# Reports

## Marine Lava Cave Fauna: Composition, Biogeography, and Origins

Abstract. *An assemblage of endemic cavernicolous marine invertebrates, including taxa found on both sides of the Atlantic Ocean of great phylogenetic age or with affinities to deep sea organisms, inhabits the Jameos del Agua cave, a sea water–flooded Holocene lava tube cave on Lanzarote in the Canary Islands. This marine cave contains both relicts from Tethyan times, such as an apparently new crustacean family belonging to what had been the monotypic class Remipedia, and relicts of groups that are now common only in the deep sea as well as species that occur outside the cave.*

In general, marine caves contain relict fauna; that is, species derived from groups that were formerly widespread and diverse (*1*) but now survive as endemics in a particular cave system (*2*) possibly because of reduced competition or predation (*3*). The marine fauna of the Jameos del Agua lava tube cave (Table 1) are classified as four distinct groups: (i) Tethyan (*4*) cave-limited relict species, some of which are of great phylogenetic age and are closely related to inhabitants of marine caves in the western regions of the Atlantic Ocean; (ii) deep sea cave-limited species that may or may not be relicts derived from now deep sea (bathyal) stocks; (iii) ubiquitous species, those that seek out caves but can also occur outside them; and (iv) accidental species, those that are rarely found in caves and cannot survive there for long. These fauna are similar in many respects to those of marine limestone caves in Bermuda, the Bahamas, and the Caribbean region (*5*) and have similar origins (*6*). Their presence in a geologically young lava tube shows the mobility of such species and indicates the existence of habitats other than the typical limestone caves for cavernicolous fauna.

The Jameos del Agua cave is the seaward-most segment of a 7-km-long lava tube formed 3000 to 5000 years before present by a volcanic eruption on the island of Lanzarote in the Canary Islands (Fig. 1). The cave's diverse fauna consume food transported by strong tidal currents and diatoms living in the indirectly illuminated lake. Although the Jameos cave was the first to be recognized as biologically significant (*7*) and was subsequently investigated (*8, 9*), no in situ underwater studies were conducted. We now describe the composition, biogeography, and origins of the fauna of the Jameos cave as revealed by our investigations of the underwater tube.

The marine fauna of the Jameos cave consist of at least 14 invertebrate species, eight of which are endemic. These include an apparently new family from the class Remipedia, which had been considered monotypic. This primitive, eyeless, unpigmented crustacean was observed and collected during our dives in the totally dark lava tube connecting the Jameos cave with the sea. Remipedia were originally discovered in a marine cave on Grand Bahama Island (*10*), although what appear to be three additional species have been discovered in another inland marine cave in the Caicos Islands (*11*). The presence of the phylogenetically ancient Remipedia in isolated marine caves of both the eastern and western regions of the Atlantic Ocean probably resulted from continental drift and indicates a Tethyan origin predating

Table 1. Composition and inferred origin of the fauna of the Jameos del Agua cave, Lanzarote, Canary Islands.

| Fauna | Geographic affinities and distribution | | | Index of time in caves | Habitats | | | |
|---|---|---|---|---|---|---|---|---|
| | Endemic | East and west Atlantic distribution | Affinity to deep sea species | Eyes and dark pigment ± reduced | Macroporous interstitia | Free swimming | On bottom | Littoral |
| Remipedia family new, genera new, species new (Crustacea) | + | + | | + | | + | | |
| *Curassanthura* species new (Paranthuridae, Isopoda) | + | + | | + | + | | | |
| *Heteromysoides cotti* (Heteromysini, Mysidacea) | + | + | | + | | + | | |
| *Hadzia acutus* (Gammaridea, Amphipoda) | + | + | | + | + | | | |
| *Halophiloscia canariensis* (Oniscoidea, Isopoda) | + | + | | + | | | | + |
| *Tethyan or deep sea or both* | | | | | | | | |
| *Spelaeonicippe buchi* (Pardaliscidae, Amphipoda) | + | + | + | + | | | + | |
| *Deep sea* | | | | | | | | |
| *Munidopsis polymorpha* (Galatheidae, Anomura) | + | | + | + | | | + | |
| *Gesiella jameensis* (Polynoidae, Polychaeta) | + | | + | + | | | + | |
| *Ubiquitous* | | | | | | | | |
| *Stenopus spinosus* (Stenopodidea, Natantia) | | | | | | | + | |
| *Typosyllis cornuta* (Syllidae, Polychaeta) | | | | | | + | | |
| *Parhyale hawaiensis* (Talitroidea, Amphipoda) | | | | | | | | + |
| *Accidental* | | | | | | | | |
| *Cestus veneris* (Acnidaria) | | | | | | | | |
| Unidentified Echinoidea | | | | | | | + | |
| Unidentified Holothuroidea | | | | | | | + | |

