Cambridge University Press
978-0-521-82846-8 — Cave Biology: Life in Darkness
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Excerpt
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1 · *A brief history of cave biology*

Some specialist books include a short introduction or brief chronology of the major historical events related to the branch of knowledge they cover. In this book there is an entire chapter on the history of biospeleological ideas. This is because it is essential to explain why biospeleology as a science in general, and our understanding of cave biology in particular, lags so far behind in mainstream organismal biology, particularly in terms of evolution and ecology. In fact, the author argues that this is so because many biospeleologists have failed to understand the historical framework in which this science has developed. This has led many to uncritically accept both concepts and lexicons that are inconsistent with current biological thought. Thus, this chapter provides a historical explanation of the ideological framework surrounding the majority of biospeleological research. This chapter also contains a number of illustrations (Figs. 1.1–1.5) related to the historical narrative presented here; more illustrations on this topic may be found in Romero (2001b).

1.1 Conceptual issues

An understanding of the history of any particular area of scientific inquiry is essential in order to really appreciate the significance of current knowledge and the voids that need to be filled. Most scientists are not particularly interested in pursuing such a task because the history of science is influenced by philosophy, politics, religion, and other expressions of human activities whose comprehension requires interdisciplinary approaches that go beyond what scientists have been normally trained for in universities. Yet, the history of science has demonstrated again and again that errors, fashion, and conceptual inertia have often delayed the development of certain areas of knowledge (Horder 1998). This chapter demonstrates that biospeleology is a perfect example of that.

There are two major ways to present the history of a particular branch of science: one is simply an uncritical chronological narrative, and the other is a critical examination of ideas that influenced the development of that area of study. Here, the second route is taken, because an appreciation of the historical background in which biospeleological ideas developed is necessary to understand why the full incorporation of modern biological thought in biospeleology has been delayed. As Ernst Mayr put it 'When scientists concentrate on the study of isolated objects and processes they seem to operate within an intellectual vacuum.' (Mayr 1982, pp. 66–7). Evidence is also provided that geography and religion played a major role in how this science evolved, first in the Protestant USA, and later in Catholic France.

To date there is still no comprehensive published history of biospeleology: Vandel (1964, pp. xxiii–xxiv) outlined a few historical facts; Barr (1966) wrote a brief history of biospeleology in the United States; Bellés (1991) wrote a largely chronological and anecdotal narrative on the subject; Shaw (1992) in his treatise on the history of speleology provided little information on biospeleology *per se*, and Romero's (2001b) article on hypogean fish research dealt mostly with the history of evolutionary ideas.

This chapter demonstrates that the most important issue regarding cave biology has been and continues to be the origin and evolution of cave fauna. Because of that, Darwinism is a central event in the development of biospeleology as a science but not for the reasons most people would assume. In fact, we can say that the history of biospeleology can hardly be depicted as another triumph of Darwinism as an idea. As will be shown, Charles Darwin, who was the first scientist who really tried to provide a scientific explanation about the origin of cave fauna and the phenomenon of what he called 'rudimentation' in the form of reduction and/or loss of the visual apparatus, espoused a rather neo-Lamarckian stance on the topic, to the point that his explanations were not fully Darwinian in the modern sense of the word. Furthermore, because of this and the fact that biospeleology developed mostly in France, where Lamarckism and its philosophical allies were very strong, not even the modern synthesis seriously changed the interpretation that most biospeleologists had of biological phenomena in caves.

Therefore, the following is a history of biospeleology focusing on five particular historic, intellectual, and/or geographic areas, each characterized by the dominance of a particular idea or set of ideas and mostly overlapping chronologically. These are: (1) pre-Darwinian thought (before 1859), (2) Darwinism and American neo-Lamarckism (1859–1919), (3) European selectionism and the death of the controversies

(1880–1921); (4) biospeleological ideas in France and elsewhere in continental Europe (1809–1950); and, (5) the impacts of the modern synthesis (1936–1947). There then follows a discussion of the roots of current intellectual inertia. This outline does not follow a strict chronological order but rather expresses the influence of culture on the development of ideas as delineated by geographic and intellectual boundaries. In order to make the narrative more fluid, this chapter contains a number of footnotes, which provide some biographical information on the major actors mentioned in the main text as well as explanations of philosophical terms so the reader can better appreciate the context in which many of these developments took place.

