Biology of Underwater Caves

by Tom Iliffe, PhD

Recent speleological investigations in coastal areas have confirmed that anthropogenic pollutants can have potentially devastating effects on the fresh groundwater lenses and adjacent open water marine ecosystems including coral reefs, mangroves and sea grass. Many species of cave animals are listed as critically endangered. These animals are a barometer of the health of the environment and virtual missing links that help to explain the evolution of life in the sea and the evolution of life on earth.

The subterranean aquatic environment consists of interstitial (small, water-filled spaces between unconsolidated sediments) and cave (larger voids within bedrock, either formed by solution or volcanic action) ecosystems. The water in underground environments can vary from completely fresh to fully marine salinities. Such habitats are characteristically lightless, environmentally stable and have limited input of food due to the absence of photosynthetic plants and barriers to external input.

Ecologically, aquatic cave animals can be subdivided into stygobites (cave-adapted species restricted to subterranean waters), stygophiles (species inhabiting caves and completing their entire life cycle there, but which also occur in similar open water habitats) stygoxenes (species common in caves, but which must leave the cave to feed or reproduce), and accidentals (species that wander or are washed into caves, but which cannot survive there for very long). The prefix “styg” refers to the subterranean River Styx which from Greek mythology circles through Hades or the underworld. Thus, stygobites are literally the “aquatic cave life”, stygophiles the “aquatic cave lovers”, and stygoxenes the “aquatic cave guests”.

Although cave-adapted animals have long been known and studied from freshwater caves, the discovery of similar animals from marine caves is a recent event brought to light by cave diving explorations. Anchialine (tidal, water-filled voids near the coast) caves typically possess a highly stratified water column with deeper, fully marine waters separated by a halocline from overlying fresh or brackish water. Cave diving technology has been an essential tool to explore and study the deeper waters in such systems.

Anchialine caves include the cenotes of Mexico’s Yucatan Peninsula, the blue holes of the Bahamas and Belize, as well as numerous limestone and volcanic caves, mostly on islands, around the Caribbean, Mediterranean and Indo-Pacific. Seven of the ten longest underwater caves in the world are anchialine caves from the Caribbean coast of Yucatan. This anchialine cave habitat is characterized by the absence of light, a salinity and temperature stratified water column, very limited food resources, low levels of dissolved oxygen and stable environmental conditions.

Anchialine and freshwater stygobites are mostly crustaceans, and include several higher groups of crustaceans found only or primarily in subterranean habitats. Such animals include:

- Remipedes – primitive, anchialine, “living fossil” crustaceans with highly segmented bodies, reminiscent of the segmented worms from which crustaceans are thought to have evolved. Remipedes have paired hollow fangs for capturing prey and are among the top predators in this habitat. They are up to 4.5 cm in length, usually colorless and blind, with elongate, centipede-like bodies. Seventeen species of remipedes inhabit fully marine, oxygen-deficient waters in caves in the Bahamas, Caicos Islands, Cuba, Yucatan Peninsula, Canary Islands and Western Australia.
• **Thermosbaenaceans** – small (4 mm or less), eyeless or eye-reduced, anchialine and freshwater crustaceans with a dorsal brood pouch in females. Their wide distribution in caves and thermal springs around the Mediterranean and Caribbean, as well as Australia and Cambodia, suggests an origin along the coastline of the Tethys Sea, a shallow sea separating the continents during the early Mesozoic some 200 million years ago. They include at least 34 species.

• **Mictaceans** – small (3-3.5 mm), eyeless and depigmented, non-predatory crustaceans represented by a single species in anchialine caves in Bermuda.

• **Spelaeogriphaceans** – small (less than 1 cm long) freshwater crustaceans represented by species from caves in South Africa, Brazil and Western Australia. They are most closely related to the mictaceans. This widely separated distribution implies an early origin for the group, at least 200 million years before present in the Tethys Sea.

• **Bochusaceans** – small (1.2-1.6 mm), semi-transparent and eyeless crustaceans that include two anchialine species from the Bahamas and Cayman Islands and three deep-sea species.

• **Copepods** – a large and diverse group, comprising the most common animals in marine plankton. Platycoelooid, misophrioid, cyclopid, harapacticoid and epacteriscid calanoid copepods inhabit anchialine caves in tropical regions around the globe.

They are small (typically 1-2 mm long) and have a short, cylindrical body with head and thorax fused into a cephalothorax. Most are planktonic filter-feeders, but some such as the harapacticoids and cyclopoids are benthic.
- **Ostracods** – small (approximately 0.5-2 mm), benthic or planktonic bivalve crustaceans. Halocyprid ostracods include anchialine species with a distribution and co-occurrence similar to that of remipedes. More than 300 species of podocopid ostracods have been found in springs, caves and anchialine habitats.

