Review
The Dark Side of Relict Species Biology: Cave Animals as Ancient Lineages

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Abstract Due to their fascinating biology and phenomena belonging to the realm of scientific curiosity, cave animals have been objects of study for zoologists for numerous decades. This chapter not only focuses on the extremes (e.g., absence of eyes, specialization to extreme environments), but also serves as an introduction to understand the geographic distribution patterns and history of these highly diverse ecological groups with their relict characteristics. After an introduction to the subterranean environment in Sect. 1, we briefly review the biology and ecology of cave animals with their regressive and progressive evolutionary tendencies in order to understand the innate reasons for restricted distribution patterns (Sect. 2). In Sect. 3, we summarize the main aspects of our knowledge regarding the distribution of these species, especially in the Holarctic; and finally in Sect. 4, we highlight the relict characteristics of cave animal distribution and the ancient phylogenetic splits between cave and surface lineages.

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1 The Subterranean Environment

The environmental conditions of caves and other cavities in massifs have frequently been investigated in conjunction with studies on cave animals. The first studies were carried out in the 19th century in a region known as Karst or Kars (in Slovenia), located between Ljubljana and Trieste. It was rapidly understood that the so-called karst processes tend to create specific geomorphology and landscape with crevices, caves, dolines, or karrens when the land is formed by soluble rocks. In the case of the Slovenian Karst, the land is formed by carbonated rocks (mainly, limestone and dolomite), the type of rock which is most important worldwide for the development of caves. Other soluble rocks, such as evaporate rocks (e.g., gypsum, salty rocks, some quarzites), can also undergo karst processes, sometimes, however, only slowly. Today, a landscape in which the main features of rock, soil, and hydrology are predominantly caused by dissolution of bedrock, is called "karst", from the Slovenian word for the above-mentioned region (Ginés and Ginés 1992).

Rock solubility is one of the main prerequisites for the formation of crevices and cavities. In the case of limestone, the main constituent is calcite which is not very soluble in pure water. However, under natural conditions water contains some acids, and this increases the solubility of calcite. The most important of these acids is carbonic acid, formed from water and carbon dioxide present in the atmosphere and soil (as a consequence of biological activity of roots, animals, protozoa, and bacteria). Other acids from the soil or from other rocks (e.g., humic acids) also have the potential to solubilize calcite. The dissolution of calcite and thus of limestone depends on several chemical dissociation and hydration reactions, both involving complex interplay of physico-chemical equilibria (Herman 2005) which, under specific conditions, cause secondary deposits in caves, e.g., stalagmites, flowstones, helictites, gypsum flowers, and columns.

The progressive dissolution of rock results in the development of fissures allowing infiltration of water into the inner parts of the karst massif, a process which tends to disarticulate the superficial hydrological network. This feeds the karst aquifer, and a subterranean hydrological network develops which promotes progressive dissolution and erosion of the inner parts of the karst massifs. Together with break-down processes, rock solubility is the main force involved in the formation of characteristic karst phenomena such as caves, karrens, dolines, crevices, fissures, and karst springs (Culver and White 2005).

Caves can also be developed by other geological processes (e.g., pseudokarst, cryp-tokarst, or volcanism), but most caves are located on limestone in karstic areas. Since most work on cave animals has been conducted in limestone caves in temperate and Mediterranean climates, the following section also focuses on this type of habitat.

In general, the physical environment in caves varies much less than the surrounding and/or superficial habitats (Culver 1982; Culver et al. 1995; Wilkens et al. 2000; Culver and White 2005). The lack (or at least reduction) of diurnal and annual rhythms results in an environment without (or with strongly reduced) temporal coordination of animal activity. Especially, in the inner part of large caves or karst

massifs the temperature varies less than 1ºC in the course of the year and is, moreover, close to annual mean temperature (e.g., Juberthie 1969). Relative humidity and physico-chemical parameters of cave water are also relatively stable. Additionally, due to the decelerating effect of fissures and crevices, drainage basins in karst massifs have moderate flood peaks compared to other drainage basins (Culver 1982).

In the 1980s, the so-called superficial underground compartment (="milieu souterrain superficiel," MSS) was discovered in the Pyrenees and subsequently in many other regions with a temperate or Mediterranean climate. The MSS corresponds to both the underground compartment (caves) and the deeper horizons of the top soil. It consists of a system of heterogenous macroporal voids in rocky material underneath the soil (mesocavernous habitats; for a detailed description of the MSS, see Juberthie et al. 1980). Due to its intercrossing nature, between the underground and the surface, the MSS shows numerous intermediate conditions; however, the microclimate in some MSS seems to be more stable than in some large caves, due to the absence of air circulations which change in caves from winter to summer.

