428. Romero, A. 2004. Biospeleologists. pp. 151-154, *In*: J. Gunn, Ed. *Encyclopedia of Cave and Karst Science*. New York: Fitzroy Dearborn.

BIOSPELEOLOGISTS

This entry provides short biographical sketches of researchers, now deceased, who were known for either "firsts" in biospeleological discoveries or for their influence on biospeleological ideas. The order is chronological, according to the time in which they made their major contribution to speleology.

In 1537, the Italian poet and scholar Giovanni Giorgio (GianGiorgio) Trissino (1478–1550) recorded what must have been a form of cave amphipod (probably *Niphargus*) from a cave in northern Italy. He also wrote detailed accounts of Italian caves. However, it is thought that the first printed report of a cave organism was by Yi-Jing Jie, who described an eyeless hyaline fish from the Alu caves of Yunnan in China in 1541. This species, *Sinocyclocheilus hyalinus*, was not scientifically described until 1994. The French engineer and mathematician Jacques Besson

(*c.*1530–73) reported little eels (*petites anguilles*) in a cave stream somewhere in Europe in 1569. However, he did not give a locality, and neither did he describe the fish as blind or depigmented (Romero & Lomax, 2000).

Athanasius Kircher (1602–80), a German-born Jesuit polymath, wrote *Mundus Subterraneus* in 1665, probably the first printed work on earth science to include speleology. There he enumerated numerous cave organisms, including mythical beasts such as dragons, although none of the animals that he mentioned displayed the typical features associated with troglomorphic animals: blindness and depigmentation. (Romero, 2000). In 1674, the English naturalist Martin Lister (1639–1712) published the earliest reference to underground fungi.

The Slovenian historian and naturalist Janez Vajkard [Johann Weichard] Valvasor (1641–93) published the first systematic study of caves in a particular area, and explained the mystery of disappearing karst lakes by a system of underground rivers and reservoirs (see also Speleologists). In his 1689 book *The Glory of the Duchy of Carniola*, Baron Valvasor described the discovery of the blind cave salamander *Proteus anguinus* at a karst spring near Vrhnika. This was the first troglobite to be scientifically described and named, by the Viennese zoologist Josephi Nicolai Laurenti in 1768.

In 1748, Marc-René Marquis de Montalembert (1714–1800), a French aristocrat, reported a blind, subterranean fish in a spring at Gabard, Angoumois, near one of his estates in southwestern France in 1748. However, no drawings or specimens were preserved and his description remains unconfirmed (Romero, 1999a).

The first study of underground plants was published in 1772 by the Italian naturalist Giovanni Antonio Scopoli (1723–88) (Scopoli also sent specimens of *Proteus anguinus* to other researchers in Europe, and it was one of these specimens that Laurenti examined). Green plants in the mines of Freiburg that had not fully developed due to lack of light were described in 1793 by the German naturalist and geographer Alexander von Humboldt (1769–1859). In 1799 he visited Guácharo Cave in Venezuela, and described the nocturnal oilbird, *Steatornis caripensis*, flocks of which emerge from the cave at night. In 1805 he published a description of a freshwater species of catfish ejected from an underground volcano in Quito, Ecuador, although this discovery remains unsubstantiated (Romero & Paulson, 2001).

Karl Franz Anton von Schreibers (1775–1852) performed the first detailed anatomical studies of *Proteus anguinus*, on one of Scopoli's specimens stored in the Vienna Natural History Museum. He also bred *Proteus* in artificial underground caves.

In 1842, August Otto Theodor Tellkampf (1812–83), a German physician who emigrated to America, visited Mammoth Cave, and later described several species of invertebrates from the cave fauna. He also contributed detailed descriptions of the northern cavefish *Amblyopsis spelaea* and concluded that its eyes and those of blind cave crayfishes had become rudimentary from lack of use (Romero, 2002)

Jean Louis Rodolphe Agassiz (1807–73), a Swiss anatomist who emigrated to the United States and served as Director of the Harvard Museum of Comparative Zoology from 1859 to 1873, in 1847 proposed a plan to raise individuals of *A. spelaea* under different light conditions, to study the influence of illumination on its eyes and pigmentation. A creationist, he thought only of the effects of the environment on development, not of the environment influencing evolution. He never carried out the experiments, but several of his students also showed a great deal of interest in cave fauna, and later developed his ideas (Romero, 2002).