a relatively narrow separation of the Atlantic Ocean.

Of three other genera, each with only two known species—one from the eastern and one from the western region of the Atlantic—at least two are also Tethyan relicts: (i) the anthurid isopod genus *Curassanthura*, with *C. halma* Kensley from Curaçao and a new species from the Jameos cave; and (ii) the mysid *Heteromysoides*, with the spongicolous *H. spongicola* Bacescu from Cuba and *H. cotti* (Calman) from the dimly lit Jameos lake. *Heteromysoides cotti* has brown pigmentation and eyes with a small number of facets. In these features it differs from the other Tethyan species in the Jameos cave, which lack dark pigmentation and are eyeless. The third genus is the amphipod *Spelaeonicippe*, with *S. provo* Stock and Vermeulen from the Caicos Islands and *S. buchi* (Andres) from the Jameos cave. *Spelaeonicippe* belongs to the primarily abyssal family Pardaliscidae and thus could either be of Tethyan origin or a recent descendant of now bathyal species. In addition, the amphipod *Hadzia acutus* (Andres) which lives in the macroporous interstitia of the Jameos tidal lake and the supralittoral isopod *Halophiloscia canariensis* Dalens are both probably Tethyan (*12*).

A second group of species from this cave has close affinities with deep sea organisms. Since the cave and deep sea habitats have many similarities (for example, total darkness, low food supply, nearly constant temperatures, and the absence of perturbation by waves or storms), bathyal species are predisposed for life in caves. The galatheid *Munidopsis polymorpha* Koelbel, closely related to the eastern Atlantic region deep sea species *M. simplex, M. curvirostra*, and *M. bispinata*, exhibits an unusual feature of the eyes: although facets and lenses are absent, light is perceived by sensory cells in the eye stalk rudiment (*9*). The monospecific polychaete *Gesiella jameensis* (Hartmann-Schröder) and *S. buchi* are two other such species closely related to the deep sea fauna. These species could either be bathyal relicts possibly of Tethyan age, or the result of a recent invasion of the cave via the undersea tube; this question remains until more is known about the composition of the deep sea fauna around the Canary Islands.

A third group consists of ubiquitous species which live in the Jameos cave, but which can also be occasionally observed outside. *Stenopus spinosus*, a red shrimp possessing well-developed eyes, was collected 700 m into the underwater tube near a small hole connecting to the overlying open sea. The cosmopolitan amphipod *Parhyale hawaiensis* Dana occurs around the Jameos tidal lake, while the globally distributed polychaete *Typosyllis cornuta* Rathke inhabits macroporous interstitia within this lake.

A fourth group consists of those species that are accidentally drawn by tidal currents into the cave but cannot complete their life cycle within it. Single specimens of an echinoid and a holothurian were observed near the opening at 700 m penetration, while the Venus girdle *Cestus veneris* Lesueur is observed occasionally in the Jameos lake (*9*). These lack the necessary preadaptations, especially viviparity, to found cave populations as individuals (*9, 13*).

The case of *Spelaeonicippe* lends support to the theory of Tethyan origin of species restricted to marine caves rather than recent origin. It has been argued (*14*) that *Spelaeonicippe* is a relatively recent addition to the caves, presumably derived from the related genus *Nicippe* found on the continental shelf and slope. This would have required independent colonization of caves on both sides of the Atlantic and subsequent convergent evolution to produce what appears as a single genus with two similar species. Since *Nicippe* and *Spelaeonicippe* differ in 13 developmentally unconnected characters, the chance of convergence producing such similarity is unlikely. Since three other genera from the Jameos cave show the same distribution as *Spelaeonicippe*, a Tethyan origin followed by separation and isolation of the species by continental drift is a more plausible explanation.

