaces around tree roots, ant nests, mosses, and vertebrate burrows and nests in the terrestrial realm, and interstitial habitats in shallow lakes in the aquatic realm.

All of these SSHs share another feature in addition to the absence of light—the presence of species with reduced or absent eyes and reduced or absent pigment. These characteristics, which are likely molded by natural selection in an aphotic environment (Culver and Pipan 2019), or perhaps are the result of selectively neutral genetic processes (Wilkens and Strecker 2017) indicated absence of light is an important feature of SSHs.

However, the boundary between aphotic and photic habitats is not always sharp. There are number of habitats, typically ecotonal in nature (see Gibert et al. 1990), that have very low levels of light, typically one lux or less. These include the twilight zone of caves, springs, leaf litter. For example, the depigmented (but eyed) planarian, *Phagocata morgana,* is widespread in cold-water streams and springs in the mid-Atlantic region of the USA (Culver et al. 2012; Kenk 1972). Luštrik et al. (2011) report co-occurrences of surface-dwelling and stygobiotic amphipods in springs. Symphyla, both eyeless and depigmented, are common denizens of leaf litter (Scheller 1986). Vignoli and Prendini (2009), on the basis of their phylogeny of the scorpion family Typhlochactidae, proposed that troglomorphic cave scorpions gave rise to troglomorphic leaf litter species. Along a similar vein, Heads (2010), in his study of spider crickets, suggested that troglomorphic characteristics in spider crickets evolved in the leaf litter.

In one of the most thorough studies to date, Mejía-Ortíz et al. (2018) found a variety of terrestrial subterranean invertebrates in a cave with dim light throughout almost all of the cave (Fig. 10.14). In their study of Sistema Muévelo Rico, they found at least six troglomorphic taxa in the twilight. It appears that it is advantageous for these species to forage in the organically richer photic habitats in spite of the presence of a number of eyed predators. These twilight habitats are worth much further study. For example, it is not clear that light at intensity of less than one lux is sufficient for predators to form a search image. Additionally, nothing is known about the response of subterranean specialists to these low light levels. All light response experiments that we are aware of, use much brighter light (e.g. Friedrich et al. 2011).

One key piece of data that is missing from an analysis of these twilight habitats is the distribution of light, both spatially and temporally. As a starting point, both a rocky stream bottom and leaf litter may have a mosaic of light intensities, with overall intensity declining with depth. From the organism's point of view, it may be possible to avoid light entirely or, conversely, to avoid darkness. Thus, there may be aphotic habitats within the leaf litter and the stream benthos, and this may explain the presence of species with some troglomorphic features, and the presence of photic habitats within the leaf litter and the stream benthos, would explain the presence of species without any troglomorphic features.

As a group, SSHs, with the possible exception of calcrete aquifers, share, not only the absence of light but also intimate contact with the surface. With the exception of some lava tubes, SSHs showed annual and often daily variation (Culver and Pipan 2014). This variation has several important implications, including cyclicity itself which can be important in setting circadian clocks and especially for input of organic carbon and nutrients. These characteristics are in contrast with deeper subterranean environments, including caves and deep phreatic water.

A feature that narrow sense SSHs (hypotelminorheic, epikarst, hyporheic, MSS and calcrete aquifers) also share is

Table 10.6 Caves with more than 25 stygobionts (A) or 25 troglobionts (B). Modified from Culver and Pipan (2019). There are a few non-cave subterranean sites with this level of species richness

Site name	Country	Number of species	Region/Ecology
A. Stygobionts			
Postojna Planina Cave System	Slovenia	48	Dinarides
Vjetrenica	Bosnia and Herzegovina	40	Dinarides
Walsingham Cave	Bermuda	37	Anchialine/chemoautotrophic
Jameos del Aqua	Lanzarote, Canary Islands, Spain	32	Anchialine/chemoautotrophic
Križna jama	Slovenia	29	Dinarides
Logarček	Slovenia	28	Dinarides
Šica-Krka System	Slovenia	27	Dinarides
B. Troglobionts			
Postojna Planina Cave System	Slovenia	36	Dinarides
Cueva de Felipe Reventón	Tenerife, Canary Islands, Spain	36	Lava tube
Vjetrenica	Bosnia and Herzegovina	30	Dinarides
Peştera Movile	Romania	29	Chemoautotrophic
Cueva del Viento	Canary Islands, Spain	28	Lava tube
Sistema Purificación	Mexico	28	Tropics
Mammoth Cave	Kentucky, USA	26	Longest cave

habitat dimensions intermediate between the large open spaces of caves and the tiny spaces between soil particles or sand grains. When all SSHs are considered, a wide range of habitat sizes occur. It is also a repeated observation that habitat size (pore size) is a major determinant of body size, especially for the small pore habitats such as soil. Indeed, the only clear morphological pattern to emerge, aside from eye and pigment loss, is the correlation of body size and habitat size (Pipan and Culver 2017) (Fig. 10.15). Pipan and Culver presented a simple model, based on likely factors of natural selection (Fig. 10.16).