As the author explains the major ideas that have influenced biospeleology, he argues that many of those ideas by themselves do not represent paradigms in the Kuhnian sense of the word (Kuhn 1970, p. 10). They were never original ideas, but borrowed in both form and substance from neo-Lamarckism,and at the same time they ignored the pre-eminence of natural selection as an effective mechanism for the explanation of the evolution of cave organisms. Because of their restrictive nature and their incompatibility with the neo-Darwinian framework, these neo-Lamarckian ideas provide little opportunity for further elaboration and development.

1.2 Pre-Darwinian thought (before 1859)

1.2.1 From prehistory to mythology

Caves have been of human interest since prehistoric times, serving both as a shelter and as a source of artistic expression (Morgan 1943; Shaw 1992; Cigna 1993a; Romero 2001b). The earliest known human representation of cave fauna dates back to *c.* 22,000 YBP (years before the present) (Upper Paleolithic). It is a carved drawing of a wingless cave cricket, *Troglophilus* sp., on a bison (*Bison bonasus*) bone found in the Grotte des Trois Frères (Three Brothers Cave) in the central Pyrenees, France (Chopard 1928) (Fig. 1.1).

From the beginning of history humans have developed a close mythic–religious association among caves, the underworld, and death. Burials in caves have been common among many cultures (see, for example, Watson 1974; Stone 1995; Clottes 2003). The underworld or Hades (Ἅδης) in Greek mythology was believed to be the 'Kingdom of the Dead' to which one could gain access via caves (Mystakidou *et al.* 2004). Not surprisingly,

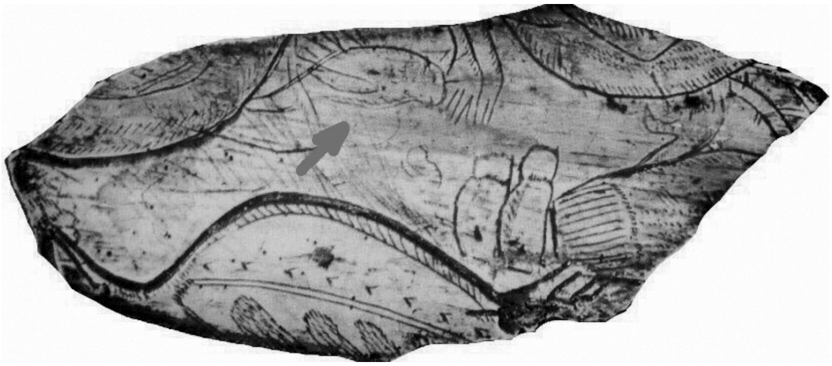

Figure 1.1 The earliest known human representation of cave fauna dates back to *c.* 22,000 YBP (years before the present) (Upper Paleolithic). It is a carved drawing of a wingless cave cricket, *Troglophilus* sp., on a bison (*Bison bonasus*) bone found in the Grotte des Trois Frères (Three Brothers Cave) in the central Pyrenees, France (Chopard 1928). Line drawing by Amy Awai-Barber from a photograph of the original. (See Plate 1.)

ideas about cave creatures were, from the beginning, a mixture of myth and reality. Dragons and other imaginary beasts had been described by many authors since before the invention of the printing press.