Due to the general absence of photoautotrophic organisms, cave communities and their food web are based on decomposers. Food enters caves only as organic matter in streams and vertical shafts (also via the MSS, see Gers 1998, as dissolved organic matter in water), and by feces of animals which regularly visit caves (e.g., bats). Only a few chemoautotrophically-based cave ecosystems have primary producers (e.g., Sarbu et al. 1996). In the underground and the superficial underground compartment, Collembola and Acarina function as "underground plankton" because of their basal position in many subterranean food webs. In general, decomposers (e.g., Diplopoda and Diplura) and first- and second-order predators (e.g., Coleoptera, Chilopoda, and Aranea) occur. For many cave animals, food is scarce and its availability is more stochastic and unpredictable in superficial habitats; its pattern of occurrence also seems to be more clustered (Gers 1998).

2   Biology and Ecology of Cave Animals

Cave animals are adapted to the above-mentioned special habitat conditions, which include reduced environmental variation and darkness. Loss of eyes, loss of wings in insects, and reduction of pigments are elements of regressive evolution; prolongation of extremities and increased sensory systems are elements of progressive evolution which occur in cave animals. The development of such features associated with cave life is known as troglomorphy (Christiansen 2005). In many cases, these features evolved convergently (e.g., the head flattening in cave vertebrates, a strong enlargement of elytra, but not of the abdomen – known as pseudophysogastry – in different lineages of beetles) and resulted in a special habitus of many cave-adapted animals (Figs. 1–3). These adaptations to the special environment are the reason why true cave animals are not able to survive outside of their underground habitats. The members of this ecologically characterized group which live exclusively in caves (or the MSS) during their whole life cycle are termed *troglobionts* or troglobites.
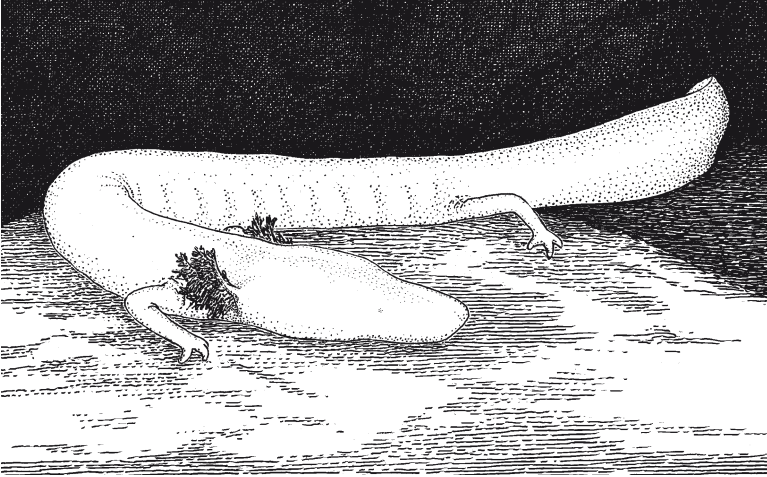
Fig. 1 European cave salamander or olm (*Proteus anguinus*), larva (drawn by Peter Schüle)

Troglophiles are capable of spending their entire life cycles either in underground or in surface habitats. *Trogloxenes* are vagrants or animals which can spend part of their life in caves, but are not able to develop in the underground. The latter terms are mainly used for terrestrial species. *Stygobionts* or stygobites live exclusively in subterranean waters (including cave and interstitial habitats), whereas stygophiles are able to develop in subterranean and in surface water bodies (cf. Culver and White 2005).

Regressive evolution, in particular, is not yet well understood. The simple neutral mutation hypothesis implies that regression is caused by random mutations in genes involved in the development of a given character. Under the relaxed selective pressure of the cave environment, these random mutations can accumulate and lead to the loss of the given character. Jeffery (2005, 2008) reviewed studies of regressive evolution in the Mexican Blind Cavefish (*Astyanax mexicanus*) and concluded that pigmentation regression is probably best explained by the neutral mutation hypothesis, whereas eye degeneration may be caused by adaptive evolution and pleiotropic effects of the genes also involved in the development of eyes. A review on the regressive evolution of cave fishes, in general, is given by Jeffery (2009).

As a consequence of eye reduction, the circadian rhythm of many cave animals is also reduced. Extremely evolved cave animals exhibit no or only weakly developed circadian rhythms of locomotory activity and resting. However, it was shown that light can induce clear activity rhythms in troglobite species (Lamprecht and Weber 1979, 1992).