Since the Jameos cave is geologically young, the discovery of endemic relict fauna of Tethyan age showing extreme reduction of body pigment and eyes may seem surprising. Although there are no other known large caves in the Canary Islands, there are undoubtedly smaller caves in older rocks that could have served as the original habitat for these species. Some of the oldest rocks on Lanzarote are located immediately adjacent to and beneath the lava flow forming the Jameos cave. Volcanism in Lanzarote extends from the Tertiary Period (*15*) to the present day. The eastern islands of the Canaries, including Lanzarote, are thought to have separated from Africa in the early Cenozoic Era (*16*). Anchialine pools (*17*) on other

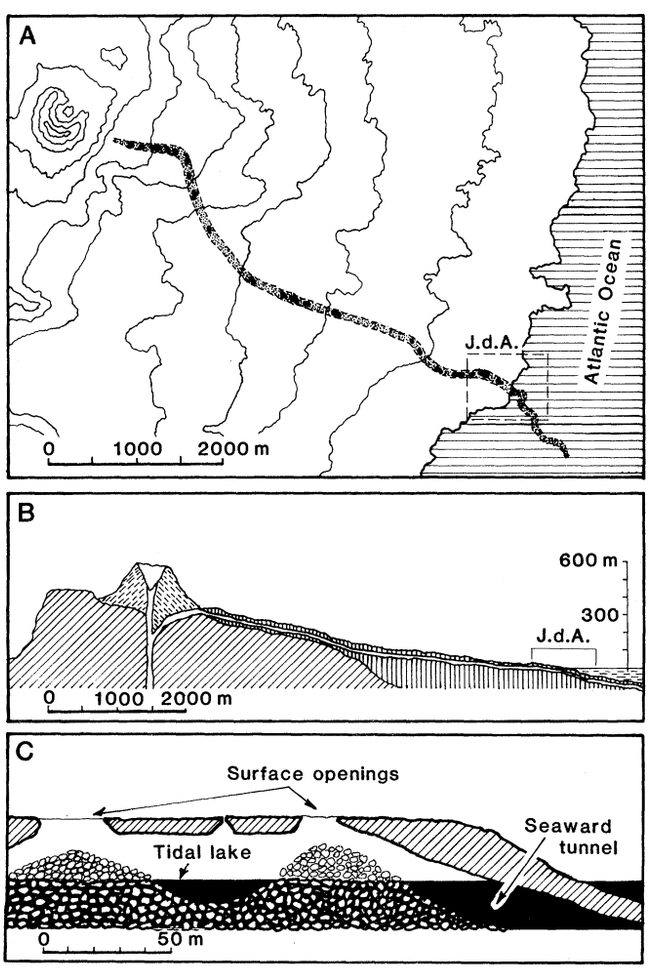


Fig. 1. Map (A) and profile view (B) of the lava tube and lava field of La Corona volcano on Lanzarote in the Canary Islands. The Jameos del Agua (*J.d.A.*) section of the lava tube (C) consists of two skylight openings where the cave roof has collapsed, isolating an indirectly illuminated tidal lake between two breakdown mounds. An intact continuation of the tube extends underwater past the coastline and beneath the sea floor for an explored distance of 1377 m. The average diameter of the tube is 10 to 15 m. The tidal range in the lake is 2 m, and the salinity of the lake water is nearly equal to that of the open sea.

volcanic islands contain cavernicolous shrimp (*18*), indicating that habitats other than caves can support these fauna. Terrestrial cavernicolous fauna have colonized Hawaiian lava tubes as soon as 100 years after the formation of the tubes (*19*). The high tidal range and corresponding strong currents in the Jameos cave would provide a means of sweeping larvae or weakly swimming species into the cave. Since the underwater tube was at a depth of 53 m and still descending at the limit of our diving explorations, deep water species or their larvae may also be drawn directly into the cave. Furthermore, at least some deep sea species have been shown to have two distributional maxima, one in the deep sea and another in shallow marine caves (*13*). Thus, it is possible that the Jameos cave fauna could have entered the cave by local dispersion from adjacent and older caves, other suitable habitats, or even the deep sea in a relatively short period of time.

