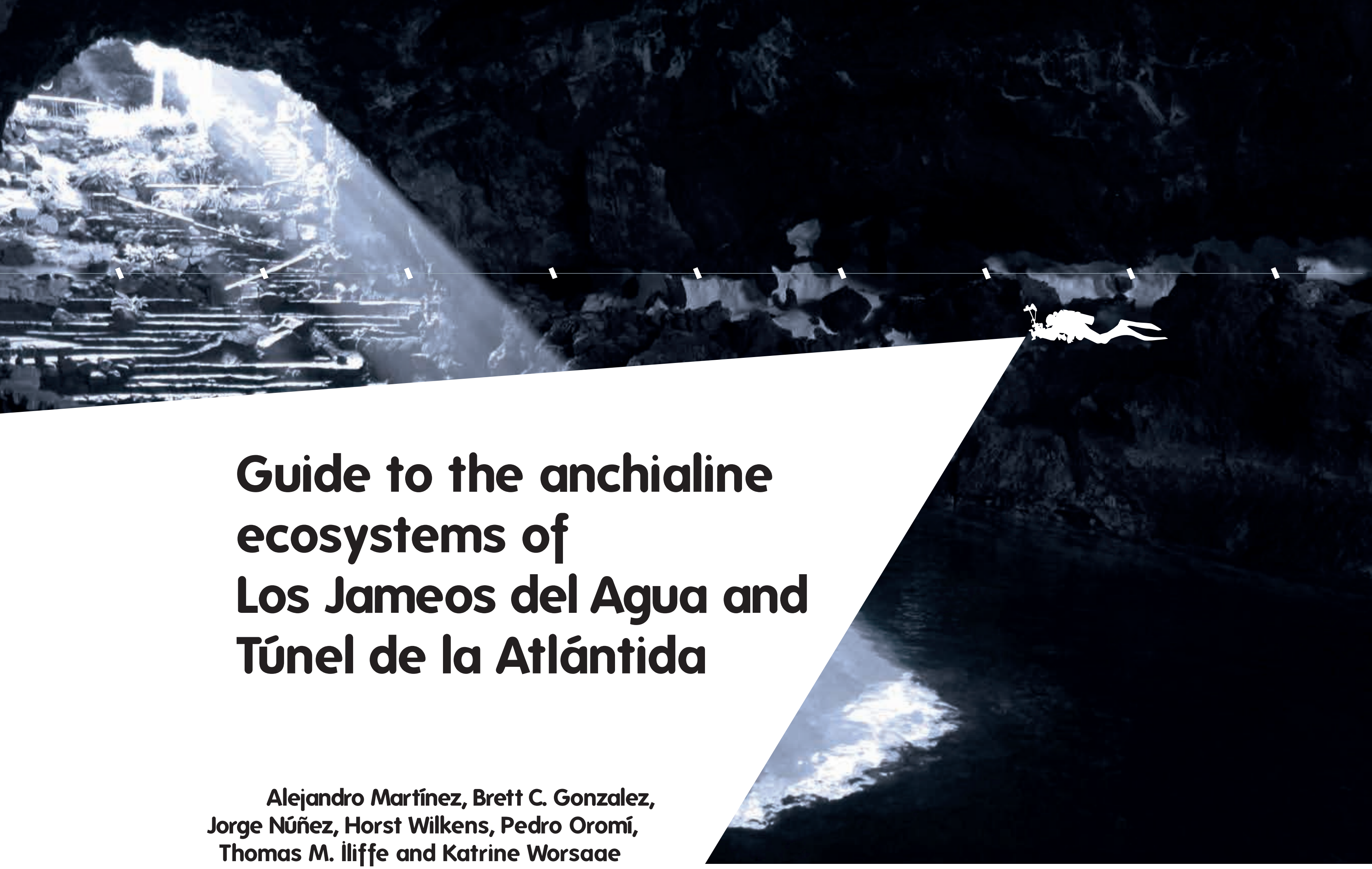

Guide to the anchialine ecosystems of Los Jameos del Agua and Túnel de la Atlántida

Alejandro Martínez, Brett C. Gonzalez,
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Thomas M. Iliffe and Katrine Worsaae

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Guide to the Anchialine Ecosystems of Los Jameos del Agua and Túnel de la Atlántida

Lanzarote, 2016

Guide to the anchialine ecosystems of Jameos del Agua and Túnel de la Atlántida

CABILDO DE LANZAROTE

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Área de Medio Ambiente
President: Pedro San Ginés Gutiérrez

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Guide to the Anchialine Ecosystems of Los Jameos del Agua and Túnel de la Atlántida

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…even amongst the flooded darkness, they shined…

Preface

La Corona lava tube is one of the most remarkable anchialine caves in the world. Already to the original settlers of Lanzarote it had a great significance, continuing nowadays, being visited by thousands of people from all over the world each year. During the last 125 years, more than 50 scientists have investigated this cave, producing numerous technical publications about its geology, fauna, and ecology, mainly accessible for the scientific community.

This book is intended to merge the past 125 years of scientific research into a single synopsis, accessible and understandable to all. We have organized all the information into four chapters addressing the Geology, Fauna, and Ecology of La Corona lava tube, as well as a comprehensive İntroduction to the Science of Subterranean Biology. İn the construction of each chapter we have taken into account the most recent scientific findings and methods to bridge the gap between old and new trends in subterranean biology in order to provide the readers with a comprehensive overview.

The authors of this book represent three generations of scientist in subterranean biology, from original explorers and taxonomists to upcoming experts in the field. Together, we hope this book will spread our knowledge and foster curiosity and respect for these relatively unknown environments, ensuring their protection.

Alejandro, Brett, Jorge, Horst, Pedro, Katrine and Tom

Presentation

Túnel de la Atlántida is the longest flooded lava tube in the world, offering a 1.6 km pathway into the bowels of the Earth, similar to those described in the novels by Jules Verne. This natural tunnel was formed approximately 21,000 years ago by the lava emissions from lateral vents of Volcán de la Corona, at the northern tip of Lanzarote during the last Glacial Maximum. Lava headed towards the sea, flowing over ancient lava fields previously left behind by Los Helechos and La Quemada volcanoes. With the melting of the ice caps during the last sea transgression, the last 1600 meters were flooded, resulting in the development of anchialine ecosystems in the costal underground areas flooded by sea water.

People from Lanzarote have taken pride in this work of nature throughout history; the curiosity and admiration of thousands of people from all over the world who visit Jameos del Agua; and the research of scientists from many parts of the globe who have provided their data and theories to the international scientific community, agreeing on its definition as one of the most significant anchialine caves in the world, with 36 known endemic species.

This unique summary gathering 125 years of research called "Guía Interpretativa de los ecosistemas anquialinos de Jameos del Agua y Túnel de la Atlántida", edited by the Cabildo of Lanzarote and written by Alejandro Martínez, Brett C. Gonzalez and Katrine Worsaae of the University of Copenhagen; Jorge Nuñez and Pedro Oromí of the University of La Laguna, Horst Wilkens of the University of Hamburg, Thomas M. Iliffe of Texas A&M University at Galveston, with photographs by Juan Valenciano (Lanzarote) and Enrique Domínguez (Tenerife), shows a compilation of Secrets of geology, fauna and ecology hidden behind one of the most important anchialine caves in the world. İts aim is to spread the word on this natural wonder, increase curiosity and respect for these relatively unknown ecosystems, and in turn ensure the preservation and protection of this natural legacy.

İ hope you go through these pages with as much keenness and eagerness as the authors who have put together an inspiring work that allows everyone to love one of the great wonders and legacies that Lanzarote provides to the world.

Pedro San Ginés Gutiérrez
PRESİDENT OF CABİLDO DE LANZAROTE

Acknowledgments

This book was only made possible due to the initiative and enthusiasm of Elena Mateo Mederos, who always provides her full support to our scientific inquiries to further knowledge of the subterranean treasure in Lanzarote. A special thanks goes to the members of our team: Enrique Domínguez, Carola D Jorge, Luis E Cañadas, Ralf Schoenermark, Juan Valenciano, Antonio Martín We thank the Speleological Group Uesteyaide, especially Alexandre Perdomo. Gismacan Canarias financially supported the 2014 Expedition to Lanzarote. We will never forget Suso Fontes and the staff in Jameos del Agua for their support during our long nights of diving in Túnel de la Atlántida. Thanks to the staff in Aula de la Naturaleza for accommodation. Management was facilitated by Miguel Ángel Rodríguez and Juan Escobar of Tragsatec, and Jan Andersen and Saeeda Vally, University of Copenhagen. We are indebted to Karsten Kristiansen for supporting our project.

Additional artwork and photography found throughout this book was generously provided by Sergio González, Jill Heinerth, Kirsten Kvindebjerg, Jaume Mora, Leopoldo Moro, Peter R. Møller, Ana María Palmero, Sofia Pyateava, Tomás Abel Rivero, Emilio Rolán, Andreas Schmidt-Rhaesa, Simon Richards, Ulrike Strecker, and Tamara Thomsen. Species identification as well as unpublished data was provided by Tom Artois, Alberto Brito, Jordi Corberá, Marco Curini-Galetti, Gustavo Fonseca, Damià Jaume, John Pohlman, Emilio Rolán, and Antonio Todaro. Virginia Martínez provided helpful suggestions towards the geology chapter.

This book was mainly prepared and written at the Marine Biology Section, University of Copenhagen "Salaries, expedition and laboratory costs were supported by the University of Copenhagen and the Carlsberg Foundation (grant # 2013_01_0779)". Scanning electron micrographs were performed at the Natural History Museum, University of Copenhagen, Denmark.

Ashley Paige Marmottin and Fernando Pardos reviewed the English and Spanish manuscripts, greatly improving the language and shape of the texts.

A debt of gratitude to all the pioneers who have devoted their life to diving exploration and scientific achievements, laying the foundations on top of which this book is written.

Index

Geological Origin of La Corona Lava Tube Anchialine Ecosystems

CHAPTER

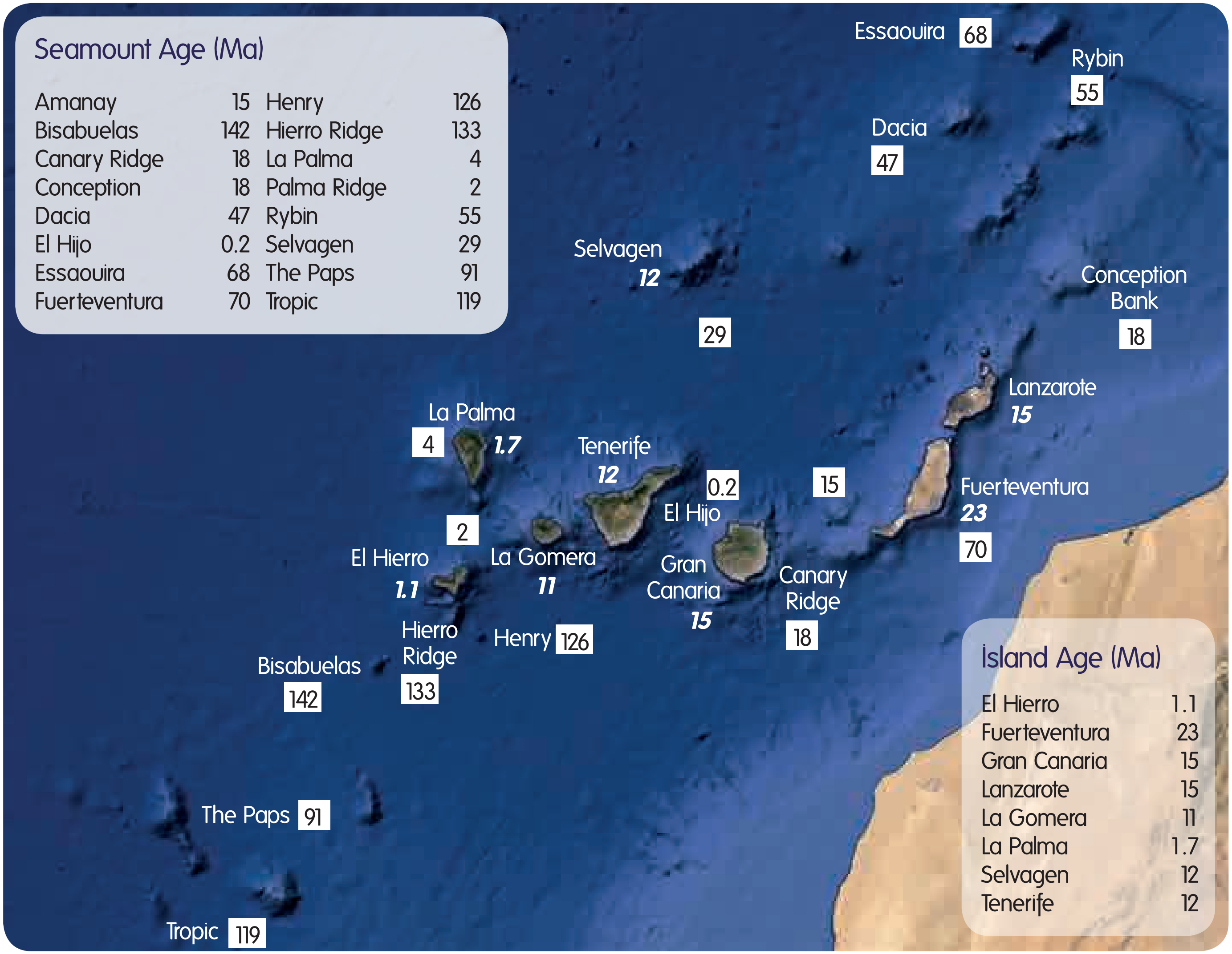
1

Geological Origin of Lanzarote

The Canary Islands are an oceanic archipelago of volcanic origin, located on the African Oceanic Plate, 100 km off the coast of West Africa (Map 1). They are composed of seven major islands and several islets, with nearly every island constituting independent seamounts separated by depths ranging from 2,000 to 3,000 m. Formed from the same seamount and separated by the 40 m deep El Río and La Bocaini Straights, La Graciosa, Lanzarote, and Fuerteventura are an exception. The Canary Islands Seamount Province is scattered over 1300 km of Atlantic Ocean floor (Map 1). Recently obtained dredged material from throughout the Canary Islands Province has dated the oldest seamount to 142 million years ago (Ma), measured with ^{40}Ar/^{39}Ar dating methods (see below). However, the present-day Canary Islands are not uniform in age (see ages on Map 1). At 23 Ma, Fuerteventura is the oldest island while Lanzarote and Gran Canaria are next, estimated at 15 Ma. The youngest island in the archipelago is El Hierro, at 1.1 Ma. Therefore, the oldest sea mounts in the Canary Islands Seamount Province formed as the Atlantic began to open, while the oldest aerial islands emerged at least 100 Ma afterward.

The origin of Lanzarote is geologically complex (Map 2). It began as a seamount with the formation of the basal complex, which are the first rocks of the island, characterized by the presence of pillow lavas with intrusions of marine sediments. The seamount emerged as an island during the Lower Miocene (23-5 Ma). As a newly formed island, Lanzarote continued to experience constructive and erosive periods. The constructive periods were characterized by intense volcanic activity that increased the overall landmass of the island. During erosional periods, volcanic activity ceased and the landscape was scoured by wind and rain. It is thought that during these long periods without volcanic activity, an overall reduction in the size of the island occurred. Ancient lava fields are still visible today throughout the island and corroborate the alternating periods between volcanism and erosion.

The first subaerial constructive period of Lanzarote led to the formation of Los Ajaches and Famara massifs (groups of mountains) (Fig. 1 A and C). Los Ajaches is located on the eastern edge of Lanzarote, and Famara on the northwest, having formed approximately 14.5-13.5 Ma and 10.2-3.8 Ma respectively. Los Ajaches appears to have been created in a single fast volcanic episode, while Famara involved at least three separate eruptions. The evidence supporting these three eruptions in Famara is marked by the presence of burned paleosoils between the three lava flows. Although today Los Ajaches and Famara consist of nothing more than two dry and highly eroded ridges reaching maximums of 560 m and 671 m respectively,

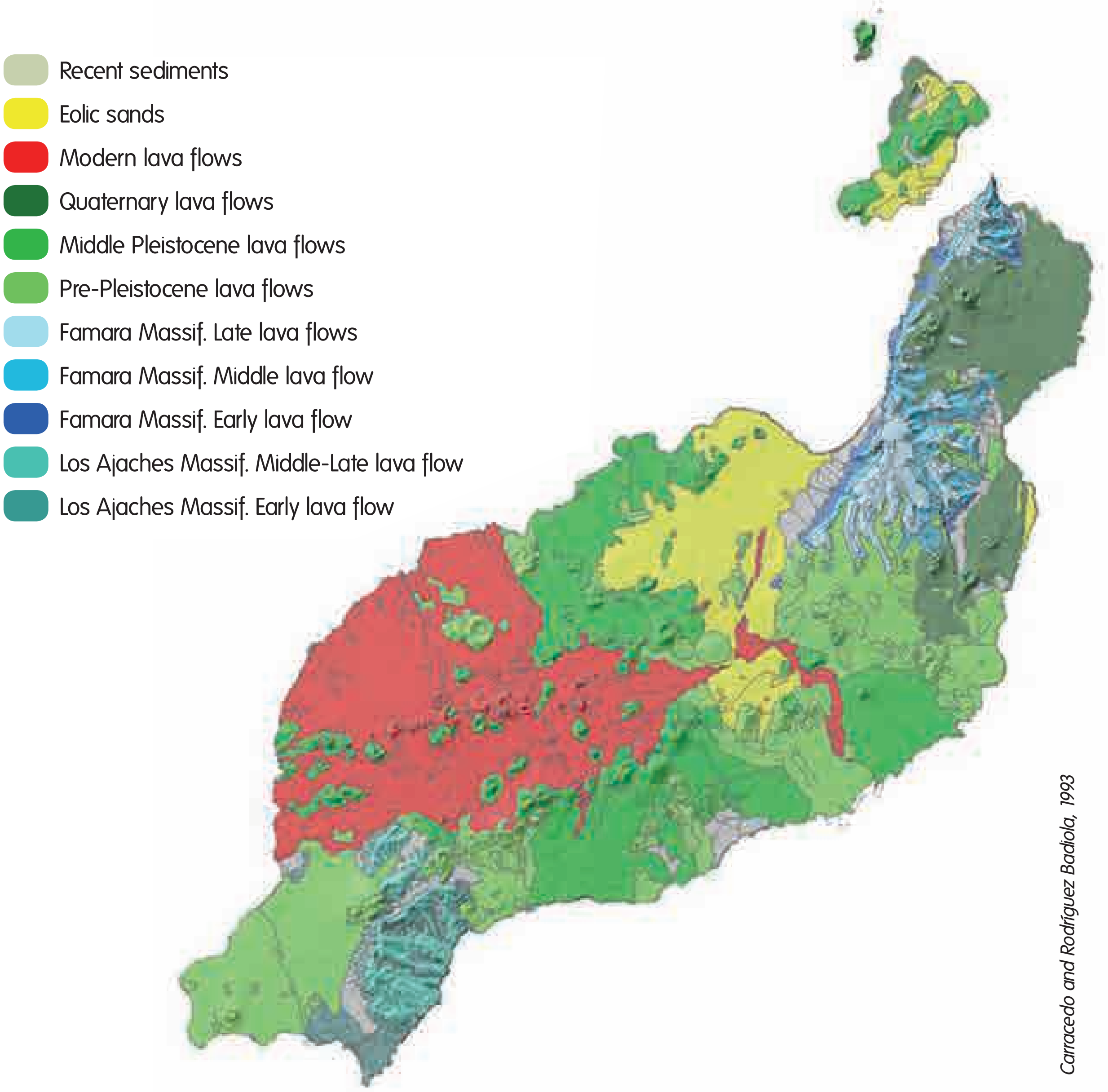


Van den Bogaard, 2013

Map 1. Map showing the age of seamounts and islands in the Canary Islands geological province.

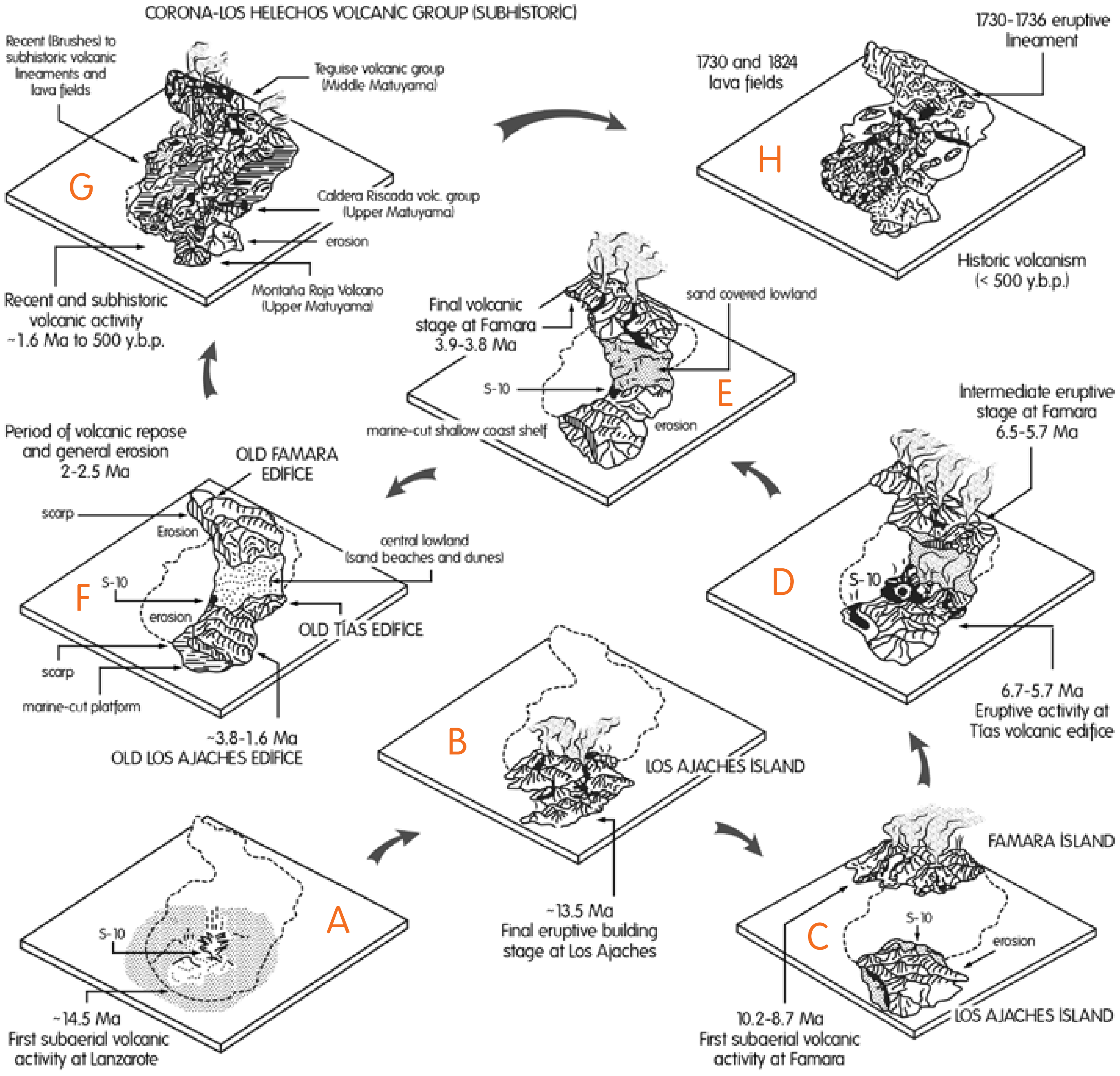
geologist think that these ancient massifs were once higher than 4000 m and, in their infancy, capable of collecting the humidity of the passing trade winds.

The increased moisture would have produced frequent precipitation to support laurel forests and dense vegetation on these ancient mountains. As a



Carracedo and Rodríguez Badiola, 1993

Map 2. Geological composition of Lanzarote.



Modified from Carracedo and Rodríguez Badiola, 1993

Figure 1. Geological evolution of the island of Lanzarote (see text for explanation).

consequence of this, the ancient climate of Lanzarote was comparable to that of the present day islands of Tenerife or La Palma. The resulting precipitation infiltrated the porous lava rock, forming a shallow freshwater aquifer, thicker in the interior and tapering towards the island's edges. Millions of years later, this aquifer played a crucial role in the survival of the human settlers on the island (see Chapter 2 and 3). During the Late Miocene (6.1 Ma), the massifs of Los Ajaches and Famara were connected by a third volcanic episode, producing the Tías volcanic complex (Fig. 1 D and E). Lava from this episode is uncommon and only visible close to the settlement of Tías as well as near Los Ajaches massif (Map 2).

After these constructive episodes, volcanic activity was dormant for approximately 2.5 Ma during the Pliocene (5.3-2.6 Ma, Fig. 1 F), when Lanzarote was in an erosive period. As erosional processes were acting on Los Ajaches and Famara, microscale climate changes also ensued on the landscapes below. Erosional processes eventually altered the capture of trade-wind precipitation, which led to the overall shrinking of the freshwater aquifer. After the Pliocene, a second period of volcanic activity, characterized by fissure eruptions, covered the older geological structures. Eruption epicenters were located in Montaña Roja, Caldera Riscada (near Los Ajaches), Teguise, and La Corona (near Famara) (Fig. 1 G). These eruptions primarily ejected highly porous vesicular basalts and scoria, created when dissolved gases are forced out of solution to form vesicles as the lava decompresses upon reaching the surface. The only two recent and historical volcanic eruptions occurred in 1730 and 1824 in Timanfaya, on the western coast of Lanzarote (Fig. 1 H). These events briefly interrupted the ongoing erosional processes.

Geological Origin of Malpaís de La Corona and its Lava Tube

Malpaís de La Corona (La Corona badland) is a stark, jagged lava field at the northern tip of Lanzarote that originated from eruptions of La Corona volcano (Fig. 2). This lava field partially covers the Pliocene age Famara massif that formed during the second constructive period on Lanzarote (Map 2, Fig. 3 A and B). Emerging from the lava field, three cinder cone volcanoes, La Quemada, La Corona, and Los Helechos, are arranged in a line from north to south (Map 2, Fig. 3).

One of the most remarkable geological structures in La Corona lava field is La Corona lava tube, a 7.8 km long lava tube that crosses the Malpaís lava field in a southeast direction from La Corona volcano towards the sea (Fig. 3). This lava tube was formed from pahoehoe lavas erupted from a lateral vent near the base of the volcano. Pahoehoe lavas are characterized by their high temperature (1100 to 1200°C) and lower content of gases, making them more fluid than other types of lavas. Due to their viscous nature, pahoehoe lavas flow slowly and solidify at their surface to form distinctive ropy or smooth crusts. This partially hardened skin is dragged and compressed by the flow of the lava below into a series of wrinkles and ridges that produce the pahoehoe's typical ropy texture. Due to these properties, pahoehoe lava flows favor the formation of lava tubes. As the uppermost surface of the lava flow cooled, it formed a viscous, and eventually solid, external crust. Molten lava continued to flow in a tubular conduit within, insulated by the ceiling above (Fig. 4). Once the volcano ceased its eruptions and the main flow of lava drained out of the tube, a hollow cave-like conduit (the lava tube) remained. Lava tubes, like other products of volcanic eruptions, are very influential in shaping landmasses and islands. However, because they form near the surface of the earth and are more vulnerable to erosional and tectonic processes, lava tubes are geologically short-lived when compared to other type of caves, such as limestone caves.The exact age of the initial formation of La Corona lava tube is still debated. However, many geologists agree with the latest estimate, which indicates the lava tube was formed above the sea level approximately 21,000 ± 6,500 years ago as measured with the Ar/K method. Ar/K is a radiometric dating method based on the measurement of radioactive decay of an isotope of potassium (^{40}K) into argon (^{40}Ar). The long half-life (1.25 billion year) of ^{40}K allows the method to be used to calculate the absolute age of samples older than a few thousand years, making it very useful in many fields of geology and archeology. The age estimated for La Corona lava tube with this method corresponds with the last glacial maxima. This was a period in the Earth's climate history when ice sheets were at their most recent maximum extension, covering most of Europe, between 26,500 and 19,000 years ago. The maximum depth of the submerged portion of the tube provides additional support to the radiometric measurements. It coincides with the estimated sea levels 20,000 years ago, nearly 100 m lower than today, and it has been shown that shallow lava tubes (as La Corona) cannot be formed under water. Just before the termination of the submerged lava tube, a small cupola or dome is present and then the tube pinches out. This structure is thought to have been caused by an abrupt interruption of lava flow due to sudden cooling of the lava flow at the contact with the Atlantic Ocean. Flooding of La Corona lava tube occurred more recently, after the last glacial maxima, when sea level rose to its present position (Fig. 5).

Brett C. Gonzalez

Figure 2. Malpaís de La Corona photographed near Los Jameos del Agua.

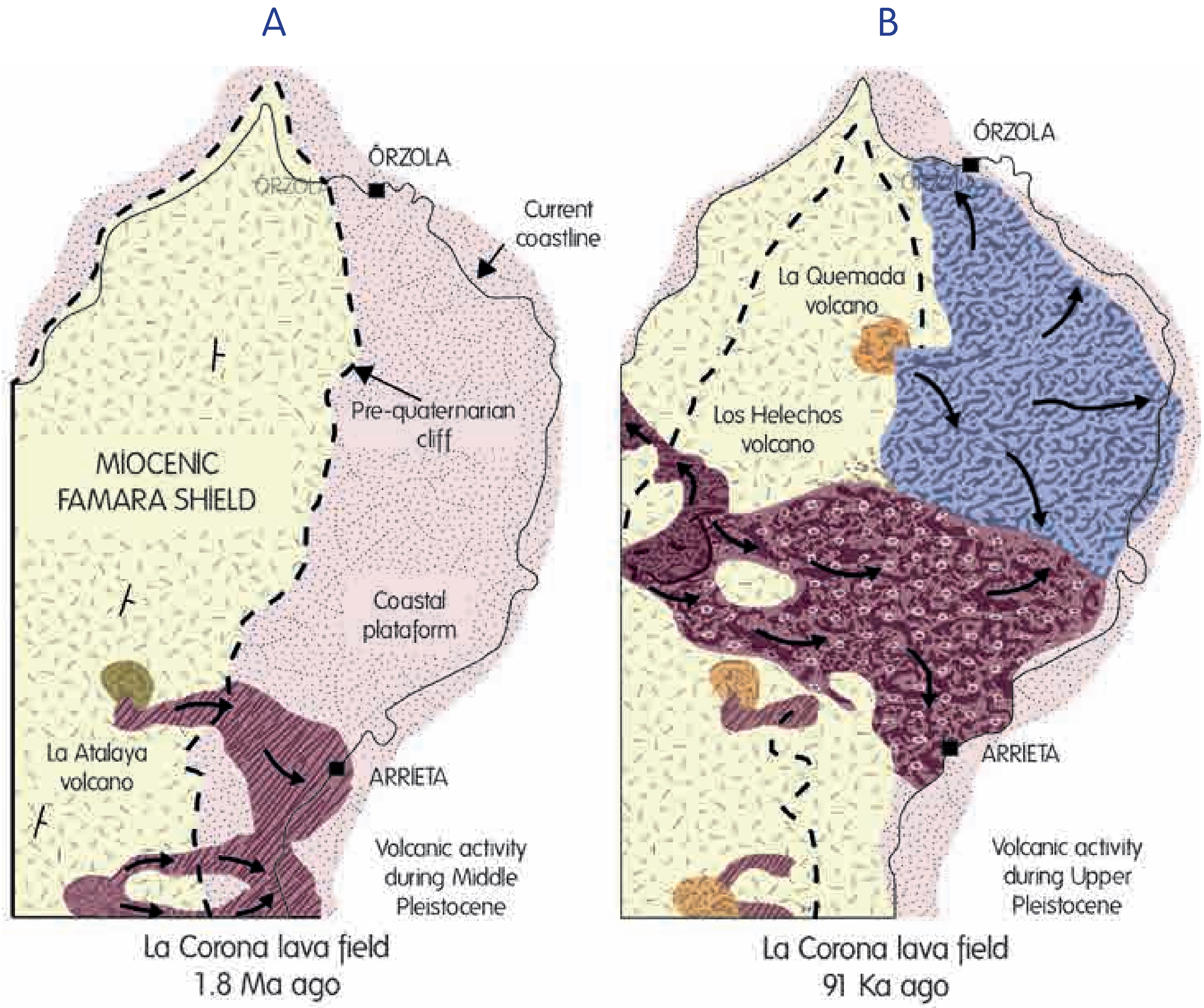
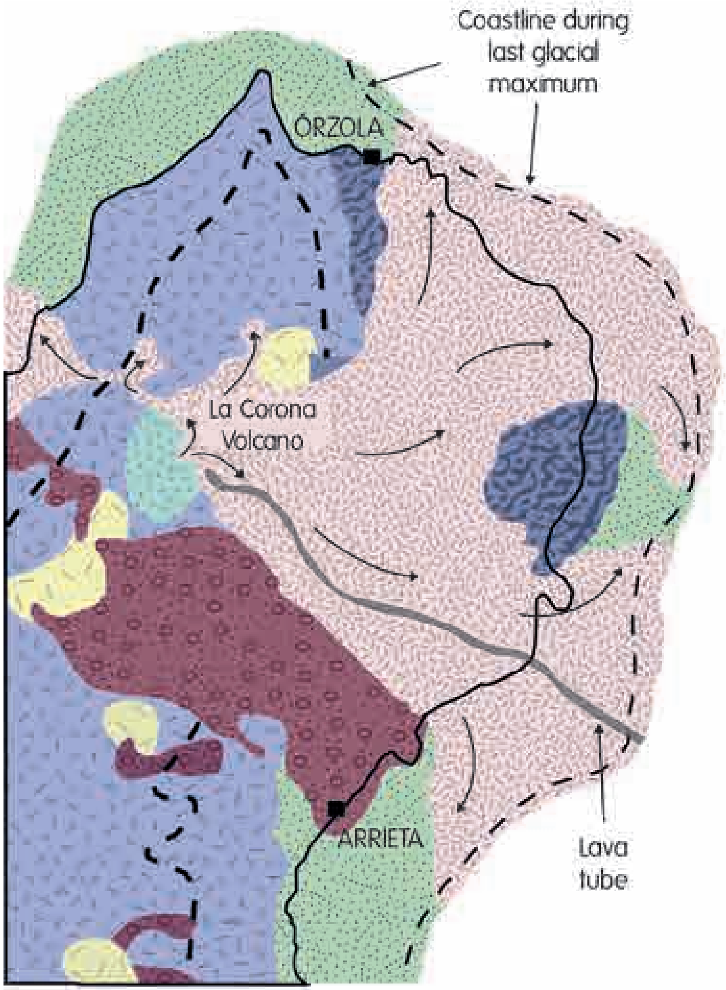


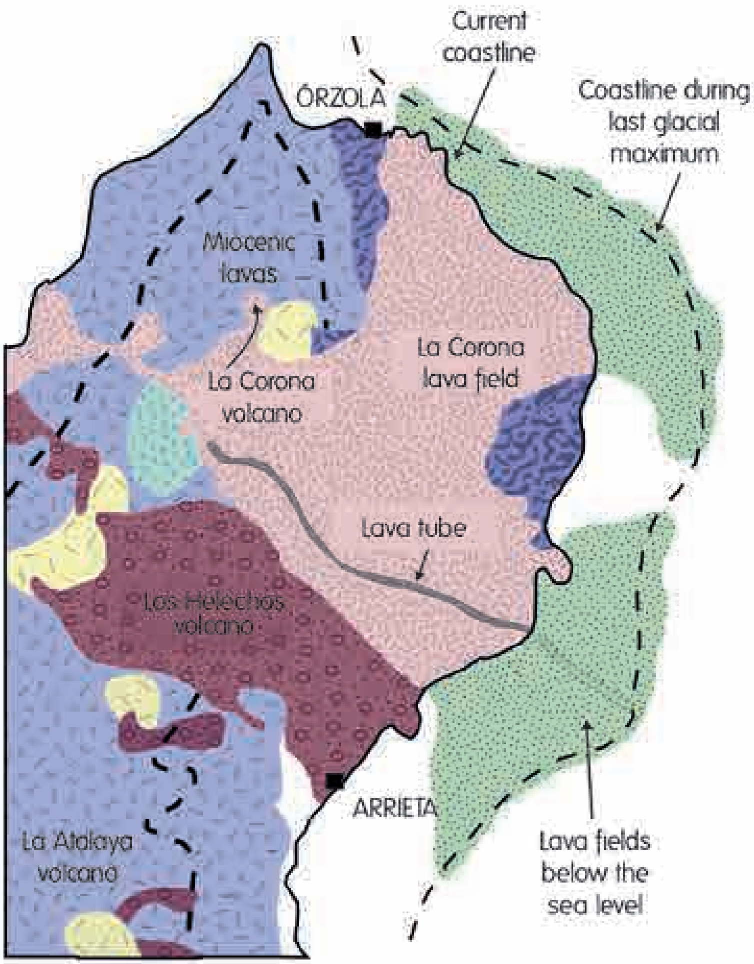
Figure 3. Origin of La Corona lava field and lava tube (see text for explanation).

C

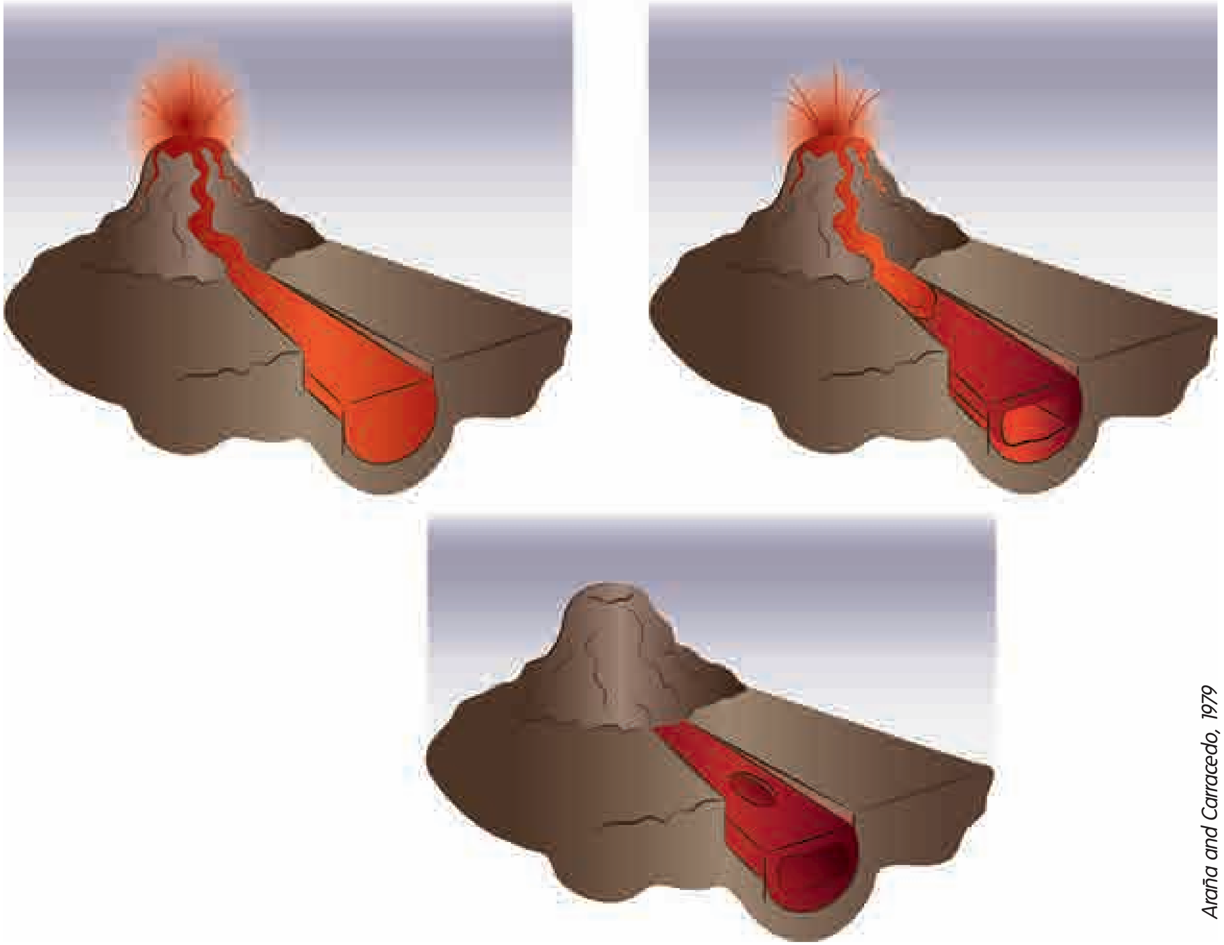


La Corona lava field 20 Ka, during last glacial maximum (Sea level 120 m lower)

D



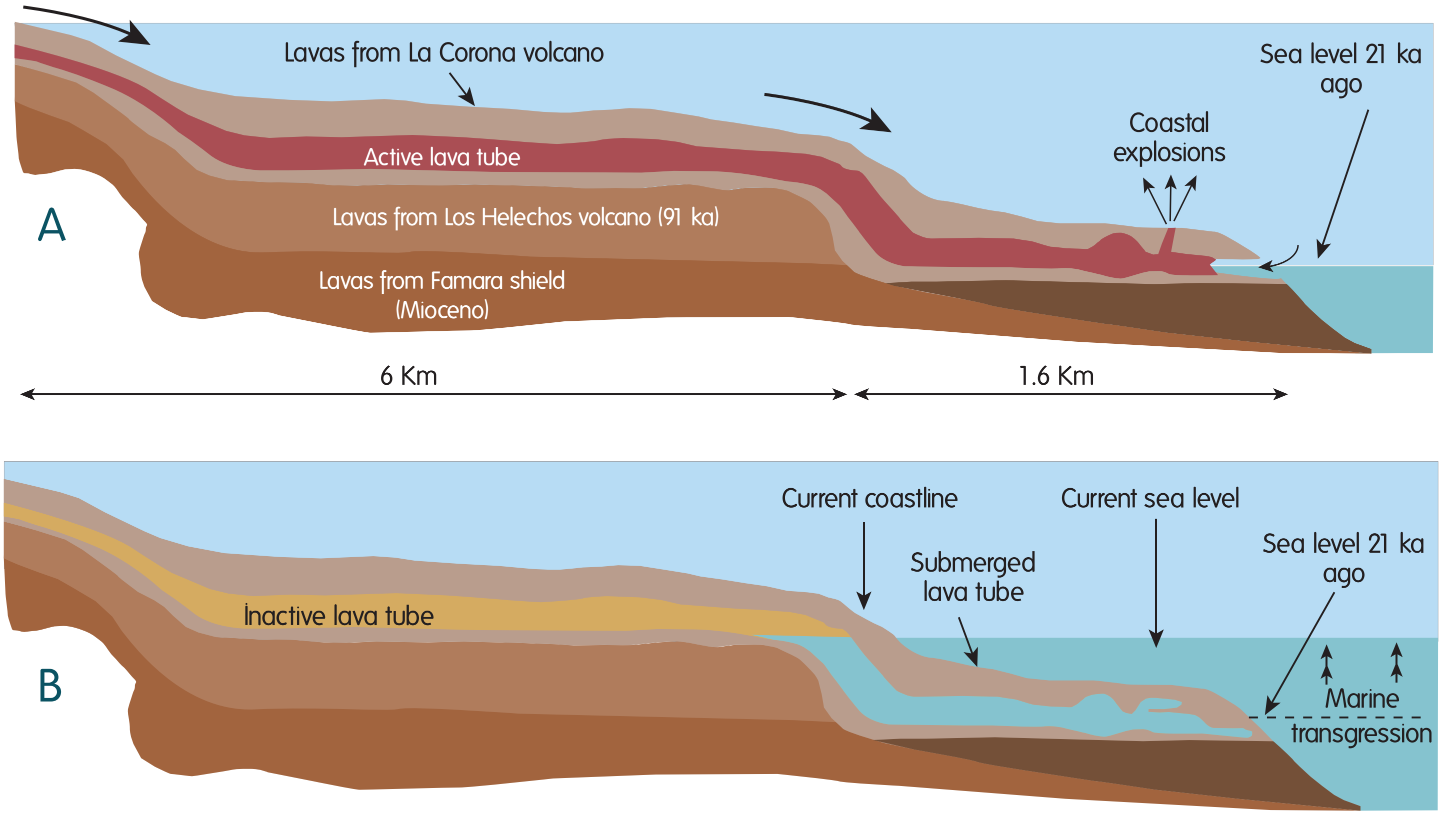
La Corona lava field today



Araña and Carracedo, 1979

Figure 4. Schematic process of lava tube formation.

The overall length of La Corona lava tube, including both terrestrial and underwater portions, is 7.8 km, with diameters up to 30 m. The lava tube is oriented in a linear fashion with no side branches, running perpendicular to the coastline on the northeast side of Lanzarote (Map 1). La Corona lava tube has 17 entrances (Fig. 6), some of which are skylights formed by collapse and have a talus mound below, while others, instead are blowhole vents, as the entrance between Jameo Grande and Jameo



Modified from Carracedo et al, 2003

Figure 5. Diagram showing the formation and posterior flooding of La Corona lava tube.
A. Representation of the lava tube during its formation.
B. Representation of the lava tube today.

Chico, above Los Jameos del Agua lake. Blowhole vents are formed by increased gas pressure inside the lava tube, leading to explosions that break the roof or walls. The fragments of the roof are normally still viscous when thrown by the violent release of gases, and they can stick near the entrances, as is observed near the blowhole in Los Jameos del Agua. Locally, skylights and blowholes are known as *jameos*, an aboriginal term that stems from the Majos people of Lanzarote and means cavity or depression in the ground. These entrances permit the exploration of the lava tube below, but may also be associated with talus mounds that block the entire gallery of the lava tube, dividing it into

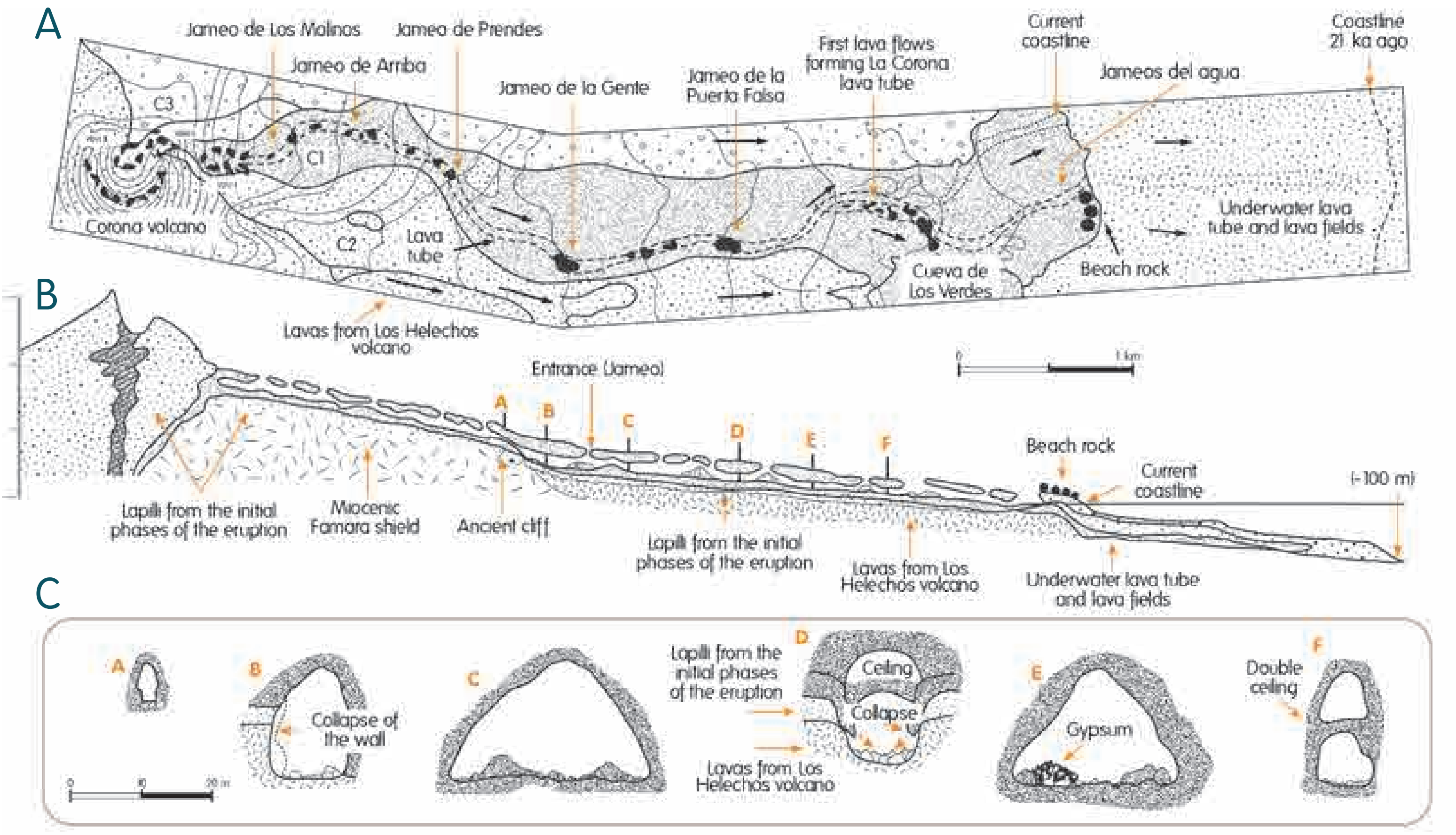
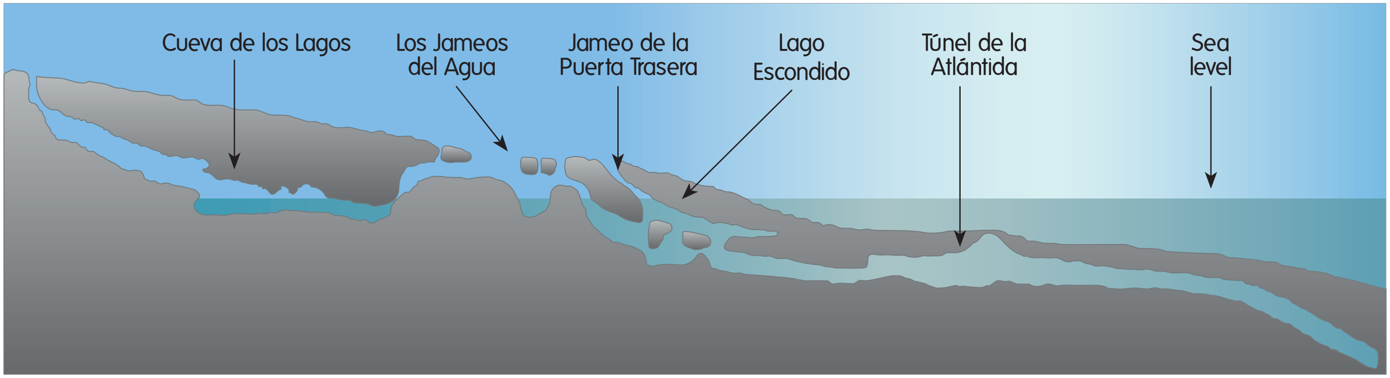


Figure 6. Map of La Corona lava tube, in groundview (**A**) and profile view (**B**), showing the main skylight (Jameos). The lower scheme (**C**) shows the sections of the cross section of the areas indicated at the profile view map.

separate sections. Although a number of segments can be distinguished in the lava tube, for the purpose of this book we considered it as divided into four major units: (1) a terrestrial dry section from La Corona to the entrance of Cueva de los Lagos; (2) a partially flooded section terminating in a sump in Cueva de los Lagos; (3) the tidal pool of Los Jameos del Agua; and (4) the completely submerged section of Túnel de la Atlántida, mostly extending further from the coastline into the sea.

Subterranean intrusion of marine groundwater penetrates at least 600 m inland in La Corona lava tube, where it can be observed in Cueva



Modified from Martíez et al, 2009

Figure 7. Map of the anchialine sections of La Corona lava tube. Only the flooded portions of the cave are illustrated.

de los Lagos (Fig. 7). From here, heading towards the ocean, there are three additional entrances at the tourist center of Los Jameos del Agua: Jameos Chico, Jameo Grande, and Jameo de la Cazuela. From Jameo Chico an entrance pool leads to Túnel de la Atlántida, the completely submerged portion of the lava tube. The last entrance before the lava tube crosses under the coastline is Jameo de la Puerta Trasera (Fig. 8), which opens near the tourist center of Los Jameos del Agua at approximately 200 m from the coastline. Though blocked by breakdown, Jameo de la Puerta Trasera connects to Lago Escondido, a section of the cave running parallel to and above to the main passage of Túnel de la Atlantida. Túnel de la Atlántida extends 1,600 m as a completely submerged passage beyond the present-day coastline of the island and out under the floor of the Atlantic Ocean. The cave terminates in a cul-de-sac at 64 m depth with no direct connection known between the cave and the ocean. As is evidenced by marine debris and open-ocean fauna, the only direct communication between the sea and the lava tube is a small hole directly above the Montaña de Arena (Fig. 9), a conical pile of loose white sand at 750 m penetration from the coast, where percolation into the cave occurs, similar to sand dropping into an hourglass. Indirect communication between the ocean and the lava tube also occurs through cracks, fissures, and the natural porosity of the basalt.

Inside the lava tube, several important geological features can be observed, including speleogens (relief features that are part of the surrounding bedrock, such as lateral benches and levees) and speleothems (secondary mineral deposits formed in the cave, i.e., stalactite-like lavacicles). These structures provide additional information on the

Brett C. Gonzalez

Figure 8. Jameo de la Puerta Trasera leads to the air-filled passage on the shallow side of Lago Escondido. However, Jameo de la Puerta Trasera is completely filled by large boulders making Lago Escondido only accessible through Túnel de la Atlántida.

Figure 9. Montaña de Arena, at 750 m of linear penetration inside the lava tube is a 20 m high accumulation of coarse sand that entered the cave from the sea.

Jill Heinerth - We are water

height and turbulent nature of the various flows, which occurred within the lava tube. One of the most prolific speleogens are the lateral benches, which are catwalk-like suspended protrusions at differing heights on the walls of the cave, illustrating the fluctuating amounts of flowing lava at the late-stages of the lava tube formation. (Fig.10). Other common speleogens are the parallel levees or banks, formed by a stream of lava moving along the floor of an existing lava tube, which cools first near the sides, creating a free-standing vertical remnant along the edge (Figs. 10 and 14). Finally, "tube-in-tube" formations resulting in a second section atop the main passage can be observed in Cueva de los Verde and Túnel de la Atlántida, the latter known as Lago Escondido (Fig. 7). These secondary galleries are formed when the lateral benches in the opposite walls of the lava tube get progressively closer until they collide, creating a false floor. Once eruptions cease and molten lava drains from the tube, a smaller secondary tube remains perched atop the larger main tube. The most common speleothems in the cave are lavacicles (lava stalactites, Figs. 11 and 13). They are present in varying sizes in many sections of La Corona lava tube. Some of these lava stalactites formed as the level of lava fluctuated inside the lava tube. When the level fell, lava that coated protrusions on the ceiling or below the lateral benches dripped off, forming broadly shaped sharktooth stalactites (Fig. 11). Alternatively, splash stalactites formed when turbulent lava flows or breakdown pieces falling into the flowing lava, splashed molten material upward that cooled as it dripped. Ropey pahoehoe lava (Fig. 12), encountered on the cave floor, represents the last of the molten lava to flow through the tube at the end of the volcano's eruptive processes. It formed when the thin, partially solidified crust of a flow was slowed or halted by an obstruction while the lava beneath continued to move forward, dragging and compressing the crust above into a series of wrinkles and ridges. Occasionally, the floor of the lava tube may be covered by breakdown blocks – large boulders that broke loose from the cave ceiling and now cover the floor (Fig. 13). Breakdown blocks are welded to the floor if they happened to fall when the lava was hot enough to partially fuse the collapsing rocks to molten lava on the floor (Fig. 14). A conspicuous feature mostly found in the submerged sections of the lava tube is a white carbonate cement, up to 5 cm or more in thickness, that occurs on the uppermost surfaces of breakdown blocks, benches, and the cave floor (Figs. 12 and 14). It is likely that this carbonate cement formed either by precipitation from supersaturated carbonates in the cave water or from a cementing together of lime mud that entered the cave from the seafloor above. These deposits can be localized, surrounding the pores in the basalt, (Fig. 15) or forming small prominent knobs (Fig. 16).

Juan Valenciano

Figure 10. Lateral bench photographed in Túnel de la Atlántida after La Sima restriction (150-350 m from the entrance). In this section, lateral benches are well developed and densely covered by lavacicles and splash marks. Below the lateral bench, additional formations are visible including lava aprons and a lava levee. Contraction cracks appear along the passage wall. Loosely compacted carbonates have been deposited throughout.

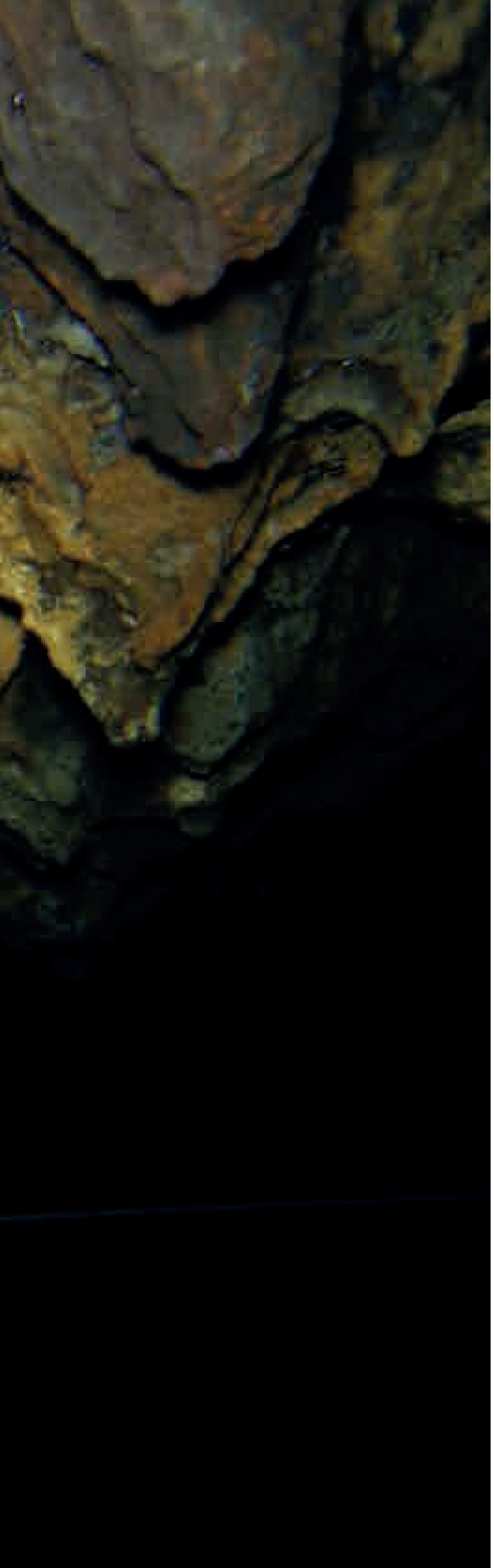

Enrique Domínguez

Figure 11. Sharktooth lavacicles observed on the ceiling near La Sima. The length of the biggest speleothem is approximately 30 cm.

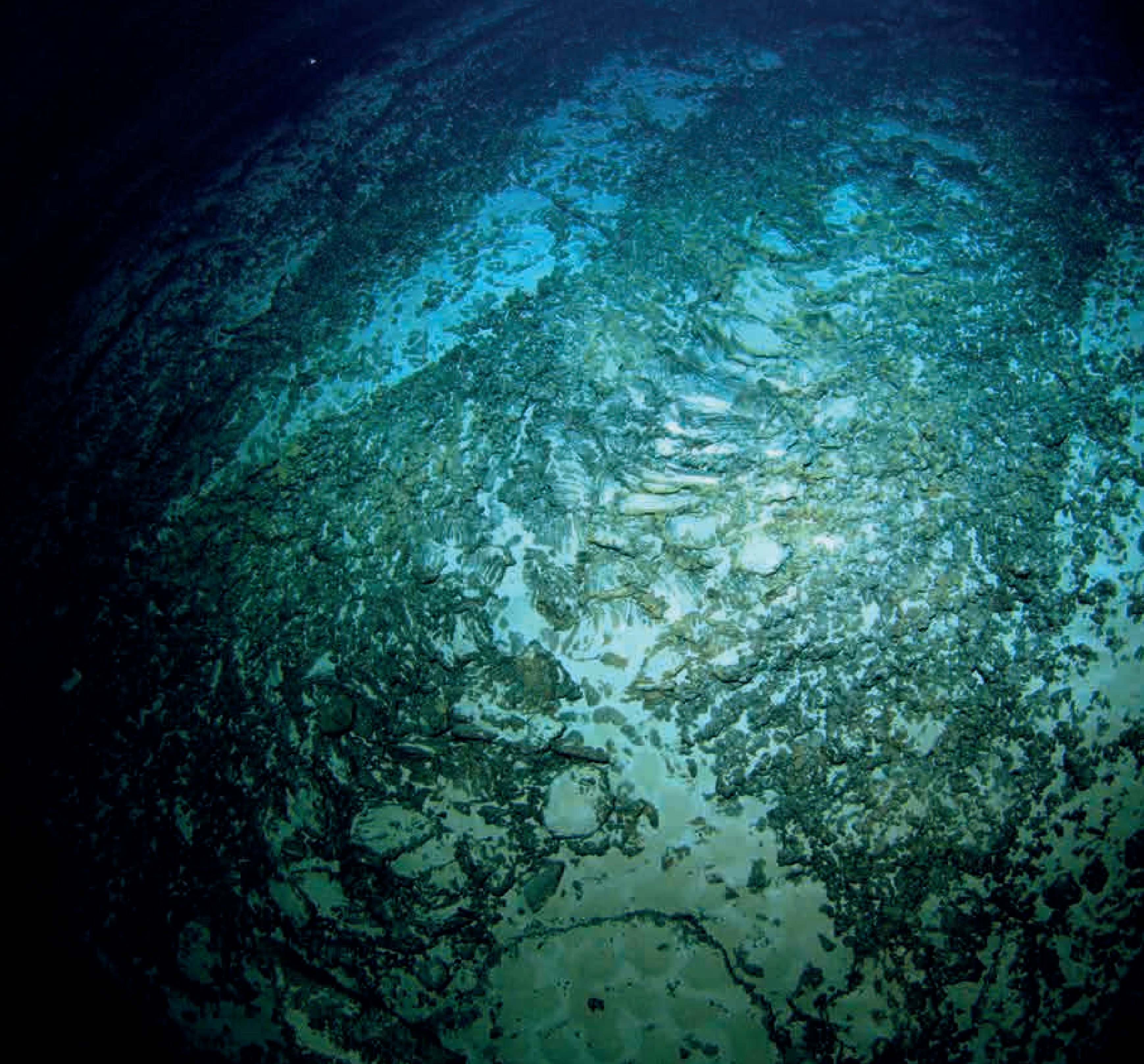
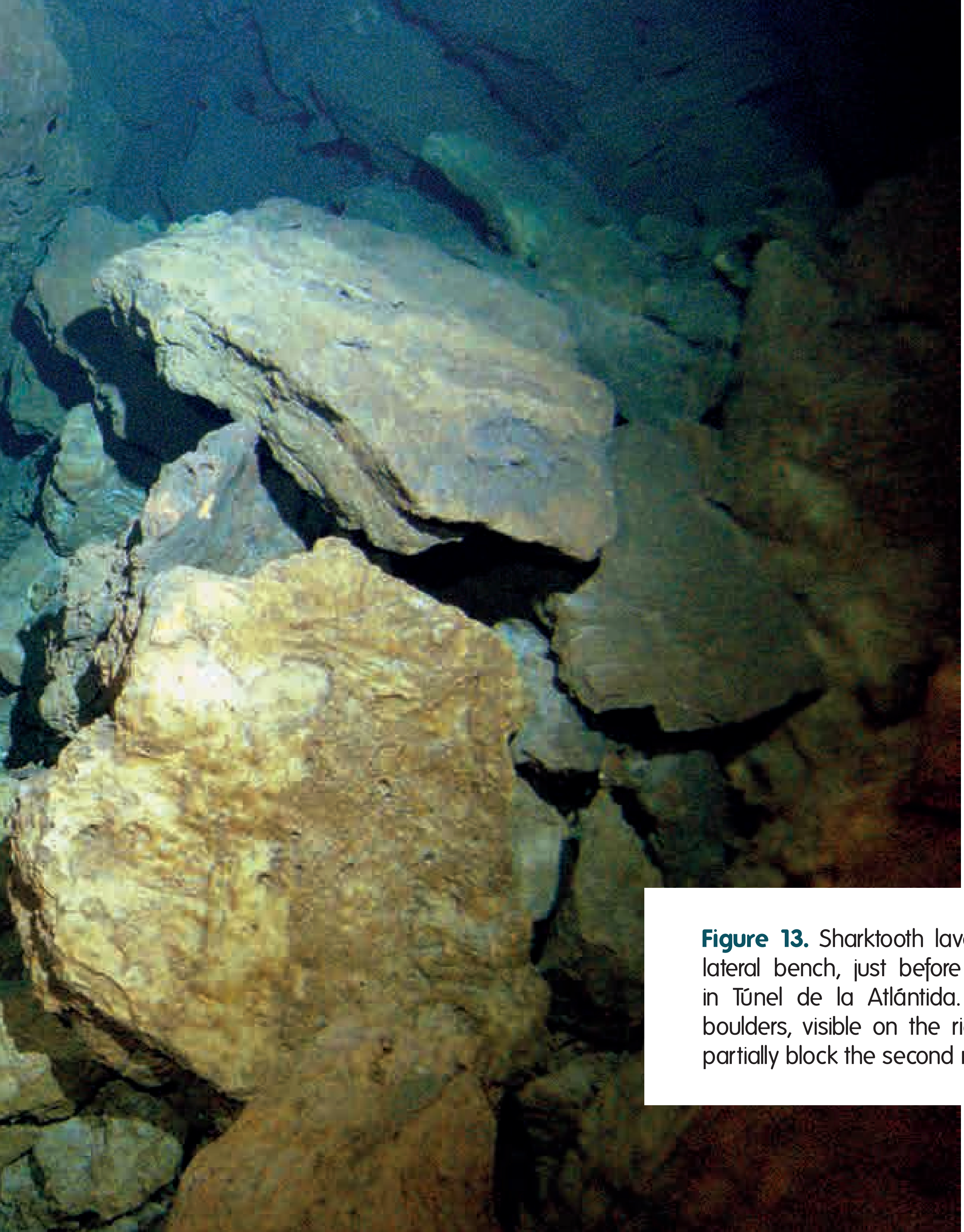


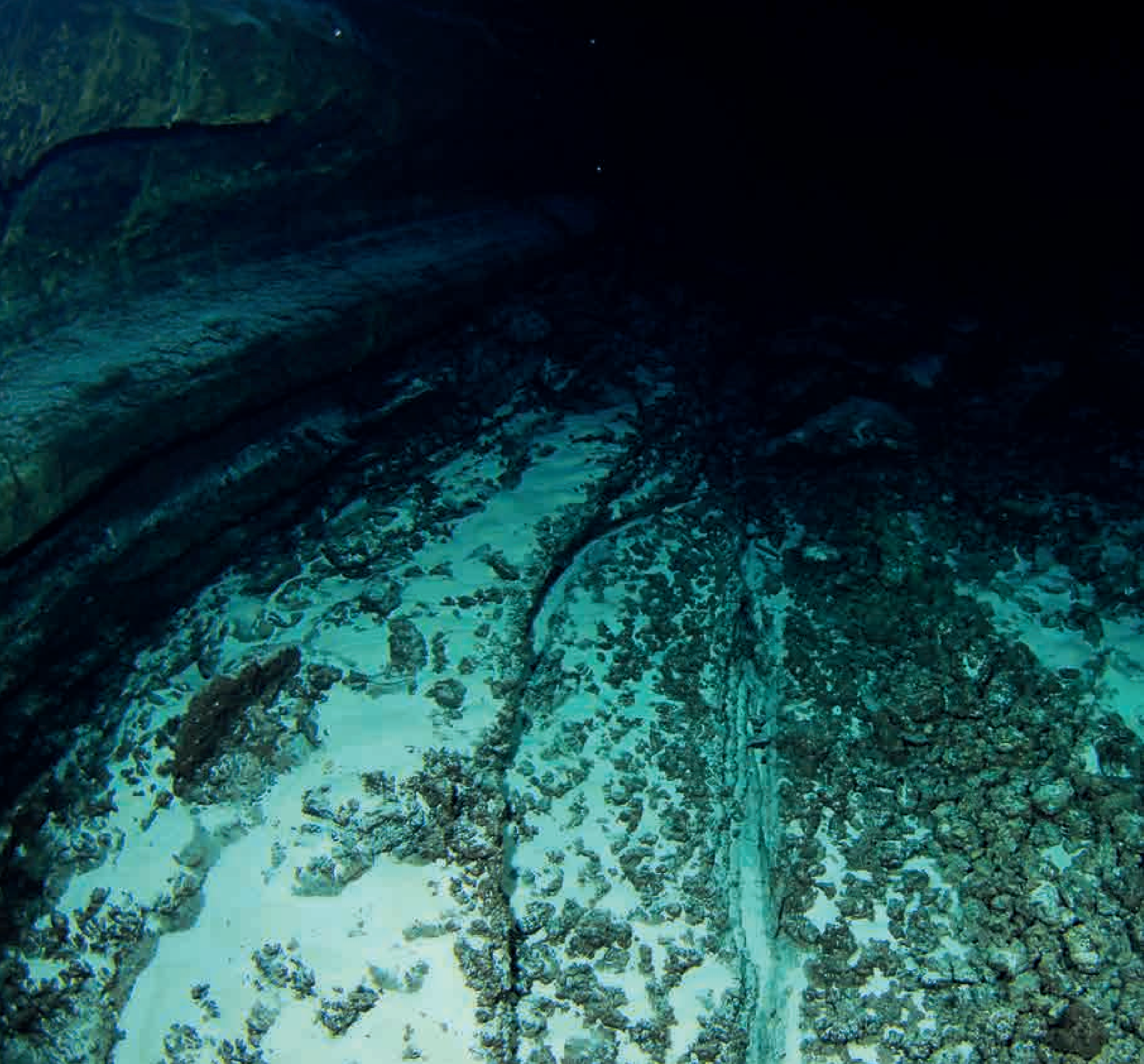
Figure 12. Ropey pahoehoe lava covers the bottom of the main passage after the second window to Lago Escondido. These flows have been secondarily covered by calcium carbonate.

Enrique Domínguez



Enrique Domínguez

Figure 13. Sharktooth lavacicles hanging from a lateral bench, just before the second restriction in Túnel de la Atlántida. The large breakdown boulders, visible on the right side of the picture, partially block the second restriction.