Such views of cave life survived up to the seventeenth century. For example, in 1665 a polymath Jesuit priest, Athanasius Kircher,[1] published what might be considered as the first book whose title gave the impression of being devoted solely to caves: *Mundus Subterraneus* (Kircher 1665). This was a gigantic, two-volume, folio-sized tome totaling 892 pages, whose second edition, published in Amsterdam in 1678, contained lengthy additions about caves in Switzerland, Austria, Italy, and the Greek Islands. This latter edition would be the one that achieved more popularity and became the standard geology text in the seventeenth century. Despite its title, Kircher dealt with many more topics than just caves, such as alchemy, chemistry, and metallurgy, among others.

Unfortunately, this was an extremely uncritical book full of inaccuracies and odd explanations of how water circulated underground (Fig. 1.2). It also contained descriptions of supposed cave fauna that included dragons, unicorns, and giants (he even provided illustrations of such alleged creatures). However, no blind and/or depigmented creature was included. Kircher was an uncritical repeater of other people's tales.

[1] *b.* Geisa, Germany, 2 May 1602; *d.* Rome, 28 November 1680.

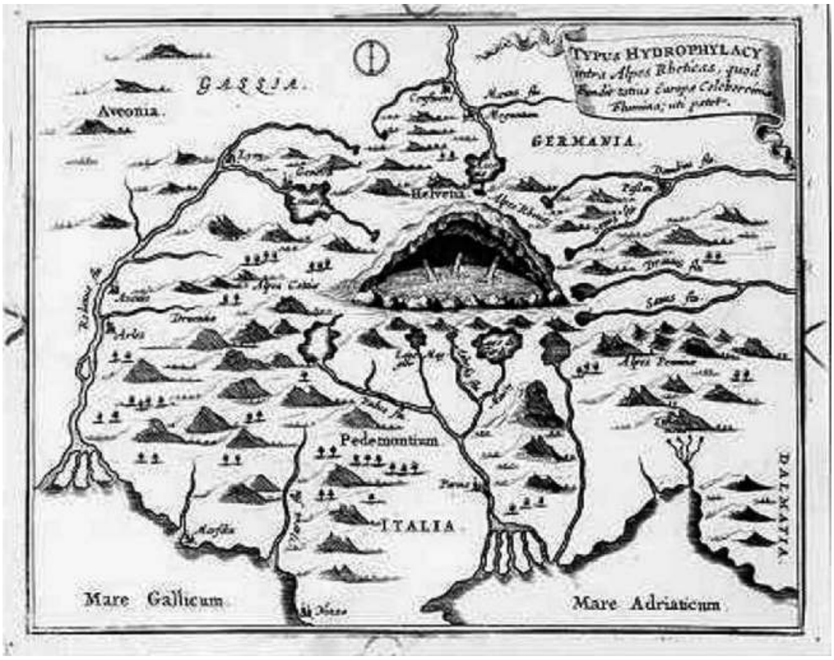

Figure 1.2 Illustration of 'hydrophylacy' from Kircher's *Mundus Subterraneus* (1665).

However, he was a very popular author because of his position as professor of the Collegio Romano (the Vatican's University), his reputation for being able to read 16 languages, having published 44 books (most of them huge in size, in large print and with impressive illustrations) on a great array of topics, and having written more than 2,000 manuscripts and letters (that have survived) (Romero 2000).

However, there is very little in Kircher's work of any value and his book is only a footnote in the history of biospeleology. The first real contributions would take place during the Renaissance in Europe and at the peak of ancient Chinese civilization.

1.2.2 European Renaissance and Ming Dynasty

Both the Renaissance (*c.* 1450–1650) in Europe and the Ming Dynasty (1368–1644) in China were characterized as eras of exploration. They provided the first significant contributions to our knowledge of the world fauna since antiquity. In Europe that was particularly true for animals that were new to the ones mentioned in the Bible or by ancient Greek and Roman authors.

