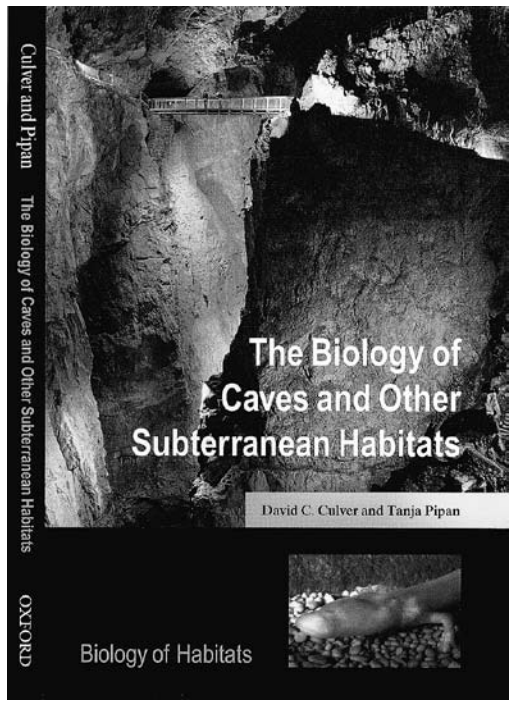
THE BIOLOGY OF CAVES AND OTHER SUBTERRANEAN HABITATS



David C. Culver and Tanja Pipan 2009: The Biology of Caves and Other Subterranean Habitats
Oxford University Press, Oxford. 256 pp., ISBN 978–0–19–921992–6 (Hardback), ISBN 978-0–19–921993–3 (Paperback). Price: 66 EUR Hardback and 33 EUR Paperback.

The prosperity of any scientific discipline depends critically on the quality and quantity of the record of knowledge it has accumulated. In this respect, subterranean biology can be considered quite fortunate. Several eminent publishers have included special "subterranean" volumes in their series on ecosystems, habitats and biodiversity. A number of encyclopedic works are dedicated, in full or in part, to cave animals and other subterranean life. Several countries have published monographs of national or international significance, many of which are available in English. Nevertheless, a certain type of book, most beneficial for the future of a discipline, has been missing: a clear and concise introduction, a textbook so to say.

The number of Biospeleology, Speleobiology, or Subterranean Biology classes taught at universities throughout the world is probably quite small. This might be the main reason why no textbook has been published until now. The interested student had to work his way through using literature either to voluminous (Encyclopaedia biospeologica), too technical, too trivial, or too scattered for efficient study. In this review I shall try to show that Culver and Pipan have succeeded in filling the gap. Criticisms should be read having in mind the needs of the student, rather than the intellectual satisfaction of the specialist.

The text is structured into 10 chapters covering most, but not all areas of contemporary subterranean biology. It starts with an overview of different kinds of subterranean environments and their physical and geochemical properties. An ecosystemic introduction follows in two different chapters (two and four). The first is about energy sources, the second dealing with the gross function of subterranean ecosystems with emphasis on the fate of organic carbon as limiting factor. Special attention is devoted to the ecology of sulphidic caves with entire pro- and eukaryotic communities depending on the chemoautotrophy of sulphur-oxidizing bacteria. The two ecosystemic chapters are separated by a concise and appealing systematic overview of subterranean life. This

is the largest chapter of the volume as it not only presents the (numerically) most important groups of cave inhabitants, but also issues concerning the classification of cave life (troglo-biont, -phyle, -xene), and methods of study. The fifth chapter is dedicated to the structure of subterranean communities and interactions between species such as predation and competition for resources. Although here both authors have conducted research of their own, biotic interaction and community ecology remain among the most underrepresented parts of subterranean biology. Those interested in subterranean communities may continue reading at chapter 9 in which some representative subterranean communities in all important subterranean habitats from several continents are described. Again, due to the deficiency of research results in this field, the accounts are descriptive and qualitative rather than quantitative. Comparisons based on species dominance or diversity indices are not possible. The finest subterranean biology has to offer comes in chapters six (on selection and adaptation) and seven (on colonization and speciation). The subjects of these two chapters have a long history of investigation and are covered by a large body of literature. Most of the research here has been hypothesis-driven, and is continuing to thrive by the use of modern molecular and computational approaches. The authors make good use of these advantages, not forgetting Darwin's infamous digression on the evolution of cave animals. Next, geographic diversity patterns are presented and tentatively explained. This is one of the youngest of the major fields of subterranean biological research, as exemplified by the recency of the references. Hence, it is not surprising that several exciting new discoveries like new diversity hotspots and regional rank lists still lack explanation, and first vague hypotheses are just being proposed. The biodiversity chapter sets a context for the last and, in a sense, most important part of the book, dealing with threats and conservation of subterranean environments and their biotas. A succinct section at the end of each chapter summarizes the most important information and concepts. Read alone, these summaries suffice as an overview of what subterranean biology actually is. Students shall find them useful as they recap the relevant key words and phrases.