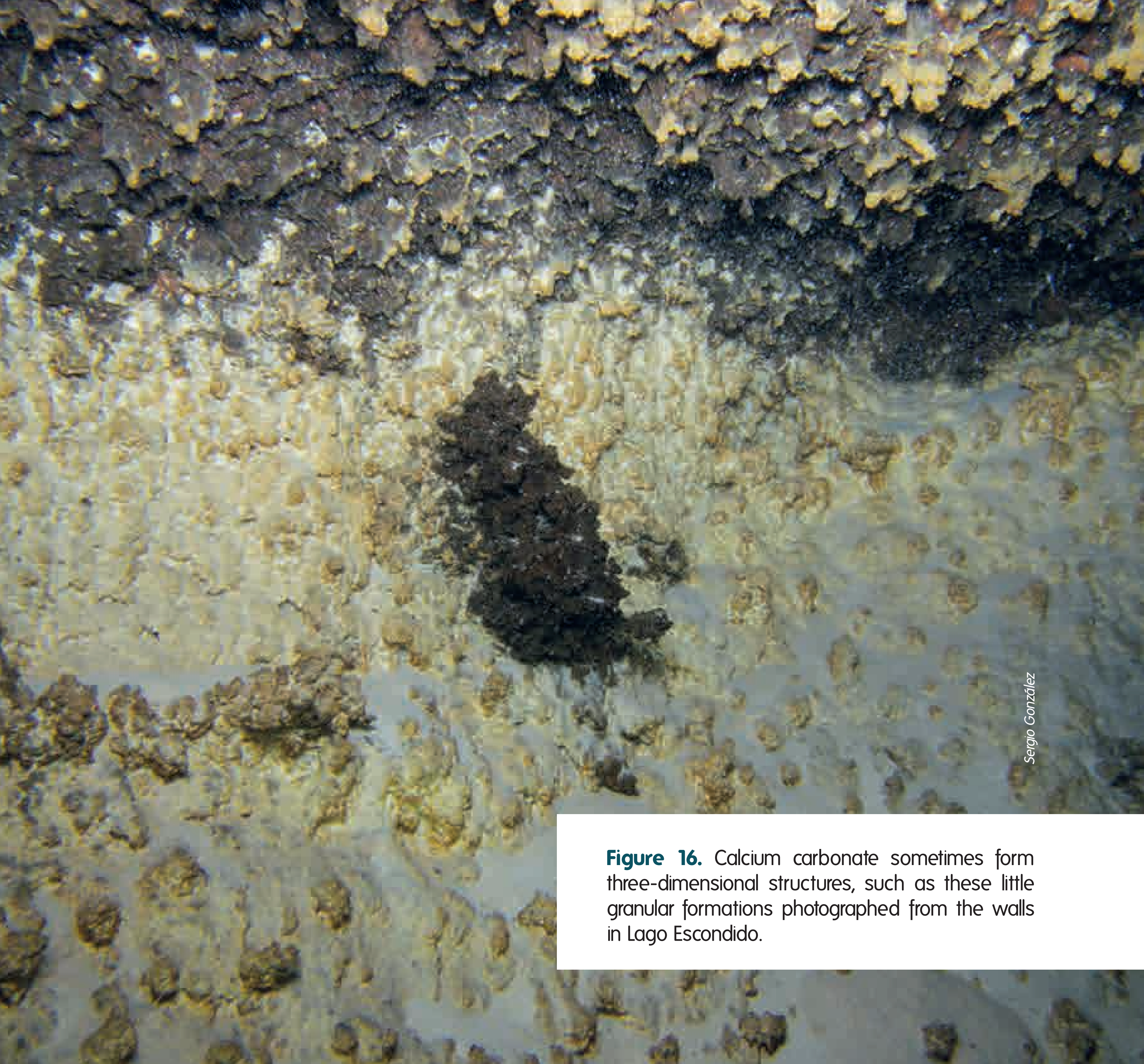


Enrique Domínguez

Figure 14. Welded breakdowns are often seen covering the bottom of Túnel de la Atlántida. The image shows other speleothems: lateral benches on the wall and, a lava levee between the wall and the melted break down. All these features originated during the lifetime of active lava flow in the tube. The white crusts of calcium carbonate were originated afterwards, both before and after the cave was flooded.

Sergio González

Figure 15. Calcium carbonate often precipitates around the vesicles of the lava, as shown in this picture taken from a wall in Lago Escondido.



Sergio González

Figure 16. Calcium carbonate sometimes form three-dimensional structures, such as these little granular formations photographed from the walls in Lago Escondido.

Morphology of the Anchialine Sections of La Corona Lava Tube

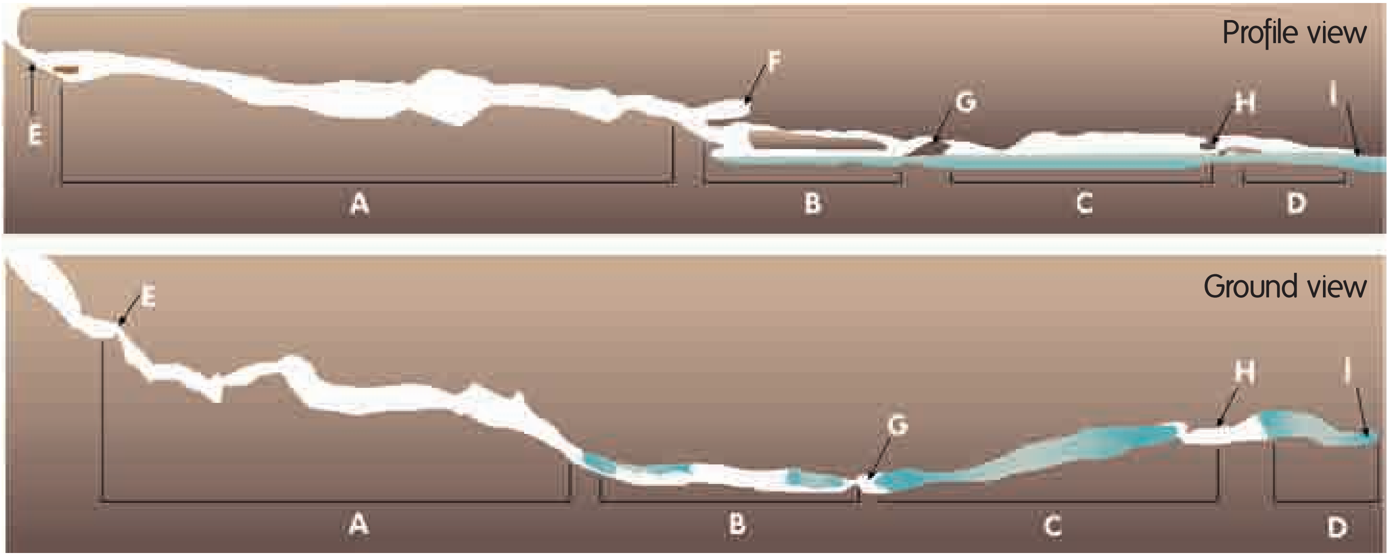


Figure 17. Map of Cueva de los Lagos showing some major features. The completely flooded section after the terminal sump is not represented. **A**. Dry section. **B**. First Lake. **C**. Second Lake. **D**. Third Lake, until the terminal sump. **E**. Entrance. **F**. "Tube-in-tube" structure leading to a secondary gallery above the cave. **G**. First sump, connecting first and second lakes. **H**. Second sump, connecting second and third lakes. **I**. Terminal sump.

Cueva de los Lagos (Fig. 17) marks the farthest point inland that seawater penetrates into the lava tube, approximately 600 m from the nearest point on the coast. The entrance to this section of the lava tube is located in the interior of La Corona lava field, 210 m from the road between Los Jameos del Agua and Cueva de los Verdes. Looking down from the surface of La Corona lava field, there is a 12 m vertical drop to the top of a talus mound (Fig. 18), followed by a restriction just below which opens into a wide lava tube extending over 700 m to the southeast. The first 400 m of the lava tube past the restriction is completely dry (Fig. 17 A), with the cave floor covered with loose sediment and large breakdown mounds.

Figure 18. Cueva de los Lagos is located in the middle of La Corona lava field. The entrance (shown here) is located at the bottom of a nearly vertical rock face. At the time when this picture was taken (2010) the reinforced steel gate, which today protects the cave from uncontrolled visitors, had not been installed.

Kirsten Kvinderbjerg

Figure 19. The first of three lakes present in Cueva de los Lagos. The three subterranean lakes are connected by completely flooded narrow passages (sumps). The white crusts on the walls are a result of calcium carbonate deposition. Two parallel lateral benches are visible at each side of the passage.

Suso Fontes

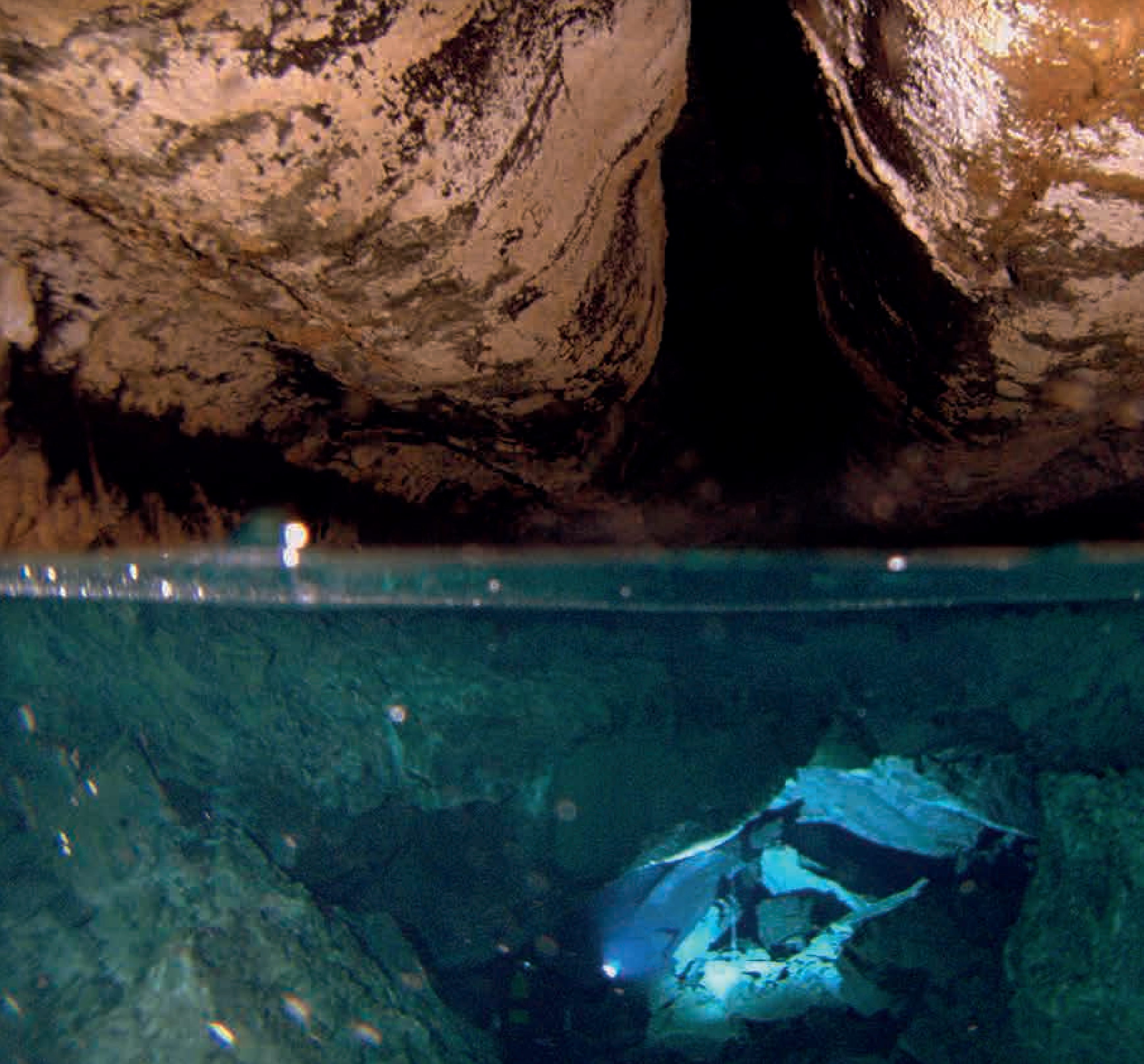


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Figure 20. Illuminated in the foreground of the lower center of the picture is the sump between the first and second lake. At this point the passage becomes completely submerged and can only be explored by trained cave divers. A set of lava aprons is visible above the waters surface.

Farther into the cave, the lava tube gradually descends to the water table, where a lake is reached (Fig. 19). This tidal anchialine lake ranges from 1 to 2 m in depth and is divided into three parts (Fig. 17 B and D) by collapses that have partially blocked the tunnel (Fig. 17 G and H). These three lakes, locally *lagos*, provide the name for the cave.

An upper level of the lava tube connects over the breakdown separating the first two lakes (Fig. 17 B). Alternately, the three lakes are interconnected underwater through submerged cave passages that require specialized cave diving equipment and training (Fig. 17 G and H). The first sump (between lakes one and two) consists of approximately 25 m of low horizontal passage at a depth of 3 m (Figs. 20 and 21). This is followed by a second sump, between lakes two and three, that extends for about 15 m at the same depth. At the end of the third and final lake (Fig. 22), the cave continues underwater for approximately 150 m at 5 to 9 m in depth before ending. The first half of the sump is narrow, with the roof covered by lavacicles and the floor partially consisting of welded breakdown (Fig. 23). After passing a bulbous protrusion in the cave ceiling named La Tortuga (Fig. 24), the gallery gets wider (Fig. 25) until it finishes in a dead end. At one time, the sump after the third lake was connected to Los Jameos del Agua, but this was blocked during construction of the auditorium in Los Jameos del Agua tourist center.

Lava speleothems are present throughout the lake passages, while boulders cover the bottom of the cave, sometimes partially blocking the passages and forcing the divers to get out of the water before they can continue their dive (Fig. 26). Lateral benches are well developed, but often partially broken (Fig. 27). The walls of the tube at levels between the high and low tide marks are covered by a thick layer of white, crystalline, calcium carbonate which contrasts to the otherwise dark greys and browns of the lava itself (Fig. 19). The variable size of the breakdown debris within this section of the cave provides interstitial and crevicular habitats (Fig. 28). Whereas interstitial habitats are voids amongst unconsolidated sediments, crevicular habitats refer to the bigger spaces among gravel or formed by cracks in porous consolidated rocks. Both types of environments are commonly inhabited by a variety of obligate cave-dwelling (stygobitic) organisms which are well adapted to marine water in caves and are never found outside them.

Los Jameos del Agua (Fig. 29) is a portion of the cave developed as a major tourist attraction. It contains three skylights flanking a 50 m long by 25 m wide lake with a maximum depth of 10 m at high tide (Figs. 29 and 30). The side walls of the lava tube are penetrated by numerous small cracks and fissures. Each end of the lake is enclosed by a cement capped talus mound to provide visitors access.

The original state of the lake has undergone several alterations since the beginning of the construction of the Los Jameos del Agua tourist center in 1968 by the local artist César Manrique, although the original dimensions and most of the features of the lake were preserved. The eastern, seaward facing edge

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Figure 21. The sump connecting the first and second lakes is approximately 25 m, and partially blocked with breakdown. The white guideline, visible in the center of the image, has been laid for safety and directs divers between lakes. Small lavacicles capped by calcium carbonate decorate the edge of the lateral bench visible at top right.

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Figure 22. Underwater view leaving the third lake in Cueva de los Lagos and heading into the terminal sump.

of the lake has steps leading into the water (Fig. 31), below which the depth drops steeply to the boulder covered bottom at 9-10 m depth. At the opposite end of the lake, where the maximum depth is about 5-6 m, large accumulations of cinders dumped during tourist construction, cover the natural bottom (Fig. 32). Volcanic cinders are particles expelled during eruptions, with sizes ranging from 200 to 64 mm. In Lanzarote, volcanic cinders are traditionally mined for use in construction and agriculture. Atop the cinders, diatoms grow as dense patches (Fig. 33). Growth of diatoms is possible due to the presence of sunlight penetrating from the natural entrances above (see Chapter 4). These entrances consist of two natural collapses with talus mounds, named Jameo Chico at the eastern side, and Jameo Grande at the western side; as well as a smaller blowhole above the middle of the lake. The bottom of the lake contains coins from varying countries as the lake has been wrongly regarded as a natural "wishing well" by visiting tourists. This activity has gone on for at least the last 20 years despite the presence of signs prohibiting it. Periodic attempts have been carried out to gather the corroding coins since metal, particularly toxic copper, is leaching from them, but coins are still present and can be seen from the surface. It is unclear how much copper has been added in this manner to the cave water column and what long lasting effects it is having on the endemic and endangered fauna.

Túnel de la Atlántida (Map 3) is the terminal section of La Corona lava tube that extends beyond the coastline of the island and below the seafloor (Fig. 34). It is the longest underwater lava tube in the world with a length of 1726 m, diameters greater than 30 m and a maximum water depth of 64 m.

The cave begins at a small entrance pool near Jameo Chico, at the southeast end of the tourist center of Los Jameos del Agua (Fig. 35). This 3 by 8 m lake is at the base of a breakdown slope below a tourist overlook, that is adjacent to the restaurant bar area of Los Jameos del Agua. Artificial lighting permits the growth of various colored algae on the lava tube walls, with different species and colors appearing at different tidal levels (Fig. 35). Artificial illumination is restricted to the entrance pool and only penetrates 20-30 m, whereas thereafter the remainder of the lava tube continues in complete darkness (Fig. 38). Underwater from the entrance pool, a slope of cinders continues to the bottom of the tube at 9 m water depth (Figs. 36 and 37). As the tube levels off, scattered breakdown blocks of various sizes are welded to the bottom with either lava or carbonate cement.

Progressing past the entrance area, the depth gradually increases over the length of the underwater tube. There are two restrictions (i.e., smaller diameter openings with correspondingly stronger tidal currents) in the submerged tunnel. The first restriction at 150 m linear distance from the entrance pool called La Sima (Figs. 39 and 48), literally translated as a gap or chasm, where the depth of the lava tube increases from 15 m to an average of 25-30 m. About 250 m linear distance after La Sima and approximately 350 to 400 m from the entrance, a second restriction is present the lava tube has been partially blocked by secondary collapse of the ceiling (Fig. 40). A small opening on the right side of this breakdown allows divers to access the rest of the cave. Lateral benches (Figs. 10 and 41), lavacicles (Figs. 11 and 13), and ropey pahoehoe lava (Fig. 12) are present between these restrictions. Past the second restriction, the tunnel continues at a depth of 30 to 35 m. At 750 m linear distance from the entrance, a 25 m high conical sand dune, Montaña de Arena (Figs. 9 and 42), is composed of white carbonate sand entering the cave from the sea floor above (Fig. 43). This dune formed over several thousands of years from a small crack in the roof, permitting sand to penetrate, grain by grain, from the ocean above. This is the only place in the cave where a direct connection with the ocean has been observed. As a result, an interstitial habitat formed deep inside the lava tube, which is otherwise devoid of sand or other loose sediment. This sand mountain harbors a remarkable animal community that is very important in understanding cave colonization processes (see Chapter 4). Upon approaching Montaña de Arena, two smaller passages can be observed. The upper passage leads into a dome, with a smaller, fossilized mountain of sand which has been cemented in place by carbonates (Fig. 44), while a lower gallery partially extending under Montaña de Arena ends in collapse (Fig. 9). Beyond Montaña de Arena, the cave widens and progressively descends towards a final collapse and small dome at 64 m depth and 1,726 m maximum penetration.

Back near the coastline, between the two restrictions, a tube-in-tube configuration occurs with a smaller tunnel above the main passage. A section of this upper passage extends above water level, forming a totally enclosed lake, known as Lago Escondido, which extends inland as a short, dry passage. This air filled passage ends where large boulders block the way (Fig. 45), but light can be seen coming in from Jameo de la Puerta Trasera (Fig. 8), the collapse sinkhole entrance located between Los Jameos del Agua tourist center and the coastline. Lago Escondido can be accessed from the lower and larger main part of this tube-in-tube through two small windows located at 110 m (Fig. 46) and 150 m (Figs. 47 and 50) linear penetration. A third connection to Lago Escondido from the main tube-in-tube portion of Túnel de la Atlántida is located at the second restriction. Here the ceiling has collapsed to form a wide bowl shaped opening among the boulders, joining the two levels. Heading away from the coastline, a shallow (2 to 5 m deep) and narrow (3-5 m diameter) extension of the Lago Escondido passage extends seaward for another 200 m directly above the main passage. This shallow passage is characterized by the presence of loosely compacted carbonate cement covering ropey pahoehoe lava on the floor (Fig. 51). Eventually, this upper passage from the Lago Escondido becomes progressively lower until it is no longer possible for a diver to pass.

Tomas Abel Rivero

Map 3. 3D reconstruction of Túnel de la Atlántida. (**A**) Ground view, (**B**) Profile view.

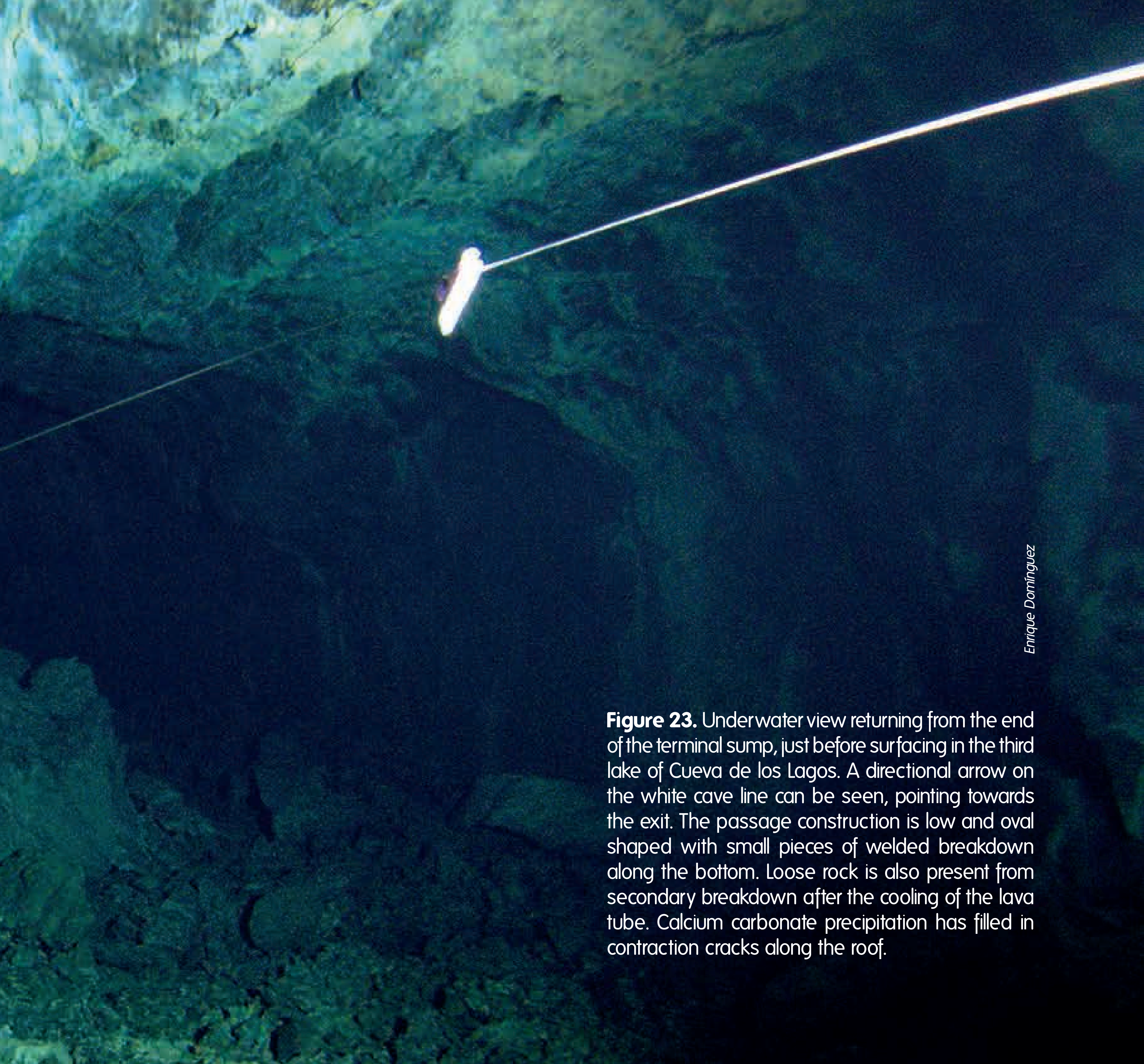

Figure 23. Underwater view returning from the end of the terminal sump, just before surfacing in the third lake of Cueva de los Lagos. A directional arrow on the white cave line can be seen, pointing towards the exit. The passage construction is low and oval shaped with small pieces of welded breakdown along the bottom. Loose rock is also present from secondary breakdown after the cooling of the lava tube. Calcium carbonate precipitation has filled in contraction cracks along the roof.

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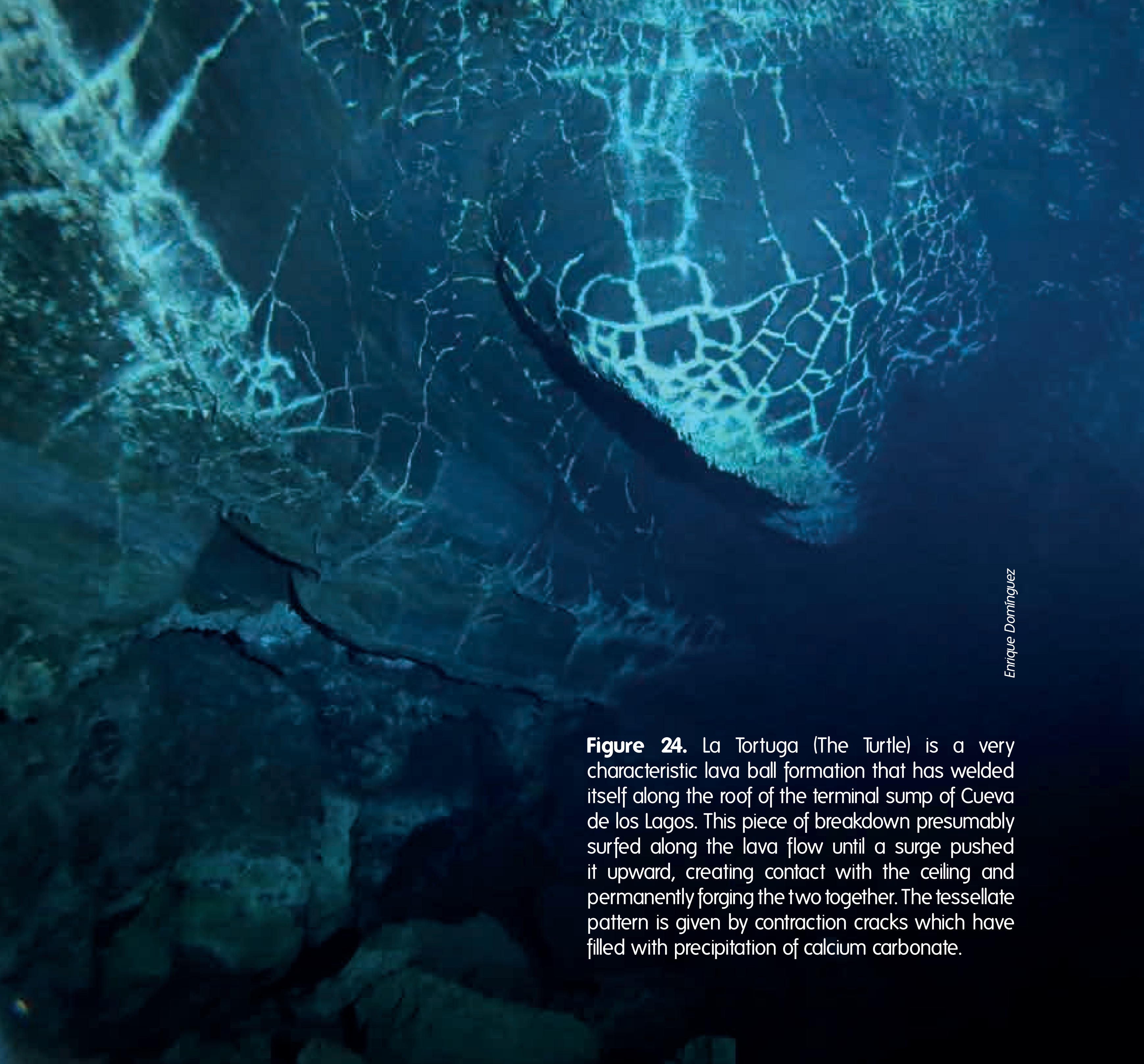

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Figure 24. La Tortuga (The Turtle) is a very characteristic lava ball formation that has welded itself along the roof of the terminal sump of Cueva de los Lagos. This piece of breakdown presumably surfed along the lava flow until a surge pushed it upward, creating contact with the ceiling and permanently forging the two together. The tessellate pattern is given by contraction cracks which have filled with precipitation of calcium carbonate.

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Figure 25. After La Tortuga the section of the terminal sump of Cueva de los Lagos widens just before ending a few meters past the viewable field in this picture.

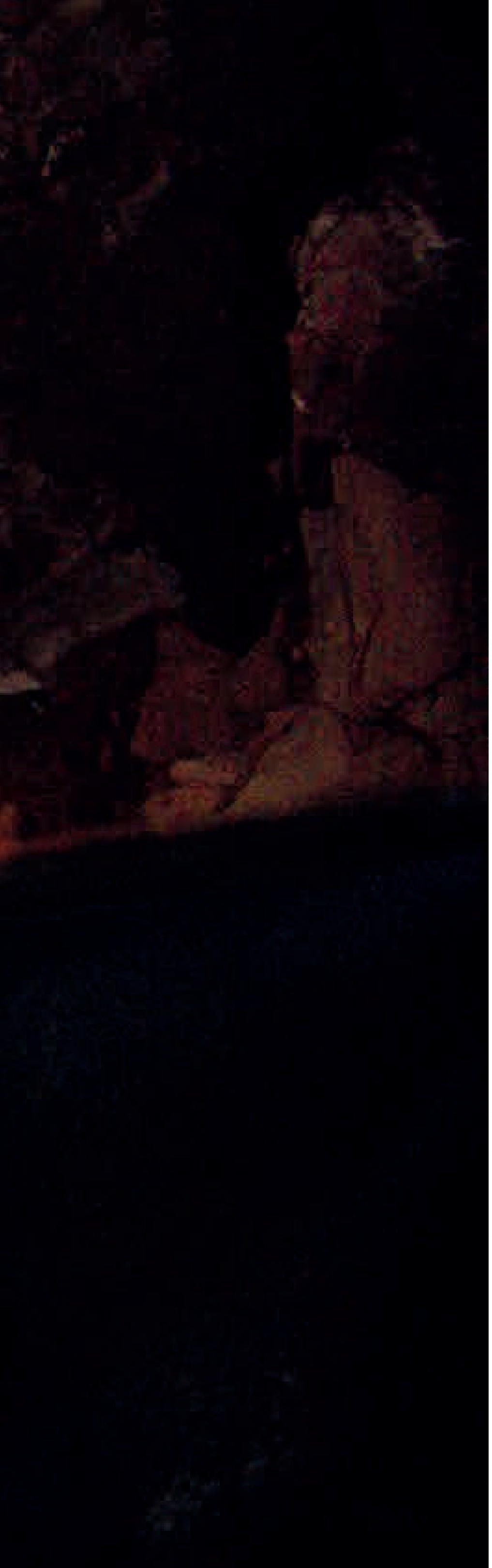

Figure 26. View from the third lake of Cueva de los Lagos before entering the last and final sump. Here the passage is partially blocked, forcing divers to crawl over large breakdown boulders, visible just at the water's edge, before continuing to the end.

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Figure 27. Lateral benches have collapsed in several points throughout the cave. Contraction cracks, as those visible in the image, are formed by the contraction of the lava during the cooling process.

Figure 28. Small pieces of breakdown or cinder have accumulated at the bottom of the sump between the second and third lake of Cueva de los Lagos. Small spaces between the cinder provide transitional habitats between the interstitial and crevicular environments, which harbor interesting assemblages of animals. White and yellow lines indicate new and old lines laid by cave divers.

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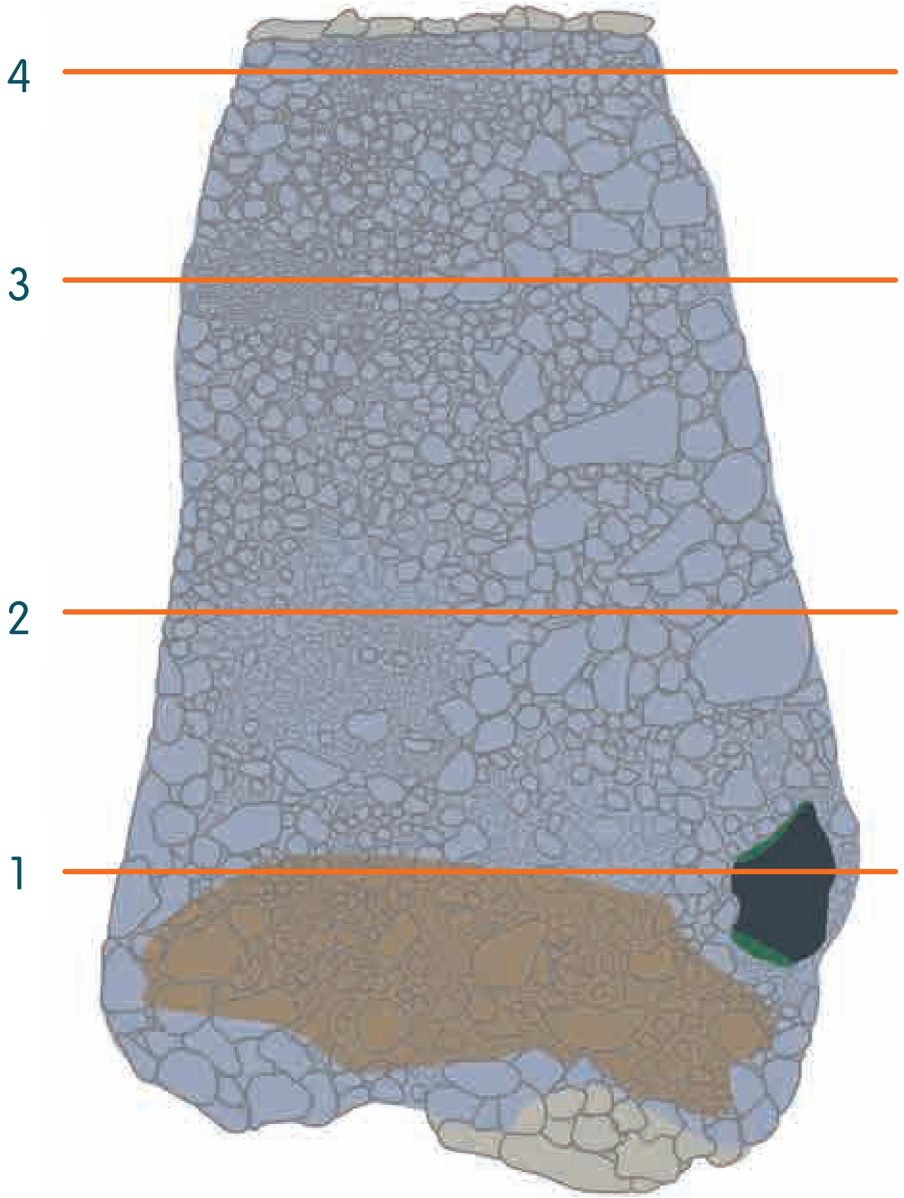

Figure 29. Map of Los Jameos del Agua lake. The red lines and numbers correspond to profiles represented in Figure 30. The brownish area represents the carpet of diatoms, the black area on the right represents a rock above the water, whereas the grey areas towards the top and the bottom are stairs which access the lake.

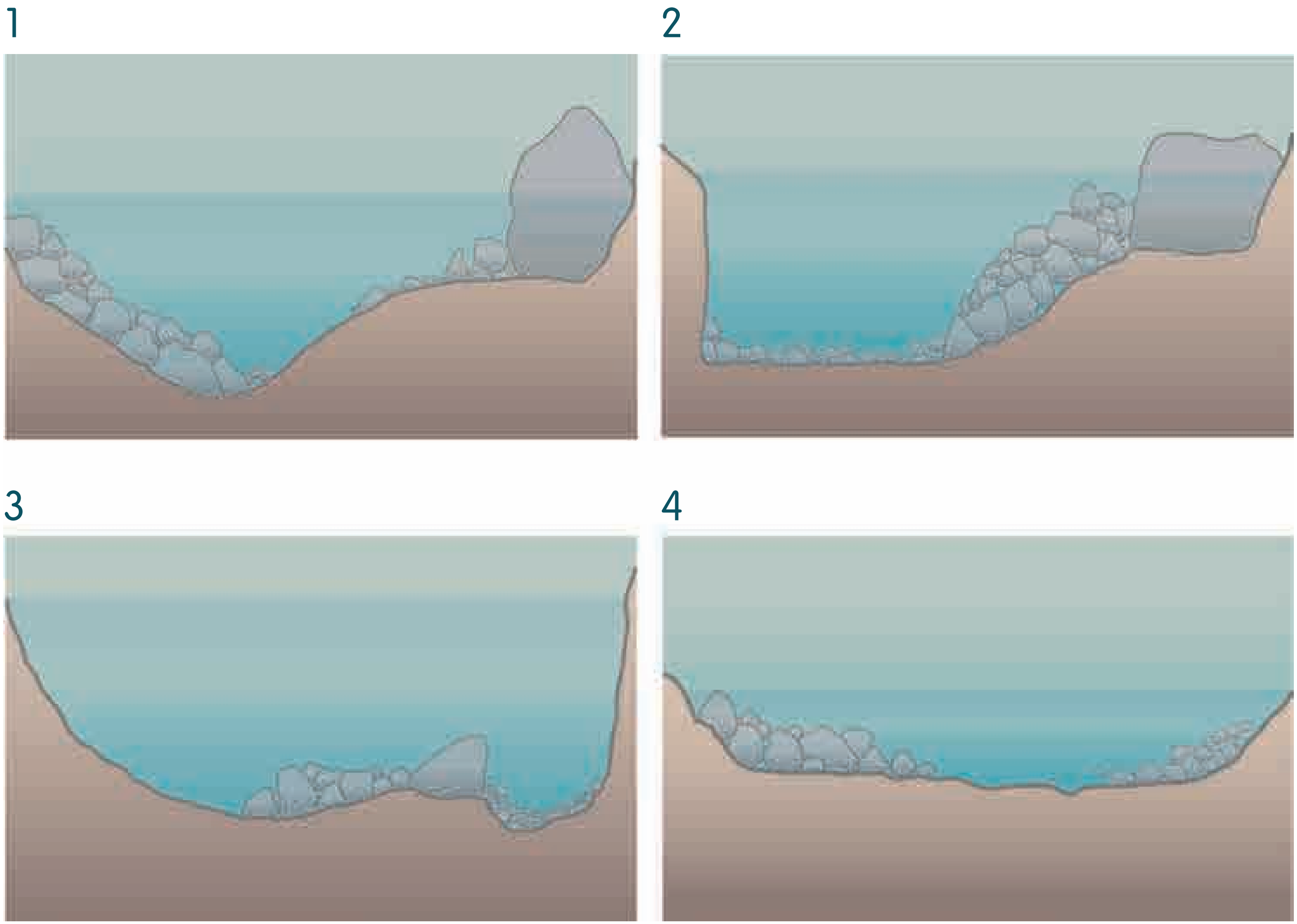

Figure 30. Transverse profiles of the bottom of Los Jameos del Agua. Figure 29 shows the relative position of each profile in the lake (see text for explanation)

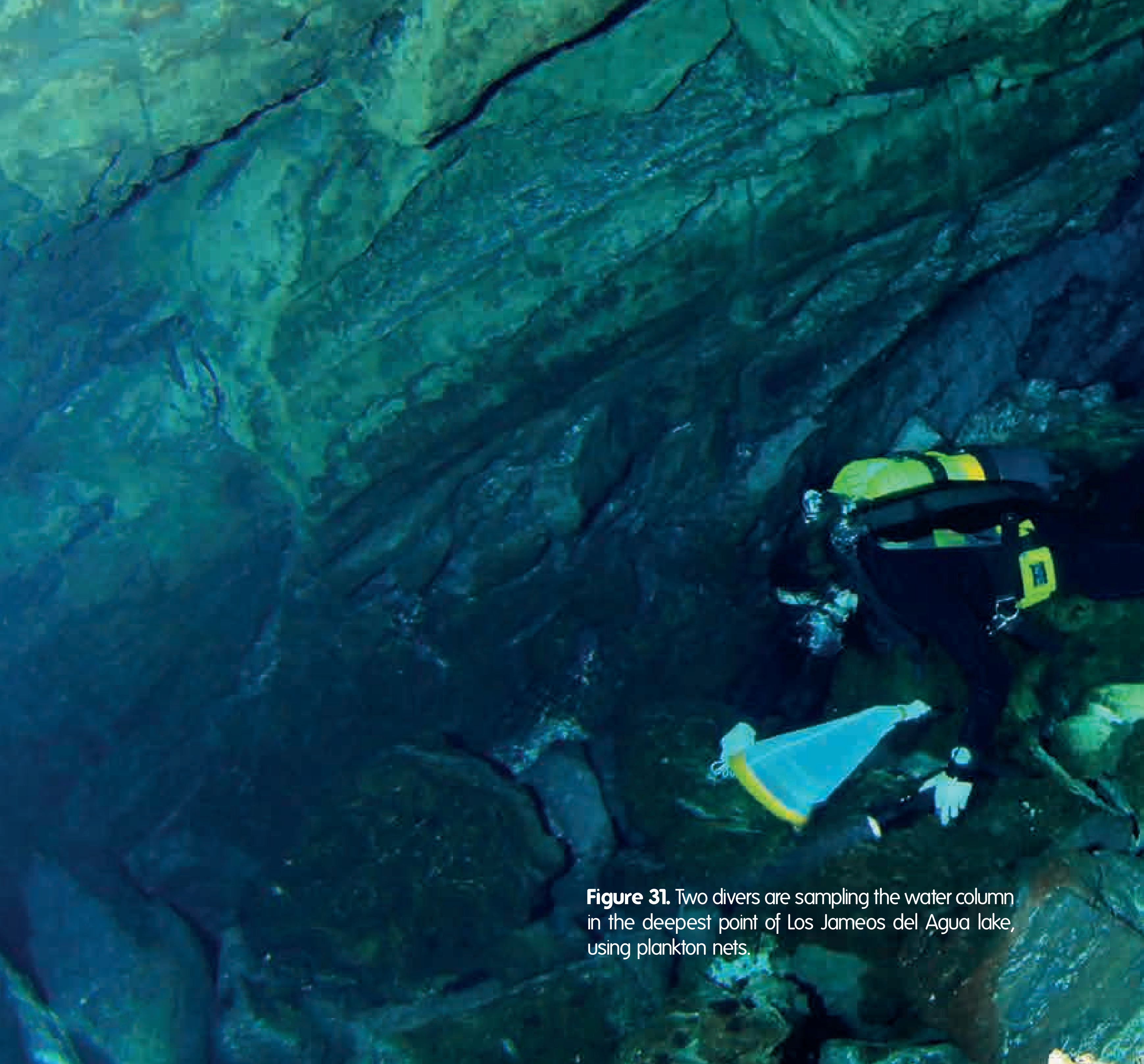

Figure 31. Two divers are sampling the water column in the deepest point of Los Jameos del Agua lake, using plankton nets.


Juan Valenciano

Figure 32. An artificial platform built on the talus mound at the eastern side of Los Jameos del Agua lake offers visitors the chance to observe the dense populations of the endemic galatheid squat lobster *Munidopsis polymorpha,* visible here as small white spots.

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Figure 33. The western side of the lagoon (0.5-2 m deep) has been filled in with introduced cinder and has now become home to a dense carpet of diatoms (brown film). White spots throughout the image are the galatheid squat lobster *Munidopsis polymorpha*.

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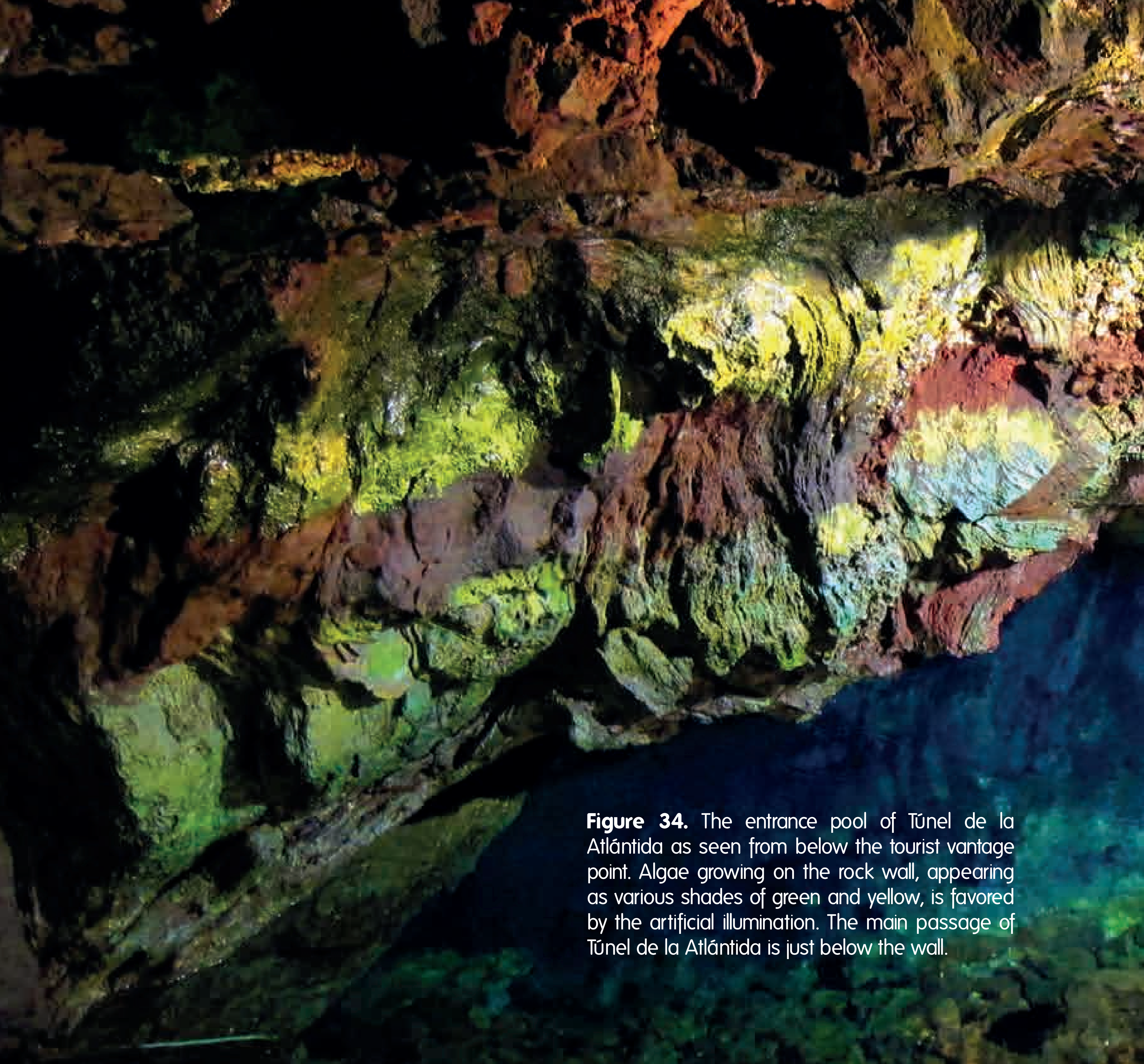

Figure 34. The entrance pool of Túnel de la Atlántida as seen from below the tourist vantage point. Algae growing on the rock wall, appearing as various shades of green and yellow, is favored by the artificial illumination. The main passage of Túnel de la Atlántida is just below the wall.

Brett C. Gonzalez

Enrique Domínguez

Figure 35. Entrance pool of Túnel de la Atlántida, just below the surface. Artificial lighting from above penetrates into the passageway for several meters before vanishing.

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Figure 36. Small mound of cinder, just past the entrance of Túnel de la Atlántida. Areas like this are scattered throughout the tunnel and harbor several endemic species specialized to this transitional interstitial crevicular environment.

Enrique Domínguez

Figure 37. Looking into the labyrinth of Túnel de la Atlántida, an illuminated diver hovers just past the entrance pool above the irregular bottom of the lava tube. The guideline can be seen on the left side of the passage.

Enrique Domínguez

Figure 38. Taken from the shallow side, La Sima is the first restriction at the main passage of Túnel de la Atlántida, at 150 m from the entrance. Just past the restriction, the depth of the water increases from 15 to 25 m. The narrowing diameter of the passage creates strong tidal currents within the restriction.

Juan Valenciano

Figure 39. La Sima, view from the deepest part. Immediately after this restriction, the cave opens up into a wide gallery that continues over 250 m until the second restriction.

Figure 40. A diver emerging from beyond the second restriction. This restriction is narrower than La Sima as it is partially blocked by collapse boulders from the roof.

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Figure 41. Contraction cracks are common along Túnel de la Atlántida, often associated with areas of collapse of lateral benches. Loosely compacted white calcium carbonate is present along the bottom and sides.

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Jill Heinerth - We are water

Figure 42. Closer view of Montaña de Arena. The diver collecting sediments near the base of the dune shows its size.

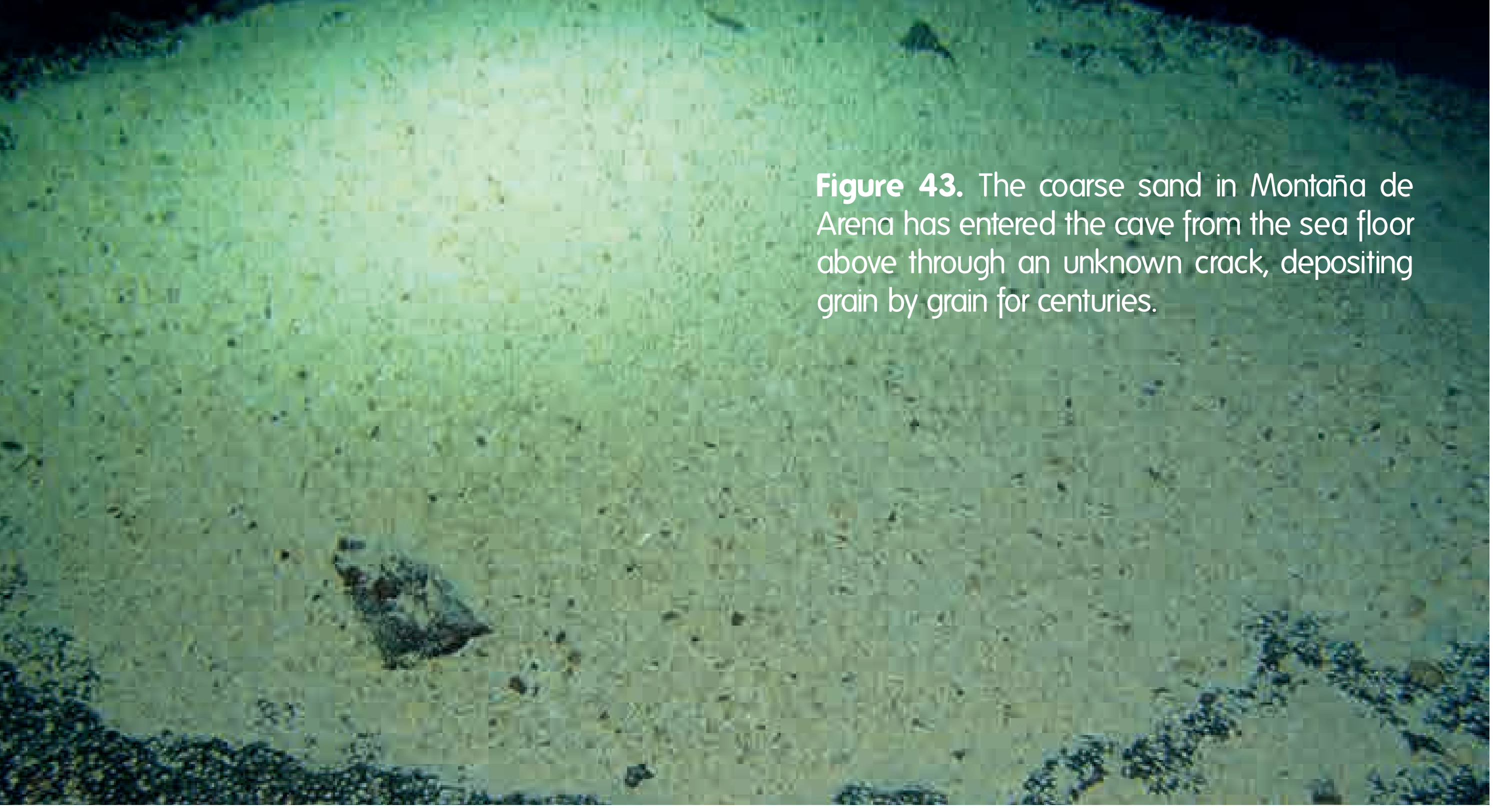

Figure 43. The coarse sand in Montaña de Arena has entered the cave from the sea floor above through an unknown crack, depositing grain by grain for centuries.

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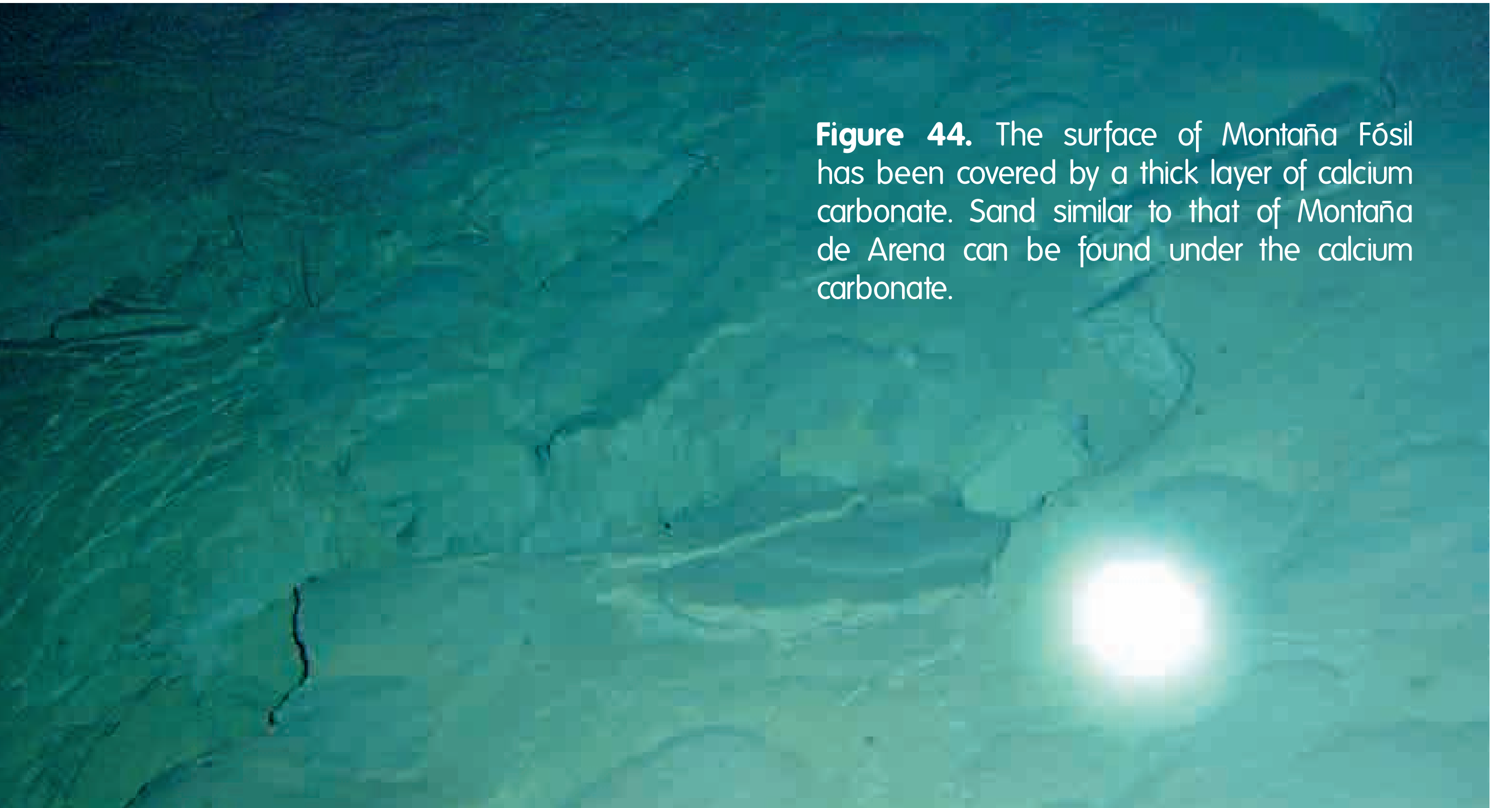

Figure 44. The surface of Montaña Fósil has been covered by a thick layer of calcium carbonate. Sand similar to that of Montaña de Arena can be found under the calcium carbonate.

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Figure 45. Lago Escondido photographed from the second entrance. The water surface is visible above the diver. The bottom of the passage is covered by welded breakdowns and calcium carbonate crusts. Lateral benches are absent throughout Lago Escondido.

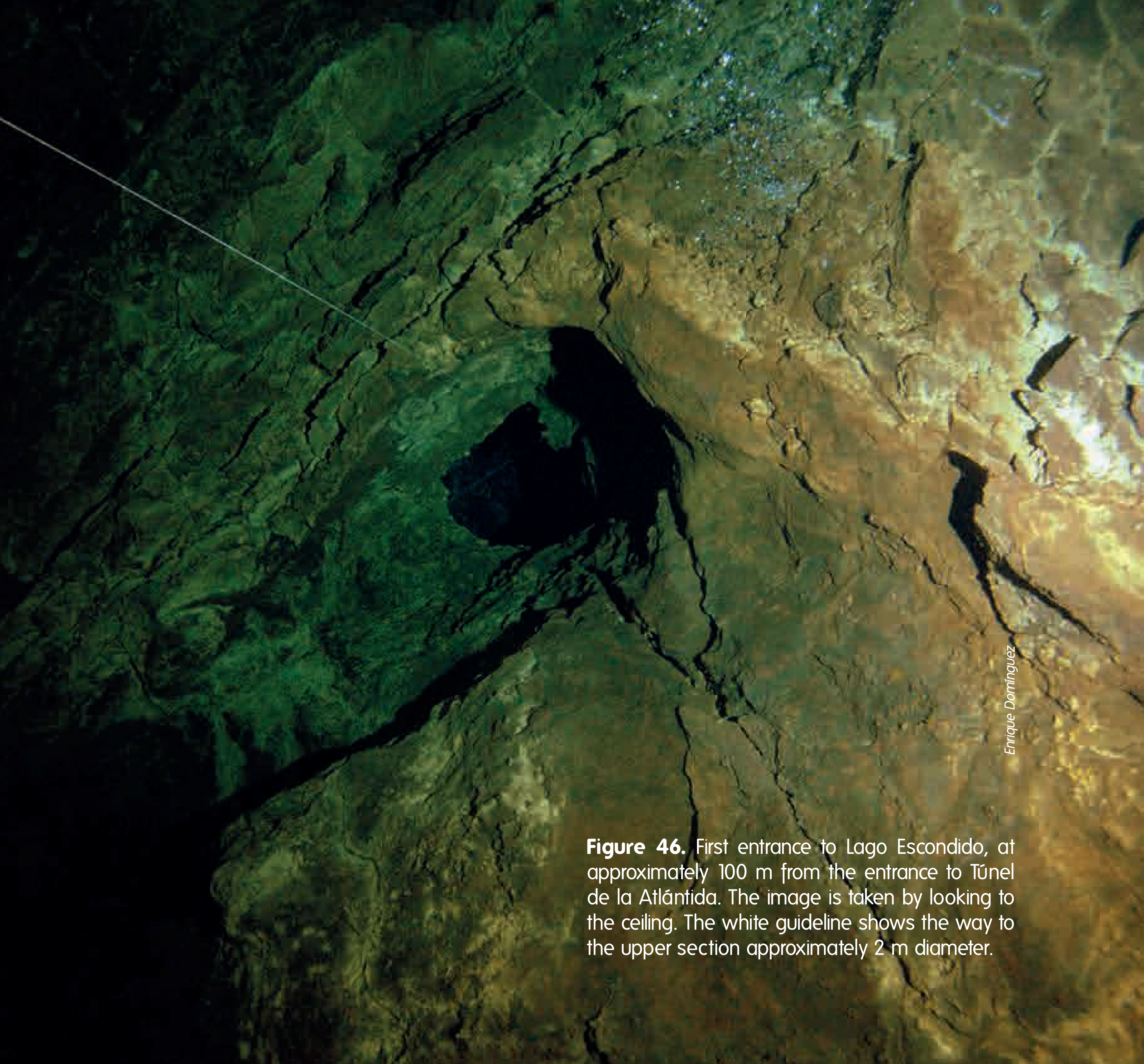
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Figure 46. First entrance to Lago Escondido, at approximately 100 m from the entrance to Túnel de la Atlántida. The image is taken by looking to the ceiling. The white guideline shows the way to the upper section approximately 2 m diameter.

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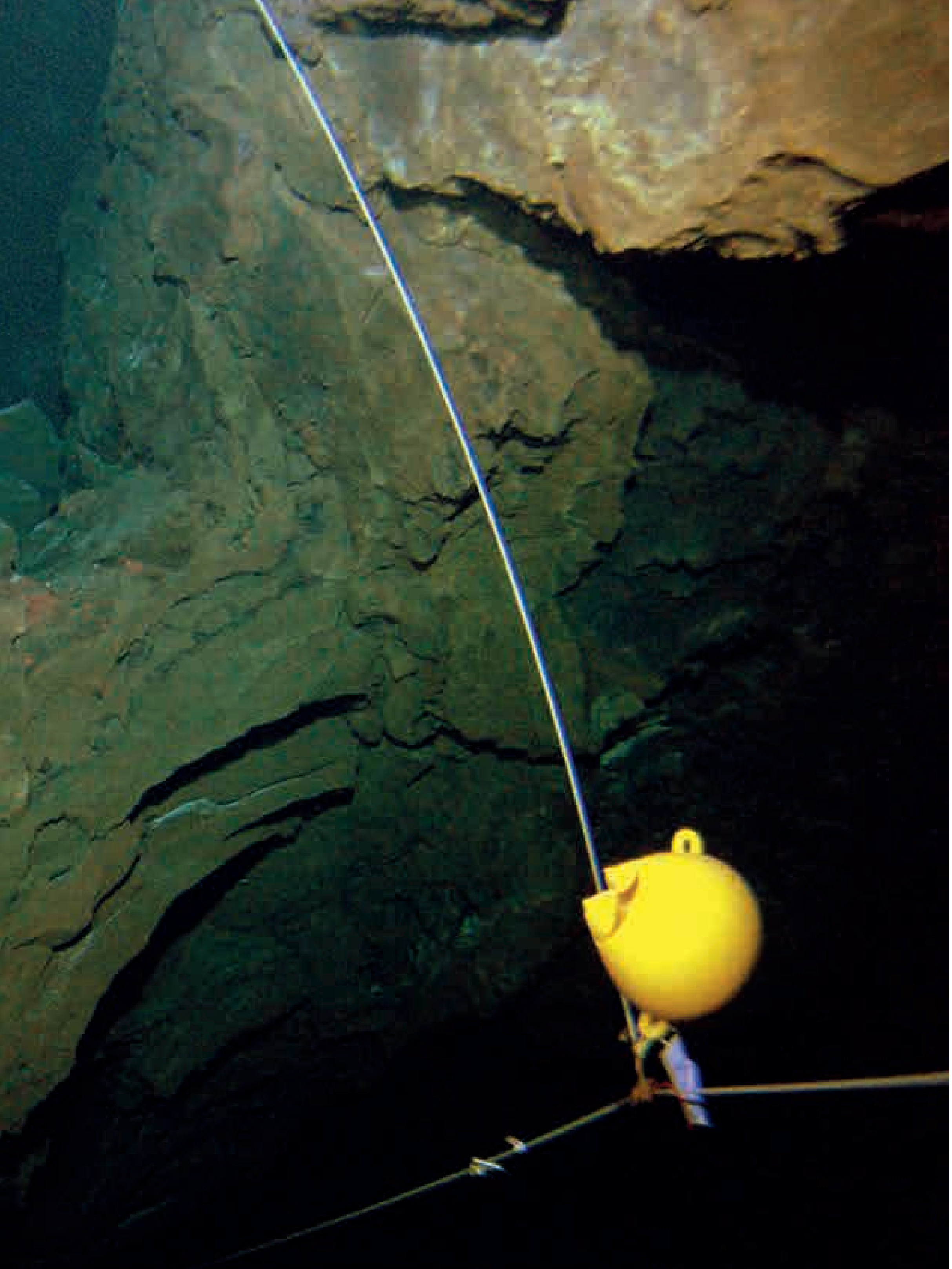
Figure 47. Intricate lavacicles adorn the walls of the lava tube above and below a second opening into Lago Escondido.

Figure 48. The second window to Lago Escondido at 200 m from the entrance pool and approximately 50 m past La Sima. The entrance at the lower level is approximately 5 m long and 3 m wide. The yellow buoy marks the line to the upper passage. Several expedition markers have been left at this junction over the years.



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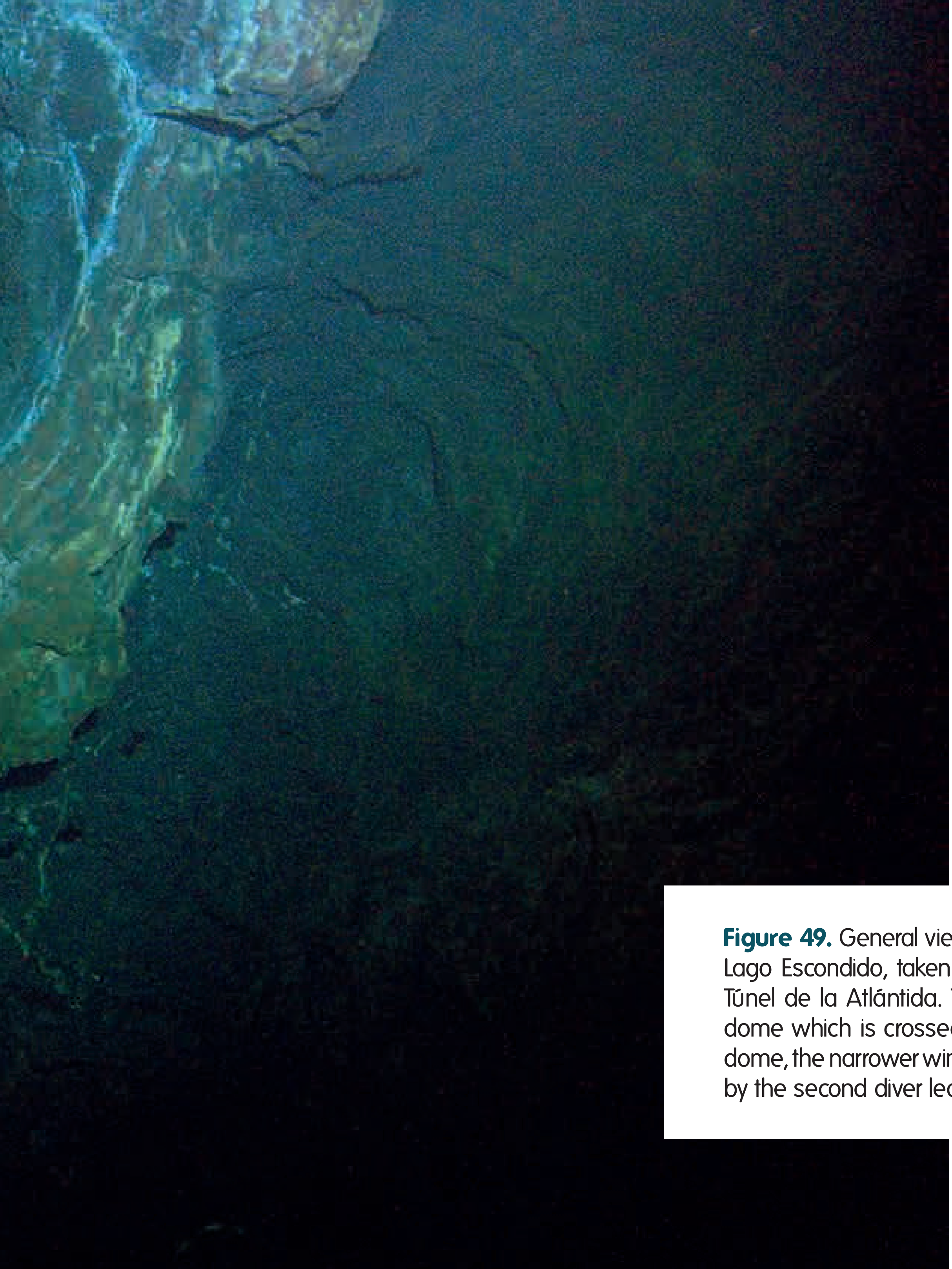

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Figure 49. General view of the second entrance to Lago Escondido, taken from the main passage of Túnel de la Atlántida. The first window leads to a dome which is crossed by the first diver. After the dome, the narrower window which is being crossed by the second diver leads to Lago Escondido.

Juan Valencia

Figure 50. Hovering above the second window in Lago Escondido, this image shows the 1.5 x 3 m long opening leading back into Túnel de la Atlántida, corresponding to the entrance.

Enrique Domínguez

Figure 51. The bottom at Lago Escondido is covered by carbonates and welded breakdown. The picture is taken from the air-filled passage looking downward towards the floor. Rounded carbonate mounds are visible near the bottom of the picture.

Introduction to Subterranean Biology

CHAPTER

2

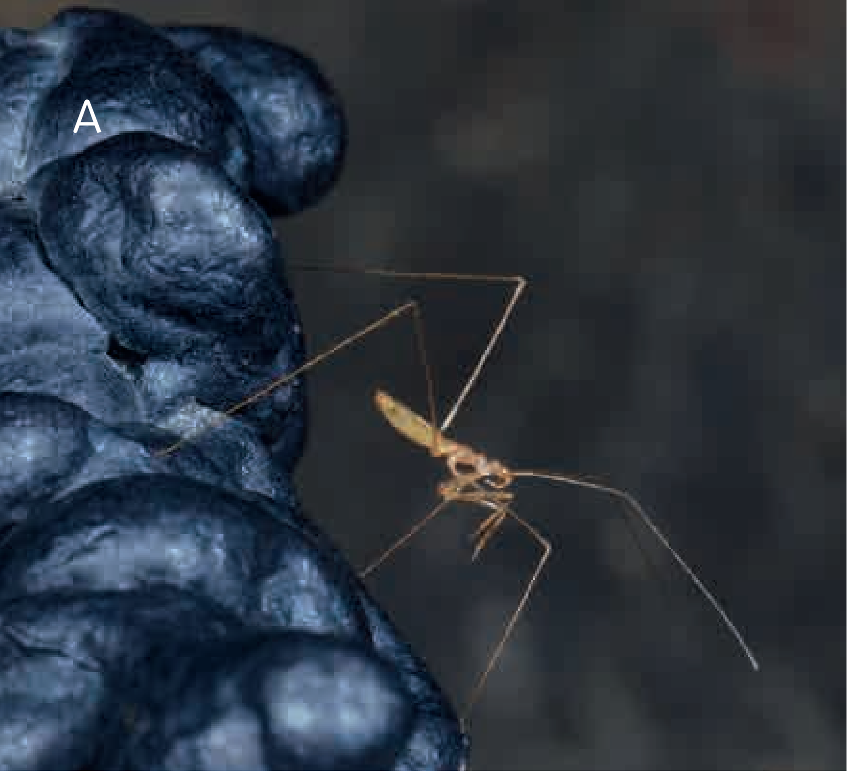
Anchialine environments contain extreme ecosystems which represent one of the Earth's last unexplored frontiers in terms of biodiversity, ecology, and evolutionary processes. Within the last two decades, cave diving biologists have discovered hundreds of novel invertebrate species, with remarkable adaptations to lightless, food poor environments nearing anoxia. The potential for continued discovery appears limitless with many thousands of such caves worldwide never having been explored or scientifically investigated. But in order to better understand these environments, it is important to first consider the historical origin and concepts that have led scientists to where we are today in biospelelology, the science of cave biology.

