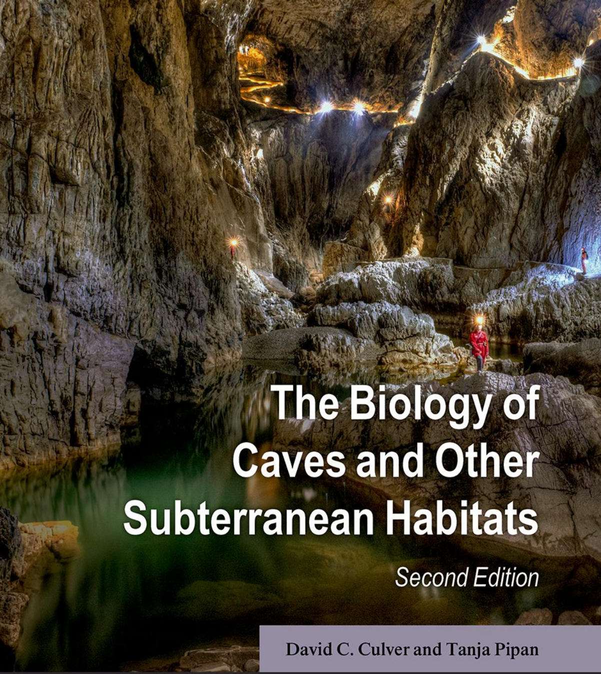

The Biology of Caves and Other Subterranean Habitats

Second Edition

David C. Culver and Tanja Pipan

Biology of Habitats

The Biology of Caves and Other Subterranean Habitats

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Preface to the Second Edition

We are in a golden age of the study of subterranean biology. Thirty-five years ago, when one of us (DCC) wrote a book on the biology of caves, it was easy to read and discuss all the non-taxonomic literature on cave biology written in English. Today, there are well over 200 papers per year published on the biology of subterranean habitats. Thirty-five years ago, for American speleobiologists, but much less so for European biologists, speleobiology meant the biology of caves. There was scarcely any recognition or awareness of non-cave subterranean environments among American speleobiologists. The scope of speleobiology has expanded to include those subterranean[1] habitats whose inhabitants include blind, depigmented species with compensatory increases in other sensory structures. In fact, there has been so much research on these non-cave subterranean habitats, that five years ago we wrote a book devoted to these habitats that are very close to the Earth's surface—*Shallow Subterranean Habitats: Ecology, Evolution, and Conservation.*

Since the publication of the first edition, a number of books on various aspects of speleobiology have been published, including general treatments by Romero (2009) and Fenolio (2016), a book on the microbiology of caves (Engel 2016), four! books on cavefish—Keene *et al.* (2016), Trajano *et al.* (2010), Wilkens and Strecker (2017), and Zhao and Zhang (2009), and a second edition of the *Encyclopedia of Caves* (White and Culver 2012). In addition, there have been more than 1000 research papers on speleobiology published since the first edition of this book.

Our strategy in the second edition has been to update information in the first edition, while still focusing on a relatively small number of well-studied cases. We have replaced some of the case studies from the first edition but have not changed others just because there have been more recent publications on the topic. The growth of information has, of course, not been uniform across subdisciplines. Phylogeography, biodiversity, and evo-devo have in particular experienced a growth spurt. All in all, we have added approximately 125 references published since the first edition.

[1] We use subterranean in the sense of organisms living in natural spaces. The word subterranean is also frequently applied to organisms that create their own spaces—especially mammals such as mole rats, termites, and plant roots. The word hypogean is sometimes used in the sense we use subterranean, but its use is uncommon, and we use enough uncommon words as it is. There are many precedents for the way we use the word, such as the International Society for Subterranean Biology and its journal *Subterranean Biology.*

We hope that this book is accessible to a wide variety of readers. We have assumed no training in biology beyond a standard university year-long course, and we have tried to make the geological and chemical incursions self-contained. An extensive glossary should help the readers through any terminological rough spots.

We have organized this book around what seem to us to be the major research areas and research questions in the field. To provide a context for these questions, we review the different subterranean environments (Chapter 1), what the energy sources are for subterranean environments given that the main energy source in surface environments—photosynthesis—is missing (Chapter 2), and the main inhabitants of these underground domains (Chapter 3). The research areas that we focus on are as follows:

- How are subterranean ecosystems defined and organized, and how in particular does organic carbon move through the system (Chapter 4)?
- How do species interact and how do these interactions, such as competition and predation, organize and constrain subterranean communities (Chapter 5)?
- How did subterranean organisms evolve the bizarre morphology of elongated appendages, no pigment, and no eyes (Chapter 6)?
- What is the evolutionary and biogeographical history of subterranean species? Are they in old, relic lineages (Chapter 7)? How does their distribution relate to past geological events?
- What is the pattern of diversity of subterranean faunas over the face of the Earth (Chapter 8)?

We close by 'putting the pieces together' and examining some representative and exemplary subterranean communities (Chapter 9), and how to conserve and protect them (Chapter 10).

With the exception of Chapters 1–3, where we have attempted to provide a comprehensive geographical and taxonomic review of the basics, we have focused on a few particularly well-studied cases. Although we have provided case studies from throughout the world, readers from Africa, South America, and Asia will no doubt find a North American and European bias. Of this we are certainly guilty, but in part this bias is because of longer traditions of study of subterranean life in Europe and North America. We have added several case studies from Asia and South America. We have provided an extensive bibliography and hope that interested readers will pursue the subjects further. Where English language articles are available, we have highlighted them, but we also have not hesitated to include particularly important or unique papers in other languages.

