INTERVIEW WITH DAVID CULVER "FOR MOST OF ITS HISTORY, BIOSPELEOLOGY HAS BEEN A POOR COUSIN OF THE OTHER SPELEOLOGICAL DISCIPLINES"

Conducted by IVO LUČIĆ

Our series of interviews with leading karstologists now turns to cave biologist. David Culver, an emeritus professor of environmental science at the American University (Washington DC, USA), talks about his relationship to karst and what subterranean biology has given to the geoscientific disciplines and what it has taken from them. His science approach is well reflected in the statement: "In the last few decades, I have done valuable little completely independent research, and collaboration with people with different skill groups has been critical".

PERSONAL AND BEGINNING

What attracted you to study biology connected to karst?

When I was a first year student at Grinnell College, I did an independent study project on the morphology of cave Collembola in Kenneth Christiansen's laboratory. I was immediately fascinated with them in part because as a young student I was interested in evolution. I got this interest from my father who was a high school biology teacher. Ken was interested in puzzling out why the claw of Collembola was different in cave populations from surface populations, and that the cave populations were different in the same way, even though they were from different geographic regions. So, I spend the next three years studying *Pseudosinella hirsute.* What I understood about the cave environment was largely from looking at specimens. I didn't even get into a cave for over a year after I started the project, and then it was in Iowa caves, which are relatively depauperate, being in a glaciated region.

What or who influenced you to select it for your entire career: childhood experiences, scientific interest, or some important persons from the karst world?

Kenneth Christiansen was the first person who got me interested in caves and cave biology. His primary interest at the time I was an undergraduate (the mid 1960's), was in adaptation, and he was very much part of what has come to be called neo-Darwinism. It was certainly a minority view in cave biology in the mid 1960's, which was dominated by anti-selectionist views of French cave biologists, such as Vandel and Jeannel. Together with Thomas Barr at University of Kentucky and Thomas Poulson at Yale University, he developed what is sometimes called the North American selectionist school of biospeleology. I went to graduate school at Yale to study with Thomas Poulson. While Ken was deeply rooted in taxonomy and systematics, Tom was a comparative physiologist and ecologist, and his interest in comparative, hypothesis driven studies set me on a course of studying the evolutionary ecology of simple cave communities. The time of my graduate studies was a very exciting one in the field of evolutionary ecology. The mathematical models and hypothesis testing of Robert MacArthur and Richard Levins were all the rage, and

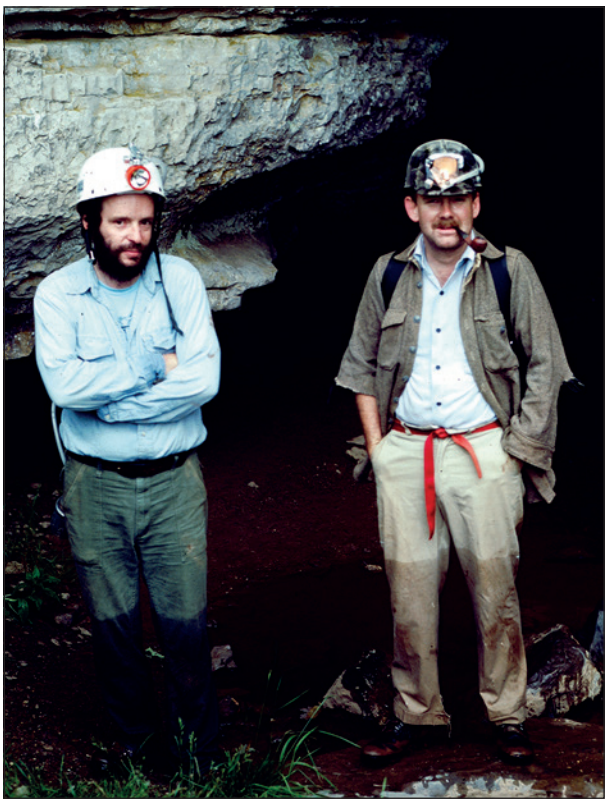

Fig. 1: David Culver with Bill Jones (right) at the entrance to Sinks of Gandy, ca. 1975 (Photo: W.K.Jones).

I took nearly as many math course in grad school as I did biology course. I also had the great good fortune to do a post doc with Richard Levins, and his approach to ecological questions, even though he never was even in a caves, stayed with me permanently.