THOMAS M. ILIFFE
*Bermuda Biological Station for Research, Ferry Reach 1-15, Bermuda*
HORST WILKENS
JAKOB PARZEFALL
*Universität Hamburg, Zoologisches Institut und Zoologisches Museum, 2000 Hamburg 13, West Germany*
DENNIS WILLIAMS
*Box F-931, Freeport, Bahamas*

### References and Notes

1. Some examples of relict species from marine caves are a new family of ostracods and a new order of peracarid Crustacea from Bermuda, and a new family of shrimps from the Caicos Islands.
2. Although most true cavernicolous marine species inhabit only a single cave system or caves from a small area, some, such as the shrimp *Barbouria cubensis* from Bermuda, Cuba, the Bahamas, and the Cayman Islands, are widely dispersed by as yet unknown mechanisms.
3. D. C. Culver, *Cave Life: Evolution and Ecology* (Harvard Univ. Press, Cambridge, Mass., 1982), pp. 96–133.
4. The period about $10^8$ years before present when the continents clustered around the Tethys Sea, a paleographic sea ancestral to the present Mediterranean which came into existence in early Permian time.
5. B. Sket and T. M. Iliffe, *Int. Rev. Gesamten Hydrobiol.* **65**, 871 (1980); J. H. Carpenter, in *Proceedings of the Eighth International Congress of Speleology*, B. F. Beck, Ed. (National Speleological Society, Huntsville, Ala., 1981), vol. 1, p. 24.
6. T. M. Iliffe, C. W. Hart, Jr., R. B. Manning, *Nature (London)* **302**, 141 (1983).
7. A. Vandel, *Biospeleology: The Biology of Cavernicolous Animals* (Pergamon, Oxford, 1965), pp. 8–9.
8. K. Koelbel, *Ann. K. K. Naturhist. Hofmuseums* **7**, 105 (1892); W. T. Calman, *Ann. Mag. Nat. Hist.* **7**, 213 (1904); L. Fage and T. Monod, *Arch. Zool. Exp.* **78**, 97 (1936); W. Harms, *Zool. Anz.* **52**, 101 (1971).
9. H. Wilkens and J. Parzefall, *Ann. Speleol.* **29**, 419 (1974); J. Parzefall and H. Wilkens, *ibid.* **30**, 325 (1975).
10. J. Yager, *J. Crust. Biol.* **1**, 328 (1981).
11. _____, personal communication.
12. J. Stock, *Studies on the Fauna of Curaçao and Other Caribbean Islands* **55**, 1 (1977); L. de Castro, *Biol. Mus. Nac. Rio Janeiro* **238**, 1 (1962).
13. R. Riedl, *Biologie der Meereshöhlen* (Verlag Paul Parey, Hamburg, 1966).
14. J. Stock and J. J. Vermeulen, *Bijdr. Dierkd.* **52**, 3 (1982).
15. E. M. Driscoll, G. L. Henry, K. J. Tinkler, *Geol. J.* **4**, 321 (1964).
16. A. Abdel-Monem, N. D. Watkins, P. W. Gast, *Am. J. Sci.* **271**, 490 (1971).
17. The term anchialine refers to "pools with no surface connection with the sea, containing salt or brackish water, which fluctuates with the tides".
18. F. A. Chace and R. B. Manning, *Smithson. Contrib. Zool.* **131**, 1 (1972); L. B. Holthuis, *Zool. Verh. Rijksmus. Nat. Hist. Leiden* **128**, 1 (1973); T. Monod and P. Cals, *Miss. Zool. Belge Iles Galapagos Ecuador* **2**, 57 (1970); J. A. Maciolek, *Bull. Mar. Sci.* **33**, 606 (1983).
19. F. G. Howarth, *Science* **175**, 325 (1972).
20. We thank S. Exley, K. Fulghum, C. Pitcairn, R. Power, and M. van Soeren—all members of the Jameos del Agua International Expedition 1983—for cave diving assistance. We also thank the Cabildo Insular de Lanzarote for assistance to our scientific studies, and H. Dalens, G. Hartmann-Schroder, L. B. Holthuis, W. Sterrer, and M. Turkay for valuable information. Supported by grants from the National Science Foundation (BSR-8215672) and the National Academy of Sciences to T.M.I.