A cautionary word about place names. Many species are limited to a single cave, well, or underflow of a brook, and, if for no other reason, this makes it important to accurately give place names. Throughout the book we have identified the country and state or province in which a site is located. We have, whenever possible, retained the spelling of the local language. Translation runs the risk of confusing anyone trying to identify a particular cave or site, and also runs the risk of repeating the word cave in different languages, as in Postojnska jama Cave (Postojna Cave Cave). Postojnska jama already has names in three languages (Slovene, Italian, and German) and there is no need to add a fourth. A list of sites mentioned in the text is provided.

Even to us, the field of subterranean biology seems especially burdened with obscure terminology. While there is a temptation to ignore it as much as possible, it is widespread in the literature and some of it is even useful. We have defined many terms in the text when we first use them, and have included an extensive glossary to aid readers.

Besides the fascination of their bizarre morphology (which cannot really be overrated), there are two main reasons for biologists to be interested in subterranean faunas. One is numerical. Nearly all rivers and streams have an underlying alluvial system in which its residents never encounter light. Approximately 15 per cent of the Earth's land surface is honeycombed with caves and springs, part of a landscape called karst that is moulded by the forces of dissolution rather than erosion of rock and sediment. In countries such as Cuba and Slovenia, this is the predominant landform.

But there is a more profound reason for biologists to study subterranean biology. Subterranean species can serve as model systems for several important biological questions. As far as we can determine, it was Poulson and White (1969) who first made this notion explicit but it is implicit in the writings of many subterranean biologists. This is a recurring theme throughout this book, and we list just some of the possibilities here:

- Subterranean ecosystems can serve as models of carbon (rather than nitrogen and phosphorus) limited ecosystems and ones where most inputs are physically separated from the community itself.
- Subterranean communities can serve as a model of species interactions because the number of species is small enough that all pairwise interactions can be analysed and then combined into a community-wide synthesis.
- The universal feature of loss of structures (regressive evolution) is especially obvious in subterranean animals, with a clear basis that in turn can allow for detailed studies of adaptation.
- The possibilities of dispersal of subterranean species are highly constrained and so the species (and lineages) can serve as models for vicariant biogeography.
- The highly restricted ranges and specialized environmental requirements can serve as a model for the protection of rare and endangered species.

Whatever reasons you have for reading this book, we hope it leads you to a fascination with subterranean biology, one that lasts a lifetime.

Acknowledgements

The field of subterranean biology is blessed with a strong, cooperative group of scholars from all over the world, and we could not have written this book without the help of many of them. We especially thank Peter Kozel for reading the entire manuscript of the second edition and making many helpful suggestions. Cene Fišer, Daniel W. Fong, and Mike Slay all read selected chapters and helped us avoid many mistakes. Several colleagues provided photographs and drawings for the first and/or second editions—Gregor Aljančič, Magda Aljančič, Matej Blatnik, Marie-Jose Dole-Olivier, Annette Summers Engel, the late Horton H. Hobbs III, Hannelore Hoch, William R. Jeffery, Arthur N. Palmer, Borut Peric, Slavko Polak, Megan Porter, Mitja Prelovšek, Nataša Ravbar, Andreas Wessel, Jill Yager, and Maja Zagmajster. Colleagues also provided us with preprints and answered sometimes naive questions—Gergely Balázs, Louis Deharveng, Marie-Jose Dole- Olivier, Stefan Eberhard, David Eme, Annette Summers Engel, Daniel W. Fong, Franci Gabrovšek, Janine Gibert, Benjamin Hutchins, Lee Knight, Florian Malard, Georges Michel, Pedro Oromí, Metka Petrič, Megan Porter, Graham Proudlove, Katie Schneider, Trevor Shaw, Boris Sket, Peter Trontelj, Rudi Verovnik, and Maja Zagmajster. Franjo Drole of the Karst Research Institute ZRC SAZU devoted many hours to scanning and producing diagrams. Maja Kranjc, and later Janez Mulec, in charge of the magnificent library at the Karst Research Institute, have helped with our requests for books and journals.

We are especially grateful to the Karst Research Institute ZRC SAZU, especially the head of the institute, Dr Tadej Slabe and the administrative assistant, Sonja Stamenković, for making the writing go as smoothly as possible. Tadej Slabe provided time for TP to work, space for DCC to work, and an appointment to DCC as Associate Researcher. Financial support was provided by Ad Futura (Javni sklad Republike Slovenije za razvoj kadrov in štipendije) to DCC during his stay in Slovenia.

We thank Ian Sherman of Oxford University Press for providing us with the opportunity to write both editions of the book, Helen Eaton for shepherding through the first edition, and Bethany Kershaw for shepherding through the second edition.

A project of this magnitude was a burden on both of our families, and we are especially grateful to our spouses, Gloria Chepko and Miran Pipan, for providing both understanding and support.

Postojna, Slovenia
April, 2018

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List of Sites

A list of sites from 29 countries mentioned in the text. General references to countries or large regions are omitted. Specific reference to the sites can be found in the appendix. While most of the sites are caves, there are a number of specific regions, e.g. Cape Range in Australia, that are listed.

Abkhazia (Georgia)

- Veryovkina

Australia

- Bayliss Cave (Queensland)
- Bundera sinkhole (Western Australia)
- Bungonia Cave (New South Wales)
- Cape Range (Western Australia)
- Pilbara (Western Australia)
- Robe River (Western Australia)
- Sturt Meadows (Western Australia)
- Tantabiddi well (Western Australia)
- Yilgarn (Western Australia)

Austria

- Danube Flood Plain National Park
- Lobau wetlands

Belgium

- Walloon

Bermuda

- Walsingham Cave

Bosnia & Hercegovina

- Dabarska pećina
- Popovo polje
- Trebišnjica River System
- Vjetrenica

Brazil

- Atlantic Coastal Rain Forest
- Lapa da Fazienda Extrema I (Goiás)
- São Mateus Cave (Goiás)