Phenomena of progressive evolution characterize many cave animals. The prolongation of extremities in arthropods and the increased number of receptors for environmental information (especially, for olfactory stimuli) are features of most cave animals (Juberthie 1979; Culver 1982; Christiansen 2005). The spectrum of
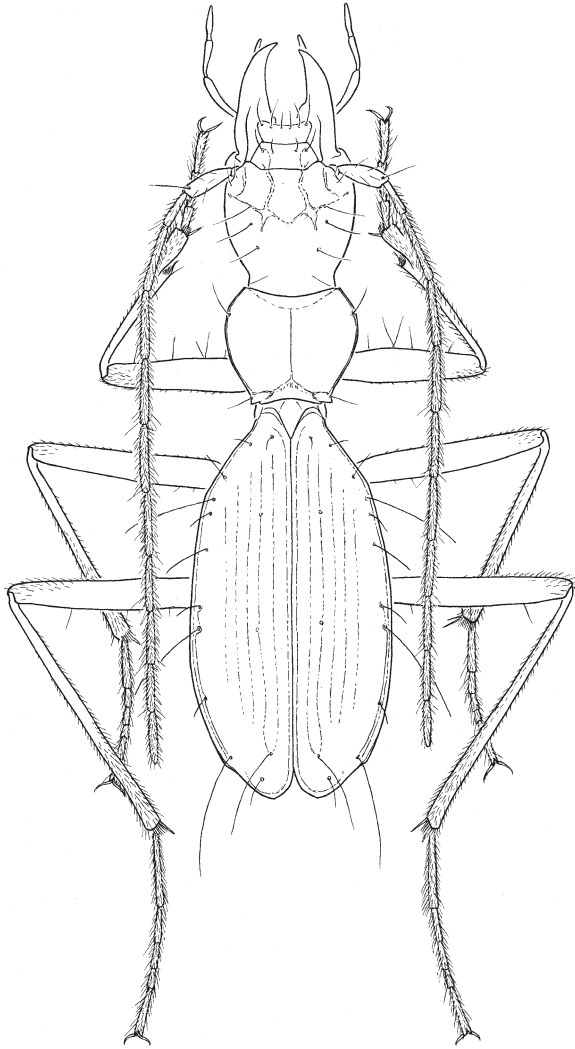
Fig. 2 Carabid cave beetle *Aphaenopidius kamnikensis*. Adapted from Assmann and Lompe (2006) and Drovenik et al. (2008), modified

consumed food ranges from feces, litter, and rotten wood to living prey. Some predators are specialized (e.g., *Neaphaenops tellkampfii* with its preference for eggs of the cave cricket *Hadenoecus subterraneus*, Kane and Poulson 1976), while some others are polyphagous (e.g., *Aphaenops crypticola*, Gers 1996). The reduced and stochastic availability of food seems to have resulted in selection pressure to a lower metabolic rate which allows both greater resistance to starvation and a comparably higher availability of energy for reproduction. Generally, but not in all
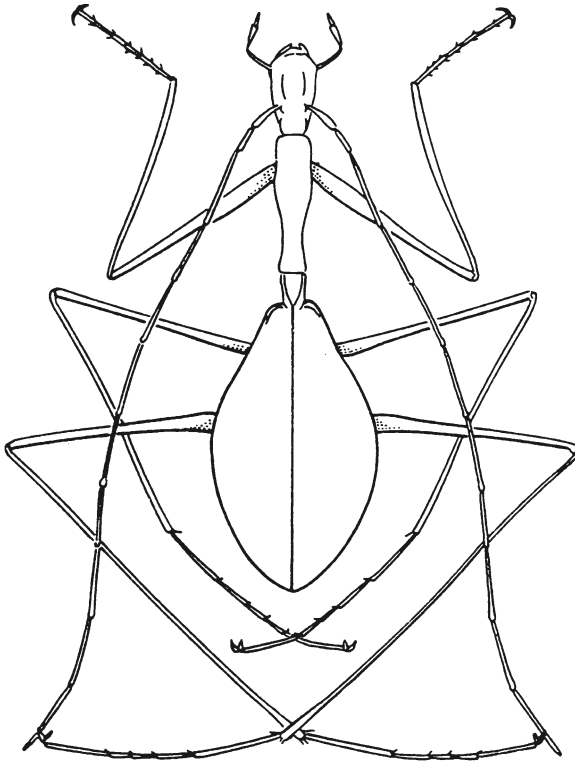
Fig. 3 Cholevid cave beetles *Antroherpon dombrowski*. Adapted from Jeannel (1924)

animal groups, cave species show a lower metabolic rate than their relatives that inhabit epigeic habitats (Vandel 1965; Culver 1982; Hüppop 2005).