Outlooks on Subterranean Fauna

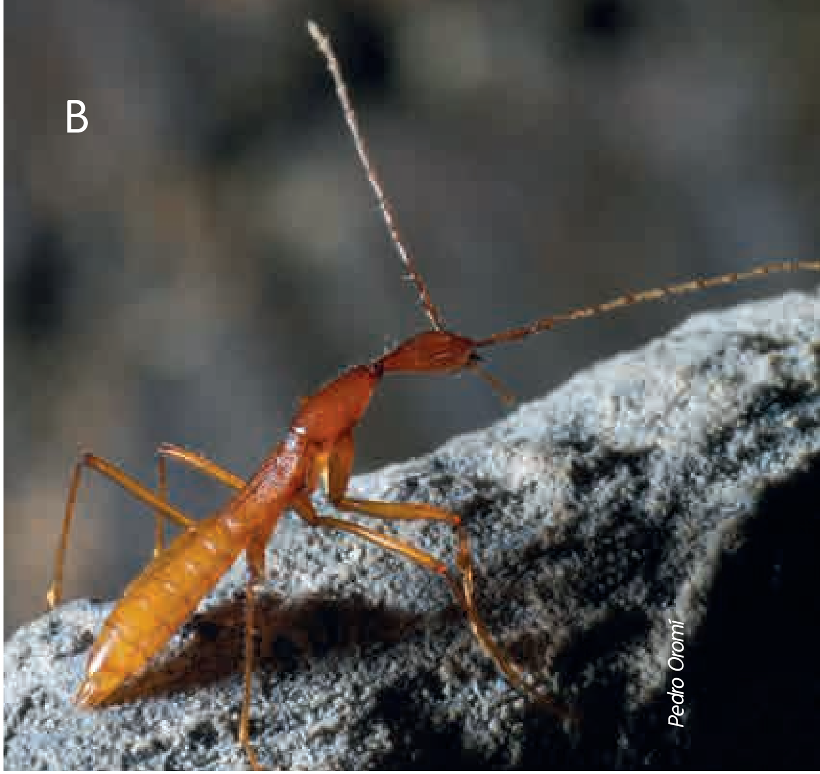
A vast part of the biosphere is found underground, in the subterranean domain, is known as this hypogean environment. Although the term "cave" refers to only a small fraction of the hypogean environment that is physically accessible to humans, we here use it as an acceptable simplification of the whole.

Classification of subterranean animals

All cave-dwelling animals are termed as cavernicoles, a classification scheme first proposed by Austrian entomologist İgnaz Rudolph Schiner in 1854, while observing various arthropods living in caves. Schiner divided cavernicoles into (i) troglobites or "cave life" -obligatory cavernicoles only surviving in caves or similar subterranean habitats and showing a significant or total loss of vision and pigmentation; (ii) troglophiles or "cave lovers"- facultative cavernicoles that can live and complete their life cycle within caves, but can also be found in suitable habitats outside caves; usually typically exhibiting varying levels of eye and pigmentation reduction; (iii) trogloxenes or "cave guests" -animals which occur in caves, but, periodically return to the surface for food, e.g., bats, cave crickets. Later, European biologists reserved the prefix "troglo-" to refer to terrestrial cavernicoles, while "stygo-" (derived from Styx, the Greek name for the river surrounding Hell), as in stygobite, stygophile, and stygoxene, was used for aquatic cave fauna. By extension, all these terms derived from stygo- and troglo- are also applied to animals from any other subterranean habitat different than caves, such as Shallow Subterranean Habitats (SSHs), river beds, etc.



Pedro Oromí



Pedro Oromí

Pedro Oromí

Figure 1. Several troglomorphic troglobite arthropods from the Canary Islands. (**A**) The assassin bug *Collartida anophthalma*, without eyes or pigmentation, and exhibiting a remarkable elongation of appendages. (**B**) The beetle *Domene volcanica*, with a significant reduction of pigmentation and elongation of the body. (**C**) The endemic cockroach *Loboptera troglobia*, without eyes and with long sensory antennae.

Most endemic cave species display a set of common convergent adaptations, including blindness and depigmentation, which were referred to by American biologist Kenneth Christiansen (1962) as troglomorphic/stygomorphic characters (Fig. 1). This shift in emphasis from ecological (troglobite, stygobite) to evolutionary (troglomorph/stygomorph) has broadened biospeleology, i.e., the science of cave biology, far beyond the classical discipline of discovering and describing new species.

The concept of "living fossil"

Romanian zoologist, speleologist, and Antarctic explorer Emil G. Racovitza established biospeleology as a science in 1907. He considered subterranean environments as isolated and extreme, inhabited by a variety of invertebrates and fish that he considered "living fossils", a term originally coined and discussed in Charles Darwin's famous 1859 book, "On the Origin of Species". Living fossils exemplified species with primitive features, showing little evolutionary modifications from their ancestors, with no close living relatives. As morphological investigations expanded, it became apparent that a number of anchialine species exhibited such primitive features retained from their ancestors without modification (Box 1 in Chapter 3). For example, six out of the ten known major groups of copepods are represented in anchialine caves by species that exhibit what were considered ancestral characters, as in the platycopioid copepod *Antrisocopia prehensilis* from anchialine limestone caves in Bermuda. However, more refined studies have often contradicted the idea of "living fossils", as exemplified by the case of the iconic cave exclusive class Remipedia (p. 232, Chapter 3). The first remipede was discovered in the Bahamas in 1979 with additional species subsequently found in anchialine caves in Lanzarote, on opposite sides of the Atlantic Ocean, and from Western Australia. Due to their restricted distribution only in anchialine caves, low population sizes, and presence of several features interpreted as primitive (e.g., segmentation, serial repetition of legs), remipedes were interpreted as living fossils. However, analyses of evolutionary history and detailed morphological investigations, including studies of the brain and nervous system, indicate that Remipedia evolved comparatively late within the arthropods (Boxes 1 and 4, Chapter 3). Although Racovitza's evolutionary concept behind "living fossils" may have deviated as a result of today's modern sciences, it continues to have an influence on cave biologists throughout the world.

Figure 2. Not all troglobites are troglomorphic, e.g., the spider *Meta menardi* exclusive from caves in the Canary Islands presents well developed eyes and dark pigmentation.

The hypogean archetype

The hypogean archetype is a relict concept dating from early investigations of cave biology in efforts to put forth an evolutionary model explaining the presence or absence of observable morphological characters. It is important to note that these early distinctions were based on investigations of terrestrial caves. Research into subterranean aquatic habitats, especially anchialine, occurred much later in the history of biospeleology. Most morphological changes observed are a result of the lack of light in the subterranean environment and thus has been considered a rule for troglomorphic organisms. Nevertheless, there are several exceptions and research has found that troglomorphic features may be highly variable even among representatives of the same species. It is well known that many species inhabit caves and the subterranean environment, but show no degree of troglomorphism in the traditional interpretation of the term (e.g., many cave fish and annelids) (Fig. 2). Consequently, not all troglomorphisms are driven by the lack of light or paucity of food, but may also be in response to other parameters differing between caves and the ancestral aquatic habitats. Therefore, the concept of a hypogean archetype is useful as an initial approximation to understand the evolutionary processes in caves; however, it may underestimate the diversity of ongoing processes and the extent to which they affect new cave colonizers.

For decades, it was widely accepted that troglomorphic features were the result of the preadaptation in which new niches were colonized by organisms that already expressed characteristics favoring the distinctive environmental conditions present in the subterranean realm. However, the two most easily recognizable troglomorphic features, blindness and depigmentation, are novel characteristics in many cases. To further complicate this issue, there is large number of intermediate forms within populations that vary in degrees of eye reduction and depigmentation.

To elucidate the origin of anchialine cave species, studies in developmental biology suggest that stygobites are derived from hypogean or epigean species through morphological plasticity through which species can continuously alter their expre-ssed characters. Such variation in expressed characters is sometimes seen in subterranean animals in the form of paedomorphism (retention of juvenile traits in adults still capable of reproduction) or neoteny (animals with slowed growth), especially among vertebrates. Some of the troglomorphic characters seen throughout stygobiont taxa should therefore be interpreted as a result of natural selection, through which genetic variability is expressed under appropriate conditions. Other times, features are lost due to accumulation of neutral mutations, without any role of natural selection.

Concepts of Anchialine Environments

Anchialine habitats are well known in tropical and subtropical areas of the world with large numbers in the Caribbean and Mediterranean Basins, as well as in certain oceanic islands with volcanic origin (e.g., Canary Islands, Christmas Island, Palau, Hawaii, Galapagos, and Bermuda). These habitats are predominantly concentrated in tropical limestone, but are also present in volcanic rocks, and along continental margins and peninsulas. Anchialine habitats may occur as water-filled pools and depressions (Hawaiian Islands), coastal tectonic faults and fissures ("grietas" in the Galapagos Islands), flooded lava tubes ("jameos" in the Canary Islands), solutionally dissolved limestone conduits ("cenotes" in Yucatan or "casimbas" in Cuba), deep vertical shafts ("blue holes" in the Bahamas), and combinations of each (Fig. 3). These habitats often lead underground and exhibit a halocline where freshwater mixes with intruding seawater (Fig. 4).

Dutch biologist Lipke B. Holthuis coined the term "anchialine" in 1973 based on his discovery of a variety of unusual shrimp inhabiting comparable coastal pools in locations including Hawaii, Micronesia, and the Sinai Peninsula. Derived from the Greek word ‘αγχί-άλός (meaning near the sea), he described these habitats as unique bodies of water that have "*...no surface connection with the sea, containing salt or brackish water that fluctuates with the tides*". As cave diving investigations have expanded in the recent decades, our understanding of anchialine habitats have broadened and the concepts behind the term ‘anchialine’ has thus been revised. In 1984, the definition was modified as follows: "*Anchialine habitats consist of bodies of haline waters, usually with a restricted exposure to open air, always with more or less extensive subterranean connections to the sea, and showing noticeable marine as well as terrestrial influences.*"

In 2012, discussions by a group of leading cave biologists led to a further revision of the term which states that an anchialine habitat is "*a tidally-influenced subterranean estuary located within crevicular and cavernous karst and volcanic terrains that extends inland to the limit of seawater penetration*". This new definition includes the term "subterranean estuary" defined as the underground mixing zone between fresh and saltwater in a coastal aquifer (i.e, underground layer of water-bearing permeable rock). Although anchialine caves had not been previously categorized as estuaries, caves such as inland blue holes and cenotes with their characteristic haloclines are clearly areas where underground freshwater meets intruding saltwater (Fig. 5). While fusing the concept of a subterranean estuary into the definition of anchialine holds true for the majority of anchialine localities, not all caves with anchialine fauna exhibit the hydrological characteristics of esturaries. Submarine lava tubes

Figure 3. The Bahamian blue holes are formed by the collapse of the roof of dissolutional caves. They are characteristically rounded holes, usually leading to extense subterranean systems. Although they were formed above the sea level, these entrances can be found both in (**A**) land or (**B**) marine coastal areas.

B

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Figure 4. A diver swims at the level of the halocline in Taj-Mahaa cenote, near Tulum, in the Yucatán Peninsula (México). The mixing between freshwater and saltwater can be observed over the back of the diver, as a blurry cloud due to differences in density.

from Lanzarote, tidal saltwater pools in Hawaii, and sub-seafloor caves in the Bahamas and Belize lack mixing zones and only show minimal interactions with meteoric freshwater.

The aphotic (dark) zones of anchialine ecosystems have been compared to deep sea abyssal plains, sharing absolute darkness, isolation, paucity of nutrients, stable temperatures, and low dissolved oxygen levels. Complete darkness of the cave interior limits photosynthetic production to their entrances. Without photosynthetic production, most nutrients in anchialine environments were originally thought to be derived from surface environments which entered by being carried in via water or animals. However, recent studies have shown that chemosynthetic bacteria can produce organic matter from inorganic compounds in several anchialine ecosystems (Fig. 6). These same bacterial mediated processes are known to support entire subterranean ecosystems in some regions of the world.

The water column in anchialine cave systems is highly complex, exhibiting distinct stratification within physico-chemical parameters (Fig. 7). Marked similarities among these various parameters are present in anchialine caves from the Yucatan Peninsula of Mexico, many Caribbean İslands, Bermuda, and Western Australia (Figs. 8 and 9). A freshwater lens is formed when freshwater from precipitation overlays denser saltwater from the sea, forming distinct boundaries or haloclines. This freshwater layer becomes thicker with increasing distance from the coastline, due to recharge by rainfall, reduced tidal disturbances, and retention by the land. Some caves are distinctly different, having hydrogen sulfide (H_2S) layers or temperature and oxygen inversions. Especially at the halocline, physico-chemical parameters change in well defined patterns with microhabitats being identified in vertical intervals as small as one centimeter. Temperature maxima and minima are found at surface pools, entrances, or at depth depending on the season, geographic location, and/or water circulation. Temperature increases are usually associated with the halocline (salinity boundaries) and temperature stabilization normally occurs at depth in the saltwater layer.

İlluminated surface waters of anchialine ecosystems commonly exhibit nearly saturated levels of dissolved oxygen due to constant atmospheric exchange and photosynthetic oxygen production. Dissolved oxygen levels usually show a marked decrease across the halocline as a result of microbial oxidation of organic matter and continue to decline with increasing depth. Occasionally however, dissolved oxygen levels rebound in areas where horizontal water flow from the sea occurs. Dissolved oxygen levels at depth are often less than 1,0 mg/l, and rarely exceed very low or dysoxic (2.0-0.2 mg/L) concentrations, demanding special adaptation in many stygobitic organisms (see below). Low levels of oxygen occurring at depth in anchialine caves may be caused by enhanced microbial oxidation at the chemocline (halocline) or by long residence time of the water in the subterranean environment removed from photosynthetic oxygen production.

Tamara Thomsen

Figure 5. A diver collects small animals under the halocline of a Bahamian blue hole. The presence of microscopic algae in the freshwater is seen by the green color of the water layers above the diver. The algae are absent in the black saltwater where the diver swims.

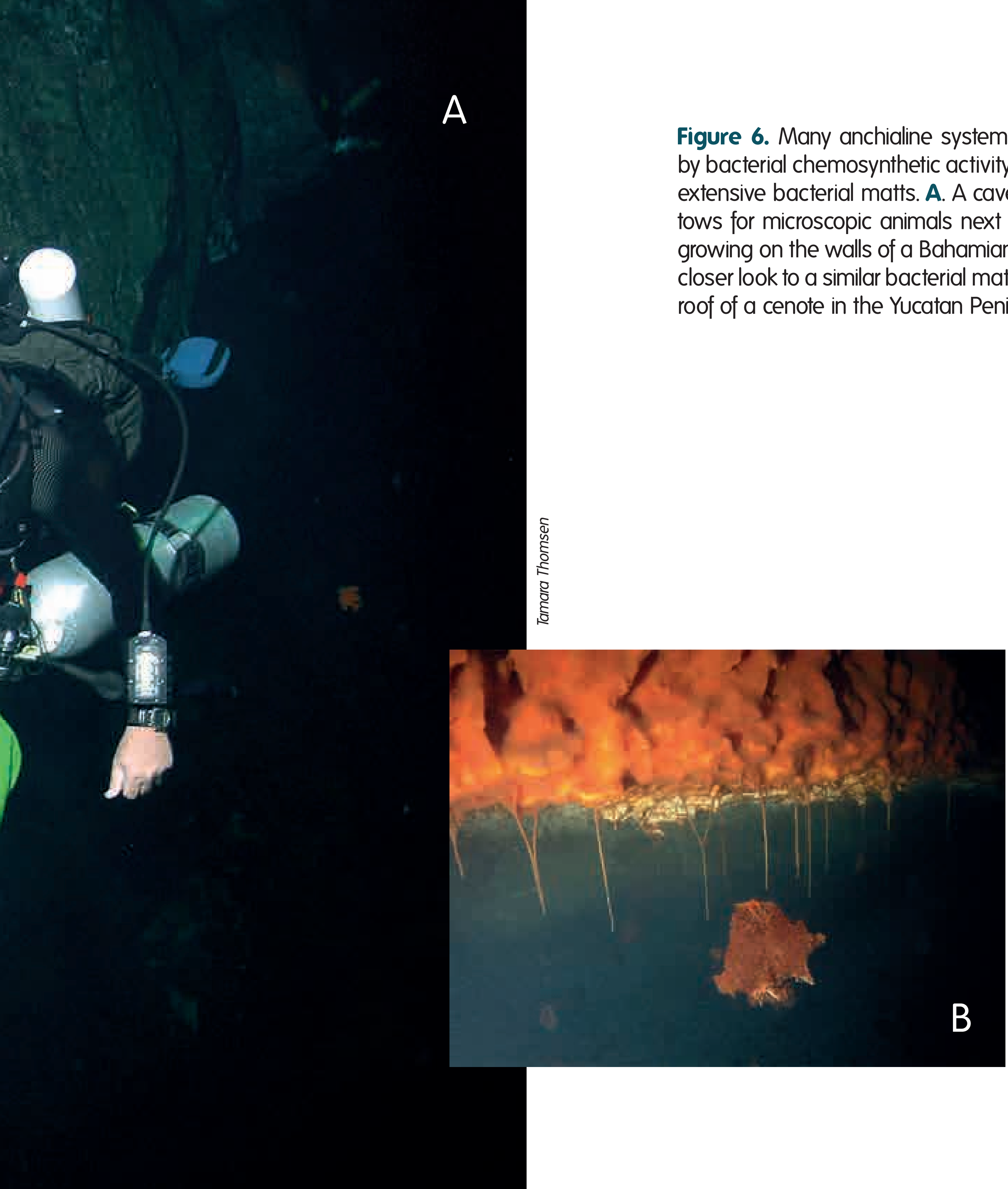

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Figure 6. Many anchialine systems are sustained by bacterial chemosynthetic activity, and may form extensive bacterial matts. **A**. A cave diver plankton tows for microscopic animals next to the bacterial growing on the walls of a Bahamian blue hole. **B.** A closer look to a similar bacterial mat growing on the roof of a cenote in the Yucatan Peninsula, Mexico.

Tamara Thomsen

Figure 7. The water column of many cave systems is strongly stratified, as shown in the picture. The diver swims in the freshwater layer, green in color due to the presence of microscopic algae; above the black saltwater layers. Both water masses are separated by the halocline, with a characteristic whitish color due to the presence of hydrogen sulfide.

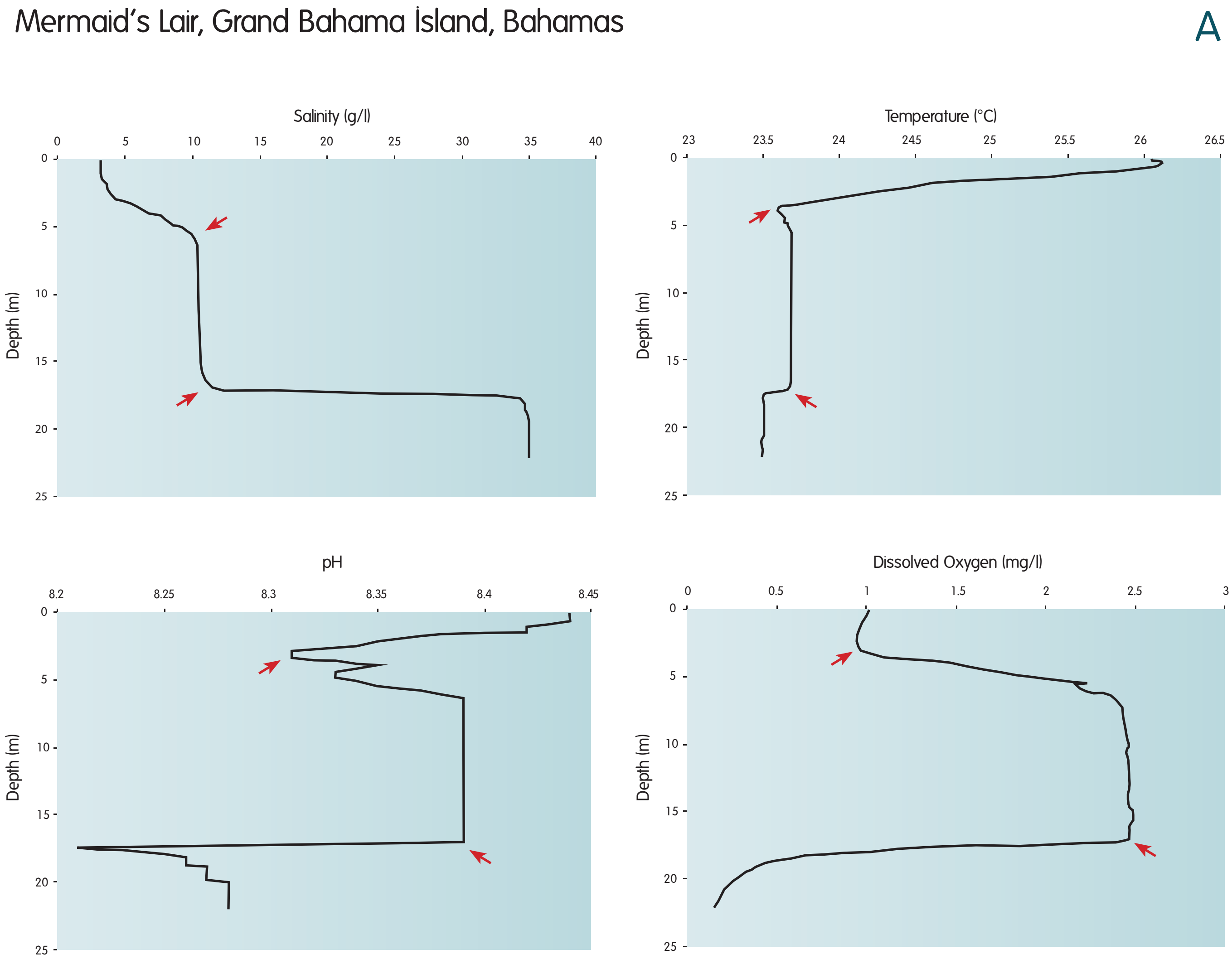
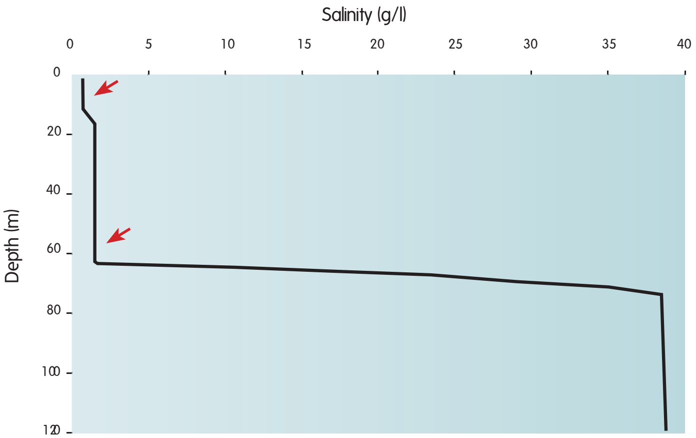
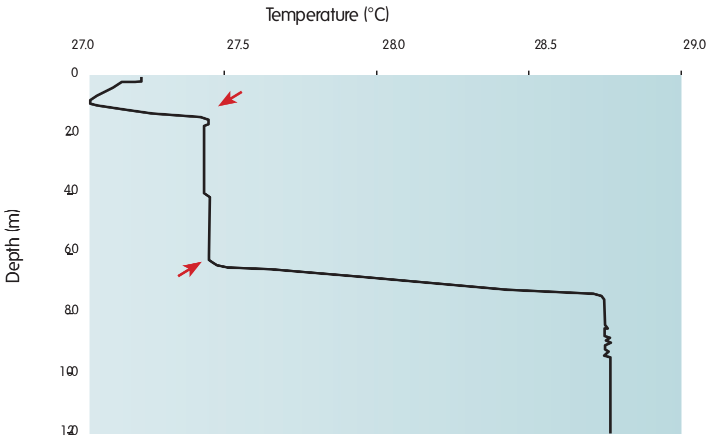


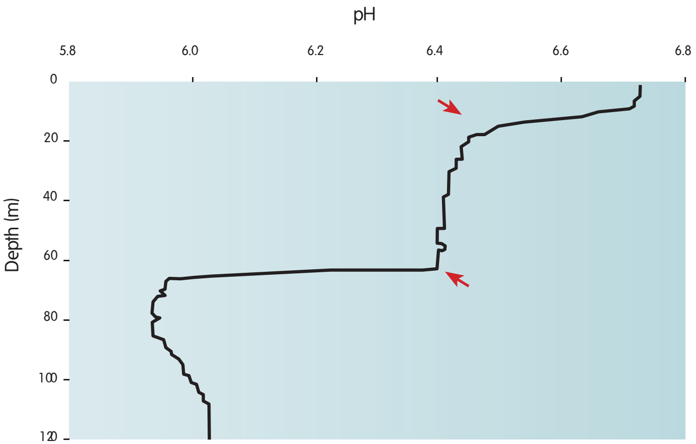
Figure 8. Water profiles from two different anchialine caves (**A**) the Bahamas and (**B**) Yucatan Peninsula; both very similar despite the relatively large geographical distances between localities. The vertical axis shows the depth, whereas the horizontal axis reflects the values for the different measured parameters. The halocline (arrows) is at the depth where all the parameters exhibit a sharp change in their values.

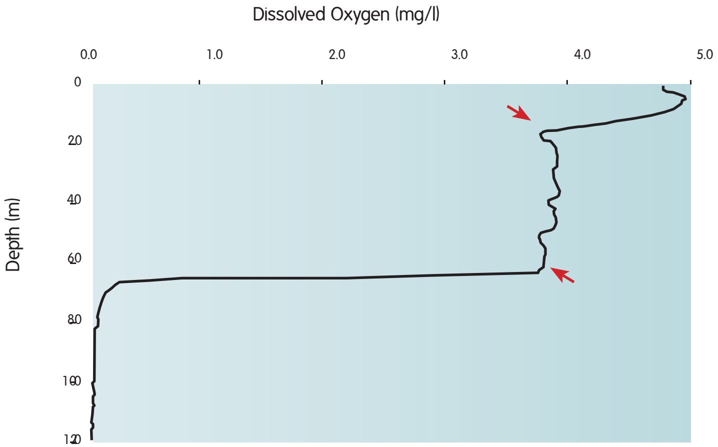
Cenote Sabac Ha, Yucatan, Mexico

B


Salinity (g/l)


Temperature (°C)


pH


Dissolved Oxygen (mg/l)

Lanzarote has limited annual precipitation (12.5-15 cm/yr) and freshwater is heavily pumped from aquifers, causing saltwater to intrude into the depleted freshwater aquifer of the island. Not all of the freshwater aquifers have been drained in Lanzarote and can still be found localized throughout the island (e.g., Famara Massif and Haría Valley) (Fig. 10). A subterranean aquifer is however absent from the coast at La Corona badlands. Due to the lack of fresh groundwater in the area, haloclines are therefore absent in La Corona lava tube. However, La Corona lava tube still qualifies as an anchialine cave since the water column shows at least a minimal degree of stratification, tidal exchange with the ocean, and typical anchialine fauna including remipedes, thermosbaenaceans, and thaumatocyprid ostracods (see Chapter 3).

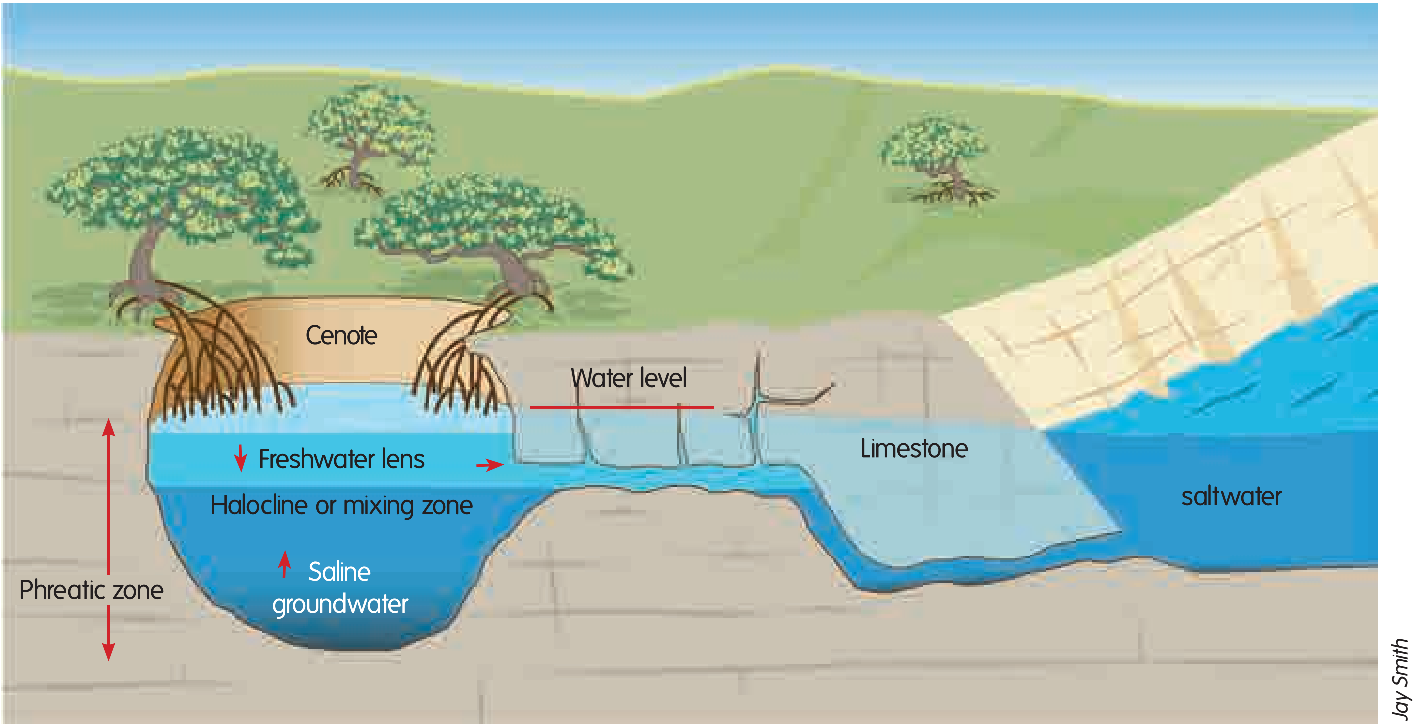
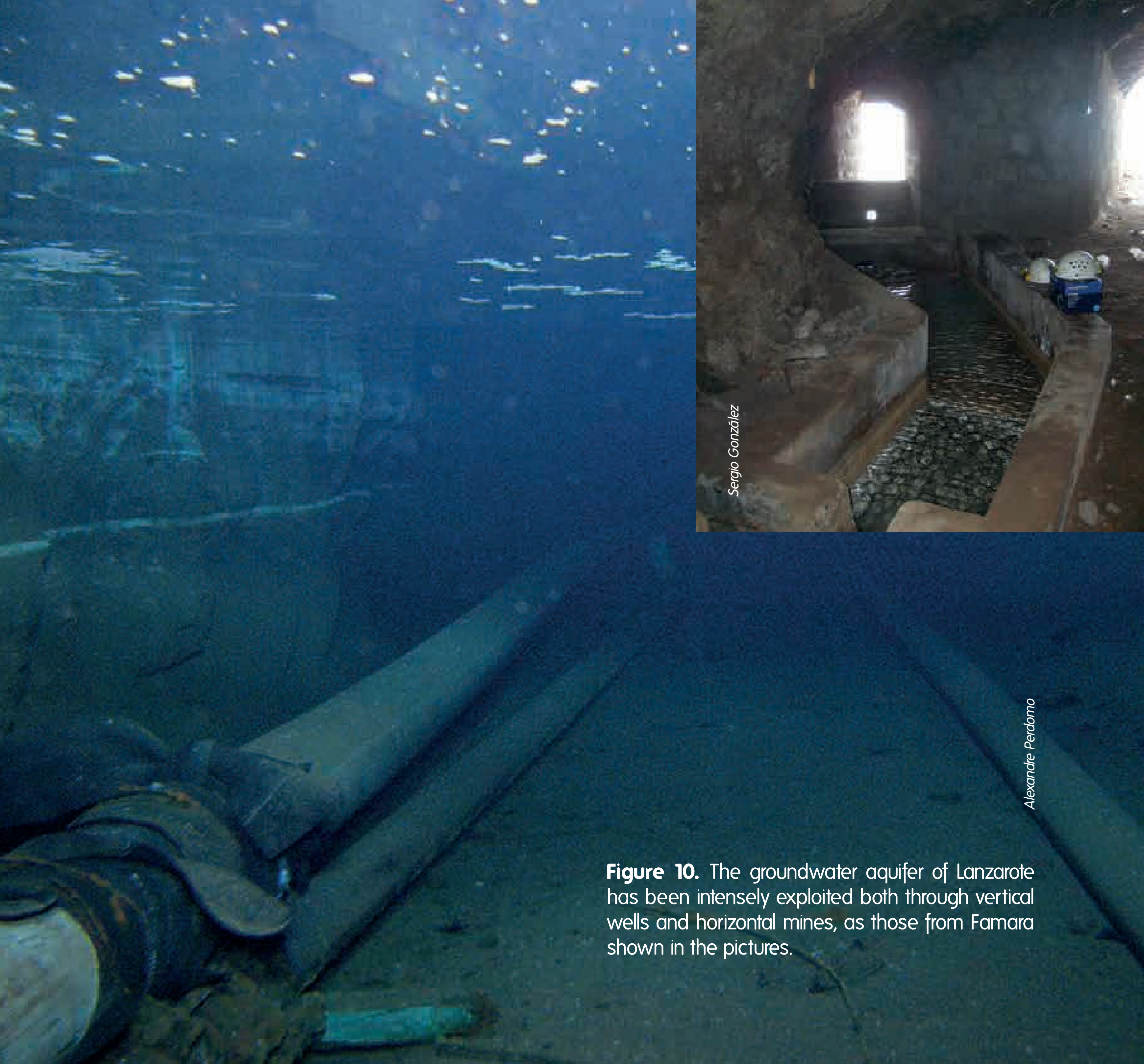


Figure 9. Diagram showing the area of freshwater and saltwater interaction (see text for explanation).



Sergio González

Alexandre Perdomo

Figure 10. The groundwater aquifer of Lanzarote has been intensely exploited both through vertical wells and horizontal mines, as those from Famara shown in the pictures.

Surviving in Anchialine Caves

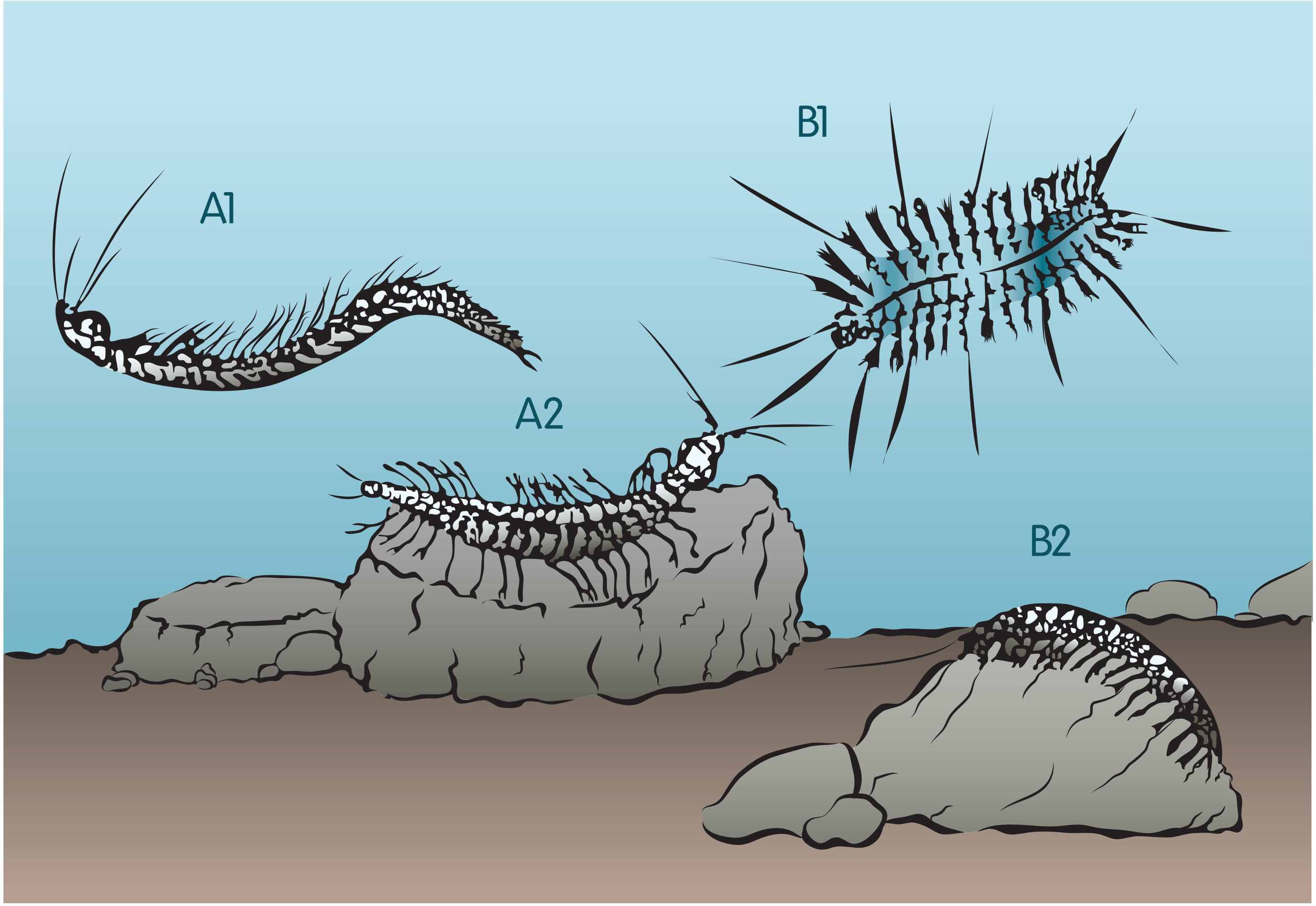
Anchialine stygobites as extremophile organisms

Due to the lack of light and low levels of dissolved oxygen and food, anchialine caves are often defined as extreme environments, and therefore, many stygobites are referred to as extremophiles. Extremophiles are organisms which thrive in an extreme environment whereby survival is difficult, forcing them to adopt special adaptations, sometimes employing drastic changes in behavior, morphology, and metabolism in order to persist and reproduce. Obviously, this term is coined from an anthropomorphic perspective which considers varying degrees of severity in physical (such as temperature, radiation, or pressure) or geochemical parameters (such as desiccation, salinity, pH, dissolved oxygen).

For organisms to survive in similar extreme environments, they must possess common sets of adaptations. These adaptations are represented in stygobites by distinct suites of changes, mostly directed to optimize their effectiveness in obtaining food and successful reproduction. Such adaptations vary in different types of organisms, but they can be categorized into three groups depending on whether they affect behavior, morphology (implying both gain and loss of features), or metabolic traits, and include reduction in eyes, loss of pigmentation, elongation of appendages, a thinner cuticle (mostly seen in terrestrial troglobites), reduced metabolism, fewer but larger eggs, increased lifespan, and a tendency towards k-strategies (reduced offspring but increased parental investment).

Behavioral adaptations

Changes in an organism's behavior are probably the first solution that many species undertake in order to survive in the anchialine environment. Behavior is versatile and can change without being associated to genetic changes (Fig. 11). Over many generations, evolutionary modifications shape the morphology and metabolic characters of cave-dwelling species. In La Corona lava tube, as in many other caves, trophic resources are found in the water column in the form of either particulate organic carbon (entering through percolation or water flow) or bacteria (including those living on rock surfaces or within sediments). Since the ability to access these areas is crucial

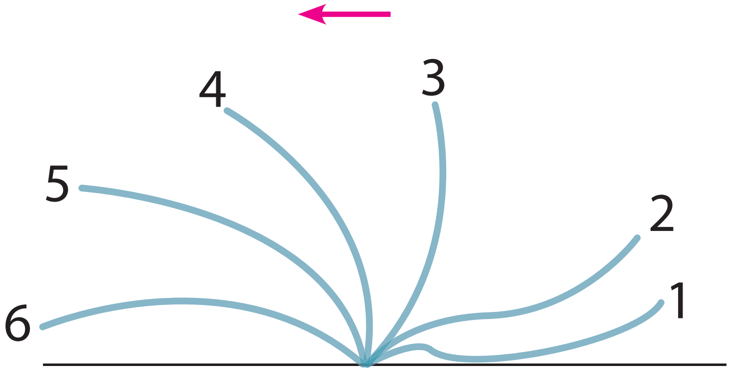


Redrawn from Parzefall, 1978

Figure 11. The investigations on the behavior of stygobitic species began in the middle of the 20th century, with interesting contributions based on the anchialine fauna from Lanzarote. In the image, made by Jakob Parzefall (1978), showing the different swimming (**1**) and resting (**2**) behavioral patterns by *Morlockia ondinae* and *M. atlantida* (**A**) and the annelid *Gesiella jameensis* (**B**) from Túnel de la Atlántida.

A

Forward (power) stroke



B

Backward (recovery) stroke

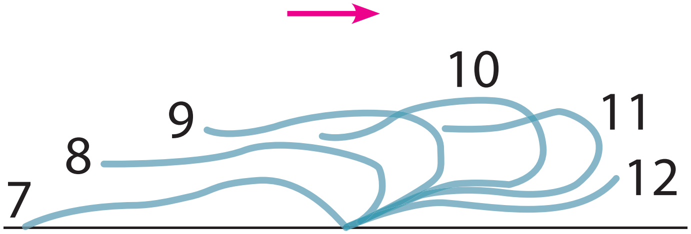
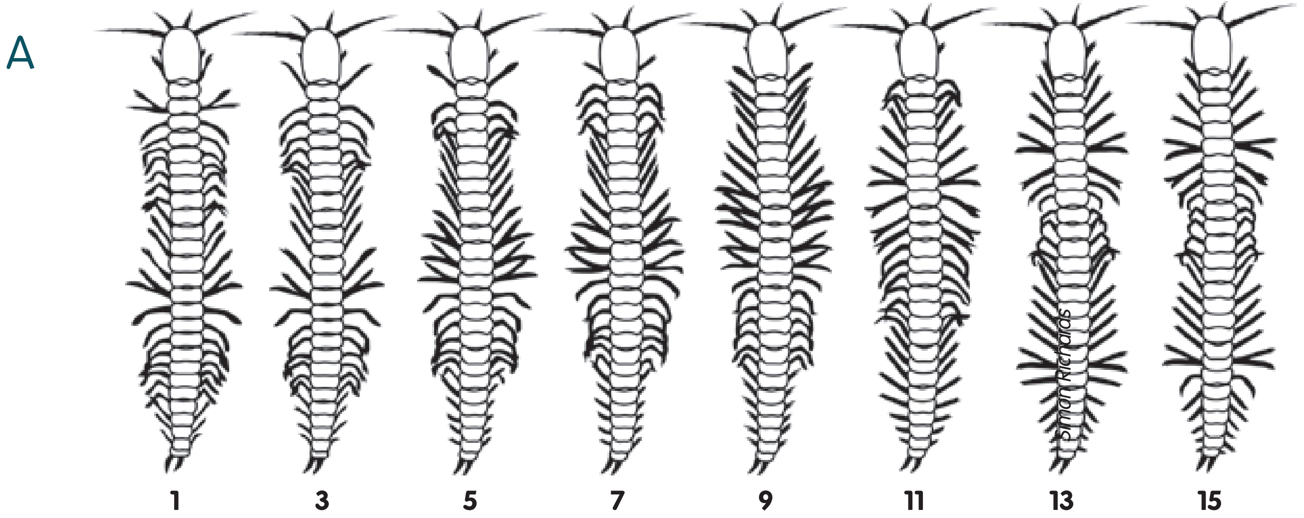


Figure 12. The coordinated beating of the cilia arranged as bands in different zones of the body provides enough buoyancy to small annelids, such as nerillids or protodrilids, to keep the position in the water column. The beating of an individual cilia is assymetrical and consists of a (**A**) power stroke and a (**B**) recovery stroke.



Simon Richards

Kohlhage & Yager, 1994

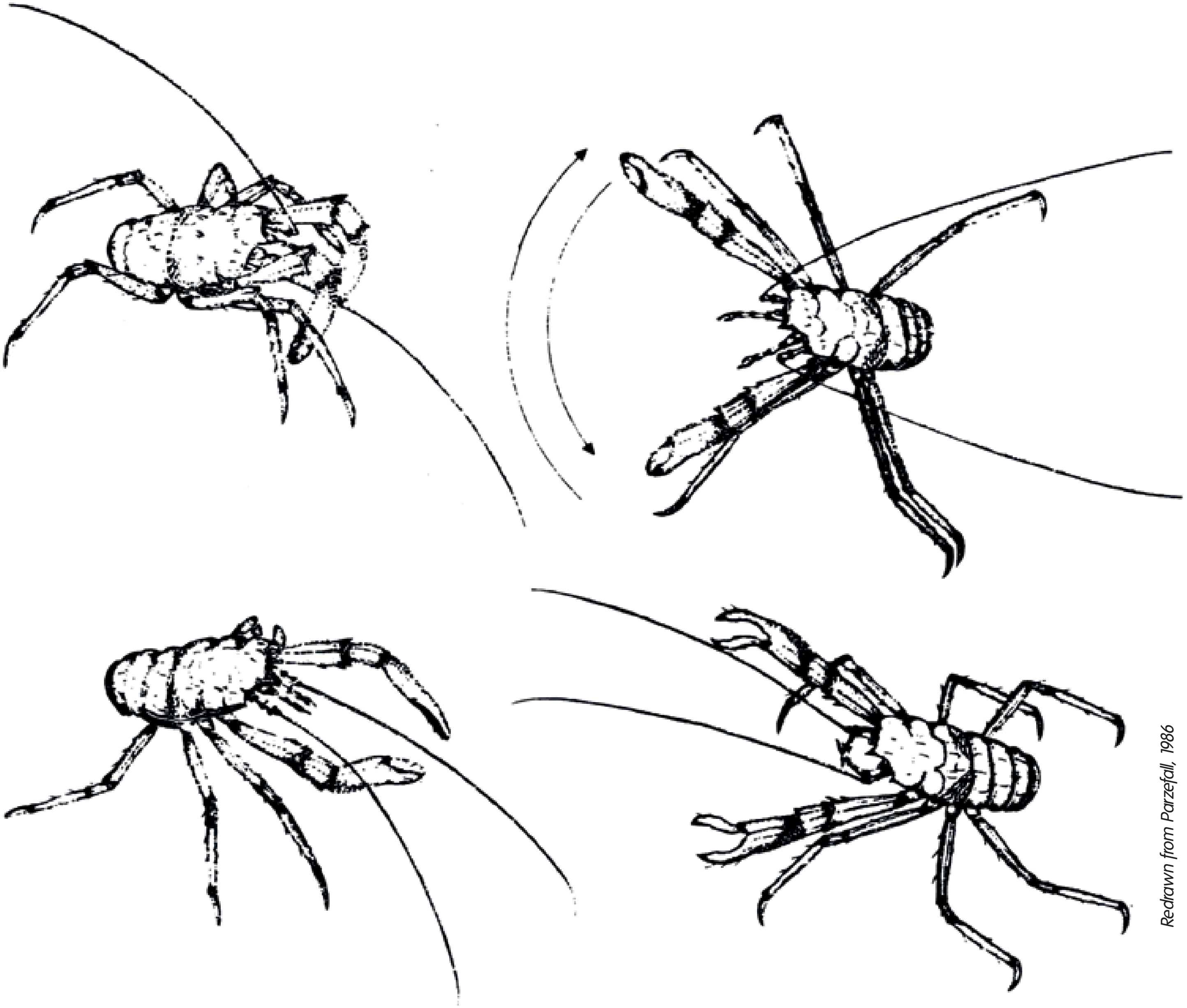
Figure 13. The metacronal beating of appendages serially repeated on the trunk of certain crustaceans (e.g., remipedes) or annelids (e.g., polynoids) is a common strategy for swimming with low energy consumption. This strategy has been studied in detail in (**A**) remipedes, such as (**B**) *Speleonectes lucayensis*.

Simon Richards

to many stygobites, many of them are able to effortlessly drift or swim throughout the water column. This drifting strategy can be observed across organisms ranging from small meiofauna (microscopic animals smaller than 1 mm) to larger cave crustaceans, and has been shown to be an effective behavior in reducing energy use. In small animals, this behavior is achieved by bands of beating cilia arranged in rows (Fig. 12), concentrated in various parts of the body, as seen in some small cave annelids belonging to the families Nerillidae and Protodrilidae (see below and Chapter 3). As the animals' bodies become larger or more robust, ciliary beating becomes inefficient in providing and maintaining both a vertical and horizontal position in the water column. Larger animals, such as shrimp and fish, can overcome this by accumulating lipids, thereby increasing buoyancy. At the same time, the storage of lipids provides a valuable source of energy when food is scarce. This strategy is sometimes combined or substituted in some amphipods and annelids by the development of long or paddle-like body appendages that increases their overall body surface.

Drifting is often combined with other locomotive strategies to minimize energy utilization. Generally, most anchialine species take advantage of the minimal or reduced water currents in anchialine systems (which in La Corona is limited to tidal currents that are nearly imperceptible unless within one of the restrictions) by swimming slowly with intermediate breaks, taking advantage of their forward progression while resting. Many cavefish often swim by using a glide-and-rest technique that conserves energy in their search for food. Annelids and some arthropods, such as remipedes, (p. 232, Chapter 3) swim by metachronal beating of their parapodia or legs (Fig. 13). In remipedes, the power stroke is produced by serially arranged appendages that are extended outward to maximize pull. This initial stroke naturally produces drag and small eddies alongside the body. To overcome these water perturbations, the recovery stroke is initiated with folded legs, avoiding eddies produced by the first stroke.

Dense populations of organisms are typically rare in anchialine systems due to limited food availability. However, a few cases are known from caves or particular sections of a cave that contains increased organic inputs. One particular case that has been studied in great detail is the stygobitic squat lobster *Munidopsis polymorpha* which exhibits its greatest abundance in Los Jameos del Agua (Fig. 14) (p. 248, Chapter 4). In order to cope with the increased densities, each animal defends a small territory defined by the length of the second antenna so every individual has sufficient access to resources.



Redrawn from Parzefall, 1986

Figure 14. *Munidopsis polymorpha* is a territorial species that defends a small territory determined by the length of its second antennae. When one invades another's territory, it is often violently attacked by its owner.

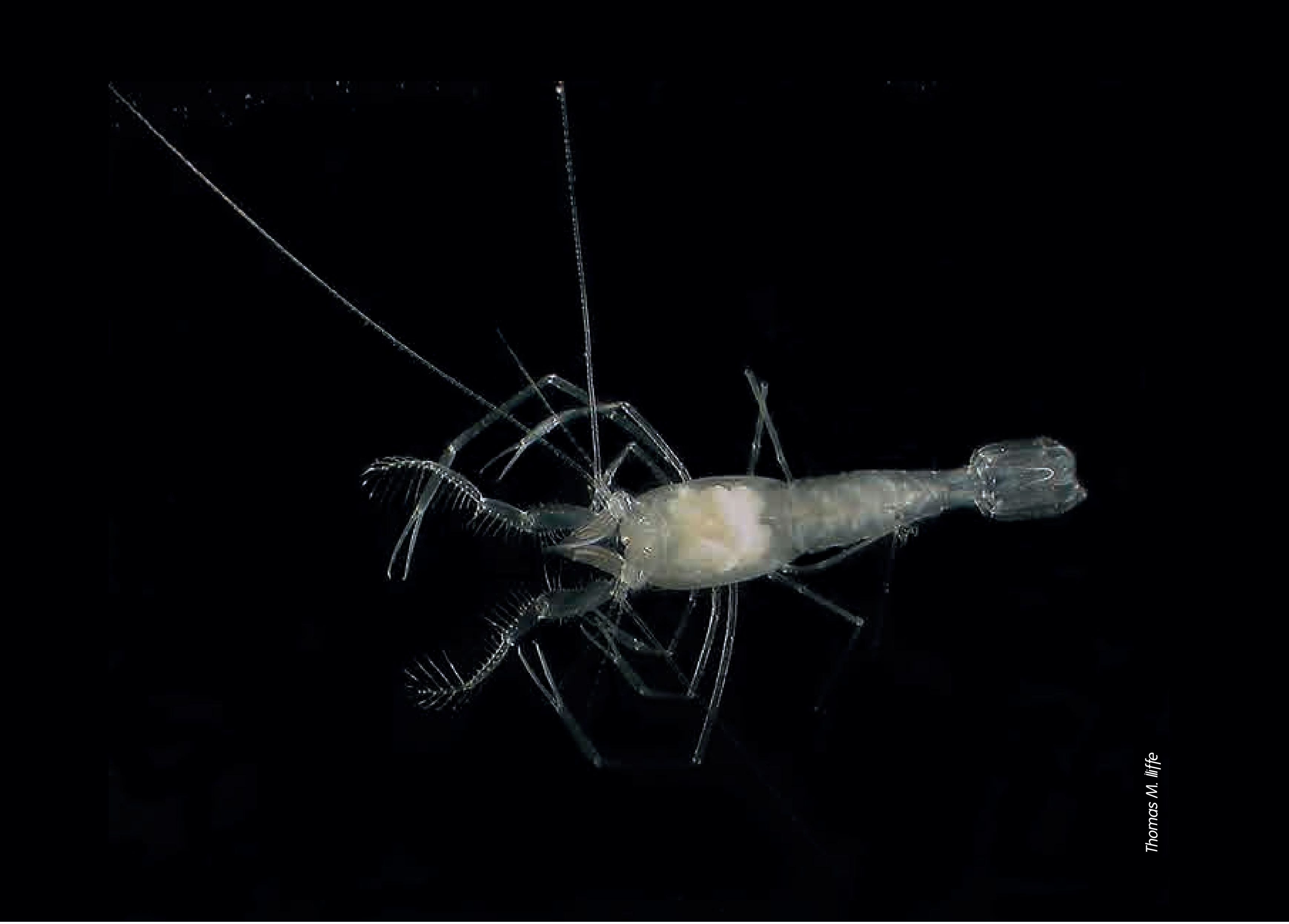

Thomas M. Iliffe

Figure 15. The shrimp *Macromaxillocaris bahamensis* is exclusive from few "blue holes" in the Bahamas. It represents a classic example of stygomorphic adaptations, lacking pigmentation and eyes, as well as significantly long appendages.

Morphological adaptations

Morphological adaptations to subterranean habitats vary widely among cave species. These adaptations are often categorized into constructive and regressive adaptations depending on whether they enhance or reduce a certain organ system compared to its epigean counterparts living outside of caves. It is important to recognize that the use of the word "regressive" in this context only indicates the reduction or loss of a structure that was present in the ancestor. This does not imply any considerations as to whether this loss was due to selection of a more beneficial feature resulting in an advance in evolutionary terms, or conversely arises from mutations that neither help nor harm the organism. Most of the described constructive adaptations involve the development of increased sensory structures that favor foraging or reproductive strategies. In crustaceans and certain annelids, development of sensory structures is often related to enlargement of certain appendages such as antennae or cirri, that possess increased numbers of sensory mechano or chemoreceptors (Fig. 15). Other types of constructive adaptations involve the development of specialized feeding structures, which have been recorded in several annelids including species of Protodrilidae (p. 155), Scalibregmatidae (p. 148), and Nerillidae (p. 158).

Regressive features involve the loss of structures that no longer have a biological function in the subterranean realm. Eyes and pigmentation are the two most commonly lost structures. It has been proposed that their loss prevents metabolic energy from being spent on structures which have no functionality in lightless subterranean environments. In a given habitat, eyes and pigmentation may show varying degrees of reduction among species, while for other species, little to no reduction of such characters occurs. Sometimes, the degree of reduction can also vary across populations of the same species depending on the specific environmental conditions, for example, individuals inhabiting illuminated versus lightless sections of the same cave. This is illustrated by the endemic mysid *Heteromysoides cotti* which is widespread throughout the anchialine environments of Lanzarote, occurring in permanently illuminated areas such as Los Jameos del Agua and anchialine surface pools, or in complete darkness hundreds of meters into the lava tube. Although these different populations have not been investigated in detail, *Heteromysoides cotti* exhibits polymorphisms with regards to pigmentation and compound eyes. This is most likely a response to the environmental parameters, with blind and unpigmented morphs living deep inside the lava tube, while pigmented and oculated individuals being found in Los Jameos del Agua and the anchialine pools present along the coastline of Lanzarote.

Metabolic adaptations

Resources in anchialine environments are often scarce or patchy, requiring organisms to cope with long periods of limited food and depleted dissolved oxygen. Hypogean organisms, especially those inhabiting anchialine caves, deal with these periods through shifts and modifications in their metabolism. These metabolic shifts may be observed as retention and accumulation of lipids, or by reducing ATP (adenosine triphosphate: a source of chemical energy within cells that is used for metabolism) expenditures on a molecular level through changes in motility, prey capture, and duration of digestion.

When comparing crustaceans living in epigean habitats versus those inhabiting hypogean environments (i.e., anchialine caves), hypogean crustaceans tend to have a higher percentage of lipids than their epigean relatives. Lipids serve as energy reserves allowing the organism to survive during periods when food is not available. Additionally, the stored lipids are less dense than water and aid in maintaining a vertical position within the water column, reducing energy used. In order to decrease their energy expenditure, hypogean organisms avoid metabolic pathways which demand molecular oxygen, which is scarce within many anchialine environments. Hypogean organisms therefore commonly produce their ATP through less efficient anaerobic pathways which do not require oxygen, in place of the more efficient aerobic metabolic pathways. These shifts to anaerobic pathways are often correlated with a reduction of overall body size and mass.

In La Corona lava tube, dissolved oxygen levels are relatively high and have not been measured below oxic conditions (>2.0 mg/L) as is commonly present in other anchialine environments (e.g., the Bahamas). Due to the greater availabilty of dissolved oxygen in La Corona, metabolic rates in the fauna are significantly higher when compared to those species found from other anchialine caves. Most anchialine environments show a direct correlation between depth and dissolved oxygen, decreasing as depth increases to nearly anoxic conditions (<2.0 mg/L). Since La Corona lava tube lacks significant haloclines while tidal circulation from the sea is substantial, dissolved oxygen levels tend to be relatively high and unchanging as depth increases. Stygobites from La Corona lava tube were compared to congeneric cave-dwelling species from low oxygen caves in the Bahamas to test the effects of oxygen availability on the morphology and physiology. While organisms from these two localities did not always have evolutionary ties to low oxygen environments, they are all capable of surviving periodic decreases. Since the selective pressures of oxygen and food reduction have been removed, oxygen consumption in anchialine fauna from La Corona was significantly higher as compared to similar genera from the Bahamas. In addition to the higher oxygen demand, the size and mass of stygobitic fauna from La Corona lava tube showed an overall increase in comparison to species from the same genus inhabiting Bahamian caves, thus highlighting the observation that low oxygen environments tend to harbor organisms with reduced oxygen demand, resulting in a smaller size. These findings suggest that the reduction of metabolic rates commonly observed in anchialine and other extreme environments might have evolved as a response to limited oxygen consumption rather than to low food availability.

-BOX 1- Anchialine metabolism: Case studies

Although few opportunities exist to observe active cave colonization events, the barbourid shrimp, *Barbouria cubensis*, found in anchialine environments in the Bahamas, Cuba, Yucatan, and Jamaica, provides an example of a recent cave colonizer capable of living in both fully illuminated anchialine pools as well as in aphotic dysoxic (approaching anoxia) anchialine cave systems. These shrimp show varying degrees of eye and pigment reduction between epigean and hypogean populations. *Barbouria cubensis* has been considered a model cave organism to determine if physiological preadaptations are needed for animals to successfully colonize the subterranean environment. It was observed that *B. cubensis* demonstrates both morphological and physiological adaptations to the cave environment, with those shrimp residing in full aphotic environments being poised for further metabolic adaptation. While metabolic enzymes were similar between the epigean and stygobitic populations, only stygobitic populations used anaerobic pathways to acquire energy, relying heavily on glycolysis that produces only 2 ATP per molecule of glucose, instead of more efficient aerobic pathways yielding up to 36 ATP per glucose. These results indicate that some species can secondarily evolve metabolic adaptations in order to successfully colonize subterranean habitats that are depleted in nutrients and dissolved oxygen. These recent findings are contradictory to earlier investigations of metabolic physiology in the Mexican blind cave fish *Astyanax fasciatus*, which showed little to no difference between epigean and hypogean populations, thus suggesting preadaptation was not needed for successful cave colonizaton in *Astyanax*. However, these studies of *Astyanax*, and several cave amphipods, did not investigate nutrient availability in the cave system or water parameters such as dissolved oxygen and temperature, both which affect metabolic rates. While these latter results seem to conflict with more recent studies of *Barbouria*, they do not represent organisms which inhabit anchialine environments, and are instead used to illustrate and identify the physiological variation and metabolic strategies employed by various groups of subterranean fauna.

Anchialine Fauna of Lanzarote

CHAPTER

3

Historical Introduction

Since their discovery at the end of the 19th century, the anchialine ecosystems in Lanzarote have stimulated the interest of many scientists who, during the last 125 years, have focused on understanding interactions among organisms and their environment in this unique ecosystem, as well as describing its distinctive fauna (Fig. 1).

Roughly speaking, it is possible to distinguish three periods in the study of La Corona lava tube fauna. The first period (1892-1940) corresponded to single visits by European researchers who investigated Jameos del Agua, collecting and describing the most common species occurring in the lake. Karl Koelbel, a zoologist from the Natural History Museum of Vienna (Austria), first described *Munidopsis polymorpha* in 1892 (previously collected by Oskar Simony in 1888) as part of his work on the crustaceans in the Canary Islands. In his early work, he was already surprised by the adaptations of this squat lobster to the darkness of the cave and its similarity with deep sea forms. Concurrently, zoologist Jürgen Harms from the University of Marburg (Germany) worked on the anatomy of the reduced eyes of *Munidopsis*. He was also the first to record the presence of the echiuran annelid *Bonellia viridis* and the comb jelly *Cestum veneris*, commonly known as "Venus girdle", in the lake. The description of *Munidopsis polymorpha* was completed in 1932 by zoologist William Calman from the University College of Dundee (Scotland), who also described the crustacean mysid *Heteromysoides cotti*, previously collected and brought to him by British explorer and zoologist Hugh Cott. Observations from these previous works were summarized and the ecology of Jameos del Agua described in a short monograph published in 1936 by zoologists Louis Fage and Théodore Monod from the Muséum National d'Histoire Naturelle de Paris. They also recorded the presence of the mollusc *Monodonta turbinata* (later renamed as *Phorcus atratus*) and the amphipod *Parhyale fasciger*, which was later redescribed by Dutch biologist Jan Stock as *P. multispinosa*.

After a hiatus of nearly thirty years, a very fruitful second period of discoveries began in the late 1960s with numerous contributions by zoologists Horst Wilkens and Jakob Parzefall from the University of Hamburg (Germany). Their investigations focused on the biology and behavior of several species from the lava tube, paying special attention to *Munidopsis polymorpha. As a result of intensive sampling, they published studies on the ecology of Los Jameos del Agua.* This sampling effort led to the discovery of the endemic stygobitic isopod *Curassanthura canariensis*, ostracod *Humphreysella wilkensi*, harpacticoid *Neoechinophora karaytugi*, and annelid *Gesiella jameensis*. Wilkens and Parzefall also systematically sampled wells and anchialine pools along the coast of Lanzarote, where they found some of the same species as in Los Jameos del Agua. At the same time, Jan Stock, and his team from the Zoological Museum of Amsterdam, conducted several sampling trips to Lanzarote where they concentrated their efforts on subterranean crustaceans. They mostly sampled in wells and anchialine pools discovering the presence of endemic species including the copepods *Stephos canariensis* and *Boxshallia bulbantennulata*, as well as the amphipods *Parhyale multispinosa* and *Bogidiella uniramosa.* Since these last amphipods also occur in Jameos del Agua, Wilkens, Parzefall, and Stock provided the first evidence for connectivity among the island's anchialine habitats, thereby laying the foundation for later theories of dispersal between distant caves through the crevicular habitat.

However, the most impressive discoveries came with a third period, started by the advent of cave diving explorations of Túnel de la Atlántida. The most remarkable discovery was the remipede *Morlockia ondinae* in 1983 by an international team of cave divers led by bioespeleologist Tom İliffe (then at the Bermuda Biological Station) and including Sheck Exley, Clark Pitcairn, Ken Fulghum, Rob Power, Mary Van Soeren, and Dennis Williams. This remipede was described in 1984 by zoologist Antonio García-Valdecasas from the Museo Nacional de Ciencias Naturales in Madrid. This and subsequent diving expeditions by İliffe yielded additional discoveries of a variety of endemic stygobitic crustaceans including the thermosbaenacean *Halosbaena fortunata*, ostracods *Humphreysella phalanx* and *Eupolycope pnyx*, misophiorid copepods *Expansophria dimorpha*, *Palpophria aestheta*, and *Dimisophria cavernicola*, and epacteriscid calanoid *Enantronia canariensis*.

During the late 1990s, and in parallel with these cave diving expeditions, the first studies of the interstitial communities living in the cinder were conducted by Jorge Núñez and his team from Universidad de La Laguna, Tenerife. Focusing mainly on the interstitial communities at Jameos del Agua, they discovered the interstitial annelid stygobites *Fauveliopsis jameoaquensis, Leptonerilla diatomeophaga, Macrochaeta* n. sp, and *Mesonerilla* n. sp.

The most recent publications on the fauna of the cave appeared in a special issue of the journal Marine Biodiversity containing the results from the 2008 Atlantida Cave Diving Expedition. This expedition, lead by Prof. Tom İliffe (Texas A&M) included the scientist Stefan Koeneman (Univ. Hannover), Horst Wilkens and Ulrike Strecker (Univ. Hamburg), Alejandro Martínez (Univ. La Laguna) and Rene Bishop (Pennsylvania State University), as well as the cave divers Terence Tyssal, Jill Heinerth and Jim Rossi. During this international investigation, sampling focused on the water column of the cave, as well as sediments from Montaña de Arena. This led to the discovery of a second species of remipede, *Morlockia atlantida*, and new annelids *Meganerilla cesari* and *Sphaerosyllis iliffei.* In the same issue, a review of the fauna from La Corona lava tube recorded 77 species, 32 of them known exclusively from Lanzarote anchialine ecosystems. The majority of these species were crustaceans (31 species), followed by 25 species of annelids. Although the numbers of crustaceans and annelids were nearly equivalent, the degree of endemism was very different. Whereas 70% (22 species) of the crustaceans were endemic from the cave, only 40% (10 species) of the annelids were unequivocally endemic. Molluscs were the third group in terms of species richness, although all the 13 recorded species were of open water marine origin. Additionally, there were two nematodes, two cnidarians, and one species each of Priapula, Ctenophora and Echinodermata were recorded for the cave at that time.

After these results were published, other expeditions have subsequently investigated the lava tube; all organized by the University of Copenhagen. Amongst them was the First Workshop on Marine and Anchialine Meiofauna in Lanzarote in 2012. This expedition, organized by Katrine Worsaae and Alejandro Martínez, included the biologists Maikon Di Domenico (Univ. Campinas, Brazil), Tom Artois and Toon Janssen (Univ. Hasselt, Belgium), Marco Curini-Galletti (Univ. Sassari, Italy), Antonio Todaro (Univ. Modena, Italy), Diego Fontanetto (Inst. Ecosystem Study, Italy), Jon Norenburg and Francesca Leasi (Smithsonian Inst., USA), Kirsten Kvinderbjerg and Asrin Partavian (Univ. Copenhagen), and divers Enrique Domínguez, Carola de Jorge, Ralf Schoernermark, Luis Cañadas, Juan Valenciano, and Antonio Martín (all from the Canary Islands). During this expedition, many marine and cave environments in Lanzarote were surveyed, yielding more than 500 new records for the fauna of the Canary Islands. These remarkable results, continue to highlight the huge diversity present in marine and anchialine ecosystems of Lanzarote, which is still far from being comprehensively investigated.

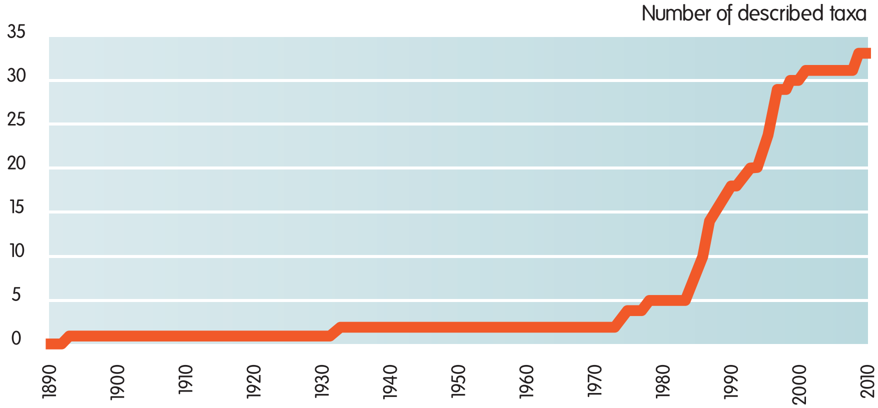


Figure 1. Number of endemic species described in La Corona lava tube since the description of *Munidopsis polymorpha*. The sudden increase of discoveries in the last 30 years corresponds to the beginning of cave diving explorations in the cave.

-BOX 1- Systematics: How do we classify living organisms?

Over the last 300 years, zoologists have described approximately 1.3 billion species of animals grouped in 35-40 phyla, depending upon the classification scheme. This enormous number only represents a small part of the actual animal diversity which is estimated between 10-200 billion species. When biologists name a new species, they follow a nomenclatural system created by the Swedish botanist Carolus Linnaeus (1707-1778) of the University of Uppsala. İn his book Systema Naturae published in 1735, Linnaeus proposed assigning a unique binomial name to each known species. The first part of the name corresponds to the genus (see below), while the second defines the species. Once named, described species are grouped into hierarchical categories. Thus, the Animal Kingdom is subdivided into phyla, a phylum into classes, a class into orders, an order into families, a family into genera, and finally a genus into species. The Linnean System is still used by biologists today since it does not contradict the principle of evolution by natural selection, despite predating Charles Darwin's work by almost 125 years.