Since my post-doc, a number of colleagues have focused my interest in various aspects of cave biology. I have been like a sponge, soaking up ideas and approaches. Among those with the largest impact are Dan Fong, who sharpened my interest in rigorously testing adaptationist hypotheses; Thomas Kaine, who showed me how molecular genetic studies complemented more traditional approaches; Mary Christman, who taught me how to frame interesting hypotheses in a statistical way; and Tanja Pipan, who got me to understand community-wide and ecosystems approaches.

Fig. 2: Culver using a Bou-Rouch pump in Rock Creek, Washington, D.C., 2004 (Photo: W.K.Jones).

How would you define exactly your discipline, its name and subject, as well as its connection to karst?

For Americans, this is both a difficult and complicated question. To begin with, there are no research or teaching positions for biospeleologists or cave biologists. Until very recently, there were no institutes devoted to the study of karst. American cave biologists have found jobs as evolutionary biologists, as geneticists, as microbiologists, etc. Hence the name speleobiologist is perhaps more descriptive than biospeleologist. Even this is too restrictive because we must also be ecologists, evolutionary biologists, or some other major branch of the life science. This is not to say that some American cave biologists are not deeply conversant with cave geology and other non-biological aspects of speleology. Examples that come to mind include Thomas Barr, John Holsinger, and Matthew Niemiller, but it is certainly not universal. However, that knowledge was and is not part of their job description.

SUBTERRANEAN BIOLOGY DEVELOPMENT

How did the world of biospeleology appear at the start of your career in the late 1960's?

Of course, the world of science in the 1960's was much more fragmented than it is now. Travel was much more expensive and difficult, especially between the eastern and western blocs. Additionally, the language barrier was much greater, and in particular, relatively few scientists out side of anglophone countries knew English. Biospeleology tended to be much more national in character, and different language groups were much more isolated. The discipline itself was dominated by taxonomic description, and there was relatively less more general writing. The one book that was widely available was Albert Vandel's 1964 *Biospéologie,* which was translated into English in1965. The book was very useful as a catalog of species adapted to caves, as well as a summary of what was known about their biology and ecology. Its utility was limited because of its anti-Darwinian stand, which was entirely unacceptable to American speleobiologists. Briefly, Vandel held that animals were not blind because they were in caves, but were in caves because they were blind! Christiansen's classic studies of adaptation in cave Collembola were a response and challenge to the views of Vandel. In North America, neo-Darwinian studies of cave animals were flourishing. Working in Germany on captive populations of the Mexican cavefish *Astyanax,* Horst Wilkens provided a counterweight to adaptationist views by proposing the eye and pigment loss were the result of neutral mutation. European work tended to be more ecological than North American work, with an emphasis of community structure and the occurrence of eyeless, depigmented organisms in non-cave subterranean habitats, such as the underflow of streams. This work went largely unnoticed in the U.S.A., mostly because papers were mostly in French and other European languages. But perhaps the most salient feature of biospeleology in the mid 1960's was how many really interesting cave organisms there were, and their potential as model systems for various aspects of biology.

Where were the centers of biospeleological research at that time?

The main center was certainly the Laboratoire Souterraine in Moulis, France. It housed a number of prominent researchers, especially Christian and Lysianne Juberthie and Raymond Rouch. Scientists from all over the world spent time there, and it had both excellent biologists and and exceptional fauna. It had a geosciences component as well, including Alain Mangin. The Laboratoire Souterrane had an excellent library as well, and was supported by CNRS. By the mid-1960's the research group at University of Claude Bernard at Lyon 1 (headed by René Ginet) was very active, somewhat later the Subterranean Ecology and Hydrobiology Research Team was formed by Janine Gibert. The Emil Racovitza Institute of Speleology in Cluj and Bucharest was also very active at the time, but travel to and from Romania

Fig. 3: Culver with the late Horton H. Hobbs III exiting a wet West Virginia cave in 2005 (Photo: W.K.Jones).

made it much less prominent. Individual researchers were scattered, and important researchers were in former Yugoslavia (especially Slovenia), Italy, Germany, and USA.

What was the perception of biospeleology in karstology's circles in that time? How did you feel as a biospeleology researcher compared to colleagues of others karstology disciplines, like geography, geology…?

For most of its history, biospeleology has been a poor cousin of the other speleological disciplines. In textbooks of speleology, biospeleology is relegated to a chapter at the end of the book. In accounts of individual caves, biology is often not treated, although there are notable exceptions, especially the account of Vjetrenica in Bosnia & Hercegovina by Lučić and Sket. Part of this is understandable since much of biospeology, including systematics and biodiversity, is largely independent of the other karst disciplines. However, there are two areas of direct connection, areas that are receiving attention from other speleologists. These are ecosystem studies and the role of microbes in speleogenesis. What is certainly true is that more biospeleologists know more about physical speleology than in the past.