The first written record of a true cave organism was in the form of a letter dated in 1537 written by the Venetian poet and philologist Giovanni Giorgio (GianGiorgio) Trissino.[2] In that letter he mentioned a cave amphipod ('*gamberetti picciolini*', probably *Niphargus costozzae*) from Monti Berici, Veneto, northern Italy. That letter was later reported by the Dominican friar and historian Leandro Alberti[3] in his most famous book, *Descrittione di Tutta Italia* (1550, pp. 471–2) in which he portrayed numerous Italian caves in detail (Hill 1974).

The first known written account of a cave fish came from China just three years after Trissino's letter. It was a travel report written in 1540 by Yi Jing Xie,[4] a local government official. This never published report was found in the records of Luxi County in 1905 by Ying Huang, the local governor, who had it engraved as an inscription on a stele (Y. Zhao, pers. comm.). In this document Xie referred to the hyaline fish(*Sinocyclocheilus hyalinus*) from the Alu caves, Yunnan, China. This fish was not collected for scientific purposes until 1991 and was not scientifically described until 1994 (Chen *et al*. 1994).

That these two discoveries took place almost simultaneously in Europe and China is not totally surprising since, as mentioned above, both cultures were experiencing their golden age of geographic discoveries. For China the sixteenth century, which coincided with the first half of the Ming Dynasty, was a century after the Chinese had embarked on impressive maritime explorations. However, by that time, the Yang Ming system of thought established by Shouren Wang[5] had replaced that of Xi Zhu.[6] Whereas Zhu, the most significant Confucian rationalist, insisted on the importance of observation and that learning should be based on reason and the 'investigation of things' (see his *Four Books*), Wang believed in the 'learning of the mind,' through intuition. This was, unfortunately, a reverse of the change in thought that occurred in Ancient Greece when the idealism of Plato,[7] based on the recognition

[2] *b*. Vicenza, Republic of Venice [today Italy], 8 July 1478; *d*. Rome, 8 December 1550.
[3] *b*. Bologna, Italy, 1479; *d*. Bologna, 1552? [4] Xie, Yi Jing (*b*. ?; *d*. ?).
[5] Wang, Shouren (Yangming) (*b*. Yuyao, Zhejian Province, China 1472; *d*. Nan'an, Jiangxi, China, 1528).
[6] Zhu, Xi (*b*. Yuxi, Fujian Province, China, 18 October 1130; *d*. China, 23 April 1200).
[7] *b*. Athens [?], 427 BC; *d*. Athens, 348/347 BC.

of tangible objects via individual perceptions was replaced by the logic based on observation by his student Aristotle.[8]

Aristotle's legacy would have a tremendous importance because it helped to establish one of the fundamental tenets of Western science (particularly in biology) after the Renaissance: knowledge via observation, not pure speculation. On the other hand, Chinese civilization declined owing to internal factors and invasions by Mongols and Westerners.

Thus, new scientific discoveries would continue to take place mostly in Europe instead of elsewhere, even when some of those discoveries represented unconfirmed findings and false starts. That was the case of the French engineer and inventor Jacques Besson,[9] who reported alleged underground little eels (*petites anguilles*) somewhere in Europe. In his book, Besson (1569) did not indicate the locality nor give a description of the fish in question. He did not mention the fish as being blind and/or depigmented (these would have been extraordinary characteristics to even the casual observer). Thus it is unclear whether Besson observed true hypogean fish, actual eels (*Anguilla anguilla*), or European freshwater fishes with eel-like bodies that are sympatric with the areas in which he traveled (France and Switzerland). Those possible fish families include Petromyzonidae, Cobitidae, Siluridae, and Clariidae (Blanc *et al.* 1971). Therefore, this description remains unconfirmed (Romero and Lomax 2000).

Another example of an unconfirmed report of underground fauna was that of Marc-René Marquis de Montalembert,[10] a French general and military engineer famous for devising simplified polygonal designs for fortresses that became the standard blueprint for European fortifications until the nineteenth century. Montalembert reported a blind, subterranean fish in a spring at Gabard, Angoumois, near one of his estates in southwestern France (Montalembert 1748). No specimen was preserved, and his description remains unconfirmed (Romero 1999a).