Burma

- Farm caves

China

- Ma San Dong Cave
- Shihua Cave

Croatia

- Krk Island
- Markarova pećina
- Miljacka pećina
- Pincinova jama
- Rupeciča
- Šipun

France

- Ardèche
- Ariège
- Baget basin
- Bellissens
- Canal di Mirabel
- Col des Marrous
- Dorvan-Cleyzieu
- Grand Gravier
- Grotte du Cormoran
- Grotte du Pissoir
- Grotte de Sainte-Catherine
- Heraut
- Isère River
- Jura Mountains
- Lachein Creek
- Las Hountas
- Rhône River at Lyon
- Roussilon
- Tour Laffont

Germany

- Aach Spring
- Segeberger Höhle

Indonesia

- Batu Lubang (Halmahera)
- Gua Sulukkan (Sulawesi)
- Niah Caves (Sarawak)

Israel

- Ayalon Cave

Italy

- Abisso di Trebiciano
- Grotta Azzurra
- Grotta di Frasassi
- Lessinian Mountains

Malaysia

- Lubang Nasib Bagus (Sarawak)
- Sarang karst (Borneo)
- Subis karst (Borneo)

Mexico

- Cueva Chica
- Cueva de la Curva
- Cueva de Los Sabinos
- Cueva da Villa Luz
- Cueva de El Pachón
- Sierra del Abra
- Sistema Zacatón
- Sotano de al Tinaja
- Sotano de las Golandrinas

Montenegro

- Dormitor National Park

Papua New Guinea

- Kavakuna Matali system

Phillipines

- Bohol Island caves
- Montalban caves
- Taninthayri caves

Portugal

- Azores lava tubes
- Serra da Estrela

Romania

- Peştera Movile
- Peştera Urşilor

Slovakia/Hungary

- Baradla/Domica

Slovenia

- Črna jama
- Huda luknja
- Jelševnik
- Kompolska jama
- Krim
- Križna jama
- Mejama
- Otovski breg
- Logarček
- Malo okence
- Paka karst
- Pivka jama
- Pivka River
- Planinska jama
- Postojna–Planina Cave System
- Postojnska jama
- Rak River
- Šica–Krka system
- Škocjanske jame
- Tular

Spain

- Cantabrica
- Cueva del Felipe Reventón (Canary Islands)
- Cueva del Mattravies
- Cueva del Naciemento del Arroyo de San Blas
- Cueva del Viento (Canary Islands)
- Jameos del Agua (Canary Islands)

Thailand

- Central Plain
- Tham Chiang Dao
- Tham Phulu
- Tham Thon

Ukraine

- Zoloushka Cave

United Kingdom

- Otter Hole Cave (Wales)
- Swildon's Hole (England)

United States

- Alpena Cave (West Virginia)
- Blue Lake Rhino Cave (Oregon)
- Bracken Cave (Texas)
- Carlsbad Caverns (New Mexico)
- Cave Spring Cave (Arkansas)
- Cesspool Cave (Virginia)
- Classic Cave (New Mexico)
- Coldwater Cave (Iowa)
- Columbia River basalt (Washington)
- Devil's Hole (Nevada)
- Dillion Cave (Indiana)
- Edwards Aquifer (Texas)
- Fern Cave (Alabama)
- Fisher Cave (Missouri)
- Flathead River (Montana)
- Floridan Aquifer (Florida)
- Glenwood Caverns (Colorado)
- Greenbrier Valley (West Virginia)
- Hellhole (West Virginia)
- Hering Cave (Alabama)
- Hidden River Cave (Kentucky)
- Howe Caverns (New York)
- Inner Space Caverns (Texas)
- Kartchner Caverns (Arizona)
- Kazumura Cave (Hawaii)
- Lanikai Cave (Hawaii)
- Lava Tubes National Monument (California)
- Lechuguilla Cave (New Mexico)
- Limrock Cave (Alabama)
- Logan Cave (Arkansas)
- Lower Kane Cave (Wyoming)
- Lower Potomac (District of Columbia)
- Mammoth Cave (Kentucky)
- McClean's Cave (California)
- Ogalalla Aquifer (Nebraska)
- Old Mill Cave (Virginia)
- Organ Cave (West Virginia)
- Parker Cave (Kentucky)
- Pless Cave (Indiana)
- Robber Baron Cave (Texas)

- Scott Hollow Cave (West Virginia)
- Scotts Run Park (Virginia)
- Shelta Cave (Alabama)
- ShenandoahValley (Virginia)
- Silver Spring (Florida)
- South Platte River (Colorado)
- Sunnyday Pit (West Virginia)
- Thompson Cedar Cave (Virginia)
- Thornhill Cave (Kentucky)
- Tony Sinks (Alabama)
- Ward's Cove (Virginia)
- Young–Fugate Cave (Virginia)

Vietnam

- Halong Bay
- Tan phu lava tubes

Plate 1 Photo of the karst landscape of Halong Bay, Vietnam. Karst landscapes take many different shapes and forms in different regions. Among the most spectacular are the towers and pinnacles of Halong Bay, a UNESCO World Heritage site. The remaining limestone is slowly being dissolved away. See page 5 in text.

Plate 2 Photo of Pivka River sinking at the entrance to Postojnska jama, Slovenia. Photo by M. Petrič, used with permission. See page 11 in text.

Plate 3 Photo of Unica Spring, the resurgence of the Postojna–Planina Cave System, Slovenia. Photo by M. Blatnik, used with permission. See page 12 in text.

Plate 4 Photograph of the authors at a hypotelminorheic site at Scotts Run Park, near Washington, DC, USA. Photo by W.K. Jones, with permission. See page 18 in text.