- **Mysids** – small (approximately 3-20 mm), shrimp-like crustaceans including stygobitic species found in freshwater and anchialine habitats in Africa, the Caribbean, Mediterranean, and India. Their distribution suggests that they were stranded in caves by lowering of sea levels in the Tethys and Mediterranean.

- **Isopods** – dorsoventrally compressed body (flattened from top to bottom); occurring in terrestrial, freshwater and marine habitats. Stygobitic isopods range from several millimeters to several centimeters in length.

- **Amphipods** – laterally compressed body (flattened from side to side), occurring in freshwater and marine habitats. Stygobitic representatives are present in the bogidiellid, crangonyctid, hadziid and nephargid families of the amphipod suborder Gammaridea. They are very widely dispersed with large numbers inhabiting caves in Central and Southern Europe, the Mediterranean, eastern and southern North America, and the Caribbean.

- **Decapods** – possess five pairs of pereiopods or legs (hence the name Decapoda). Anomuran crabs (e.g., hermit, porcelain, mole and sand crabs) inhabit a freshwater cave in Brazil and an anchialine lava tube in the Canary Islands. Stygobitic crayfish are present in caves in North America and Cuba. Brachyuran crabs (i.e., true crabs) are widely distributed from caves in the tropics and subtropics. Caridean shrimp include freshwater and anchialine representatives from caves mostly in tropical latitudes.

- **Fish** – nearly 100 species of stygobitic fish are presently described, primarily from tropical and subtropical regions. They occur principally in freshwater caves, but anchialine fish are present in Caribbean islands and Yucatan. The principle stygobitic fish are cyprinids (carps and minnows), balitorids (river loaches), and siluriform fishes (catfish). Six species of amblyopsid cave fish occur in the southern and eastern United States.

Anthurid isopods occur in anchialine and freshwater caves in the Canary Islands, Caribbean and Indian Ocean islands, Mexico and South America. Asellot isopods inhabit anchialine and freshwater caves in the Caribbean, Europe, Galapagos, India, Indonesia, Japan, Malaysia, North and Central America and Polynesia. Cirolanid isopods have been found in freshwater and anchialine caves clustered in Mexico and the Caribbean as well as in Europe and the Mediterranean.

- **Salamanders** – Ten species of stygobitic salamanders are known, including Proteus, the 25-30 cm long world-famous blind salamander from caves near the Adriatic Sea, and nine species from the US (Tex-
as, southwestern Ozark Plateau, Tennessee, Alabama, Georgia and Florida).

Most of these animals have lost their eyes and pigmentation in response to life in the constant and total darkness of the cave. A number of less-obvious evolutionary modifications have also occurred. In comparison to their surface relatives, cave animals tend to be longer-lived, produce fewer but larger eggs, have lower rates of metabolism, possess more abundant tactile and chemo-receptors, have longer antennae and long, thin, body forms.

Dr. Tom Iliffe and Dr. Wolfgang Sterrer examine a specimen at the Bermuda Zoological Society, Aquarium and Zoo. Photo: Jill Heinerth

To date, more than 350 new species of anchialine crustaceans have been collected and described, mostly from caves in the Bahamas, Bermuda and Yucatan Peninsula. Other hotspots for anchialine cave species include the Galapagos Islands in the eastern Pacific, Cape Range Peninsula in Western Australia, Canary Islands in the eastern Atlantic and Balearic Islands in the Mediterranean. Continued exploration is still turning up new discoveries at a high rate.

Despite being limited to caves, many groups of anchialine organisms are widely separated, e.g., on opposite sides of oceans or even opposite sides of the earth, and seemingly isolated from one another on a global scale. One theory attempts to explain such distributions by suggesting that cave organisms originated more that 100 million years ago when all continents were combined into one supercontinent and subsequently were dispersed by plate tectonic rafting as the continents separated and moved to their present positions. A number of other anchialine animals show close relationships with present deep-sea species implying a possible deep-sea origin for cave fauna. Finally, some cave animals are thought to have been 'stranded' in their present locations by receding waters of the Tethys Sea.

Unfortunately, many of these unique and fascinating animals are threatened with extinction due to the actions of man. In Bermuda alone, 25 species of cave animals are internationally recognized as “critically endangered.” This is the highest level of threat and roughly equates to a 50% chance of the species going extinct if nothing is done. All too frequently, anchialine cave animals can be considered endangered since 1) they have very limited distributions, commonly being known only from a single cave, and 2) environmental conditions in these caves are often deteriorating through the effects of water pollution or cave destruction.