The Linnean nomenclatural system deals with the task of naming and grouping species, but it leaves open the problem on how to establish these groups. This task is undertaken by the science of Systematics, which attempts to establish natural groups based on the criteria of common ancestry following cladistics. Cladistics was introduced by the German entomologist Willi Hennig in 1950 as a method to establish natural groups (clades) of organisms. The criterion to define these groups was the presence of shared features from their last common ancestor, but absent in other organisms outside the group. İn order to do that, Cladists define a series of characters corresponding to the morphological (e.g., presence of eyes) or molecular (protein or DNA sequences) features that they observe in the organisms. These characters are further divided into different states according to their variability (e.g., eyes: "absent/present"). The different states are then organized into a matrix (Fig. 2) coded for all species being studied (Species 1 - eyes: "present"), which is then analyzed, yielding a hypothesis for the relationships of the coded species. These relationships are then presented as a branching diagram called "cladogram" or "phylogenetic tree" (Fig. 3). Phylogenetic trees are normally calculated with special software that implements algorithms based on various assumptions, but a complete explanation is out of the scope of this text. For general purposes, it is important to keep in mind that phylogenetic trees are mere hypotheses derived from data sets, and do not represent established facts. Our ideas of classification constantly change by obtaining additional evidence (e.g., discovery of new species, re-evaluation of the morphological characters, obtaining additional molecular data) or the advent and refinement of the available methods (new algorithms, more accurate methods). Accordingly, systematists are continuously gathering new data and producing new methods in order to progressively obtain more reliable phylogenetic trees.

The following terms, coined by Willi Hennig, are used to describe different types of characters according to the information they contain about relationships among organisms (Fig. 4).

- **Plesiomorphy** or **ancestral state** is a character state that that a species or a group of species have retained from their ancestors. When two or more species share a **plesiomorphy**, it is refered to as a symplesiomorphy. However, symplesiomorphies do not mean that the taxa sharing that character state are closely related.

- **Apomorphy** or **derived state** is a novel feature present in a species or a group of species, shared by its most recent common ancestor. İf the apomorphy is present in a single species it is known as **autoapomorphy**, but this does not say anything about the relations of the species to others. However, if an apomorphy is shared by several species (**synapomorphy**), it indicates a potential relationship between the species into a clade, or group of organisms believed to have evolved from a common ancestor.

- **Homoplasy** or **convergence** refers to characters that are shared by two species but were absent from their last common ancestor, evolving independently in each species.

Finally, according to the relationships recovered in a given tree, groups of species will be considered as either (Fig. 5):

- **Monophyletic** (monophyly): a group which includes all descendants from a common ancestor, often referred to as natural groups. Monophyletic groups are defined by the presence of one or more synapomorphies (shared apormophies or derived character states) present in the first member of the clade and inherited by all its descendants, but not by any other species.
- **Paraphyletic** (paraphyly):a group of species characterized by the presence of one or more plesiomorphies or ancestral character states, i.e., characters present in their last common ancestor but not in all its descendants. Paraphyletic groups can also be seen as groups of species that do not include all of the clades from an other monophyletic group.
- **Polyphyletic** (polyphyly): a group of species characterized by the presence of one or more homoplasies, or characters that have converged or reverted so they look the same although they have not been inherited from a common ancestor.

	subjects				
	1	2	3	4	5
a-us	0	0	0	0	0
b-us	1	1	0	0	1
c-us	1	1	1	1	2
d-us	1	1	1	1	2

Figure 2. Data matrix of morphological characters. Top horizontal row labeled as 'subjects' represent observed morphological characters (1-5) selected for comparison throughout selected taxa. Horizontal rows labeled a-us to d-us represent different species. Scored character states (0,1,2) for each subject with regards to taxa is illustrated inside the table. Modified lectures series of K. Fitzhugh.

Figure 3. Comparing DNA sequences (image left) of species x-us, y-us and z-us is used to calculate a phylogenetic tree (image right) which represents a hypothesis for the relationships among the three taxa. The letters in the matrix correspond to DNA nucleotides (A, adenine; C, cytosine; G, guanine; T, thymine). Dashes or "gaps" represent gains (insertion) or losses (deletion) of nucleotides which have occurred during evolution. Modified lectures series of K. Fitzhugh.

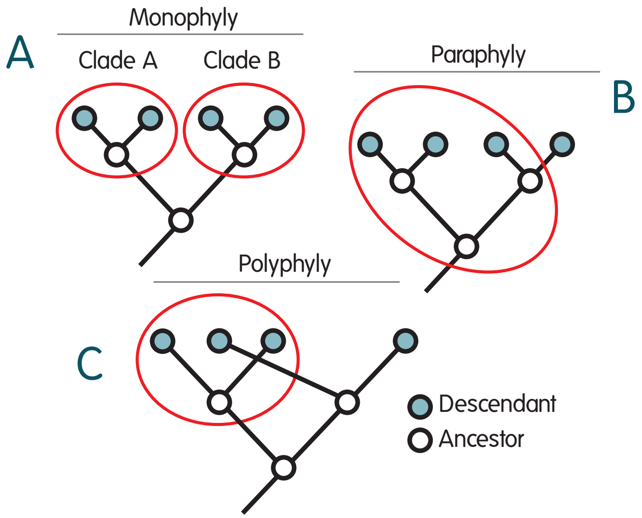


Figure 4. Terms above each circled clade are used to describe different groupings of animals according to their ancestry (see text for explanation).

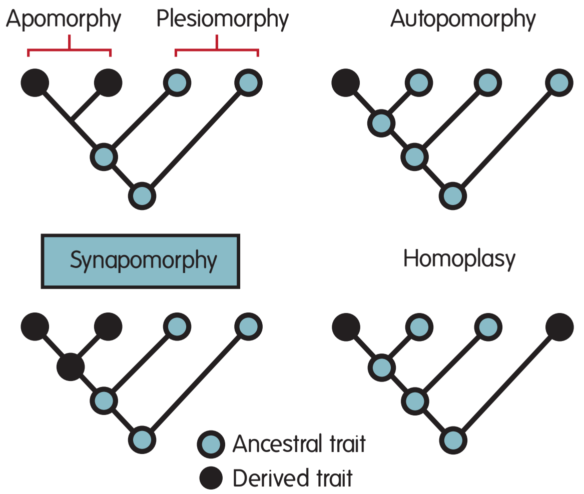


Figure 5. Terms used to describe different types of characters (see text for explanation).

-BOX 2- Animal Tree of Life

Understanding of the evolution of animals and their relationships has been the goal of many zoologists since the 19th century. From the first hand-drawn attempts made by the German zoologist Ernst Haeckel in 1866 to the modern phylogenetic trees calculated from large datasets with supercomputers, the main goal of these phylogenetic hypotheses is to explain the similarities observed among different groups of animals within the paradigms of Darwinian evolution. Although many questions remain, the principle branches of the Animal Tree of Life are progressively becoming better understood as shown by several well defined clades summarized in Fig. 6. All members of the Animal Kingdom share a common ancestor and form a monophyletic group known as the **Metazoa**, which is divided into 36 major groups or phyla, all sharing the presence of certain molecular characters (collagens, protein kinase C for cell signaling, and RFamide and acetylcholine as neurotransmitters) as well as similarity in producing gametes (sexual cells).

Recent molecular studies consistently recovered a large clade, **Bilateria**, gathering all animals with bilaterian symmetry, that is, with a front and back end, as well as an upside and downside, and therefore a left and right. Bilateria is sister to those clades lacking in bilaterail symmetry such as Ctenophora (comb jellies), Porifera (sponges), Placozoa (strange, poorly known small animals), and Cnidaria (jellyfish, corals, etc), although the relationships among these four remain controversial. Bilateria is divided into clades Acoelomorpha (soft-bodied small animals, externally similar to flat worms), Deuterostomia, and Protostomia. Deuterostomia includes all the animals in which the blastopore or embrionic mouth becomes the anus in the adult, and the adult mouth develops as a new opening during development. The clade includes Echinodermata (i.e., starfish, sea urchins, and sea cucumbers), Cephalochordata (small, fishlike, filter-feeding animals), Urochordata (tunicates or sea squirts) and Craniata (including Vertebrates). Prostostomia is more difficult to define morphologically, although traditionally it has been considered as those animals in which the blastopore becomes the mouth in the adult, and share a similar mode of mesorderm (a third germ layer) formation. Prostostomia is divided into clades Ecdysozoa (all molting animals which shed their cuticle throughout their life) and Spiralia (all animals with spiral cleavage, a particular pattern in the division of early embryonary cells). Ecdysozoa includes Nematoda (roundworms, p. 138), Nematomorpha (horsehair worms), Tardigrata (waterbears), Onychopora (velvet worms), Arthropoda (insects, spiders, crustaceans, etc., p. 169), Priapula (penis worms, p. 142), Loricifera (very small to microscopic marine sediment-dwelling animals), and Kinorhyncha (mud dragons). Spiralia is separated into Polyzoa (diverse colonial marine or freshwater animals), Trochozoa (marine animals with ciliated, free-swimming trochophore larva) and Platyzoa (flat animals).

Polyzoa includes Bryozoa (moss animals), Entoprocta (small, mostly sessile aquatic animals) and Cycliophora (small animals living attached to the bodies of cold-water lobsters); while Trochozoa comprises Annelida (segmented worms, p. 141), Mollusca (snails, bivalves, octopus and squid, p. 164), Nemertea (ribbon worms or proboscis worms), Brachiopoda (lamp shells) and Phoronida (horseshoe worms); and Platyzoa contains Gastrotricha (hairybacks), Platyhelminthes (flatworms), and the Gnathiferan phyla Gnathostomulida (jaw worms), Micrognathozoa (with only a single known species living between sand grains) and Rotifera.

-BOX 2- Animal Tree of Life

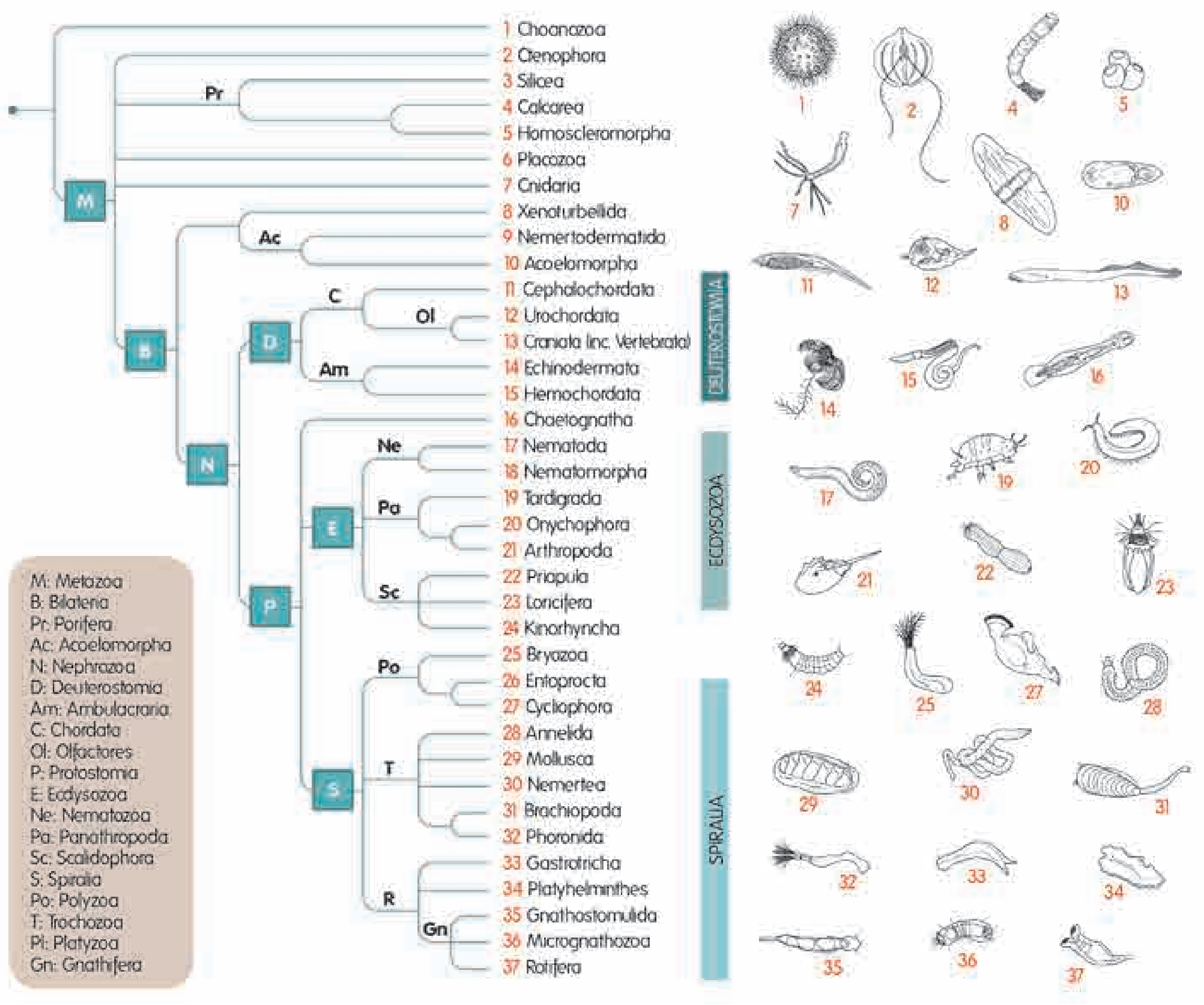


Figure 6. Summary of the relationships among animals (see text for explanation).

Organization of the species records

Group of animals

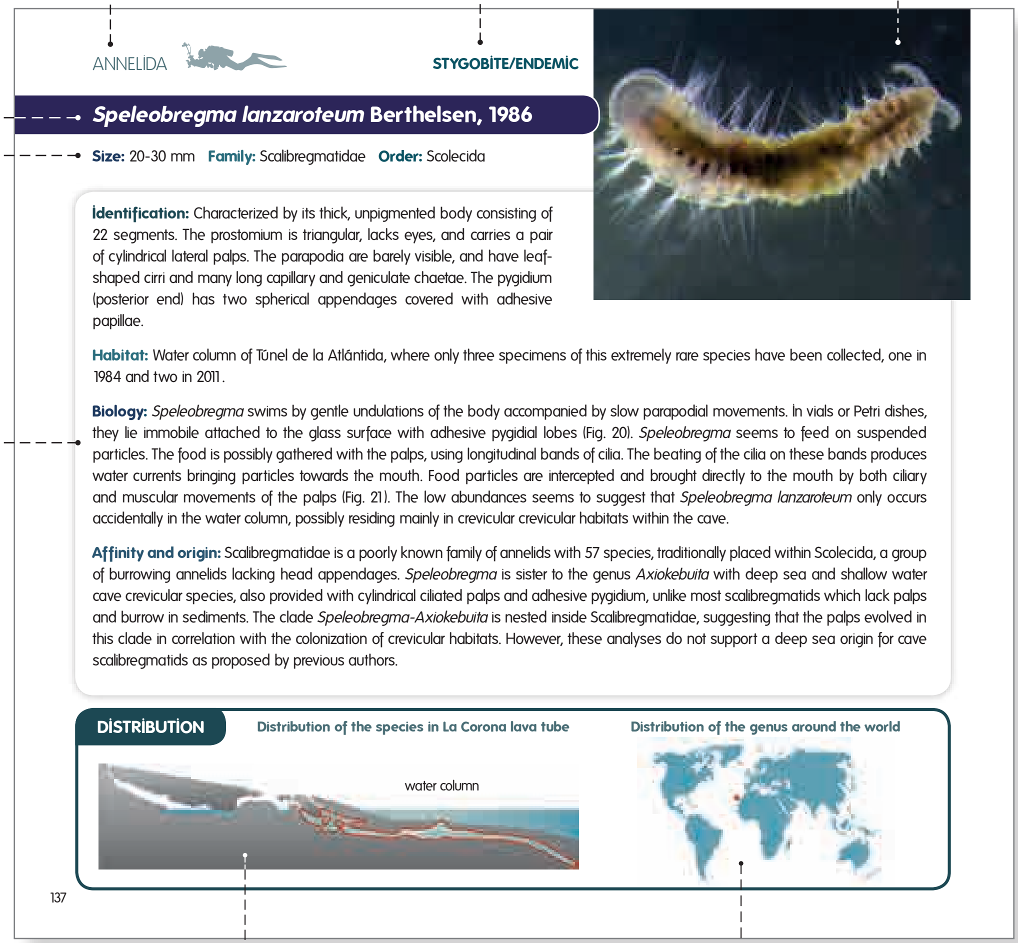
Degree of adaptation and exclusivity:
Stygobite (exclusive from subterranean environments)
Endemic (exclusive from a particular geographical area)

Main image of the species. If not indicated, the image is taken from the original description

Scientific name

Size ranges; Family and Order names

Information about how to identify the species, as well as its habitat, biology, and phylogenetic affinities



ANNELIDA

STYGOBİTE/ENDEMİC

***Speleobregma lanzaroteum* Berthelsen, 1986**

Size: 20-30 mm **Family:** Scalibregmatidae **Order:** Scolecida

İdentification: Characterized by its thick, unpigmented body consisting of 22 segments. The prostomium is triangular, lacks eyes, and carries a pair of cylindrical lateral palps. The parapodia are barely visible, and have leaf-shaped cirri and many long capillary and geniculate chaetae. The pygidium (posterior end) has two spherical appendages covered with adhesive papillae.

Habitat: Water column of Túnel de la Atlántida, where only three specimens of this extremely rare species have been collected, one in 1984 and two in 2011.

Biology: *Speleobregma* swims by gentle undulations of the body accompanied by slow parapodial movements. In vials or Petri dishes, they lie immobile attached to the glass surface with adhesive pygidial lobes (Fig. 20). *Speleobregma* seems to feed on suspended particles. The food is possibly gathered with the palps, using longitudinal bands of cilia. The beating of the cilia on these bands produces water currents bringing particles towards the mouth. Food particles are intercepted and brought directly to the mouth by both ciliary and muscular movements of the palps (Fig. 21). The low abundances seems to suggest that *Speleobregma lanzaroteum* only occurs accidentally in the water column, possibly residing mainly in crevicular crevicular habitats within the cave.

Affinity and origin: Scalibregmatidae is a poorly known family of annelids with 57 species, traditionally placed within Scolecida, a group of burrowing annelids lacking head appendages. *Speleobregma* is sister to the genus *Axiokebuita* with deep sea and shallow water cave crevicular species, also provided with cylindrical ciliated palps and adhesive pygidium, unlike most scalibregmatids which lack palps and burrow in sediments. The clade *Speleobregma-Axiokebuita* is nested inside Scalibregmatidae, suggesting that the palps evolved in this clade in correlation with the colonization of crevicular habitats. However, these analyses do not support a deep sea origin for cave scalibregmatids as proposed by previous authors.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube

Distribution of the genus around the world

137

Distribution of the species in La Corona. *The sections of the cave are highlighted in red when the species is present along the entire section; red dots indicate it is restricted to a particular zone*

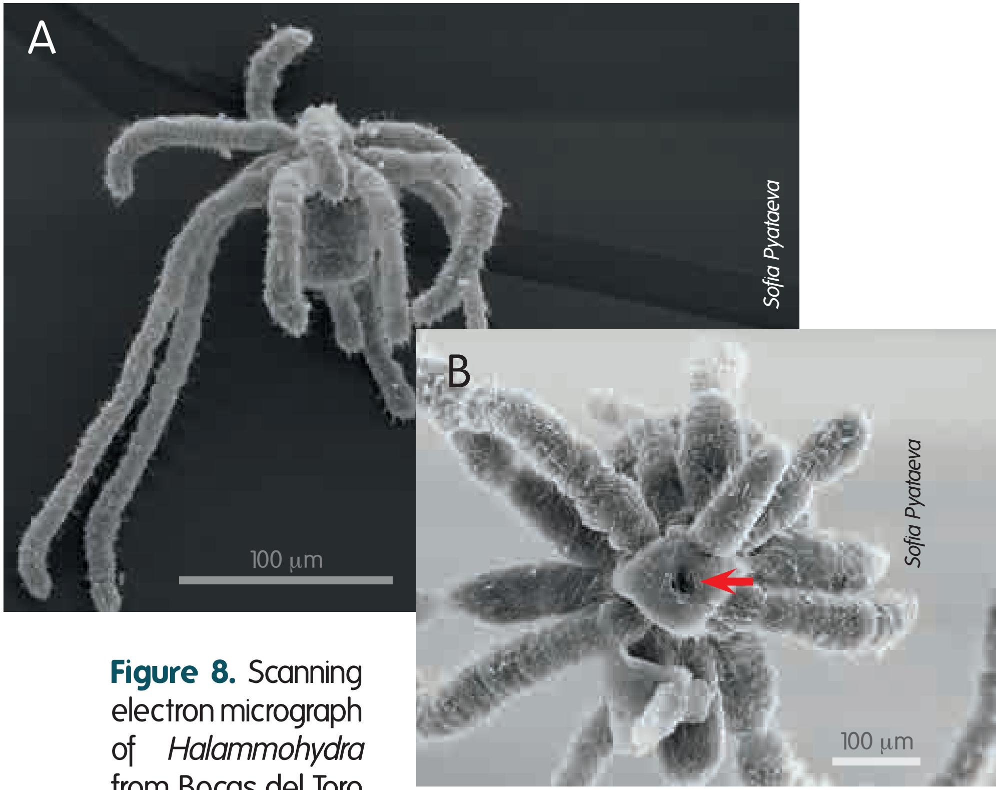
Distribution of the genus in the world. *Red dots indicate the presence of species in caves; orange areas indicate the presence of the species in the ocean*

CNIDARIA

Cnidarians consist of more than 9,000 described species that are mostly marine, and include corals, jellyfish, and sea anemones. The Cnidaria, meaning nettle, gets its name from the presence of cnidocytes, a type of stinging cell used to capture prey. Cnidarians are considered simple, without a distinct head or brain, and having a combined oral and anal opening. They lack organ systems and most of their life functions are performed by groups of specialized cells. Cnidarians typically have a relatively complex life cycle with alternation of generations from sessile individuals called polyps (as in corals or anemones) to pelagic floating forms called medusae (as in


Sofia Pyataeva

Figure 7. The genus *Halammohydra* consists entirely of minute interstitial species. Specimens collected from Tunel de Atlantida are morphologically similar to those collected elsewhere. Photograph and specimen above from Bocas del Toro, Panama.



Sofia Pyataeva

Sofia Pyataeva

Figure 8. Scanning electron micrograph of *Halammohydra* from Bocas del Toro showing detailed structures; (**A**) whole body and (**B**) mouth opening (arrow).

Figure 9. *Caryophyllia inornata* is an accidental species found near Montaña de Arena. It is a solitary stony coral common in rocky bottoms and marine caves throughout the Canary Islands.

Figure 10. *Telmatactis cricoides,* photographed near Montaña de Arena in Túnel de la Atlántida.

jellyfishes), although in some groups, only one of these stages is present.

Cnidaria is an ancient group, having diverged from a common ancestor before the origin of bilateral animals which possess more complex brains. Four classes are recognized within the phylum: Hydrozoa (hydroids, fire corals and Portuguese man-of-war), Scyphozoa (true jellyfish), Cubozoa (box jellies) and Anthozoa (anemones, stony corals and soft corals).

Cnidarians in subterranean environments and in La Corona lava tube

Although cnidarians are common in anchialine habitats, they are primarily represented by marine species concentrated around cave entrances. Only 25 species of cnidarians are considered stygobitic. One of the most remarkable species of hydrozoan cnidarians is *Velkovrhia enigmatica,* the only freshwater stygobitic hydrozoan, known exclusively from caves in Dinaric karst of the Balkans.

The three species of cnidarians found in La Corona lava tube are marine accidentals.

Halammohydra sp. (Figs. 7 and 8) is found interstitially in the sediments of Montaña de Arena. It is a minute hydrozoan, 0.3-1.3 mm, highly modified to interstitial life among sand grains. Approximately 10 species have been described within this genus, all exclusive to marine sediments from around the world. Other species of the genus are relatively common in coastal marine sediments in the Canary Islands.

Small populations of the solitary coral ***Caryophyllia inornata*** (Fig. 9) and the sea anemone ***Telmatactis cricoides*** (Fig. 10) have also been found on the cave walls near Montaña de Arena where the proximity to the marine connection seems to provide them sufficient nutrients. Both species are common in marine caves throughout the Canary Islands.

NEMATODA

There are more than 25,000 known species of nematodes or roundworms including free living forms on land and in marine ecosystems, as well as forms parasitic to a variety of animals and plants. This number most likely only represents a small percentage of the actual diversity of the group, which is estimated to contain around a million species. The morphology of nematodes is relatively simple, consisting of a cylindrical, thread-like

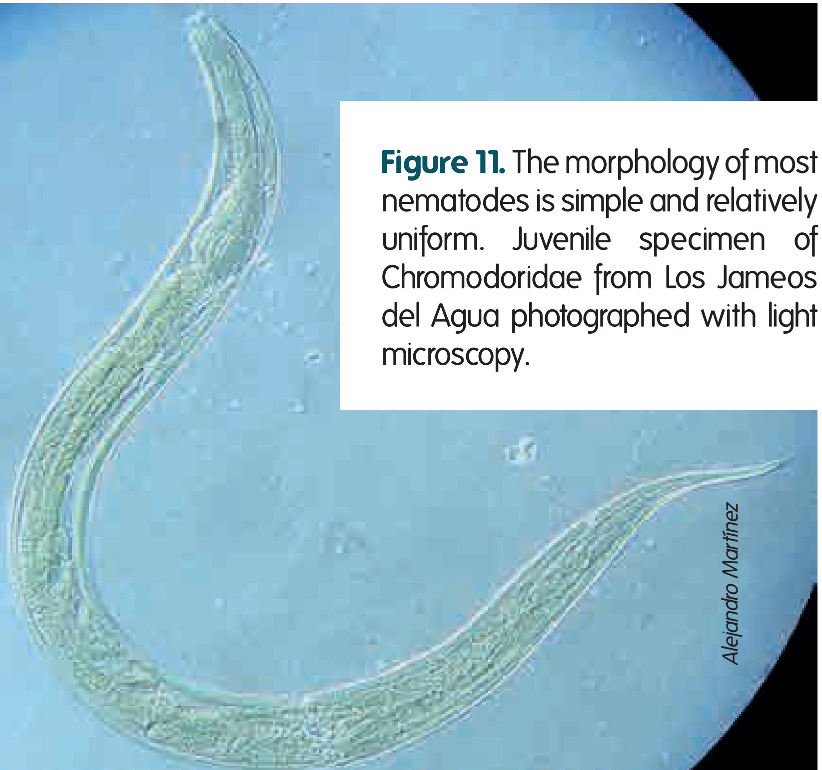
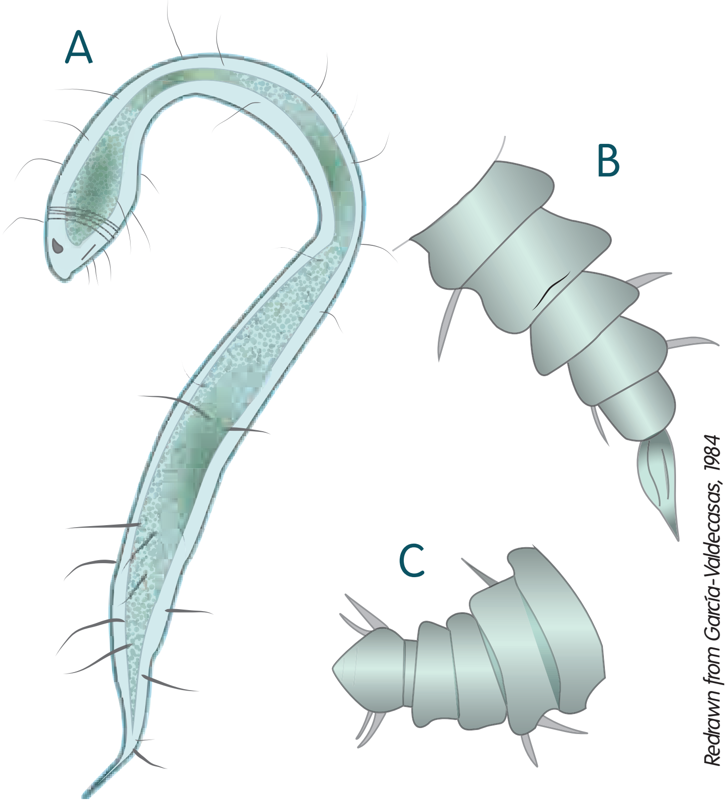


Figure 11. The morphology of most nematodes is simple and relatively uniform. Juvenile specimen of Chromodoridae from Los Jameos del Agua photographed with light microscopy.

Alejandro Martínez



Redrawn from García-Valdecasas, 1984

Figure 12. (**A**) *Draconema* and (**B-C**) *Quadricoma* (anterior and posterior ends) contain some of the strangest looking marine nematodes. Both are found in Montaña de Arena.

body without apparent appendages. Only a few exceptions to this effective homogeneous body organization are known. These include highly modified parasitic forms and the free living interstitial dragon nematodes (Draconematidae). Previously, nematodes were placed with other worm-like animals including kinorhynchs (mud dragons), gastrotrichs (hairbacks), and priapulids (penis worms), within the Aschelminthes. However, with the advent molecular genetic analyses, the relationship between nematodes, arthropods, and other molting animals has been confirmed in a clade called Ecdysozoa (Box 2).

Nematodes in subterranean environments and in La Corona lava tube

Although nematodes are common in anchialine caves, their diversity has not been well investigated. The few records known correspond to marine species near cave entrances or accumulations of sand within caves (Fig. 11). İn La Corona lava tube, nematodes are reported from Jameos del Agua and the interstitial habitats of Montaña de Arena. The few genera recorded are widespread in marine habitats and include *Draconema* (Fig. 12 A), *Quadricoma* (Fig. 12 B), *Croconema, Calyptronema*, and *Serysthomina.*

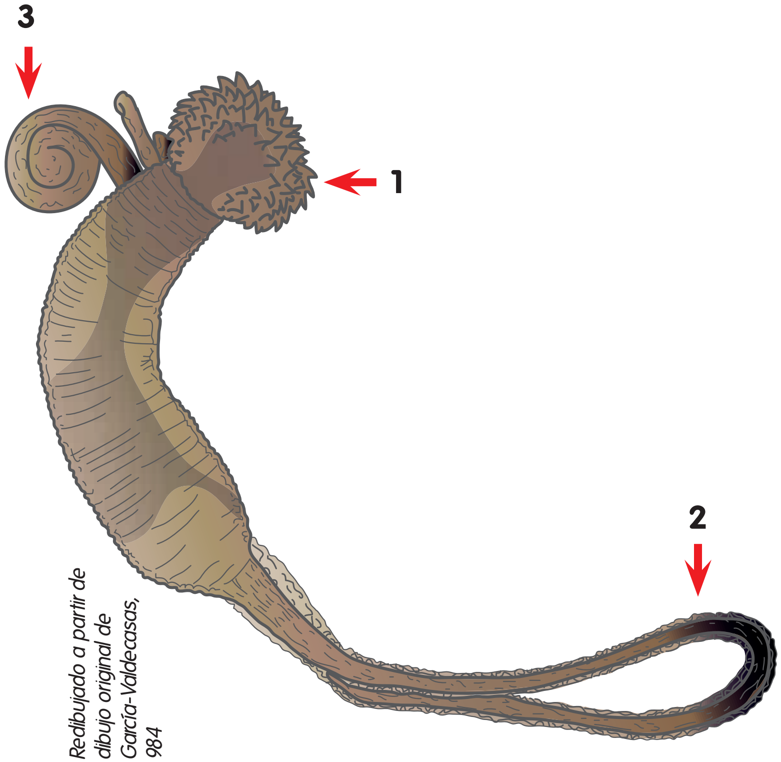
PRİAPULİDA

Priapulids, or penis worms, consist of only 18 described species, all inhabiting marine sediments where they burrow using an extensible spiny proboscis combined with peristaltic movements of their body in order to feed on organic matter in the sediments. However, some microscopic species are considered to be interstitial, crawling among sand grains. The body of priapulids is divided into introvert and trunk. The introvert consists of a proboscis with numerous denticles and adhesive tubes, and can evert and retract in order to move, burrow or collect food particles. The trunk is cylindrical and normally ends in a single tail or several appendages. Priapulids are placed within Ecdysozoa (Box 2) and grouped together with Kinorhyncha and Loricifera (two groups of marine meiofaunal animals), forming the clade Scalidophora, which is characterized by a circular brain and the presence of an introvert with scalids (small spines).The Priapula is divided into five families with the macrofaunal burrowing Priapulidae, Halicryptidae, and Chaetostephanidae, and the minute interstitial Tubiluchidae and Meiopriapulidae.

Priapulids in subterranean environments and in La Corona lava tube

Priapulids are uncommon in anchialine environments, except for the interstitial *Tubiluchus* which are found in cave sediments from Bermuda (*T. corallicola* in Walshingham Cave), İtaly (*T. troglodytes* in Ciolo Cave Salento), and the Canary İslands (T. lemburgi from Tenerife and Lanzarote, Fig. 13).

This latter species has been found in several marine caves, including La Corona lava tube, where adult and juvenile individuals inhabit the sediments in Montaña de Arena and cinder patches in Jameos del Agua (Fig. 14). The species is identified by the arrangement of the genital area of the males (Fig. 15).



Redibujado a partir de dibujo original de García-Valdecasas, 984

Figure 13. *Tubiluchus lemburgi* from Montaña de Arena. The rounded spiny structure above is the introvert (**1**) used in feeding and locomotion; whereas the posterior adhesive tail (**2**) provides attachment to the sand grains. The gut (**3**) is visible near the introvert (**3**). Entire animal about 1 mm in length.

Andreas Schmidt-Rhaesa

Figure 14. Scanning electron micrograph *Tubiluchus lemburgi* collected in a marine cave in Tenerife.

Figure 15. Scanning electron micrograph of the male copulatory organ (between brackets) of *Tubiluchus lemburgi* from Montaña de Arena. The shape of the genital area, as well as the number and arrangement spines, are important features in distinguishing species. The anterior end of the animal at the left.

ANNELİDA

Annelids, or segmented worms, are a diverse group of animals with approximately 15,000 described species. They are ecologically ubiquitous, occurring in almost every environment on Earth. Most species of annelids live in marine waters and include familiar forms such as nereis worms, fan worms, and stinging fire worms. Although less diverse, terrestrial and freshwater annelids such as earthworms and leeches are also well known and are important in agriculture and medicine. İn contrast, other annelids are poorly known, even by experts. For example, a little known group, the formerly termed archiannelids, has been found to be composed of several non-related families of externally simple worms that mostly live among sand grains. Also myzostomids, which are rounded worms living as commensals of echinoderms, are also understudied. Some annelids, such as the peanut worms (Sipunculida) and spoon worms (Echiurida), are so morphologically divergent that researchers needed to use molecular techniques before they could properly place them within the annelids.

Although annelids are morphologically highly variable, they typically have a well-defined head or prostomium, sometimes with a pair of palps and three antennae. The prostomium is followed by a trunk formed by serially repeating segments. The last segment of the trunk, called pygidium, is morphologically distinct and usually possesses the anus. Paired fleshy appendages, or parapodia, normally project laterally on both sides of each trunk segment. Each parapodium typically bears one or two bundles of chaetae, which are hard chitinous bristles mainly used for locomotion.

Previously, annelids were grouped together with arthropods in a clade called Articulata. However, analyses based on large molecular datasets revealed a sister group relationship between annelids and molluscs with both groups now belonging to Trochozoa. The internal relationships among annelids are still controversial. Morphological analyses revealed three major clades of which Clitellata (earthworms) and Hirudinea (leeches) were sister to Polychaeta (brittle worms). Polychaeta was divided into several orders according to varying morphological organization. However, molecular studies have placed Clitellata (earthworms) and Hirudinea (leeches) among the marine bristle worms, suggesting that many complex features have been lost as well as appeared during the evolution of segmented worms, undoubtedly having a long history.

Annelids in subterranean environments

Stygobitic annelids, mostly clitellates (i.e., earthworms) from terrestrial and freshwater caves, are represented by approximately 522 described species. Annelids inhabiting anchialine caves are becoming increasingly known and might even equal or surpass that of crustaceans in coming years. So far the annelid families found in anchialine caves include the Polynoidae, Nerillidae (most diverse), Spionidae, Fauveliopsidae, Nereididae, Hesionidae, Protodrilidae, Scalibregmatidae, Syllidae, Acrocirridae, Flabelligeridae, Sabellidae, and Serpulidae. Most of these stygobitic species occur in fully marine waters, except for *Troglochaetus beranecki* (Nerillidae, with an amphi-atlantic distribution), *Marifugia cavatica* from Dinaric caves (the world´s only freshwater stygobitic tube worm), and at least three species of *Namanereis* (Nereididae) from the Canary Islands (Gran Canaria and Fuerteventura) and the Caribbean.

Annelids in La Corona lava tube

La Corona lava tube contains 25 species of annelids, although only 11 are endemic stygobites. Marine annelids are common in Jameos del Agua, including several deposit feeding species which take advantage of the abundant food provided by diatoms in Jameos del Agua. Numerous marine interstitial and infaunal annelids are also found in Montaña de Arena. Stygobitic annelids primarily inhabit aphotic (dark) zones, and can be found swimming in the water column or crawling within the benthos in cinders and crevices (small spaces amongst rocks).


Juan Valenciano

Gesiella jameensis (Hartmann-Schröder, 1974)

Size: 10-40 mm **Family:** Polynoidae **Order:** Aphroditiformia

İdentification: *Gesiella* is the only unpigmented scale worm found in La Corona lava tube. İt can be recognized by the presence of transparent scales attached to the dorsal side of the body, which alternate with long dorsal cirri (slender filaments). The head lacks eyes and bears three antennae and two long palps (Figs. 16 and 18). The parapodia possess chaetae and a unique ciliated wheel organ, only found in this species.

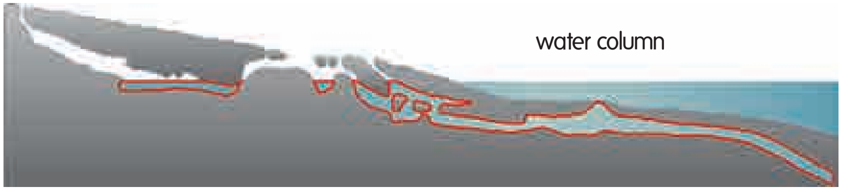
Habitat: İt is one of the most commonly observed species in the flooded lava tube with numerous individuals seen during a single dive.

Biology: Very few details of the feeding biology are known for *Gesiella*, but indirect evidence indicates that it probably scavenges and may be a predator of small crustaceans and polychaetes. Most individuals of *Gesiella* are found drifting in the water column of the cave (Fig. 17), maintaining their position by extending their parapodia and long cirri. *Gesiella* also possess a parapodial wheel organ, which may aid in swimming, respiration, and brooding/dispersal of gametes. When it needs to move longer distances or escape predators, *Gesiella* swims by metachronal beating of its parapodia combined with undulating movements of the trunk. Resting animals can be found on the rocks or the bottom, partially within crevices of the lava rocks (Fig. 16).

Affinity and origin: Polynoidae is a diverse family of annelids, with more than 1200 species divided into many subfamilies and genera. They are found everywhere in the ocean, occurring from intertidal flats to bathyal depths in all possible marine habitats. *Gesiella* belongs to the subfamily Gesiellanae, sister to Macellicephalinae, both phylogenetically nested within Polynoidae. *Gesiella* is the sister species to the genus *Pelagomacellicephala*, which consists entirely of stygobitic polynoids from anchialine caves of the Bahamas. These two genera are related to deep sea species suggesting that the common ancestor of *Gesiella* and *Pelagomacellicephala* colonized anchialine caves from the deep sea possibly through seafloor crevices or crevicular habitats. The diversification of this lineage might be related to vicariance (i.e., splitting of populations) relation to the opening of the Atlantic Ocean or dispersal, possibly through deep sea crevicular habitats

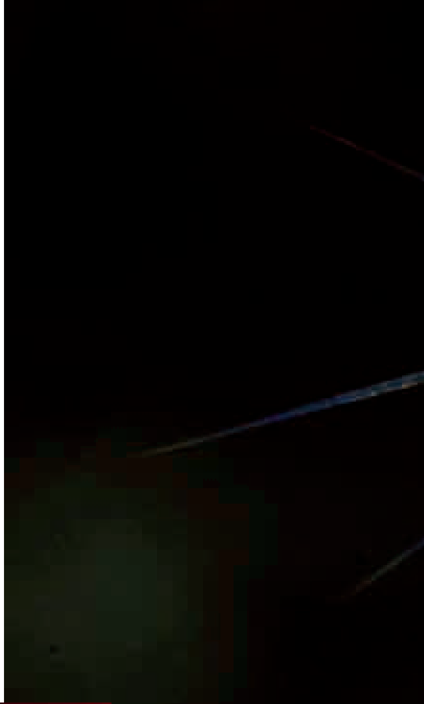
DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

Figure 16. *Gesiella jameensis* remaining stationary on a rock surface below the entrance pool of Túnel de la Atlántida. Parapodia and chaetae provide motility, while transparent scales, visible on the dorsal side of the body, act as a shield to soft underlying body parts.



Juan Valenciano

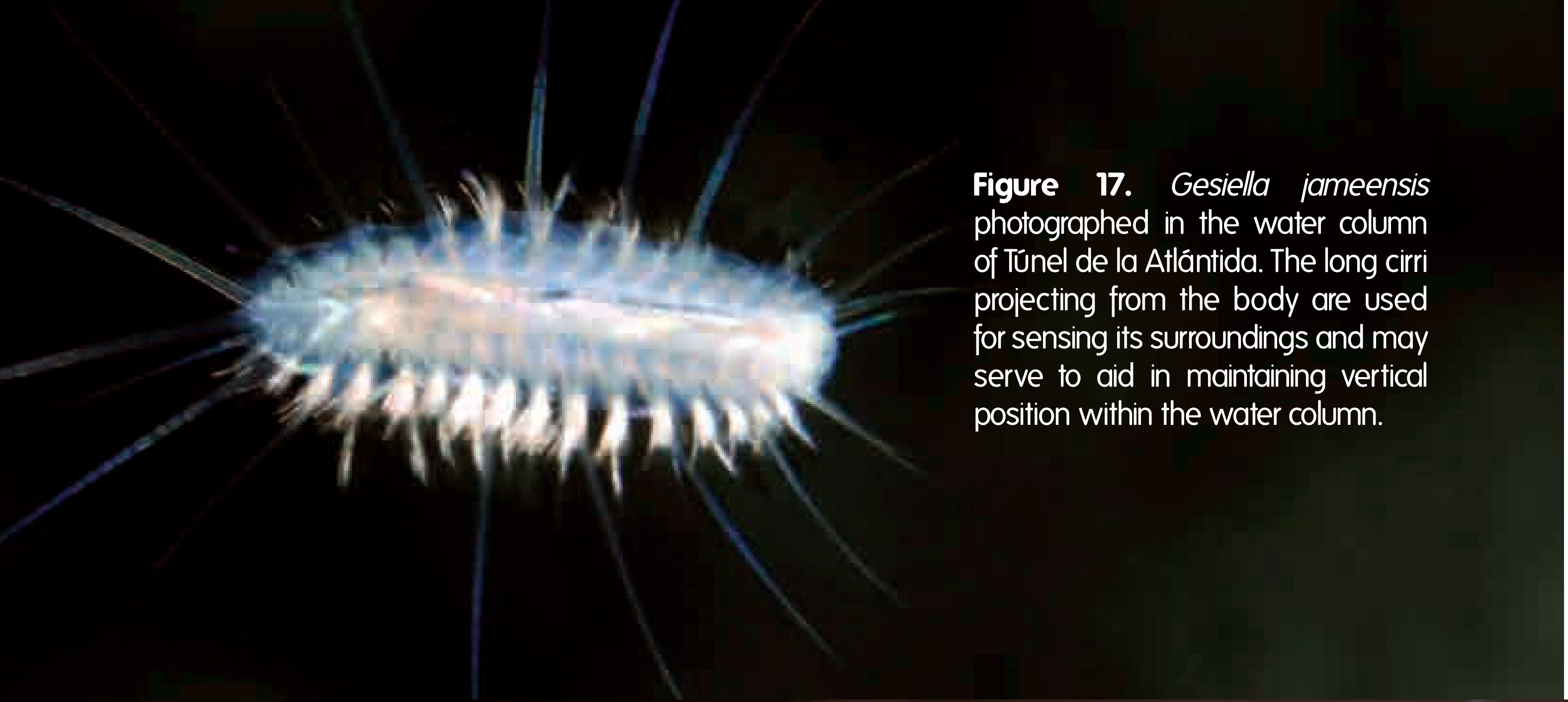


Figure 17. *Gesiella jameensis* photographed in the water column of Túnel de la Atlántida. The long cirri projecting from the body are used for sensing its surroundings and may serve to aid in maintaining vertical position within the water column.

Juan Valenciano

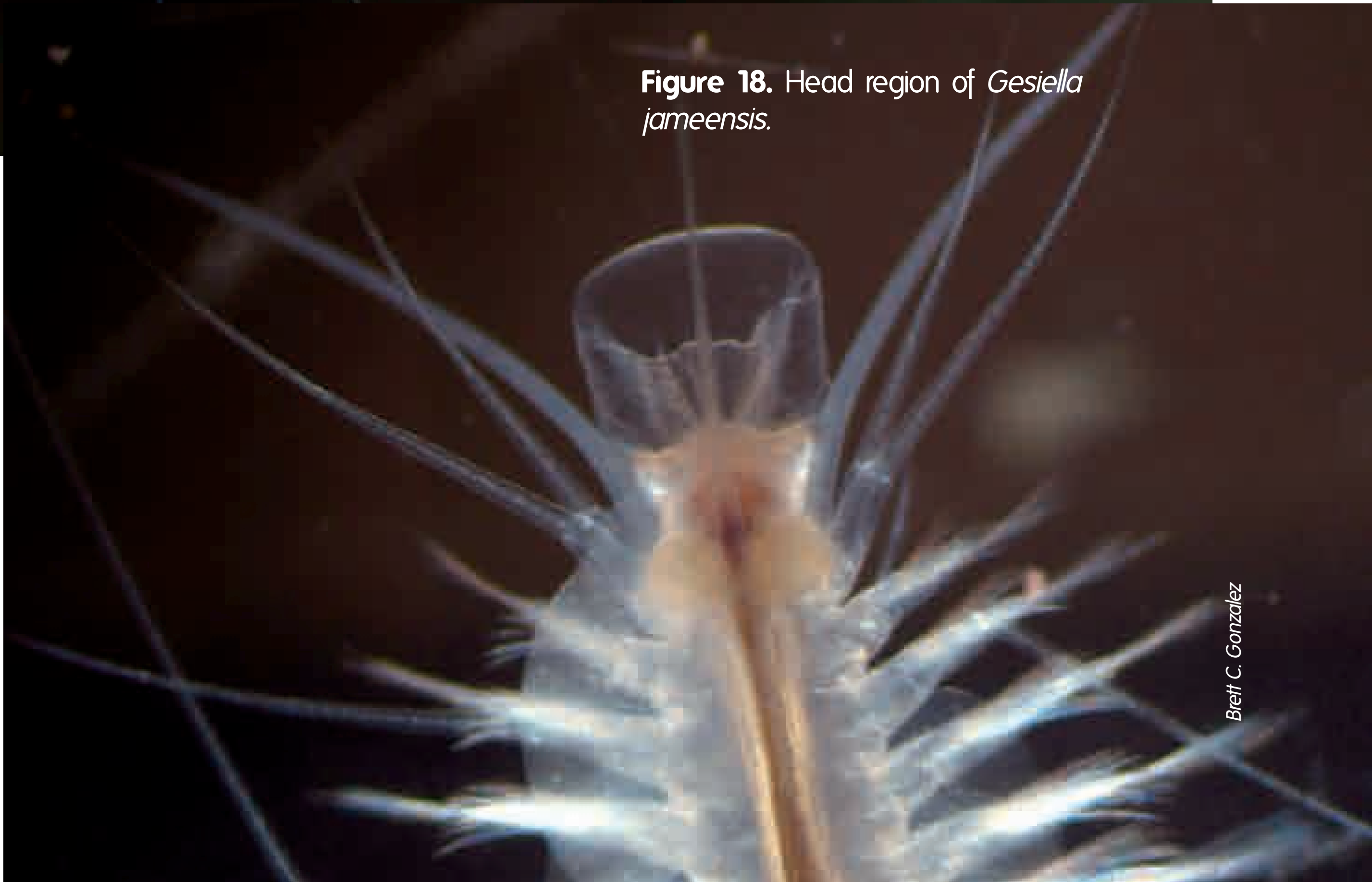
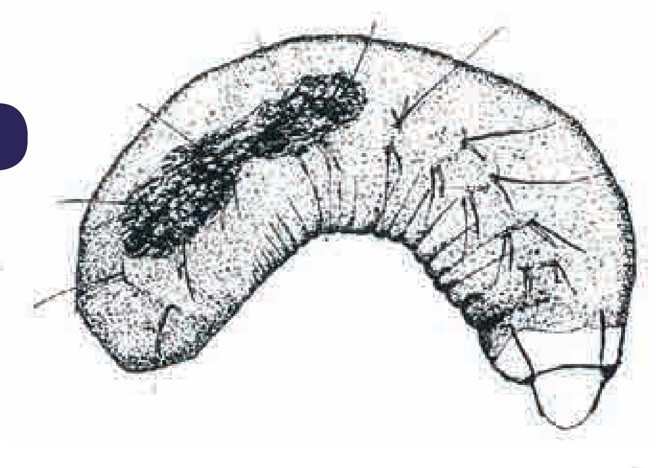


Figure 18. Head region of *Gesiella jameensis.*

Brett C. Gonzalez

Fauveliopsis jameoaquensis Núñez, 1997

Size: 0.5-1 mm **Family:** Fauveliopsidae **Order:** Terebellida



İdentification: *Fauveliopsis jameoaquensis* is a small, brownish annelid with a cylindrical body divided into 10 segments. İndividual segments bears reduced biramous (with two lobes) parapodia, each with only one capillary thin and slender and one acicular (needle-shaped) chaeta in each (projecting lobe). The head is poorly differentiated and retractable into the anterior segments. (Fig. 19).

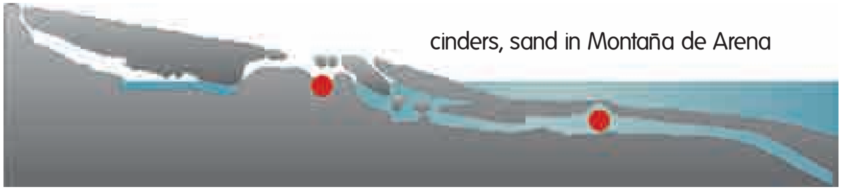
Habitat: Cinder patches and fecal deposits of *Bonellia viridis* in Jameos del Agua, as well as coarse sand of Montaña de Arena from Túnel de la Atlántida.

Biology: *Fauveliopsis jameoaquensis* moves slowly through the sediment by contraction of their muscles but gaining further progress by everting and retracting their proboscis. İn the sediments, *Fauveliopsis* feeds on deposits of organic matter collected with the eversible proboscis. Details of the reproductive biology are unknown, but sexes are separate and mature females bear only 1-2 immature eggs in the posterior end of the body.

Affinity and origin: Fauveliopsidae is a relatively poorly known family of annelids, with two genera and 15 described species. Most species occur in cold to temperate waters in a variety of habitats ranging from mud or empty gastropod shells, to bathyal (1000 to 4000 m) or abyssal (4000 to 6000 m) depths. Based on morphological studies, Fauveliopsidae has been placed in the clade Cirratuliformia, together with Acrocirridae, Flabelligeridae, and Cirratulidae. However, this position has yet to be confirmed by molecular analyses. *Fauveliopsis jameoaquensis* is the only fauveliopsid considered as a stygobite, as well as the smallest species of the family. Similar morphology is shared by two other undescribed stygobitic species collected from silty sediments in Yucatan (Mexico) and Mallorca (Spain). Although phylogenetic analyses are incomplete, the abundance of Fauveliopsidae in the deep sea suggests a putative deep sea affinity for this stygobitic species.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

Alejandro Martínez

Figure 19. Scanning electron micrograph of *Fauveliopsis jameaquensis*, an interstitial annelid living in the cinders of Los Jameos del Agua. The entire animal measures approximately 1 mm.

Speleobregma lanzaroteum Berthelsen, 1986

Size: 20-30 mm **Family:** Scalibregmatidae **Order:** Scolecida


Alejandro Martínez

İdentification: *Speleobregma lanzaroteum* is characterized by a thick, unpigmented body consisting of 22 segments. The prostomium is triangular, lacks eyes, and carries a pair of cylindrical lateral palps. The parapodia are barely visible, and have leaf-shaped cirri and many long capillary and geniculate (bent at a sharp angle) chaetae. The pygidium (posterior end) has two spherical appendages covered with adhesive papillae (small rounded protuberances).

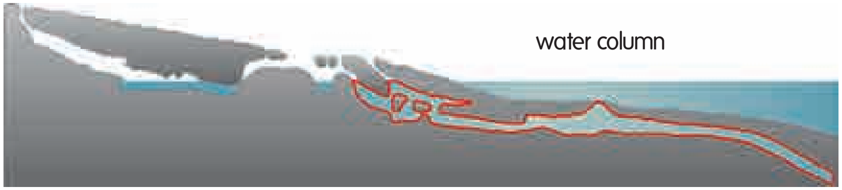
Habitat: Water column of Túnel de la Atlántida, where only three specimens of this extremely rare species have been collected, one in 1984 and two in 2011.

Biology: *Speleobregma* swims by gentle undulations of the body accompanied by slow parapodial movements. İn vials or Petri dishes, they lie immobile attached to the glass surface with their adhesive pygidial lobes (Fig. 20). *Speleobregma* seems to feed on suspended particles. The food is possibly gathered with the palps, using longitudinal bands of cilia. The beating of the cilia on these bands produces water currents bringing particles towards the mouth. Food particles are intercepted and brought directly to the mouth by both ciliary and muscular movements of the palps (Fig. 21). The low abundance seems to suggest that *Speleobregma lanzaroteum* only occurs accidentally in the water column, possibly residing mainly in crevicular habitats within the cave.

Affinity and origin: Scalibregmatidae is a poorly known family of annelids with 57 species, traditionally placed within Scolecida, a group of burrowing annelids lacking head appendages. *Speleobregma* is sister to the genus *Axiokebuita* with deep sea and shallow water cave crevicular species, which also possesses cylindrical ciliated palps and adhesive pygidium, unlike most scalibregmatids which lack palps and burrow in sediments. The clade *Speleobregma-Axiokebuita* is nested inside Scalibregmatidae, suggesting that the palps evolved in this clade in correlation with the colonization of crevicular habitats. However, molecular analyses do not support a deep sea origin for cave scalibregmatids as proposed by previous authors.

DİSTRİBUTİON

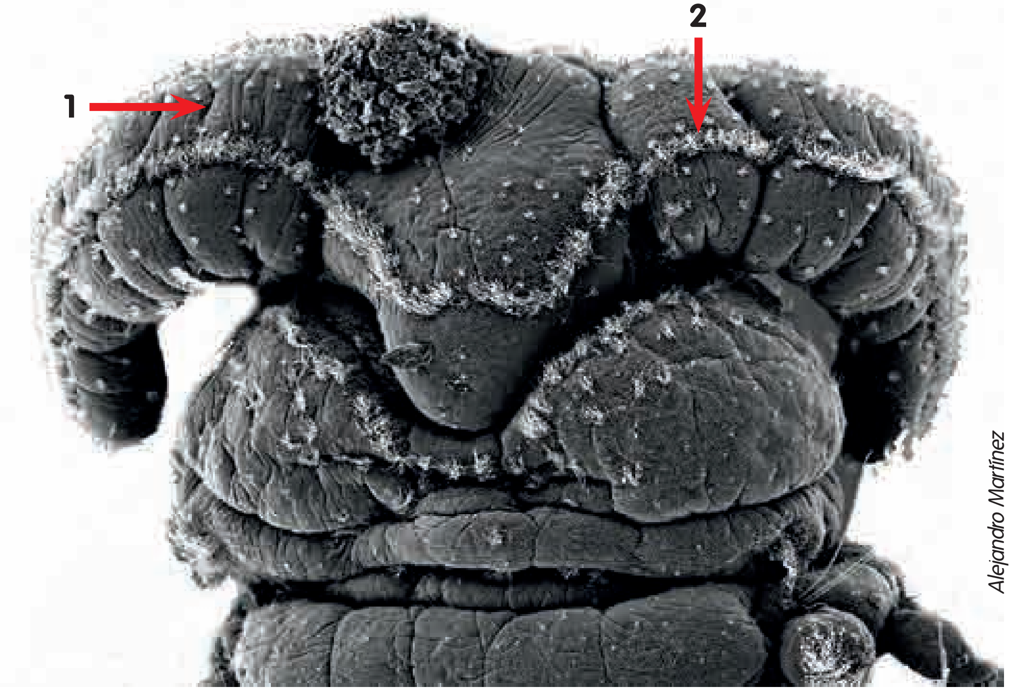
Distribution of the species in La Corona lava tube



Distribution of the genus around the world

Alejandro Martínez

Figure 20. Pygidium of *Speleobregma lanzaroteum*. The rounded structures are covered by adhesive papillae that the animal possibly uses to attach to the rocks in crevicular habitats.



Alejandro Martínez

Figure 21. Scanning electron micrograph of head region of *Speleobregma lanzaroteum* from Túnel de la Atlántida showing two thick palps (**1**). The brighter bands along both palps (**2**) are cilia used to produce water currents and collect food particles.

Bonellia viridis (Rolando, 1921)

Size: females, 15 cm; males, 1-3 mm **Family:** Bonellidae **Order:** Echiura


Juan Valenciano

İdentification: Females of *Bonellia viridis* are easily recognized by their large, spoon-shaped body, vivid green color and bilobed proboscis, several times longer than the maximum length of the body. Males are microscopic, entirely ciliated and live inside the kidney of the females.

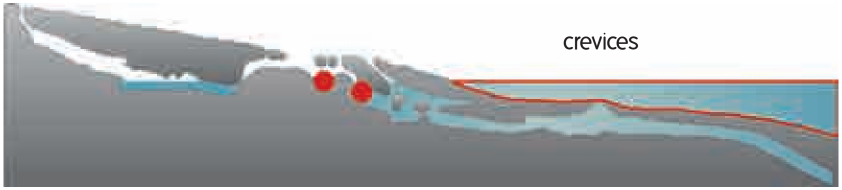
Habitat: Crevices in the illuminated sections of Jameos del Agua and Túnel de la Atlántida. *Bonellia viridis* is widely distributed in the Canary İslands, including twilight zones of many marine caves.

Biology: *Bonellia viridis* is one of the better studied species of echiurids. İt feeds on deposited organic matter which it collects using its long proboscis while keeping its body safely hidden in crevices and rock cracks. Ciliary bands and mucous glands in the proboscis work together in producing currents, which transport adhering particles towards the mouth. *Bonellia* daily ingests large quantities of particles, producing significant amounts of fecal matter (Fig. 22). These deposits accumulate along the bottom of the basin, creating adverse consequences for the ecology of the lake (p. 250, Chapter 4). Bo*nellia* is extremely sexually dimorphic. Females are large while males are microscopic packages of sperm no bigger than 1-3 mm and live exclusively inside females. Up to 20 males are often found inside a single female. Free swimming larvae are undifferentiated and sex determination depends on the spot of settlement. İf the larva settles on the proboscis of a female, it becomes a male, whereas if it settles elsewhere, it becomes a female.

Affinity and origin: *Bonellia* belongs to Echiura, a group of annelids with approximately 140 species. They are found in all oceans, but are more common in littoral zones of tropical and subtropical regions. The position of echiurids within the annelids has been long debated since they lack external segmentation and possess a unique proboscis not found in other annelids. However, evolutionary analyses indicate that they are closely related to earthworms within the so-called sedentary annelids.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the species around the world

Jorge Núñez

Figure 22. *Bonellia viridis* resting on its own excrements (white powdery material) accumulate on the bottom of Los Jameos del Agua. This animal is approximately 50 mm in length.


Alejandro Martínez

Prionospio n. sp. in Martínez *et al.* unpublished

Size: 50-60 mm **Family:** Spionidae **Order:** Spionida

İdentification: This undescribed species has a long, yellowish cylindrical body with short parapodia bearing leaf-shaped lobes. The head lacks eyes or antenna, but has a pair of long thread-like palps (Fig. 23 A and B). The pygidium bears two leaf-shaped lateral lobes separated by a median triangular lobe (Fig. 24).

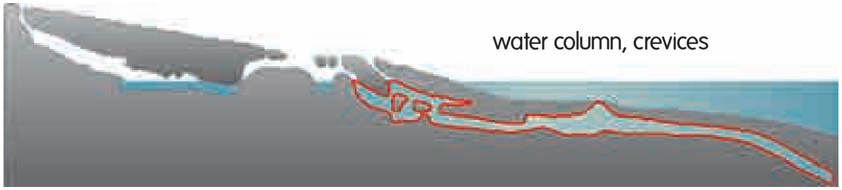
Habitat: Specimens were collected on four occasions from the water column of Túnel de la Atlántida.

Biology: *Prionospio* n. sp. is a recently discovered, rare species. Most of the details about its biology remain unknown. This annelid is most likely a suspension feeder, collecting suspended organic matter and bacteria with its long ciliated palps. When present in the water column of the cave, it swims by gently looping the anterior half of the trunk back and forth, while dragging the posterior half and the pygidium behind the body (Fig. 25). İts uncommon occurrence in the water column and its swimming behavior similar to the escape reaction observed in other spionids suggest that it inhabits cracks and crevices, being dislodged by exhaust bubbles from passing divers.

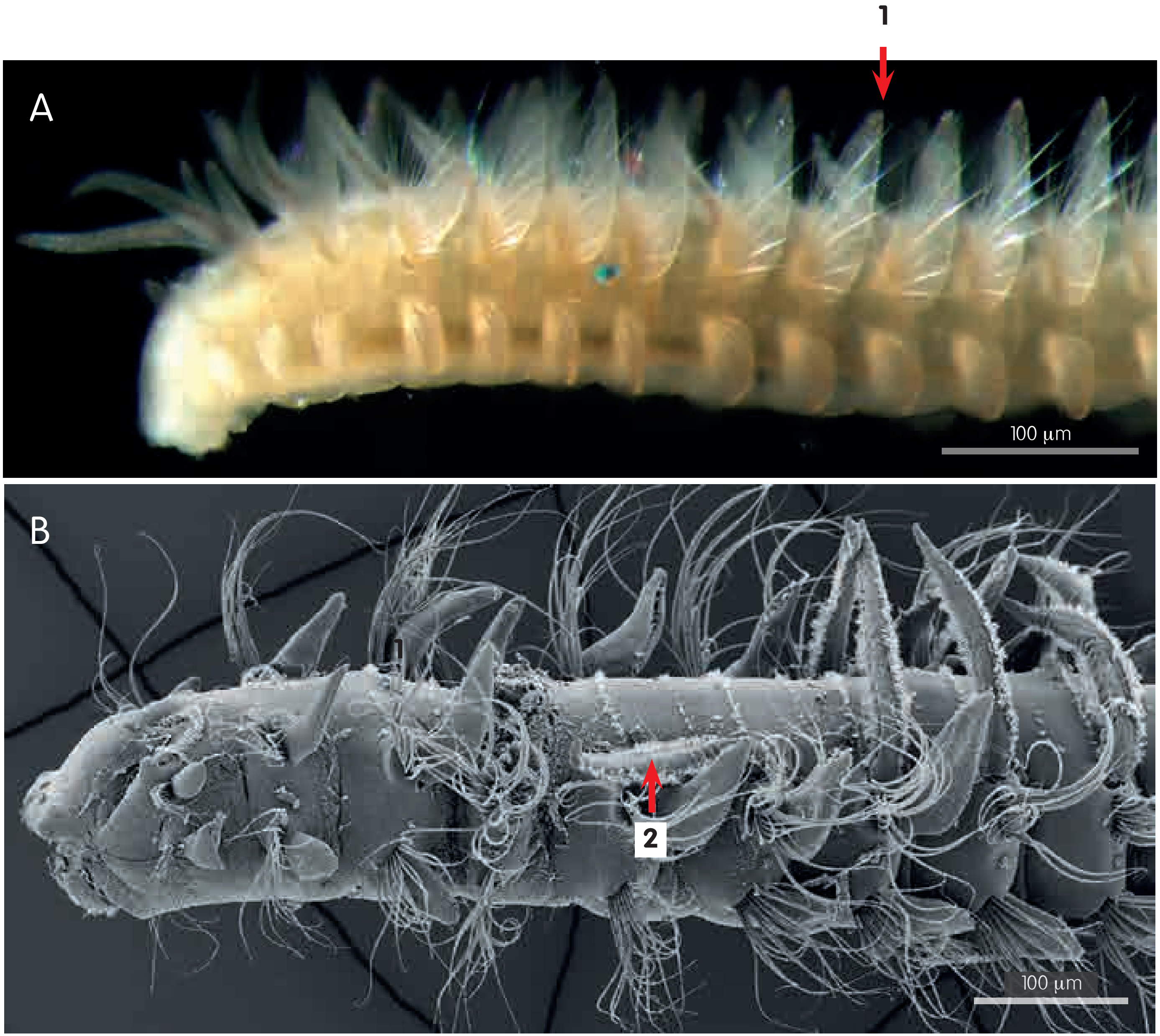
Affinity and origin: *Prionospio* n. sp. belongs to the family Spionidae, which are widespread and common through the marine environments with more than 1,000 described species. Four other stygobitic species of *Prionospio* are known from anchialine caves in Western Australia, Christmas İsland, the Bahamas, and Yucatan. The presence of several shared morphological features among these five species unequivocally distinguishes them from other marine spionids and indicates a close relationship despite their disjunct full-Tethyan distribution.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world



Alejandro Martínez

Figure 23. *Prionospio* n. sp. from Túnel de la Atlántida (**A**) light and (**B**) scanning electron micrograph of the head. The long palps are broken off in the pictures. Leaf-shaped parapodial lobes (**1**) and ciliated branchiae (**2**) are visible on the dorsal side of the body in both figures.

Alejandro Martínez

Figure 24. Detail of the posterior end of *Prionospio* n. sp. under light microscopy.

Figure 25. *Prionospio* n. sp. swims by twisting and looping its entire body. These pictures show the varying strokes of the swimming movement; taken in a lab aquarium.

Juan Valenciano

Megadrilus pelagicus Martínez, Kvindebjerg, İliffe & Worsaae, 2016

Size: 1-2 mm **Family:** Protodrilidae **Order:** Protodrilida

İdentification: İt is easily identified by its long, whitish and externally simple body, lacking body appendages except for a pair of long palps projecting anteriorly from the head. The anterior end of the trunk is cylindrical, tapering towards the pygidium with a dorsal keel. The pygidium is trilobed, with one triangular dorsal and two leaf-shaped lateral lobes.

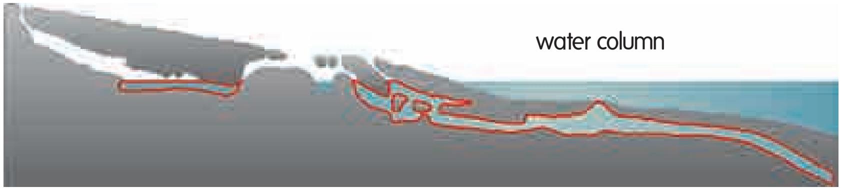
Habitat: Water column of Túnel de la Atlántida and Cueva de los Lagos.

Biology: *Megarilus pelagicus* is the only suspension feeding protodrilid. İt collects suspended food particles while drifting in a characteristic j-position in the water column of the cave (Fig. 26 A), and achieves neutral buoyancy by the beating of transverse and longitudinal bands of cilia. Food particles are intercepted by mucous secretions on the palps and brought towards the mouth by muscular movements (Fig. 26 B). Water currents produced by mouth cilia allow the food to be ingested. When disturbed, *Megadrilus pelagicus* swims by undulatory muscular movements. Sexes are separate and fertilization is presumed to involve the production of a spermatophore (a package containing sperm that the males deliver to the female) like in other species of the family.

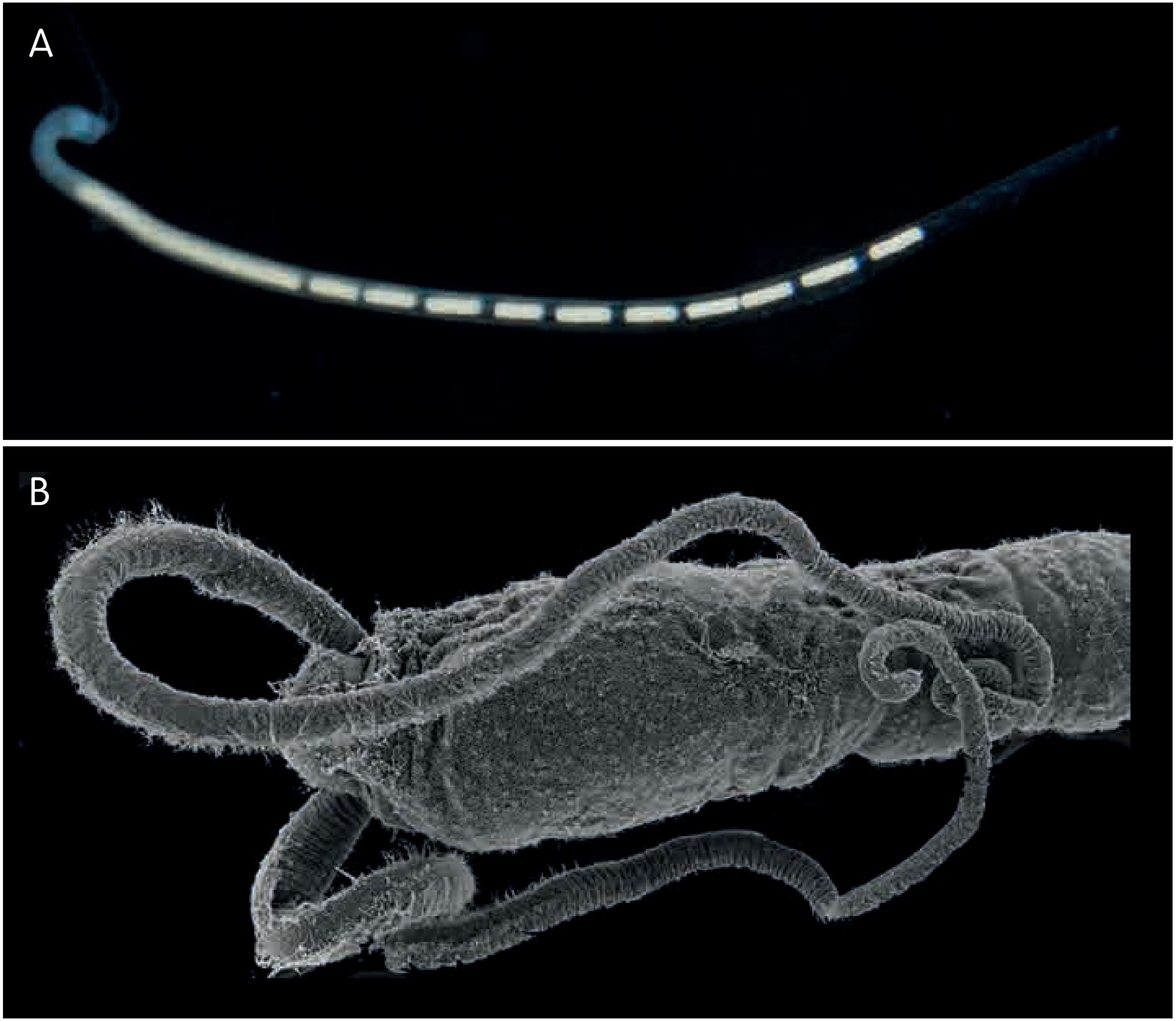
Affinity and origin: Protodrilidae is one of the most diverse families of interstitial annelids with 34 described species and several still undescribed. The family has a worldwide distribution in shallow water marine sediments with the highest diversity recorded from beach environments and shell gravel at 0-15 m depth. *Megadrilus* is a genus nested within Protodrilidae. Except for *Megadrilus pelagicus*, the remaining species of the genus are all marine, dwelling in shallow, coarse, gravel sediments. The genus is known from Australia, Central America, Caribbean, Canary İslands, Europe, and Brazil. Phylogenetic analyses of the genus support a sister position of *Megadrilus pelagicus* to the remaining marine species and suggest that this species originated from a shallow water interstitial marine ancestor.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



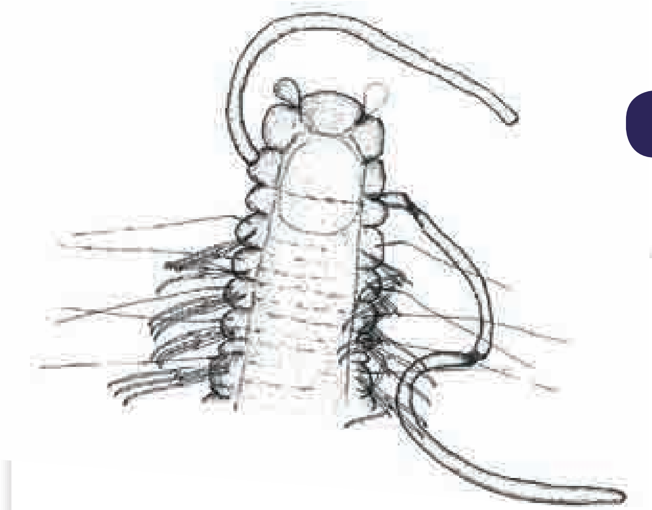
Distribution of the genus around the world



Juan Valenciano

Alejandro Martínez

Figure 26. (**A**) *Megadrilus pelagicus* feeding in the water column. (**B**) Electronic micrograph of the head showing the long, ciliated palps.



