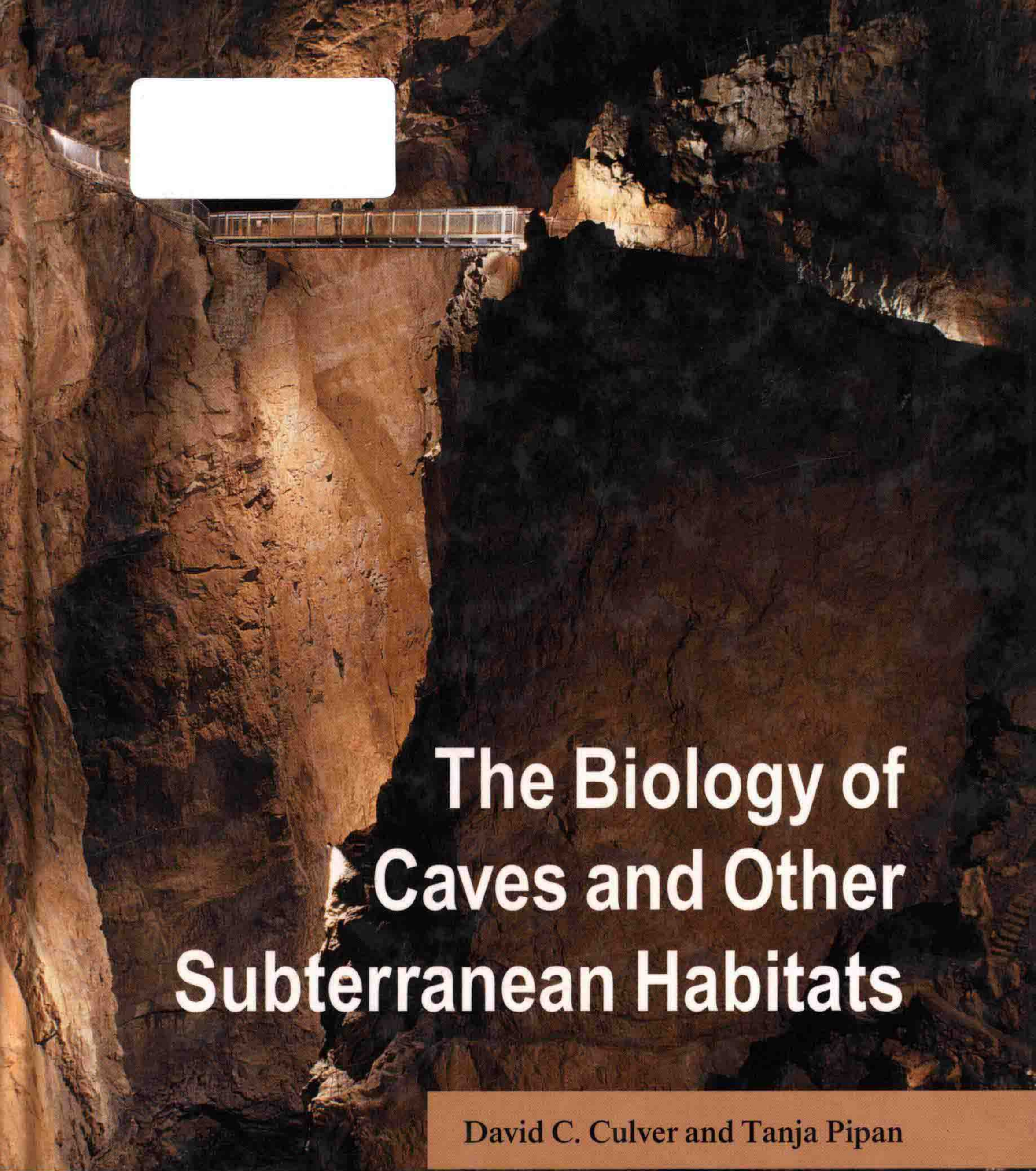

# The Biology of Caves and Other Subterranean Habitats

David C. Culver and Tanja Pipan

Biology of Habitats

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# The Biology of Caves and Other Subterranean Habitats

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# Preface

We are in a golden age of the study of subterranean biology. Twenty-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. The only book length treatment of cave biology at that time in English was the translation from the French of Albert Vandel's *Biospeleology*. Most speleobiologists were not writing in English and the discipline remained largely a national one. Art Palmer, the author of a recent introductory text on cave geology, points out that theories of cave development were developed independently (and in strikingly parallel ways) three times—first in Serbo-Croatian, next in French, and finally in English. Speleobiologists as well kept reinventing the wheel—who knows how many biologists discovered and rediscovered that the Pleistocene may have driven animals into caves. Twenty-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.

How times have changed. 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. The globalization of subterranean biology and collaboration among speleobiologists has been made possible, especially because of Internet and World Wide Web. The growing and now nearly universal use of English as the language of scientific communication has opened up new avenues for cooperation and collaboration. New technology, including the possibility of sequencing DNA molecules (Porter 2007), the availability of increasingly sophisticated software for phylogenetic reconstruction, and the possibility

[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*.

of storing and analysing large quantities of spatial information (especially databases and Geographic Information Systems), has created new potentialities in the analysis of subterranean species and communities. This combined with new conceptual advances, such as vicariance biogeography, the joint analysis of evolution and development (evo-devo), and ecosystem models, has led to the current golden age, with an accompanying explosion of published information.

