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CONTRASTING APPROACHES TO THE STUDY OF SUBTERRANEAN LIFE: BIOSPELEOLOGY AND SPELEOBIOLOGY

KONTRASTNA POGLEDA NA RAZISKOVANJE PODZEMELJSKEGA ŽIVLJENJA: BIOSPELEOLOGIJA IN SPELEOBIOLOGIJA

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David C. Culver & Tanja Pipan: Contrasting Approaches to the Study of Subterranean Life: Biospeleology and Speleobiology

The study of subterranean life in general and cave life in particular has been given several names, most especially biospeleology and speleobiology. Historically, biospeleology came first, and signalled that biological study was part of speleology, the science of caves. Speleology itself has come to have several meanings beyond the science of caves, but as a discipline it has not fully developed. Speleobiology emphasizes the connection with biology, especially ecology and evolutionary biology. Biospeleology can be construed as the taxonomic and distributional aspects of the biology of caves while speleobiology can be construed as the aspects pertaining to general biological principles such as evolution.

Keywords: Cave biology, cave science, karst, subterranean biology, speleology

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David C. Culver & Tanja Pipan: Kontrastna pogleda na raziskovanje podzemeljskega življenja: biospeleologija in speleobiologija

Preučevanje podzemeljskega življenja nasploh in zlasti jamskega življenja je dobilo več imen, predvsem biospeleologija in speleobiologija. Zgodovinsko gledano je bila biospeleologija prva in je nakazala, da je biološko proučevanje del speleologije, znanosti o jamah. Speleologija sama je imela več pomenov, ki presegajo znanost o jamah, vendar se kot disciplina ni v celoti razvila. Speleobiologija poudarja povezavo z biologijo, predvsem ekologijo in evolucijsko biologijo. Biospeleologijo lahko razlagamo kot taksonomske in distribucijske vidike biologije jam, medtem ko lahko speleobiologijo razlagamo kot vidike, ki se nanašajo na splošna biološka načela, kot je evolucija.

Ključne besede: jamska biologija, znanost o jamah, kras, podzemeljska biologija, speleologija

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1. THE SCIENCE OF SPELEOLOGY

The term speleology[1] was coined by Émile Rivière in 1890 to denote the scientific study of caves (Mattes, 2015). The term has come to have several meanings, including (1) the original meaning of a scientific discipline devoted to the study of caves, (2) an expanded definition to include subterranean environments in general, (3) a discipline that includes non-professional cavers (variously called citizen scientists, amateurs, and autodidacts, see Pérez, 2015) as well as professionals, and (4) the hobby of exploring caves (the "sporting science of speleology" according to Mencarini et al., [2021]). The "sporting science" is also used to include citizen science (Pérez, 2015), especially the mapping and description of caves and their locations. There are different nuanced meanings for the term, including French and German, but we limit ourselves, for the most part, to its English language use.

In the original, restricted meaning of a distinct scientific discipline, perhaps the clearest parallel to the term is oceanography, the study of oceans and the marine environment (Gèze, 1965). The vision of many early speleologists, e.g., Martel in France, was the creation of departments and institutes of speleology, such as exist for oceanography. More generally, Goodlad (1979) lists the requirements of an academic discipline, which are:

1) a distinctive object of research;
2) specialized knowledge;
3) a unique terminology and technical language;
4) specific empirical methods for examination;
5) effective theories for organizing the accumulated knowledge and giving reason to the methods used; and
6) a history of undergoing institutionalization in the form of scientific societies and independent research departments.

Certainly, speleology, even as a young discipline, satisfied the first three criteria. The object of research, at least in its simplest form, was caves, and more generally the subterranean realm (see below), which requires a specialized knowledge, and certainly has developed a unique terminology (Field, 2002). Whether there are specific empirical methods and effective theories for organizing accumulated knowledge is debatable. In the years leading up to World War II, many professors and departments opposed the creation of a speleology institute at University of Vienna because it would, in their view, simply take a piece of their department away without any real addition (Mattes, 2015). Mattes quotes the amusing aphorism attributed to Franz Seuss that "cave research is not a science, a cave is a hole." Nevertheless, for several decades there was a speleology department at the University of Vienna, but is became a vehicle for pro-Nazi elements at the university, and was eliminated after the war. To our knowledge, there are no speleology departments at any university, but there are several very active research institutes whose main area is karst and caves, especially the Karst Research Institute ZRC SAZU in Postojna, Slovenia, and the Emil Racoviță Institute of Speleology in Bucharest and Cluj, Romania. In the 1960's and 1970's there was an Institute of Speleology at the University of Kentucky, founded by Thomas Barr, a biologist. Its research focus was Mammoth Cave, but it remained small and eventually disappeared.