Macrochaeta n. sp. in Núñez *et al.* 1997

Size: 1.5-2 mm **Family:** Acrocirridae **Order:** Terebellida

İdentification: *Macrochaeta* n. sp. is a small annelid with a long and slender body, covered by papillae. The head bears a pair of short, club-shaped palps and three to four pairs of filamentous branchiae. The trunk segments have small parapodia with large compound neurochaetae (ventral chaetae) and simple capillary notochaetae (dorsal chaetae).

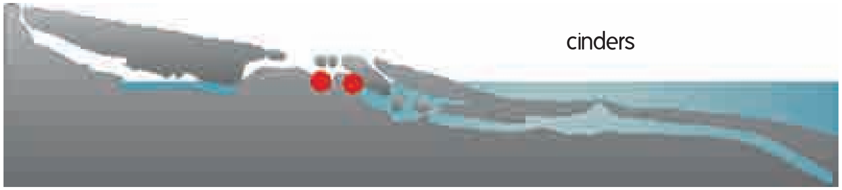
Habitat: Cinder accumulations in Jameos del Agua and at the entrance of Túnel de la Atlántida

Biology: Most of the biology of *Macrochaeta* n. sp. is unknown and based upon the observations from only a few individuals. The feeding ecology is also unknown, but it presumably feeds on organic matter, diatoms, and bacteria among the cinder grains.

Affinity and origin: *Macrochaeta* consists of 13 described species, most of them marine interstitial in coarse, shallow water sediments. Several records have come from similar sediments of marine caves in Tenerife and another stygobitic species is known from a cave in the Yucatan Peninsula, Mexico.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

NERİLLİDAE

Size: 1-1.5 mm **Family:** Nerillidae **Order:** Orbiniida

İdentification: Nerillids possess a short transparent body with 8-9 segments. The head is rounded and bears paired palps (club-shaped in *Leptonerilla* and *Mesonerilla*, long and cylindrical in *Meganerilla*, and thread-like in *Longipalpa*) and three antennae (except for *Meganerilla* which lacks antennae). Each trunk segment has bundles of compound chaetae with two (in *Leptonerilla*) or one (in the remaining species) interramal cirri arising between them. Chaetae are compound (consisting of two articulated parts) in all species found in the cave except for *Meganerilla*. The pygidium bears a pair of cirri in all species except for *Longipalpa*, which instead has a pair of ciliated lobes used for swimming.

Biology: Nerillidae contains 43 species in 14 genera and is found worldwide in all types of habitats, with the highest diversity in marine, subtidal sand. Most nerillids feed on organic matter, microalgae, and bacteria deposited among the sand grains. İnterstitial nerillids glide between the sand grains using special bands of cilia along the midventral axis of the body. Muscular escape responses are recorded in most of the species and consists of short periods of hectic undulatory swimming. *Mesonerilla* exhibit direct development, with females brooding their offspring on their posterior body segments. *Meganerilla cesari* most likely produces larvae as found in other species of this genus. The development of *Leptonerilla* and *Longipalpa* remains unknown. Except for *Mesonerilla armoricana* and *Longipalpa*, all species have separated sexes. *Longipalpa* is the only exclusively pelagic nerillid living in the water column of anchialine caves. *Longipalpa* swims with specialized bands of cilia and a pair of ciliated posterior lobes while it collects and feeds on suspended organic matter and bacteria with long ciliated palps.

STYGOPHYLE / NON ENDEMİC

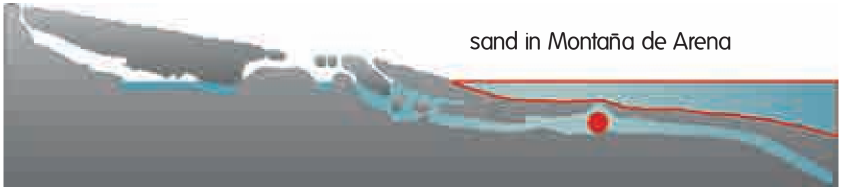
Mesonerilla armoricana Swedmark, 1959

Alejandro Martínez

Comments: Recorded at the sandy sediments in Montaña de Arena. The species is also common in coastal sediments from Europe and the Canary İslands.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world


Alejandro Martínez

STYOGOBİTE / ENDEMİC

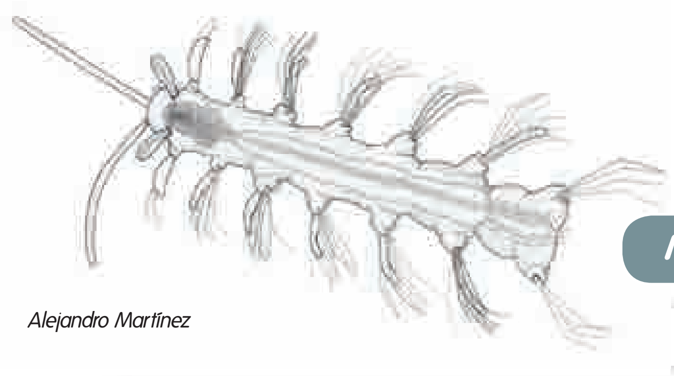
Mesonerilla n. sp. 1 in Worsaae, Martínez & Núñez, 2009

Comments: Only known from La Corona lava tube where it inhabits cinder patches and the sandy sediments at Montaña de Arena. This species is probably derived from marine shallow water ancestors.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube

Distribution of the genus around the world


Alejandro Martínez

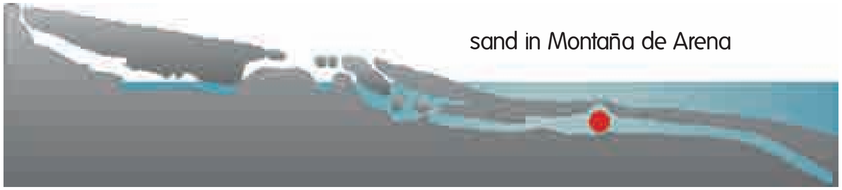
STYGOPHİLE /ENDEMİC

Mesonerilla n. sp. 2 in Worsaae, Martínez & Núñez, 2009

Comments: Only known from the sandy sediments of Montaña de Arena.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

STYGOPHİLE /ENDEMİC

Mesonerilla n. sp. 3 in Worsaae, Martínez & Núñez, 2009

Alejandro Martínez

Comments: Only known from the sandy sediments of Montaña de Arena.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube

Distribution of the genus around the world

STYGOPHİLE /ENDEMİC

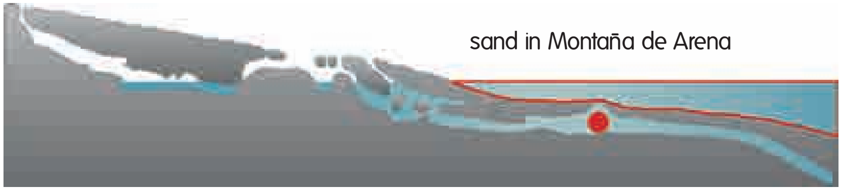
Meganerilla cesari Worsaae, Martínez & Núñez, 2009

Alejandro Martínez

Comments: Originally described from the sandy sediments of Montaña de Arena, it was later found from interstitial environments on Gran Canaria. The species was named after the famous Lanzarote artist, César Marinque, who designed Los Jameos del Agua tourist center.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world


Alejandro Martínez

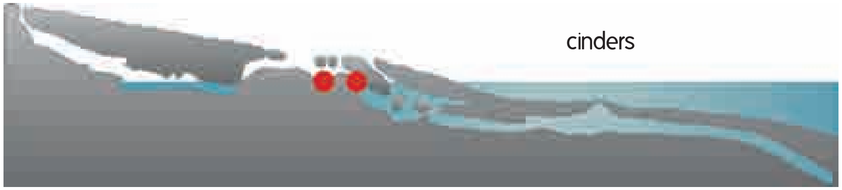
STYGOBİTE /ENDEMİC

Leptonerilla diatomeophaga (Núñez, 1997)

Comments: Found in the cinder patches and diatoms at Los Jameos del Agua and Túnel de la Atlántida. İt occurs in gravel from two other caves in Tenerife. Several species of the genus, most of them still undescribed, were collected in caves from Sardinia, Mallorca, Bermuda, and Bahamas. *Leptonerilla* is closely related to *Mesonerilla neridae*, known from hydrothermal vents in the Pacific Ocean.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world


Alejandro Martínez

STYGOBİTE/ENDEMİC

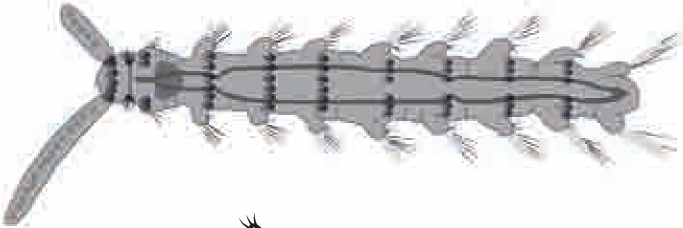
Longipalpa n. sp.

Comments: *Longipalpa*, exclusively found in the water column, is the most specialized nerillid from La Corona. *Longipalpa* n. sp. is closely related to at least three additional stygobitic species known from Bermuda, the Bahamas, Cuba, and Yucatan. How microscopic cave-limited annelids exhibit such a disjunct distribution remains a mystery. Some authors propose ancient colonization of caves with vicariance related to the opening of the Atlantic Ocean. Others instead, suggest dispersal through crevices in the sea floor.

DİSTRİBUTİON

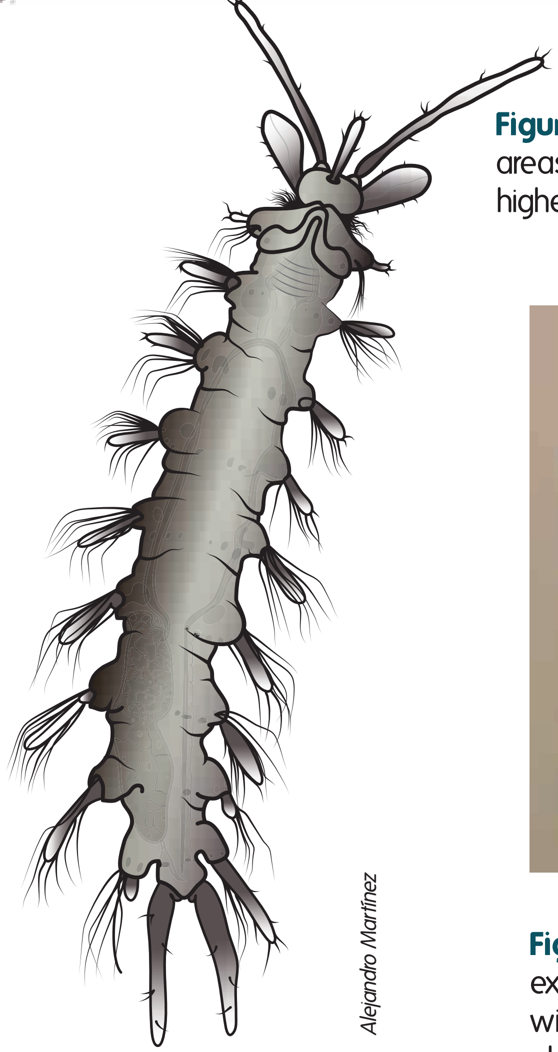
Distribution of the species in La Corona lava tube

Distribution of the genus around the world



Alejandro Martínez

Figure 27. *Meganerilla cesari* (1-1.5 mm in length) is found in the Montaña de Arena, at a depth of 30 meters and 750 meters of linear penetration from the entrance of Túnel de la Atlántida. It also occurs in shallow marine waters throughout the Canary Islands in coarse sandy sediments.

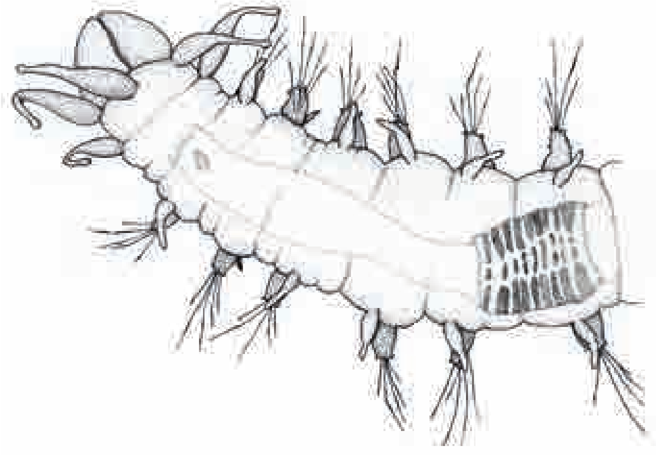


Alejandro Martínez

Figure 28. *Mesonerilla* n. sp. (approximately 0.7 mm) is found in areas of cinder rubble throughout La Corona lava tube; however higher abundances occur in Jameos del Agua.

Alejandro Martínez

Figure 29. *Longipalpa* n. sp., a nerillid annelid (less than 1 mm) occurs exclusively in the water column throughout La Corona lava tube. It swims with the pair of ciliated posterior lobes, visible on the right side of the photo, and collects suspended food particles with the very long palps, seen on the left.



All STYGOPHİLE /NON ENDEMİC except
***Sphaerosyllis* STYGOPHYLE/ENDEMİC**

Exogone gambiae Lanera, Sordino & San Martín, 1996
Miscellania dentata Martín, Alós & Sardá, 1990
Sphaerosyllis iliffei Núñez, Martínez & Brito, 2009
Syllis beneliahuae (Campoy & Alquézar, 1982)
Syllis garciai (Campoy, 1982)
Syllis gerlachi (Hartmann-Schröder, 1960)
Syllis parapari San Martín & López, 2000

Size: 1-10 mm **Family:** Syllidae **Order:** Phyllodocida

İdentification: Syllids from La Corona are clearly segmented with a well-defined head. The head bears three antennae, one pair of palps, which may be partially fused at the base. All, except *Sphaerosyllis iliffei*, have eyes. Parapodia are biramous and carry both compound and simple chaeta. The most distinctive feature of the family is the presence of strongly muscularized part of the digestive tract behind the pharynx opening (a proventriculus), which is visible through the skin as a dark cylindrical, light reflecting, barrel-shaped organ. İdentification to the species level is complicated due to the high number of species.

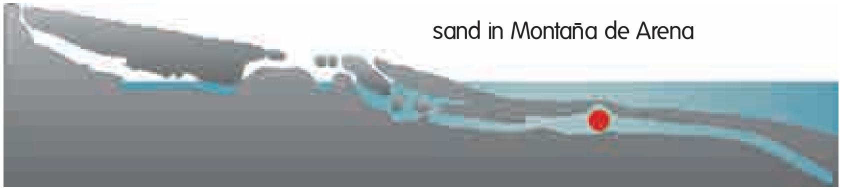
Habitat: Diatoms and cinders in Jameos del Agua and sediments of Montaña de Arena.

Biology: Syllids are found throughout most the marine environment. Although most of the species live in both hard and soft substrates along the continental shelf. Symbiotic syllids also exist, associated with sponges, cnidarians, echinoderms, or crustaceans. Except for *Sphaerosyllis iliffei*, all syllids recorded in La Corona lava tube are also found in marine habitats outside the cave.

Affinity and origin: Syllidae constitute a large family of annelids with approximately 700 described species. This family is placed in Errantia within the annelids and is related to other well-known annelid groups such as Nereididae, Hesionidae, and Nephtydae. *Sphaerosyllis iliffei* is the only described stygobitic syllid from a genus widespread in marine waters inhabiting hard to soft substrates. *Sphaerosyllis iliffei* has been only found from coarse sand at Montaña de Arena in La Corona lava tube. İt lacks eyes and pigmentation, although these features are also highly variable among marine species of the genus. *Sphaerosyllis iliffei* is further characterized by the arrangement of the chaetae as well as the presence of elongate ventral cirri at segment 13 which are to play a role in reproduction. The only described mature female was carrying a single embryo, unlike other species of the family that carry multiple. This might point towards a further adaptation to the cave environment.

DİSTRİBUTİON

Distribution of the *Sphaerosyllis iliffei* in La Corona lava tube



Distribution of the of the genus *Sphaerosyllis* around the world

MOLLUSCA

Mollusca is one of the most diverse animal phyla on Earth with more than 90,000 living species and 70,000 described fossils, numbers only surpassed by arthropods (p. 169). They are well known not only to zoologists, but are also highly appreciated for their culinary value, sought for their beautiful shells and important in producing useful drugs. Molluscs such as the octopus and cuttlefish are considered to be the most intelligent marine invertebrates. The fascinating morphology and variability in size of some of these animals have even led to myths; including the legend of the terrible Kraken, inspired by the giant squid Architheuthis.

Despite their morphological diversity, molluscs are characterized by the presence of a shell which might consist of one, two, or eight plates. The shell however is highly variable and may only consist of external spicules, calcareous or cartilaginous internal structures, or be lost altogether. Molluscs also present an unusual ribbon of teeth, called the radula, that they use to scrape along hard surfaces to graze on algae or bacterial film or allow predation of incrusting organisms. Similar to the shell, the radula is also extremely adaptable among the groups, consisting of a variable number of toothed rows, modified into harpoons connected to venomous glands, or completely absent.

Molluscs are placed within the protostome clade Lophotrochozoa (Box 2), probably sister to annelids in a clade called Trochozoa characterized by the presence of trochophore larvae. Molluscs are traditionally divided into ten classes including Caudofoveata and Solenogastres (worm-like molluscs bearing spicules), Polyplacophora (chitons), Monoplacophora (deep sea limpets with a cap-like shell), Gastropoda (snails and slugs), Bivalvia (clams and mussels), Scaphopoda (tusk shells) and Cephalopoda (octopus, squids and cuttlefish).

Molluscs in subterranean environments

Molluscs are abundant in subterranean habitats, where they are represented by at least 450 stygobitic species, mostly gastropods. The family Hydrobiidae is the most diverse, occuring in freshwater caves and groundwater. In anchialine and marine systems, Neritiliidae is the richest in species number especially in the Indopacific. The species *Neritilia margaritae* is the only neritilid recorded from the Canary Islands, endemic from a cave in Tenerife. Other gastropod families are less diverse but still contain stygobitic species, such as Tornidae with the species *Teinostoma* brankovitsi recently described from Yucatan caves, or Caecidae, with two known stygobitic species from Bermuda, *Caecum caverna* and *C. troglodyta*. Stygobitic bivalves are rare, with the remarkable exception of the three relict stygobitic species of the genus *Congeria*, endemic from freshwater


Figure 30. The gastropod *Phorcus atratus,* considered an accidental, is occasionally found in Los Jameos del Agua but has not formed a successful breeding population.

Juan Valenciano

caves in the Dinaric Karst and considered as a living fossils.

Diversity of molluscs in La Corona lava tube

Ten species of gastropods and three species of bivalves have been recorded from La Corona lava tube. Most of these species are common littoral and subtidal inhabitants that are also occasionally recorded in Los Jameos del Agua and the entrance pool to Túnel de la Atlántida. These species rarely form significant populations and their presence in the cave is accidental. Some of these species correspond to large and typically intertidal animals

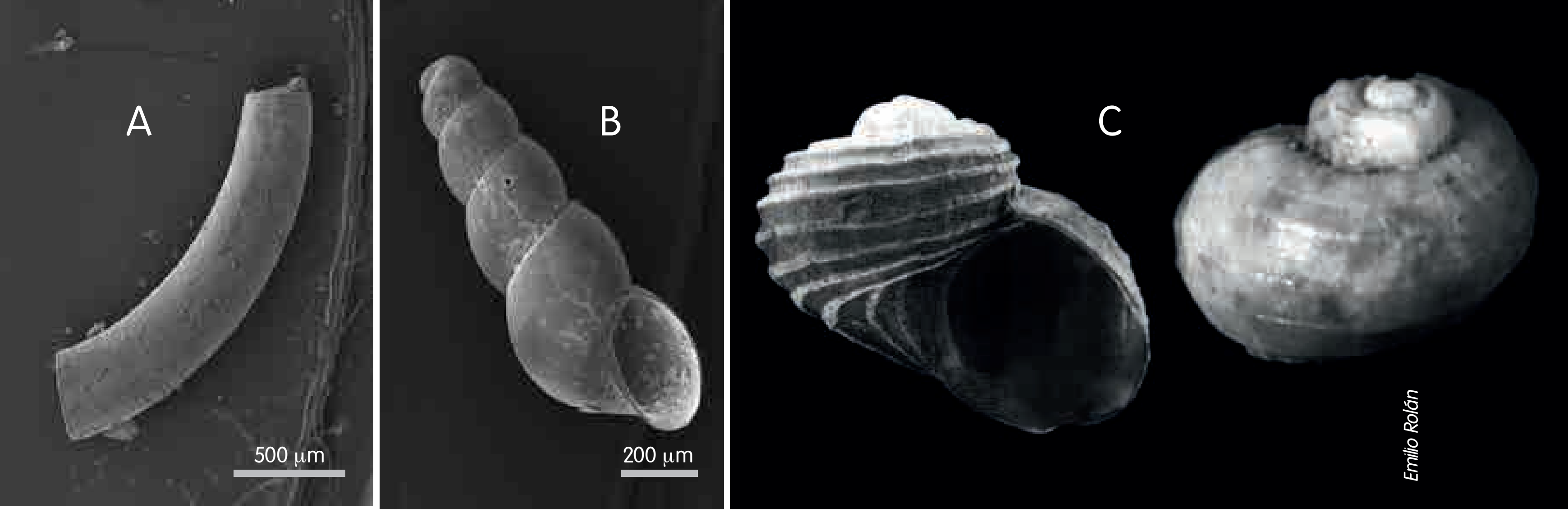


Figure 31. Scanning electron micrographs of interstitial gastropods common in the sediments of Montaña de Arena, 30 m depth and 750 m horizontally from entrance pool: (**A**) *Caecum clarkii*, (**B**) *Pseudobis jameoensis*, (**C**) *Cima minima*.

such as *Jujubinus exasperatus* (recorded at Los Jameos del Agua in 1969 and 2006), *Phorcus atratus* (Fig. 30) (recorded in Los Jameos del Agua in 1936, 1969, and 2014), *Littorina striata* (recorded once in Los Jameos del Agua and once in Cueva de los Lagos), and *Bolma rugosa, Patella ulyssiponensis, Columbella adansoni, Stramonita haesmatoma, Pinna rudis,* and *Spondylus senegalensis* (all recorded once in 1969). Other accidental gastropods are micromoluscs, including the cerithiid *Bittium reticulatum*, the rissooid *Manzonia unifasciata*, and *Botryphallus epidauricus*, this latter species also found in Cueva de los Lagos.

Additionally, populations of stygophilic interstitial gastropods inhabit the sediments of Montaña de Arena: *Caecum clarkii* (Fig. 31 A), is a caecid common in interstitial environments throughout the Canary Islands characterized by its tubular shell adapted to move among the sand grain; the tiny skeneid *Pseudorbis jameoensis* (Fig.31 C), first described from Montaña de Arena, but subsequently found in marine sediments in Gran Canaria; and *Cima minima* (Fig. 31 B), a cosmopolitan species belonging to the family Cimidae, common in interstitial environments and algae mats throughout the Canary Islands.

ECHİNODERMATA

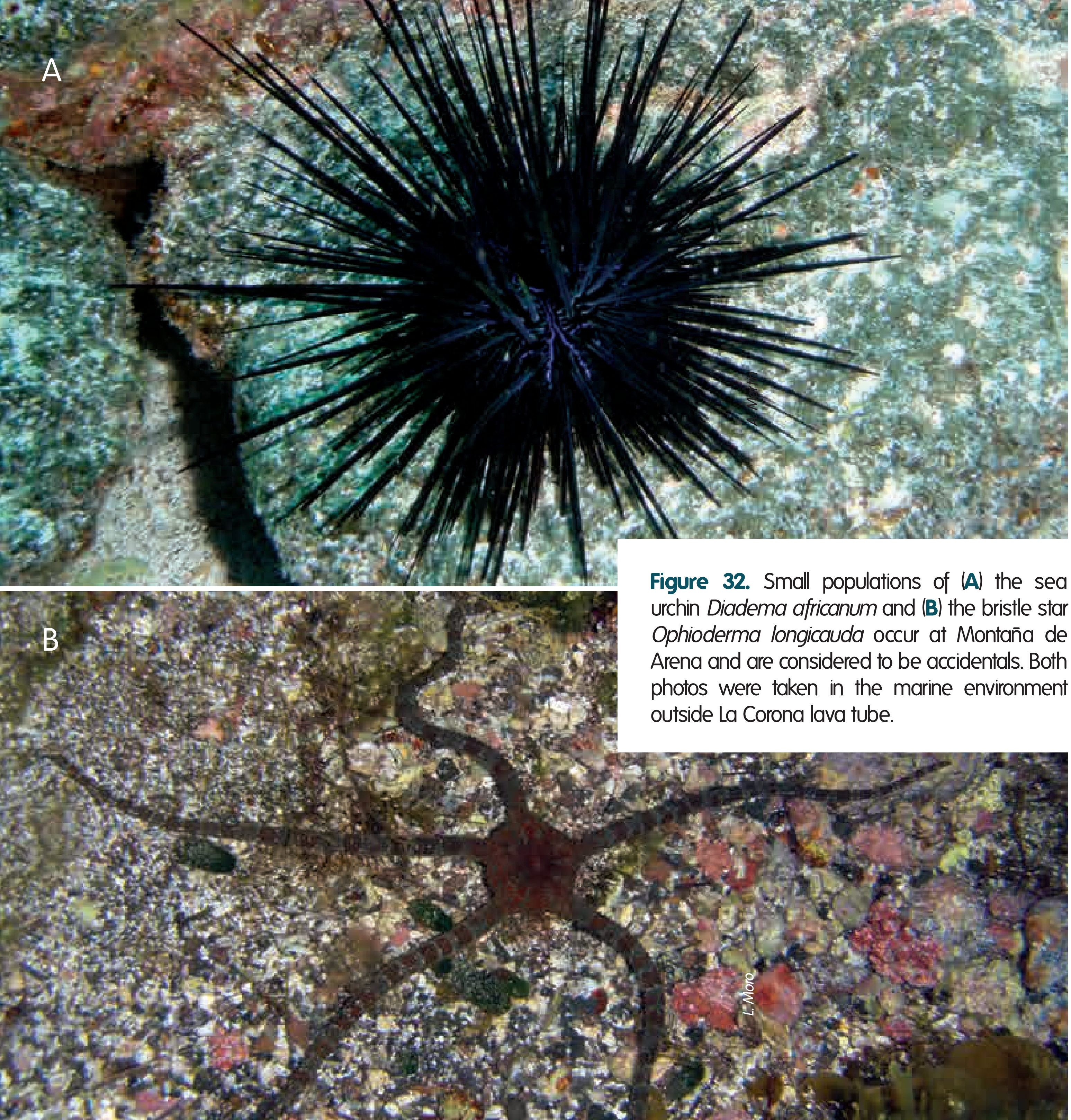
Echinoderms, meaning spiny skinned, are exclusively marine animals with approximately 6000 described species, including sea urchins, seastars, brittle stars, basket stars, sea cucumbers, and sea lilies. Most species are benthic, moving along the sea floor or found burrowing in sediments, with few highly specialized interstitial forms. Echinoderms may be suspension feeders like crinoids and some brittle stars, grazers such as many sea urchins, or predators like the seastars. Some echinoderms are vital to coral reef and other hard bottomed ecosystems as regulators of algal growth. Alternatively, overfishing of natural predators to the sea urchin *Diadema africanum* has allowed dense populations to form in some areas of the Canary İslands. This has had a devastating effects on the algal populations and causes dramatic changes to the shallow water rocky ecosystems of the islands.

Echinoderms have a calcareous endoskeleton lying just below the epidermis as well as a complex water vascular system connected to a series of tentacle-like projections, the ambulacral system, that is involved in locomotion, respiration, and sensory functions. However, the most distinctive features of echinoderms is the loss of bilateral symmetry during larval development with adults becoming pentaradially symmetrical.

The position of echinoderms is well established by molecular and morphological data (Box 2). They belong to the clade Deuterostomia which is closely related to Hemichordata. Echinodermata is divided into five classes which include Crinoidea (sea lilies), Asteroidea (seastar), Ophiuroidea (brittle stars), Echinoidea (sea urchins), and Holothuroidea (sea cucumbers).

Echinoderms in subterranean environments and La Corona lava tube

Echinoderms are sometimes found in caves, although in most instances they are represented by marine accidental species that colonize entrance areas of the cave. Two stygobitic species have been described including an anchialine seastar from Cozumel (México), and a brittle star from San Salvador İsland (the Bahamas). Only two marine species have been recorded in La Corona: the urchin *Diadema africanum* (Fig. 32 A) and the brittle star *Ophioderma longicauda* (Fig. 32 B), both found only at Montaña de Arena in Túnel de la Atlántida.



Antonio Martin

Leopoldo Moro

Figure 32. Small populations of (**A**) the sea urchin *Diadema africanum* and (**B**) the bristle star *Ophioderma longicauda* occur at Montaña de Arena and are considered to be accidentals. Both photos were taken in the marine environment outside La Corona lava tube.

ARTHROPODA

Arthropods are the most diverse group of animals on Earth, comprising approximately 85% of all described species. They are known from all ecosystems, ranging from the deepest seas to the highest mountains. Arthropods colonized the land during the Silurian (443-419 Ma) and radiated to become one of the most common and abundant groups of animals outside the ocean. İnsects account for most of the terrestrial arthropod diversity, sometimes acting as ecosystem builders and exerting strong influence on the evolution of many other groups of organisms, with fascinating examples of coevolution between land plants and pollinating insects. Terrestrial arthropods were also the first group of metazoans capable of flight, conquering the air in the Carboniferous (320 Ma), much earlier than any vertebrate. İn the ocean, crustaceans are one of the dominant groups and a very important component of marine food chains, with copepods and krill being the main prey of many species of fish and marine mammals. Arthropods also influence humans, holding a love and hate relationship with us since the early days of our species. On one hand, arthropods are important as a source of food, pollinators, and producers of many material goods such as honey, wax, and silk; but on the other hand, they are pests, vectors of diseases, and a source of stings and bites. The influence of arthropods in human culture is reflected in many old traditions and legends, as well as in contemporary movies and tales, in which insects or crustaceans often become heroes or villains.

Although they look very different, all arthropods present a body divided in segments grouped into functional units or tagmata. The segments in each tagma normally bear a pair of appendages with two rami, an endopod (internal branch), and an exopod (external branch), modified for specific functions. The first tagma constitutes the head and normally bears appendages modified as mouthparts and sensorial organs, whereas the subsequent tagma, the thorax and the abdomen are provided with appendages used for locomotion and reproduction.

Arthropods were traditionally grouped with annelids in the clade Articulata, first proposed by French zoologist George Cuvier in the 19th century. However, recent analyses consistently recovered arthropods as grouped with other molting animals in the clade Ecdysozoa (see Box 2). The internal relationships among the Arthropoda are quite complex and still debated. A more detailed overview, based on the latest studies focused on those groups with anchialine representatives, is provided in Box 3.

-BOX 3- The Arthropoda Tree of Life

The relationships among arthropods have been debated for more than 200 years. These debates mostly focus on the relationship of five key well-supported groups: Pycnogonida (sea spiders), Euchelicerata (spiders, scorpions, mites), Myriapoda (millipedes and centipedes), Hexapoda (insects), and Crustacea (shrimps, crabs) (Fig. 33). These five groups are monophyletic in most analyses except for Crustacea, which includes Hexapoda. Although several issues remain open, the last two decades of research have progressively increased our certainty with several relationships, allowing us to have a general overview at least on the major relationships of arthropods.

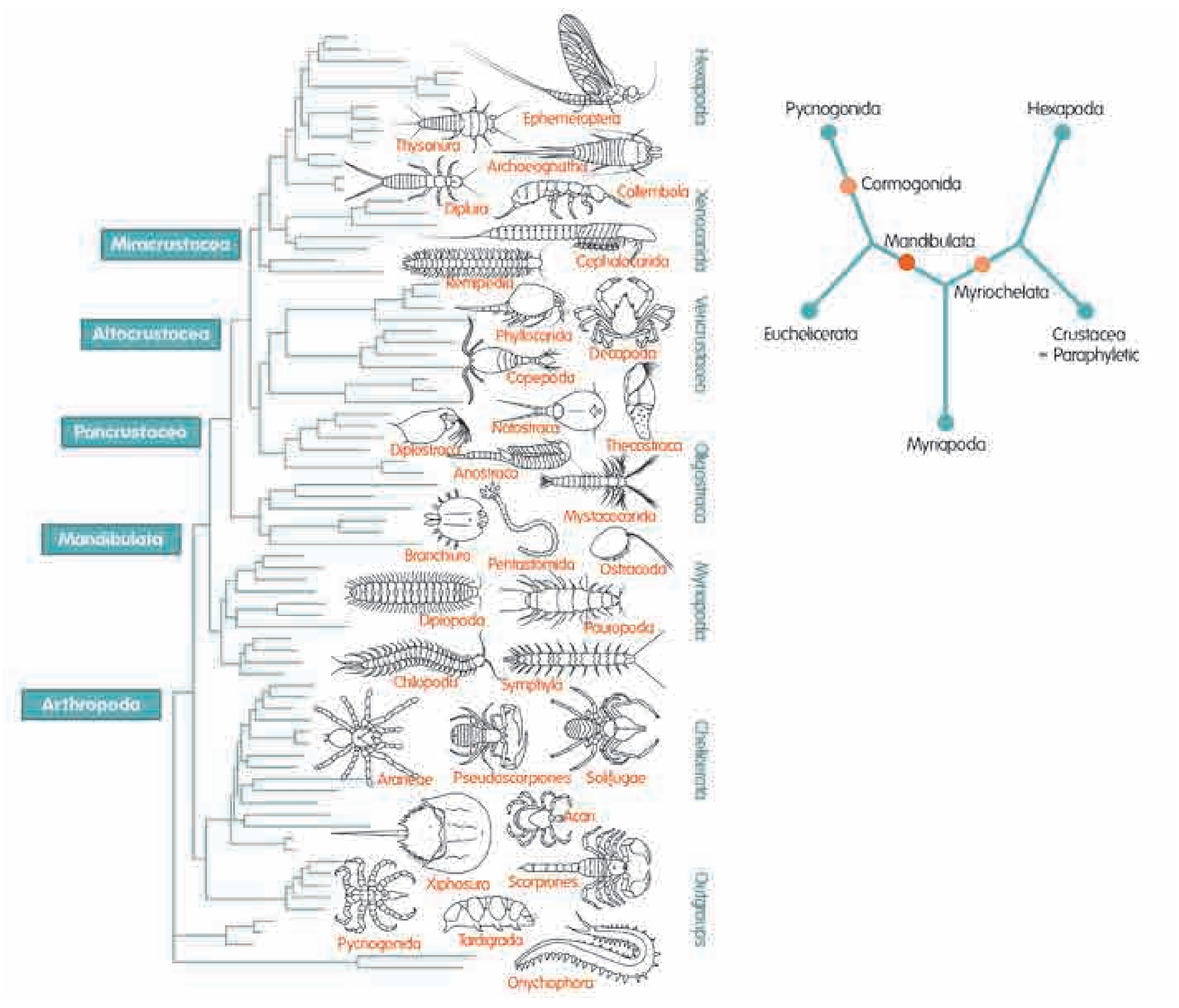
Phylum Arthropoda is divided into two major lineages, Chelicerata, grouped into Pycnogonida and Euchelicerata, and Mandibulata consisting of Hexapoda, Myriapoda, and Crustacea (Fig. 33). **Chelicerata** is characterized by special fang-like mouthparts called chelicerae, which are only present in this clade. The group is further divided into Pycnogonida (sea spiders) and true chelicerates or Euchilicerata, this latter subdivision splitting off into Arachnida (spiders, scorpions, harvestmen) and Merostomata, including the horseshoe crabs (Xiphosura) and the extinct sea scorpions.

Mandibulata is characterized by the presence of mandibles and splits off as two clades, Myriapoda (centipedes and millipedes) and Tetraconata (crustaceans and insects). **Tetraconata**, which is named after the presence of squared ommatidia (compound eyes), is very diverse and its internal relationships remain poorly understood. Tetraconata splits into four clades: Oligostraca, Vericrustacea, Xenocarida (which include the anchialine cave crustaceans described below) and Hexapoda.

- **1.** Oligostraca includes four lineages of strange-looking crustaceans, with Ostracoda (mussel shrimp) being the most diverse and the only one with known anchialine species (p. 173). The remaining three oligostracan lineages, the interstitial Mystacocarida, and the parasitic Pentastomida and Branchiura, have few species and have never been found in anchialine caves.

- **2.** Vericrustacea includes all the common crustaceans, splitting into Branchiopoda and Multiscrustacea clades.
    - **Branchiopoda** includes several groups of small freshwater crustaceans such as tadpole shrimp (Notostraca), cladocerans (Diplostraca), and artemia and their relatives (Anostraca). Although some species of these groups occur in subterranean freshwater habitats, they are scarce in anchialine environments and absent in La Corona lava tube.
    - **Multicrustacea** includes the majority of the crustaceans known in anchialine habitats. The clade is subdivided into three groups, **Copepoda** (p. 180) sister to **Thecostraca** (barnacles) and **Malacostraca** (shrimps, amphipods). Malacostraca can be further subdivided into **Phyllocarida**, which includes Caribbean anchialine species; **Hoplocarida**, including mantis shrimps (Stomatopoda); and **Eumalacostraca** including Syncarida (Bathynellacea and Anaspidacea), very common in freshwater caves; Eucarida (Decapoda, Euphasiacea and Amphionidae) and Pericarida. The Pericarida include Amphipoda (p. 201), Cumacea (p. 200), İsopoda (p. 219), Lophogastrida (shrimp-like animals from deep sea), Mictacea, Spelaeogriphacea, Mysida and Stygiomysida (p. 192), Tanaidacea and Thermosbaenacea (p. 198). Lophogastrida is the only group not presently found in subterranean anchialine.
- **3. Xenocarida** is a small clade that includes the Cephalocarida and Remipedia. Cephalocarids are strange crustaceans exclusively dwelling among sand grains, whereas remipedes are exclusively found swimming in marine waters from anchialine caves (p. 232). Xenocarida is the sister group to **Hexapoda**, which includes all insects, although this relationship is poorly supported morphologically.

-BOX 3- The Arthropoda Tree of Life



Regier et al, 2010.

Figure 33. Summary of the relationships among Arthropoda.

OSTRACODA

Ostracoda, also called mussel shrimp or seed shrimp, are a peculiar group of crustaceans with 5,650 described living species. They have a very characteristic appearance due to their bodies being enclosed in a bivalve carapace impregnated with calcium carbonate, somewhat resembling the shells of bivalve molluscs. Most ostracods are small marine species, barely reaching a few millimeters in length. Because of the presence of a mineralized carapace, the fossil record of Ostracoda is very rich, with more than 10,000 described fossil species dated back to the Cambrian (650 Ma).

The carapace of ostracods is formed by two valves joined by a dorsal hinge line consisting of a non-calcified strip of cuticle. These valves can be closed by the contraction of several transverse adductor muscles, inserted near the center of each valve. The morphology of the carapace is highly variable and used to recognize different species. It can be smooth or decorated with conspicuous ornamentation including pits, tubercles, or irregular projections and chitinous setae. Inside the carapace, the head constitutes most of the body of ostracods, while the trunk is highly reduced and lacks segmentation. The most conspicuous appendages are antennae and maxillae. Trunk appendages are reduced to only one or two pairs. The morphology of the appendages is quite variable, ranging from leg-like structures to those modified for swimming, feeding, clasping, or grooming the carapace.

The phylogenetic position of Ostracoda within crustaceans is not fully resolved, although recent analyses recovered the group within the clade Oligostraca (Box 3). Ostracods are divided into two major groups: Myodocopa and Podocopa. Myodocopa is characterized by a poorly calcified carapace with a non-concave ventral margin and the presence of a notch in the anterior margin of both valves, which permits the protrusion of the antennae when the valves are closed. All of these features are absent in Podocopida. Additionally, in myodocopans, the exopod of the second antenna is longer than the endopod, whereas in podocopans, the exopod is short and the endopod much longer.

Ostracods in subterranean environments

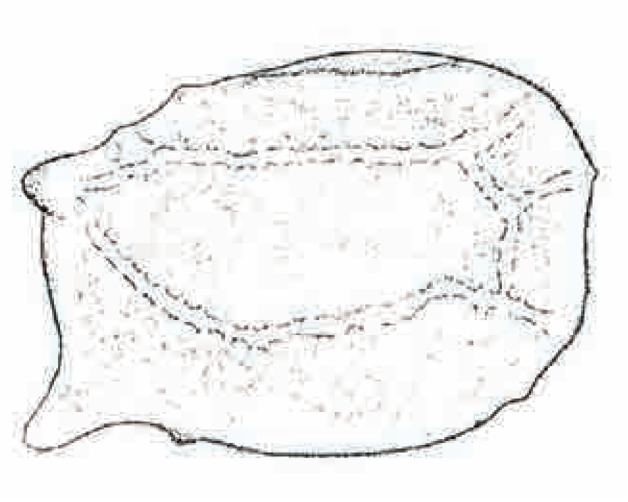
Ostracods are very common in caves with about 310 described stygobitic species. Podocopans are relatively well studied in anchialine habitats of the Galapagos, Bahamas, Bermuda, and Australia. However, they mostly consist of marine or freshwater species, capable of surviving in certain cave habitats, such as cave entrances or pools.

From an evolutionary perspective, cave myodocopans are more interesting, represented by three exclusively stygobitic lineages with disjunct distributions in the Caribbean, Canary Islands, Australia, and

Christmas Island indicating ancient colonizations and subsequent radiations into anchialine habitats. These lineages include the exclusively stygobitic family Deeveyidae with the genera *Deeveya* (seven species in the Bahamas and adjacent Turks and Caicos Islands) and *Spelaeoecia* (12 species in Bahamas, Bermuda, Cuba, Jamaica, and Yucatan); and the family Thaumatocyprididae, consisting of two deep sea genera, *Thaumatoconcha* and *Danielopolina*, sister to the two entirely stygobitic lineages *Humphreysella* and *Welesina* (see below). Cave-dwelling myodocopan species are described in other families, but always related to typically marine genera (possibly indicating more recent cave colonization events).

Ostracods in La Corona lava tube

Four species of ostracods are recorded from La Corona lava tube. *Humphreysella phalanx* and *H. wilkensi* represent true stygobites, whereas *Eusarsiella bedoyai* and *Eupolycope pnyx*, in spite of being endemic from the cave, belong to genera widespread in the open ocean.



Eusarsiella bedoyai Baltanás, 1992

Size: 1-1.5 mm **Family:** Sarsiellidae **Order:** Myodocopida

İdentification: *Eusarsiella bedoyai* can be identified by the shape of its carapace, with two strong posterior processes. The surface of the carapace is decorated by a u-shape cordon, with one ramification towards each of the posterior processes and three ramifications towards the anterior margin.

Habitat: Coarse sand sediments in Montaña de Arena.

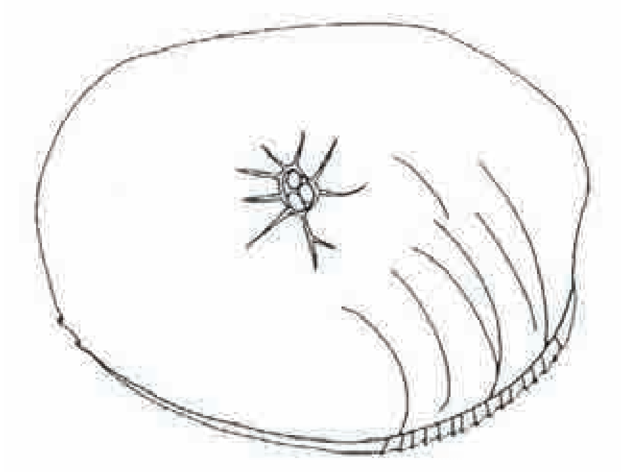
Biology: *Eusarsiella bedoyai* is probably an interstitial species, feeding on detritus among the sand grains.

Affinity and origin: The genus *Eusarsiella* includes more than 50 described marine species from all over the world. Most species of the genus inhabit shallow waters, although a few of them are recorded from bathyal depths. Another species of the genus, *Eusarsiella styx,* is described from anchialine caves in Bermuda. Both species are found in marine-like habitats within caves and are most likely not true stygobites, but instead marine species capable of establishing populations in these cave habitats, while also likely to exist in the open ocean.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube

Distribution of the genus around the world



Eupolycope pnyx Kornicker & İliffe, 1995

Size: 0.1-0.2 mm **Family:** Polycopidae **Order:** Halocyprida

İdentification: This species can be recognized by the small size of the carapace, which is completely rounded and without processes or conspicuous ornamentation.

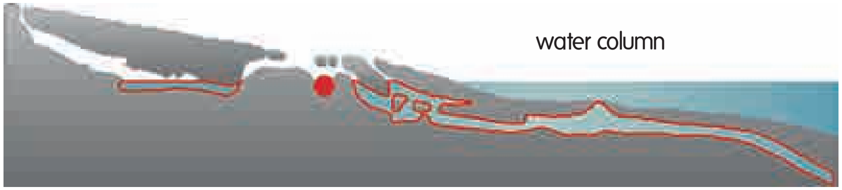
Habitat: Water column in Túnel de la Atlántida.

Biology: *Eupolycope pnyx* possibly feeds on suspended particles in the water column. İt is a relatively common species, frequently collected in plankton tows.

Affinity and origin: *Eupolycope pnyx* is the only stygobitic species of the genus, which otherwise consists of seven described species from shallow water marine environments in the Northern Hemisphere. This species possibly colonized the cave from marine shallow water environments.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

Humphreysella wilkensi (Hartmann, 1985)
Humphreysella phalanx (Kornicker & İliffe, 1995)

Size: 1-1.5 mm **Family:** Thaumatocyprididae **Order:** Halocyprida

İdentification: *Humphreysella* are small unpigmented ostracods, lacking eyes. The carapace is oval, with anterior and anterior-posterior processes. The two stygobitic species from Lanzarote are distinguishable by the presence of a posterodorsal process and reticulation in the carapace in *H. wilkensi* (Fig. 34 A), both features absent in *H. phalanx* (Fig 34 B).

Habitat: Water column of La Corona lava tube and anchialine wells around the island.

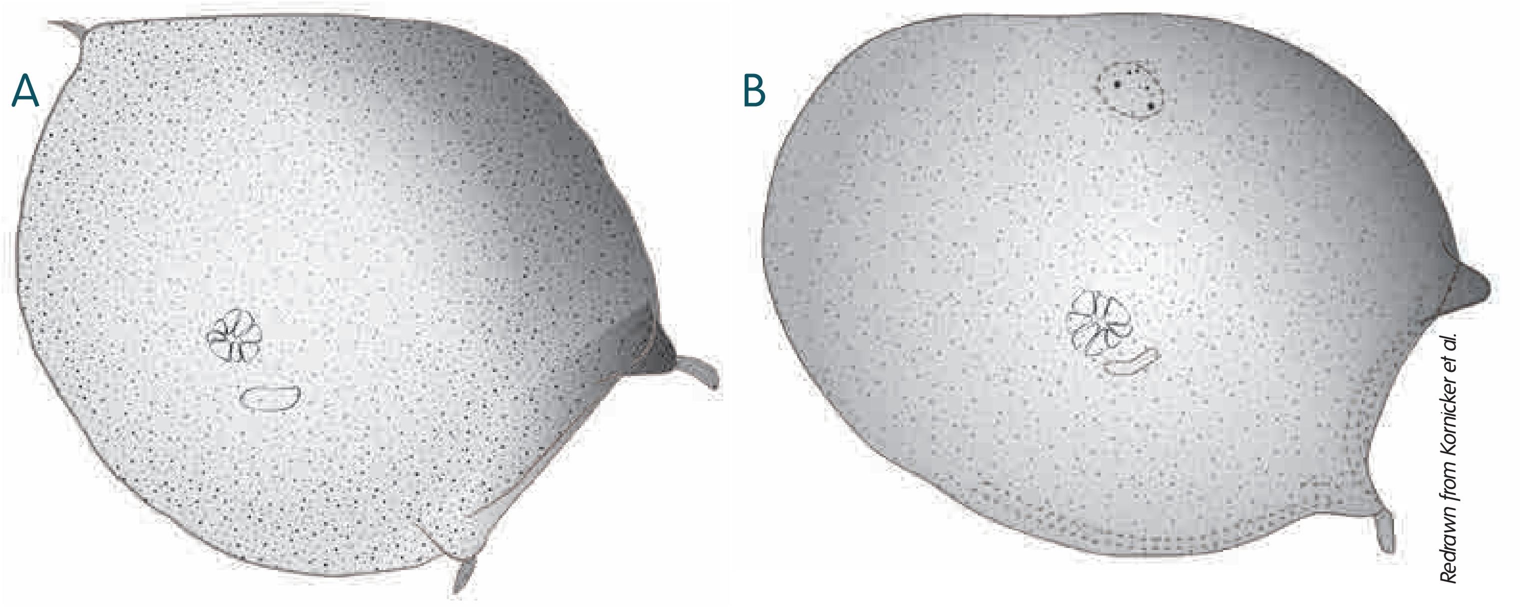
Biology: *Humphreysella* are relatively common in La Corona lava tube, although they are difficult to observe due to their small size. Both species swim by stroking the second antennae (Fig. 35), the only prominent appendages (Fig. 36). The gut is often filled with amber or brown organic particles lacking recognizable fragments of animals, suggesting that they might feed on detritus or bacteria. Collection of several specimens using baited traps supports the idea that *Humphreysella* can also act as a scavenger. The presence of *H. wilkensi in* anchialine wells around the island indicates that they can likely disperse through anchialine crevicular environments. İn contrast to other ostracods, *Humphreysella* never occurs in sediments, being unable to burrow or colonize interstitial spaces.

Affinity and origin: *Humphreysella* belongs to Thaumatocyprididae, which consists of seven genera: *Pokornyopsis* and *Thaumatomma* (only known from fossils), *Thaumatocypris*, *Danielopolina* and *Thaumatoconcha* (which inhabit the deep sea) and *Welesina* and *Humphreysella* (which are exclusively anchialine). The species within *Welesina* and *Humphreysella* were initially described in the genus *Danielopolina*, but cladistic analyses showed a lack of synapomorphies for the group (Box 1). *Welesina* currently consists of a single anchialine species in Western Australia, whereas *Humphreysella* contains the ten remaining described anchialine thaumatocypridids, found in the Caribbean, Canary İslands, Christmas İsland, and Galapagos. Although evolutionary analyses suggested that the common ancestors of *Welesina* and *Humphreysella* probably colonized anchialine habitats from the deep sea, it has been argued that this scenario contradicts paleogeographical evidence, instead depicting a Tethyan shallow water ancestry followed by vicariant events related to plate tectonics.

DİSTRİBUTİON

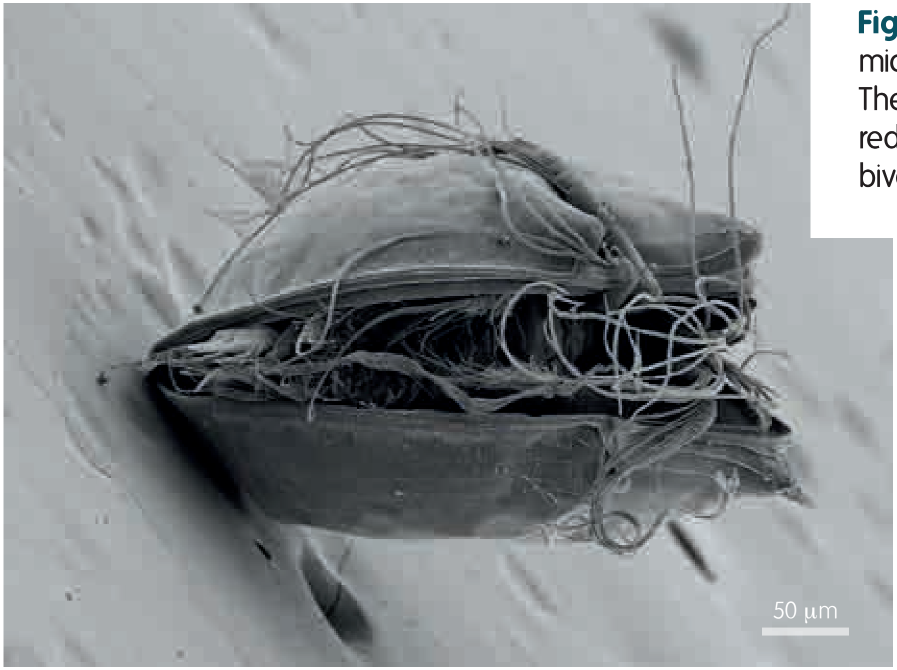
Distribution of the species in La Corona lava tube

Distribution of the genus around the world



Redrawn from Kornicker et al.

Figure 34. (**A**) *Humphreysella wilkensi* is characterized by the presence of three projecting processes in the carapace, whereas (**B**) *Humphreysella phalanx* has only two.



Alejandro Martínez, Brett C. Gonzalez

Figure 35. Scanning electron micrograph of *Humphreysella phalanx*. The body of all ostracods is very reduced and packed tightly inside the bivalved carapace.

Figure 36. *Humphreysella wilkensi* (approximately 1 mm) swims in the water column using its second pair of antennae. This specimen was photographed under a stereomicroscope.

COPEPODA

Copepoda is the largest and most diverse group of crustaceans with more than 24,000 described species, classified into 2,400 genera and 210 families. Although most species are marine, the group is also abundant in freshwater and semi-terrestrial environments, such as mosses, soil-water films, and leaf litter. Parasitic and symbiotic species also exist. Some parasitic forms attach under scales of fish or in their gills, occasionally becoming a serious pest to commercial fish farms. Others are beneficial to humans, as they act as biological vectors to remove disease-bearing mosquito larvae that are responsible for malaria or dengue. In the ocean, copepods are a very important component of trophic levels, being one of the most abundant constituent of the plankton in terms of biomass, but also acting as a link between primary producers and higher trophic levels in the marine pelagic food web.

Copepods are small, ranging between 1-5 mm. They are generally cylindrical, anteriorly rounded or pointed, and tapering towards the posterior end. The body is divided into the anterior prosome and the posterior urosome by a major articulation. The prosome includes the cephalothorax, consisting of the head fused with the first 1-2 thoracic segments and covered by a cephalic shield, as well as several free visible thoracic segments. The head bears a median naupliar eye which may be absent in many cave species, two pairs of antennae, and several pairs of mouth parts. The antennae consist of a variable number of segments (group specific), and present setae (long sensory hairs) and thick tubular chemosensory structures called aesthetascs. The first antenna is uniramous and generally longer than the second biramous antenna. The antennae are often used for swimming and are modified in males for holding the females during copulation. Additionally, the prosome has the maxillipeds used for feeding and five pairs of legs for locomotion. The urosome consists of five segments that are normally narrower than the prosomal segments, and lacks appendages, except for a single pair of caudal rami.

Copepoda are related to Cirripedia (barnacles) within the clade Vericrustacea (Box 4). The internal systematics of Copepoda have been reviewed several times during the last several decades. Currently, copepods are divided into nine orders grouped in three classes, although the relationships among these orders are still debated. Two of these orders (Monstrilloida and Siphonostomatida) include mostly symbiotic or parasitic species, with the remaining orders (Calanoida, Cyclopoida, Gelyelloida, Harpacticoida, Misophrioida, Mormonilloida, Platycopioida, and Poecillostomatoida), mostly consisting of free-living species. Stygobitic copepods are described in the orders Harpacticoida, Calanoida, Cyclopoida, Misophrioida, Gelyelloida, and Platycopioida, but only the first four are present in La Corona lava tube and considered here. Harpacticoida are mostly benthic Calanoida are mostly planktonic; and Cyclopoida include both planktonic and epibenthic species. Misophrioida, contains few described species, but a relatively high diversity of stygobites, some of them represented by genera with disjunct distributions (see below).

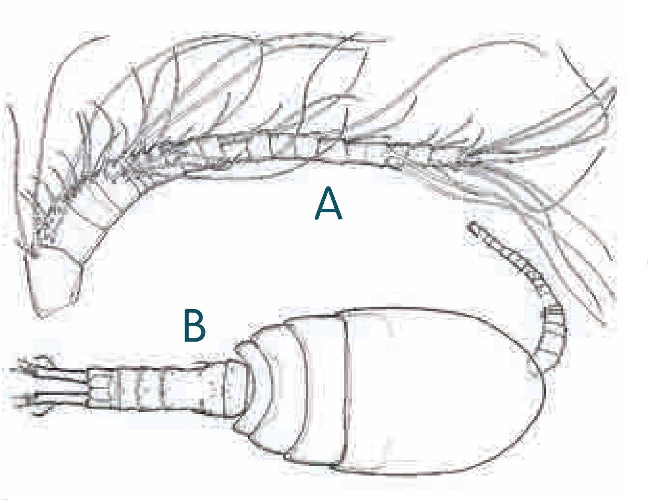
Copepods in subterranean environments

Copepoda are the most diverse group of crustaceans in caves, with at least 1,000 described species, of which many inhabit anchialine caves. ***Misophrioida*** is very relevant from a biogeographic point of view, as it consists of approximately 25 stygobitic species. Some misophrioids belong to lineages with disjunct distributions, while others are related to deep sea or shallow water hyperbenthic species. ***Calanoida*** is also very rich in stygobitic species, including several closely related families with abundant stygobites, such as Epacteriscidae, Ridgewayiidae, and Arietellidae. Other families of calanoid copepods with stygobites are Boholinidae, Diaptomidae, Fosshagenidae, Pseudocyclopidae, and Stephidae. ***Cyclopoida*** includes several stygobitic species, mostly belonging to widespread marine genera. The exception is the exclusively anchialine family Speleoithonidae, with three endemic species from Bermuda and the Bahamas. Finally, ***Harpacticoida*** has the highest diversity of species in subterranean habitats, although is poorly studied in anchialine caves. The two main harpacticoid families known to have stygobitic anchialine species are Superornatiremidae and Rotunidiclipeidae.

-BOX 4- Identification of the four main anchialine copepods lineages

Although the identification of copepods to the species level is complicated, even for specialists, classifying copepods within an order can be generally done with the aid of a stereomicroscope. The following chart aims to help the non-specialist. Listed below are the key characters of the four orders found in La Corona lava tube, as well as behavioral observations.

- **Calanoida**: The prosome and urosome articulate between the 5th and 6th segments, with the urosome much narrower. The first antenna is usually as long as the body and much longer than the second, which is difficult to observe. Normally pelagic, they swim in short jumps using their antennae.
- **Cyclopoida**: The prosome and urosome articulate between the 4th and 5th segments, with the urosome much narrower. The first antenna is usually much shorter than the body and equal or longer than the second. Pelagic and epibenthic species swim using their antennae, moving in short jumps.
- **Misophrioida**: The prosome and urosome articulate between the 4th and 5th segments, with the urosome much narrower. The first antenna is usually much shorter than the body and equal to or longer than the second. The antennae consist of a comparatively large number of segments. Caudal rami are often very long. Pelagic and epibenthic species swim in an undulating fashion such that the body is in continuous motion.
- **Harpacticoida**: The prosome and urosome articulate between the 4th and 5th segments, with the urosome and prosome of equal width. The first antennae is much shorter than the second. Normally benthic, they are poor swimmers and often crawl on the substratum using their legs.



Oromiina fortunata Jaume & Boxshall, 1997

Size: 0.9-1 mm **Family:** Smirnovipinidae **Order:** Cyclopoida

İdentification: *Oromiina fortunata* can be identified by the lack of eyes and pigmentation. The cuticle is ornamented with small tubercles. The prosome includes four segments, but only three are visible since the first one is hidden below the cephalic shield (**B**). The first pair of antennae is symmetrical and in females consists of 17 segments having long setae and short aesthetascs (**A**). The urosome includes five segments with a frilled anterior margin. The first two segments of the urosome are fused.

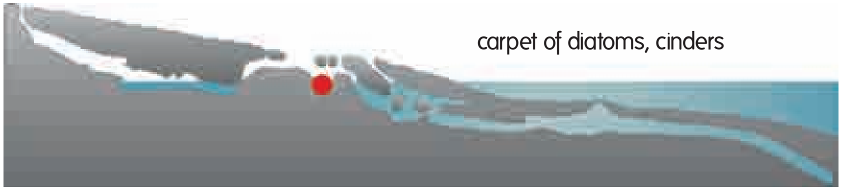
Habitat: Cinder patches and diatoms in Los Jameos del Agua.

Biology: *Oromiina fortunata* probably feeds on detritus and bacteria among cinders and diatoms.

Affinity and origin: The family Smirnovipinidae has been recently proposed for the genera *Costanzoia*, *Cyclopinoides*, *Oromiina,* and *Smirnovipina*, formely included in the Cyclopinidae. The family consists of about 10 species, most of them marine, except for the genera *Costanzoia* and *Oromiina*, which consist entirely of stygobitic species. *Oromiina* is a monotypic genus (with only one species), characterized by the retention of many characters considered to be ancestral for Cyclopoida.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube

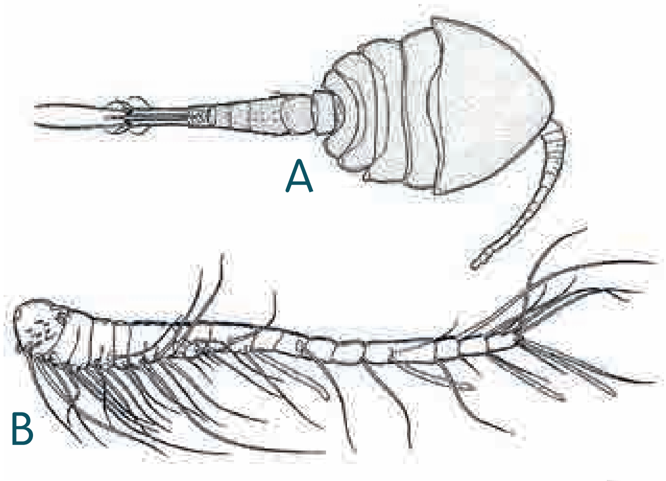


Distribution of the genus around the world

STYGOBİTE/ NON ENDEMİC

Muceddina multispinosa Jaume & Boxshall, 1997

Size: 0.7-1 mm **Family:** Schminkepinellidae **Order:** Cyclopoida



İdentification: *Muceddina multispinosa* can be distinguished from other cyclopoids La Corona lava tube by the lack of eyes and pigmentation. The cuticle is covered with tiny tubercles. The prosome consists of four segments, all of which are visible (**A**). The first pair of antennae is symmetrical and consists of 15 segments in females, with long setae and aesthetascs (**B**). The urosome includes five segments with a frilled anterior margin. The first two urosomal segments are fused.

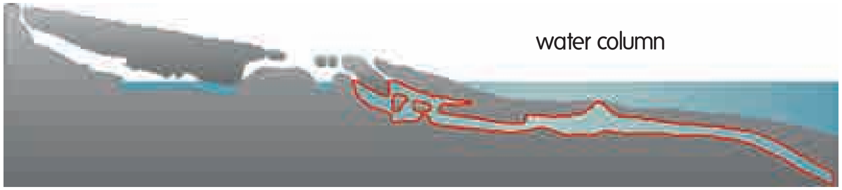
Habitat: Water column of Túnel de la Atlántida. The species is also known from anchialine caves in Mallorca and Capo Caccia (Sardinia).

Biology: *Muceddina multispinosa* is problaby a suspension feeder of detritus and bacteria.

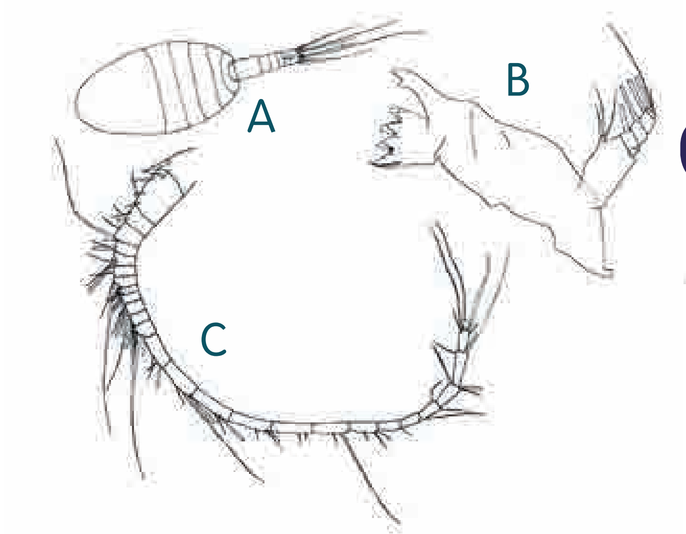
Affinity and origin: The family Schminkepinellidae is widely distributed in marine environments, more often in brackish zones, beaches, or infralitoral marine habitats. Some species are interstitial. The populations, identified morphologically as *Muceddina multispinosa* in anchialine caves in Lanzarote, Mallorca, and Sardinia, might comprise a single species, with dispersal capabilities between these localities. Alternatively, they might represent morphologically identical but genetically different cryptic species, which originated from a past vicariant event without subsequent morphological differentiation.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world



STYGOBİTE/ ENDEMİC

Enantronia canariensis Fosshagen, Boxshall & İliffe 1991

Size: 1.5-2 mm **Family:** Epacteriscidae **Order:** Calanoida

İdentification: *Enantronia canariensis* can be distinguished from other calanoids of La Corona lava tube by the lack of eyes and pigmentation as well as their comparatively large size. The prosome consists of five visible segments (**A**). The first pair of antennae is long and symmetrical, with antennal segments longer towards the tip, long setae and short aesthetascs (**C**). The urosome includes four segments, all visible. The caudal rami consist of five pairs of setae. The second innermost setae of the left caudal ramus is longer than the urosome. The second innermost setae of the right caudal ramus is shorter than the urosome and gives an asymmetrical arrangement to the caudal rami.

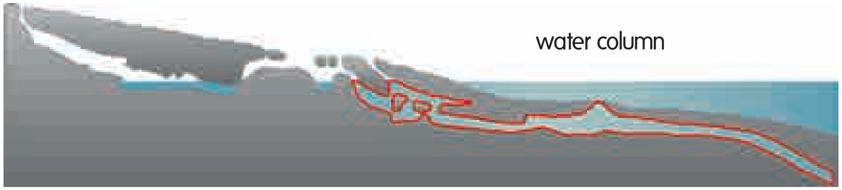
Habitat: Water column of Túnel de la Atlántida.

Biology: *Enantronia canariensis* is a predator, like other members of the family. Differences across the structure in the raptorial appendages (**B**) in epacteriscids suggest a specialization among the species to different prey types, most likely separate species of copepods. The males of this species have yet to be found found.

Affinity and origin: Epacteriscidae includes 20 genera, most consisting of only one known species. Most epacteriscids live in anchialine caves in the Canary İslands, Bermuda, the Caribbean basin (Bahamas, Turks and Caicos İslands, Belize, Mexico, Cuba), and the İndo-Pacific (Palau, Fiji, Galapagos, Western Australia). Members of genera *Epacteriscus* and *Enantiosis* are also found in marine shallow water environments, whereas the genus *Miheptneria* is exclusive to the deep sea. Anchialine epacteriscids exhibit varying degree of specialization. Species of the genus *Epacteriscus* are pigmented and typically found in the entrance areas, whereas other species lack pigmentation and only occur in deep isolated sections of anchialine caves. Although phylogenetic analyses have not been published yet, the diversity and distribution patterns of Epacteriscidae suggests that the family is ancient and have undergone a radiation in anchialine habitats. The family Ridgewayiidae, closely related to Epacteriscidae, also consists of a large number of stygobitic species, although most of them have a lesser degree of association to subterranean habitats, suggesting several colonization events.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube

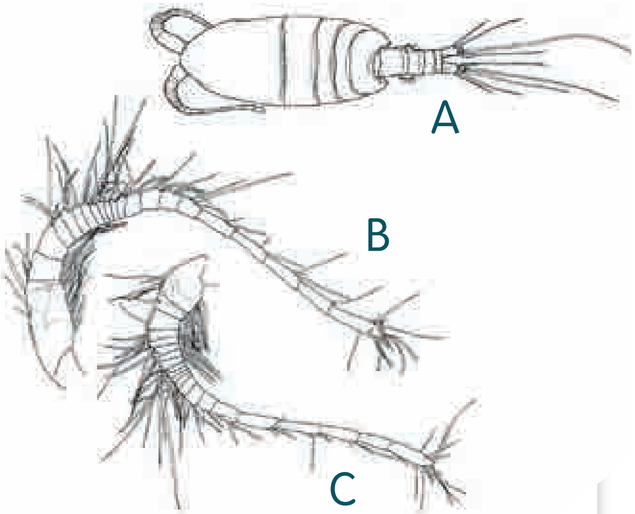


Distribution of the genus around the world

STYGOBİTE/ ENDEMİC

Paramisophria reducta Ohtsuka, Fosshagen & İliffe, 1993

Size: 1.5-2 mm **Family:** Arietellidae **Order:** Calanoida



İdentification: The prosome consists of four visible segments as the fourth and fifth true segments are fused (**A**). The first pair of antennae is asymmetrical with the right shorter than the left and with the greatest difference in length between the most basal antennal segments (**B**,**C**). Right and left first antennae are densely covered with setae, especially near insertions into the head. The urosome consists of four segments. Each caudal ramus has five caudal setae with the second innermost setae of both rami as long as the urosome.

