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The Corona lava tube, Lanzarote: geology, habitat diversity and biogeography

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Abstract The Corona lava tube on the Canarian island of
Lanzarote is a unique subterranean ecosystem comprising
both dry and submerged cave sections with a total length of
almost 8 km. Here, we present the results of a diving
exploration of the lava tube that took place from 11 to 25
March 2008. Environmental characteristics are given for
ecologically disparate sections of the cave, including the
Cueva de los Lagos, the Jameos del Agua, and the Túnel
de la Atlántida. Moreover, we compare various habitats
within the lava tube, and discuss the origin of the diverse
hypogean fauna, including new species of remipede
crustaceans and polychaete worms discovered during the
expedition.

Keywords Anchialine caves · Sub-seafloor caves ·
Marine biodiversity · Hypogean fauna · Mesozoic distributions

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Introduction

The Corona lava tube on Lanzarote, Canary Islands is the
15th longest lava tube in the world at 6,100 m (Gulden
2009), as well as the longest underwater cave of this type,
extending to 1,618 m (Isler 1987). The first scientific
reference to the cave was by the Austrian taxonomist
Koelbel (1892) in his description of the galatheid crab
Munidopsis polymorpha, probably the best-known endemic
species from the lava tube. A preliminary ecological survey
of the Jameos del Agua, a tidal lagoon within the lava tube,
was performed by Harms (1921), who mainly focused on
the histology of the depigmented and reduced eyes of *M.
polymorpha*. Subsequent early studies on the cave fauna
were carried out by Calman (1904, 1932) and Fage and
Monod (1936).

In the early 1970s, a new phase of intensive studies
started with emphasis on the biology and behavior of *M.
polymorpha* and the ecology of the Jameos del Agua
(Wilkens and Parzefall 1974; Parzefall and Wilkens 1975;
Wilkens et al. 1990). In connection with these investiga-
tions, several eyeless and depigmented new species of
amphipods, polychaetes and isopods from the hypogean
lagoon were described by Andres (1975, 1978), Hartmann-
Schröder (1974) and Wägele (1985).

Diving investigations of the totally submerged section of the lava tube, the Túnel de la Atlántida, commenced in 1983 (Iliffe et al. 1984) and resulted in the remarkable discovery of the first and, until now, only remipede so far known from the eastern Atlantic, *Speleonectes ondinae* (García-Valdecasas 1984) (Schram et al. 1986). Another comprehensive study was performed shortly after this by García-Valdecasas (1985).

As a result of these previous studies and our current investigations reported in this special issue, 77 species including 37 endemic were found to inhabit the anchialine sections of the lava tube. Listed in order of abundance, stygobiont species include 11 copepods (Boxshall and Iliffe 1987; Ohtsuka et al. 1993; Huys 1996; Jaume and Boxshall 1997; Fosshagen et al. 2001), 9 annelids (Hartmann-Schröder 1974; Bertelsen 1986; Núñez et al. 1997; Worsaae et al. this issue), 4 ostracodes (Baltanás 1992; Kornicker and Iliffe 1995, 1998), 4 amphipods (Andres 1975, 1978), 2 remipedes (García-Valdecasas 1984; Koenemann et al. this issue), as well as a single species of thermosbaenacean (Bowman and Iliffe 1986), thecostrata (Ohtsuka et al. 1993), mysidacean (Calman 1932), decapods (Koelbel 1892); isopods (Wägele 1985), and molluscs (Rubio and Rodríguez-Babío 1991).

This paper reviews the results of previous studies in the light of the new discoveries made during the "Atlántida 2008 Cave Diving Expedition to the Túnel de la Atlántida". We present a more complete picture that reflects our current state of knowledge of the diversity and origin of the fauna inhabiting the Corona lava tube.

The Atlántida 2008 cave diving expedition

In March 2008, a cave diving expedition including divers and scientists from Spain, Germany and the United States was conducted to investigate and collect specimens of the anchialine fauna of the Túnel de la Atlántida as well as to document water quality and tidal circulation. Closed circuit rebreathers, which release no exhaust bubbles and recycle exhaled gases, were used by the dive team to extend dive times and reduce decompression obligations. All diving was carried out following standards set by the National Speleological Society – Cave Diving Section (NSS-CDS) and the American Academy of Underwater Sciences (AAUS).

The primary objectives of the expedition were to (1) collect biological specimens for taxonomic, physiologic, and molecular examination or analysis, (2) investigate and sample the Montaña de Arena at 700 m horizontal penetration into the cave, and (3) study water quality and tidal circulation through use of an electronic water quality analyzer moored for 2-day periods at 300, 700 and 1,000 m penetrations into the Túnel de la Atlántida.

Another important goal was to collect specimens of the remipede *Speleonectes ondinae* for molecular genetic comparison with its congeners inhabiting caves on the opposite side of the Atlantic. An extraordinary and totally unexpected discovery involved our collection of a second, new species of *Speleonectes* (Koenemann et al. this issue), representing the second species of Remipedia (Crustacea) in the Eastern Atlantic.

Zooplanktonic organisms from the water column were identified visually and collected individually along with ambient water in clear, wide-mouth bottles. Under these conditions, animals remained alive and in good condition for at least 24 h, allowing them to be photographed and examined, or used in physiological experiments to measure their oxygen consumption and metabolic rates (Bishop and Iliffe this issue).

Still and video photographic documentation of the natural color patterns and behavior was carried out while specimens were still alive. Photographs were taken either through a macro lens directly on the camera or through a photo adapter tube on a trinocular dissecting microscope. Specimens were fixed in molecular grade 96% EtOH for subsequent morphologic examinations and DNA extractions.

Sand samples were collected in a 4-l bottle from the surface of the Montaña de Arena, and interstitial animals sorted while alive by suspending and decanting the supernatant through a 63-µm mesh sieve. Organisms were anesthetized in isosmotic $MgCl_2$ solution, then fixed in 2% glutaraldehyde in seawater, and stored in cacodylate buffer with 0.3 M sucrose.