Differences in body size may serve as an important constraint on the colonization of SSHs by species living in different SSHs. For example, the morphological differences between soil and cave Collembola are extensive and cast doubt about the likelihood of soil Collembola being ancestral to cave Collembola. Just as the MSS is more than a dispersal corridor between karst areas, SSHs are more than staging areas for colonization of deeper subterranean habitats. They are habitats in their own right and may not be staging areas at all.

A final feature that unites all SSHs (and deep subterranean habitats for that matter), is the presence of some obligate species that have not lost their eyes and pigment. There are a few rare cases where eyed species are unknown from a subterranean habitat, e.g. the cave Vjetrenica in Bosnia and Hercegovina (Lučić and Sket 2003) and epikarst drips in Županova jama (Pipan 2005), but these are the exceptions rather than the rule. Most SSHs and most caves have non-troglomorphic species that are not stygobionts or troglobionts (Pipan and Culver 2012a).

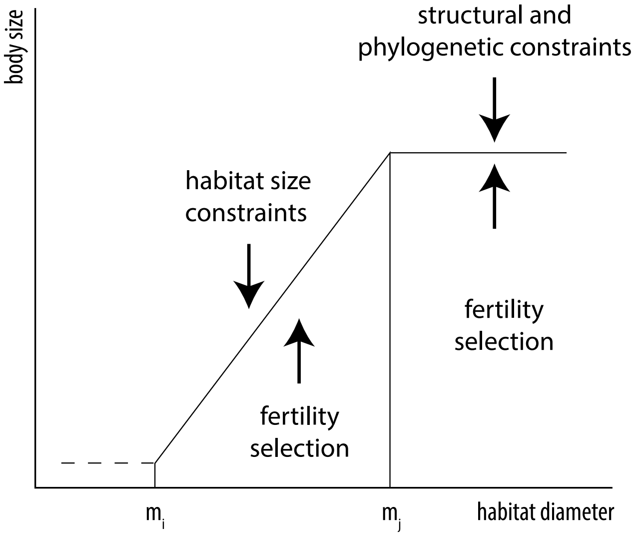


Fig. 10.16 Hypothetical relationship between subterranean habitat diameter (pore size) and body size, with selective forces indicated by arrows. Below a minimum (m_i), there is not sufficient space for animals to occur without burrowing. Above a maximum (m_j), body size is likely constrained by other factors, such as phylogenetic and structural constraints. The relationship need not be linear but is presented as such for simplicity. Modified from Pipan and Culver (2017)

10.4.2 What Divides SSHs?

Each SSH type has a characteristic distribution of habitat (pore) sizes (Fig. 10.15), and these are potential divergent selective pressures on different SSHs (Table 10.7). In

Table 10.7 Hypothesized pattern of selective pressures with respect to habitat. Habitat is taken to mean different shallow subterranean habitats as well as caves. From Culver and Pipan (2014)

Convergent among and within habitats	Divergent among and convergent within habitats	Divergent among and within habitats
Absence of light	Pore (habitat) size	Interspecific competition
	Organic carbon and nutrient flux	
	Cyclicity and connections with surface	

addition, SSHs, both within a particular type and among types, will differ in the organic carbon flux and in cyclicity of the environment. Whether these are important selective factors remains to be demonstrated in most cases. The documentation of adaptation to low organic carbon and nutrients is mostly with species at the top of the cave food web, especially fish (Hüppop 2000), and the extent of its importance for species in lower trophic levels remains largely untested.

The ground-breaking work of Friedrich (2013) on the connection between microphthalmy and circadian clocks implies that species must in some way "sample" light in order to reset the circadian clock. Thus, distance to light may be an important feature of SSHs. In the absence of other information, depth below the surface is at least an estimate of this distance.

10.5 Conclusion

While the dichotomy between shallow and deep subterranean habitats is arbitrary in the details of the division, e.g., how deep can shallow be, it is a useful dichotomy nonetheless because it brings into focus several important features of subterranean habitats. First, it highlights the impact of the surface landscape on subterranean habitats, in terms of organic carbon and nutrient input, cyclicity and even light. Second, the connection between SSHs and twilight habitats emphasizes how little we know about light regimes in both these habitats. Third, it draws attention to the question of pre-adaptation and expectation of the deep subterranean fauna. The combination of habitat delineation and phylogenetic analysis is beginning to give some idea of the path of colonization and the importance, or lack thereof, of expectation and pre-adaptation (e.g. Arnedo et al. 2007). Fourth, it re-emphasizes the importance of non-cave subterranean habitats, and idea with a long and rich European tradition (Racoviţă 1907).

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