In the past 20 years, several milestone books on subterranean biology have been published, including *Groundwater Ecology* (Gibert *et al.* 1994a), the three-volume *Encyclopaedia Biospeologica* (Juberthie and Decu 1994–2001), *Subterranean Ecosystems* (Wilkens *et al.* 2000), *Encyclopedia of Caves* (Culver and White 2005), and *Encyclopedia of Caves and Karst Science* (Gunn 2004). Collectively they have advanced the field of subterranean biology by leaps and bounds, but none of them are introductory accounts. Hence this book.

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 biogeographic history of subterranean species? Are they in old, relict lineages (Chapter 7)? How does their distribution relate to past geologic 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 geographic 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 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 provided an extensive bibliography and hope that interested readers will pursue the subjects further. When English language articles were 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. Maps of sites mentioned in the text are 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% of the Earth's land surface is honeycombed with caves and springs, part of landscape called karst that is moulded by the forces of dissolution rather 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 just list 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 Janez Mulec for reading the entire manuscript and making many helpful suggestions. Daniel W. Fong, Horton H. Hobbs III, William R. Jeffery, William K. Jones, Megan Porter, Peter Trontelj, and Maja Zagmajster all read selected chapters and helped us avoid many mistakes. Several colleagues provided unpublished photographs and drawings—Gregor Aljančič, Marie-Jose Dole-Olivier, Annette Summers Engel, 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—Louis Deharveng, Marie-Jose Dole-Olivier, Stefan Eberhard, Annette Summers Engel, Daniel W. Fong, Franci Gabrovšek, Janine Gibert, Benjamin Hutchins, Florian Malard, Georges Michel, Pedro Oromi, Metka Petrič, Megan Porter, Katie Schneider, Boris Sket, Peter Trontelj, Rudi Verovnik, and Maja Zagmajster. Jure Hajna and Franjo Drole of the Karst Research Institute ZRC SAZU devoted many hours to scanning and producing diagrams. Maja Kranjc, in charge of the magnificent library at the Karst Research Institute, has constantly helped even in the face of increasingly panic-stricken requests for books and journals. Daniel W. Fong, Benjamin Hutchins, Karen Kavanaugh, and Wanda Young cheerfully handled our many requests for materials from American University while we were writing the book at the Karst Research Institute in Slovenia.

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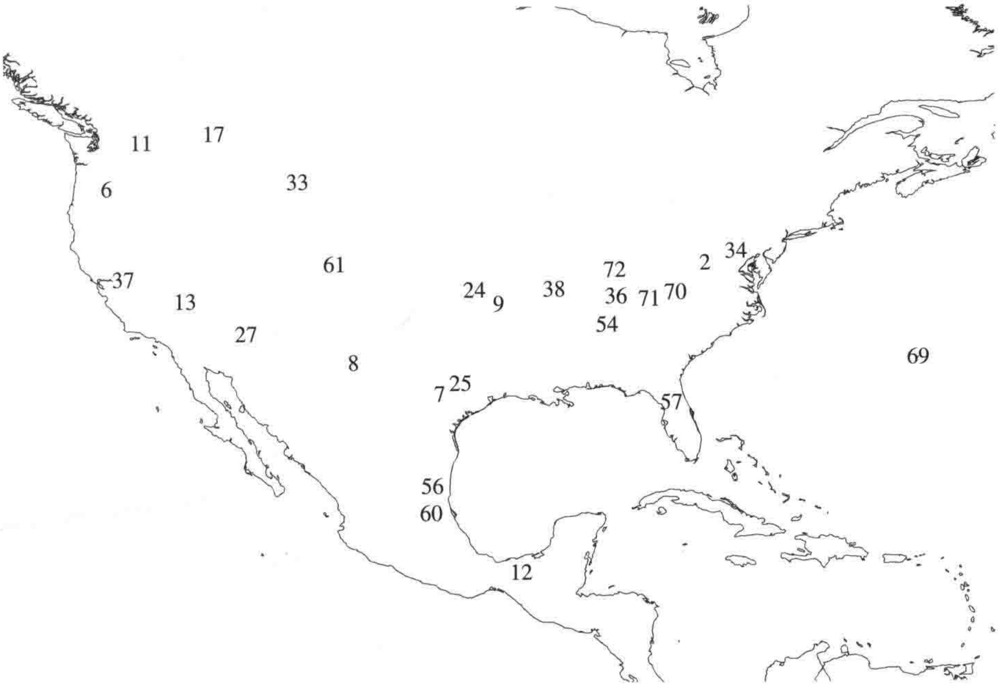
A project of this magnitude was a burden on both of our families, and we are especially grateful to our spouses, Gloria Chepko and Miran Pipan, for providing both understanding and support.