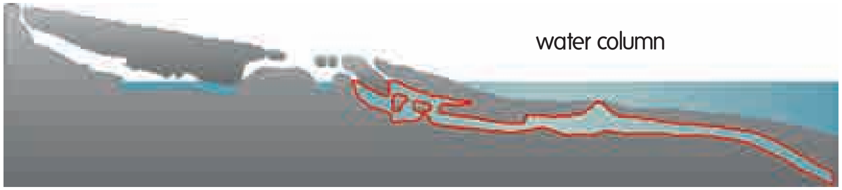
Habitat: Water column of Túnel de la Atlántida.

Biology: The asymmetrical body of *Paramisophria* is correlated with their unique swimming behavior, with the left side of the body parallel to the bottom during swimming motion. İn some of the species inhabiting lower littoral and upper sublittoral zones, this morphology is interpreted as an adaptation to maintain positioning with regards to bottom sediments in areas of increased wave activity. Gut contents suggest predation on small organisms and detritus.

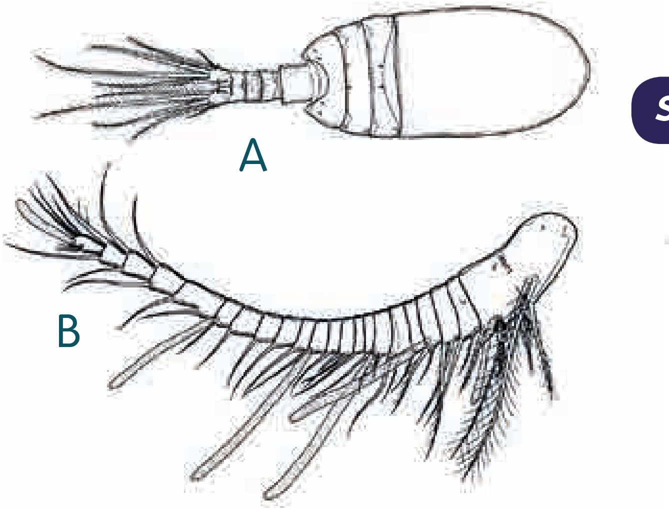
Affinity and origin: *Paramisophria* includes 18 species of small, heavily built copepods from caves as well as marine shallow water and deep sea habitats. The stygobites in the genus occur at the Canary İslands, Bahamas, Bermuda, the Mediterranean, and the Galapagos; whereas marine species are described from the North Atlantic, Brazil, Japan, Australia, and New Zealand. Phylogenetic analyses based on morphological data support a shallow water origin of the cave species in the genus, representing relatively recent and independent colonization events into cave systems.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world



Stygocyclopia balearica Jaume, Fosshagen & İliffe, 1999

Size: 0.5-0.6 mm **Family:** Pseudocyclopiidae **Order:** Calanoida

İdentification: The prosome consists of three visible segments and the urosome of four (**A**). The first pair of antennae is short, thick, and symmetrical, consisting of relatively short antennal segments (**B**). Each antennal segment bears a long setae and variable numbers of long aesthetascs. Each caudal rami has five setae, with the second innermost setae of both rami equal to the length of the urosome.

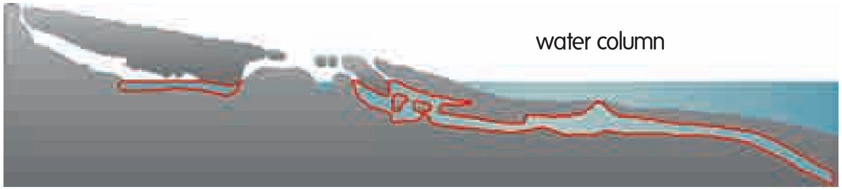
Habitat: Water column of Tūnel de la Atlántida and Cueva de los Lagos, as well as from several wells along the coast of Lanzarote. The species is also known from anchialine caves in Mallorca and Cabrera.

Biology: İt probably feeds on suspended detritus and bacteria in the water column of the cave.

Affinity and origin: *Stygocyclopia* belongs to the family Pseudocyclopiidae, consisting of 13 species grouped in five genera. Although most of the species are marine, the genera *Paracyclopia*, *Thompsonopia,* and *Stygocyclopia* contain stygobitic species. The genus *Stygocyclopia* consists of two additional stygobitic species: *S. australis* from Bundera Sinkhole (Western Australia) and *S. philippensis* from caves in Philippines. The distribution pattern of *S. balearica* is similar to that found in the cyclopoid copepod *Muceddina multispinosa* (p. 184) and could reflect similar dispersal mechanisms across caves in the Mediterranean and the Canary İslands or a common vicariant event.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube

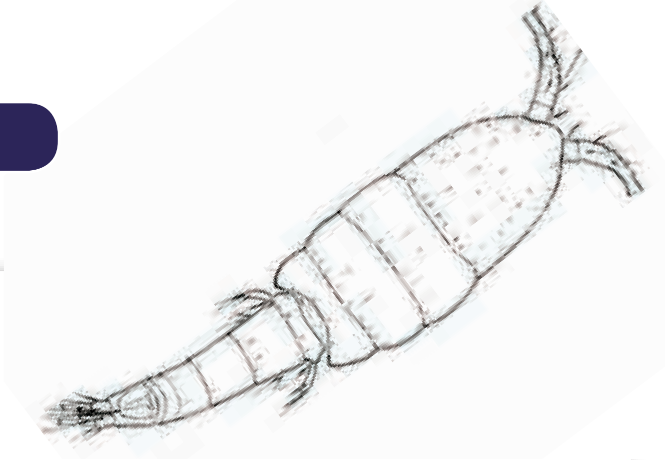


Distribution of the genus around the world

STYGOBİTE/ ENDEMİC

Neoechinophora karaytugi Huys, 1996

Size: 0.5-0.6 mm **Family:** Superornatiremidae **Order:** Harpacticoida



İdentification: *Neoechinophora karaytugi* can be recognized by its relatively cylindrical body with the prosome and urosome of similar width. The first and second pairs of antennae are short, bearing only few setae without aesthetascs

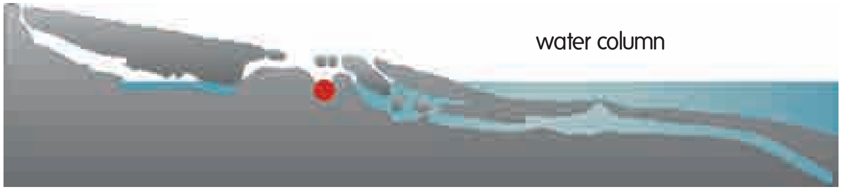
Habitat: The single specimen known from this species was collected with a hand-net in Los Jameos del Agua.

Biology: İt is presumed to feed on particulate organic matter like other species of the family.

Affinity and origin: Superornatiremidae is a stygobitic family of anchialine copepods with ten described species, classified in four genera. Except for *Gideonia*, with one species, the remaining genera entirely consist of anchialine stygobites described from Bermuda, Canary İslands, and Mallorca, as well as undescribed from Bahamas and Belize. The family is unique due to the presence of a stylet-like mandible combined with an oral cone, similar to that present in the order Siphonostomatoida. Superornatiremidae retains several ancestral harpacticoid features, placing it within the tisbimorph complex, a highly diverse group of harpacticoid copepods commonly occurring in groundwater.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

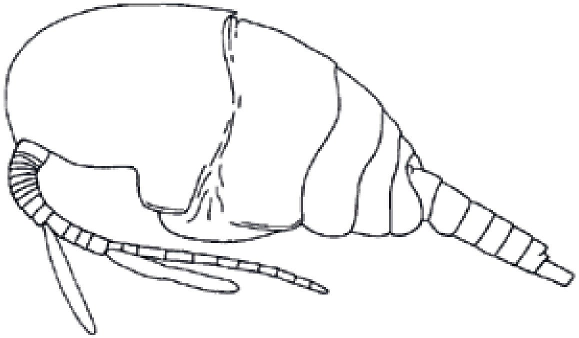
MİSOPHRİOİDA

İdentification: See Box 4

Habitat: All four misophrioids from La Corona lava tube are found within the water column, and occasionally in cinder patches or the sediments of Montaña de Arena.

Biology: Misophrioids probably feed on suspended organic matter and bacteria from the water column.

Affinity and origin: Misophrioida is an order with approximately 50 species classified into three families. Speleophriidae consists mostly of anchialine species, Palpophriidae has one species endemic from La Corona lava tube, and Misophriidae consists mostly of hyperbenthic marine species. Cladistic analyses based on morphological data has attempted to unravel the origin of the stygobitic misophrioids. These analyses have become good examples on how discoveries of new taxa can completely modify our interpretation of the evolutionary history of a group. İnitial analyses of the species described up to 1989 identified two main lineages, Speleophriidae and Misophriidae, with deep sea species splitting sister to anchialine speleophriids and marine hyperbenthic misophriids, favoring a deep sea origin for anchialine misophrioids. However, the discovery of more basally splitting, *Palpophria* and *Speleophriopsis*, has changed the entire picture by favoring a shallow water origin for the cave species in the group.



STYGOBİTE / ENDEMİC

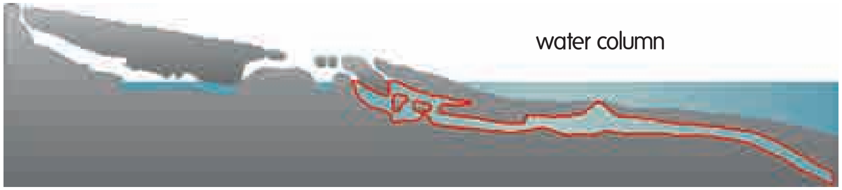
Expansophria dimorpha Boxshall & İliffe, 1987

Size: 0.45-0.6 mm **Family:** Speleophriidae **Order:** Misophrioida

Comments: Three additional species are known from the genus, *E. apoda*, *E. galapaguensis* and *E. sarda*, from anchialine caves in Bermuda, Galapagos, and Sardinia, respectively.

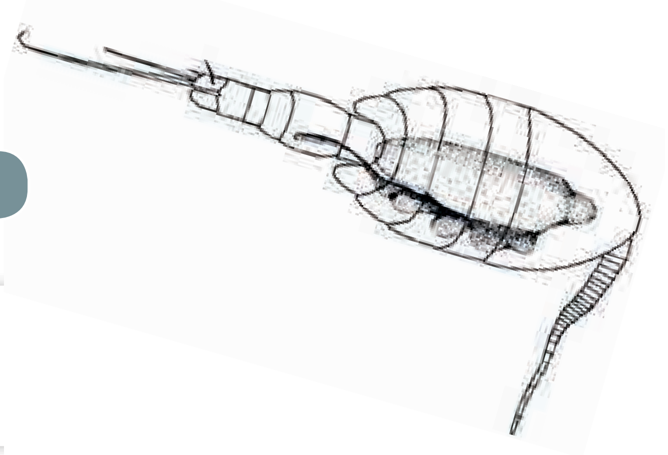
DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

STYGOBİTE / ENDEMİC



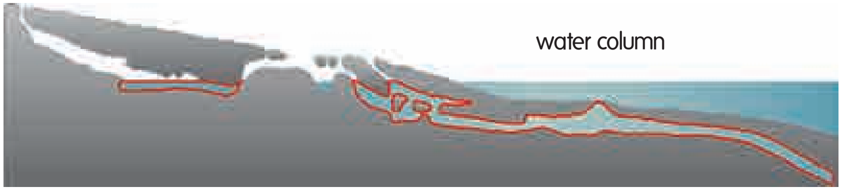
Dimisophria cavernicola Boxshall & İliffe, 1987

Size: 0.3-0.4 mm **Family:** Misophriidae **Order:** Misophrioida

Comments: *Dimisophria cavernicola* is the only described species in the genus. The phylogenetic position is not fully resolved since it presents a combination of characters from the families Speleophriidae and Misophriidae. Thus its placement in Speleophriidae is tentative.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

STYGOBİTE /ENDEMİC


AM&BCG

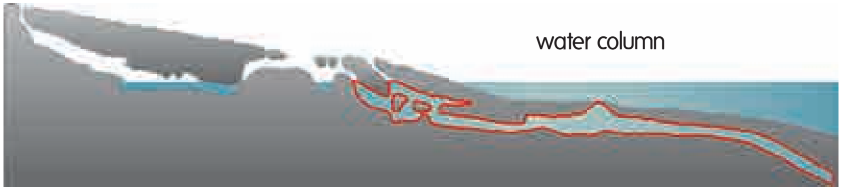
Speleophriopsis canariensis Jaume & Boxshall, 1996

Size: 0.6 mm **Family:** Speleophriidae **Order:** Misophrioida

Comments: Three additional species are described in the genus, *S. balearicus*, *S. scottocarloi*, and *S. campaneri*, from anchialine caves in Mallorca, Bermuda, and Palau, respectively.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

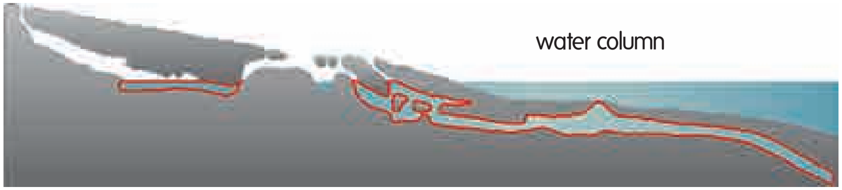
Palpophria aestheta Boxshall & Jaume, 1997

Size: 0.3-0.4 mm **Family:** Palpophriidae **Order:** Misophrioida

Comments: The species is characterized by the presence of an extraordinarily long mandibular palp, clearly visible under the stereomicroscope. This is the only described species of the family Palpophriidae.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

MYSİDA

Mysids or "opossum shrimp" are relatively common in aquatic environments with more than 780 described marine and freshwater species, mostly pelagic or hyperbenthic, swimming near the bottom. While some species are solitary, many mysids form large swarms and are an important component of the diet of a variety of marine animals.

Mysids look like small shrimp, with the body divided into a abdomen and the head and thorax. However, the head and the thorax are covered by a carapace as in true shrimp. However, in mysids the carapace is posteriorly loose and not attached to the last 4-5 thoracic segments. The head bears two pairs of antennae as well as two stalked compound eyes, which can be absent in stygobitic species. The carapace extends anteriorly forming a rostrum of variable length. The first and sometimes the second thoracic appendages are modified as maxillipeds for feeding. The remaining thoracic appendages are similar, with filamentous exopods often having swimming setae. The abdominal appendages (pleopods) are often much reduced. Both thoracic exopods and pleopods are used for swimming. The uropods are paddle-shaped, forming a tail-like structure, and possess a pair of statocysts, which are sensory organs specialized in gathering information on the relative position of the animal within the water column. Sexes are separated with females incubating the embryos in a ventral marsupium formed by the base of the last thoracic legs.

Mysida was originally placed in the order Mysidacea, together with Lophogastrida and Stygiomysida. The order was defined based on the presence of a series of shared plesiomorphic (ancestral) characters including the stalked compound eyes, well-developed carapace, thoracic gills, long tubular heart, and the presence of antennal and maxillary glands. Based on the retention of so many plesiomorphies, many specialists have suggested that Mysida might represent one of earliest evolving lineages in Peracarida. However, more recent phylogenetic analyses have shown that Mysida, Lophogastrida and Stygiomysida represent in fact independent evolutionary lineages within Peracarida, and that Mysida evolved relatively late within Peracarida. The internal relationships within Mysida are still poorly understood.

Mysids in subterranean environments

Mysids are common in anchialine caves, sometimes represented by marine species that can form resident populations using the twilight areas as refuge, and other times represented by anchialine stygobites. Approximately 30 stygobitic mysids are known, mostly belonging to the family Mysidae inhabiting marine, anchialine, and freshwater caves in North Atlantic islands, Africa, the Caribbean, the Mediterranean, and İndia. The origin of different groups of cave mysids have been explained through several evolutionary pathways, although in many instances, adaptation to caves fits the so called "zonal model" where species become progressively more adapted to subterranean habitats through adaptation to twilight zones, such as cave entrances and twilights zones.

Juan Valenciano

Heteromysoides cotti Calman 1932

Size: 5-10 mm **Family:** Mysidae **Order:** Mysida

İdentification: *Heteromysoides cotti* is the only mysid found in La Corona lava tube. İt has a shrimp-like body with the head and the thorax covered by a carapace (Fig. 37) with two pairs of long lateral antennae. A pair of small reddish eyes are present in some specimens (Figs. 38 and 40). The thorax possesses several leg-like appendages and the abdomen is segmented with reduced appendages. The uropods at the end of the abdomen are paddle-shaped and form a fin-like structure.

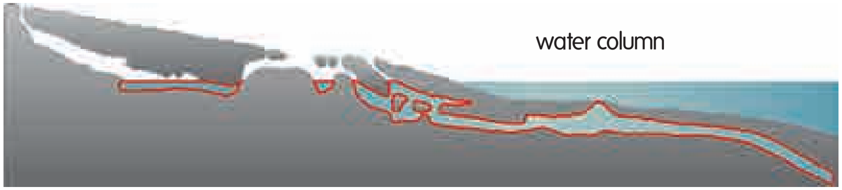
Habitat: Water column and crevicular habitats within La Corona lava tube, in addition to anchialine wells and pools around the island.

Biology: *Heteromysoides cotti* feeds on detritus which it collects using the thoracic appendages. Several specimens were collected using baited traps indicating that the species is also a scavenger. İt forms large swarms in Los Jameos del Agua, whereas inside Túnel de la Atlántida only solitary individuals are found swimming among rocks near the bottom. *Heteromysoides cotti* can also be found in wells and anchialine pools where it migrates during the night for feeding, hiding during the day in adjacent subterranean crevicular spaces. Two distinct morphologies can be found within the species. İndividuals collected at Los Jameos del Agua are pigmented and have reddish reduced eyes (Fig. 39 A and B), in contrast to the specimens found in wells and the lava tube, which are unpigmented and lack eyes (Fig. 39 C and D). The pigmented form seems adapted to the light and the abundant food of Los Jameos del Agua, while the unpigmented form is more specialized to the darkness of the lava tube and other subterranean crevicular habitats on the İsland. *Heteromysoides cotti* has separate sexes with females incubating a single pair of embryos in two voluminous marsupia formed by modified segments of each of the last thoracic appendages (Fig. 40).

Affinity and origin: *Heteromysoides* includes nine species from both marine and subterranean environments. The subterranean species include *H. stenoura* and *H. spongicola* from Grand Cayman, *H. dennisi* from Grand Bahama and *H. simplex* from Okinawa (Japan), all collected in fully marine waters. The origin of these cave species remains to be investigated, but they seem to be derived from a shallow water marine ancestor since all their closest relatives inhabit coastal marine habitats.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

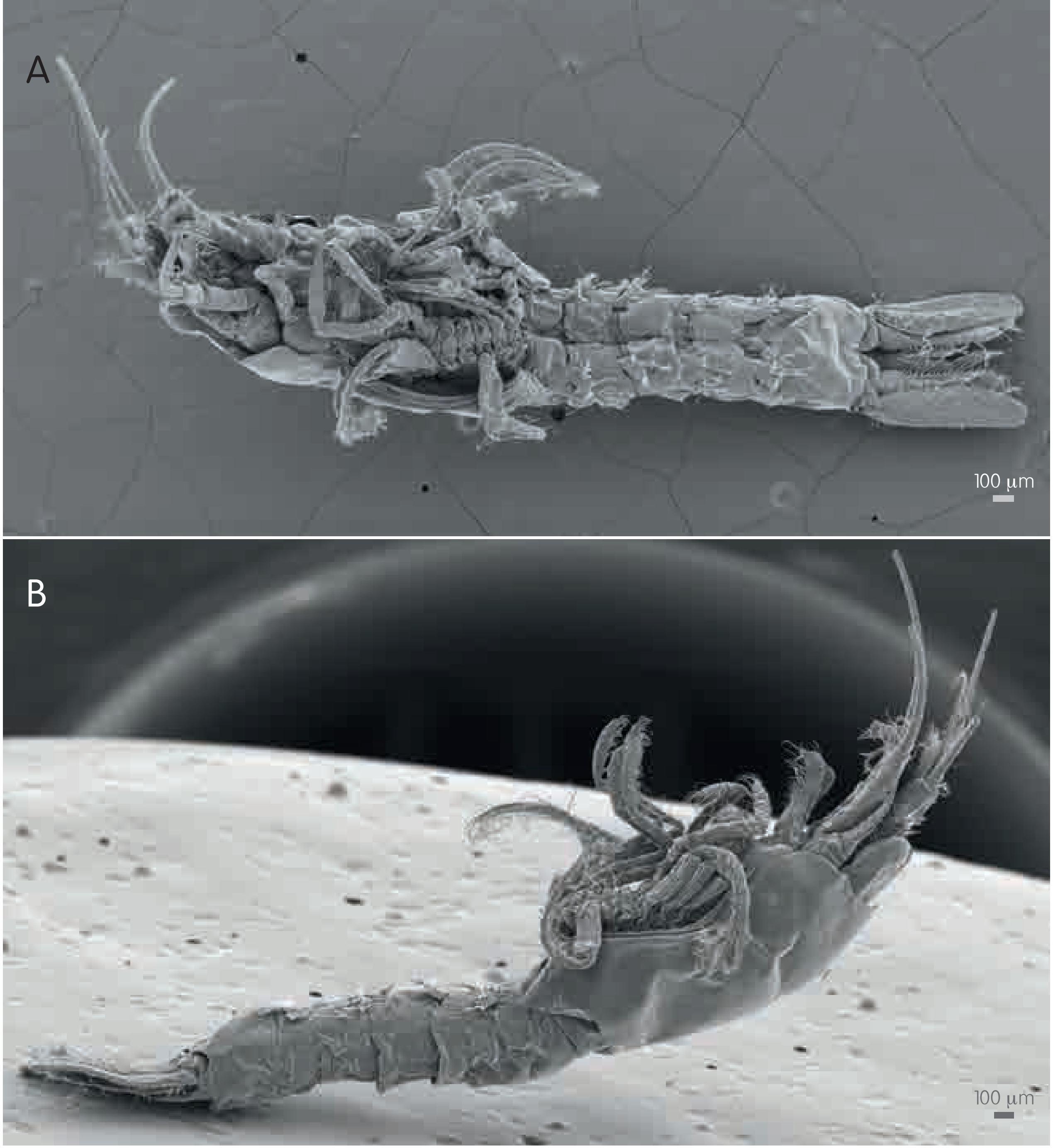


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Figure 37. Scanning electron micrographs of *Heteromysoides cotti* from Los Jameos del Agua in (**A**) ventral and (**B**) lateral.

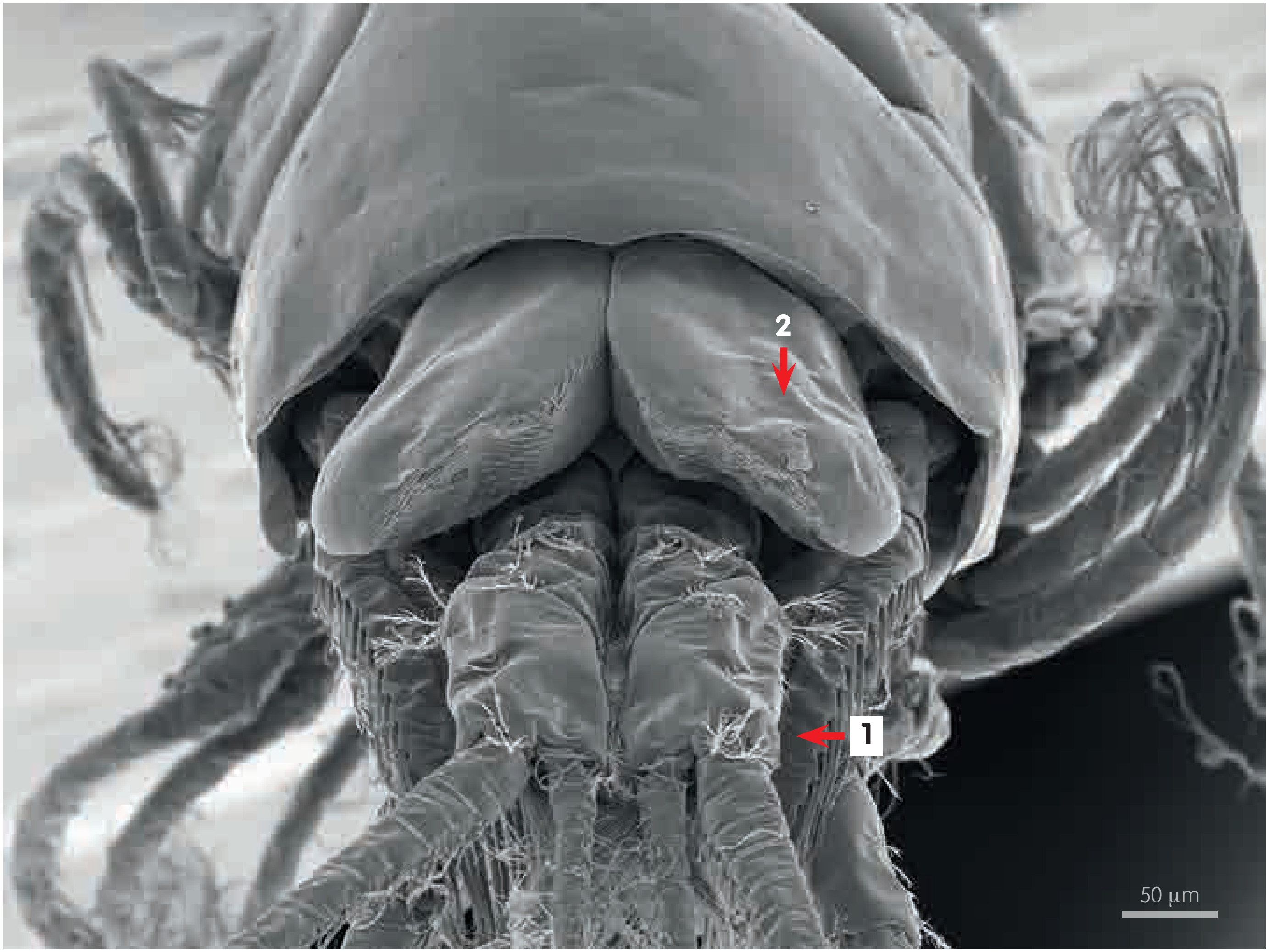

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Figure 38. Scanning electron micrographs of the anterior end of *Heteromysoides cotti* from Los Jameos del Agua. Clearly visible in the foreground are a pair of biramous antenna (**1**) below the eye stalks (**2**).

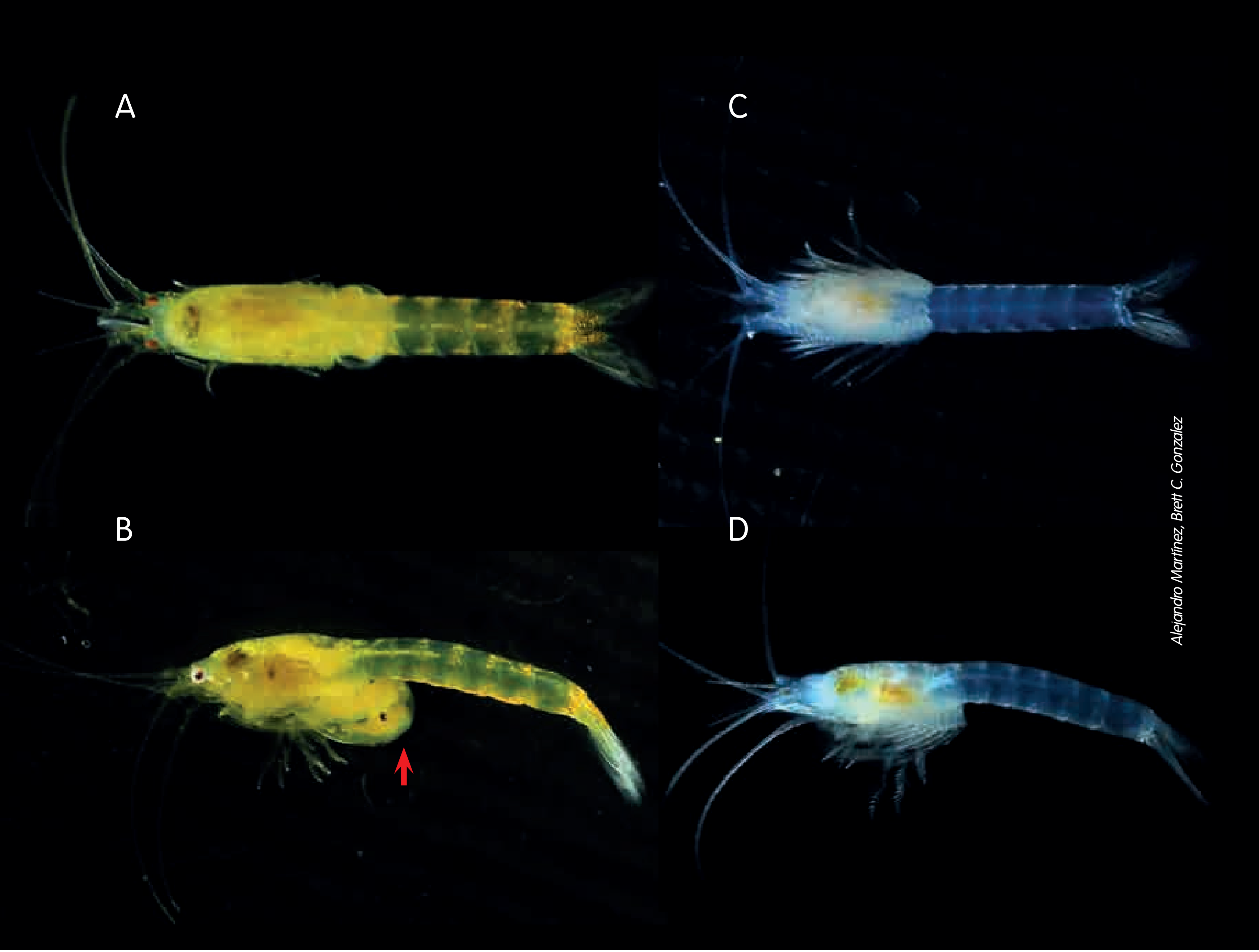

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Figure 39. *Heteromysoides cotti* from (**A-B**) Los Jameos del Agua and (**C-D**) Túnel de la Atlántida. The specimens from Túnel del Atlántida are unpigmented and blind, whereas those from Los Jameos del Agua are pigmented with red eyes. The brooding chamber (arrow) is clearly visible on the midline axis on the ventral side of the body of the pigmented specimen.

Juan Valenciano

Figure 40. Gravid *Heteromysoides cotti* from Los Jameos del Agua carrying two developing eggs in the marsupium (arrow) at the end of the thorax.

THERMOSBAENACEA

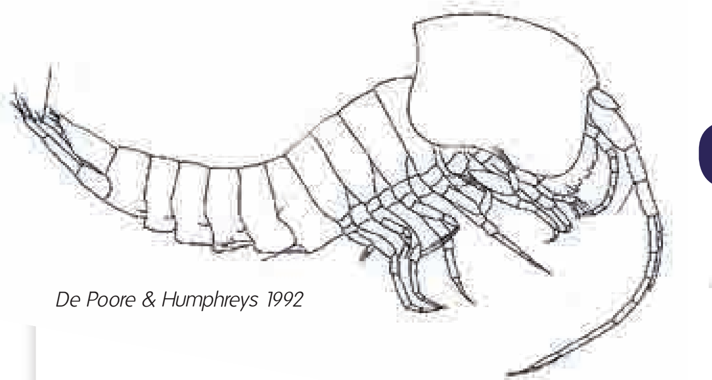
Thermosbaenacea is a small group of strange peracarid crustaceans with about 34 known species. Originally described from thermal hot springs in northern Africa, most subsequent discoveries have been from subterranean waters. Although they seem to be derived from a marine ancestor, most known thermosbaenaceans live in subterranean freshwater and only five species occur in fully marine waters. Although many thermosbaenaceans inhabit caves, several species have been collected from deep layers of gravel accumulated in the tidal zone or in river beds.

All thermosbaenaceans are eyeless and unpigmented. The body is roughly cylindrical, with a short carapace covering the head and the first thoracic segments. The thorax consists of seven segments. The first thoracic segment possesses a pair of maxillipeds used for feeding, in combination with the mouth parts. The remaining thoracic segments carry pairs of biramous appendages, with leg-like endopods used for locomotion and paddle-like exopods used for respiration. The abdomen consists of six segments with very short appendages only on the first two segments. The telson bears several appendages articulated with the last abdominal segment. Thermosbaenaceans have separate sexes and incubate the eggs and embryos near the head, in a dorsal brood pouch derived from the carapace.

Although thermosbaenaceans have been traditionally placed in Peracarida, their inclusion in the group is still under debate since they incubate the embryos in a dorsal brood pouch derived from the carapace, and not in ventral thoracic marsupia as in other peracarids (see Mysida). The internal relationships within Thermosbaenacea are also poorly investigated, and the group is currently divided into four families: Monodellidae, Thermosbaenidae, Halosbaeinidae, and Tulumellidae.

Thermosbaenaceans in subterranean environmentss

Thermosbaenaceans are known exclusively from groundwater with their distribution matching the ancient coastline of the Tethys Sea. Thermosbaenaceans are considered relicts of a widespread shallow water Tethyan fauna stranded in interstitial and crevicular groundwater during episodes of marine regressions.



De Poore & Humphreys 1992

Halosbaena fortunata Bowman & İliffe, 1996

Size: 2-2.5 mm **Family:** Halosbaenidae **Order:** Thermosbaenacea

İdentification: *Halosbaena fortunata* is the only thermosbaenacean found in Lanzarote. İt superficially resembles *Heteromysoides cotti*, but *Halosbaena* completely lacks eyes and eye stalks. *Halosbaena fortunata* has a shorter cephalic carapace covering only the anterior thoracic segments and lacks abdominal appendages, except for the most anterior ones. Females incubate their embryos dorsally in a brood pouch derived from the carapace and not in a ventral thoracic marsupium as in *Heteromysoides cotti.*

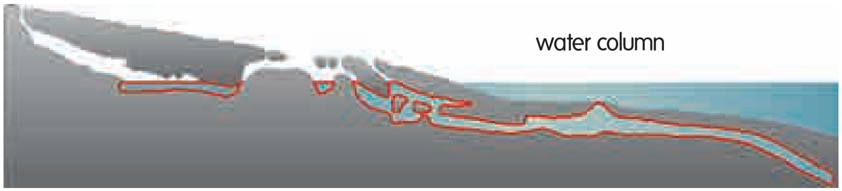
Habitat: Water column of Túnel de la Atlántida and Cueva de los Lagos. Occasionally found in anchialine wells around Lanzarote.

Biology: Few details are known on the biology of *H. fortunata.* This is a relatively rare species, usually found as individuals swimming several meters away from the cave walls. The distribution of *Halosbaena* found in several anchialine wells around the island indicates a mode of crevicular dispersal.

Affinity and origin: *Halosbaena* consists of four species recorded in caves and interstitial environments in the Canary İslands, Caribbean, Japan, and Australia. *Halosbaena acanthura* from the Caribbean, and *H. fortunata* from the Canary İslands are found in fully saline waters, whereas *H. daitonensis* from Japan and *H. tulki* from Australia inhabit in freshwater pools inside caves. The genus displays a full Tethyan distribution, with species present in areas corresponding with the ancient coast of the Tethys Sea.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube

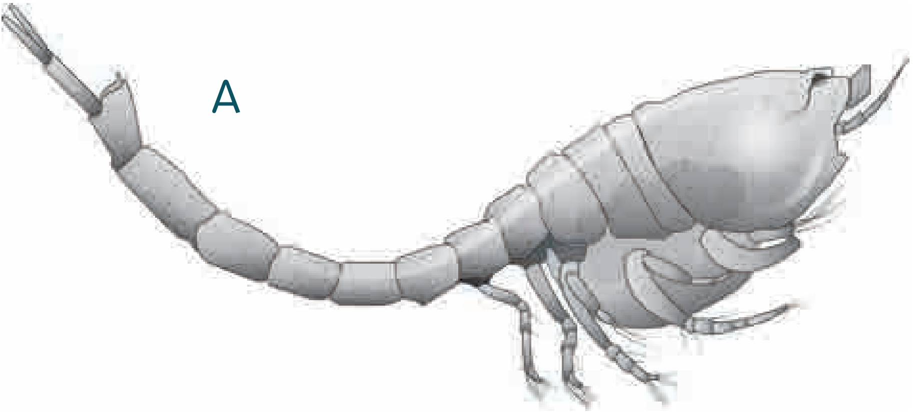


Distribution of the genus around the world

CUMACEA

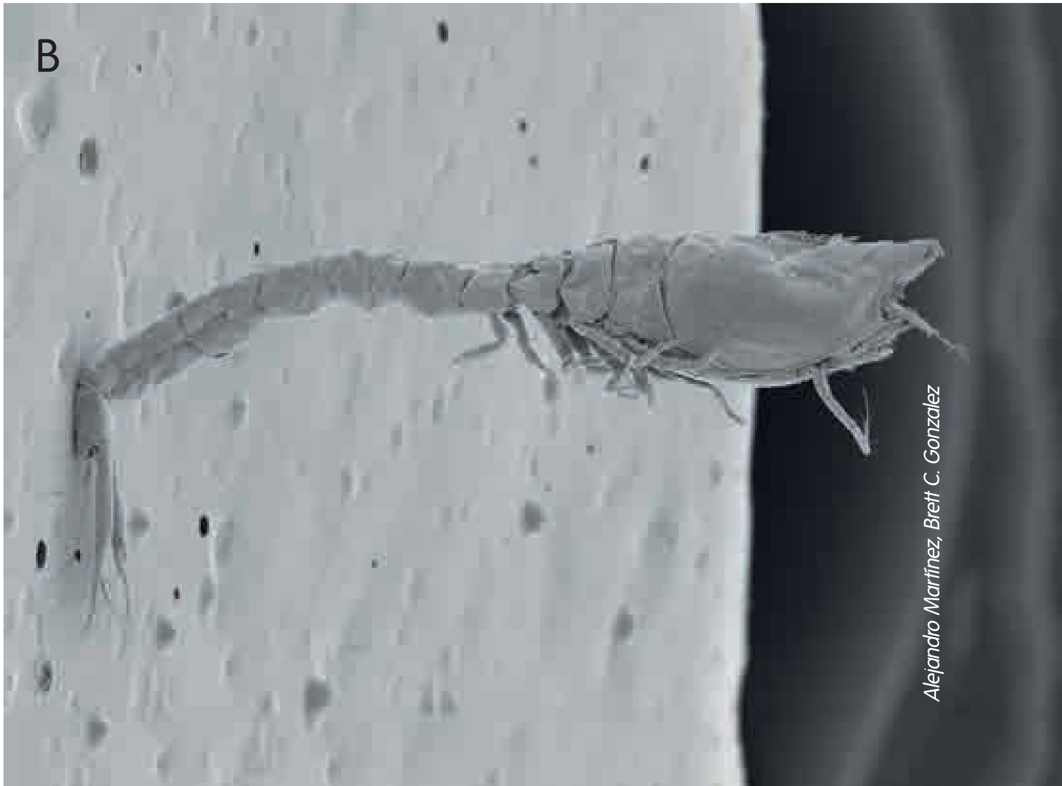
Cumacea includes 1,400 species of marine peracarid crustaceans living in muddy and sandy marine sediments, especially those with abundant organic matter, where they typically show patchy distributions and abundances. Most species live in the surface layers of the sediments and burrow into it backwards using their hind legs. As a result, the animal ends up in an inclined position with its head projecting above the sediment surface. Most cumaceans are regarded as deposit feeders, scraping organic matter from the surface of the sand grains, while a few species are either tube building suspension feeders or predators of small organisms.

The body of cumaceans is distinctly shaped with the head and thorax enlarged, though the abdomen is very narrow, terminating in slender elongated uropods. The head possesses a very pronounced rostrum, with the eyes inserted at its base when they are present. The first antennae have two flagella (whip-like extensions near the base) with the outer one longer than the inner. The second antennae show



Redrawn from García-Valdecasas, 1982

Figure 41. (**A**) Schematic drawing of *Speleocuma guanche* and (**B**) scanning electron micrograph of *Iphinoe* cf. *canariensis*. Both species occur in the sediments of Montaña de Arena, as well as in other marine caves throughout the Canary Islands.



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a marked sexual dimorphism, short in females and long and well-developed in males. The thorax bears several pairs of leg-like appendages primarily used for locomotion.

Cumaceans are placed within Peracarida, although their phylogenetic position within the group has yet to be resolved. The group is internally divided into eight families and about 100 genera; however, the relationships among the families have been poorly investigated.

Cumaceans in subterranean environments

Cumaceans are relatively common in marine and anchialine caves, although mostly represented by marine species that establish populations in sediments within caves or in the entrances and twilight areas. Most of the published data correspond to records in oceanic blue holes in the Bahamas, marine connected caves in Jamaica and Bermuda, and shallow lava tubes or erosional marine caves along the coastline in the Canary İslands.

Cumaceans in La Corona lava tube

Speleocuma guanche (Fig. 41 A) and ***İphinoe* cf. *canariensis*** (Fig. 41 B) are the only cumaceans found in La Corona lava tube, both from the coarse sediments at Montaña de Arena in Túnel de la Atlántida. *Speleocuma guanche* is common in marine caves in the Canary İslands and belongs to the monospecific genus *Speleocuma*, seemingly related to the Northwestern Atlantic genera *Mancocuma, Pseudoleptocuma* and *Spilocuma*. The origin of *Speleocuma guanche* is associated with a vicariant event related to the opening of the Atlantic Ocean (130 Ma). İn contrast, *İphionoe canariensis* is common in coastal marine sediments throughout the Canary İslands, and belongs to an entirely marine genus with 40 known species.

AMPHİPODA

Amphipoda is a large order of crustaceans with 7,000 described species classified in more than 100 families. The group is widely distributed and although it mainly consists of marine species, many freshwater and even a few terrestrial species are known. Most amphipods are relatively small, although some deep sea species can reach up to 34 cm. The smallest species are those adapted to live among sand grains with modified, worm-like bodies barely reaching 1 mm in length.

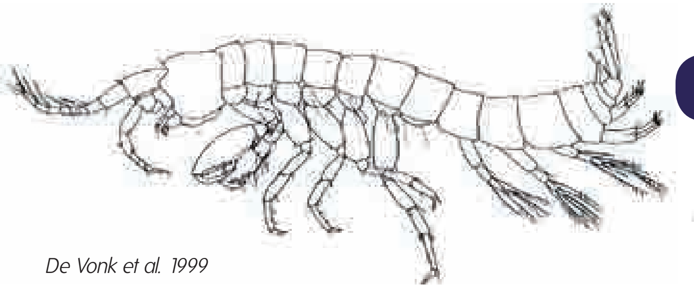
Amphipods generally have a laterally compressed body with a shrimp-like appearance. However, in contrast to shrimp (Caridea), amphipods lack a carapace, their eyes are sessile, and the abdomen is not demarcated from the thorax. The head bears two pairs of normally well-developed antennae. The thorax is typically comprised of eight segments, each of them with paired appendages or pereiopods (legs). The coxae (first segment of the pereiopod and point of attachment to the thorax) is normally enlarged and extended dorsoventrally, enhancing the compressed appearance of the body. The first pair of thoracic appendages is modified as maxillipeds for feeding, whereas the second and third pairs are enlarged, subchelate gnathopods adapted for. The remaining leg-like appendages are used for locomotion. The abdomen normally consists of six segments. The first three abdominal segments (pleosome) bear paired appendages called pleopods used for swimming, respiration, and ventilation of the eggs. The last three abdominal segments (urosome) bear three pairs of appendages or uropods, directed backwards and used for jumping, burrowing, or swimming, depending on the species.

Amphipods belong to the order Peracarida, in the class Malacostraca, which contains most of the well-known crustaceans (Box 3). Amphipods are traditionally divided into three suborders: Gammaroidea (gammarids), İngolfiellidea (worm shrimp), and Caprelloidea (skeleton shrimp). Gammarids have the highest diversity of species, inhabiting a variety of environments. İngolfiellids consist of approximately 50 species, mostly interstitial in marine and freshwater sediments, while the exclusively marine caprellids with more than 200 species are common in hard bottom habitats.

Diversity of subterranean amphipods

Currently, almost 12% of the 7,000 described species of amphipods inhabit subterranean environments, both freshwater and marine, and include stygobitic and stygophilic species. Most subterranean amphipods are concentrated in 12 families, with the majority in Bogidiellidae, Crangonyctidae, Hadziidae, Pseudoniphargidae and Niphargidae (Gammaroidea), as well as in İngolfiellidae (İngolfielloidea). The lineages of subterranean amphipods have evolved through different evolutionary pathways. Many groups seem to have evolved by vicariance related to tectonics or changes in sea levels (i.e., Crangonyctidae, Niphargidae, and Pseudoniphargidae), while the Pardaliscidae are thought to have colonized cave habitats from deep sea ancestors.

***İngolfiella* sp.** is exclusively found in the sediments of Montaña de Arena. Two other species of ingolfiellids are known in the Canary İslands: *İngolfiella similis* from freshwater wells in Fuerteventura, and *İngolfiella canariensis* from marine intertidal environments at Tenerife and El Hierro.



De Vonk et al. 1999

Bogidiella uniramosa Stock & Rondé-Broekhuizen, 1987

Size: 1.5-2.5 mm **Family:** Bogidiellidae **Order:** Gammaridea

İdentification: *Bogidiella uniramosa* differs from other stygobitic amphipods of Lanzarote in its small size, slender and laterally compressed body, lack of eyes and pigmentation. The antennae have few segments, with the first pair of antennae longer than the second. Gnathopods are comparatively small, only bearing a few strong internal spines. Uropods are simple, with a group of terminal spines.

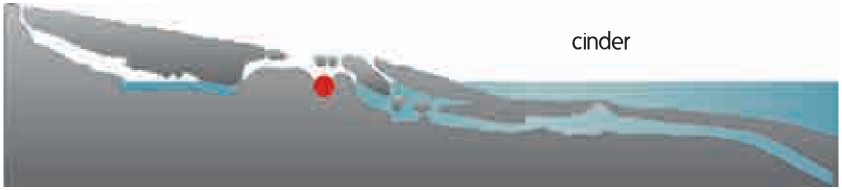
Habitat: İnterstitial in cinders and gravel in Jameos del Agua, as well as several wells, salt works, and marine coastal localites of Lanzarote.

Biology: Possibly feeds on detritus which it collects from the sediments.

Affinity and origin: *Bogidiella uniramosa* belongs to the family Bogidiellidae, which consists of more than 110 species known worldwide in subterranean marine, brackish, and freshwater environments. Most of the species are concentrated around the Mediterranean as well as in the Caribbean. Bogidiellids probably originated as a marine group which underwent several independent colonizations into freshwater and subterranean habitats. *Bogidiella uniramosa* probably colonized caves in Lanzarote from similar marine interstitial environments.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world


Juan Valenciano

Liagoceradocus acutus (Andres, 1978)

Size: 7-10 mm **Family:** Hadziidae **Order:** Gammaridea

İdentification: *Liagoceradocus acutus* is a large amphipod, lacking eyes and pigmentation. İt resembles *Speleaonicippe buchi*, but these species can be distinguished by the first pair of antennae being longer than the second, smaller gnathopods covered with setae (Figs. 42, 43 A and B), and characteristic leaf-shaped uropods in *L. acutus*.

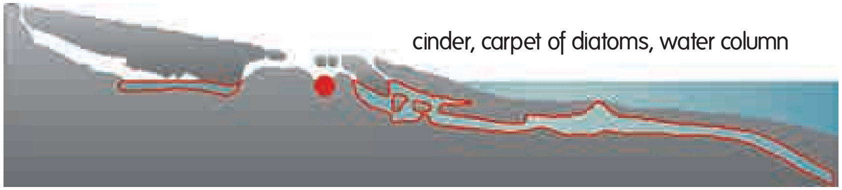
Habitat: Water column and cinders in Los Jameos del Agua, Tũnel de la Atlántida, and Cueva de Los Lagos. Large populations occur in many anchialine wells around the island.

Biology: İn the lava tube, solitary individuals of *Liagoceradocus* are commonly observed drifting in the water column with extended pereiopods to maintain their position in the water column (Fig. 45). Short periods of swimming are carried out through the use of their periopods. İn wells and in Los Jameos del Agua, the species is found in larger groups, normally close to the bottom. *L. acutus* is a scavenger, feeding on detritus and dead animals, and commonly collected in baited traps.

Affinity and origin: Hadziidae is a very diverse and cosmopolitan family of amphipods with numerous interstitial and crevicular species often found in caves. The systematics of the family is still debated and the validity of many genera needs to be reviewed. The genus *Liagoceradocus* consists of six species. Except for *L. acutus*, the remaining species of the genus inhabit İndo-Pacific caves and anchialine ponds in Cape Range and Barrow İsland (Western Australia), Australia, in addition to caves in the İndo-Pacific (Western Samoa, Solomon İslands, Fiji, and Hawaii). Since the validity of the genus *Liagoceradocus* is still debated and the relationship of *L. acutus* to its congeners is unknown, it is difficult to propose a hypothesis for the origin of this cave species.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

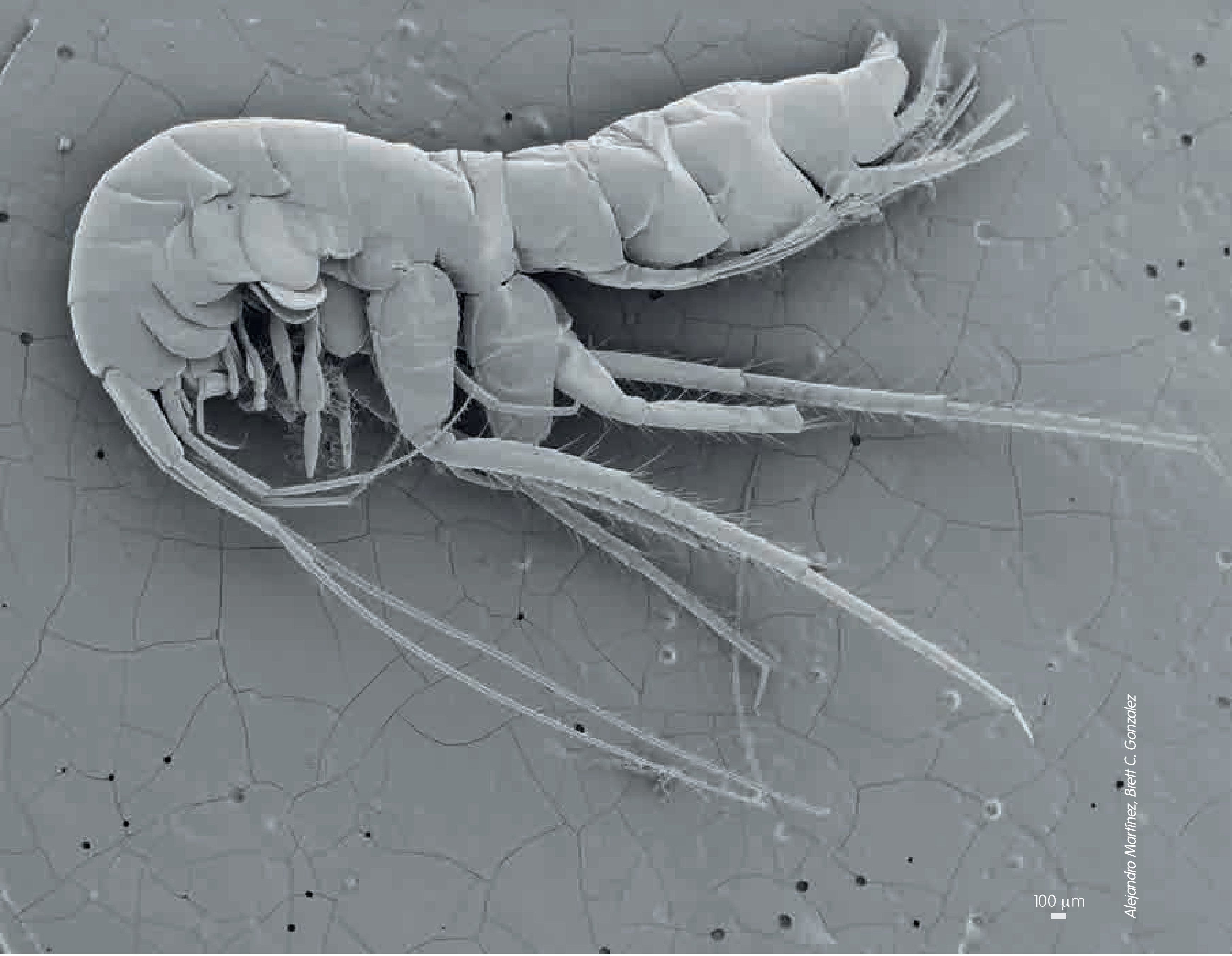


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Figure 42. Scanning electron micrograph of *Liagoceradocus acutus*.

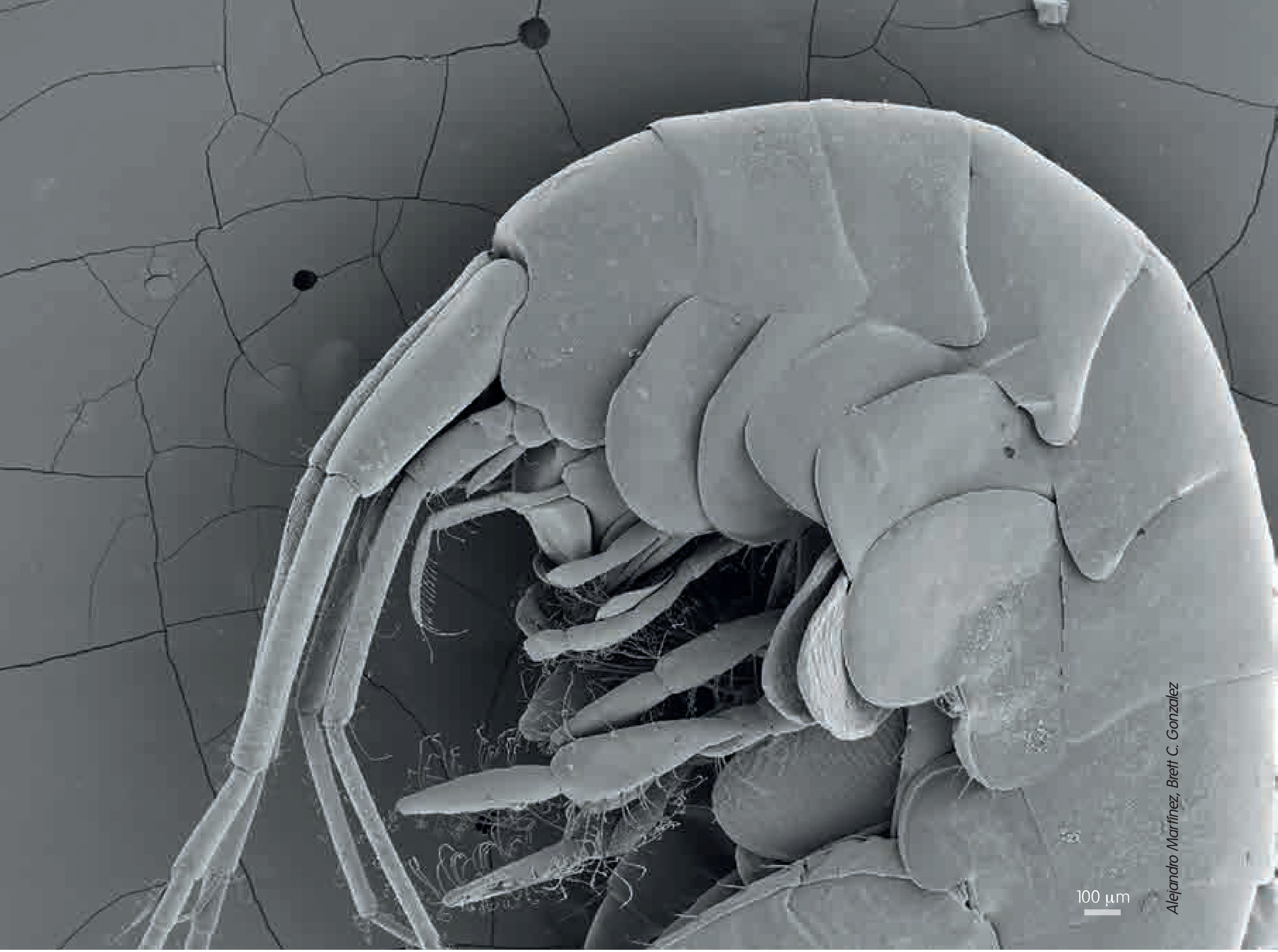

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Figure 43. Scanning electron micrograph of head of *Liagoceradocus acutus*.

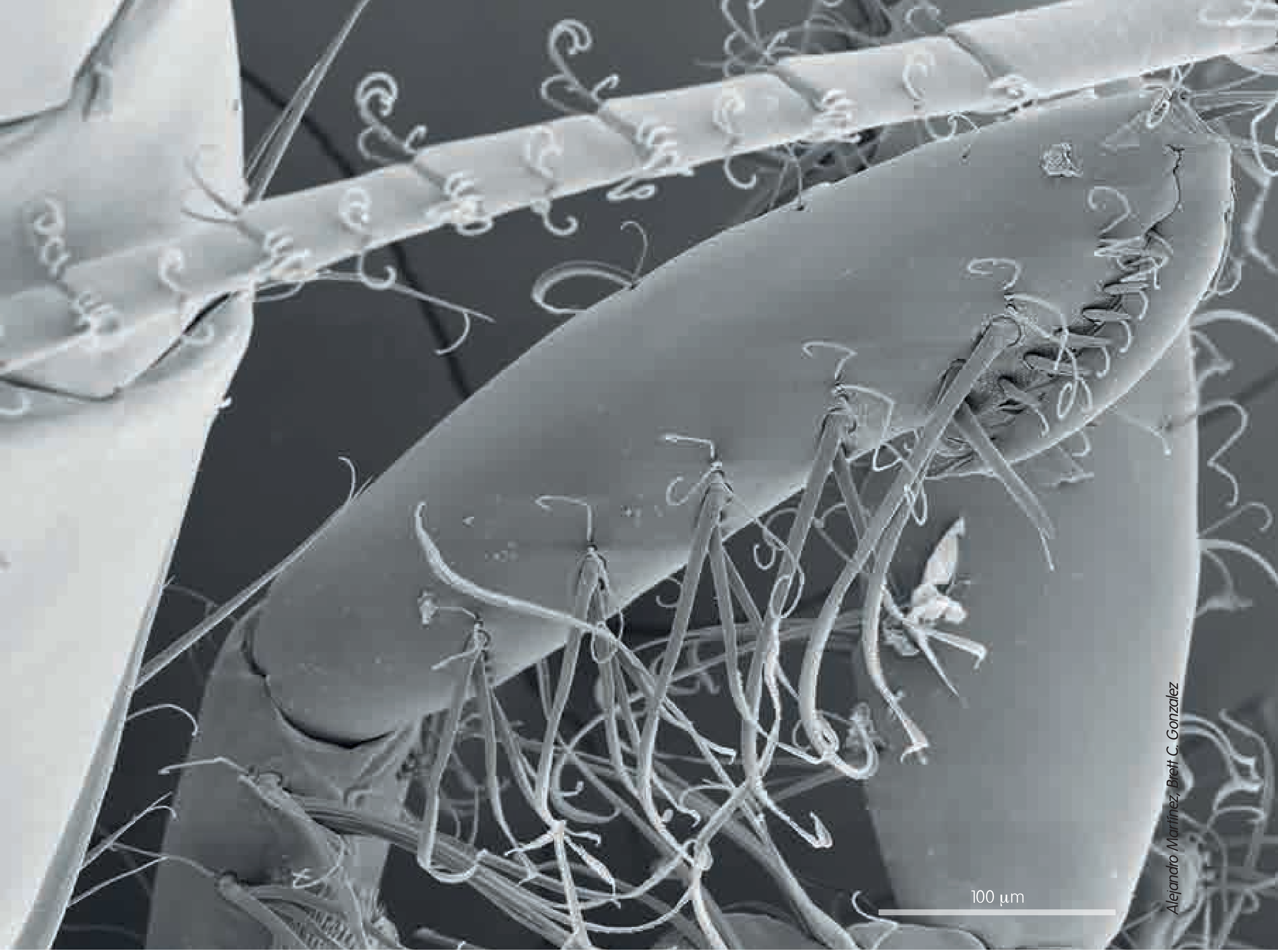

Figure 44. Scanning electron micrograph of the second gnatopod of *Liagoceradocus acutus*.

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Figure 45. *Liagoceradocus acutus* in the water column.


Sergio González

Parhyale multispinosa Stock, 1987

Size: 5-12 mm **Family:** Hyalidae **Order:** Gammaridea

İdentification: *Parhyale multispinosa* can be recognized by the presence of a pigmented body with well-developed compound eyes, large and wide coxae of the thoracic legs (Fig. 46), short and robust gnathopods (Figs. 47 and 48), and relatively short uropods (Fig. 49).

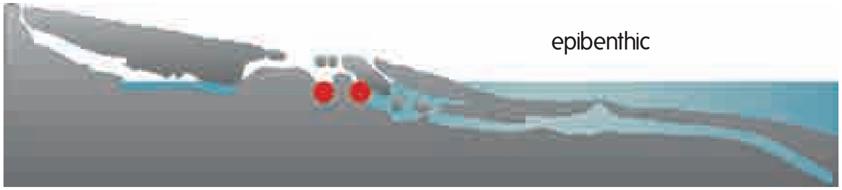
Habitat: Epibenthic in the illuminated sections of Los Jameos del Agua and Túnel de la Atlántida. They have also been observed in in high abundance from anchialine pools throughout Lanzarote.

Biology: *Parhyale multispinosa* is a benthic species, crawling or swimming near the bottom in relatively high densities (Fig. 50). İt feeds on detritus, but can also act as a scavenger and can be collected by the hundreds with baited traps in many anchialine pools of the island.

Affinity and origin: *Parhyale* is a widely distributed genus of marine amphipods common in intertidal pools in tropical and subtropical areas. *Parhyale multispinosa* lacks any troglomorphic adaptations and it is likely that it evolved from marine intertidal ancestors. Other marine species of *Parhyale* are common in anchialine pools in Hawaii and La Palma (Canary İslands). İt has been postulated that the genetic separation of *P. multispinosa* from marine ancestors is related to the presence of the extensive anchialine groundwater on Lanzarote, which might have favored isolation and speciation.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

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Figure 46. Scanning electron micrograph of *Parhyale multispinosa* in lateral view.

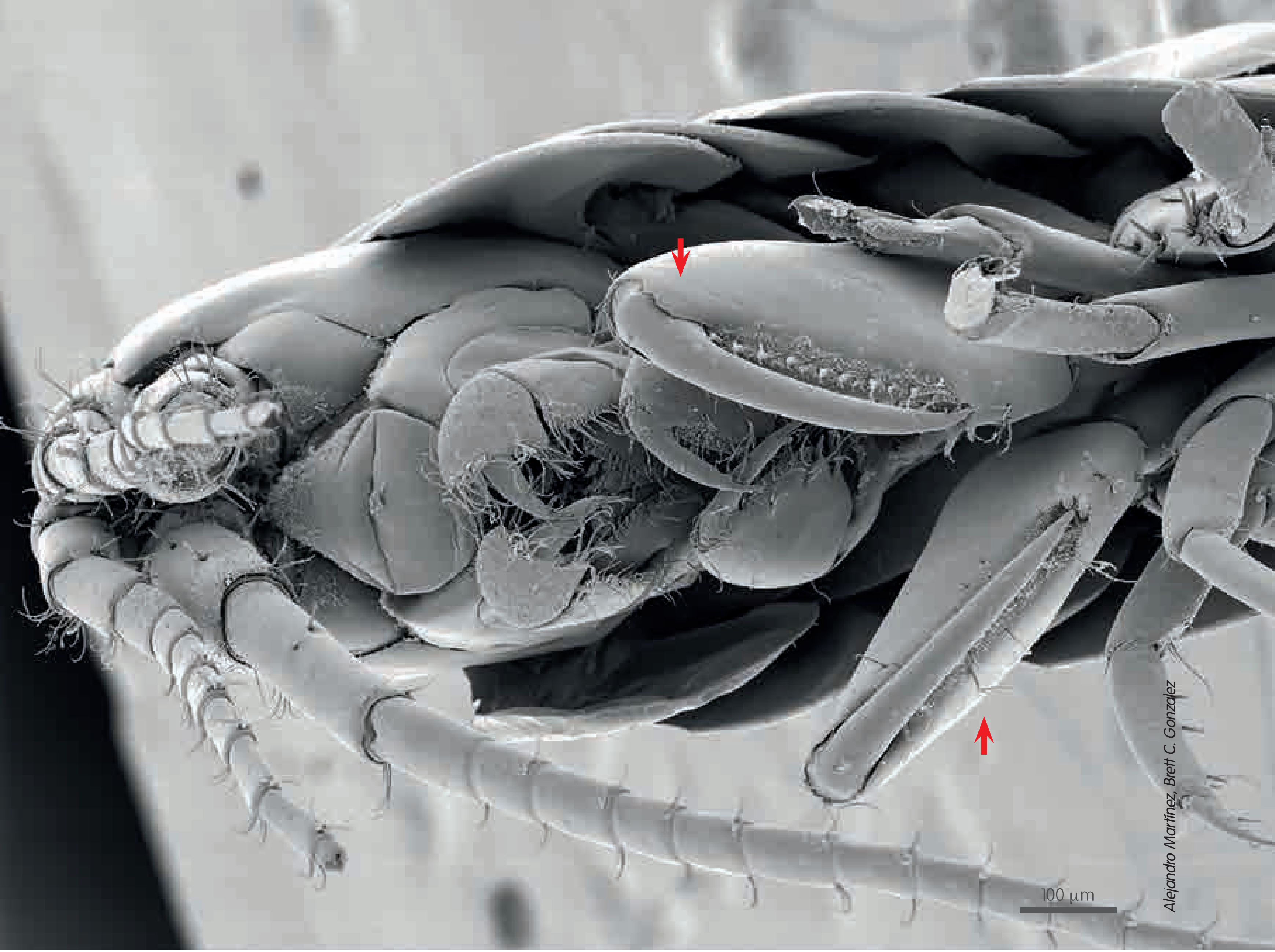

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Figure 47. Scanning electron micrograph of the mouthparts of *Parhyale multispinosa*. Notice the large prominent second pair of gnathopods (pincers; arrows).

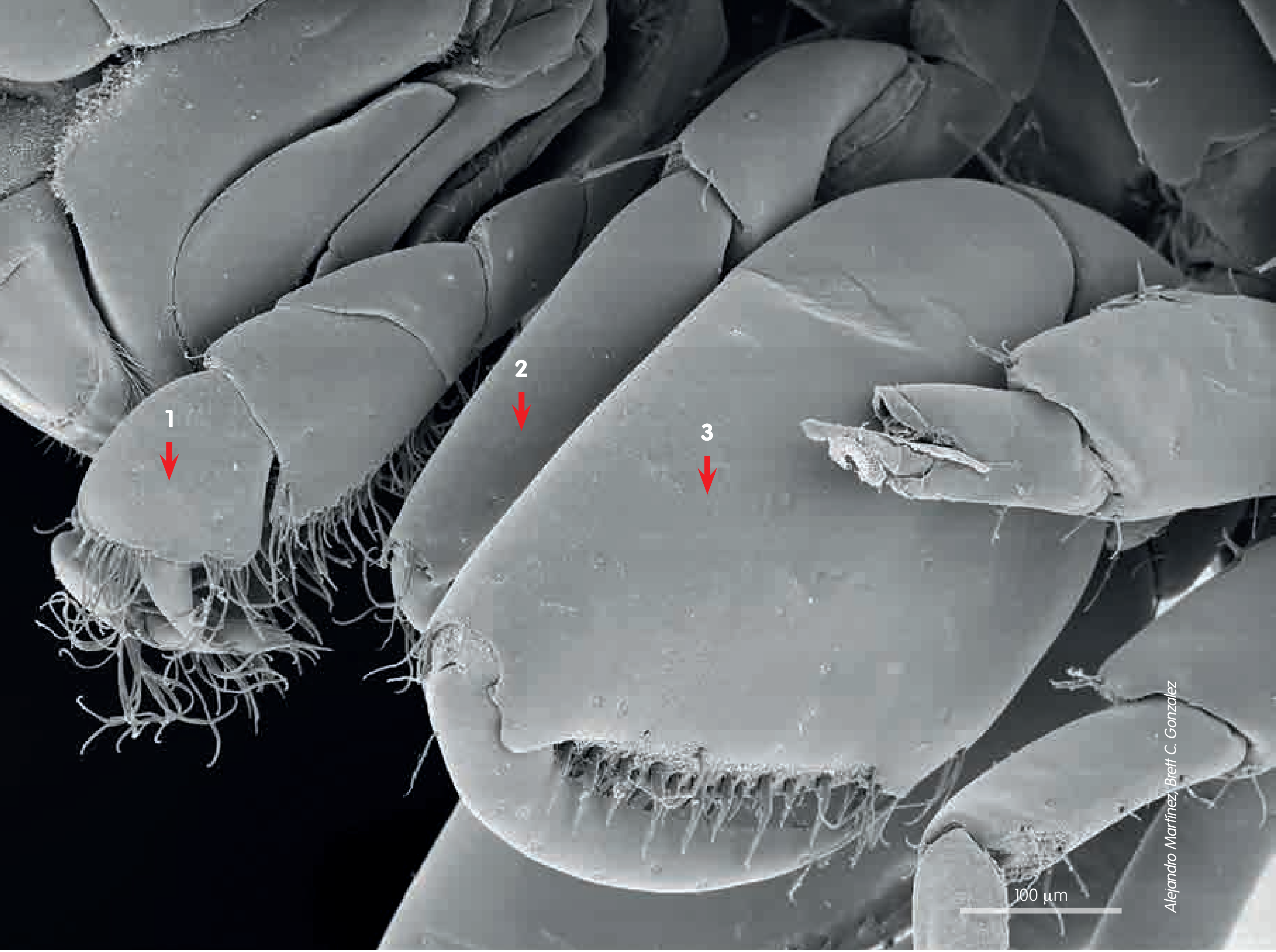

Figure 48. Scanning electron micrograph of mouth appendages (**1**) maxilliped, (**2**) first gnathopod, and (**3**) second gnathopod of *Parhyale multispinosa*.