Water quality investigations involved the placement of a YSI 600XLM electronic water quality analyzer (sonde) at 300, 700 and 1,000 m distances into the wholly submerged Túnel de la Atlántida. These locations are all beyond the coastline and situated under the sea floor. The sonde was programmed to take data at 2 min intervals and log data on depth, salinity, temperature, pH, dissolved oxygen, and redox potential. Since the tides in Lanzarote are semi-diurnal, logging runs were scheduled for 2 days to cover multiple tidal cycles. Data were plotted as a function of time and depth (tidal fluctuation) on each graph to document the tidal cycle.

We measured abiotic parameters of the sediment using a fraction of the samples, before processing them for faunistic studies. Granulometric analysis was performed manually in a sieve column according to the Wentworth scale (Buchanan 1984). Determination of organic matter content was carried out using the Walkley and Black method (Buchanan 1984). The carbonate content was obtained with a calcimeter using the Bernard method.

Geology and morphology

The Canary Islands are an oceanic archipelago with volcanic origins, composed of seven major islands and several islets of different geological ages, ranging from 22 to 0.7 million years (Carracedo et al. 1998). The island of Lanzarote is one of the oldest in the archipelago, with an estimated age of 15.5 million years. Processes involved in forming the island were complex and concerned several periods of volcanism, followed by subsequent erosional periods with less volcanic activity (Carracedo et al. 2003).

The Corona lava tube is located near the northern tip of Lanzarote in the Malpaís de la Corona (Figs. 1, 3a), a lava field resulting from the activity of the volcanoes La Quemada, La Corona and Los Helechos during several eruptive episodes in the Pliocene and Pleistocene (Carracedo et al. 2003). The lava tube formed during one of the most recent phases of this process, from materials ejected by a lateral throat of the Corona volcano under subaerial conditions. This volcanic phase was recently determined to have occurred 21,000±6,500 years ago by ^{40}Ar/^{39}Ar direct dating methods, corresponding with the last glacial maximum at 21,000 to 18,000 years ago (Carracedo et al. 2003). Thus, in spite of its relatively young age, the cave is older than proposed by former indirect dating studies based on geomorphology, fossil associations, or paleosoils (Bravo 1964; Zazo et al. 1997, 2002; Zöller et al. 2003).

The dry section of the lava tube has a total length of 6.1 km and extends to the southeast from the base of the volcano towards the coastline. Seawater reaches approximately 600 m into the cave from the coastline, where it is first encountered in the Cueva de los Lagos (Figs. 2, 3c). A tidal seawater lagoon, located between two collapse entrances, is present in the Jameos del Agua section of the cave, just inland from the coast (Figs. 2, 3b). At the seaward end of the Jameos del Agua cave, another seawater pool provides diving access to the remainder of the cave, the wholly submerged Túnel de la Atlántida. This section of the lava tube continues a further 1,618 m into the sea, where it terminates 64 m below sea level in a cul-de-sac (Isler 1987). The length and depth of the submerged tube is consistent with an origin approximately 21,000 years ago, at a time when the glacial sea level was 100 m (or more) lower than today. In this scenario, the cave is assumed to have formed under subaerial conditions, only to be flooded during subsequent post-glacial sea level rise (Carracedo et al. 2003).

The diameter of the Corona lava tube varies to more than 30 m in some sections of the Túnel de la Atlántida, and is wider than 20 m along most of its length. The tube is also complex in relation to its geomorphology. Both dry and submerged sections consist of a single conduit without side passages, but occasionally with upper and lower levels separated by a false floor between them (Fig. 3d). More than 20 collapse skylight entrances are scattered along the length of the dry cave, while only a single, very small opening above the Montaña de Arena is present in the Túnel de la Atlántida (Fig. 3e). Lavacicles (i.e., lava stalactites) are present throughout the cave. Gypsum crusts and light colored powdery dust are common in the dry

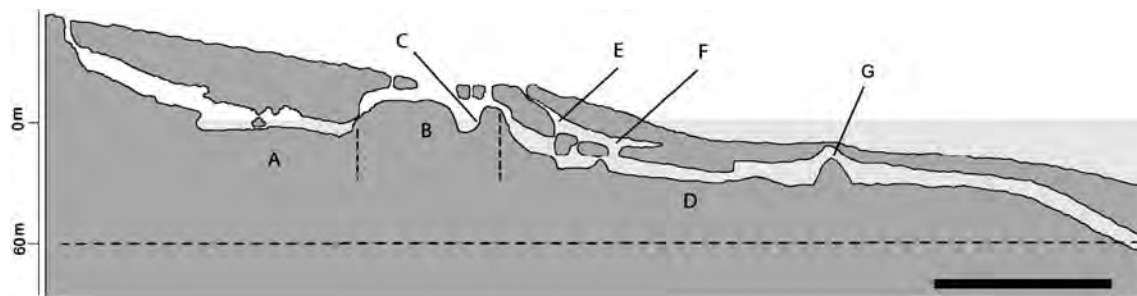**Fig. 1** Map of the Corona lava tube

Fig. 2 Schematic cross-section of the anchialine portions of the Corona lava tube. **a** Cueva de Los Lagos. **b** Jameos del Agua lagoon (*dotted transversal lines* represent the approximated area occupied by the tourist complex). **c** Position of the carpet of diatoms in the lagoon. **d** Túnel de la Atlántida. **e** Lago Escondido. **f** Dome room. **g** Montaña de Arena. *Shaded areas in light gray* Position of current sea level; *horizontal dashed line* possible position of the sea level during the formation of the cave. *Horizontal scale bar* 500 m; *vertical scale on left axis* exaggerated. Modified from Jantschke et al. 1994

cave, while white submarine cement covers the upper surfaces of many rocks in the Túnel de la Atlántida. In most parts of the dry and underwater cave system, substantial collapse has occurred and the floor is covered with large boulders. However, in other sections, solidified lava flows cover the floor, indicating that no collapse has occurred since the cave was formed.

Only the last 2,000 m of the lava tube are flooded by seawater and harbors the fauna described in this special issue. This part is divided in three sections by natural collapses (Fig. 2). Cueva de los Lagos (Fig. 3c) marks the most inland penetration of seawater into the lava tube. It extends over ca. 700 m, but only the last 400 m are partially flooded and divided into three so-called lakes (Wilkens et al. 1993). The final 100 m of the Cueva de los Lagos are completely submerged and at one time connected to the Jameos del Agua; however, this connection was artificially closed during construction in the Jameos del Agua for tourist purposes.