Postojna, Slovenia
March 2008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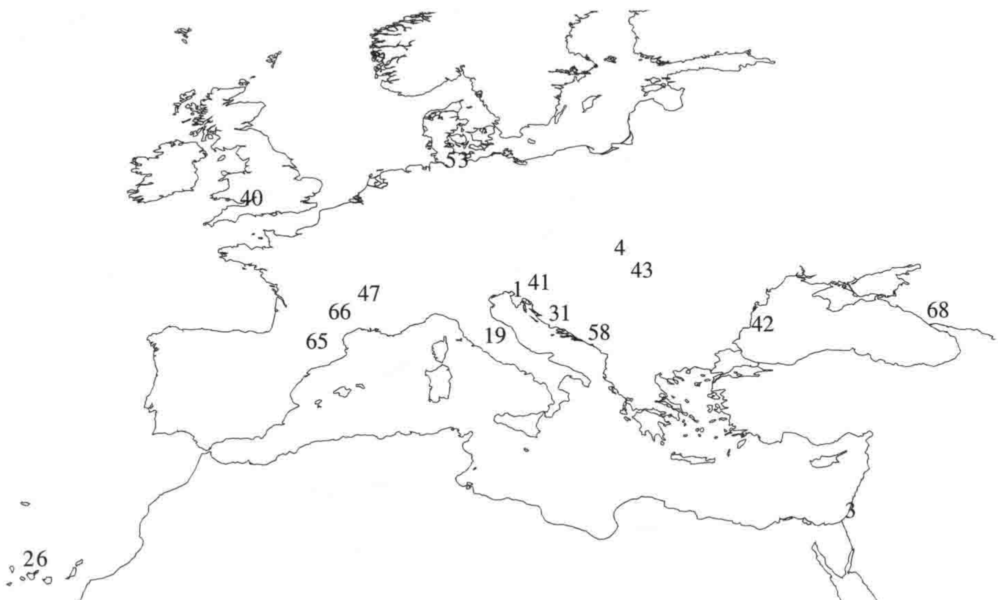
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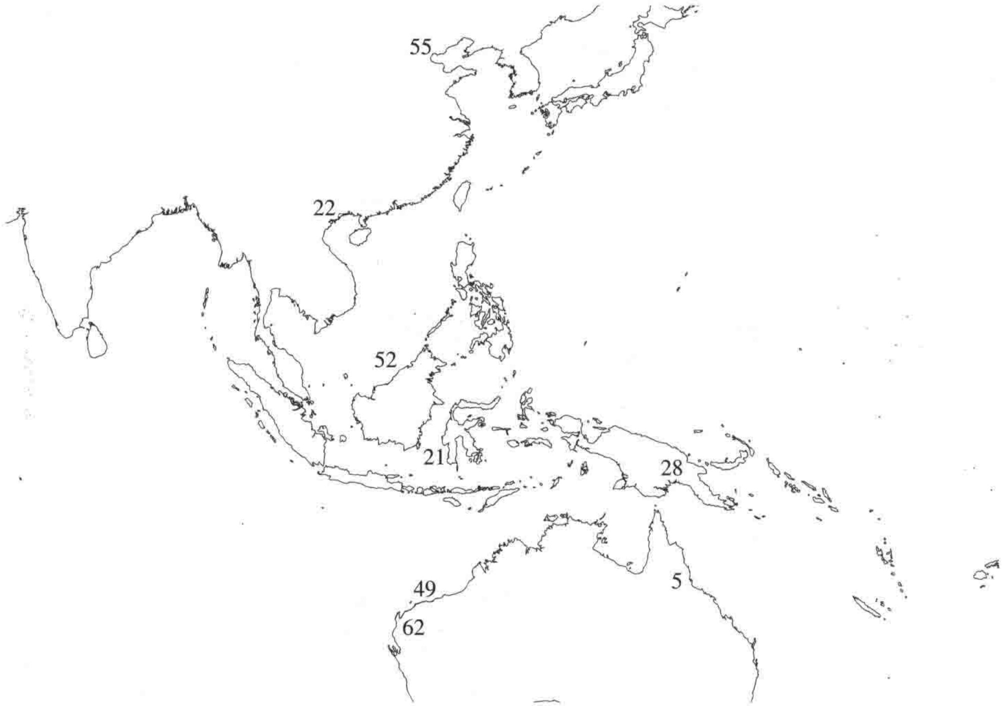
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# Site Maps and Gazetteer

List of sites mentioned in text. The associated number refers to the numbers on the maps. Several sites in Bosnia & Herzegovina, France, Slovenia, and West Virginia (USA) were so close to each other that they are represented by the same number. All sites can be found on one of the three maps, except for sites 29 and 51.

| | |
|---|---|
| Abisso di Trebiciano, Italy | 1 |
| Alpena Cave, West Virginia, USA | 2 |
| Ayyalon Cave, Israel | 3 |
| Baradla/Domica, Slovakia/Hungary | 4 |
| Bayliss Cave, Queensland, Australia | 5 |
| Bellissens, France | 65 |
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