The life span of many cave animals seems to be prolonged: The olm or European cave salamander (*Proteus anguinus*) can become older than a century (Durand 1998), and mark-recapture experiments with the microphthalmic cave ground beetle *Laemostenus schreibersi* in an Austrian cave estimated an age of more than 8 years for some individuals (Rusdea 1994, 2000). Moreover, cave animals have the tendency to produce fewer, but larger eggs and/or offsprings (Hüppop 2005). K-selection (cf. longevity, reproduction biology) seems to act on animals in the underground (see Stearns 1977 for a critique on the concept of r- and K-selection). Some members of the cholevid beetle genus *Speonomus* from the Pyrenees are an extreme example for the tendency to invest more yolk in fewer eggs. In the most extremely adapted species, only one egg ripens in a female at any given time. The hatched larva does not feed, grow, or molt, but pupates rapidly. Thus, the cycle of these species comprises only a single larval stage. This means that female invest-ment in one egg enables the development of a whole beetle (Fig. 4). Transitions to the classical life cycle of cholevid beetles with three successive larval stages are also known, however (Glacon-Deleurance 1963).
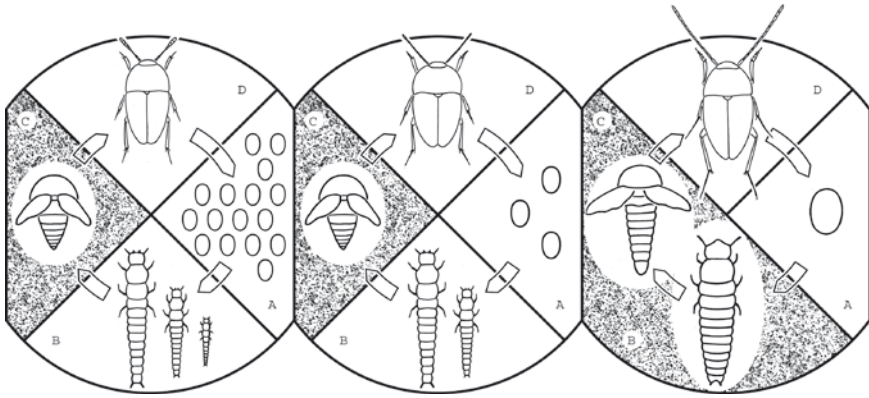
Fig. 4 Life cycles of different Cholevidae, Leptodirinae. Adapted from Glacon-Deleurance (1963) and Giachino et al. (1998), redrawn by Peter Schüle

3   Biogeography and Diversity Hotspots

The marked differences between the distribution patterns of aquatic and terrestrial troglobites were recognized by biologists several decades ago (Thienemann 1950; Vandel 1965; Lamoreux 2004). The Northern distribution limit of terrestrial troglobites does not reach as far North as that of aquatic troglobites, at least in Europe and North America. For example, members of *Niphargus*, an aquatic amphipod genus with blind species which inhabit groundwater in caves and other geological settings, are distributed Northwards as far as Ireland. Terrestrial forms (e.g., some genera and many species of blind cave Trechini beetles), however, reach their Northern limits in the so-called "massifs de refuge" at the Southern border of the Alps, in small and isolated refugia at the North-Western and North-Eastern border of the Alps, and in the Carpathians (Holdhaus 1954; Vandel 1965). The reasons for the different distribution patterns are still under discussion (cf. Lamoreux 2004).

The Southern edge of permafrost ground coincides notably with the Northern edge of the distribution range of terrestrial troglobites (Holdhaus line; see for a detailed discussion Drees et al. 2009). Due to the narrow adaptations to their habitats, terrestrial cave animals are not able to leave the massifs in which they live. Power of dispersal is, therefore, extremely restricted and it is highly probable that terrestrial cave animals survived the glacial periods within the massifs in which they are still distributed. Exceptions are known where the species have been able to colonize from nearby caves or massifs, probably using the MSS (cf. Daffner 1993).

Cave animals belong to the trophic groups of decomposers and carnivores, and their food chain depends on organic input from epigeic parts of the ecosystem. Survival of terrestrial cave animals during the glacial periods indicates a long-lasting persistence of ecosystems in the given regions.

The postglacial colonization of Eastern North America seems to be very complex, and many questions remain unanswered. However, it is known that glacial refuges

were localized in areas Northwards up to close to the Laurentide Ice Sheet (Soltis et al. 2006), and terrestrial cave animals were restricted to non-glaciated areas, with a concentration in Alabama (Culver et al. 2000). Some regions of the world lack a terrestrial cave fauna (e.g., Northern Asia), while in others their existence has been discovered only in recent decades (e.g., in the tropics, Howarth 1983). A general overview of the worldwide distribution of terrestrial and aquatic cave animals is given by Juberthie and Decu (1998).