Which phases do you see in subterranean biology development, and what do you see as milestones?

Thomas Barr, among others, have suggested phases in the development of subterranean biology, beginning with discovery and species description, and culminating in large scale evolutionary and ecological syntheses. But, in fact, all these activities occur simultaneously. Racovitza's major synthesis of biosepeology "Essai sur les problèmes biospéologiques" was written early in his career, and new species are constantly being described, even in well studied areas such as the Appalachians in the USA. What is the case is that the ready availability of comparative data in analyzable form has meant big leaps forward in our general understanding. I am thinking here of both large datasets of species distribution, such as was assembled under the European PASCALIS (**P**rotocols for the ASsessment and Conservation of **A**quatic **L**ife **I**n the **S**ubsurface) program and libraries of gene sequences. I tend to view developments in subterranean biology as part of a continuum, but the development of both the molecular techniques for large-scale gene sequencing and geospatial analyitical continues to allow for rapid progress.

Can you compare the history of biospeleology in the Dinaric Karst and other parts of the world?

I am not really the one to explore the subtleties of the history of biospeleological research in the Dinaric Karst, but that just as the Dinaric karst is the birthplace of speleology and theories of speleogenesis (Cvijić and others), it is also the birthplace of subterranean biology—the first cave animals were described from the Dinaric karst. However, it was not until Sket's pioneering pair of papers on subterranean biodiversity 1999 that the quantitative extent of subterranean diversity in the Dinaric Karst became clear. The northwest Dinaric Karst of Italy and Slovenia is still recognized as the global hotspot of subterranean biodiversity. Equally important to the preeminence of the fauna of the Dinaric karst is the strong

research group that has studied. Centered at the University of Ljubljana, the SubBioLab is a center of biospeleological research

KARSTOLOGY TODAY

Is the umbrella of karst science needed for your research?

While not all of my research has utilized or required other karst sciences, some of it has. In particular, my studies of ecosystem dynamics, especially with respect to the flux of organic carbon and my studies of the fauna of epikarst, has been, at a minimum, greatly enhanced by other karst sciences. As a practical matter, I have tried to make for a stronger umbrella for my research first by working with Tanja Pipan and her colleagues at the Karst Research Institute in Postojna, and by being on the prime movers in the establishment of the virtual institute, the Karst Waters Institute. One of the goals of KWI is the fostering of interdisciplinary and international karst research.

Can you describe your approach to biospeleology?

It has been my long-standing perception that two approaches have been applied to the study of karst problems, whether they are physical or biological. One is try to extract some overall general principles, even at the expense of detail. Wolfgang Dreybrodt and his students exemplify this in physical speleology. The other is to describe the incredible detail and diversity of both the physical aspects of caves and the biological aspects of caves. Taxonomy is a manifestation of this approach, which I think of as that of natural history. I am very much in the first camp, and in fact am a mediocre natural historian at best. Just as important for my approach has been the excellent collaborators. I have done precious little completely independent research for the last several decades, and collaboration with people with different skill sets has been critical.

Fig. 4: Culver standing next to a statue of J. Valvasor in Ljubljana in 2008 (Photo: W.K.Jones).

What do you see as your best contributions to biospeleology?

I tend to think of my most recent papers as my best papers both because I hope I have improved as a scientist over the years, and because they are my current interests. I do not have one particular contribution that it would call my best, but in terms of impact judged by number of references, the book that Tanja Pipan and I wrote, *Biology of Caves and Other Subterranean Habitats*, now in its second edition, is the most widely referenced of my publications. More generally, I think I have made interesting contributions in four areas, listed in chronological order:

- Population ecology
- Adaptation and natural selection
- Biodiversity patterns
- Non-cave subterranean habitats

What is subterranean biology today? What is its most significant interest today? What does subterranean biology see as the most crucial target now?

Like it or not, long-term sustained research requires funding, and so part of the priorities are set by funding agencies. I recognize that many in the speleological community particularly value the work done with volunteer help, and it will always be an important part of the research picture. I think that there are perhaps five threads of research today. The first is bioinventory and diversity pattern analysis, particularly when it is tied to strategies of species and habitat preservation and protection. The second is the historical biogeography (phylogeography) of subterranean colonization. The third is the microbiology of cave ecosystems, including their role in physical process like speleogenesis. The fourth is overall analysis of karst ecosystem processes, although this area desperately needs more funding. Finally, the study of evolution and development (evodevo) of the Mexican cavefish *Astyanax mexicanus* has opened many new possibilities in understanding adaptation to subterranean life, as well as providing valuale insights in to some human diseases, such as obesity. This last research area, which has its roots in the discovery of the Mexican cavefish in the 1940's has often followed a separate research agenda, partly a consequence of its heavy dependence on laboratory studies, but the overlaps with traditional subterranean biology are considerable.