8 December 1983; accepted 17 February 1984

## Raman Spectroscopy of a Coal Liquid Shows That Fluorescence Interference Is Minimized with Ultraviolet Excitation

Abstract. *The first ultraviolet resonance Raman measurements of a coal liquid are reported. The spectra detail the presence of numerous polycyclic aromatic hydrocarbons with ring systems similar to those of naphthalene, fluorene, phenanthrene, pyrene, and triphenylene. The ultraviolet resonance Raman measurements of this highly complex sample show no significant interference from fluorescence. The lack of fluorescence interference and the high selectivity indicate that ultraviolet resonance Raman spectroscopy is a powerful new technique for characterizing highly complex samples and mixtures.*

Raman spectroscopy represents only one of a myriad of spectroscopic techniques used in the study of molecular structure (*1*). However, resonance Raman spectroscopy is unique among these techniques because of its selectivity, since the resonance phenomenon permits the specific enhancement of the vibrational spectrum of one particular molecular species within a complex solution or mixture (*2*). Other species in the mixture not resonantly enhanced show Raman spectra of much lower intensity (often by a factor of $10^{-5}$). Raman spectroscopy has shown particular promise for biological investigations because the weak Raman scattering of water does not significantly interfere with measure-

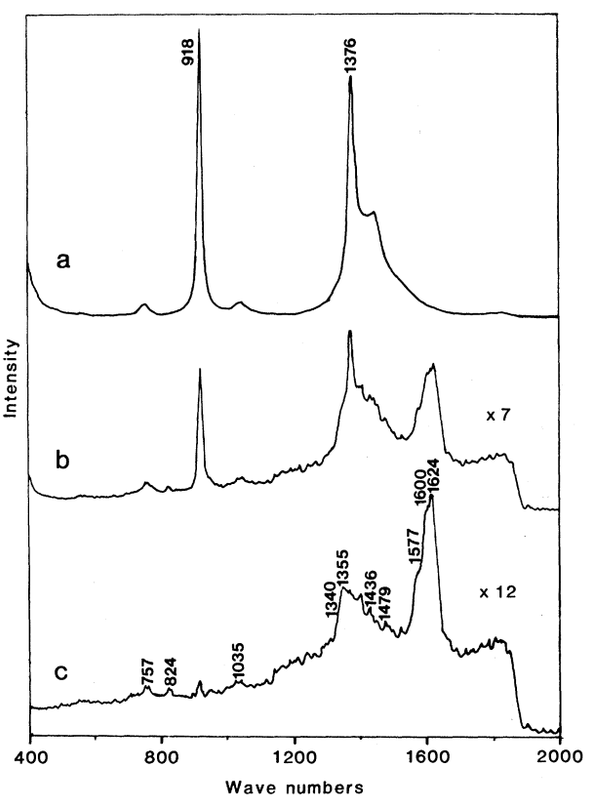


Fig. 1. Ultraviolet resonance Raman spectrum of (a) acetonitrile; (b) a coal liquid sample in acetonitrile diluted ~500 times (volume/volume); the intensity scale of (b) is expanded by a factor of 7 as compared to (a); (c) difference spectrum (b − a) showing the coal liquid resonance Raman spectrum; the intensity scale is expanded by a factor of ~12 as compared to (a). The measurement parameters were as follows: excitation wavelength, 256 nm; number of laser pulses averaged, 18,000 (15-minute scan at 20 Hz); average power, 2.0 mW; spectrometer bandpass, ~6 $cm^{-1}$.