Bizarre disjunct distribution patterns in North America and in Europe can be found in higher amphibian taxa with troglobitic or at least troglophilic species: The family of cave salamanders (Proteidae) comprises the genus *Necturus* in surface waterbodies of North America and the European cave salamander or olm (*P. anguinus*) Southeast of the Alps in Europe; troglophilic lungless taxa inhabit disjunct distribution areas in Western North America (*Hydromantes*) and in the North-Western Mediterranean (*Speleomantes* and *Atylodes*; Durand 1998; Weisrock et al. 2005). Disjunct distributions are also known from groups of blind ground beetles which occur in North America and in the Palearctic (the so-called "série phylétique" of *Aphaenops*, Trechini; Casale and Laneyrie, 1982). Such disjunct small distribution areas on two continents are strong arguments for ancient splits in the phylogeny of the given groups. Without doubt, these taxa are ancient relicts of a former wider distribution.

One of the "hottest hotspots" of terrestrial cave fauna is located in the Western Palearctic realm, probably with a center in the Northern part of the Mediterranean region (Culver and Sket 2000; Gibert and Culver 2005; Culver et al. 2006). Ground beetles are a good example of "clustered" cave species richness: Casale et al. (1998) cite more than 50 genera of troglobitic ground beetles of the tribe Trechini from the Mediterranean realm (mainly from Southern Europe; and 13, 4, and 7 genera from North America, South America, and Australia, respectively). Another important hotspot seems to be Southeast Asia (more than 30 genera listed by Casale et al. 1998, and numerous newly described taxa, cf. Lorenz 2005). More than 600 of a total of more than 1,000 troglobitic trechine species from the Western Palearctic have been described.

The species number of some cave genera is low and there are even some monotypic genera (e.g., *Ameroduvalius*), whereas others are extremely rich in species, e.g., troglobitic ground beetles with >250 *Pseudanophthalmus* species in North America, and a similar number of *Duvalius* species in the Palearctic (Casale et al. 1998; Culver et al. 2003). Extraordinary species richness is also a feature of some aquatic cave animal groups, especially of the amphipod families Niphargidae and Crangonyctidae (both *Niphargus* and *Stygobromus* comprising about 200 species in Europe and North America, respectively, Peck 1998; Gibert and Culver 2005). In general, however, the species richness of aquatic fauna is lower than that of terrestrial species (Culver et al. 2003). The reasons for the different species richness patterns have not yet been conclusively ascertained (cf. Lamoreux 2004).

The invertebrates inhabiting the underground are still poorly studied, from a systematic point of view. Species richness of ground beetles inhabiting underground habitats in the Palearctic has not yet reached an asymptote (Fig. 5), whereas overall species richness of carabids in most European and North African countries reached a clear asymptote during the 20th century (Schuldt and Assmann 2009).
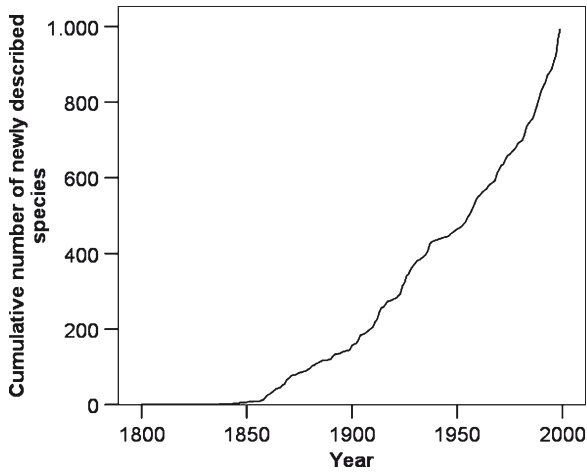
Fig. 5 Cumulative number of carabid taxa inhabiting underground habitats (troglobionts and troglophiles, including blind species from the superficial underground compartment) described from the Palearctic (1800–1999). Generated from the Catalog of Palearctic Coleoptera, Löbl and Smetana (2003)

4 Relict Status of Cave Animals

Biospeleologists agree that cave animals share a common ancestor with epigeic species. These ancestors lack features of progressive and regressive evolution which is related to the progress of troglobite evolution. According to the "Pleistocene-effect theory", ancestral forms are thought to have adapted ("taken refuge") to caves when "postglacial climates became warmer and drier, and thus inimical to ancestors preadapted to cool, wet microhabitats" (Vandel 1965; Culver 1982; Barr and Holsinger 1985 p. 331; Moldovan 2005).