The Jameos del Agua (Fig. 3b) contains a 50-m-long and up to 10-m-deep anchialine lagoon. Two larger collapse entrances on either side of the Jameos lagoon and a small vent hole directly above it allow mostly indirect daylight to reach the water. In contrast, all other lakes within the lava tube are in total darkness (Wilkens and Parzefall 1974).

The Túnel de la Atlántida (Fig. 3f) is the longest and most complex section of the flooded cave. Except for its entrance pool at the back of the Jameos del Agua cave, the remainder of the tube is completely submerged and crosses the coastline, heading out to sea. Atlántida contains several features not found in other parts of the cave. For example, at 400 m penetration into the underwater cave, a breakdown mound allows divers to reach a second part of the tube lying above the main tunnel and extending inland to an isolated air room, the Lago Escondido, as well as seaward for several hundred meters before the tunnel becomes too low for divers to continue. In addition, the Montaña de

Arena is an impressive, 11-m-high conical mound of loose, white sand, located at 700 m inside the lava tunnel (Fig. 3e). It is formed by calcareous sand entering through a small hole in the ceiling from the overlying sea floor.

Ecology

Although the various sections of the Corona lava tube have a common geological origin and all parts are interconnected, the different submerged parts show ecological differences for which varied abiotic factors are responsible. With respect to the influence of daylight, the submerged section of the lava tube can be partitioned into two parts. Whereas the Cueva de los Lagos and the Túnel de la Atlántida are true lightless biotopes, limited daylight that enters the Jameos del Agua lagoon allows a carpet of benthic diatoms to flourish, at least in shallow, more well-illuminated depths. The availability of this food source in an otherwise nutrient impoverished environment has a profound impact on the trophic dynamics and faunal composition.

Direct infiltration of marine water plays an important role in the Túnel de la Atlántida in providing a source of nutrients to the cave ecosystem. The trophic input is probably composed of dead organic matter as well as smaller planktonic organisms. This is demonstrated by the presence of the ahermatypic solitary coral *Caryophyllia* cf. *inornata* on the cave ceiling, near the sand mound, where water influx from outside is taking place during the rising tide. This is furthermore proven by relatively high abundances of shrimps on the sand mound surface and meiofaunal organisms in its sediment (see Martínez et al. this issue). Since the water column merely moves back and forth in the lava tunnel, the nutrient content of the water most likely diminishes as the distance from openings to the sea—such as the one at the Montaña de Arena—increases.

Fig. 3 a The Corona volcano (northwestern view), with a collapse section of the lava tube in the foreground. **b** The Jameos del Agua lagoon in the tourist complex. **c** Diver in the Cueva de Los Lagos section. **d** Upper level passage at approximately 300 m penetration. **e** Divers at the sand mound Montaña de Arena. **f** Team of three divers in the Túnel de la Atlántida. All photos courtesy of Jill Heinerth

The Cueva de los Lagos, as the most inland extension of seawater into the lava tube, presumably derives minimal benefit from the oceanic infiltration input, because of its significant distance from the sea. Probably very little of the tidal waters entering the Túnel de Atlántida penetrate to this innermost zone, and if they do, only with a long delay. It is more likely that, during the winter rainy season, precipitation falling on the overlying lava field seeps through the thin layers of bedrock into the cave. In this way, terrestrial organic matter could be transported from the surface into the Cueva de los Lagos.

In contrast to other sections of the lava tube, the Jameos del Agua presents a quite different ecological situation because it is exposed to daylight, which enables primary production. However, the low light intensity is only sufficient for the development of diatoms, which are in

turn fed upon by locally abundant populations of the crab *Munidopsis polymorpha* and the mysid shrimp *Heteromysoides cotti*.

Environmental characteristics

All three anchialine sections of the Corona lava tube, i.e., Cueva de los Lagos, Jameos del Agua, and Túnel de la Atlántida, contain tidally influenced, fully marine waters. As with most anchialine caves, the timing of the tides within the cave is delayed in comparison with open ocean tides and the amplitude is reduced. The exact entry point for the exchanging tidal water is not known. Only one location, a small opening in the cave ceiling directly above the peak of the Montaña de Arena, shows clear signs of direct communication with the open sea, as evidenced by the presence of filter-feeding offshore animals such as sponges and solitary corals at this site. However, on several occasions when divers visited the opening, strong currents could not be detected. An alternate explanation for the source of tidal waters within the cave is that the walls of the entire Túnel de la Atlántida are pervious and allow

exchange with the open sea. To determine what kind of water quality fluctuations occur at specific locations in the cave and how these relate to the tides, a YSI 600XLM sonde was moored for 2 day intervals at three locations with increasing distances into the Túnel de la Atlántida. The sonde was first placed in a somewhat restricted part of the cave passage at 300 m distance from the entrance pool. The second station was on the ceiling in the Montaña de Arena section at 700 m, while the third station was in large passage at 1,000 m penetration (Figs. 4, 5).