The expansion of the scope of speleology from caves to other subterranean habitats corresponds, on the physical side of speleology, to a shift in emphasis from caves to the landscape, in particular the karst landscape of caves, dolines, blind valleys, poljes, etc., exemplified by the title of Alfred Bögli's influential text, *Karst Hydrology and Physical Speleology* (1980, 2012). The biological expansion of habitat was a bit different, depending on where animals were found. In fact, the word karst signals this change in emphasis to the landscape, and is popular term in the title of many books on the physical aspects of caves and karst:

- White's *Geomorphology and Hydrology of Karst Terrains* (1988)
- Ford and Williams' *Karst Hydrogeology and Geomorphology* (2007)
- de Waele and Gutierrez's's *Karst Hydrology, Geomorphology, and Caves* (2022)

Karst is also a popular name for research institutes dedicated to the study of subterranean environments:

- Karst Research Institute at ZRC SAZU in Slovenia (founded 1947),
- National Cave and Karst Research Institute in USA (founded 1998)
- Karst Waters Institute in USA (founded 1994)

[1] There has been a debate among French scientists as to the proper word. Louis du Nussac in 1892 proposed spéologie as a more euphonious term, but its use has died out (Mattes, 2015).

- Karst Dynamics Laboratory in China (founded in 1997)

The term speleology is retained by the older Emil Racoviță Institute of Speleology in Romania (founded in 1920) and the University of Kentucky's Institute of Speleology, now defunct. The change in names has accompanied a change in emphasis towards analysis of the total karst landscape, including sinkholes, springs, poljes, uvalas, and caves etc., rather than a focus on caves, for which the word speleology is more appropriate. This contemporary trend is countered by Arthur Palmer and the late Alexander Klimchouk's (2015) view that speleology and speleogenesis should be central. Hence Palmer's book is entitled *Cave Geology* (Palmer, 2007).

The third definition, which explicitly includes non-professionals, has a somewhat complex and obscure history. For example, in the introduction to the 1976 edition of *The Science of Speleology,* T.D. Ford and C.H.D. Cullingford claim that speleology was begun by "gifted amateurs, who, by careful observation and recording of their interests, turned them into science." In the 1953 edition, only one of 13 authors was a professional scientist in the discipline. This was no doubt a matter of necessity rather than a matter of choice, and by 1976, ten of 22 contributors had academic positions. However, this is perhaps misleading since most of these the ten professors actually did their primary research in other fields. A good example of this is William White, the sole American contributor and a dominant figure in at least North America for physical aspects of cave and karst studies, had his primary appointment at Pennsylvania State University in Materials Science, where he did ceramics research. Of the two editors, one was a professional geologist and one was a cleric turned school administrator.

By a combination of necessity and choice, the tradition of non-professional[2] scientist continues in several branches of speleological science. There are aspects of speleology (more about biospeleology below) that are likely to stay in the realm of citizen science. At least in most industrialized countries, it seems unlikely that the exploration and mapping of caves will be in the hands of professionally trained, paid researchers, although this may not be the case for highly technical surveys of underwater caves and deep vertical caves. Exploration and mapping is the realm of citizen science, and as such it is celebrated by many participants. As a number of people have pointed out, it is rare for scientists to depend on citizen scientists (cave mappers) to the extent that speleologists do. Of course the line between citizen scientist and scientist is blurred because a number of professional researchers are also avid sport cavers (e.g. Špela Borko [Slovenia] see https://www.jakopin.net/portraits/Spela_Borko/index.php and Benjamin Schwartz [USA]. Winner of Lew Bicking Award in 2023, the top award of the National Speleological Society for cave exploration). Both are professional biologists with academic positions.