Plate 5 Main trunk passage in Lower Kane Cave, Wyoming, USA. White, filamentous microbial mats dominated by sulfur-oxidizing bacteria are present in shallow sulfidic water, beginning at the lower right corner (water flows from the lower right to upper left). The microbial mat extends for approximately 20 m with an average thickness of 5 cm. From Engel (2012). Photo by A.S. Engel, with permission. See page 26 in text.

Plate 6 Photograph of drip water in Organ Cave, West Virginia, USA which percolates into the cave from the epikarst. Photo by H.H. Hobbs III, with permission. See page 31 in text.

Plate 7 Dead raccoon at the base (10 m depth) of Sunnyday Pit, West Virginia, USA. Photo by H.H. Hobbs, with permission. See page 37 in text.

Plate 8 Roots of *Metrosideros polymorpha* coming through the ceiling of Lanikai Cave, Hawai'i. Photo by H. Hoch, with permission. See page 40 in text.

Plate 9 Photo of the remipede *Lasionectes entrichoma* showing male and female reproductive systems, ventral view. Photo by D. Williams and J. Yager, with permission. See page 57 in text.

Plate 10 Photograph of *Proteus anguinus.* Photo by G. Aljančič, with permission. See page 71 in text.

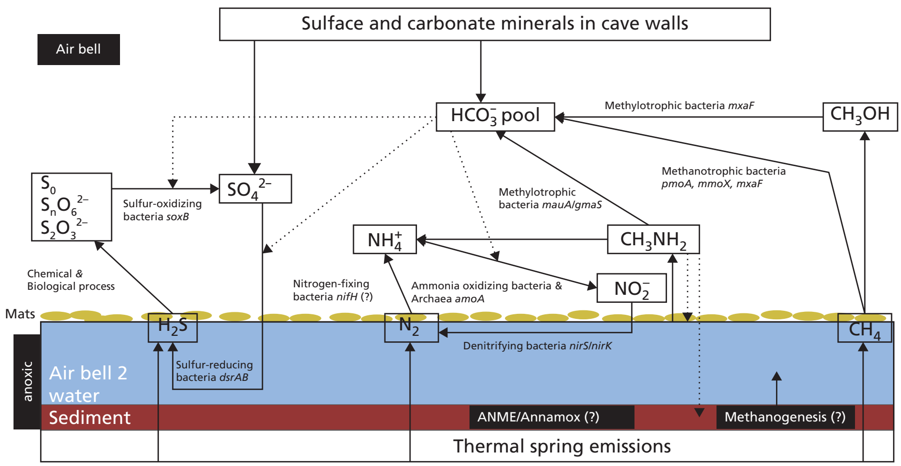

Plate 11 Schematic representation of microbial sulfur, carbon, and nitrogen cycling in Peştera Movile, Romania. Evidence for metabolic pathways comes from functional gene analyses. From Kumaresan *et al.* (2014). Used with permission of Walter de Gruyter GmBH. See page 93 in text.

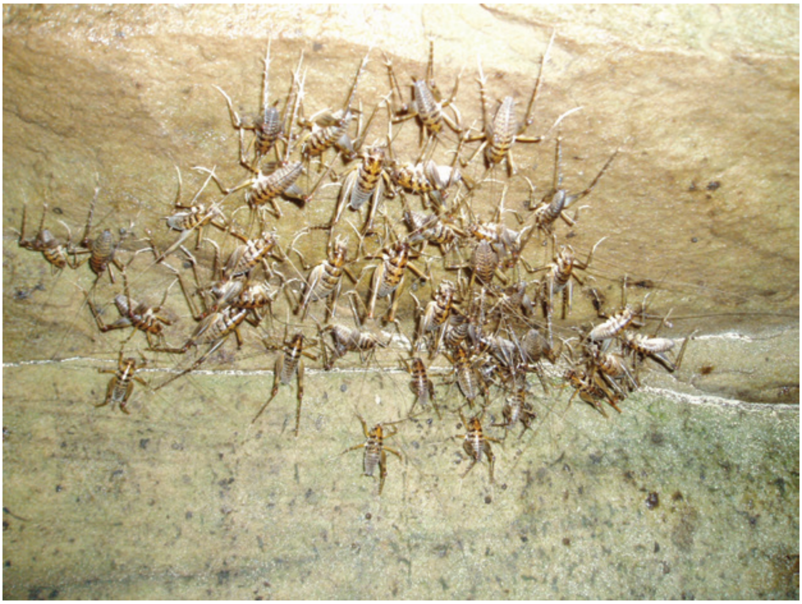

Plate 12 Concentration of cave-crickets, *Ceuthophilus stygius*, on the ceiling of Dogwood Cave, Hart Co., Kentucky, USA. Photo by H. H. Hobbs, with permission. See page 101 in text.

Plate 13 Typical (A) *Proteus anguinus anguinus* and the pigmented, eyed subspecies (B) *Proteus anguinus parkelj*. Photographs by G. Aljančič, with permission. See page 121 in text.