The Danish naturalist Jørgen Matthias Christian Schiödte (1815–84) was particularly interested in the correlations between anatomical characteristics and the biological conditions under which organisms live. Schiödte's 1849 work: *Specimen faunæ subterraneae* provided the first classification of cave animals: shade animals, twilight animals, animals in the dark zone, and animals living on stalactites.

Jeffries Wyman (1814–74), the first curator of the Peabody Museum of Yale University, studied *A. spelaea* in great detail. Although it lacked eyes, Wyman found that it had well-developed optic lobes. He proposed in 1854 that this imperfection of the eyes "might be owing to a want of stimulus through a series of generations" and that the organ of vision, however imperfect, "is more like the eyes of other vertebrates". For him, *A. spelaea* was an excellent subject for the study of evolution (Romero, 2001).

In 1854, Ignaz Rudolph Schiner (1813–73) classified cave organisms according to their degree of dependence on the underground environment: troglobites, troglophiles, and "occasional cavernicoles" (trogloxenes). This classification was later modified by Emil Racovitza, and is commonly used today.

Charles Darwin (1809–82) believed that cave fauna supported his theory of evolution. He noted that cave fauna were more closely related to the fauna of the surrounding regions than elsewhere. He first considered the mechanisms of both natural selection and disuse to explain troglomorphic features, i.e. enlargement of some sensory systems and appendages in the former and blindness and depigmentation in the latter. To him this suggested a "contest . . . between selection enlarging and disuse alone reducing these organs" (Darwin, *On the Origin of the Species by Means of Natural Selection*, 1859). However, by the third edition of his book in 1861 he relegated the importance of natural selection, eliminating his speculation about a "contest" between selection and disuse.

Alpheus Hyatt (1838–1902), a student of Agassiz, visited Mammoth Cave in 1859, and collected cave fauna. He used the specimens to demonstrate that here were animals whose phylogenetic lineage had become "old" (Romero, 2001).

In 1864, the American paleontologist and evolutionist Edward Drinker Cope (1840–97) described what he thought to be a new species and genus of troglomorphic fish, *Gronias nigrilabris*, from Pennsylvania, without presenting any evidence that such a fish had been captured in the hypogean environment (Romero, 1999b; Romero & Romero, 1999). Cope introduced the idea that evolution was directed by trends, and that when an organism travelled too far down an adaptively specialized path, as in adaptation to living in caves, it could not reverse this process. He also described the life cycles of the cave fauna of Wyandotte Cave, Indiana.

In 1871, Alpheus Spring Packard Jr (1839–1905), another former student of Agassiz, examined Mammoth Cave specimens,




Biospeleologists: Athanasius Kircher (top left); Emil G. Racovitza (top right); René Gabriel Jeannel (bottom left); Albert Vandel (bottom right).

and the fauna, particularly the fish, convinced him of their usefulness as a demonstration of Lamarckian evolution. He thought that cave fauna had a very recent origin and that the loss of certain organs was compensated for by the hypertrophy of others.

Frederic Ward Putnam (1839–1915), another of Agassiz's students, visited Mammoth Cave in 1871, and in 1874 collected a large number of specimens. He criticized Cope's interpretation that *A. spelaea* was able to survive in those waters because of its "projecting under jaw and upward direction of the mouth [which] renders it easy for the fish to feed at the surface of the water", and presented numerous examples that contradicted Cope's assertions. He viewed the amblyopsids as former marine and salt-water estuary fishes that were slowly trapped in that geographical area. He also described a new species of amblyopsid, *Chologaster agassizi*.

