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Author: Poulson, Thomas L.

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Two Very Different Books on Cave Biology

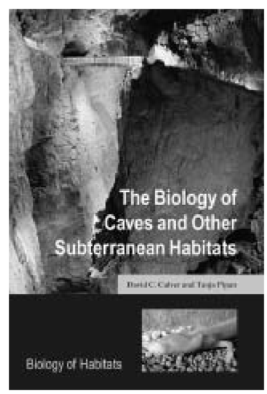
The Biology of Caves and Other Subterranean Habitats. David C. Culver and Tanja Pipan. Oxford University Press, 2009. 256 pp., illus. $60.00 (ISBN 9780199219933 paper).

Cave Biology: Life in Darkness. Aldemaro Romero. Cambridge University Press, 2009. 306 pp., illus. $62.00 (ISBN 9780521535533 paper).

The Biology of Caves and Other Subterranean Habitats is a broad review of all aspects of subterranean biology with particular emphasis on approaches and techniques that have emerged and matured since David C. Culver's 1982 book *Cave Life: Evolution and Ecology* (Harvard University Press). Culver is now professor of environmental science at American University; his coauthor Tanja Pipan is at the Karst Research Institute in Slovenia. In this new book Culver and Pipan discuss life in all subterranean habitats, not just caves.

The Biology of Caves continues the strength of the earlier volume with its blend of theory and natural history balanced with data and case studies. It includes an abundance of equations, graphs, tables, and statistical analyses. The authors discuss recent research topics, such as the use of stable isotopes, vicariance biogeography, evo-devo (evolutionary-developmental biology), DNA sequencing to construct phylogenies, and the relation of interstitial and epikarst habitats to cave habitats. Despite the book's having only 451 references, the authors describe in detail a variety of landmark studies on organisms in North America, Europe, and Australia.

Culver has been one of very few biospeleologists to use ecological and evolutionary theory in cave biology and has pioneered the use of large databases of spatial information in studies of cave biogeography. In the preface of *The Biology of Caves,* the authors review the explosion of peer-reviewed research, new techniques and approaches, books, and compendia since 1982, which has resulted in what they call "the golden age of biospeleology."



A brief history of biospeleology is provided in the chapter on adaptation; then begins the treatment of ecology with a discussion of the subterranean domain. The authors explain the importance of all kinds of subterranean spaces, including aquifers, and recount why interstitial and epikarst spaces are so important to understanding the ecology and evolution of cave organisms. Next, they discuss ecosystem function and detail the few studies of carbon input routes and processing. Another chapter covers sources of energy and gives a conventional but up-to-date treatment that includes the use of stable isotopes and the importance of biofilms. The authors emphasize the predominately allochthonous input of organic carbon by percolating water, sinking streams, wind and gravity, tree roots, and animal feces that enters and exit caves regularly. They also include impressive summaries of recent research on food webs of the few known cases in caves where autochthonous production by chemoautotophy is found.

The meat of the last ecology chapter (biological interactions and community function) consists of two case studies—Culver's own study of amphipods and isopods in cave streams, and my own research done with my students on a beetle eating cricket eggs. Culver's case studies provide enough species to study the nature of all pairwise species interactions—from +/+ mutualism to +/– predation to –/– competition—as well as indirect interactions, such as those expressed as "the enemy of my enemy is my friend." There are advantages to both systems, and the observations and experiments of each can be accomplished in the field and in the laboratory to test hypotheses about the mechanisms of competition and predation.

The first chapter on evolution in *The Biology of Caves* presents three case studies. The first system reviewed is my study of Amblyopsid fishes, which compared one surface species, one troglophilic species, and four troglobitic species that have been isolated in caves for increasing periods of evolutionary time. My emphasis was on these top predators' adaptations to apparent food scarcity in caves; Culver and others have explored adaptation in more depth, especially with amphipods, by directly demonstrating the joint effects of natural selection and neutral mutation. Culver and Pipan next review the most-studied cave organism, the Mexican surface and cave tetra *Astyanax mexicanus.* Over the past 10 years, William R. Jeffery and colleagues have added to Horst Wilkens's 35 years of morphological and genetic studies on the species with cutting-edge and elegant molecular, genetic, and developmental experiments to study how control genes affect eye degeneration.