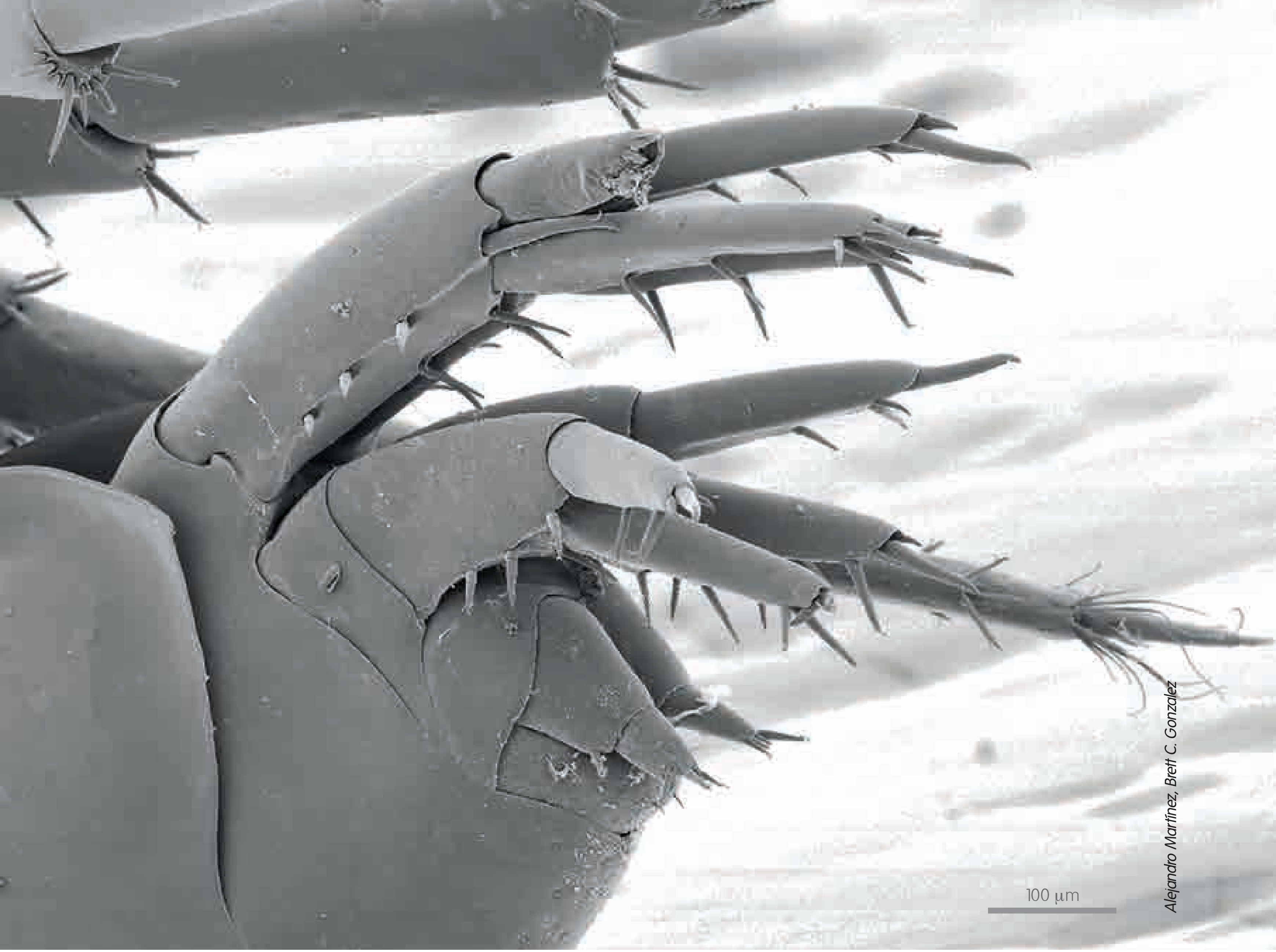

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Figure 49. Scanning electron micrograph of the posterior uropods of *Parhyale multispinosa*.

Figure 50. *Parhyale multispinosa* feeding on diatoms in Los Jameos del Agua.

Juan Valenciano


Juan Valenciano

Spelaeonicippe buchi (Andres, 1975)

Size: 6-8 mm **Family:** Pardaliscidae **Order:** Gammaridea

İdentification: *Spelaeonicippe buchi* is the largest amphipod in La Corona lava tube. İt can be recognized by the lack of eyes and pigmentation, the relative length of the second pair of antennae being longer than the first pair, large gnathopods (Figs. 51 and 52), and absence of paddle-like uropods.

Habitat: Water column throughout the cave, although it is more common in Túnel de la Atlántida, where it is one of the most abundant species.

Biology: *Spelaeonicippe buchi* drifts in the water column by extending its pereiopods to maintain its position, while short periods of swimming are achieved using its thoracic appendages (Fig. 53). Normally solitary, they stay several meters away from the walls or the bottom of the cave. They most likely feed on particulate organic matter from the water column or scavenge dead animals.

Affinity and origin: The genus *Spelaeonicippe* consists of one other described species (*Spelaeonicippe provo*) known from anchialine caves in Middle Caicos, Providenciales, and Exuma Cays in the Bahamas and Turks and Caicos islands. The genus is placed in the family Pardalisicidae, which includes otherwise deep sea species. A common deep sea ancestor has been proposed for both stygobitic species of the genus, colonizing caves through crevicular habitats.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube

Distribution of the genus around the world

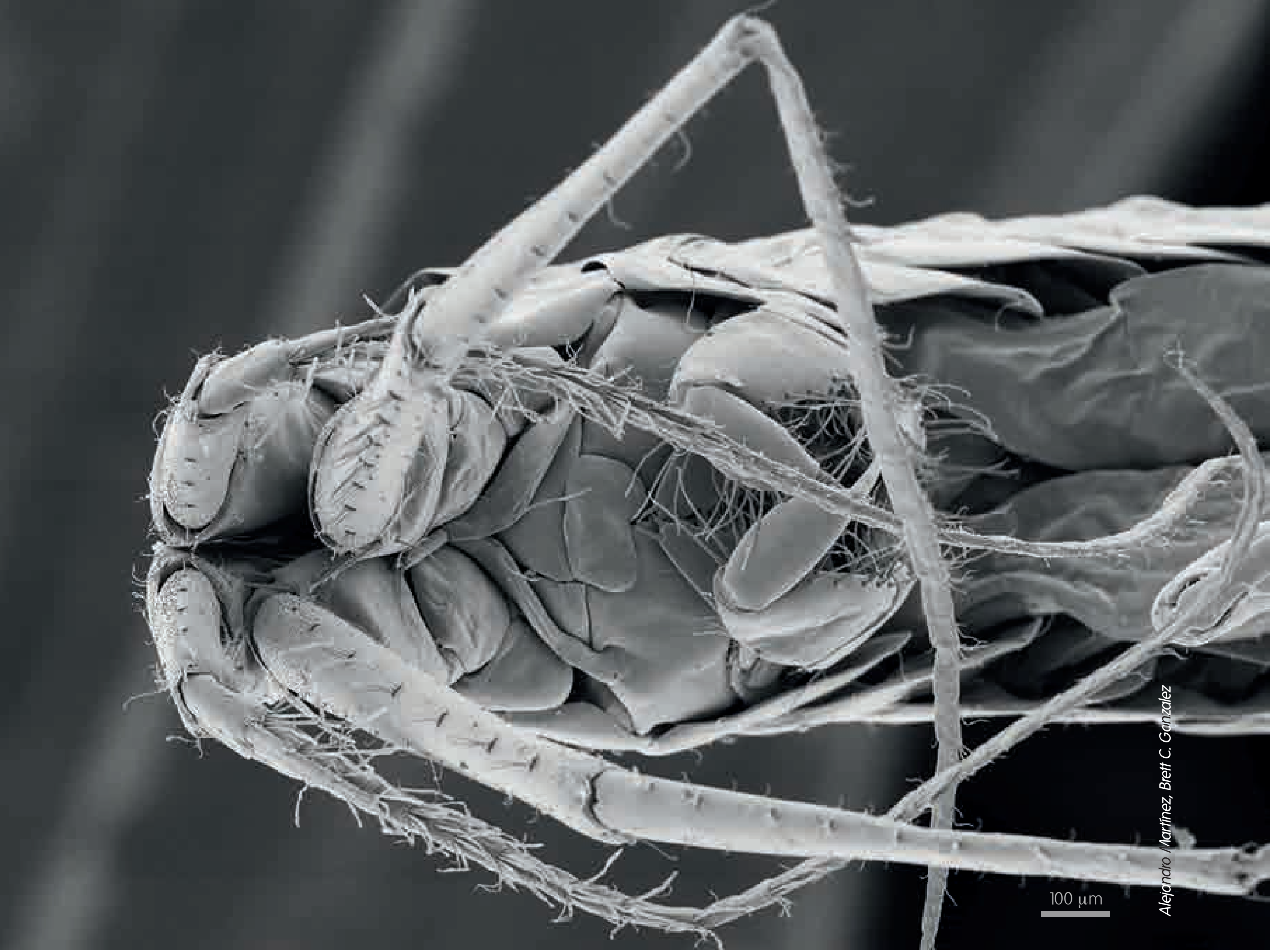

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Figure 51. Scanning electron micrograph of the head of *Spelaeonicippe buchi*, in ventral view, showing mouthparts, antennae, and gnathopods.

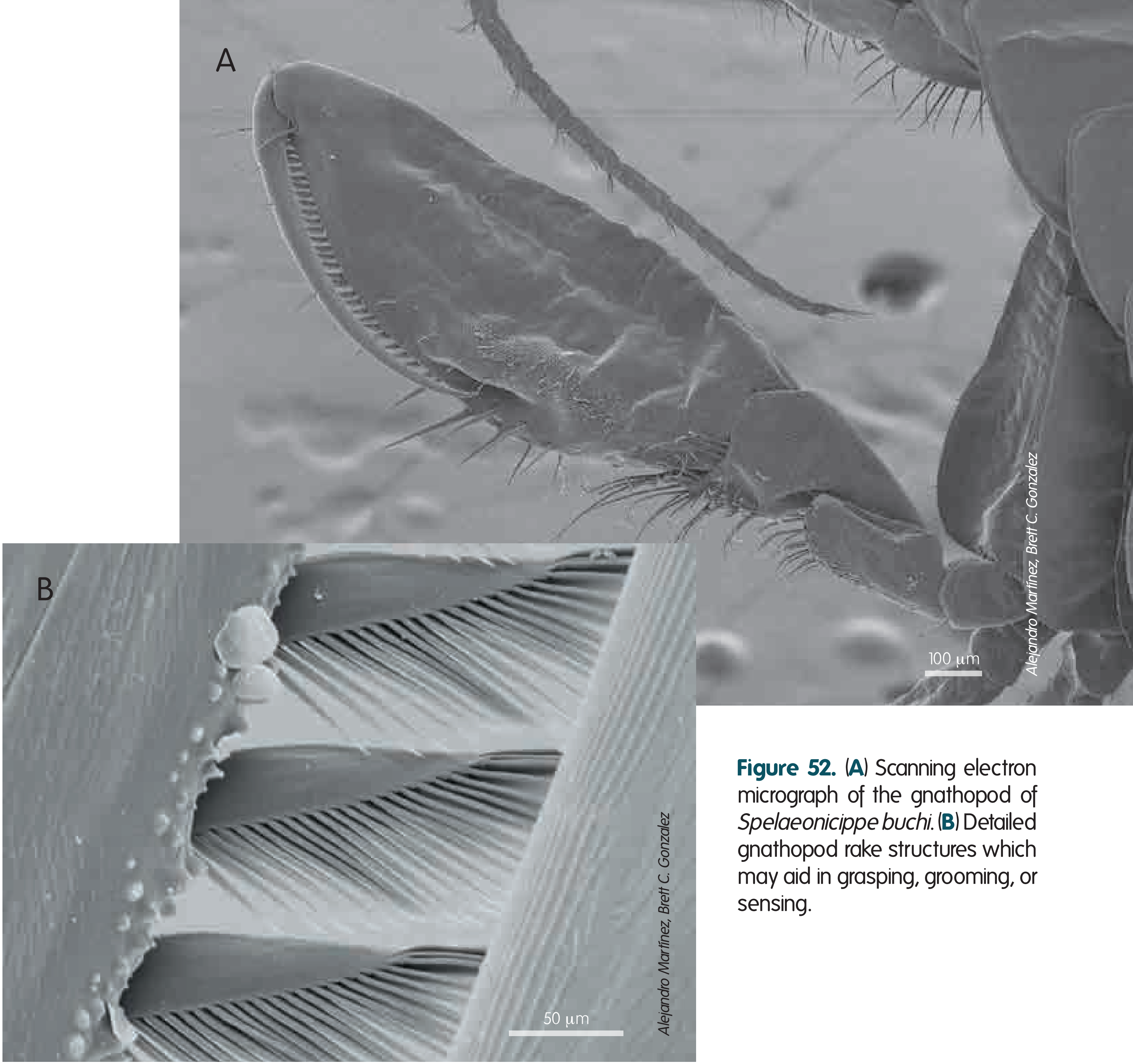

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Figure 52. (**A**) Scanning electron micrograph of the gnathopod of *Spelaeonicippe buchi*. (**B**) Detailed gnathopod rake structures which may aid in grasping, grooming, or sensing.

Figure 53. *Spelaeonicippe buchi* swimming in the water column of Túnel de la Atlántida.

İSOPODA

İsopoda is the second largest order of peracarid crustaceans, with more than 4,000 described species. Although most isopods are marine, there are also a considerable number of both freshwater and terrestrial species, including a few parasitic forms. Most isopods are benthic and adapted to crawl on the bottom, but can swim if necessary. Some specialized worm-like forms are adapted to life among sand grains.

İsopods have dorso-ventrally flattened bodies. The head is normally shield-shaped and lacks a carapace. The first antennae are normally very short or absent and eyes (when present) are sessile. The trunk is divided into a thorax and abdomen, although both regions consist of segments of similar width and are not clearly demarcated. The first pair of thoracic segments is modified as maxillipeds, whereas the rest are legs, usually adapted for crawling. İn a few groups, the first legs are modified into gnathopods for grasping and grooming. The abdomen bears pleopods, used for swimming and respiration.

Based on morphology, İsopoda belongs to the order Peracarida (Box 3). İsopoda is divided into 11 suborders, although their relationships and monophyly has yet to be tested using phylogenetic analyses.

İsopods in subterranean environments

İsopods are common in anchialine environments, with the most diverse lineage represented by the family Cirolanidae, having hundreds of stygobitic species concentrated around the Caribbean and Australia. The origin of the stygobitic cirolanids has been linked with changes in the sea level during the Cenozoic Era (55 Ma) or the Cretaceous (135 Ma). The family Asellidae has a comparable level of subterranean diversity in the Eastern Atlantic. Other families rich in stygobitic species are Anthuridae and Leptanthuridae with genera *Cyathura* and *Curassanthura* exhibiting disjunct distributions in anchialine and interstitial habitats. Members of the family Microcerberidae are also common in interstitial environments, colonizing subterranean marine and freshwater habitats.

Curassanthura canariensis Wägele, 1985

Size: 10-20 mm **Family:** Leptanthuridae **Order:** Anthuroidea

Juan Valenciano

İdentification: *Curassanthura canariensis* is a long and slender isopod that lacks eyes and pigmentation. The head is squarish and well defined, with two pairs of short antennae (Fig. 54 A and B). The trunk is long, slender, and segmented with each segment bearing a pair of uniramous leg-like appendages for locomotion (Fig. 55): except for the first pair, modified as large subchelate gnatopods (pincer-like appendages) for prey capture, grasping, and grooming. The uropods and telson at the posterior end of the body are directed posteriorly, forming a leaf-shaped structure (Fig. 56).

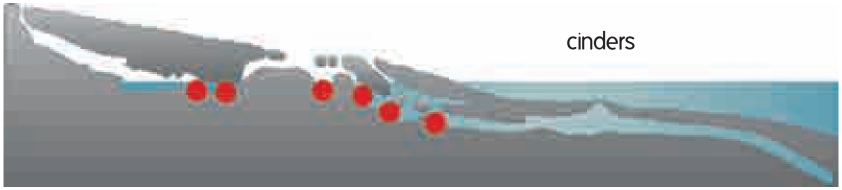
Habitat: Lives in cinders in La Corona lava tube, although more common in Los Jameos del Agua. Rarely found swimming in the water column or crawling over boulders.

Biology: *Curassanthura canariensis* is a benthic species moving through cinders and crevices. The stylet-like mouth suggests that the species might be predatory. They are negatively phototactic and avoid light, hiding quickly amongst the cinders or in crevices when they are illuminated by a dive light.

Affinity and origin: *Curassanthura* belongs to the isopod order Anthuroidea, mostly consisting of interstitial and crevicular species that are small in size with slender bodies adapted to crawl between sand grains or rocks. Although the relationships within Anthuroidea have not been investigated in detail, *Curassanthura* belongs to the family Leptanthuridae, which consists of 96 described species widespread through the ocean. The genus *Curassanthura* consists of four anchialine species: *C. canariensis* from Lanzarote, *C. halma* from Curaçao and Bonaire, *C. jamaicensis* from Jamaica, and *C. bermudensis* from Bermuda. The origin of *Curassanthura* remains problematic as the sister group of the genus is unknown. Cave colonization from marine ancestors followed by vicariance related to the opening of the Atlantic Ocean has been proposed to the origin of the genus. As an alternative, crevicular dispersal through the ocean floor has been suggested. Another cave endemic species within Leptanthuridae, *Bunderanthura bundera*, has been recently described from the freshwater layers of Bundera Sinkhole, an anchialine cave in northwestern Australia.

DİSTRİBUTİON

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

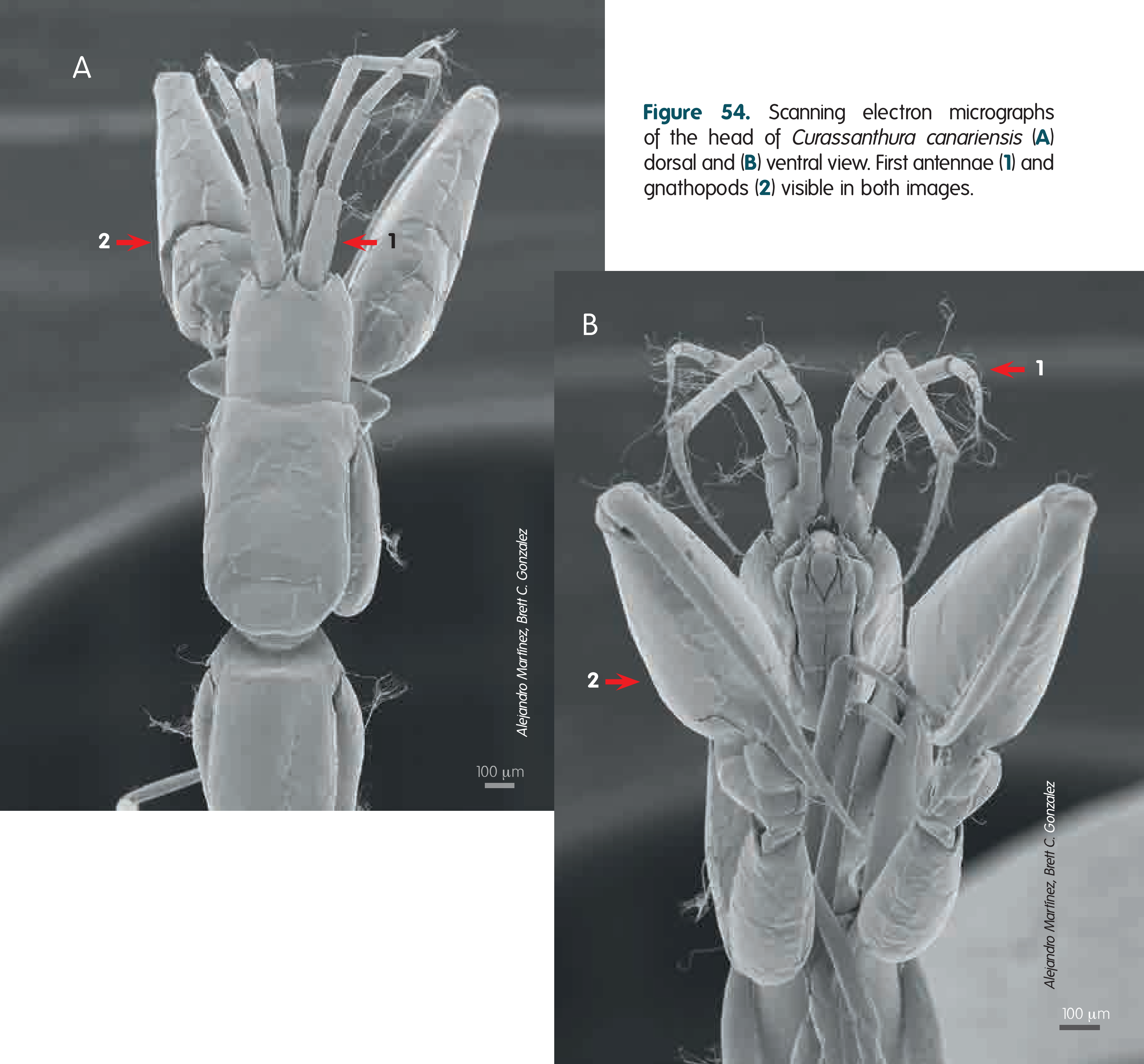


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Figure 54. Scanning electron micrographs of the head of *Curassanthura canariensis* (**A**) dorsal and (**B**) ventral view. First antennae (**1**) and gnathopods (**2**) visible in both images.

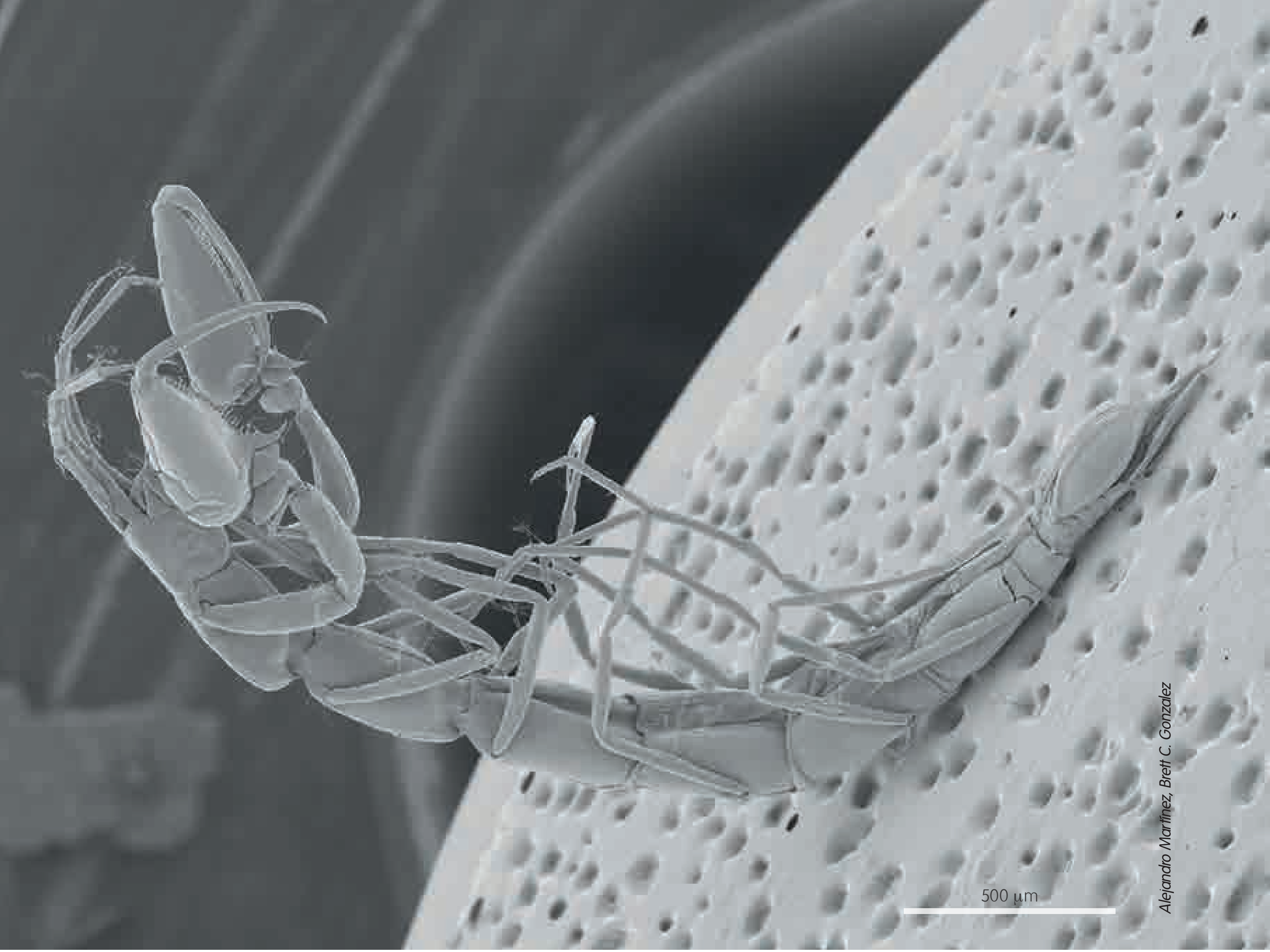

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Figure 55. Scanning electron micrograph of *Curassanthura canariensis*, lateral view.

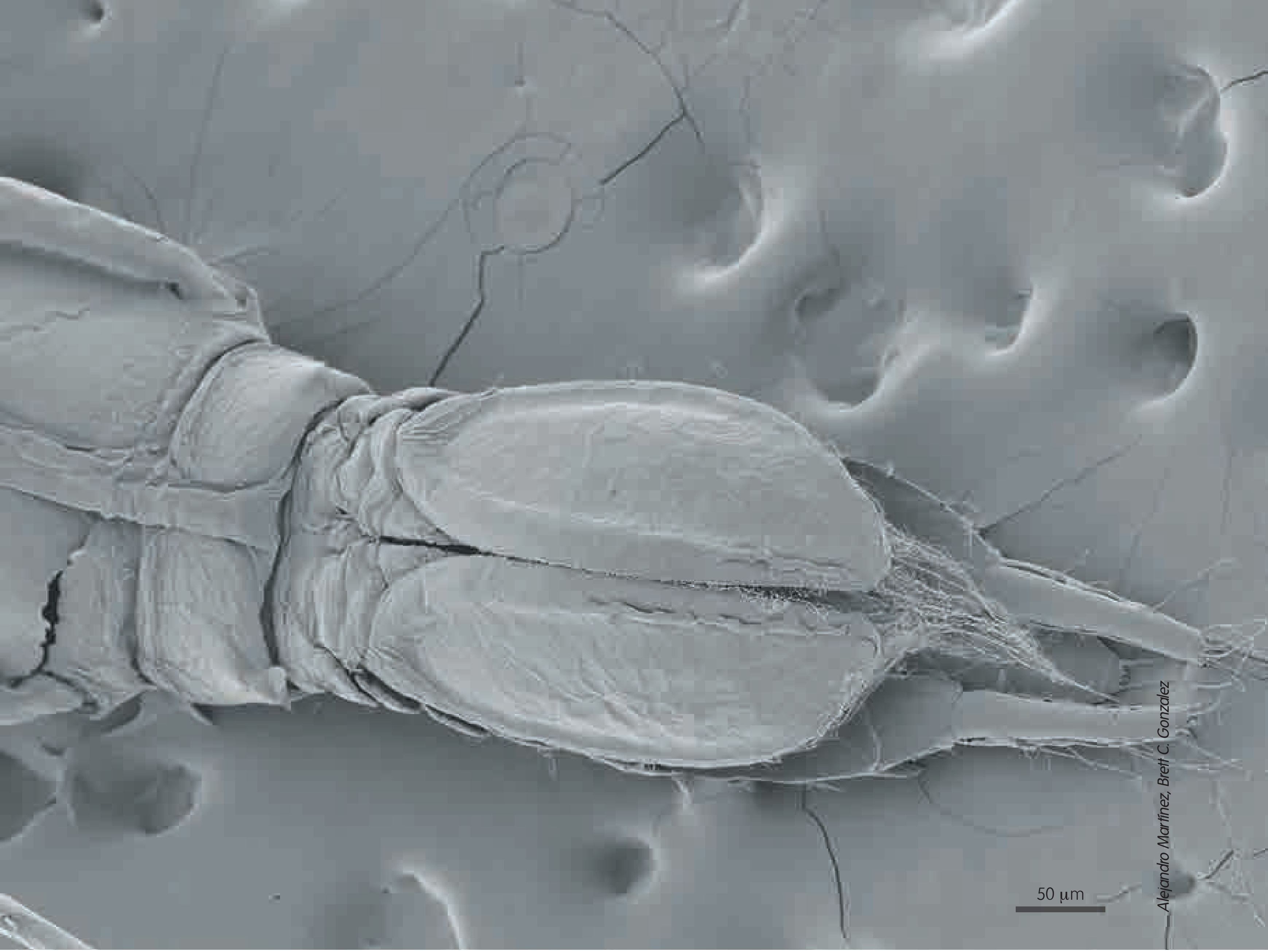

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Figure 56. Scanning electron micrograph of the posterior end of *Curassanthura canariensis,* showing the uropods.

DECAPODA

Decapoda contains approximately 15,000 species representing approximately one quarter of all described crustaceans. Most of the well-known species of crustaceans belong to this group, including shrimp, lobsters, and crabs. The majority of the decapods are marine, but they have colonized all environments. Some crayfish, shrimp, and crabs have invaded freshwater, and in the tropics, land hermit of crabs have adapted a terrestrial lifestyle. Decapods are variable in size ranging from commensal forms of a few millimeters to the Japanese spider crab which has chelipeds (pincers) spanning up to 4 m.

In decapods, the head and thorax are fused together and referred to as a cephalothorax which is covered by a protective carapace. The head normally possesses a pair of eyes, two pairs of antennae, and the mouth parts. The thorax has five pairs of appendages from which the name Decapoda is derived (10 legs). These appendages lack exopods and are unirramous. The first (and sometimes the second) of these legs is frequently enlarged and chelated, forming a pincer-like appendage mostly used to manipulate food. The remaining appendages are leg-like and primarily used for crawling or swimming. The abdomen consists of seven segments, with the anterior five bearing a pair of biramous appendages. The first two form gonopods in the males for copulation.

Decapods are placed in the clade Multicrustacea, together with Syncarida and Peracarida (Box 4). This group is divided in three major lineages: Pleocyemata, the most diverse with approximately 10,000 species including shrimp (Caridea), squat lobsters (Anomura), and crabs (Brachyura); Dendrobranchiata (prawns); and the Macrura Reptantia (lobsters and crayfish), which are less diverse, with approximately 3,050 species combined.

Decapods in subterranean environments

Decapoda are common inhabitants of subterranean environments worldwide with aproximately 150 described species belonging to all groups except for Dendrobranchiata. Macrura Reptantia include a number of stygobitic species consisting mostly of crayfish (Astacidae) inhabiting freshwater subterranean environments. Most stygobitic decapods belong to Pleocyemata, with the highest diversity occurring among the shrimp (Caridea). The families Procarididae, Agostocarididae, Xiphocarididae, and Macromaxillocarididae are exclusively stygobitic. The Procarididae have five species in the genus *Procaris* from Ascension Island, Bermuda, Christmas Island, Hawaii, and Cozumel Island (Mexico); the Agostocarididae include three species , all in the genus *Agostocaris*, from the Bahamas and Yucatan; the Xiphocarididae have two species from freshwater caves of Cuba and Jamaica; the Barbouriidae have two species both from the genus Barbouria inhabiting anchialine caves and pools from Bermuda, Bahamas, Cuba, Yucatan and the Cayman Islands; and the Macromaxillocarididae have one species from the Bahamas. However, most stygobitic carideans belong to the families Atyidae, with the stygobitic genera *Typhlatya, Stygiocaris,* and *Troglocaris*, and the Alpheidae with *Yagerocaris, Bermudacaris, Hamalpheus* and *Triacanthoneus*. Several stygobites are also described from the Hippolytidae and Palaemonidae, although mostly from freshwater caves. The Brachiura and Anomura are less abundant in anchialine habitats with the highest diversity of stygobitic crabs concentrated in the Indo-Pacific (Families Gecarcinidae, Varunidae, and Xanthidae). The only stygobitic squat lobster belongs to the family Munidopsidae, and it is represented by *Munidopsis polymorpha* from Lanzarote.

Decapods in La Corona lava tube

Four species of decapods have been recorded in La Corona lava tube; the most noteworthy being the stygobitic galatheid squat lobster *Munidopsis polymorpha*, while the other three are accidental marine species. The shrimp *Athanas* sp. (Fig. 57) and *Stenopus spinosus* (Fig. 58) have been found near Montaña de Arena in Túnel de la Atlántida, either burrowing in sand or living in rock crevices. These are marine species commonly occurring in similar open water environments throughout the Canary Islands. The hermit crab *Clibanarius* sp. was reported only once in the 1970s in Los Jameos del Agua but has not been found since then, while remaining common in littoral environments of Lanzarote.

Figure 58. Individuals of *Stenopus spinosus* have been found near Montaña de Arena and are considered to be accidental inhabitants. The specimen here was photographed in a small marine cave in Tenerife.

Jaume Mora

Figure 57. *Athanas* sp., accidental resident of Montaña de Arena.

Alejandro Martínez

Munidopsis polymorpha Koelbel, 1892

Size: 40-60 mm **Family:** Galatheidae **Order:** Anomura


Juan Valenciano

Identification: *Munidopsis polymorpha* is easy recognizable by the squat shape of the body, large white or orange carapace, reduced eye stalks (Figs. 59 and 61) and rostrum of variable length (Fig. 60). Because of this latter feature, *Munidopsis* was given the name of "polymorpha" by Koelbel. The abdomen is segmented and normally bent below the body with the telson forming a fin-like structure. The well developed chelipeds (pincers) are followed by three pairs of uniramous appendages used for walking. A fifth pair of appendages is highly reduced and used for carrying the eggs (Fig. 61).

Habitat: Rocks and crevices throughout La Corona lava tube, but more commonly observed in Los Jameos del Agua and the first 100 m of Túnel de la Atlántida, where more food is available. Occasionally, *M. polymorpha* was found one anchialine pool and wells along the coast of Lanzarote.

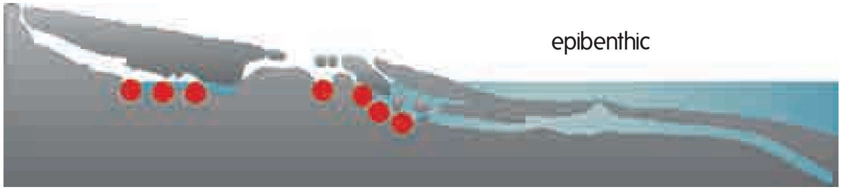
Biology: *Munidopsis* is an opportunistic omnivore, feeding on detritus, diatoms, or dead animals. They are negatively phototactic and can be found hiding in crevices and under rocks during periods of the day when portions of the caves are illuminated. During the night, *M. polymorpha* come out to feed, and at this time densities can reach up to 150 individuals per square meter in Los Jameos del Agua. *Munidopsis* is territorial, basing individual territories according to the length of their second antenna, and thus giving each individual sufficient room to graze. When an individual invades another's territory, its presence is detected by their antennae and the invader is aggressively attacked with extended chelipeds.

Munidopsis polymorpha has separate sexes, although the population in Los Jameos del Agua is dominated by females. Males can grow slightly larger than the females. The only distinction between sexes is the genital pore present at the base of the third pair of thoracic legs in the females. Reproduction takes place throughout the year, although more ovigerous females can be found in spring. The eggs are relatively large, containing a higher quantity of yolk than other investigated species of *Munidopsis*. Eggs have a diameter of 1.2-1.3 mm and are yellowish in color. Each female is typically found with 1-3 eggs, but has been observed carrying up to 8-10 eggs ventrally in the pleon. Ovigerous females continuously clean and oxygenate the eggs with their fifth pair of legs. Females take care of the embryos until the first larval stage, the zoea, when at this point, they are released. After 10-14 days the zoea molts into a second zoea stage (Fig. 62). Both zoea stages are very similar, measuring around 3 mm and can only be distinguished by details in the morphology of the pleopods. In the first larval stages, eyes are present, but they are partially covered by the base of the large and dorsally concave rostrum. These first stages are non-feeding and are nourished by a large supply of yolk. Both stages are benthic and are almost unable to move except for small movements achieved by beating of the pleon with the larvae telson. After 3-4 weeks, the second zoea stage of *M. polymorpha* molts into a small squat lobster which is morphologically similar to the adult. At this point, the yolk is still not completely consumed.

Affinity and origin: *Munidopsis polymorpha* belongs to a genus consisting of approximately 300 species, most of which inhabit the deep sea. *Munidopsis polymorpha* is the only cave species of the genus and the only stygobitic squat lobster described in the world. Since most other members of the group inhabit the deep sea, the origin of this stygobitic species has been explained by colonization of the shallow water cave environment by a marine deep water ancestor.

DISTRIBUTION

Distribution of the species in La Corona lava tube



Distribution of the genus around the world

Figure 59. *Munidopsis polymorpha* from Los Jameos del Agua showing the squat body, large robust chelipeds, long antennae and head with small reduced eye stalks.

Juan Valenciano

Figure 60. *Munidopsis polymorpha* perched on lava rock in Los Jameos del Agua. The animal is about 50 mm.

Alejandro Martínez

Figure 61. Detail of the head of *Munidopsis polymorpha*, showing the "eyeless" eye peduncles (arrow).

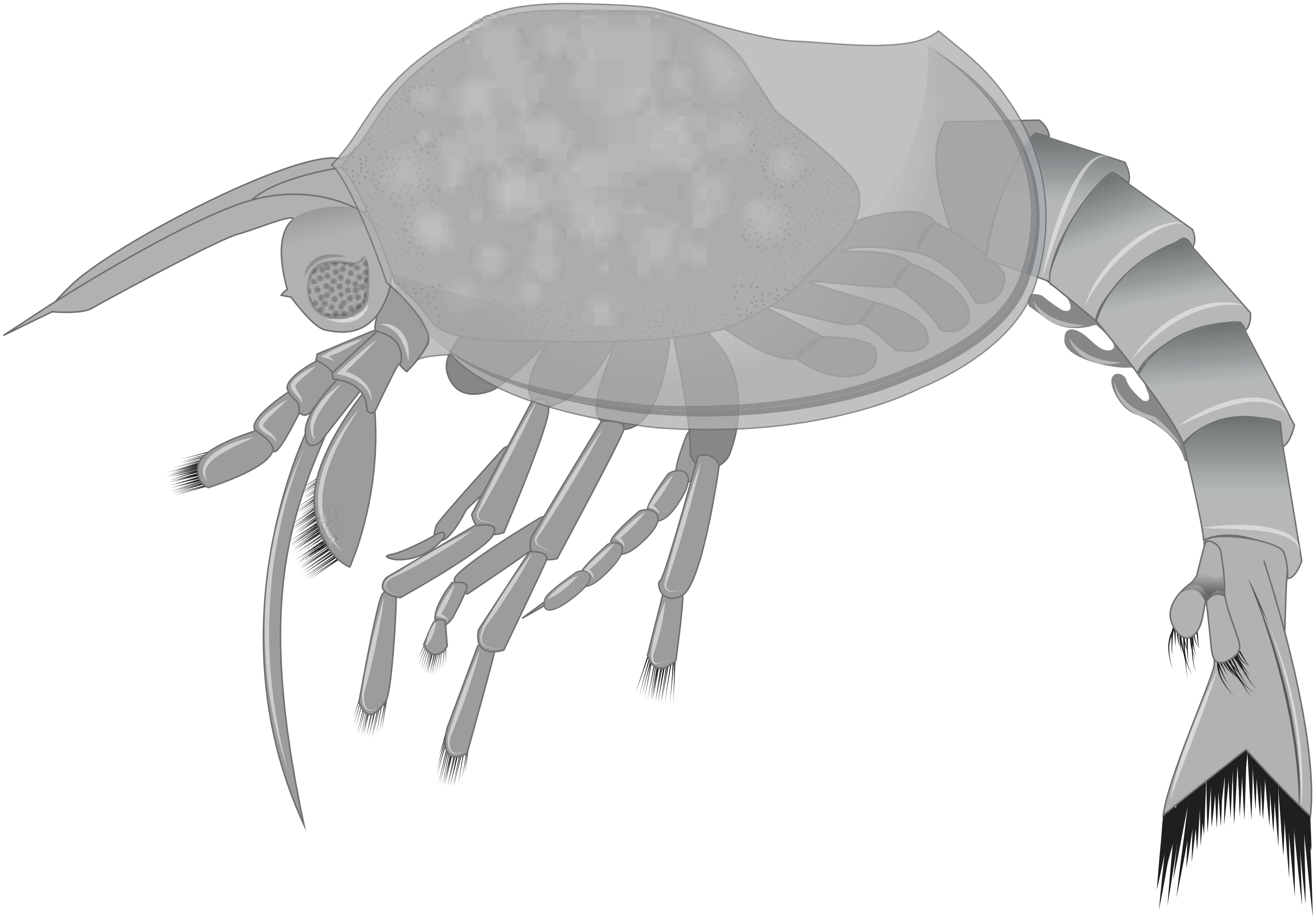
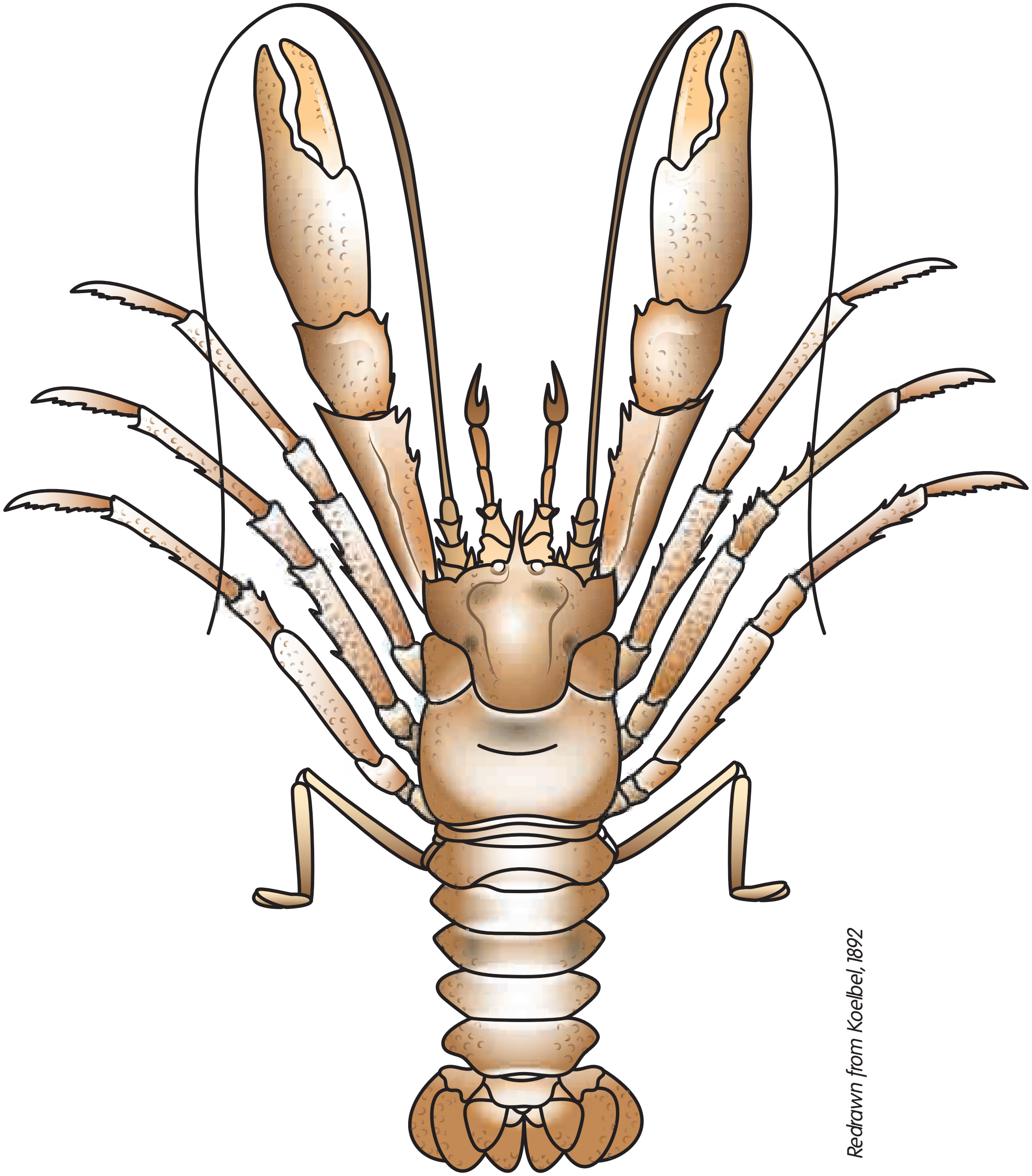


Figure 62. Second larvae stage or zoea of *Munidopsis polymorpha*. The larvae are about 1 mm.



Redrawn from Koelbel, 1892

Figure 63. *Munidopsis polymorpha.*

REMİPEDİA

The discovery of a highly unusual swimming arthropod that superficially resembled a centipede in anchialine caves from the Bahamas in 1979 set the stage to erect the crustacean Class Remipedia, regarded as one of the major zoological discoveries of the 20th century. Remipedes are one of the most enigmatic classes of arthropods. The 27 described species of remipedes are hermaphroditic predators which exclusively live in fully marine waters from the depths of anchialine caves. They are highly adapted to this environment, showing little pigmentation and no eyes. Remipedes generally exhibit low population densities; however, there are a few exceptions including Cenote Crustacea in the Yucatan Peninsula and Old Blue Hill Cave in Providenciales (Turks and Caicos İslands) which harbor comparatively dense populations. İn Cenote Crustacea, it is possible to observe hundreds of specimens on a single cave dive. This high density has not been fully explained, but might be attributed to high numbers of the stygobitic atyid shrimp *Typhlatya pearsei*. The explanation for the high densities of shrimp is also unknown; however, the shrimp serve as readily available prey for the remipedes.

The external morphology of remipedes is easily recognizable and unique among arthropods. All remipedes are eyeless with limited pigmentation and vermiform bodies consisting of 16-42 serially repeated segments or somites. The head is well defined and covered by a cephalic shield. Ventrally, the head is equipped with six pairs of appendages: pairs of sensory antennules and antennae, and pairs of powerful mandibles, maxillules with venom injecting fangs, maxillae, and maxillipedes used for capturing prey and feeding. The mouth opens between the antennae and the mandibules. The trunk somites, termed sclerites, are composed of three parts, referred to as tergal, pleural, and sternal sclerites. Each somite bears a pair of paddle-shaped, biramous swimming appendages. Swimming movements are generated by the metachronal beating of these appendages. The last segment lacks swimming appendages and instead has a pair of caudal rami projecting posteriorly.

The position of Remipedia within Arthropoda is an active topic for current investigations. İnitially based on the particular morphology of the group with metamericaly repeating trunk segments as well as their limited distribution to caves, remipedes were believed to represent basal branches of Mandibulata. This was supported by the fossil record, with the most likely sister group of remipedes being the fossil arthropod *Tesnusocaris,* known from the Devonian (419-359 Ma). However, the highly organized and well differentiated brain of remipedes is matched in complexity only by the brain of "higher" crustaceans. Furthermore, molecular analyses suggest that remipedes and Cephalocarida (an exclusively interstitial lineage of arthropods) are sister taxa to insects. The phylogenetic relationships within Remipedia have been investigated recently using molecular data, reorganizing the class into seven families and 12 genera. As a result of this reclassification, Lanzarote remipedes were removed from the genus *Speleonectes* and placed in *Morlockia*, a genus named after Morlocks, the futuristic subterranean humanoids in H.G. Wells' 1895 novel, *The Time Machine*.

Remipedes in subterranean environments

Remipedes are exclusively known from anchialine habitats, exhibiting typical disjunct distribution patterns, similar to other anchialine stygobitic lineages. Twenty-seven species of remipedes are described from anchialine caves in the Caribbean (Bahamas, Yucatan, Cuba, Belize, and Hispaniola), Lanzarote, and Western Australia. Dan's Cave on Abaco İsland in the Bahamas contains six species of remipedes representing five genera, while Sagittarius Cave on Sweetings Cay, Bahamas is inhabited by seven species, all from different genera. However, 17 species of remipedes are known to exclusively inhabit a single cave. Since many thousands of anchialine caves have yet to be scientifically explored, the potential for discovery of new species is great. The higher diversity of remipedes in the Caribbean, particularly the Bahamas archipelago with 19 species, may be related to the higher habitat availability of the region and to the isolation that occurs between caves on islands or shallow water platforms separated from one another by channels reaching oceanic depths.


Ulrike Strecker

Morlockia atlantida (Koenemann, Bloechl, Martínez, Iliffe, Hoenemann & Oromí, 2009)
Morlockia ondinae García-Valdecasas, 1984

Size: 15-20 mm **Family:** Morlockiidae **Order:** Nectiopoda

Identification: Although remipedes in general are easy to identify (see above), the two species within the lava tube are from the same genus and difficult to distinguish without detailed morphological examinations. *Morlockia atlantida* can be differentiated from *M. ondinae* by the presence of a more slender and loose arrangement of the trunk somites, long and slender branchium of maxilla, and a varying number of setae among the mouthparts, including comparatively shorter claws of the maxilla and maxilliped.

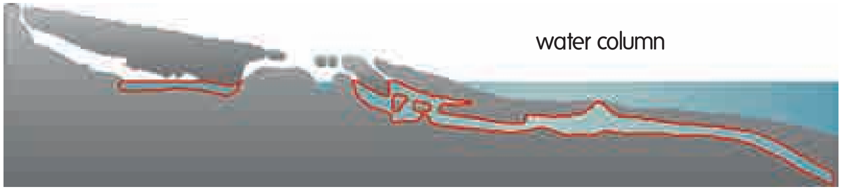
Habitat: Water column of Túnel de la Atlántida and Cueva de los Lagos.

Biology: Remipedes are the top predators in La Corona lava tube. They probably feed on other crustaceans in the cave, such as thermosbaenaceans, mysids, amphipods, and large copepods. In other caves, they have been observed preying on large animals, including shrimp. They capture the prey using their three pairs of claws, one of them with hollow fangs which inject neurotoxic venom to paralyze and kill the prey. When the prey is paralyzed, they crack the prey's carapace with their mouthparts, using their claws and the basal segments of their maxillipedes (gnatobase). In addition to their role as predators, they are suspected to occasionally act as scavengers and suspension feeders in order to obtain additional nutrients.

Affinity and origin: The extremely disjunct distribution of remipedes has motivated the proposal of the group as Tethyan relicts, colonizing the caves during the Mesozoic and speciating by vicariance related to continental drift after the extinction of their marine relatives. This hypothesis remains to be tested by phylogenetic methods, but recent molecular phylogenies do not show a clear congruent pattern between the clades and the geographical pattern. *Morlockia* consists of four species including both species from Lanzarote being sister to *M. emersoni* from Dominican Republic and *M. williamsi* from Little Bahama Bank. This relationship supports that the diversification of the clade, occurring on both sides of the Atlantic, which may have been related to vicariant tectonic events. *Morlockia* is sister to the genus *Xilbalbanus* from Yucatan, both well nested within the class Remipedia.

DISTRIBUTION

Distribution of the genus in La Corona lava tube



Distribution of the genus in caves around the world

Ecology of La Corona Lava Tube

CHAPTER 4

Anchialine water in La Corona lava tube is of marine origin and although partially isolated from the surrounding ocean, it is characterized by nearly constant environmental parameters regardless of distance or depth. The isolation and small differences in measurable components of the waters are key to understanding the fundamental ecology and the observable adaptations present in the endemic stygobitic fauna.

Hydrology

The anchialine sections of La Corona lava tube all share the same geological origin, and are interconnected through spaces between breakdown, cracks, fissures, and the porous nature of the lava rock. Hence, variations among the abiotic factors, mainly presence of light in some sections, are directly responsible for the ecological changes observed between the different parts of the cave (Fig. 1). The cave water column is weakly stratified due to mixing by the relatively strong tidal currents and limited freshwater input, primarily coming from rainfall (125-150 mm per year, most of it during the winter). As with most anchialine caves, tidal fluctuations within La Corona lava tube are delayed from the surrounding ocean nearly 1.5 hours and exhibit a reduction in high. Tidal amplitude in Túnel de la Atlántida and Los Jameos del Agua averages 1.5 m compared to 3.0 m exhibited throughout the Canary İslands. Tidal exchanges in the lava tube occur indirectly though relatively small cracks, fissures, and the porous nature of the lava rock. The only known access point for direct exchange of sea water within Túnel de la Atlántida is a small inconspicuous hole directly above Montaña de Arena, where sand enters the cave from the overlying seafloor. Previous cave diving expeditions that have reached Montaña de Arena have not observed significant tidal currents nor seen any light coming in atop the sand mountain. These observations highlight that there is no single point of tidal exchange in Túnel de la Atlántida, suggesting the entire lava tube is permeable to water exchange from the surrounding marine waters.

The salinity, temperature, pH, and dissolved oxygen values are relatively constant throughout Túnel de la Atlántida. Variations in water parameters correspond to the tidal cycles, indicated by measurements taken by an electronic water quality analyzers (sondes) placed in Los Jameos del Agua and at 300, 700, and 1000 m from the entrance pool of Túnel de la Atlántida (Fig. 2). Salinities in La Corona lava tube are very similar to that of the surrounding ocean, ranging between 34.7-35.0 ppt, with fluctuations directly related to the tides (highest values at high tide and lowest values at low tide) (Fig. 2 A and B). The slight drop in salinity at low tide could be the result of fresh

Figure 1. The light strikes obliquely on the surface of Los Jameos del Agua through Jameo Chico on the east of the lake during the morning. The light beams reach the portion of the lake where the carpet of diatoms grow.

Brett C. Gonzalez

groundwater mixing with sea water and circulating through La Corona lava tube. Water temperatures recorded in Túnel de la Atlántida hardly fluctuated during tidal exchanges (18.71-18.88 ºC) and show little to no seasonal variation throughout the year. Changes in temperature are directly related to the tide cycle at the 300 m and 700 m stations, but inversely related to it at 1000 m, suggesting that tidal currents within the lava tube flow in opposing directions. Temperature variation in the surrounding ocean ranges seasonally between 18-24°C between 0-100 m depth m. The minimal differences in water temperature of Túnel de la Atlántida are due to isolation of cave waters from daily solar insolation and local seasonal climatic changes.

The hydrogen ion concentration, or pH, in Túnel de la Atlántida ranged between 7.8-7.9, and is slightly lower than the average for surrounding marine waters (8.07). In Los Jameos del Agua, the pH has a slightly broader range (7.75-7.95). The lower pH in the lake may partially be due to the breakdown of organic matter (mostly diatoms) by bacterial processes.

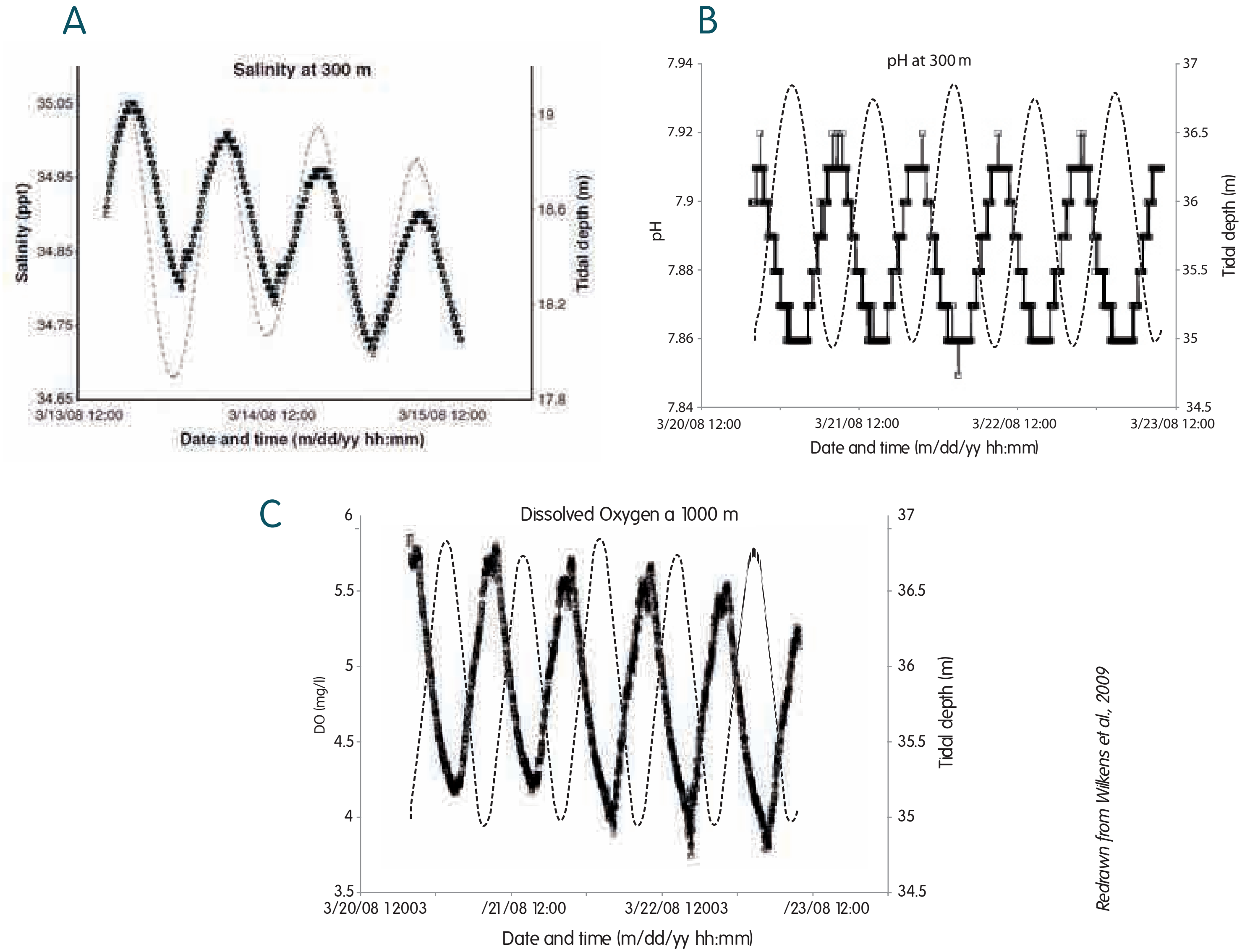
Dissolved oxygen levels in Túnel de la Atlántida are lower than the surrounding marine waters as there is no photosynthetic production within the cave. The exception to this is Los Jameos del Agua, where incident sunlight (Fig. 1) allows photosynthetic diatoms and bacteria to elevate levels of dissolved oxygen. Dissolved oxygen measured in Túnel de la Atlántida from 1000 m penetration (only available measurement) ranged between 3.7-5.7 mg/L and is inversely related to the tidal exchange (Fig. 2 C). Lower dissolved oxygen measurements at high tide are in response to tidal pumping from the surrounding ocean forcing isolated waters from deep within the lava tube upwards towards the entrance.

Chemical analyses of water from Los Jameos del Agua (Table 1) show a high degree of similarity in the chemical composition of the cave water to the ocean. However, levels of calcium, magnesium, and chloride were reduced, while concentrations of sulfate and silica increased, as these may be derived either from volcanic rocks or from diatom and bacterial mediated processes within the water column and cinders.

	Jameos del Agua	Coastal waters
Calcio (Ca^{2+})	401	428
Magnesio (Mg^{2+})	1310	1350
Sodium (Na^{+})	11120	11420
Silica (SiO_2)	2.6	<0.1
Chloride (Cl^{-})	20660	21150
Sulfate (SO^{2-})	2730	2680
Bromide (Br^{-})	70	70
Potassium (K^{+})	300	300
Borate (H_2BO^{3-})	4	4
Strontium (Sr^{2+})	6	6
Conductivity	97,8	100
pH	7.47	8.14

measurements in mg/l

Table 1. Water composition at Los Jameos del Agua lake, compared to measures taken in the open ocean in front of the cave.



Redrawn from Wilkens et al., 2009

Figure 2. Variation of hydrological parameters from Túnel de la Atlántida. (**A**) Salinity at 300 m from the entrance. Solid line represents the salinity, while dashed line represents the tidal fluctuation. (**B**) Salinity at 1000 m (thick line) is inversely related with the tides (dashed line). (**C**) Dissolved oxygen at 1000 m thick line is inversely correlated with the tides (dashed lines).

Zones of Limited Illumination: Los Jameos del Agua

Abiotic Conditions. Los Jameos del Agua is the only anchialine section of La Corona lava tube that receives natural illumination. Sunlight reaches the lake during the morning hours through the skylight of Jameo Chico, and during the evening through Jameo Grande (Fig. 4), while the roof of the lava tube shields the lake from direct sunlight and heating during most hours of the day. Growth of photosynthetic microalgae takes place in areas where light penetrates, providing nutrients to the abundant fauna from the lake. Most of the microalgae occurring in the lake are diatoms, a type of unicellular algae with characteristic carapaces called thecae, which consist of two separate valves made of silica. Although diatoms are very common in marine and freshwater environments, the high diatom abundance in Los Jameos del Agua is exceptional and likely related to high concentrations of silica in the water (see Table 2) and low light intensity, which prevents growth of most other forms of algae. The greatest density of diatoms occurs in shallow water at the western side of Los Jameos del Agua where a 1-2 cm thick carpet of diatoms covers the bottom, something which is rarely found in the open ocean (Fig. 5). The position of the skylight and the angle of incidence above the shallow depths provide the perfect conditions for elevated growth. The carpet of diatoms is predominantly composed of a single undescribed species (Table 3), characterized by its fusiform cells that form colonies of several cells arranged as rows or stars. In addition, several other species of diatoms are also present within the carpet. Measurements of chlorophyll (one of the main pigments involved in photosynthesis) from the water in Los Jameos del Agua indicate that microalgae are not only present along the bottom, but also in significant concentrations within the water column. The entrance pool of Túnel de la Atlántida also shows similar chlorophyll amounts, contributed either by the artificial illumination or by the exchange of water with Los Jameos del Agua, thus distributing the chlorophyll signal.

In Los Jameos del Agua, large amounts of organic nutrients are available due to the high densities of diatoms. Inorganic nutrients have either a a marine origin, reaching Los Jameos del Agua by tidal exchange through the porous basalts, or a terrestrial origin, percolating down through the soil layers above the cave or transported into the cave by wind or animals. Although the extent of the contribution from terrestrial nutrients is presently unknown, it may have been significantly greater

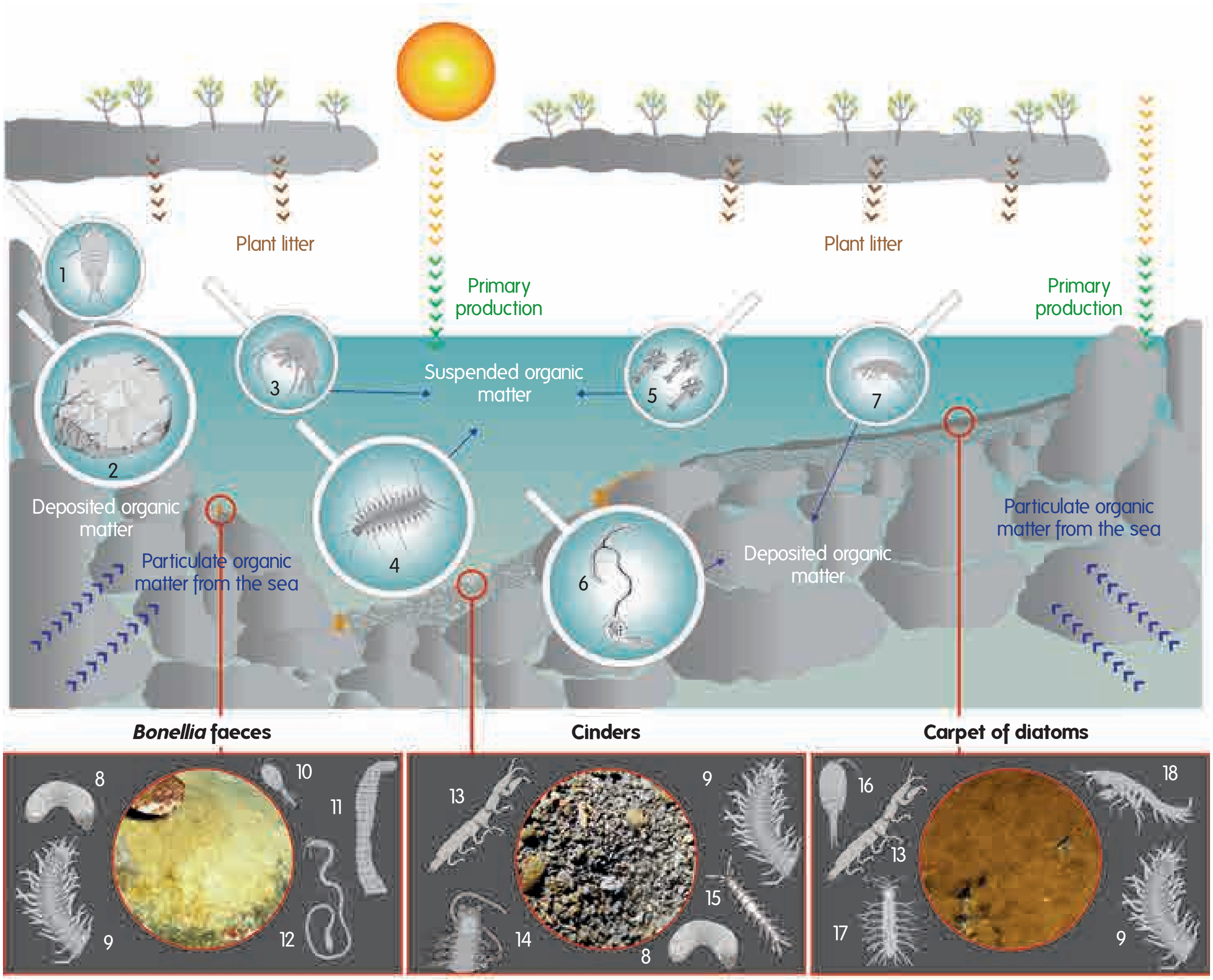


Figure 3. Trophic relationships at Los Jameos del Agua. The main scheme shows the interaction amongst the large animals which inhabit the lake. The pictures in the squares shown the assemblages of microscopic species dwelling in the bottom. **1** *Halosphiloscia canariensis*. **2** *Munidopsis polymorpha*. **3** *Spelaeonicippe buchi*. **4** *Gesiella jameensis*. **5** *Heteromysoides cotti*. **6** *Bonellia viridis*. **7** *Liagoceradocus acutus*. **8** *Fauveliopsis jameoaquensis*. **9** *Syllis* sp. **10** Cyclopoida. **11** *Notomastus* sp. **12** *Aphelochaeta marioni*. **13** *Curassanthura canariensis*. **14** *Macrochaeta* n. sp. **15** *Mesonerilla* n. sp. **16** *Oromiina fortunata*. **17** *Leptonerilla diatomeophaga*. **18** *Bogidiella uniramosa*.

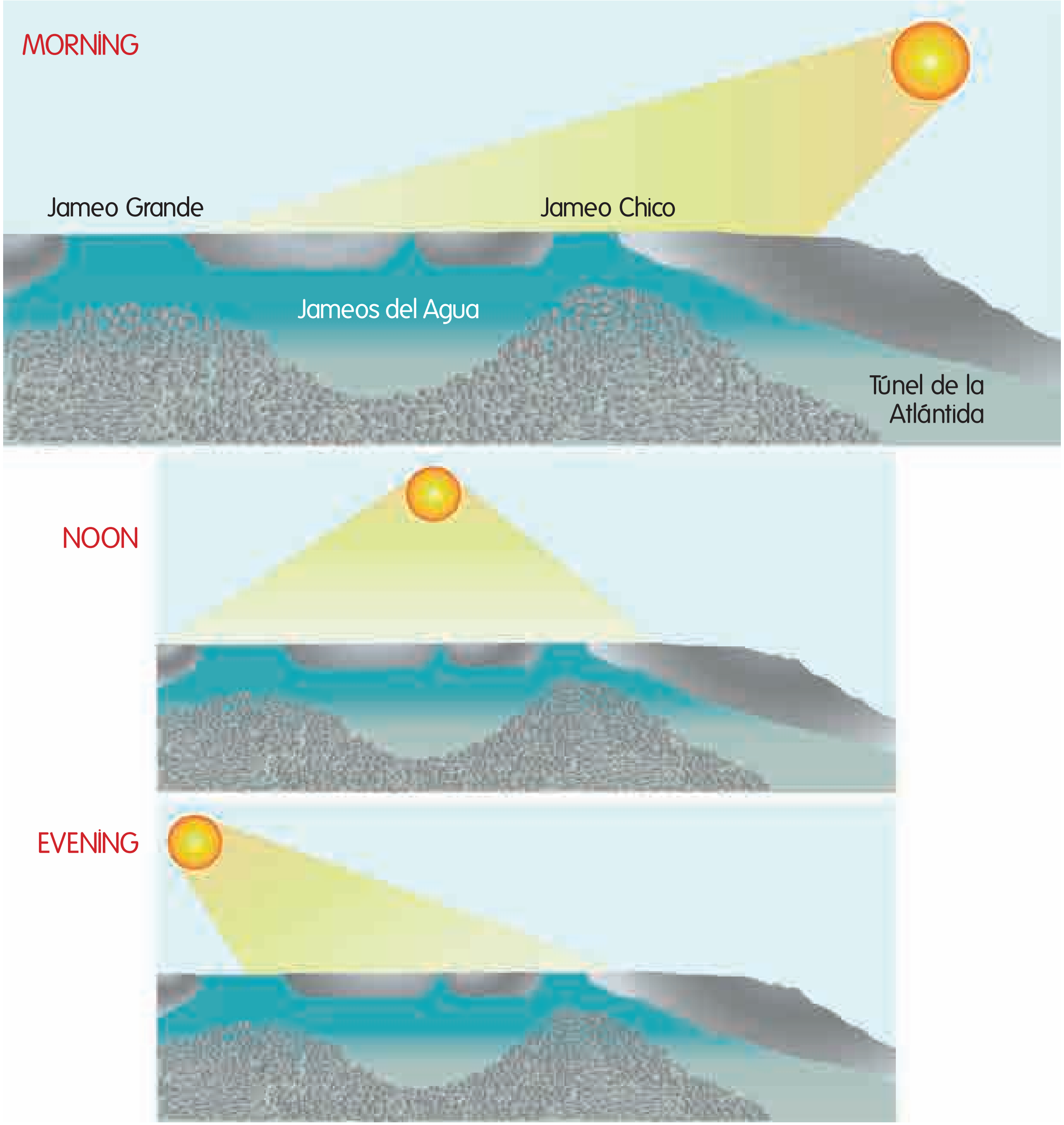


Figure 4. Diagram showing the variation of the incident sunlight in Jameos del Agua throughout the day.