Edward Ray Lankester (1847–1929), a British neo-Darwinist, proposed that blindness among cave animals was due to a special type of natural selection. In an 1893 article in *Nature*, he suggested that some animals are, by chance, born with defective eyes. Occasionally a few animals—some with normal eyes and some with defective eyes—fall or are swept into caves. In

each generation, those that have good eyes are able to see the light and escape, and eventually only those that are blind remain in the cave. He also believed that one can find organisms degenerating ontogenetically and phylogenetically. In his 1880 book *Degeneration: A Chapter in Darwinism* he defined "degeneration" as "a loss of organization making the descendant far simpler or lower in structure than its ancestor".

Carl H. Eigenmann (1863–1927) was a German-born ichthyologist who studied and worked in the United States. Much of his work between 1887 and 1909 was devoted to understanding how visual structures were lost in cave vertebrates. He described two new species of cave fish: *Amblyopsis rosae* from Missouri, and *Trogloglanis pattersoni* from the artesian waters of San Antonio, Texas. He published more than 40 papers, abstracts, and books on cave fauna—his *Cave Vertebrates of North America* (1909) being the most important. Originally a neo-Lamarckian, Eigenmann thought that the reduction or disappearance of organs among cave animals was a case of convergent evolution. He pointed out that a lack of pigmentation had to be understood as the combination of genetically fixed and epigenetically (environmentally influenced) determined characters (Romero, 1986b). He believed that cave faunas were not the result of "accidents", but rather the product of active colonization.

In 1896, Armand Viré (1869–1951), a French scientist and cave explorer attached to the Muséum National d'Histoire Naturelle, set up the world's first underground laboratory, which operated until 1914 in the catacombs of the Botanical Garden in Paris. He published several articles on European cave fauna, based on his visits to caves.

Emil G. Racovitza (Racoviţă) (1868–1947) was a Romanian zoologist who worked in France until returning home in 1920. His *Éssai sur les problèmes biospéleologiques* (1907) is considered to mark the birth of biospeleology as an independent science. He initiated an extensive international research programme called "Biospeologica" (primarily intending to document and collect cave fauna). In 1920 he founded the world's first Speleological Institute in Cluj, Romania. He explored 1200 caves in Europe and Africa, collected about 50 000 specimens of cave animals, and published 66 papers on subterranean fauna. For Racovitza, an anti-neo-Darwinist, all cave organisms were "preadapted" to the cave environment where "the function creates the organ." (Motas, 1962).

The French entomologist René Gabriel Jeannel (1879–1965) studied subterranean beetles mostly from Europe and Africa. With Racovitza he founded the journal *Biospéleologica* in 1907, became deputy manager of the Speleological Institute in Cluj, and in 1926 published *Faune cavernicole de la France*.

Charles Marcus Breder Jr (1897–1983), the director of the New York Aquarium, led the renaissance of the study of cave fishes by using *Astyanax fasciatus* as his prime subject of research. He emphasized behavioural, physiological, genetic, and ecological approaches (Romero, 1984; Romero, 1986a; Romero, 2001). Many of Breder's contributions are still cited, and several of his associates and students have studied this cave fish. Breder was the dominant figure in hypogean fish research in the 1940s and 1950s.

Curt Kosswig (1903–82), a German scientist who spent many years in exile in Turkey, used the results of his own Mendelian studies to explain the "rudimentation" or loss of structures among cave animals. He founded the cave fish team at the Zoological Museum and Zoological Institute at the University of Hamburg.

Albert Vandel (1894–1980) founded the Laboratoire souterrain de Moulis in 1948. In his highly influential book on cave biology (*Biospéologie: La Biologie des Animaux Cavernicoles*, 1964) he proposed that the evolution of cavernicoles was neither neo-Lamarckian nor neo-Darwinism, but which he called "organicist". According to him, all phyletic lines pass through several successive stages: creation; expansion and diversification; and finally specialization and senescence. The last stage of this cycle was "regressive or gerontocratic" evolution. He considered cavernicoles to be good examples of regressive evolution. However, his ideas lack empirical support.

ALDEMARO ROMERO

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Useful Websites

Biographical information on active biospeleologists can be found in web pages such as: http://members.xoom.it/bioscience/isbios/XXX.htm and http://www.cancaver.ca/bio/people.htm.