Temperature, salinity, and pH were plotted as a function of time for each of the three stations (Fig. 4). A depth-time (tidal) plot was also included to identify any relationship between observed fluctuations and the state of the tide. Changes in temperature, salinity and pH were small, but did show clear patterns of fluctuations in response to the tides. Salinity changes were directly related to the tides; for example, higher salinities were observed at high tide and lower salinities at low tide for each of the three stations. Temperature and pH behaved in a somewhat more erratic pattern. The temperature was directly related to tide at 300 and 700 m, but inversely related to tide at 1,000 m. In
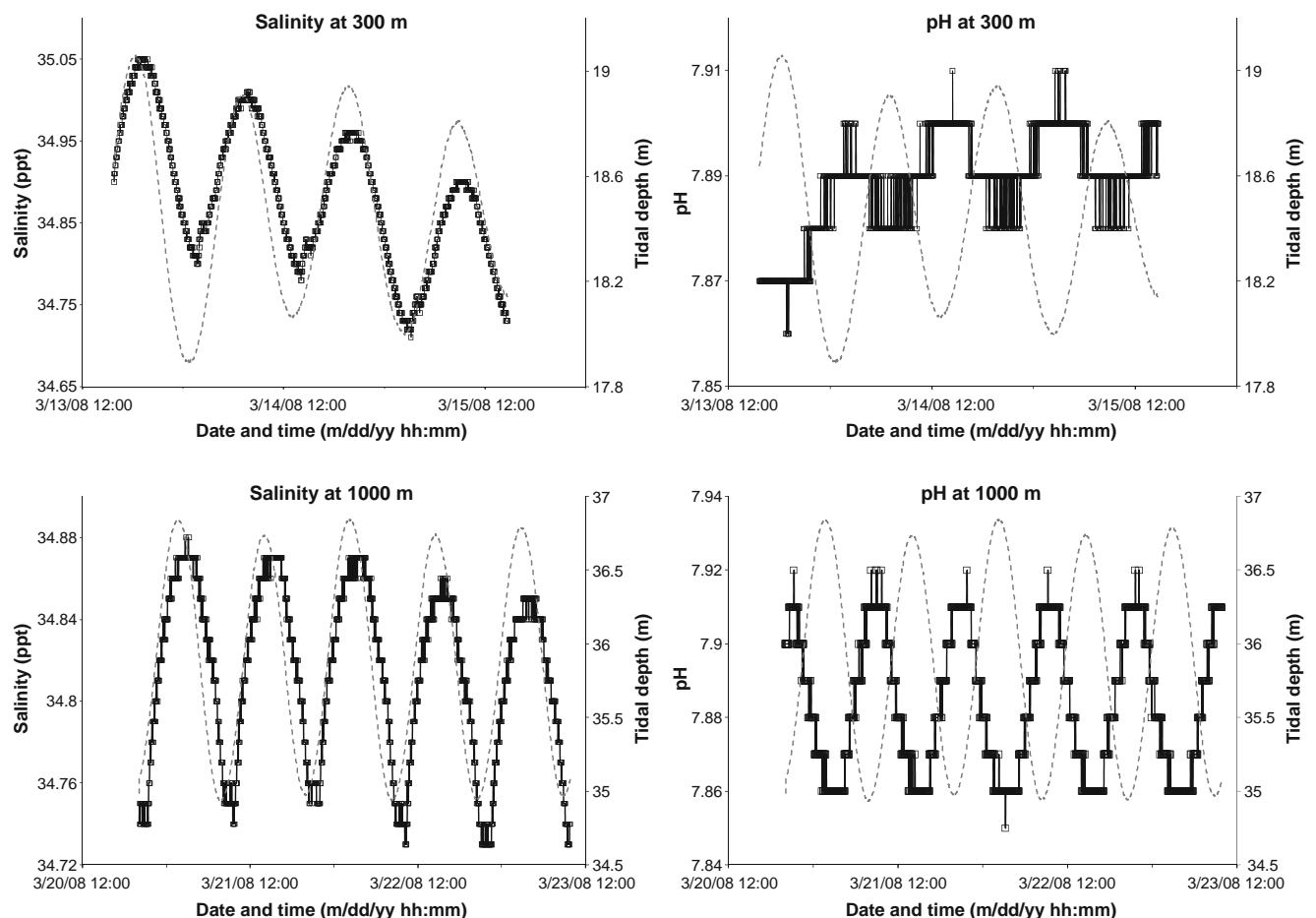

Fig. 4 Plots of salinity (*left*) and pH (*right*) as a function of time for two stations at 300 and 1,000 m penetration into the Túnel de la Atlántida. The *dashed line* represents the tidal fluctuations in water depth within the cave

Fig. 5 Depth-time (tidal) plot showing fluctuations of the amount of dissolved oxygen and the state of the tide at 1,000 m penetration into the Túnel de la Atlántida
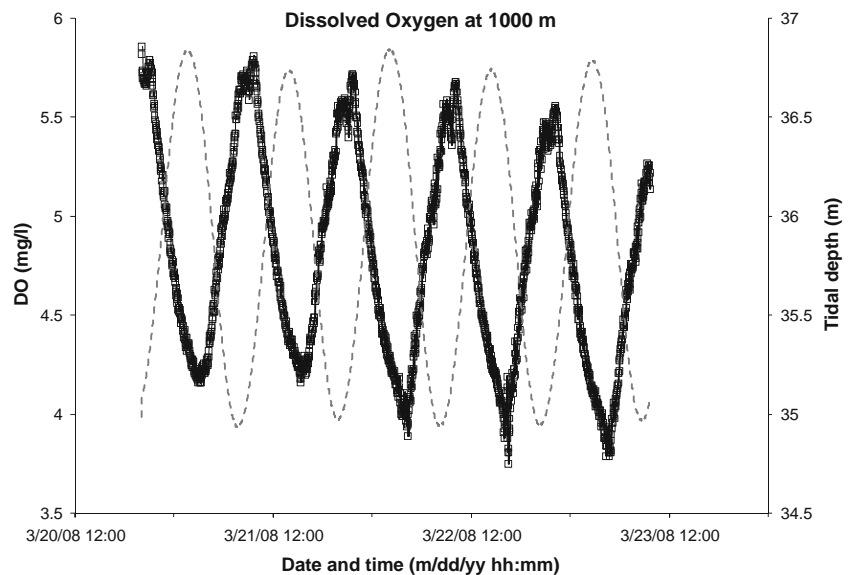
contrast, pH was directly related to tide at 700 m, and inversely related at 300 and 1,000 m. Due to problems with the membrane of the oxygen sensor, dissolved oxygen (DO) values were only obtained for the 1,000 m station, where they varied inversely with the tide, i.e., low DO occurred at high tide and high DO at low tide (Fig. 5).

Three types of water need to be taken into consideration to explain fluctuation patterns, inland groundwater, cave water, and ocean water. Groundwater should be lower in salinity than ocean water due to dilution by rain; thus, the lower salinity values observed at low tide for all three stations suggests that lower-salinity groundwater is circulating to even the most remote parts of the cave system. Fluctuations in temperature, pH and dissolved oxygen are not so easy to explain. The declining DO values on the rising tide implies that the water comes from deeper within the cave, where it has been out of contact with the atmosphere, and thus has lower DO values. It is possible that the tidal currents within the lava tube flow in opposite directions along the cave floor and the cave ceiling at any given time. This might help to account for different temperature and pH values in diverse sections of the cave.