These casual reports (whether they were confirmed or not) were typical of the natural history of the Renaissance epitomized by 'bestiaries' and were later replaced by a more rigorous view of science.

[8] *b*. Stagira, Macedonia, [in today's northern Greece] 384 BC; *d*. Chalcis, Greece, 322 BC.
[9] *b*. Colombières, France, 1530?; *d*. Orléans, France, 1573.
[10] *b*. Angoulême, Charente, France, 16 July 1714; *d*. Paris, France, 29 March 1800.

1.2.3 Modern science (*c.* 1650–1800)

Unconfirmed reports and mythical tales typical of the Renaissance were followed in the seventeenth century by the flourishing of what has been termed 'modern science', characterized by direct observation and experimentation. During that time, in which precision in description and illustration of the natural world improved considerably, we see some good examples of new accounts of underground biota.

The first of those contributions was the earliest published reference to an underground fungus by the physician and naturalist Martin Lister,[11] (Lister 1674; Carr 1973). Lister received samples of this fungus from a Mr Jessops and called it '*Fungus subterraneus*'; it was found in a mine known as 'Old Man' in Castleton, Derbyshire, central England. Lister was part of the first generation of English naturalists extremely interested in describing and illustrating natural objects, particularly animals and rocks (Unwin 1995).

The next important contribution came from the Spanish Capuchin monk and missionary Francisco de Tauste.[12] He was the first to publish a reference to a cave bird, the oilbird (*Steatornis caripensis*). Tauste wrote his report based on his study of costumes and languages of the Chaimas, an ethnic group of Native Americans of northeastern Venezuela where these birds inhabit the Cueva del Guácharo (Oilbird Cave); (Tauste 1678; Longrás Otín 2002). This species, which had been exploited for many years by the Chaimas for its oil (Anonymous 1833), was not scientifically described until 1817 by the German polymath, explorer, and, above all, holistic naturalist Alexander von Humboldt,[13] based on a specimen he collected in 1799 (Humboldt 1817). Humboldt's other contributions to our knowledge of hypogean biota include the first description of underground plants in the mines of Freiberg (Humboldt 1793) and a description of a freshwater species of catfish, which he claimed originated from an underground volcano in Ecuador (Humboldt 1805) (Fig. 1.3), yet this claim remains unsubstantiated (Romero 2001a; Romero and Paulson 2001d).

The earliest species of cave animal that underwent intense and continuous scientific study was the first species of cave salamander ever described:

[11] *b.* Radclive, Buckinghamshire, England, April 1639; *d.* Epsom, Surrey, England, 2 February 1712.

[12] *né* Miguel Torralba de Rada; *b.* Tauste, Zaragoza, Spain, 1626; *d.* Santa María de Los Ángeles del Guácharo, Venezuela, 11 April 1685.

[13] *b.* Berlin, Germany, 14 September 1769; *d.* Berlin, 6 May 1859.

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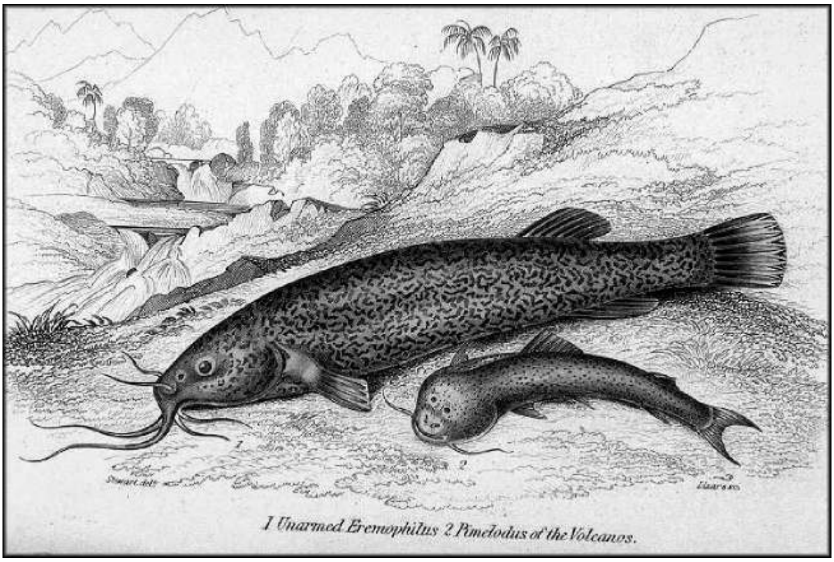