In a chapter on colonization and speciation, Culver and Pipan analyze the historical aspects of biogeography as it relates to caves. Their discussion of the four phases offers detailed

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examples of each. Within the first phase of colonization, two hypotheses are posited. First is the "climatic relic hypothesis," which theorizes that cold or dry climates caused the extinction of certain surface populations of species, of which the only survivors are found in caves. This hypothesis seems pertinent along the continental glacial borders. The alternative, which holds especially true for lava tubes, is the "adaptive shift hypothesis"; it posits that species actively invade caves that are "better" than the surface in terms of food supply and the absence of enemies. The second phase is what determines success or failure of the colonists; the third phase is the mode of speciation should the colonist succeed; the final phase is whether cave-to-cave dispersal occurs after speciation. For extant cave species, molecular genetic analyses of DNA are required to determine why populations look similar. One scenario allows for a formerly widespread surface ancestral species to colonize caves separately; the descendant species look similar because they are closely related cryptic species. In the alternate scenario, different surface species colonize caves; in this case, the descendant species look similar because the same agents of natural selection lead to a convergence in the morphology of unrelated species.

When Culver and Pipan turn to provisional explanations for patterns of species richness—at the cave, karst region, continental, and global scales—a complicated issue unfolds and no clear generalizations emerge. The authors start with statistical approaches to address the incompleteness of sampling that is exacerbated by high endemism and rarity of most cave species. Then they turn to analyses of caves as islands because of the rich theory that has grown out of MacArthur and Wilson's *The Theory of Island Biogeography* (Princeton University Press, 1967)—that distance and area are important determinants of the equilibrium between colonization and extinction in both ecological and evolutionary time. The authors find that the island theory is predictive only for certain subterranean habitats and only for some spatial scales.

Another approach pioneered by Culver and Pipan in *The Biology of Caves* is to explain global and regional patterns with statistical analyses of large databases. To me, the most interesting result of this technique is the designation of 36 global hot spots of cave biodiversity having 20 to more than 100 species per cave. These caves are hot spots either because they have especially high productivity as a result of roots in lava tubes or chemoautotrophy, or because the cave systems are very large with complex geological histories.

In a chapter on representative subterranean communities, the authors describe the faunal composition of a well-studied example for each of 15 subterranean communities. Except for seeps and caves, all of these are sampled by indirect means such as traps, nets, and pumps. A short treatment is given to each of three "superficial habitats," four "interstitial habitats," and eight "cave habitats."

Overall, the wide-angle lens of *The Biology of Caves* is refreshing and unbiased, and the book complements Culver's earlier works. By comparison, *Cave Biology: Life in Darkness,* is an idiosyncratic work that concentrates on just a few subjects and on only one subterranean habitat—caves. Author Aldemaro Romero states in his preface that "this book will challenge the conventional wisdom...[and] is likely to create controversy…and advance ideas...that in my opinion have been overlooked by many practitioners of biospeleology."

Romero is currently dean of the college of arts and sciences at Southern Illinois University and was previously a professor of biology at Arkansas State University. His research papers are on the natural history of fish at the interface of cave and surface habitats. In *Cave Biology,* his first book, Romero's discussions of the history of biospeleology and of its key people should be required reading for anyone interested in cave biology. But this book has little depth in biospeleological research and contains virtually no theory, data, or equations. It has only two graphs, a few tables, and no statistical analyses. It covers almost no modern topics, such as the use of stable isotopes to understand food webs or the use of vicariance biogeography to understand the many independent isolations of related species in even adjacent caves. Despite the book's 1151 references, most of the few case studies Romero discusses in any detail are his own and concentrate on just a few organisms, mainly the cave and surface tetras in Mexico. Curiously, he does not reference Culver's 1982 book, which covers, in more rigor and breadth, the same ground as his own newer volume.

Romero's brief history of cave biology is, by far, the best part of his book. In 60 pages he uses copious and interesting footnotes and presents a scholarly discussion. But in his two-page summary on the first modern American biospeleologists, he criticizes T. C. Barr Jr., John R. Holsinger, K. A. Christiansen, as well as Culver and myself: He writes that they "have not escaped the shadow of neo-Lamarckism and orthogenesis, by their uncritical use of such terms as preadaptation and regressive evolution." Perhaps not surprisingly, I think his tone and pages of prose far overdo this criticism.

Both books under review have surveys of subterranean organisms and use a more-or-less taxonomic hierarchy. Culver and Pipan do the job in 20 pages and cover all subterranean habitats, whereas Romero takes 67 pages and includes only caves. Romero covers all groups, but Culver and Pipan cover only groups that have 50 or more described species. Romero has more notes on the ecology of different organisms.