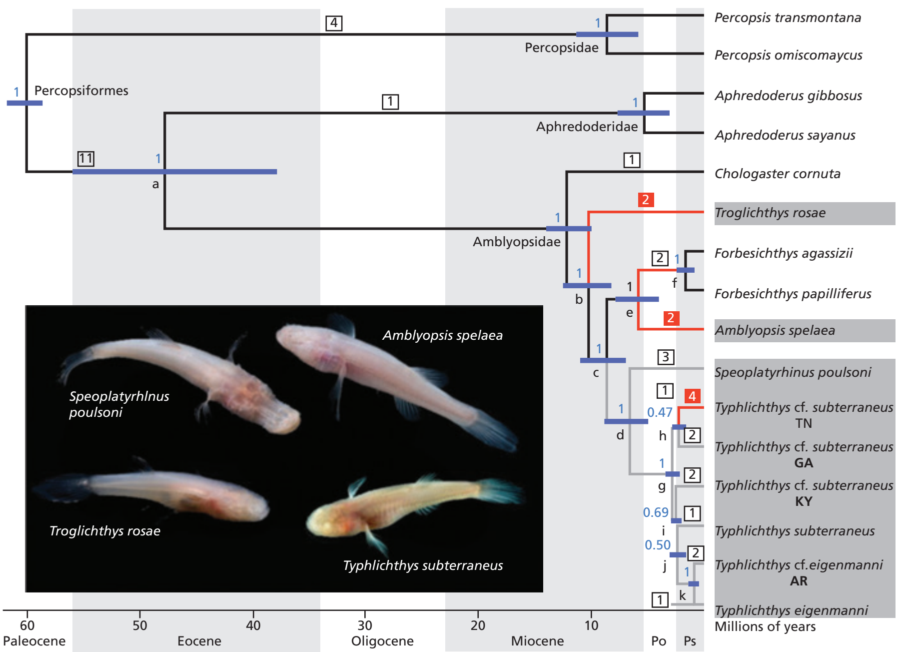

Plate 14 Molecular phylogeny of Amblyopsidae, based on Niemiller *et al.* (2012b). Used with permission of John Wiley and Sons Inc. See page 125 in text.

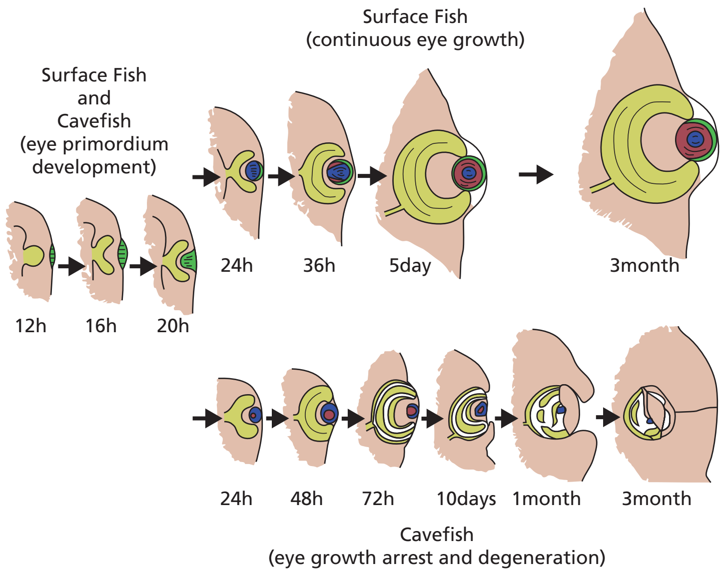

Plate 15 Eye development and degeneration in *Astyanax mexicanus.* Diagram showing the timing of eye growth and development in surface fish (top) and eye degeneration in cavefish (bottom). Drawing by W. Jeffery, with permission. See page 139 in text.

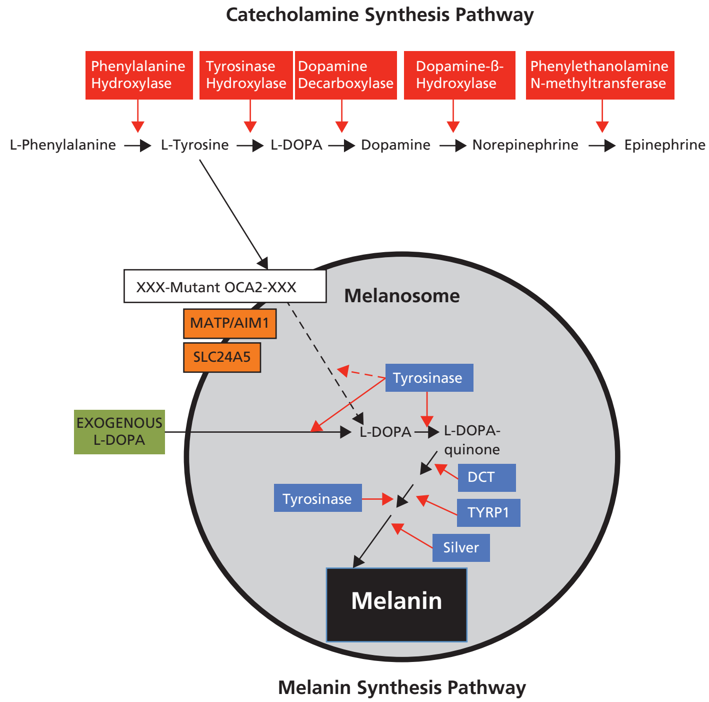

Plate 16 The relationship between the catecholamine and melanin synthesis pathways in *Astyanax* cavefish. In albino cavefish, a mutated *oca2* gene (white box with XXX) affects the first step of the pathway prior to tyrosinase function and prevents melanin synthesis. The defect caused by *oca2* loss of function can be rescued by exogenous L-DOPA. Solid lines: steps that occur in surface fish and in cavefish after L-DOPA rescue of melanogenesis. Dashed lines: steps that are absent in cavefish. From Bilandžija *et al.* (2013). See page 142 in text.