Habitat diversity and fauna

Pelagic habitat

The pelagic habitat consists of clear marine water that fluctuates back and forth in the tube in response to the tides. The volume of water exchanged between the offshore and the cave during every tide should equal the tidal range within the cave (approximately 2 m) multiplied by the area of the cave water surface from the seaward-most Lago

Escondido to the Cueva de los Lagos, the inland-most point at which water is found. Assuming the distance of seawater penetration into the lava tube is approximately 600 m for an average passage width of 10 m, the tidal exchange volume of the cave would be approximately 12,000 m^3 per tidal cycle.

Anchialine cave waters are inhabited by a diverse group of endemic, pelagic species, dominated by crustaceans, all of which are supported primarily by the marine infiltration of organic matter. Remipedes, represented by *Speleonectes ondinae* and the new species of *Speleonectes* (Fig. 6a; see also Koenemann et al. this issue), are the top predators in the cave water column, and as would be expected, are present in low numbers throughout the lava tube. Other common pelagic species include: the amphipod *Spelaeonicippe buchi* (Fig. 6c); the ostracodes *Danielopolina wilkensi* and *D. phalanx*; the thermosbaenacean *Halosbaena fortunata*; the copepods *Enantronia canariensis, Paradiaptomus allauadi, Paramisophria reducta, Stygocyclopia balearica, Dimisophria cavernicola* and *Expansophria dimorpha*; and the polychaete annelids *Gesiella jameensis* (Fig. 6d) and *Protodrilus* sp. (Fig. 6b). In the Jameos del Agua, swarms of the mysid *Heteromysoides cotti* probably subsist on the localized primary production there.

Benthic habitats

The benthic environment of the Corona lava tube is more heterogeneous than the pelagic zone and harbours a variety of habitats, namely (1) epibenthic rock surfaces of cave walls and boulders throughout the cave, (2) lapilli patches localized in some areas of the bottom, (3) calcareous sand in the Montaña de Arena area of the Túnel de la Atlántida, (4) carpets of benthic diatoms, and (5) fecal deposits of

Fig. 6 Stygobionts that inhabit the submerged parts of the lava tube. **a** *Speleonectes ondinae* (Remipedia). **b** *Protodrilus* sp. (Polychaeta). **c** *Spelaeonicippe buchi* (Amphipoda). **d** *Gesiella jameensis* (Polychaeta). **e** *Munidopsis polymorpha* (Galatheidae). **f** *Curassanthura canariensis* (Isopoda).. Animals are not shown to the same scale. Photos courtesy of U. Strecker and A. Martínez García
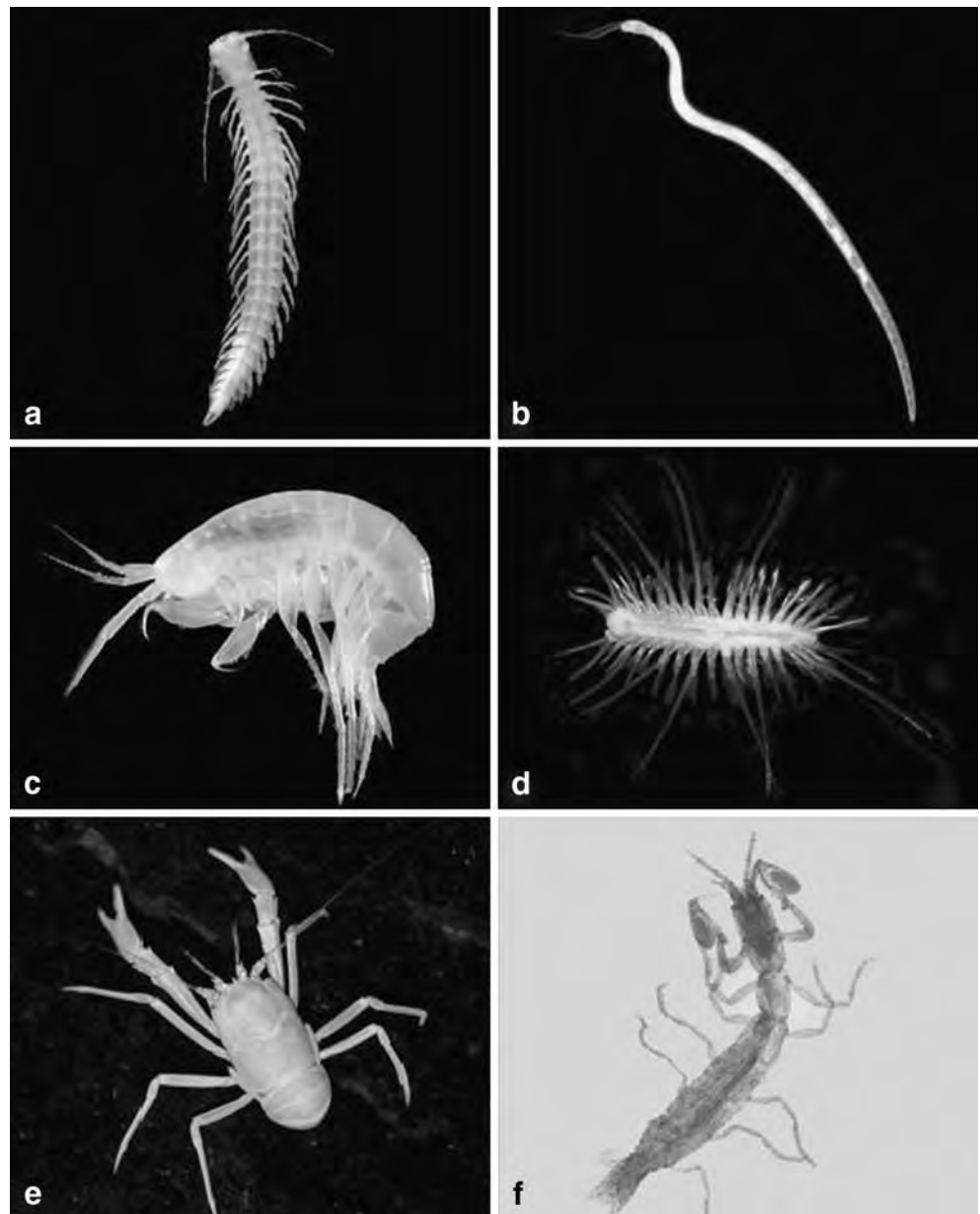
echiuran worms (*Bonellia viridis*), the latter two in the Jameos del Agua lagoon (see also Brito et al. this issue).