Both books cover the terminology for ecological and evolutionary grades of restriction to caves. Romero sets up the straw man of a "hypogean archetype" to critique the use of "troglomorphism" by many workers, and he emphasizes what he calls the "artificiality" of some ecological terms. Culver and Pipan, in contrast, find the use of "troglomorphism" useful

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to describe adaptations. And they are much more neutral about what they call the "terminological jungle" of ecological descriptors. They discuss the range of organism association with caves from "trivial or temporary to profound or permanent." Trivial inhabitants (a.k.a. accidentals) such as frogs are contrasted with temporary inhabitants (a.k.a. trogloxene, or cave guests) that may use caves for part of their life cycles, such as some salamanders and bats. Profound inhabitants (a.k.a troglophiles, or facultative species) can but do not have to complete their life cycles in caves. Troglophiles include many species that may be on the way to becoming permanent inhabitants (a.k.a. troglobites: obligate cave inhabitants).

These two volumes differ dramatically in their extent of coverage of the aspects of cave ecology. Romero limits his discussion to one chapter and several pages of another, and he does not include case studies. Culver and Pipan use four chapters for more complete coverage and include detailed case studies. Romero's chapter on the ecology of cave organisms continues his predilection for setting up straw men and criticizing what he variously calls "typological generalizations" and "allegations." But he neglects many relevant papers in the two compendia he references; as for his statement that "little is known about competition in caves," he would do well to start by reading Culver's 1982 book.

The number of pages devoted to evolution in the two books is relatively equal, but Romero covers less ground, gives only brief case studies, and continues a polemical style. His chapter on evolutionary biology is mostly a promotion of his favorite hypothesis for cave colonization. He argues that other hypotheses—"the climatic relict" and "the adaptive shift"—do not hold universally. I agree. I also agree that phenotypic plasticity, as one mode of epigenesis, has not been given enough attention in the process of cave colonization. However, I find his continued criticisms of others' use of a "hypogean archetype" and his use of the terms "preadaptation" and "regressive evolution" to be tiresome at best. No American biospeleologist takes these ideas literally anymore; all of us agree with Romero that rudimentation, especially of eyes and pigment, and elaboration, especially of extra-optic sense organs, are convergent evolutionary results of isolation in caves. Romero also does not cover the related topic of patterns of biodiversity, whereas Culver and Pipan do.

The final section of each volume addresses the conservation and management of caves. Both books emphasize the most serious threats—water pollution, especially by decomposable organic matter, and disturbance of bats, especially by poorly designed gates. Both books could do a better job in covering several topics:

- the movement of pollutants into caves by percolation or sinking streams and conduit flow transfer over long distances,
- the importance of bioaccumulation and biomagnification of toxins,
- the difference in microclimates for bat hibernacula and maternity colonies, and
- issues of artificial entrances.

Regarding conservation and management, Culver and Pipan go further than Romero in four ways: (1) They use case studies; (2) they discuss laws and conventions meant to protect caves at the international level (e.g., United Nationals Educational, Scientific, and Cultural Organization World Heritage Sites), national level (e.g., US Endangered Species Act), and local level (e.g., ownership of caves by nongovernmental organizations); (3) they explain that subterranean species, along with great endemism and many cryptic species, show "geographic rarity" more than "numerical rarity," with "habitat rarity" being very uncommon; and (4) they present an intriguing map of Europe that shows sites with high levels of species richness, endemism, and complementarity.

Only *Cave Biology* includes an epilogue; in it, Romero outlines "unanswered questions" but does not provide testable hypotheses or a suggested research program. It is too bad that he has not followed up his preliminary studies of Mexican tetras, in which he raised cave fish in the light and surface fish in the dark. This information would have given us more insight into behavioral plasticity, phenotypic plasticity, opportunistic evolution, and colonization of caves. Ultimately, I agree with Romero's statement that "this book is not saying anything essentially new." It is sad that he ends by beating the same dead horses of regressive evolution and preadaptation. His final sentence is, "many classical biospeleologists are unable to distinguish metaphor and metaphysics from science."

In summary, both books are well written, and are aimed at and accessible to educated audiences at both college and professional levels. I highly recommend *The Biology of Caves* but suggest that readers consult *Cave Biology* only to read its excellent section on history. Together, these volumes offer a complete view of biospeleology.

THOMAS L. POULSON
Thomas L. Poulson (tomandliz@bellsouth.net) is professor emeritus in the Department of Biological Sciences at the University of Illinois at Chicago.

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