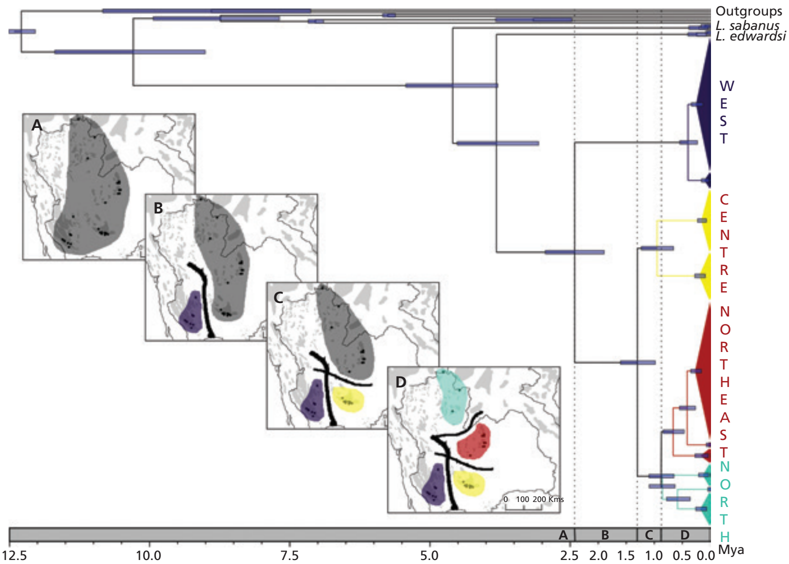

Plate 17 Dating of the most recent common ancestors with 95 percent HPD (highest posterior density), and graphical representation of the biogeographical scenario of *Leopoldamys neilli* according to four time periods A, B, C, and D. The four maps depict the hypothetical of *L. neilli* ancestral population (mid grey), western (mauve), central (yellow), northern (light blue), and northeastern (red) groups and the locations of barriers (black lines) leading to three vicariant events. From Latinne *et al.* (2012). See page 177 in text.

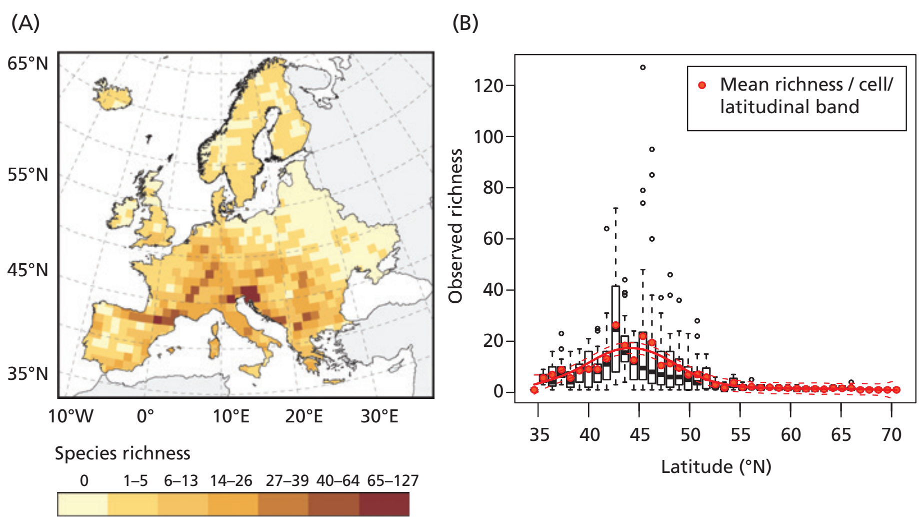

Plate 18 Map of species richness patterns of European stygobionts. A. Species richness of 10 000 km^2 cells. B. Relationship between the cell average of species richness per 0.09′ latitudinal band and latitude. Black horizontal bars and boxes show the median and interquartile range, respectively, for latitudinal bands. The maximum length of each whisker is 1.5 times the interquartile range and open circles represent outliers. The thick red line is the fit of generalized additive model to the averages of latitudinal bands. From Zagmajster *et al.* (2014). See page 200 in text.

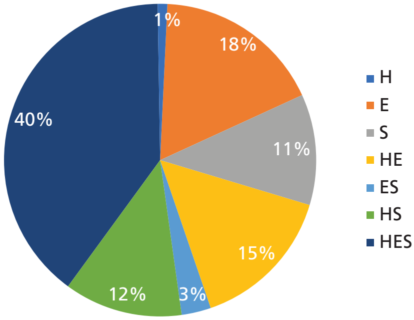

Plate 19 Pie chart of relative contributions of different combinations of drivers of species richness to the explained variance. H is historical climate stability, E is productive energy, and S is spatial heterogeneity. Data from Eme *et al.* (2014). See page 200 in text.

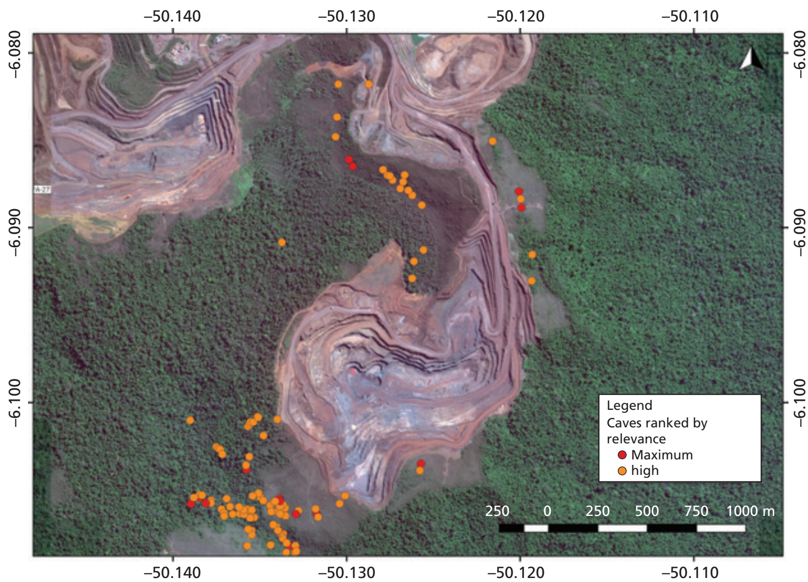

Plate 20 Iron-ore mine (N5, Serra Norte, Carajás, Brazil) showing the location of caves coloured by their classification. Caves with maximum relevance have at least one rare troglobiont; caves with high relevance have at least one troglobiont. From Jaffé *et al.* (2018). See page 215 in text.