Large boulders and rubble cover the floor in many sections of the cave and form a substratum for epibenthic species crawling over their surface, or a refuge for free-swimming species that take advantage of the large crevices. They likely accumulated during the formation of the cave, and later, massive ceiling collapses produced the various entrances. The two collapse entrances on opposite sides of the Jameos lagoon are excellent examples of this process.

Of the pelagic species that use rock surfaces as temporary substratum, the galatheid crab *Munidopsis polymorpha* (Fig. 6e) is the most commonly observed. Although it is widespread throughout the cave, it is especially abundant in the Jameos lagoon and the entrance

of the Túnel de la Atlántida, presumably feeding on algae and detritus. Other epibenthic species in the cave complex are primarily opportunistic or accidental species, and show higher abundances in the areas of the cave where offshore influence or in situ primary production is more significant. Typical representatives of epibenthic species are echiuran worms (*Bonellia viridis*) and molluscs (*Osilinus atratus, Littorina striata, Jujubinus exasperatus*, and *Botryphallus epidauricus*) in the Jameos lagoon, as well as the decapod *Stenopus spinosus* in the Montaña de Arena section.

Sessile species are also present, attached to the walls, but only in certain parts of the cave, namely the Montaña de Arena area. This sessile assemblage consists of presumably offshore species of sponges, bryozoans and cnidarians, feeding on the organic matter swept into the cave by tidal

currents entering from the open sea through a small hole in the ceiling directly above the top of the sand mound.

Lapilli patches are spread all along the cave, usually among boulders or in specific areas where the bottom morphology favors the accumulation of coarse sediments. The origin of these volcanic gravel particles is related to the formation of the cave, followed by subsequent collapse events and erosion of the cave walls. Remarkable examples of this environment are found in the Cueva de los Lagos, especially at the beginning of the first and along the second lake, in the deepest areas of the Jameos lagoon, and along the steep slope at the entrance to the Túnel de la Atlántida. This volcanic sediment is defined by its coarse grain size, with few particles smaller than 0.5 mm, and a high percentage of heavy elements reaching 98% of the total weight of the sample in some samples. In offshore areas, lapilli patches are characteristic of exposed areas, where marine dynamics do not allow sedimentation of smaller particles. Thus, the presence of relatively coarse sediment in a low-energy, anchialine environment must be considered a peculiar feature. A possible explanation is the low rate of suspended particles in this environment, where sediments from offshore are scarce or limited to special areas (such as the Montaña de Arena), so that recent sedimentary material accumulates through erosion of the cave walls. The low velocity of water currents within most of the cave explains the morphology of lapilli grains, which are characterized by low sphericity and high angularity. These features favor the development of large interstices within the patches and increase the available surface for settlement of meiofauna and bacterial colonies. Another feature increasing the surface area of the sediment is the porosity of the grains themselves, due to their volcanic origin and the presence of gases during solidification of the lava. When trophic resources are present, as is the case in the Jameos del Agua, the existence of extensive interstitial surfaces in the sediment favors the establishment of a diverse faunal assemblage. Dominant endemic species at lapilli patches include the isopod *Curassanthura canariensis* (Fig. 6f), the harpacticoid copepod *Neoechinophora karaytugi*, and several polychaetes such as *Mesonerilla* n. sp., *Macrochaeta* sp., and *Speleobregma lanzeroteum*. The scarcity of offshore species in lapilli patches throughout the cave may reflect the special conditions of this environment, when compared to interstitial offshore habitats. The abundance of offshore species appeared distinctly higher in or on the lapilli patches of the Jameos del Agua lagoon, probably due to opportune conditions at this locality, i.e., primary production. The polychaete worms *Syllis garciai*, *S. gerlachi*, *Miscellania dentata*, and *Exogone gambiae* are common among the lapilli grains in the lagoon, while they have not yet been found in the same habitat in other sections of the cave.

The calcareous sand in the Montaña de Arena section constitutes another important interstitial habitat (Fig. 3e). This section of the lava tube has been continuously building up by the slow deposition of sand sifting through a fissure in the cave ceiling that connects with a small opening in the overlying sea floor. Sedimentary particles and organisms as large as sea urchin tests drop through the hole, comparable to sand filtering through an hourglass. The high carbonate content of the sediment and the presence of abundant shell debris support the offshore source for the sand in this section (Jantschke et al. 1994). Moreover, the relatively high sphericity of the grains and their low angularity - in strong contrast with the morphology of lapilli - indicate extensive transport prior to sedimentation. This sediment, interspersed with coarse grains and intermediate organic matter, provide for a cave habitat that bears close resemblance to offshore subtidal marine environments in the Canary Islands. Thus, the abundance of typical offshore species in the sediment and their presence in only this area of the cave is not surprising. Offshore species recorded from this locality include the nematodes *Draconema* sp. and *Quadricoma* sp., the priapulid *Tubiluchus* sp., interstitial cnidarians *Halammohydra* sp., sipunculans, halacarids, and the polychaetes *Questa* sp., *Syllis garciai*, and *Protodorvillea kefersteni*. However, endemic stygobionts also inhabit the Montaña de Arena, due to the abundance of trophic resources. These include the crustaceans *Halosbaena fortunata*, *Liagodoceradocus accutus*, *Ingolfiella* sp., and *Curassanthura canariensis* (the latter in very high numbers), and the polychaetes *Speleobregma lanzeroteum*, *Mesonerilla* n. sp., *Meganerilla cesari* n. sp., and *Sphaerosyllis iliffei* n. sp.