Bermuda’s Church Cave is home to the country’s largest underground lake and many different species of unique cave adapted animals. Photo: Jill Heinerth

Threats to caves include sewage and waste disposal, deep well injection, quarrying and construction activities and diver and other human disturbances. As an example, the small oceanic island of Bermuda is the third-most densely populated country in the world and has the largest number of private cesspits per capita. Disposal of sewage and other waste water into cesspits or by pumping down boreholes is contaminating the ground and cave water with nitrates, detergents, toxic metals and pharmaceuticals; depleting the very
limited amounts of dissolved oxygen in cave water; and generating toxic levels of hydrogen sulfide. Some ocean caves such as the Blue Holes of the Bahamas have strong tidal currents sweeping through them for very considerable distances. In one such cave, plastic bottles and other trash have been observed littering the floor of the cave nearly a mile back into virgin passage. Far too many caves and sinkholes are viewed as preferred locations for the dumping of garbage and other waste products.

Jill Heinerth examines trash found inside the cave downstream of Rose Creek Swallet, Florida. Photo: Wes Skiles - from the film: Water’s Journey, Hidden Rivers of Florida.

Another serious environmental problem concerns the destruction of caves by limestone quarries or construction activities. At least half a dozen or more caves have been totally destroyed by Bermuda limestone quarries which produce crushed aggregate for construction. Untold other caves have been lost to enormous limestone mines in the Yucatan Peninsula. Many caves have been filled and built over by golf courses, hotels and housing developments in Bermuda. Recently, a series of luxury town homes were built directly on top of the largest cave lake in Bermuda.

Sometimes even seemingly innocent activities can threaten caves and cave animals. Along the Caribbean coast of the Yucatan Peninsula, many open water cenote pools are inhabited by several species of freshwater fish. Some of these fish have learned to follow divers into caves, moving in front of the dive team and voraciously darting in to devour any helpless crustaceans that chance to stray into the beam of a dive light. Considering the many hundreds to thousands of cave divers who use these systems each year, it is not surprising that the caves most heavily visited by tourist divers are now essentially devoid of life.

Even the gas exhaled by divers may have untold and unknown effects of caves and cave animals. Since anchialine caves waters typically contain extremely low levels of dissolved oxygen in the parts-per-billion range, the exhaust bubbles from open circuit and especially nitrox divers could have profound effects on the cave ecosystem. Several anchialine caves in Western Australia with unique fauna are currently off-limits to open circuit divers and may only be visited by those using rebreathers.

A boardwalk allows easy access through a tourist cave in Bermuda. Photo: Jill Heinerth

Some anchialine caves in Bermuda, the Canary Islands and Mallorca have been developed into commercial tourist attractions. Unfortunately, many of the tourists visiting these sites have viewed the deep clear water cave pools as natural wishing wells in which to throw a coin or two. Copper coins tend to rapidly deteriorate and dissolve in salt water, producing high levels of toxic copper ions in the cave waters. In one such cave in the Canary Islands off the coast of West Africa, an endemic, cave-adapted crab related to deepsea species is showing a marked decline in abundance over the last ten years or more, probably in response to high levels of copper in the cave water.

It is time that cave divers in particular begin to recognize the unique biological resources of caves and take steps to make sure such systems and organisms are protected for future generations.
A large quarry operation in Bermuda has destroyed unique cave ecosystems. Photo: Tom Iliffe

**REFERENCES AND FURTHER READING**


**ABOUT THE AUTHOR**

Tom Iliffe earned degrees in Biochemistry and Oceanography at Penn State, Florida State and the University of Texas Medical Branch. Prior to coming to Texas A&M University at Galveston, Tom worked for 11 years as a Research Scientist at the Bermuda Biological Station. It was in Bermuda that he became interested in marine cave biology. Diving explorations of Bermuda caves resulted in the discovery of more than 200 species, 70 of which were new to science.

Tom has led many expeditions worldwide to study and collect animals from underwater caves. Tom is currently a Professor of Marine Biology at Texas A&M University at Galveston where he teaches courses in Biospeleology, Scientific Diving and Tropical Marine Ecology.

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In March 2002, Tom Iliffe and his grad student Scott Webb were invited by filmmaker Wes Skiles to the Yucatan Peninsula of Mexico to carry out diving explorations and biological investigations of the Ring of Cenotes, a 180 km diameter semi-circle of water-filled caves. The Ring of Cenotes is the only surface expression of the 65 million-year-old meteorite impact crater which caused the extinction of the dinosaurs. The story of this expedition, “Watery Graves of the Maya”, is recounted in the October 2003 issue of National Geographic Magazine and on the National Geographic website.

To read about the expedition, go to: http://magma.nationalgeographic.com/ngm/0310/feature4/index.html

Dr. Tom Iliffe using his Megalodon rebreather to collect animals inside the cave.

Learn more about identifying cave animals at: www.cavebiology.com.