One way to test a book before reading it in whole is to pick a few specific topics which one associates with certain prior expectations. When in my doctoral years, I had troubles understanding the dispute of active vs. passive invasion; the alleged struggle to prove the action of natural selection in caves seemed to me like proving the obvious; and I could not get a clue about how the MSS (milieu suterrain superficiel) really looked from what I have read and heard about it. Let us see how, as a student, I might have benefited from The Biology of Caves and Other Subterranean Habitats.

To find an answer to my first problem, I searched the Index for 'Invasion' and could not find it. Culver and Pipan did not include this cumbersome heritage at all. Instead, in 'Colonization and speciation' (Ch. 7) real biological problems and testable hypotheses like vicariance and dispersal are discussed. A wise decision. A debate largely based on long refuted views like orthogenesis and different interpretations of words has no place in a concise textbook.

My second question, concerning the doubt about adaptiveness, would have been answered after I read not only the adaptation section (Ch. 6), but also the Preface. These excerpts from both parts should give a flavor of the wide-angle view the authors take:

"[More then 25 years ago] most speleobiologists were not writing in English and the discipline remained largely a national one. ... [They] kept reinventing the wheel – who knows how many biologists discovered and rediscovered that the Pleistocene may have driven animals into caves."

"Racoviță takes Darwin to task for ignoring natural selection in subterranean environments:

...he [Darwin] thinks the struggle for life does not exert itself in this environment. It has been seen that this idea is wrong (Racoviță 2006).

Enormously influential among European speleobiologists, Racoviță unfortunately had negligible impact on American speleobiologists."

Reading this helped me realize that my own view was biased – not in a negative sense, though. Studying speleobiology under Boris Sket, I was given little chance to think of troglomorphic traits outside the framework of natural selection.

Finally, my attempt to understand the nature of MSS with the help of this textbook would probably have left me slightly disappointed. It is not how the MSS is described ("Interconnected cracks and crevices in scree slopes and similar habitats") or conceptualized graphically (Fig. 1.16). These presentations are undoubtedly correct, yet the MSS remains virtually impossible to imagine for someone who has not seen it. Such an important and at the same time exotic environment deserves a clearer visual explanation. A photo, a more realistic picture, a hint on its horizontal extent, the size of rocks and in-between spaces, and an explanation of why the spaces are filled with sediments in the tropics but not in temperate zones, would be helpful.

This brings us to what I think is a potential weak point of this book if it is to serve as an independent study aid. The quality of photos and graphics does not reflect the brilliance of the text. A few pictures are difficult to

read (e.g. 1.6), some are too technical for a text book (e.g. 8.15), and some just look pathetic in black-and-white, like photos of two grey Proteus, allegedly one with pigment and the other without. Clear textbook-style color graphics are on my wish list for the next edition. Further, understanding some very substantial parts of the text requires at least basic familiarity with methods that are not or not sufficiently explained. Among them are biodiversity estimation (Chao2, jackknife, Mao-Tau), phylogeography, phylogeny, and molecular dating. As a phylogeneticist I stumbled upon the definition of "monophyletic" in the Glossary: "Having arisen from one ancestral form; in a strictest sense, from one initial population." This is a bit too wide as it applies to any arbitrary bunch of beings from this planet.

In retrospect, however, the few mistakes are rather minor and completely outweighed by the work's strengths. These are, to summarize only a few, the balanced account of all important subjects, the integrative, multidisciplinary approach, state-of-the-art and problem-oriented presentations, and last but not least, the fact that it embraces all subterranean life, not just cave fauna. Together with the new name of an old international society (International Society for Subterranean Biology) and a scientific journal called Subterranean Biology, Culver and Pipan are at the forefront of spreading this new and wider view about life in the subterranean domain.

Another book, at a first glance similar in scope and content, is fresh from the press in 2009 (Cave Biology by Aldamero Romero from Cambridge University Press). For indecisive readers it should just be said that Romero is not an entry-level text. It is challenging reading that deserves to be reviewed on its own. The Biology of Caves and Other Subterranean Habitats is beyond doubt the volume of choice when it comes to proposing a comprehensive, scholarly introductory text. There has never been anything like it in the 180 years of history of the discipline.

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