The **carpet of benthic diatoms** is limited to the sections of the Jameos lagoon exposed to incident daylight (Fig. 3b). Although diatoms grow all over the lagoon, they develop a carpet only in its shallowest areas over the lapilli, reaching up to several centimetres in thickness. It is a multispecies carpet, dominated by a species of the genus *Fragillaria* (Reboleira pers. com.). This dominance of diatoms is not common in offshore environments, and their presence in the cave has been attributed to the low light intensity, under which other algae do not survive (Wilkens and Parzefall 1974; Iliffe et al. 2000). The abundance of silicon in the water column, due to dissolution of the volcanic material, has been suggested as an alternative explanation for the dominance of diatoms (Jantschke et al. 1994). Diatom primary production provides trophic resources for potential colonizers, as can be seen in the high faunistic abundance and the presence of offshore species (Martínez et al. this issue). The nerillid polychaete *Leptonerilla diatomeophaga* is the most abundant species in the lagoon, accompanied by the endemic crustaceans *Oromiina fortunata* and *Liagodoceradocus acutus*, and the offshore polychaetes *Syllis garciai* and *Miscellania dentanta*.

The expanding population of the echiuran worm *Bonellia viridis* in the Jameos del Agua lagoon has produced large amounts of fecal sediment that has become a new habitat for some species (Brito et al. this issue). This muddy sediment is rich in organic matter favoring the settlement of offshore opportunistic species dominated by the polychaetes *Notomastus* sp., *Cyrrophorus lyra*, and *Apelochaeta marioni*. The accumulation of these sediments has been observed in the lagoon only in the last few years, and resulted in an increasing abundance of *B. viridis*.

Origin of the lava tube fauna

With respect to their distribution in the lava tube, species can be divided into at least two groups, reflecting different timing and modes of cave colonization. The first group consists of offshore species such as the echiuran *Bonellia viridis* and the decapod crustaceans *Stenopus spinosus* and *Athanas* cf. *nitescens*, among others, that colonized the cave directly from offshore environments on Lanzarote. Another example is the ctenophore *Cestum veneris*, which has been observed in the Jameos del Agua (Harms 1921).

As they lack special adaptations for the cave environment, these typical offshore species principally occur in the areas of the lava tube where trophic resources are abundant or habitats resemble offshore environments. Thus, most of these accidental and opportunistic species have been recorded either in the Jameos del Agua lagoon (with incident daylight), or on/within the calcareous sediment of the Montaña de Arena.

The second group is made up of stygobiontic species that exhibit typical morphological adaptations to the cave environment, such as lack of pigmentation, reduction of the size of the eyes, and modification of the appendages for swimming or drifting in the water column. Many of these species have also been recorded in anchialine groundwater from subterranean lava fissures on Lanzarote. Sampling surveys with baited traps at artificial wells in salt works, as well as in natural anchialine pools in several areas of the island, have revealed the presence of the crustaceans *Munidopsis polymorpha*, *Spelaeonicippe buchi*, *Heteromysoides cotti*, and *Danielopolina wilkensi* in these environments (Wilkens 1986; Wilkens et al. 1993). The local distribution of these stygobionts shows a direct connection between the lava tube and other subterranean habitats of Lanzarote (see also Koenemann et al. this issue). Within the lava tube, most of these species are concentrated in the cave water column and lapilli patches. Most of the offshore species of the first group exhibit wider distribution ranges around the eastern Atlantic and the Mediterranean Sea, whereas those included in the second group are endemic to Lanzarote.

The diversity and exclusivity of the anchialine fauna of Lanzarote reflects the unique hydrogeologic features of the island, in particular the porous volcanic material, low precipitation rates (100 mm per year, mostly in the winter months), and a relatively high tidal range. This environmental setting favours inland infiltration of marine waters and the development of marine groundwater, where anchialine communities can settle (Koenemann et al. this issue). These features also explain the unique features of the anchialine fauna on Lanzarote compared to the other Canarian islands. Even the groundwater fauna of the neighboring island of Fuerteventura is different from that of Lanzarote (Stock 1988; Boutin 1994).

The marine stygobiontic fauna of Lanzarote appears to have diverse roots. One group is represented by genera showing amphi-Atlantic distributions, with Lanzarote species having close relatives in caves and anchialine habitats on islands and continental coasts in the western Atlantic (Iliffe et al. 1984; Wilkens 1986) or even in the Pacific (Fig. 7). For example, the remipede genus *Speleonectes* currently includes 12 described species, 2 of which are from Lanzarote in addition to 7 species in the Bahamas and 1 each from Yucatan, Cuba and the Dominican Republic (Koenemann et al. this issue). Similarly, the halocyprid ostracode genus *Danielopolina* consists of 12 species, with 2 from Lanzarote, *D. wilkensi* and *D. phalanx*, 4 from the Bahamas, and 1 each from Yucatan, Cuba, Jamaica, Galapagos, Western Australia, Christmas Island, and the deep sea of the South Atlantic (Kornicker et al. 2007). Congeners of the thermosbaenacean *Halosbaena fortunata* from Lanzarote are known from Venezuela, Curaçao, and Western Australia (Poore and Humphreys 1992) and, most recently, Okinawa, Japan (Shimomura and Fujita 2009).

Several evolutionary scenarios have been proposed to explain the enigma of these disjunct global distribution patterns. For example, Boxshall (1989) suggested that deep sea relatives of misophrioid copepods and ostracodes of the genus *Danielopolina* colonized marine caves through dispersal via crevicular habitats. Proponents of alternative hypotheses have argued that ancestors of some present day stygobionts were associated with benthic shallow-water habitats, from where they colonized both cave systems and the deep sea (see Danielopol et al. 2000 and references therein).