This scenario does not seem to be true, however, from modern molecular studies on many cave animals. The DNA divergence of studied taxa indicates that biogeographic events which led to the separation of the gene pools date back some millions of years (Caccone and Sbordoni 2001; Porter 2007). Even surface and cave *Astyanax* populations seem to have diverged at least a few million years ago (Strecker et al. 2003; Strecker et al. 2004; 1.8–4.5 million years: Porter et al. 2007).

At least one population of the isopod *Asellus aquaticus* is an up to 3.9 million years old PrePleistocene "relict" of one lineage which invaded the underground. Other cave populations diverged during the glacial periods (Verovnik et al. 2004). However, despite the fact that we have molecular data only from a few related cave and surface populations/species we have to assume that the origin of many terrestrial and aquatic cave animals dates back to times (long) before the glacial periods.

Thanks to molecular studies, we are beginning to understand the evolution of speciation and colonization processes (e.g., Verovnik et al. 2005), but our knowledge of these processes in terrestrial species is still poor. Erwin (1985) developed

the taxon pulse model to explain the divergence of the hyper-diverse group of ground beetles and Casale et al. (1998) adopted it to stress the origin of subterranean lineages. However, despite its sophisticated and outstanding character, a molecular test using arboreal and epigeic ground beetles did not support the taxon pulse model (Ober 2003).

Cave animals are treated as relict species for good reasons, because in many cases they are taxa with no ancestral stock in the immediate area (Barr 1985). Taking the long-lasting divergence since the PrePleistocene times between many cave and surface lineages into account, we can denominate many ancient relicts among cave animal species. This also seems to be true for taxa with striking disjunct distributions (see biogeography and biodiversity hotspots, Sect. 3): The split from the common ancestor of *Hydromantes* (North America) on the one hand and *Speleomantes* and *Atylodes* (Europe) on the other hand occurred during the Paleocene-Eocene and both lineages can be named relicts, not only because of their ancient origin but also because of their restricted distribution areas (Vieites et al. 2007).

Despite our understanding of the biogeographic history of cave animals, numerous questions are still unanswered. Some have already been mentioned above, such as the reasons for different distribution and species richness patterns between terrestrial and aquatic troglobionts or the reason for the existence of regions without cave fauna (South of permafrost grounds during glacial periods). In addition to these gaps in knowledge, the phylogeny of many vertebrate, and even more invertebrate, species remains to be studied. For example, phylogeny is still unresolved for the European cave salamander or olm (*P. anguinus*) (Weisrock et al. 2005) described as the first eyeless cave animal by Laurenti in 1768, even though this bizarre species was already studied by Cuvier, Lamarck, and even Darwin in his famous book on "The origin of species," already one and a half centuries ago.

References

Assmann T, Lompe A (2006) *Aphaenopidius* Müller, 1913. In: Müller-Motzfeld G (ed) Carabidae. Elsevier, Heidelberg, p 149

Barr TC (1985) Pattern and process in speciation of trechine beetles in Eastern North America (Coleoptera: Carabidae: Trechinae). In: Ball GE (ed) Taxonomy, phylogeny and zoogeography of beetles and ants. Dr. W. Junk Publishers, Dordrecht, pp 350–407

Barr TC, Holsinger JR (1985) Speciation in cave animals. Annu Rev Ecol Syst 16:313–337

Caccone A, Sbordoni V (2001) Molecular biogeography of cave life: a study using mitochondrial DNA from Bathysciine beetles. Evolution 55:122–130

Casale A, Laneyrie R (1982) Trechodinae et Trechinae du monde: tableau des sous-familles, tribus, séries phylétiques, genres, et catalogue général des espèces. Mémoires de Biospéologie 9:1–226

Casale A, Vigna-Taglianti A, Juberthie C (1998) Coleoptera Carabidae. In: Juberthie C, Decu V (eds) Encyclopedia biospeologica. Tome II. Société de Biospéologie, Moulis (France), pp 1047–1081

Christiansen K (2005) Morphological adaptations. In: Culver DC, White WB (eds) Encyclopedia of caves. Elsevier, Amsterdam, pp 386–397

Culver D (1982) Cave life: evolution and ecology. Harvard University Press, Cambridge, MA

Culver D, Sket B (2000) Hotspots of subterranean biodiversity in caves and wells. J Cave Karst Stud 62:11–17

Culver D, White WB (2005) Encyclopedia of caves. Elsevier, Burlington, MA

Culver DC, Kane TC, Fong DW (1995) Adaptation and natural selection in caves. Harvard University Press, Cambridge, MA

Culver DC, Master LL, Christman MC, Hobbs HH (2000) Obligate cave fauna of the 48 contiguous United States. Conserv Biol 14:386–401

Culver DC, Christman MC, Elliott WR, Hobbs HH, Reddell JR (2003) The North American obligate cave fauna: regional patterns. Biodivers Conserv 12:441–468