Plate 21 Gate at the entrance to Fisher Cave, Missouri, USA, designed to allow unimpeded access for bats. Photo by H. Hobbs III, with permission. See page 234 in text.

Plate 22 Channelized Trebišnija watercourse in Popovo polje, Bosnia & Herzegovina in 2005. Photograph by M. Zagmajster, with permission. See page 237 in text.

1 The Subterranean Domain

1.1 Introduction

Beneath the surface of the earth are many spaces and cavities. These spaces can be very large—some cave chambers such as the Sarawak Chamber, with an area of over 21 000 000 m^3 in Lubang Nasib Bagus (Good Luck Cave) in Sarawak, Malaysia (Waltham 2004) can easily accommodate the world's largest aircraft. They can also be very small, such as the spaces between grains of sand on a beach. These spaces can be air-filled, water-filled, or even filled with petroleum. All of these spaces share one very important physical property—the complete absence of sunlight. This is a darkness that is darker than any darkness humans normally encounter, a darkness to which our eyes cannot acclimate no matter how long one waits. There are some habitats that are dark and yet have some light. The ocean abyss is nearly without light but many organisms of the abyss, such as the well-known angler fish, produce their own light with the help of microbes (Fenolio 2016). In addition, the heat of deep sea vents is high enough that light is emitted (Van Dover 2000). In subterranean habitats, with very rare exceptions, this does not happen. The most notable exception is that of glow-worms (actually fungus-gnat larvae) in a few caves in Australia and New Zealand (Broadley and Stringer 2001). But even in these special cases, organisms cannot use light to find their way about, to find food, to find mates, and so on.

Taken together, the water-filled and air-filled cavities are quite common, perhaps more common than surface habitats. Over 94 per cent of the world's unfrozen freshwater is stored underground, compared with only 3.6 per cent found in lakes and reservoirs, with the rest in soil, rivers, and the atmosphere (Heath 1982). Heath estimates that there are 521 000 km^3 of subsurface spaces and cavities in the soils and bedrock of the United States, and most of these contain water. Whitman *et al.* (1998) indicate that between 6 per cent and 40 per cent of the total prokaryotic (organisms with no nuclear membrane such as Bacteria) biomass on the planet may be in the terrestrial subsurface. The number of caves is also large—for example the Karst Research

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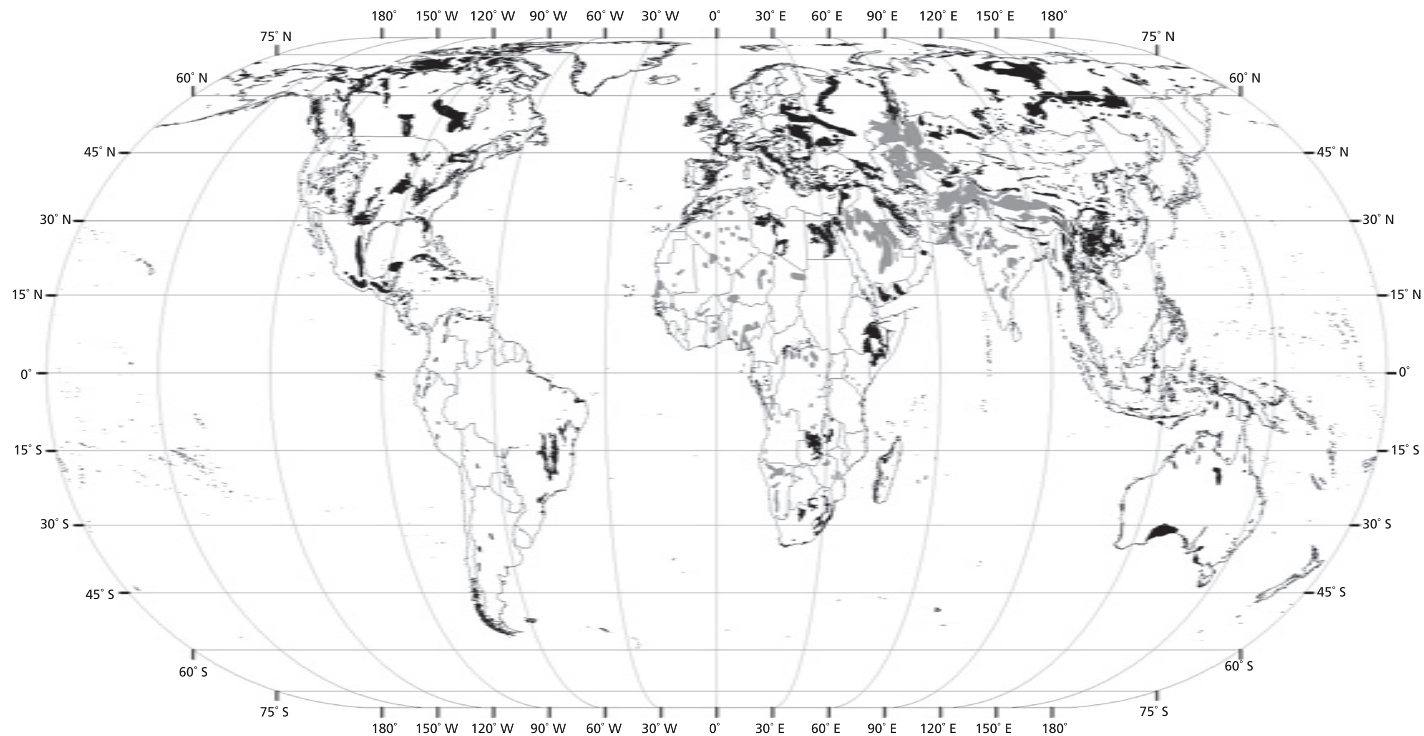

Fig. 1.1 Global distribution of major outcrops of primary cave-bearing (carbonate) rocks, shown in black. Not included in the figure are areas of volcanic rock with lava tubes. Impure or discontinuous carbonate regions are in grey. Map by P.W. Williams, used with permission.