Interestingly, most speleology textbooks, which tend to be older, cover non-geological areas, especially biology. In their book, *The Science of Speleology,* Ford and Cullingford (1976), as well as Cullingford in an earlier edition (1953), argue for an interdisciplinary science, more or less parallel to oceanography, with various discipline represented. As far as we know, no one uses the term geospeleology, perhaps because the geosciences (especially geomorphology, geology, hydrogeology, and physical geography) are so central to the discipline. However, the term biospeleology is used. Ford and Cullingford's book was followed by George Moore and G. Nicholas Sullivan's *Introduction to Speleology,* appearing in several editions from 1978 to 1997. Sullivan was a biologist and biological aspects of speleology are well represented in this book, including a survey of cave life and ecological classification of cave animals. In additon, Bernard Gèze, a geologist, covered biology in his book (Gèze, 1965), as did Herbert Trimmel (1968). Trimmel's book is also noteworthy in its use of several prefixes to speleology including bio-, geo- and anthropo-, perhaps a more acceptable use in German. As speleology expanded to include the karst landscape, biology receded into the background. None of the major karst texts (White [1988], Ford & Williams [2007], and de Waele & Gutierrez [2022]) cover non-geological and non-geograpical topics.

Some authors reserve the term speleology to the "sporting science", emphasizing the technical aspects of cave exploration (Mencarini et al., 2021), while Pérez (2015) includes both the traditional scientific aspects and the sporting aspects.

[2] What to call individuals whose career is not connected to speleology but who make professional contributions is actually a difficult decision. The phrases "non-professional", "amateur", and "auto-didact" are mildly perjorative, and perhaps the best phrase is citizen scientist.

2. THE SCIENCE OF BIOSPELEOLOGY

The study of biospeleology follows a somewhat similar track. Biologists who studied cave faunas early on the late 19th and early 20th centuries thought of themselves as biospeleologists. Hence Racoviță (1907) entitled his famous essay *Essai sur les problemes biospeologiques*. This essay, only relatively recently available in English (2006), is viewed by many European scientists as the founding document of biospeleology (Sket, 2006, Tabacaru et al., 2018). This is not the place to evaluate his work, except to point out that essays about his influence are nearly reverential in nature, his work seems to have been little known in England and North America until the 21st century, presumably due to the lack of an English translation. Romero (2009) does point out that his evolutionary thinking (as opposed to his ecological thinking) is outdated, being largely anti-Darwinian and neo-Lamarckian. Together with the French biospeleologist, Rene Jeannel, he developed a decades long research program under the title *Biospeologica,* publishing in *Archives de Zoologie Expérimentale et Général.*

Vandel (1964) entitled his book *Biospeologie* (translated into English in 1965 as *Biospeleology*). This book, until the late 1970's, was the major source book for information on subterranean life, although it was also widely criticized for its neo-Lamarckian (organicist) view of evolution. This book seems to be the last time biospeleology (or its two French versions, biospeologie and biospeleologie) appear in the title of a textbook.

The next two books to appear were René Ginet and Vasile Decu's *Initiation à la Biologie et à l'Écologie Souterraines* (1977) which abandoned the term biospeleology for the more general term subterranean biology. The absence of the word biospeleology in titles indicates dissatisfaction with the term. Culver's 1982 book, *Cave Life,* reflected the research practice of North American subterranean biologists of emphasizing cave fauna with little if any consideration for non-cave subterranean habitats and their faunas. Later books used subterranean (Eleonora Trajano et al.'s *Biology of Subterranean Fishes [*2010]), cave (Aldemaro Romero's *Cave Biology-Life in Darkness* [2009], Oana Moldovan et al.'s *Cave Ecology* [2018], and Jutson Wynne's *Cave Biodiversity* [2023]), or both (Culver and Pipan's *Biology of Caves and Other Subterranean Habitats* [2009, 2019]).

The predominant use of "cave biology" in North America reflects not only the historical bias of North American biologists toward caves per se, but also the continuing practice of paying lip service to non-cave subterranean habitats but with little analysis (but see Culver & Pipan [2014]). Biologically, the non-cave habitats are extensive both in kind and occurrence (Culver & Pipan 2014). Among the most important, at least in terms of attention, are the terrestrial milieu souterrain superficiel (MSS), first studied by Christian Juberthie and his students (Gers, 1998, Juberthie et al., 1980) and the hyporheic—the underflow of rivers. Curiously, a major subterranean habitat—the deep soil—which harbors many eyeless, depigmented species, is rarely included in the subterranean realm, or at least is studied by different researchers. The inclusion of non-cave habitats by European biologists dates back to Racoviță, and culminated, on the aquatic side, with the development of groundwater ecology by Janine Gibert and colleagues (1994) in the groundbreaking book *Groundwater Ecology.* It is noteworthy that in this book, with a deliberate shift in emphasis away from caves, the North American contributions still came from cave studies. This remained true for the 2nd edition, published in 2023 (Malard et al., 2023), which expanded to include evolutionary topics.