Figure 1.3 Illustration of the alleged subterranean fishes from a volcano in Ecuador by Humboldt (1805). (See Plate 2.)

Proteus anguinus from a region known then as Carniola, in today's Slovenia. This blind amphibian was originally identified as a 'dragon's larva' by the traveler and naturalist Janez Vajkard Valvasor[14] (Valvasor 1689). *P. anguinus* was later described scientifically by the Austrian naturalist Josephi Nicolai Laurenti[15] (Laurenti 1768) in the first post-Linnean description of a cave organism.

1.2.4 First professional studies before Darwin (1800–59)

The period between 1800 and 1859 is characterized by three major events. The first two were circumstantial in nature. One was the beginning of biology as a formal discipline and gave rise to the first generation of professional biologists; in fact, the term 'biology' began to be used around 1800 (McLaughlin 2002). The second was the discussions on evolution including the loss or rudimentation of organs such as eyes and pigmentation, a phenomenon common (but not unique) among many

[14] *b*. Ljubljana, Carniola (today Slovenia), 28 May 1641; *d*. Ljubljana, 19 September 1693.
[15] *b*. Vienna, Austria, 4 December 1735; *d*. Austria, 17 February 1805.

cave organisms. The third event was the scientific exploration of two of the most important cave systems in the world: the one occupying the southeastern regions of the United States epitomized by Mammoth Cave, and the other in what is now known as Slovenia. These factors combined to make the discussion on the biology of cave organisms an important aspect of the biological dialectic from Darwin until the end of the nineteenth century.

All this began with the first scientific description of the cave salamander, *Eurycea lucifuga* (Rafinesque 1822). This description was made by the French–American Constantine Samuel Rafinesque[16] (Fig. 1.4) when he was professor of botany and natural history at Transylvania University in Lexington, Kentucky, between 1819 and 1826. Rafinesque had been exploring the caves of that state since 1818 (Rafinesque 1832) and so was probably the first professional scientist to study them. He encountered a salamander that the locals called 'cave puppet' in 1821 in caves near Lexington. Kentucky encompasses a great deal of karst formations including large and complex cave systems. Although he did not provide too many details about the exact location, not only of the cave but in what portion of it he found this amphibian, this is one of the cave organisms most frequently encountered because it is usually seen near cave entrances. Thus, finding this salamander does not require in-depth exploration of cave systems. This discovery in itself was not particularly striking to the scientific community at that time for two reasons: first, the cave salamander is neither blind nor depigmented, so it was not particularly remarkable to the casual observer; second, Rafinesque had a poor reputation as a scientist due to his lack of critical thinking and his almost compulsive behavior in naming species (more than 6,700), many of them previously described by others or just varieties of the same one. Yet, his discovery of the cave salamander was the first indication that the biota of caves in that part of the United States was worth looking at (Ewan 1975; Warren 2004).

Rafinesque's explorations included Mammoth Cave, which since the 1830s had rapidly become a great tourist attraction. Used by Native Americans for about 4,000 YBP, this cave was first reported by people of European descent in 1797 (Goode 1986). Mammoth Cave and its fauna became famous thanks, mainly, to the exploratory work performed by

[16] *b*. Galata, near Constantinople, Turkey, 22 October 1783; *d*. Philadelphia, Pennsylvania, USA, 18 September 1840.