Another, widely accepted explanation for globally disjunct distributions of stygobiontic groups has been offered independently by numerous zoologists. It is assumed that present occurrences of some taxa that are separated by large geographic distances may represent remnants of ancient distributions that have their origin in the Mesozoic (e.g., Stock 1981; Iliffe et al. 1984; Notenboom 1991; Humphreys 1993; Holsinger 1994; Koenemann and Holsinger 1999). In this scenario, the precursors of modern stygobionts are
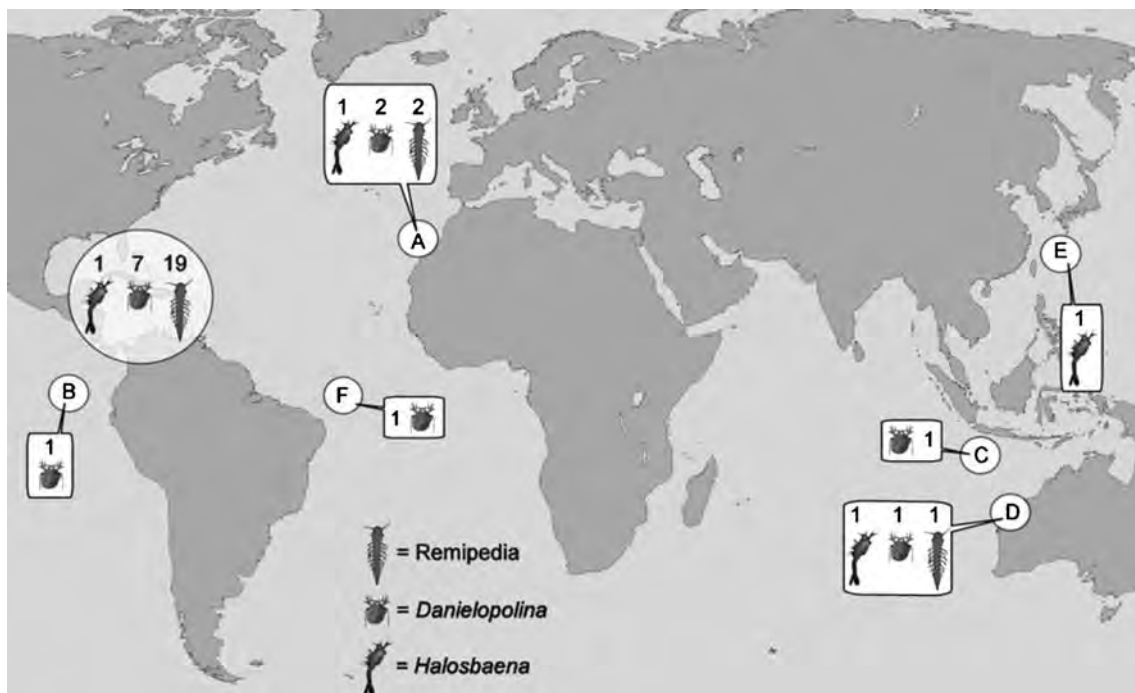
Fig. 7 Selected stygobiontic crustaceans with disjunct global distributions. Numbers of species are given for the thermosbaenacean genus *Halosbaena*, the ostracode genus *Danielopolina*, and the remipede order Nectiopoda (see detailed distribution data for Remipedia in Koenemann et al. this issue). *Small circles* represent localities on Lanzarote, Canary Islands (**a**), Santa Cruz, Galapagos Islands (**b**), Christmas Island (**c**), Cape Range Peninsula, Western Australia (**d**), Okinawa, Japan (**e**), and a species from the deep sea in the South Atlantic (**f**). The *large circle* includes localities on the Yucatan Peninsula, Venezuela and numerous Caribbean islands

believed to have inhabited the shelf regions, perhaps even marine cave systems, of the Tethyan Ocean. Subsequently, vicariance (instead of dispersal), resulting from plate tectonics ("continental drift") and marine regressions, led to regionally isolated populations, the derivative forms of which have survived until today in caves and other subterranean refugia. However, for disjunct groups occurring in Western Australia, this evolutionary model implies a global, continuous Tethyan distribution, since the geographic distance between the Australian landmass and the Proto-Caribbean and Atlantic was as vast as it is today. Such a continuous Tethyan distribution may be conceivable for taxonomically diverse taxa with a well-documented fossil record, for example, ostracodes. However, problems of interpretation could arise for remipedes which have convergently adapted to cave life and occur exclusively in such environments. For these latter groups, information from the fossil record is extremely limited and close "surface" relatives living outside caves are still unknown.

Another dilemma of ancient distribution models is the fact that extant stygobionts occur in geological terrains that are much younger than an assumed Mesozoic age. However, Humphreys and Danielopol (2006) argue convincingly that some stygobiontic species are known to occur in near-coastal Mesozoic sediments that often lie beneath the younger, emerged strata.

The processes that produced the patterns we are observing today are naturally much more complex than any singular model can predict. For example, some representatives of the marine groundwater fauna of Lanzarote are derived from deep sea forms. The crab *Munidopsis polymorpha* (Galatheidae) is one of at least 70 species of this genus otherwise distributed in the deep Atlantic Ocean (MacPherson and Segonzac 2005). Likewise, the polychaete *Gesiella jameensis* belongs to the monospecific polynoid subfamily Gesiellinae, which is closely related to the typical deep sea subfamily Macellicephalinae. Some taxa that have colonized caves of Western Atlantic islands show deep sea as well as amphi-Atlantic relationships. Such relationships are supported by the presence of *Pelagomacellicephala iliffei* (Macellicephalinae) in caves from the Bahamas or the occurrence of a single species of the ostracode *Danielopolina*, a genus otherwise exhibiting a typical anchialine distribution, in the deep sea of the South Atlantic (Fig. 7).

As concerns the age of the marine groundwater fauna of Lanzarote, it can be speculated that it could have started its evolution in relation to the emergence of the island. This would be at least about 15 million years ago. The presence

of numerous eye- and pigment-reduced species in both Lanzarote's groundwater and the Corona lava tube indicate that continuous exchange occurs between these two subterranean habitats and thus the age of the lava tube does not necessarily dictate the age of its fauna. The absence until now of remipedes in the groundwater can be explained at least in part by use of baited traps to collect groundwater fauna. Traps work well for collecting scavengers such as amphipods and crabs, but are ineffective for sampling predators such as remipedes. However, apparent morphological and molecular similarities between the two Lanzarotean remipede species support the assumption that speciation may have occurred quite recently, perhaps even within the lava tube since its formation 20,000 years ago. Preliminary results of ongoing molecular sequence analysis suggest that the closest relatives of *Speleonectes ondinae* and the newly discovered species of *S*peleonectes (Koenemann et al. this issue) are *S. gironensis* from Cuba and *S. tulumensis* from the Yucatan Peninsula (unpublished data). Remipedes probably have truly ancient origins. The discovery of remipedes at 1.6-km distances into totally subsea floor caves in the Bahamas (Daenekas et al. 2009) indicates that they may not necessarily exist in coastal or shallow water caves, but might today exist in deep water or deep sea crevicular habitats and derive food from chemoautotrophic means. Until further data are available, the origin of the amphi-Atlantic/Pacific distribution for Remipedia remains speculative.

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