3. THE SCIENCE OF SPELEOBIOLOGY

The first use of the term speleobiology is not clear, but Sket (2006) was the first to emphasize preference for the word speleobiology, rather than biospeleology. The core difference between the two is that speleobiology is a biological science, no different than "surface" biology in Sket's view (Lučić, 2021), while biospeleology is a speleological science. The research group at University of Ljubljana founded by Sket is called the *Skupina za speleobiologijo*, or informally the *SubBio laboratory*.

There is an historical component to the two terms, with speleobiology supplanting biospeleology. There is this implication in Ivo Lučić's interview (2021) with Boris Sket, where there is the sense that speleobiology is "modern" and is primarily biological, hypothesis-driven and involving contemporary technologies, particularly molecular ones. However, we think there is a useful distinction between the two and that both terms can and should be used. Furthermore, we think the implied hierarchy of speleobiology being more "scientific" and important than biospeleology is wrong.

What are the aspects of the study of caves and other subterranean environments that inform speleology? There are certainly foundational components of speleology that inform the study of subterranean life. All subterranean biologists use collections of specimens from caves, and location and maps of which are the result of work by speleologists, whether they be academic geographers or non-academic cavers (citizen scientists) who map and explore caves. This is the case even if the researchers themselves do not actively visit and explore caves. This dependence on speleology can be carried to extremes, and Aldemaro Romero (2009) highlights and laments the practice of criticism of some papers because the authors are not active cavers.

What can biologists bring to speleology? One is the growing awareness of microbiological involvement in both the formation of caves via impacts on limestone dissolution, including chemolithoautotrophy (Engel et al., 2004). The other contribution of biologists to speleology is the description of new species and the distribution of cave-limited species. While such lists are part of the database of speleology, in the same way that the names and distribution of cave minerals (Hill & Forti 1997, Onac & Forti 2011) add to the knowledge base of speleology. One of the losses resulting from the de-emphasis on the multi-disciplinary nature of speleology, especially in relation to biology, but also in relation to paleontology, is that these sciences are rarely included in regional studies of caves. For example, in the important Springer Nature series on "Cave and Karst Systems of the World", only five of 24 books in the series have any sections devoted to cave fauna—Australia (Webb et al., 2023), Lagao Santa Karst of Brazil (Auler & Pessoa, 2020), Romania (Ponta & Onac, 2019), Greenbrier Valley in West Virginia, USA (White, 2018), and Mammoth Cave in Kentucky, USA (Hobbs et al., 2017). There are a few other exceptions to this exclusion, especially Ivo Lučić's (2003) book on the Bosnia and Herzegovinan cave Vjetrenica.

Speleobiology is a branch of biology that utilizes cave organisms to illuminate and understand general biological principles. These include adaptation (Carlini & Fong, 2017), regressive evolution (Jeffery, 2009), vicariance biogeography (Trontelj et al., 2009), and even seemingly unrelated topics such as obesity (Krishnan et al., 2022) and sleep (Hutton et al., 2023). What can and have speleobiologists brought to biology? One of the earliest and most explicit attempts was that of Thomas Poulson and William White (1969) in their seminal article in *Science*—"The Cave Environment." The biologist Poulson and the geologist White both look at the question of what cave studies contribute to biology and geology. They viewed caves and natural, replicated ecological laboratories with possibilities simple communities of varying species composition that are ideal for the study of species interactions and community structure. In parallel, they see caves as evolutionary laboratories where selective pressures are clear as are predicted outcomes. Stefano Mammola (2019) provides a fifty-year progress report on this goal.

Martinez and Mammola (2021) argued that the potential for cave organisms to be model systems is largely untapped and is in fact hindered by our excessive use of terminology. The penchant of subterranean biology community for specialized terminology seems endless, and this contribution is also about terminology. Whatever we call ourselves, we can look forward to an increase in research in the biological aspects of speleology and the speleological aspects of biology.

Resting uneasily between biospeleology and speleobiology are studies of the broad scale patterns of species richness in the subterranean domain, especially caves. On the one hand it is a speleological topic because it is the culmination of lists of distribution of subterranean species, interpreted in a geographical context, including the distribution of karst. On the other hand, the geography of subterranean species richness is of interest to biogeographers in general in part because of the patterns of subterranean species richness are largely the result of processes of isolation and colonization, but with little subsequent dispersal. Whatever we call it, it is a very active research area (Zagmajster et al., 2018; Borko et al., 2021: Culver et al., 2021).

We cannot predict the future but there is a place for both speleobiology and biospeleology in it.

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