Institute of Slovenia has records of more than 12 000 caves in a country with an area of about 20 000 km^2. More than 100 000 caves are known from Europe, and nearly 50 000 are known from the United States (Culver and Pipan 2013). All of the continents except Antarctica have caves, as do most countries. A map (Fig. 1.1) of cave regions shows that North America and Eurasia are especially rich in cave-bearing rocks.

The absence of light has profound effects on the organisms living in such habitats. Eyes and the visual apparatus in general have no function there. There are no photons to capture; therefore, no increase in visual acuity will have any benefit to the organisms exclusively living in darkness. Food-finding, mate-finding, and avoidance of competitors and predators all must be accomplished without vision. As is discussed in more detail in Chapter 7, this is a profound barrier that surface-dwelling animals must overcome to successfully colonize subsurface habitats. The absence of light means an absence of both photosynthesis and primary producers (plants, algae, and some bacteria). In some rare but very interesting cases, microorganisms can obtain energy from the chemical bonds of inorganic molecules (Engel 2012), but most subsurface communities rely on food transported in from the surface. This will be taken up in detail in Chapter 2, and we just note in this chapter that the general absence of autotrophy means the amount and variety of resources are usually reduced.

For all subsurface habitats, the amplitude of variation of environmental parameters, especially temperature, is much less than that of the surface habitats. This reduction in amplitude is especially noticeable in regions where variation in surface temperatures is extreme. In Kartchner Caverns, Arizona, USA, the daily average temperature on the surface varies by more than 17°C, whereas temperatures within the cave vary less than 1°C (Fig. 1.2) (Cigna 2002). The range of variation in most spots in Kartchner Caverns was around 1 per cent or 2 per cent of the surface variation. Nevertheless, in Kartchner Caverns, as in nearly all subterranean habitats, there is still an annual temperature cycle. With the possible exception of groundwater aquifers at depths of hundreds of metres, there are no truly constant subsurface environments. In many older references (e.g., Poulson 1963, Vandel 1964), environmental constancy is over-emphasized. With the availability of better monitoring devices, especially ones taking multiple measurements, environmental variability can be detected. Other parameters besides temperature vary, including air currents, water levels, and the amount of food brought into caves. The pulse of spring flooding may be an important cue for reproduction for many cave animals (Hawes 1939). It varies in amplitude, predictability, and seasonality in different caves, but shows the general lack of constancy of the subterranean environment.

Traditionally, subsurface habitats are divided into large cavities (caves) and small cavities (interstitial habitats) (Botosaneanu 1986). We follow this division but add a third category—shallow subterranean habitats, which fit uneasily into the traditional dichotomy (Culver and Pipan 2008a, 2014).

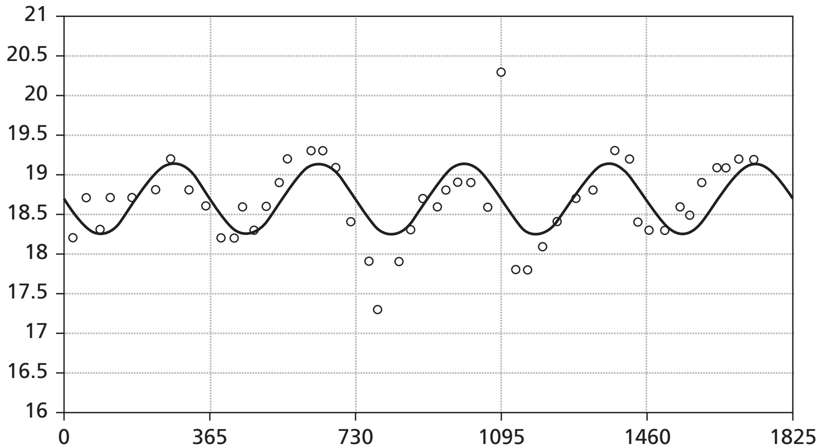

Fig. 1.2 Temperature profiles from Kartchner Caverns, Arizona, USA. Sampling began on 1 January 1996 and continued for 5 years. Solid line is a sinusoidal fit of the data. Time (in days) is shown on the *x*-axis and temperature (°C) is shown on the *y*-axis. From Cigna (2002). Used with permission of Karst Research Institute ZRC SAZU.

1.2 Caves

Caves are more difficult to define that one might expect. Geologists (e.g., White 1988) often define caves as natural openings large enough to admit a human being, but this is not an especially useful biological definition. A more useful definition is a natural opening in solid rock with areas of complete darkness, and larger than a few millimetres in diameter. The first criterion excludes spaces among sands, gravels, and stones because they are not openings in solid rock. The second criterion excludes some geographical features that are sometimes called caves, such as rock shelters and natural tunnels, which have no zone of complete darkness. The third is a more technical restriction which eliminates very tiny tubes that are too small to have turbulent water flow. Eventually, many of these tiny tubes will develop into caves but below this critical diameter processes of enlargement and dissolution are very slow indeed, taking up to hundreds of thousands of years (Dreybrodt *et al.* 2005, Ford and Williams 2007, Audra and Palmer 2015).

1.2.1 Caves formed by dissolution of rocks

Landscapes in which the primary agent moulding the landscape is dissolution rather than erosion are called karst landscapes (Fig. 1.3). That is, the features of karst landscape (caves, sinkholes, springs, blind valleys, and the like) result from the action of the hollowing out of rocks by weak acids rather than by erosion, volcanic activity, earthquakes, and so on. Caves are the most biologically interesting part of this landscape, but there are karst landscapes with very few caves (the extreme northern Shenandoah Valley in