Culver DC, Deharveng L, Bedos A, Lewis JJ, Madden M, Reddell JR, Sket B, Trontelj P, White D (2006) The mid-latitude biodiversity ridge in terrestrial cave fauna. Ecography 29:120–128

Daffner H (1993) Die Arten der Gattung *Arctaphaenops* Meixner, 1925 (Coleoptera: Carabidae). Koleopterologische Rundschau/Coleopterological Revue 63:1–18

Drees C, Matern A, von Oheimb G, Reimann T, Assmann T (2009) Multiple glacial refuges of unwinged ground beetles in Europe – molecular data support classical phylogeographic models. In: Habel JC, Assmann T (eds) Relict species – phylogeography and conservation biology. Springer, Heidelberg. yet to update

Drovenik B, Weber F, Paill WG, Assmann T (2008) *Aphaenopidius kamnikensis* Drovenik, 1987 in Kärnten. Angewandte Carabidologie 8:73–76

Durand JP (1998) Amphibia. In: Juberthie C, Decu V (eds) Encyclopedia Biospeologica II. Société de Biospéologie, Moulis, pp 1215–1243

Erwin T (1985) The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. In: Ball GE (ed) Taxonomy, phylogeny and zoogeography of beetles and ants. Dr. W. Junk Publishers, Dordrecht, pp 437–493

Gers C (1996) Stratégies alimentaires des Coléoptères troglobies du genre *Aphaenops* (Coleoptera, Trechinae). Mémoires de Biospéologie 17:35–45

Gers C (1998) Diversity of energy fluxes and interactions between arthropod communities: from soil to cave. Acta Oecol Int J Ecol 19:205–213

Giachino PM, Decu V, Juberthie C (1998) Coleoptera Cholevidae. In: Juberthie C, Decu V (eds) Encyclopaedia biospeologia. Société de Biospéologie, Moulis (France), pp 1083–1122

Gibert J, Culver D (2005) Diversity patterns in Europe. In: Culver D, White WB (eds) Encyclopedia of caves. Elsevier, Amsterdam, pp 196–201

Ginés A, Ginés J (1992) Karst phenomena and biospeleological environments. Monografias Museo Nacional de Ciencias Naturales 7:27–56

Glacon-Deleurance S (1963) Recherches sur les coléptères troglobies de la sous-famille des Bathyscininae. Ann Sci Nat 5:1–172

Herman JS (2005) Water chemistry in caves. In: Culver D, White WB (eds) Encyclopedia of caves. Elsevier, Burlington, MA, pp 609–614

Holdhaus K (1954) Die Spuren der Eiszeit in der Tierwelt Europas. Wagner, Innsbruck

Howarth FG (1983) Ecology of cave arthropods. Annu Rev Entomol 28:365–389

Hüppop K (2005) Adaptation to low food. In: Culver D, White WB (eds) Encyclopedia of caves. Elsevier, Amsterdam, pp 4–10

Jeannel R (1924) Monographie des Bathysciinae. Archives de zoologie expérimentale et générale 63:1–436

Jeffery WR (2005) Adaptive evolution of eye degeneration in the Mexican blind cavefish. J Hered 96:185–196

Jeffery WR (2008) Emerging model systems in evo-devo: cavefish and microevolution of development. Evol Dev 10:265–272

Jeffery WR (2009) Evolution of cave fish. Annual Review of Genetics 43:25–47

Juberthie C (1969) Relations entre le climat, le microclimat et les *Aphaenops cerberus* dans le grotte de Sainte-Catherine (Ariege). Annales de Spéléologie 24:75–104

Juberthie C (1979) L'évolution des coléopteres Trechinae souterrains (Coleoptera, Carabidae). In: Den Boer PJ, Thiele HU, Weber F (eds) On the evolution of behaviour in carabid beetles. Veenman and Zonen, Wageningen, pp 83–102

Juberthie C, Decu V (eds) (1998) Encyclopaedia Biologica, Tome II. Société Internationale de Biospéologie, Moulis and Bucarest

Juberthie C, Delay B, Bouillon M (1980) Extension du milieu souterrain en zone non calcaire: description d'un nouveau milieu et de son peuplement par les Coléoptères troglobies. Mémoires de Biospéologie 7:19–52

Kane TC, Poulson TL (1976) Foraging by cave beetles: spatial and temporal heterogeneity of prey. Ecology 57:793–800

Lamoreux J (2004) Stygobites are more wide-ranging than troglobites. J Cave Karst Stud 66:18–19