Which regional centers seem to you most productive and most looking forward in biospeleology?

Certainly the most productive regional centers are the SubBioLab at University of Ljubljana, which probably has more subterranean biology researchers in a single center than anywhere else in the world. They are leaders in both phylogeography and biodiversity studies. A smaller but very active research group is at the Emil Racovitza Institute of Speleology in Cluj, also with an emphasis on phylogeograhy and biodiversity studies. The largest group studying the Mexican cavefish is at Florida Atlantic University. There are many other researchers at universities and institutes throughout the world that are doing excellent research on subterranean biology, but none are of the size of the three listed above.

What are the contributions of biospeleology to general karstology, in which branches, with which techniques, topics and results?

The contributions of biology to the general science of speleology seem to lie in two areas, or at least two areas that are well integrated with the rest of speleology. The first is the role of microbial processes, a topic ably introduced and outlined in the book *Microbial Life of Cave Systems* edited by Annette Summers Engel. The second is the possibility of a general treatment of a karst basin as an ecosystem. Some initial work on this has been done by Slovenian researchers (Petrič, Pipan, and Šebela) at the Karst Research Institute but a full scale analysis is yet to be done.

USA

Please, would you sketch the main features, values, research, environmental problems, and visions in the USA?

Research in subterranean biology has always been scattered about the country and that remains the case today. There is a concentration of *Astyanax* researchers at Florida Atlantic University (Keene, Kowalko, Duboue) and individual researchers at University of Hawaii, University of Minnesota (McGaugh), Stowers Institute (Rohner), University of Maryland (Jeffery), to name a few. Microbiology has a number of researchers interested in karst systems, including Engel at University of Tennessee, Macladay at Pennsylvania State University, and Barton at University of Akron. Phylogeography and biodiversity are less well represented than in Europe but active researchers include Niemiller (University of Alabama—Huntsville), Fong (American University), and Zigler (University of the South).

DINARIC KARST

Dinaric karst is recognized as the birthplace of biospeleology and karstology at all. How do you see the role of Dinaric karst in biospeleology today?

Fig. 5: Cartoon of Culver as the cover of an invitation to the Karst Waters Institute dinner which honored him with the Karst Science Award in 2015. Sketch by Lee Elliott, used with permission.

I believe that research in the Dinaric Karst will continue to be at the forefront, especially in the areas of biodiversity and phylogeography. The first reason is of course the unparalleled richness and complexity of the subterranean fauna, but the second reason is equally important—a concentration of high quality researchers with the availability of the tools of modern molecular genetics, at least in Slovenia.

Which research centers in Dinarides have abilities to answer contemporary problems of biospeleology?

In the areas of phylogeograph and biodiversity, the SubBioLab at University of Ljubljana is a word leader. The Karst Research Institute in Postojna, with its strength in physical speleology as well as ecology, is ideally positioned to conduct long term ecosystem studies. Finally, the molecular biology lab being developed at the Ruđer Bošković Institute in Zagreb promises to become an important center for the study of molecular biology of subterranean organisms, including the Mexican cavefish.

PUBLICATIONS AND POPULARIZATIONS

How much does karstology, especially biospeleology, take care of popularizations, and how much do biospeleologists invest in its popularization?

In my view there can never be enough written about karst and subterranean biology for the general public. This kind of writing is not a skill that many scientists possess, but we are fortunate that there are several science communicators with a special interest in karst science. Dane Fenolio, a researcher at the San Antonio Zoo, has

written an excellent "coffee table book", *Life in the Dark*, a model for both writing and photography. In the realm of adventure writing, Michael Ray Taylor has included a lot of information on geomicrobiology of caves in his books, *Dark Worlds* and *Hidden Nature.* We need more of this kind of writing.

FUTURE

How do you see the future of biospeleology and karstology?

The future I would like to see for subterranean biology is two pronged. First, I would like to see a greater integration of ecosystem studies and geomicrobiology in the discipline of karstology (I strongly prefer the term karst science). Biology should no longer be relegated to a desultory single chapter treatment completely independent of the rest of the material. Second, I would like to see an increased use of cave organisms and communities as model systems for the study of not only evolution, but biogeography, development, etc.