Lamprecht G, Weber F (1979) The regressive evolution of the circadian system controlling locomotion in cavernicolous animals. In: Den Boer PJ, Thiele HU, Weber F (eds) On the evolution of behaviour in carabid beetles. Veenman and Zonen, Wageningen, pp 69–82

Lamprecht G, Weber F (1992) Spontaneous locomation behaviour in cavernicolous animals: the regression of the endogenous circadian system. In: Camacho AI (ed) The natural history of biospeleology. Museo Nacional de Ciencias Naturales, Madrid, pp 225–262

Löbl I, Smetana A (eds) (2003) Catalogue of Palearctic Coleoptera Vol. 1: Archostemata, Myxophaga, Adephaga. Apollo Books, Stenstrup

Lorenz W (2005) A systematic list of extant ground beetles of the world (Coleoptera "Geadephaga": Trachypachydiae and Carabidae, incl. Paussinae, Cicindelinae, Rhysodinae). 2nd edition. Lorenz, Tutzing

Moldovan OT (2005) Beetles. In: Culver D, White WB (eds) Encyclopedia of caves. Elsevier, Amsterdam, pp 45–51

Ober KA (2003) Arboreality and morphological evolution in ground beetles (Carabidae: Harpalinae): testing the taxon pulse model. Evolution 57:1343–1358

Peck SB (1998) A summary of diversity and distribution of the obligate cave-inhabiting faunas of the United States and Canada. J Cave Karst Stud 60:18–26

Porter ML (2007) Subterranean biogeography: what have we learned from molecular techniques? J Cave Karst Stud 69:179–186

Porter ML, Dittmar K, Perez-Losada M (2007) How long does evolution of the troglomorphic form take? Estimating divergence times in *Astyanax mexicanus*. Time in Karst – 2007 (Slovenska Akademija Znanosti Umetnosti): 173–182

Rusdea E (1994) Population dynamics of *Laemostenus schreibersi* (carabidae) in a cave in Carinthia (Austria). In: Desender K, Dufrene M, Loreau M, Luff ML, Maelfait J-P (eds) Carabid beetles – ecology and evolution. Kluwer, Dordrecht, pp 207–212

Rusdea E (2000) Langlebigkeit der Adulten – ein Faktor, der die Populationsgröße stabilisieren kann. Erläutert am Beispiel einer Langzeituntersuchung am Höhlenlaufkäfer *Laemostenus schreibersi* (Coleoptera, Carabidae). Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandten Entomologie 12:517–521

Sarbu SM, Kane TC, Kinkle BK (1996) A chemoautotrophically based cave ecosystem. Science 272:1953–1955

Schuldt A, Assmann T (2009) Environmental and historical effects on richness and endemism patterns of carabid beetles in the Western Palearctic. Ecography . doi:10.1111/j.1600-0587.2009.05763.x

Soltis DE, Morris AB, McLachlan JS, Manos PS, Soltis PS (2006) Comparative phylogeography of unglaciated Eastern North America. Mol Ecol 15:4261–4293

Stearns SC (1977) The evolution of life history traits: a critique of the theory and a review of the data. Ann Rev Ecol Syst 8:145–171

Strecker U, Bernatchez L, Wilkens H (2003) Genetic divergence between cave and surface populations of *Astyanax* in Mexico (Characidae, Teleostei). Mol Ecol 12:699–710

Strecker U, Faundez VH, Wilkens H (2004) Phylogeography of surface and cave *Astyanax* (Teleostei) from Central and North America based on cytochrome b sequence data. Mol Phylogen Evol 33:469–481

Thienemann A (1950) Die Binnengewässer XVIII: Verbreitungsgeschichte der Süsswassertierwelt Europas. Verlag Schweizerbart, Stuttgart

Vandel A (1965) Biospeleology: The biology of cavernicolous animals. Pergamon Press, Oxford

Verovnik R, Sket B, Trontelj P (2004) Phylogeography of subterranean and surface populations of water lice *Asellus aquaticus* (Crustacea: Isopoda). Mol Ecol 13:1519–1532

Verovnik R, Sket B, Trontelj P (2005) The colonization of Europe by the freshwater crustacean *Asellus aquaticus* (Crustacea: Isopoda) proceeded from ancient refugia and was directed by habitat connectivity. Mol Ecol 14:4355–4369

Vieites DR, Min MS, Wake DB (2007) Rapid diversification and dispersal during periods of global warming by plethodontid salamanders. Proc Natl Acad Sci USA 104:19903–19907

Weisrock DW, Harmon LJ, Larson A (2005) Resolving deep phylogenetic relationships in salamanders: analyses of mitochondrial and nuclear genomic data. Syst Biol 54:758–777

Wilkens H, Culver DC, Humphreys WF (2000) Subterranean ecosystems. Elsevier, Amsterdam