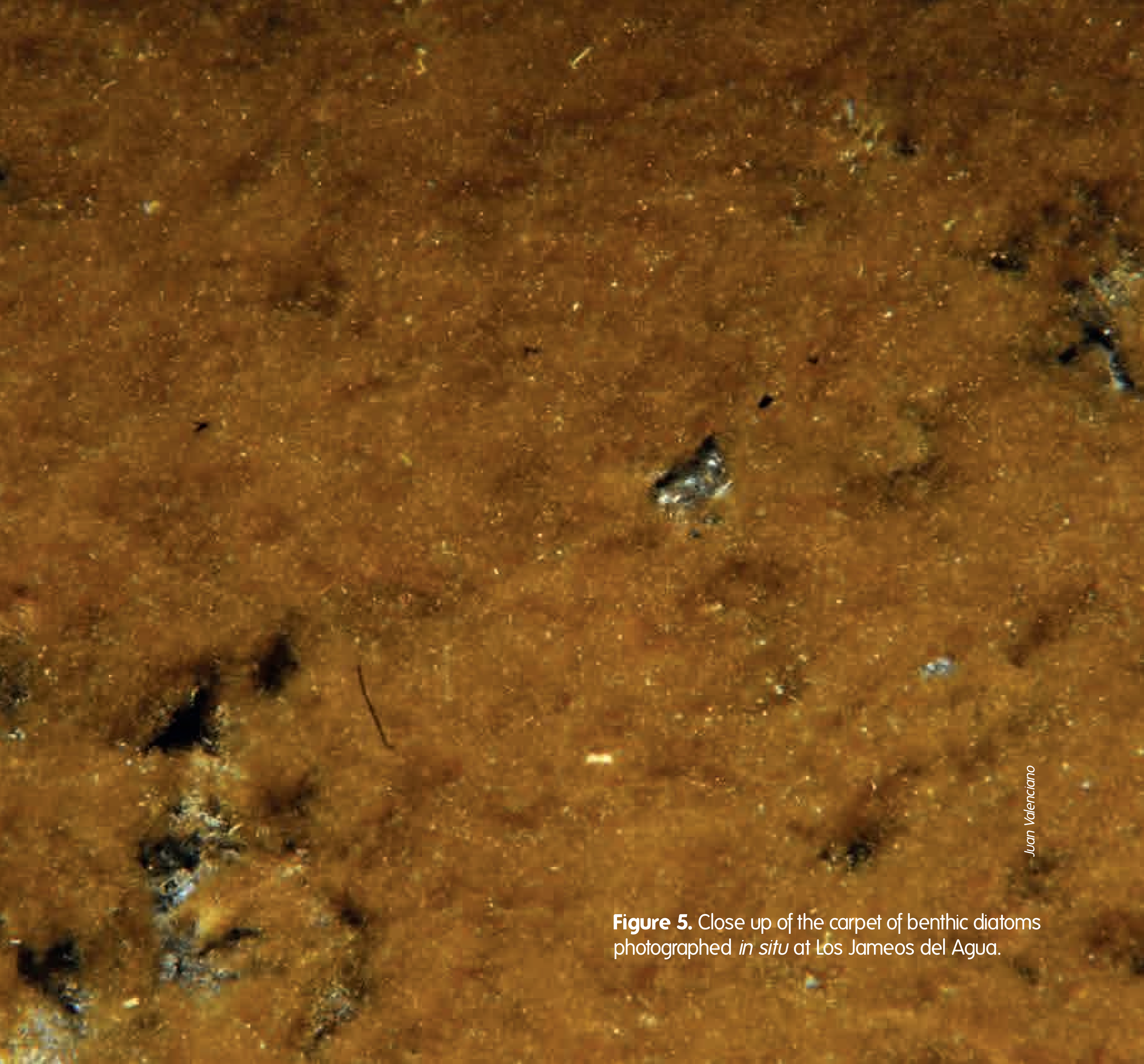


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Figure 5. Close up of the carpet of benthic diatoms photographed *in situ* at Los Jameos del Agua.

before the construction of the tourist center altered the landscape. This is evidenced through early descriptions of Los Jameos del Agua by geologist Eduardo Hernández Pacheco (1907) and biologists Fage and Monod (1936), where they describe abundant growth of native vegetation around the shores of the lake and the skylights above. This growth surely contributed to accumulations of organic debris along the bottom of Los Jameos del Agua, sustaining denser populations than those observed today for the endemic amphipod *Parhyale multispinosa* and several marine molluscs including *Phorcus atratus, Littorina striata,* and *Patella ulyssiponensis.*

Animal Assemblages and Trophic Relationships. Los Jameos del Agua is inhabited by several endemic stygobitic species, being the only section of La Corona lava tube known to support high densities of stygobitic species.

	Túnel de la Atlántida				Open ocean
	1	**2**	**3**	**4**	
Calcium (Ca^{2+})	416	416	416	421	428
Magnesium (Mg^{2+})	1330	1320	1340	1330	1350
Sodium (Na^+)	11200	11200	11230	11360	11420
Silicate (SiO_2)	2.6	2.4	2.4	2.4	<0.1
Chloride (Cl^-)	20520	20590	20870	20930	21150
Sulfate (SO^{4-})	2760	2690	2950	2670	2680
Bromide (Br^-)	70	-	-	-	70
Potassium (K^+)	300	-	-	-	300
Borate (H_2BO^{3-})	4	-	-	-	4
Strontium (Sr^{2+})	6	-	-	-	6
Conductivity	97	98.7	98.7	98.7	100
pH	7.79	7.38	7.83	7.45	8.14

measurements in mg/l

Jantschke et al., 1994

Table 2. Water composition in Túnel de la Atlántida compared to measurements taken in the open ocean just in front of the tourist center. Each column represent a different sampling station inside the cave. **1** Entrance in the Jameo Chico, **2** Lago Escondido, **3** La Sima, **4** Montaña de Arena.

Species	Family
Achnantes brevipes	Achnantaceae
Amphora spp.	Catenulaceae
Coconais scutellum	Cocconeidaceae
Coconais sp.	Cocconeidaceae
Coscinodiscus sp.	Coscinodiscaceae
Fragillaria spp.	Fragilariacieae
Melosira nummulouides	Melosiraceae
Navicola sp.	Naviculaceae
Grammaphora sp.	Striatellaceae
Grammatophora marina	Striatellaceae
Odontella spp.	Triceratiaceae
Tricerathium sp.	Triceratiaceae

Table 3. Species of diatoms recorded in Los Jameos del Agua lake.

MOLLUSCA		
GASTROPODA	BUCCİNİDAE	Buccinidae sp.
	CERİTHİDAE	*Bittium* cf. *incile* Watson, 1897
		Bittium latreilli (Payraudeau, 1826)
	EULİMİDAE	*Baleis* sp.
		Eulimidae sp.
	PHASİANELLİDAE	*Tricolia canariensis* Nordsieck, 1973
	RİSSOELLİDAE	*Rissoella* cf. *inflata* (Monterosato, 1880)
	RİSSOİDAE	*Alvania* cf. *aurantiaca* (Watson, 1873)
		Alvania watsoni (Watson, 1873)
		Alvinia scabra (Philippi, 1844)
		Crisilla beniamina (Monterosato, 1884)
		Manzonia unifasciata Dautzenberg, 1889
	SCİSSURELLİDAE	*Sinezona cingulata* d'Orbigny, 1824
	TROCHİDAE	*Clanculus bertheloti* (d'Orbigny, 1840)
BİVALVİA	UNGULİNİDAE	*Diplodonta rotundata* (Montagu, 1803)

Table 4. Checklist of species of mollusc shells collected from the sediments of Montaña de Arena. All species correspond to marine littoral species.

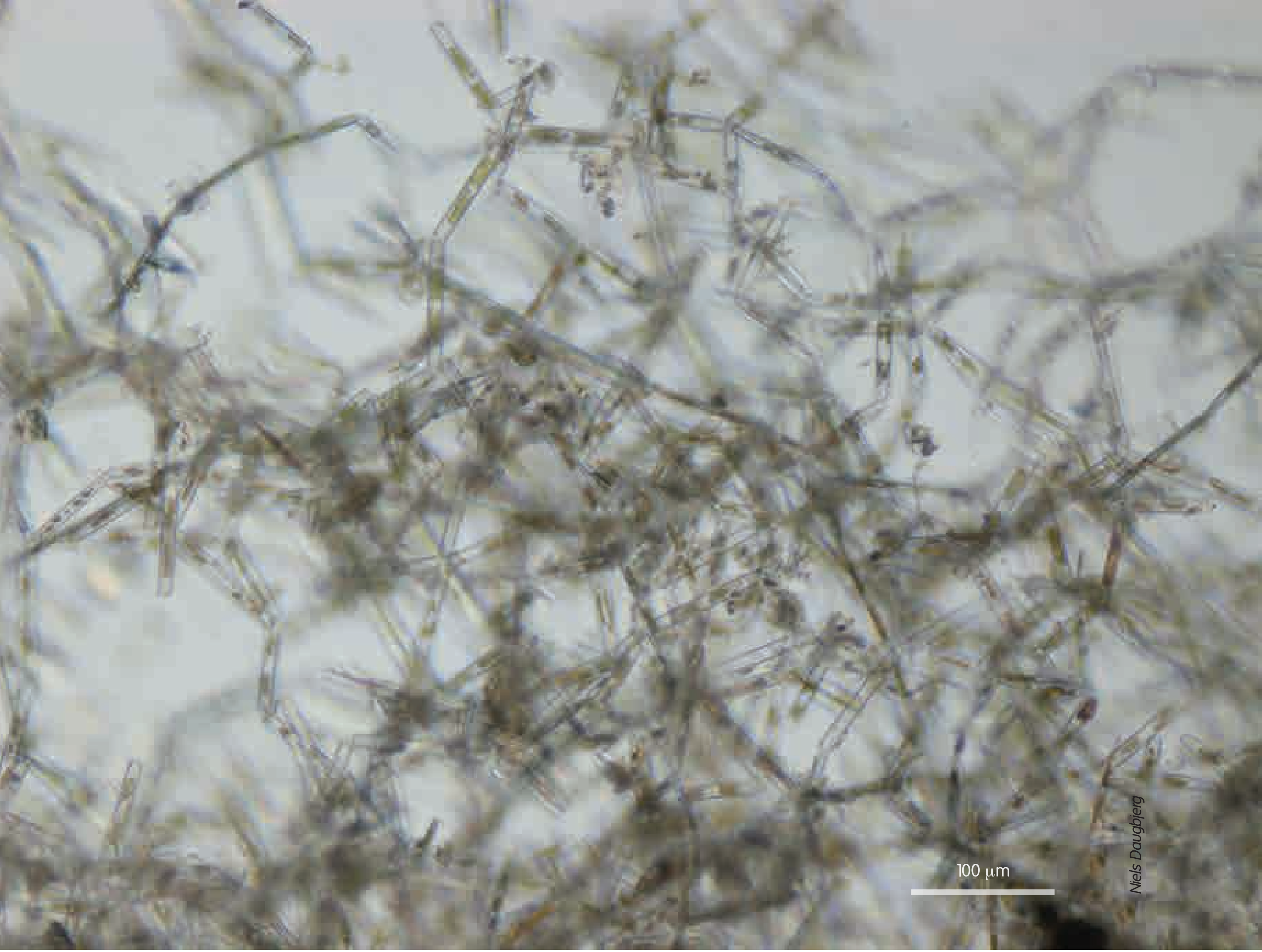
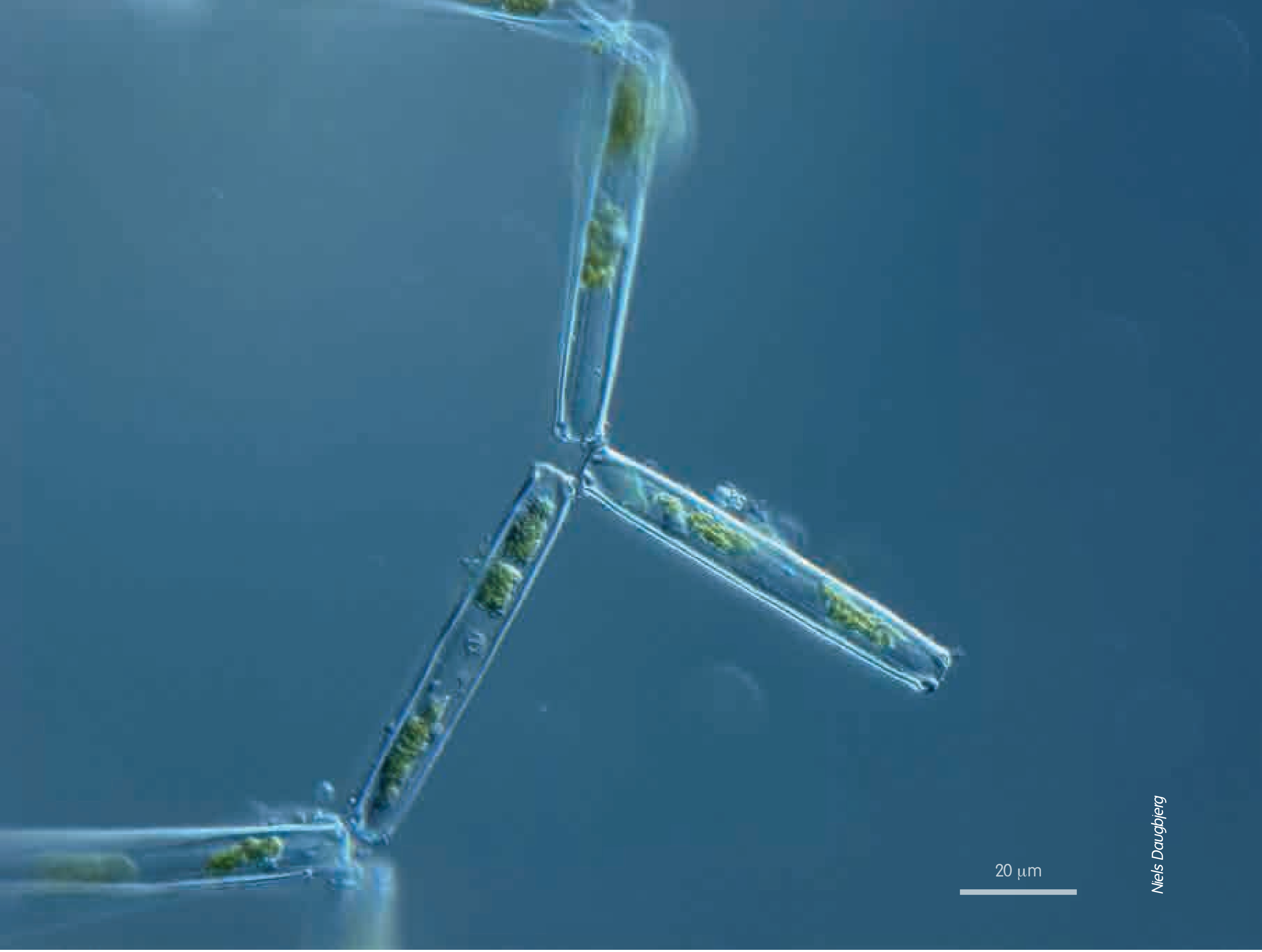


Figure 6. Light microscopy micrograph of the dominant species of diatom in the carpet of Los Jameos del Agua, showing several entangled living colonies.



Niels Daugbjerg

Figure 7. Detail of three cells of the dominant diatom species of Los Jameos del Agua. The chloroplasts (green inner material) are slightly contracted due to the stress suffered by the cells in the whole mount.

The highest densities of the mysid *Heteromysoides cotti* occur in the water column of Los Jameos del Agua. This suspension feeding mysid ingests mostly microalgae and other particulate organic matter from the water column with its specialized mouthparts (Fig. 8). *Heteromysoides cotti* is present throughout the other flooded sections of La Corona lava tube, but in much lower abundance. This polymorphic mysid exhibits yellowish pigmentation and eyes in Los Jameos del Agua, but is unpigmented and eyeless in the remaining sections of La Corona lava tube as well as in other anchialine pools and wells throughout the island (p. 193). The amphipods *Liagoceradocus acutus* and *Spelaeonicippe buchi*, as well as the annelid *Gesiella jameensis*, are also common in the water column though in much lower numbers. Despite being invisible to the naked eye, tows with fine mesh plankton nets reveal high densities of microscopic species of copepods, mostly calanoids and misophrioids, as well as the ostracods *Humphreysella wilkensi* and *H. phalanx.*

The most conspicuous benthic species in Los Jameos del Agua is the galatheid squat lobster *Munidopsis polymorpha* that attains densities up to 150 individuals per square meter (Fig. 9). *Munidopsis polymorpha* is negatively phototactic and thus prefers areas with limited or no light, making them more active and visible during the evening and night, while hiding among crevices during the day (Fig. 11). Apart from high densities of adults, ovigerous females, larvae, and juveniles are also common in the lake, which indicates they reproduce and complete their entire life cycle in Los Jameos del Agua. The stygophilic echiuran worm *Bonellia viridis* also exhibits high densities, exceeding 20 individuals per square meter (Fig. 12). Although *B. viridis* were first observed in the lake in the 1920's, their densities were much lower and did not begin to increase until the late 1990's, with continued proliferation to what is observed today. The increased abundance of *B. viridis* is of ecological concern as this echiuran produces large amounts of fine excrements that tend to accumulate in the absence of currents (Fig. 13). These accumulations could eventually limit or prevent circulation of water and nutrients in the spaces between the cinders. Additionally, *B. viridis* faeces provide suitable habitats for marine opportunistic species that compete with the endemic interstitial and crevicular stygobites, progressively replacing them. These new colonizers consist mostly of annelids (*Notomastus* sp., *Aponuphis bilineata,* and *Aphelochaeta marioni*) common to marine habitats with increased levels of nutrients.

Mostly unnoticed by visitors and divers, the highest animal diversity in Los Jameos del Agua corresponds to microscopic animals living in the carpet of benthic diatoms or among the cinder grains (Fig. 14). The microscopic community between the diatoms is dominated by the nerillid annelid *Leptonerilla diatomeophaga*, which grazes on algal cells and deposited organic matter from the bottom. Other common species in the diatom carpet include marine syllids (*Syllis garciai*, *S. gerlachi,* and *Miscellania dentata*), amphipods (*Bogidiella uniramosa* and *Liagoceradocus acutus*), isopods (*Curassanthura canariensis*), and cyclopoids (the stygobite *Oromiina fortunata* together with few oculate species). Nearly all of these species are deposit feeders or grazers with adaptations to feed on the diatoms, except for *Syllis garciai* and *Syllis gerlachi* that can also act as predators or scavengers. All these animals, together with the diatoms, provide food for the larger species of Los Jameos del Agua such as *Munidopsis polymorpha, Gesiella jameensis*, and *Bonellia viridis*.

In the deeper sections of Los Jameos del Agua, the light incidence is too low for diatom growth and a different community structure occurs in the spaces surrounding the cinders (Fig. 15). The most common animals in this microscopic cinder community are the endemic stygobitic annelids *Mesonerilla* n. sp., *Macrochaeta* n. sp., *Fauveliopsis jameoaquensis*, and a new species of *Laubierpholoe*. Several crustaceans are also present including the isopod *Curassanthura canariensis* and several species of unidentified harpacticoid and cyclopoid copepods. The marine priapulid *Tubiluchus lemburgi* is often present as well.

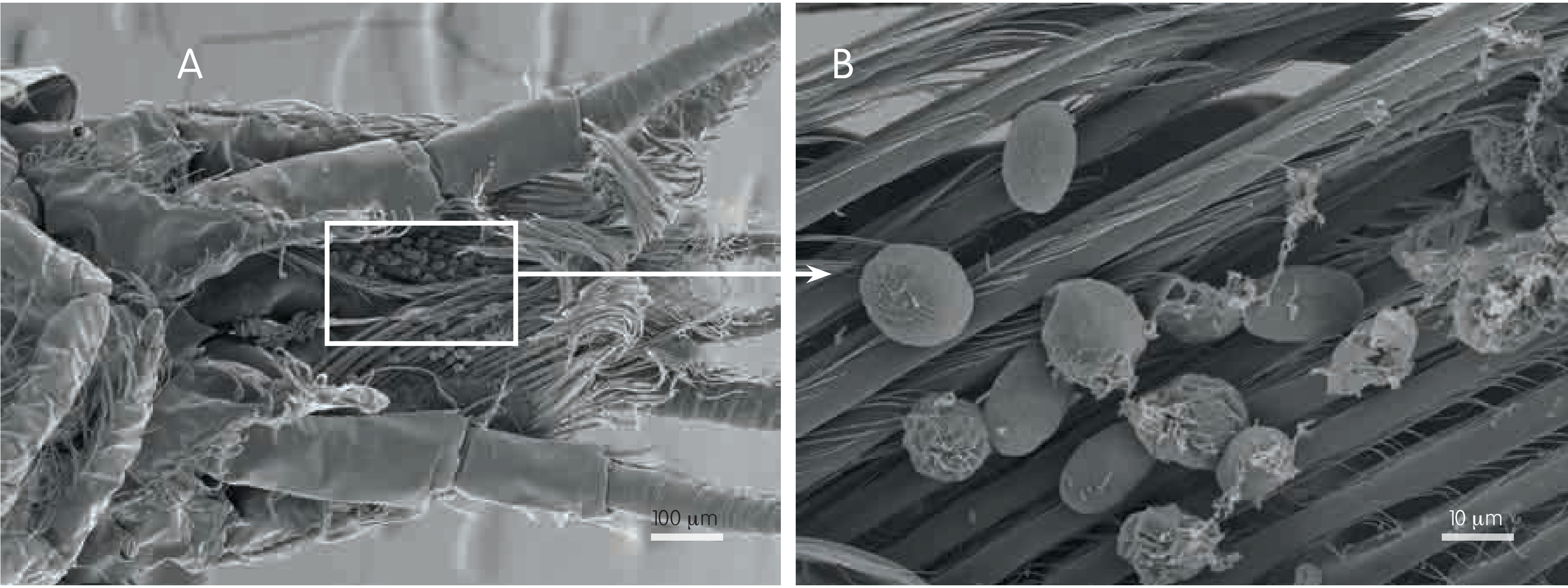


Figure 8. (**A**) Scanning electron micrograph showing the mouthparts of *Heteromysoides cotti*, bearing several cylindrical food particles. (**B**) Detail of the cells.

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Figure 9. The amphipod *Parhyale multispinosa* engaged in copulation near the shore of Los Jameos del Agua.

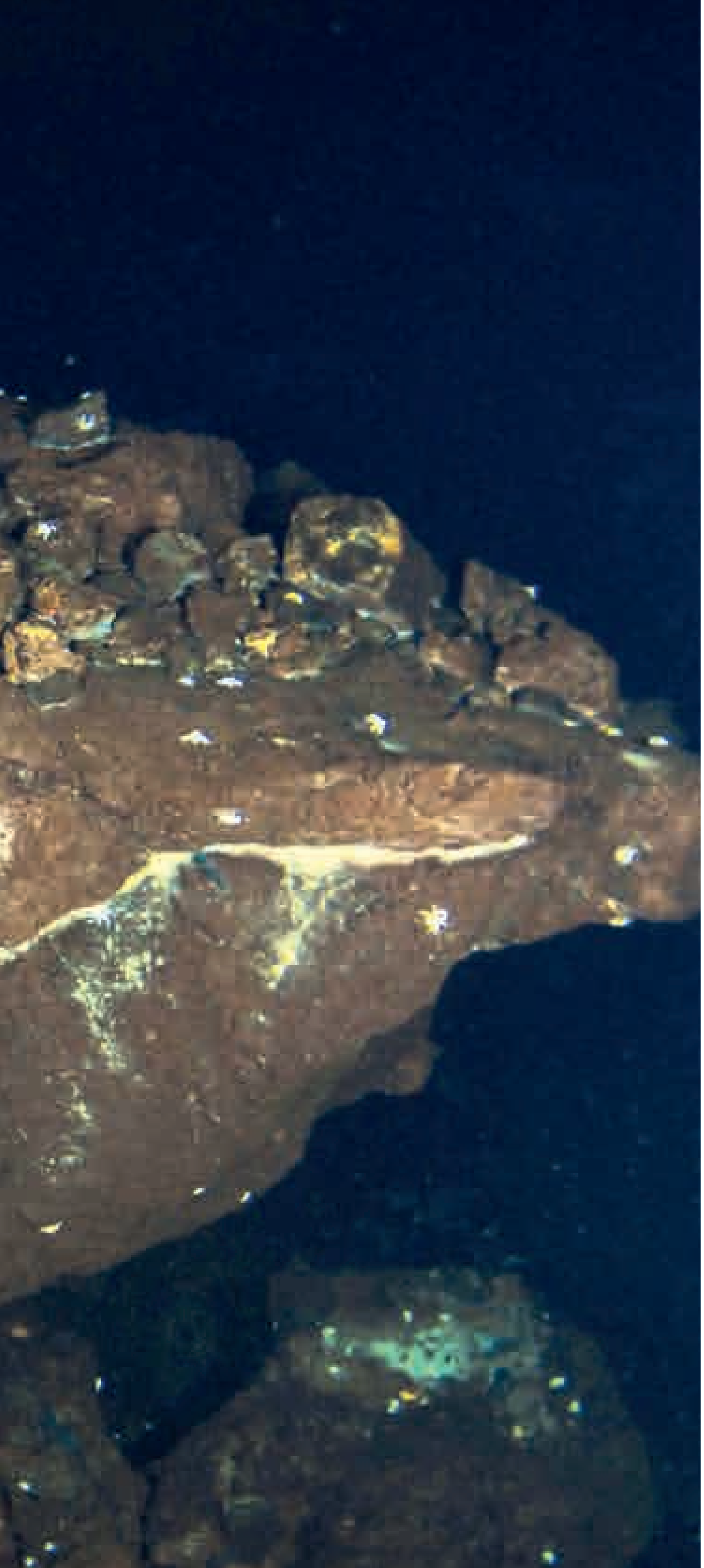

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Figure 10. Nighttime scavenging of *Munidopsis polymorpha*. Image is looking down at the substrate within Los Jameos del Agua.

Although Los Jameos del Agua is rich in stygobitic species, it is a small and relatively fragile environment. The tourist center attempts to protect this unique ecosystem from uncontrolled visitation, undesirable dumping of trash, and acts of vandalism. Unfortunately the tourist center has integrated a walkway running alongside the lake exposing the fauna and this fragile ecosystem to other types of anthropic threats. The greatest problem arising from tourists is the large number of coins thrown into the lake by poorly informed visitors who regard this water body as a natural "wishing well" (Fig. 16). Although several notices sternly forbid throwing of coins into the water, a large part of the lake bottom, especially crevices between larger boulders, is covered or filled with corroding copper coins. Divers have been employed in an attempt to remove visible coins, but many are inaccessible having slid into cracks and crevices or having corroded to mere flakes that disintegrate when touched. This is a serious situation since toxic metals, particularly copper, are leaching from the coins, becoming concentrated in the water and sediments of Los Jameos del Agua (Fig. 18 A and B) and spreading with the tides throughout Túnel de la Atlántida, having a destructive impact not only on the endangered species (Fig. 17), but the entire ecosystem.

Figure 11. *Munidopsis polymorpha* hidding in the crevices of Los Jameos del Agua during the day.

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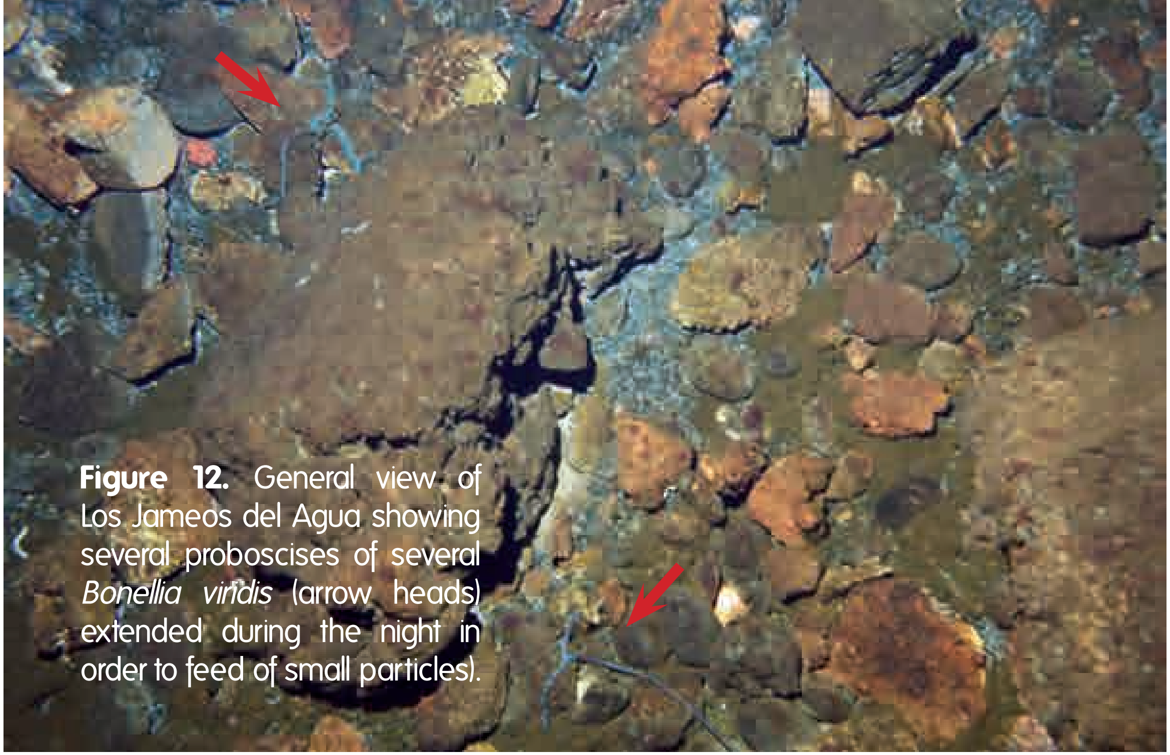


Figure 12. General view of Los Jameos del Agua showing several proboscises of several *Bonellia viridis* (arrow heads) extended during the night in order to feed of small particles).

Jorge Núñez

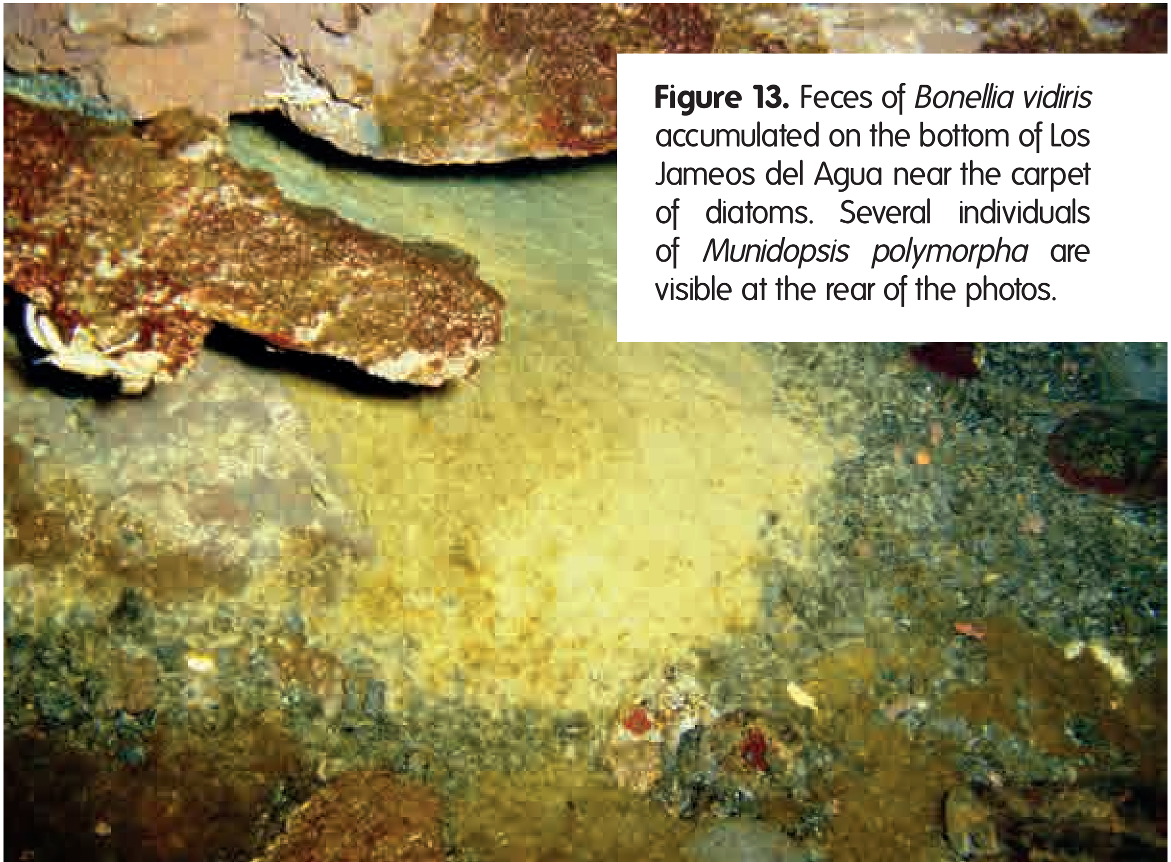
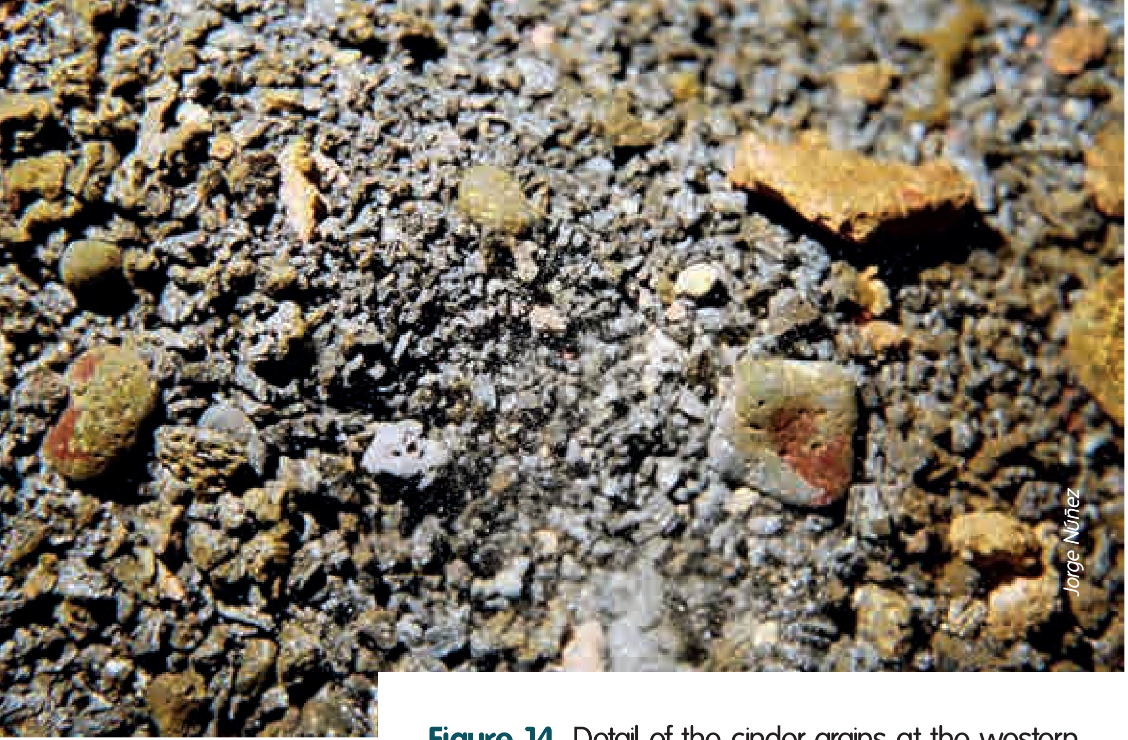


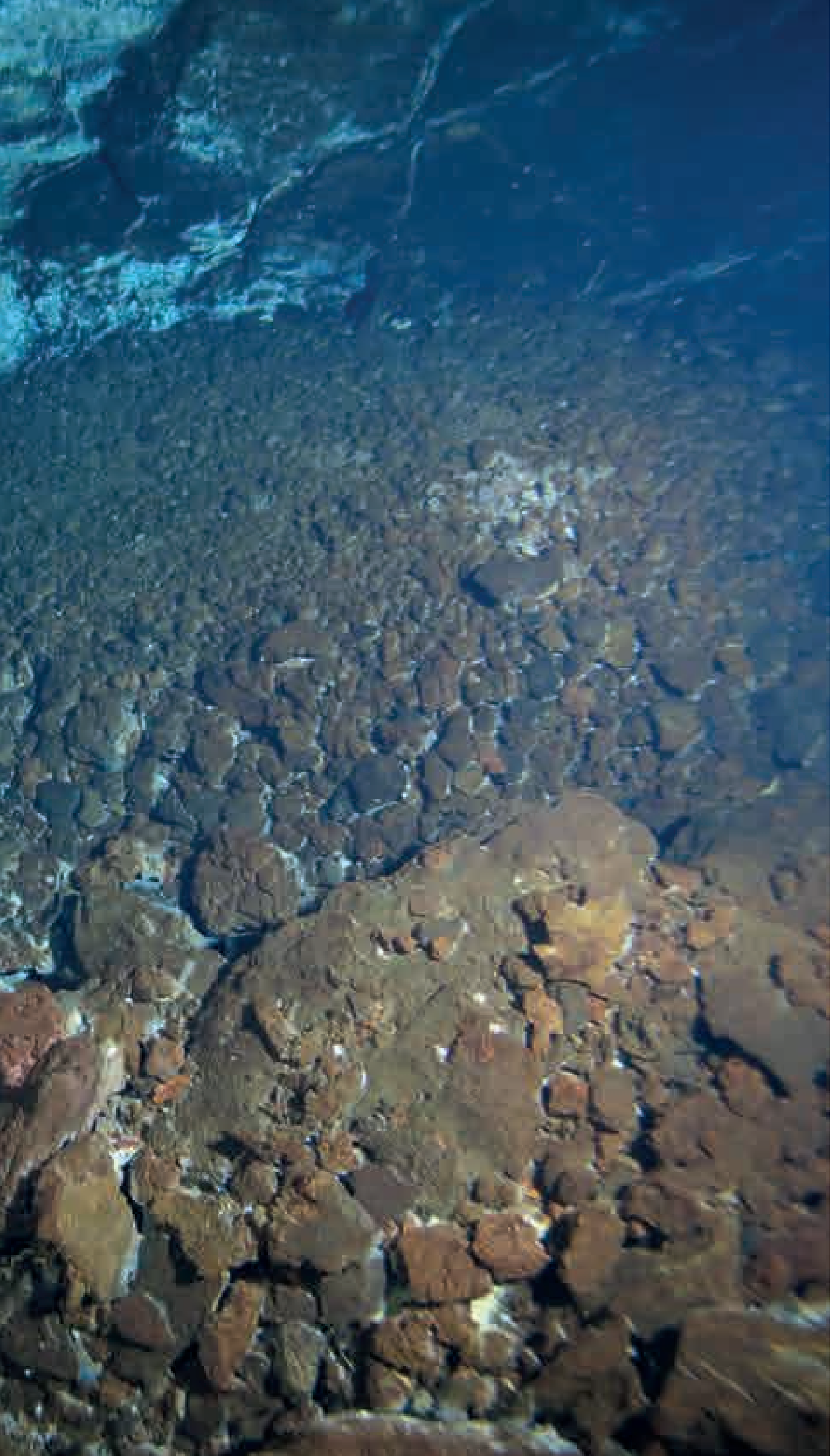
Figure 13. Feces of *Bonellia vidiris* accumulated on the bottom of Los Jameos del Agua near the carpet of diatoms. Several individuals of *Munidopsis polymorpha* are visible at the rear of the photos.

Enrique Domínguez



Jorge Núñez

Figure 14. Detail of the cinder grains at the western side of Los Jameos del Agua. The small spaces among the grains harbor a rich assemblage of animals.



Juan Valenciano

Figure 15. General view of the cinder accumulations in the deepest area of Los Jameos del Agua.

Alejandro Martínez

Figure 16. Coins from various years and countries collected during a short dive in Los Jameos del Agua.

Figure 17. Presence of corroding coins adversely affect the endemic inhabitants of Los Jameos del Agua.

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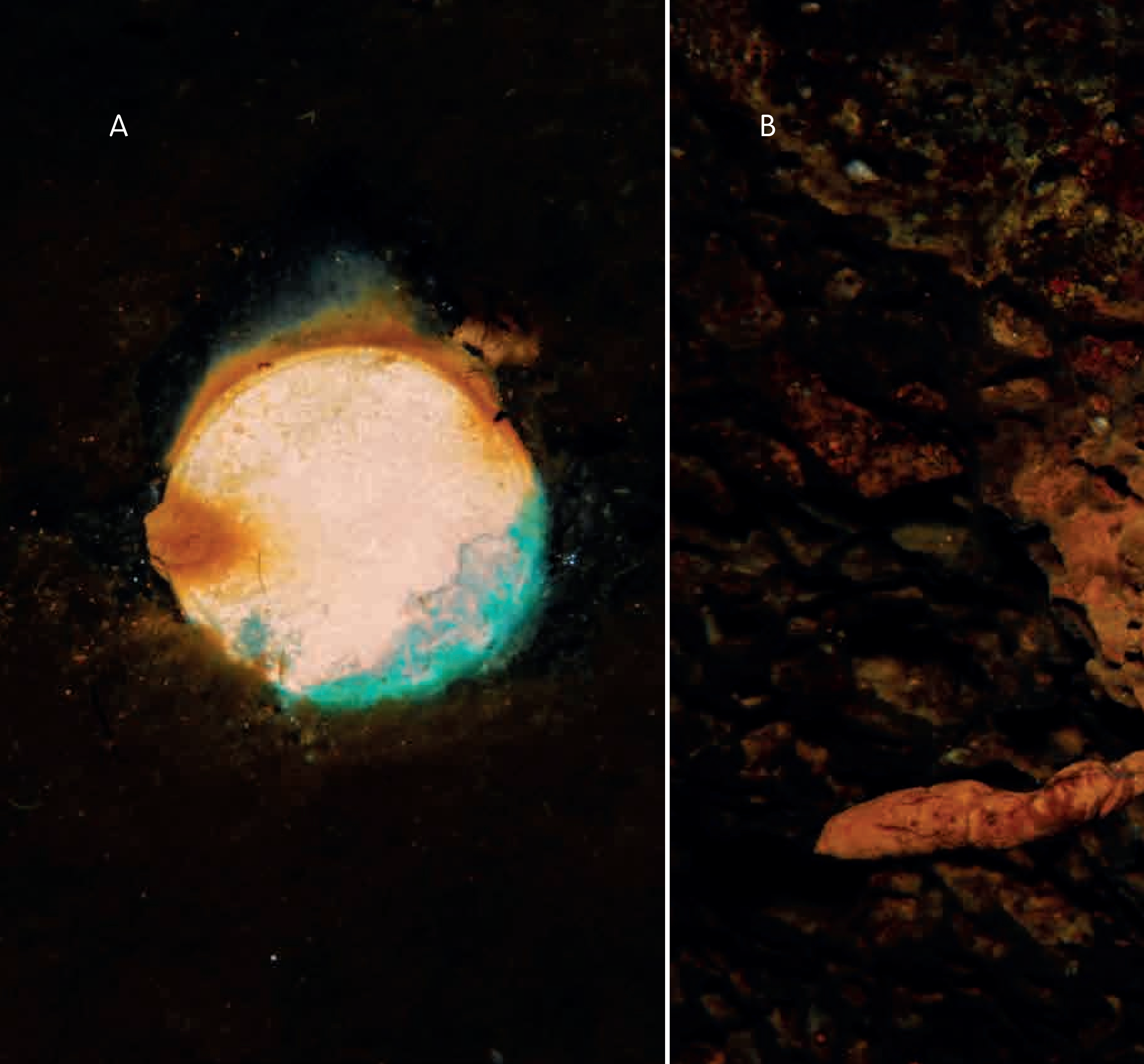
A
B

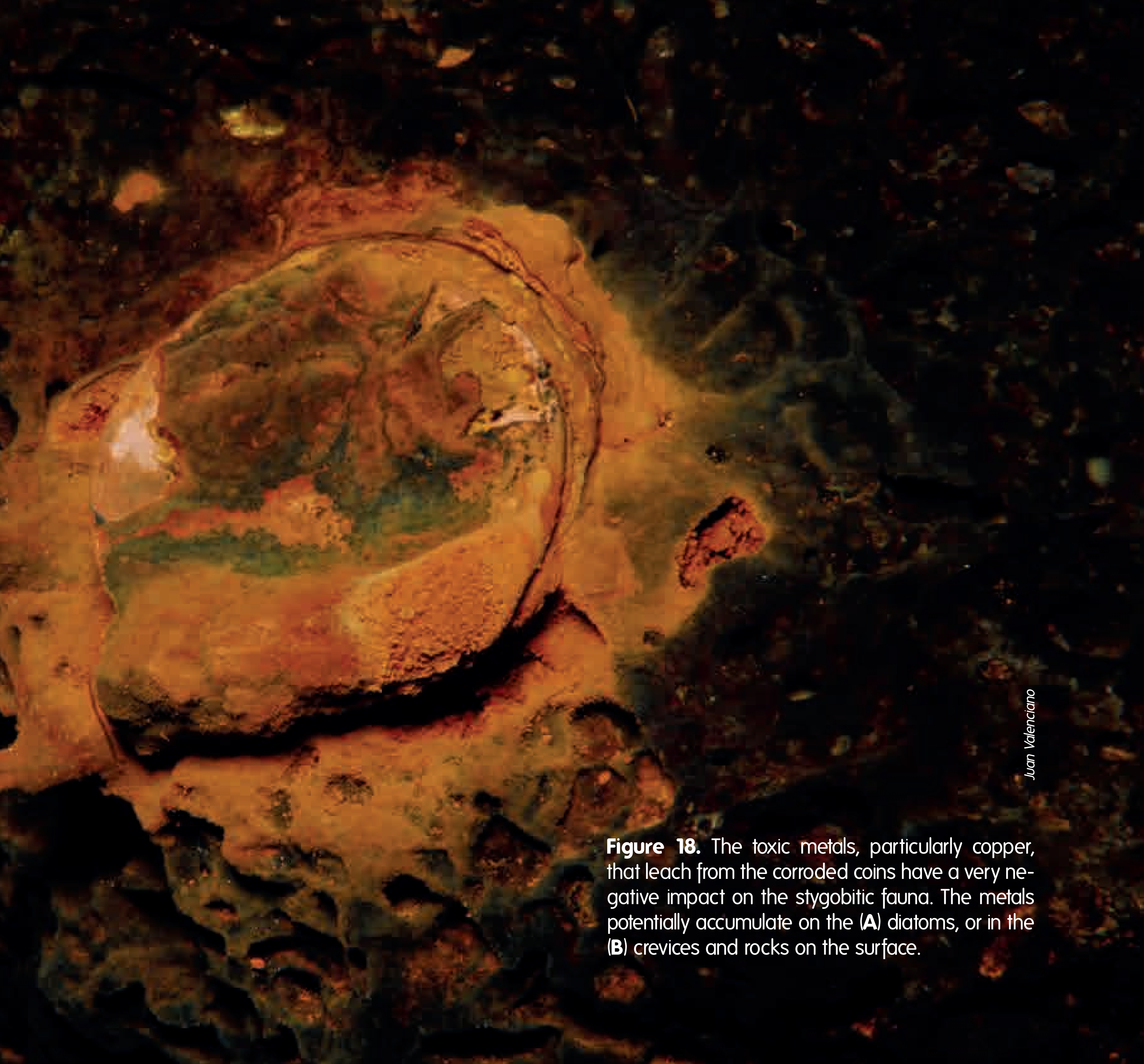

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Figure 18. The toxic metals, particularly copper, that leach from the corroded coins have a very negative impact on the stygobitic fauna. The metals potentially accumulate on the (**A**) diatoms, or in the (**B**) crevices and rocks on the surface.

Aphotic Zones: Túnel de la Atlántida and Cueva de los Lagos

Abiotic Conditions. Cueva de los Lagos and Túnel de la Atlántida are in complete darkness, with the exception of the first few meters of the latter which are illuminated by artificial light (Fig. 20). As a consequence, photosynthetic primary production is absent in both, with organisms relying on organic matter transported in from outside the cave or produced by chemosynthetic bacteria within. Cueva de los Lagos and Túnel de la Atlántida share many of the same sources of organic input, but since the latter is situated inland, while the former extends out to sea under the floor of the Atlantic Ocean, the contribution of different sources of organic matter to the ecosystem shows considerable variation. As would be expected, preliminary studies on carbon isotopes in select stygobitic fauna from Túnel de la Atlántida showed a significant fractionation of isotopes indicating a marine origin for most of the organic matter that these animals consumed. Most of the organic matter probably entered Túnel de la Atlántida from two areas: Montaña de Arena where marine sediments and waters enter the lava tube through a hole in the cave ceiling, and Los Jameos del Agua where tidal currents exchange the organic matter locally produced by photosynthetic microalgae. In contrast, the far inland location of Cueva de los Lagos suggests that stygobitic organisms there must rely on either terrestrial inputs or bacterial production, with limited contribution coming from oceanic sources. A lesser known source of organic matter may come from bacterial chemoautotrophic production within the lava tube. While no bacterial mats have been observed in the cave, bacterially mediated production of organic matter in the cave water column may utilize inorganic energy sources.

Animal Assemblages. The most unusual and diverse assemblages of stygobitic animals that inhabit aphotic (dark) zones of Túnel de la Atlántida and Cueva de los Lagos are present in the water column of both. The fact that most animals from these parts of the lava tube are found primarily in the water column strongly suggests that this is where they are getting their food, either from marine organic matter or from chemoautotrophic bacteria. These species often have evolved specialized adaptations to achieve and maintain their vertical and horizontal position within the water column without expending significant amounts of energy. These aphotic sections of the lava tube are ecologically more homogenous, with faunal communities only differing between the water column, interstitial cinder patches, and loose sand of Montaña de Arena.

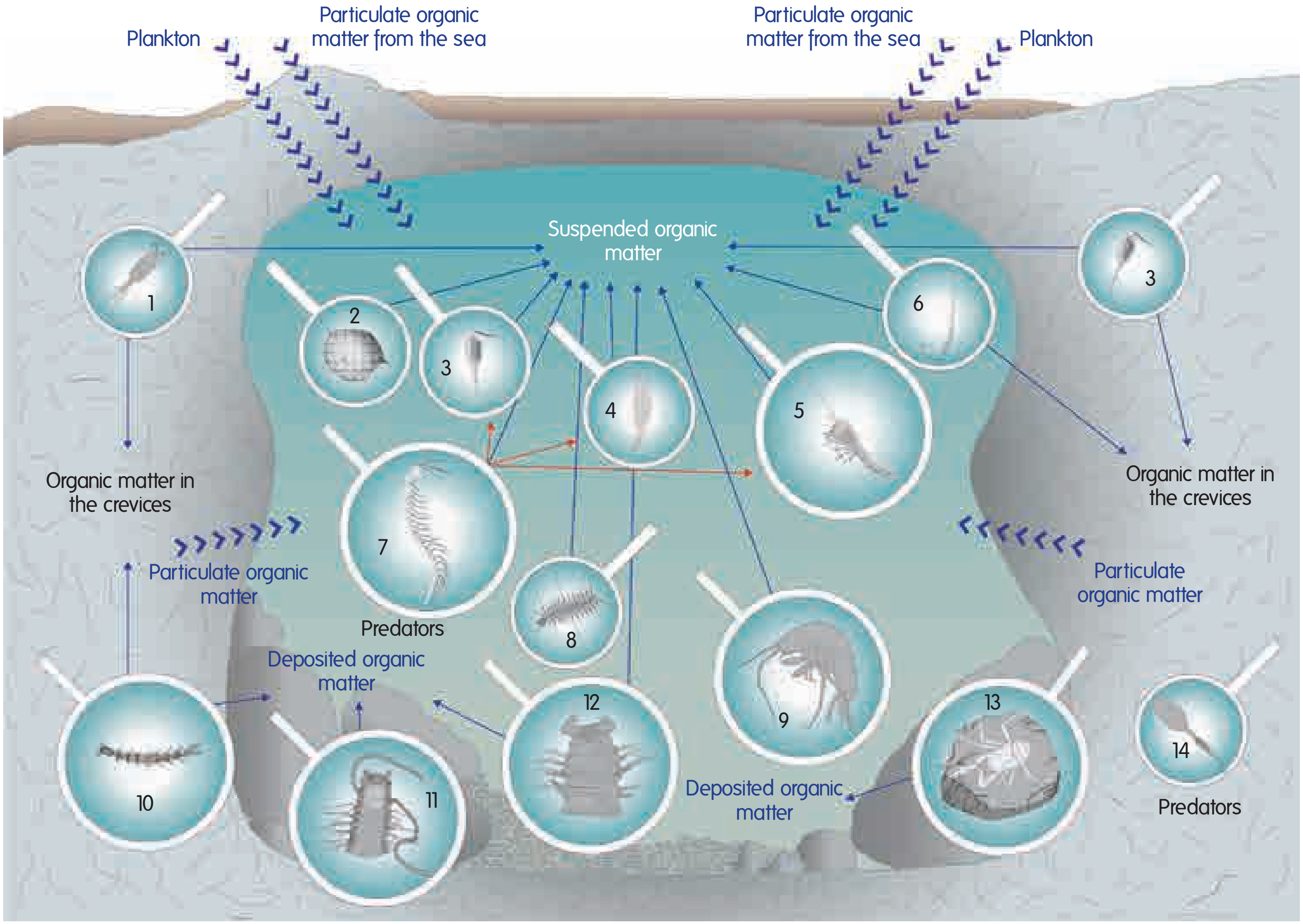
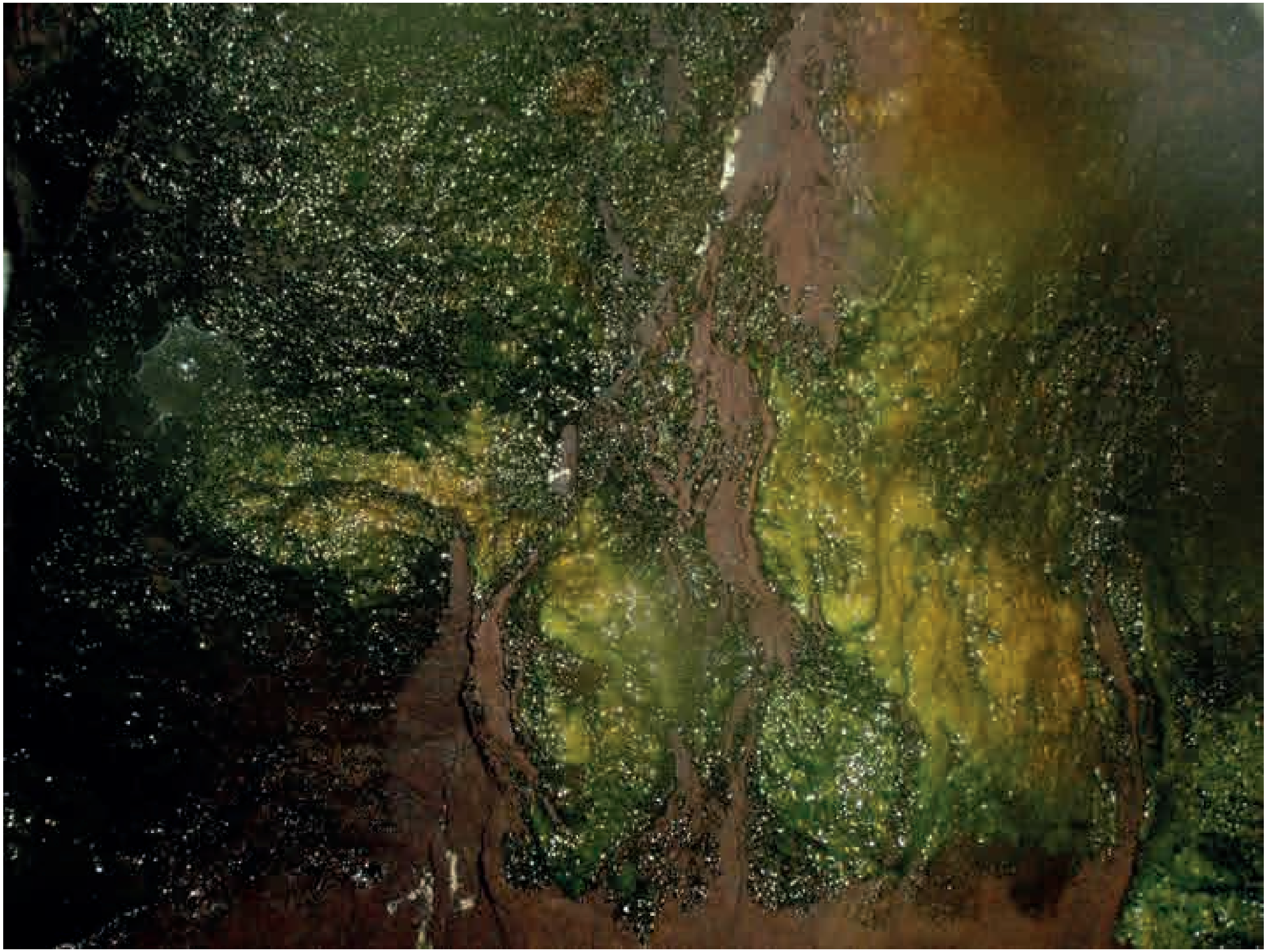


Figure 19. Trophic relationships in Túnel de la Atlántida. The particulate organic matter enters the cave through the crevices and it provides food to most of the animals in the cave (blue arrows). Few predators feed on these animals (red arrows), including remipedes and epacteriscid copepods. **1** *Paramisophria canariensis*. **2** *Humphreysella*. **3** Misophrioida. **4** *Neoechinophora karaytugi*. **5** *Halosbaena fortunata*. **6** *Megadrilus pelagicus*. **7** *Morlockia*. **8** *Gesiella jameensis*. **9** *Spelaeonicippe buchi*. **10** Nerillidae. **11** *Macrochaeta* n. sp. **12** *Speleobregma lanzaroteum*. **13** *Munidopsis polymorpha*. **14** Epacteriscidae.



Brett C. Gonzalez

Figure 20. Microscopic algae of several shades of green grow on the walls at the entrance of Túnel de la Atlántida due to the presence of high humidity and artificial light.

Figure 21. As in many other anchialine systems, remipedes are the top predators in La Corona lava tube. They are equipped with well-developed claw-like appendages on the head, the last of them connected to paired fangs with poison producing glands. The photos correspond to the Bahamian genera *Godzillius* (top) and *Cryptocorynetes* (bottom).

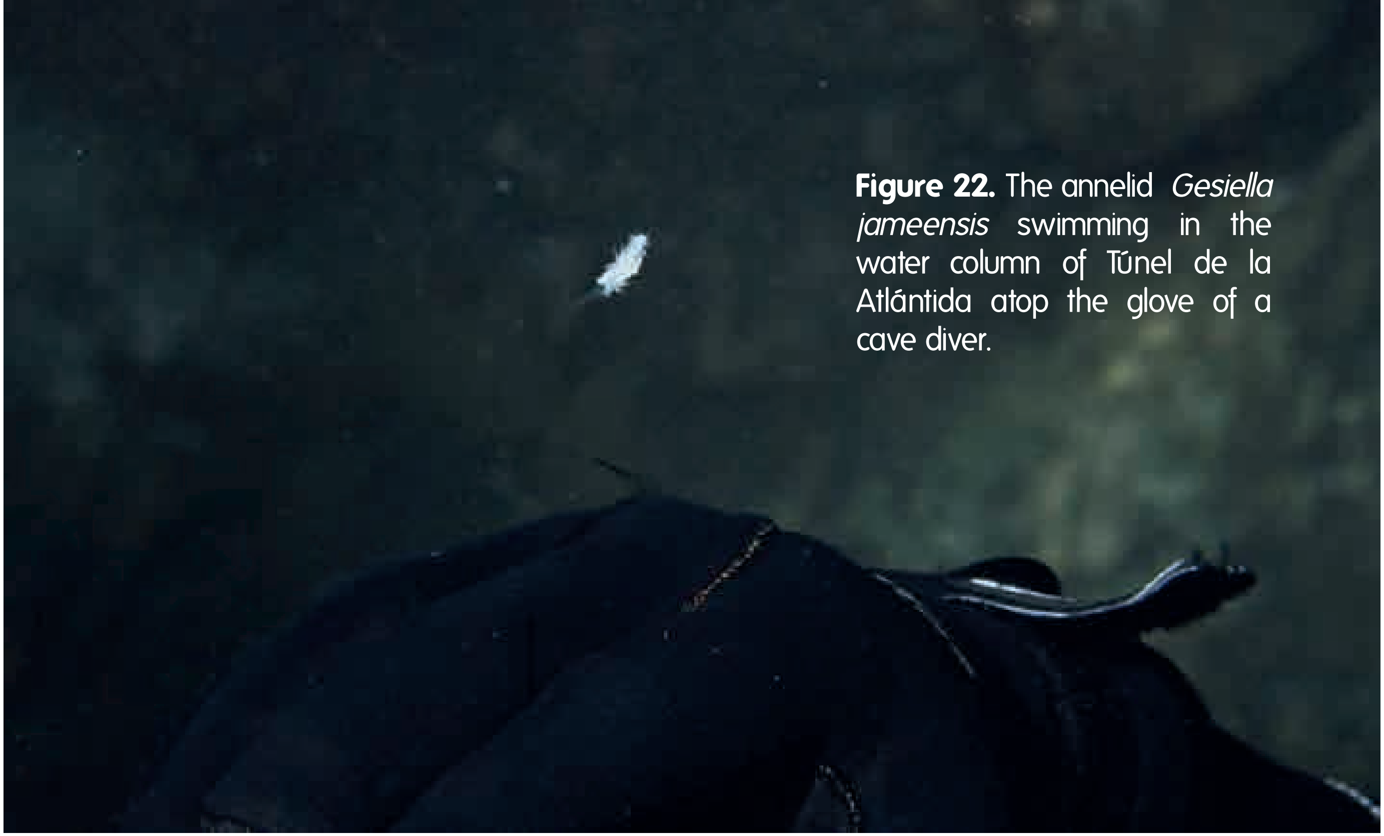


Figure 22. The annelid *Gesiella jameensis* swimming in the water column of Túnel de la Atlántida atop the glove of a cave diver.

Peter R. Møller

Figure 23. The amphipod *Spelaeonicippe buchi* in the water column of Túnel de la Atlántida.

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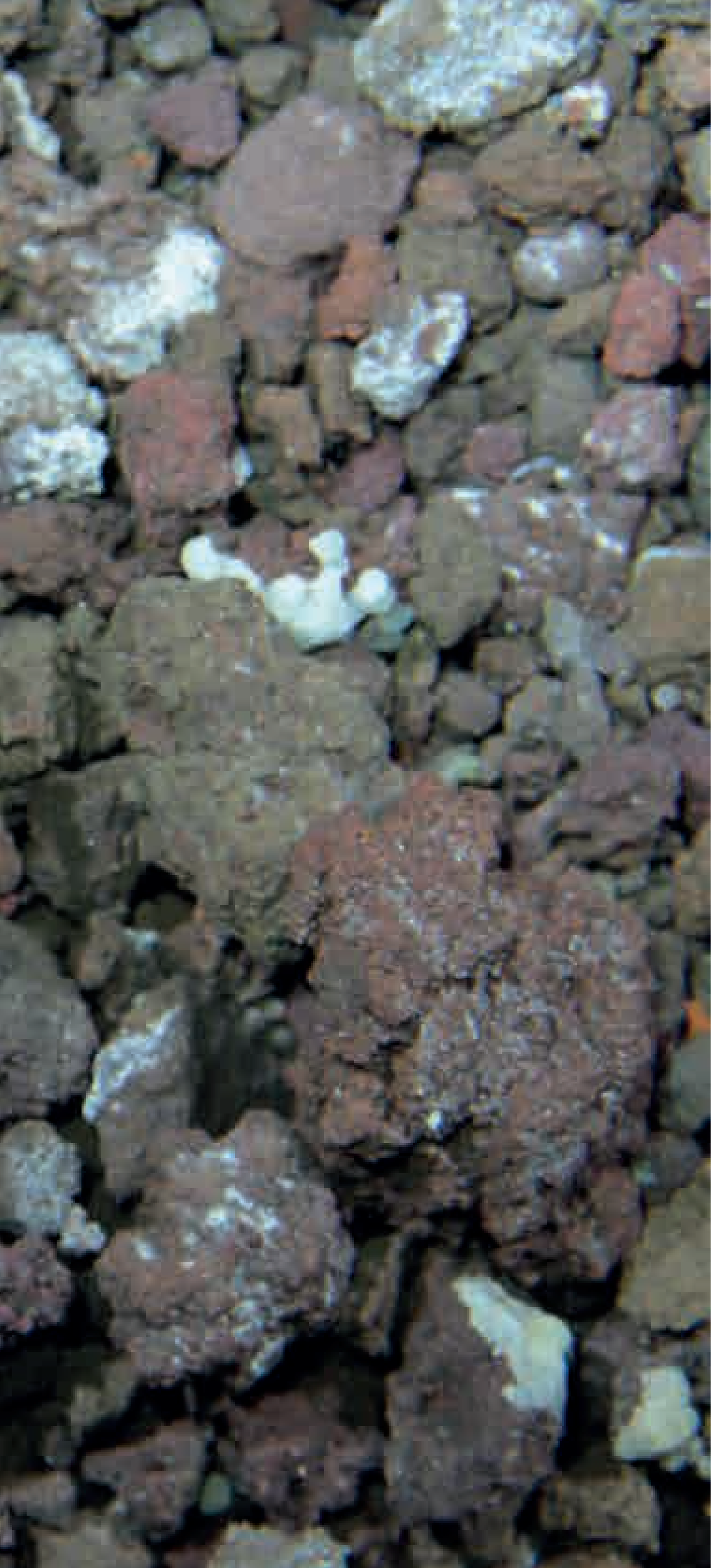
The top predators in the water column in Túnel de la Atlántida are the two species of remipedes, *Morlockia ondinae* and *M. atlantida.* They prey on small crustaceans and other invertebrates with their specialized first three pairs of appendages, one of which is equipped with a pair of venom injecting fangs (Fig. 21). Some evidence suggests that at least some species of remipedes may also be capable of feeding on detritus or suspended organic material, but this behavior has not yet been observed from remipedes in La Corona lava tube. In addition, the epacteriscid copepod *Enantiosis canariensis* is a water column predator, although at a smaller size. The details of the biology and feeding behavior of epacteriscid copepods are mostly unknown, but they possess clear and characteristic adaptations for preying on other small animals with their first pairs of appendages. The annelid *Gesiella jameensis* (Fig. 22) is possibly also a predator and scavenger like other polynoid annelids, capable of capturing small animals with its jawed proboscis.

Suspension feeders and scavengers are also present in the water column. *Megadrilus pelagicus* is a unique suspension feeder in Túnel de la Atlántida, being the only known protodrilid to employ such feeding strategies. Its dorsal keel and bands of cilia along the trunk allow it to maintain its position in the water column while it collects particles with its long palps. *Spelaeonicippe buchi* (Fig. 23) and *Liagoceradocus acutus* also collect particles in the water column, most likely with their mouth parts and gnathopods. These amphipods are commonly observed in the lava tube as solitary individuals. The mysid *Heteromysoides cotti* is also present but not in as high densities as in Los Jameos del Agua. It is typically observed in groups of 2-3 individuals, often near the bottom, swimming in and out of cracks and spaces between boulders. Rarely observed but still living within the water column are the thermosbaenacean *Halosbaena fortunata* and stygobitic annelids such as *Prionospio* n. sp. and a new species of hesionid. One of the rarest organisms described from La Corona lava tube is the scalibregmatid annelid *Speleobregma lanzaroteum,* which is only known from three specimens collected in 1981 and 2011 from the water column of Túnel de la Atlántida (Fig. 25).

The water column of La Corona lava tube also contains a large diversity of microscopic animals. Plankton tows from the water column yielded a number of stygobites, mostly ostracods (*Eupolycope pnyx*, *Humphreysella wilkensi*, *H. phalanx*), and copepods such as misophrioids (*Speleophriopsis canariensis*, *Palpophria aestheta*) and endemic harpacticoids (such as the superornatiremid *Neoechinophora karaytugi*). Plankton tows also reveal a new species of *Longipalpa,* which is a cave-dwelling genus of annelids known exclusively from anchialine caves in Lanzarote, Bermuda, Yucatan, and the Bahamas. It is characterized by a pair of long palps and a swimming behavior (as opposed to a benthic way of life) unique to the family.



Peter R. Møller

Figure 24. Cinders at the entrance of Túnel de la Atlántida.

Many of the previously mentioned species from the water column also inhabit crevices in the ceiling and walls of the lava tube, or under and between breakdown boulders. Some may only be found in the water column in response to predatory evasion or exhausted air bubbles from cave divers. The only species that have never been observed in the crevices are remipedes.

The most conspicuous benthic species is the galatheid squat lobster, *Munidopsis polymorpha*, which exhibits considerably smaller densities in Túnel de la Atlántida than Los Jameos del Agua. *Munidopsis polymorpha* appears to be concentrated near the entrance pool at Jameo Chico (Fig. 24), with densities declining deeper into the lava tube. The decreasing densities of *Munidopsis* with distance into Túnel de la Atlántida is most likely a response to availability of nutrients, being highest in the entrance pool due to water exchange from Los Jameos del Agua or from artificial lights which stimulate algal growth. The echiuran *Bonellia viridis*, can also be found in Túnel de la Atlántida, although only in very low numbers and near the entrance pool (Fig. 26).

With the exception of cinder patches and Montaña de Arena, benthic communities of Túnel de la Atlántida and Cueva de los Lagos are more depauperate than those of the water column. Accumulations of cinders provide habitat for species adapted to highly permeable interstitial environments. In cinder accumulations at the entrance pool of Túnel de la Atlántida, the annelids *Macrochaeta* n. sp. and *Leptonerilla diatomeophaga* are commonly found as well as abundant copepods, especially cyclopoids and harpacticoids. Cinder accumulations are also present in Cueva de los Lagos, but the community structure is different and the common species of *Macrochaeta* and *Leptonerilla* are absent and replaced by a new species of *Mesonerilla* currently being described. Occasionally, larger specimens of the isopod *Curassanthura canariensis* have also been observed crawling among the cinders or crevices in Cueva de los Lagos.


Enrique Domínguez

Figure 25. *Speleobregma lanzaroteum*, one of the more difficult animals to find in Túnel de la Atlántida. It is only known from three specimens.

Enrique Domínguez

Figure 26. A specimen of *Bonellia viridis* hinding in the crevices at the entrance of Túnel de la Atlántida.

Alejandro Martínez

Figura 27. *Munidopsis polymorpha* feeding in Los Charcos de Luis (Órzola) in the middle of the day.

Interstitial Environments: Montaña de Arena

Montaña de Arena is a 20 m high conical pile of sand formed some 750 m into the cave from the entrance pool of Túnel de la Atlántida (Fig. 9, Chapter 1). This submerged cone of coarse, white marine sand has its apex located directly beneath small hole in the cave ceiling where loose sand has been entering the lava tube from the overlying ocean floor for untold number of years in a process analogous to sand pouring through an hour glass. The sand particles have diameters between 0.5 and 1 mm, with smaller particles being nearly absent. The large grains and the lack of smaller particles leave relatively large interstices (Box 1). This facilitates water circulation in the superficial layers, which brings in oxygen and nutrients for the interstitial fauna. Organic matter present in the dune is similar to that found in marine sediments outside the lava tube, calculated as 0.01% of the dry weight. The mineral composition of the sediment is a direct match to the sand above, consisting mostly of biogenic carbonates, which corresponds to 98-99% of the dry weight, with only a small fraction comprised of volcanic particles. These carbonates also contain mollusc shells (Table 4) and the remains of various sea urchin species, mainly *Diadema africanum* and *Paracentrotus lividus*.

The exact position of this crack on the overlying seafloor has never been identified, but the abundant marine fauna living in and around Montaña de Arena indicates a direct connection with marine waters above. Sessile suspension feeding organisms such as sponges and cnidarians are abundant along the walls and ceiling of the lava tube above the peak of Montaña de Arena. Commonly found on the surface of the sand dune are individuals of *Diadema africanum* and the brittle star *Ophioderma longicauda,* as well as the decapods *Stenopus spinosus* and *Athanas* sp., all of which are typical littoral marine species.

The sand interstices of Montaña de Arena are inhabited by a rich community of marine species, dominated by annelids from the families Orbiniidae, Dorvilleidae, Syllidae, Acrocirridae, and Nerillidae. Additional fauna present includes species of gastrotrichs (*Urodasys* and *Macrodasys*), eight species of rhabdocoel platyhelminthes, five genera of Kalyptorhynchia, and three genera of Dalytyphloplanida, six species of proseriates platyhelminthes (belonging to *Boreocelis, Archilina, Minona, Paratoplana, Vannuccia,* and *Archimonocelis),* a cnidarian of the genus *Halammohydra*, several microscopic molluscs (e.g., *Cima minima, Caecum clarkii,* and *Pseudorbis jameoensis*), as well as copepods and ingolfiellid

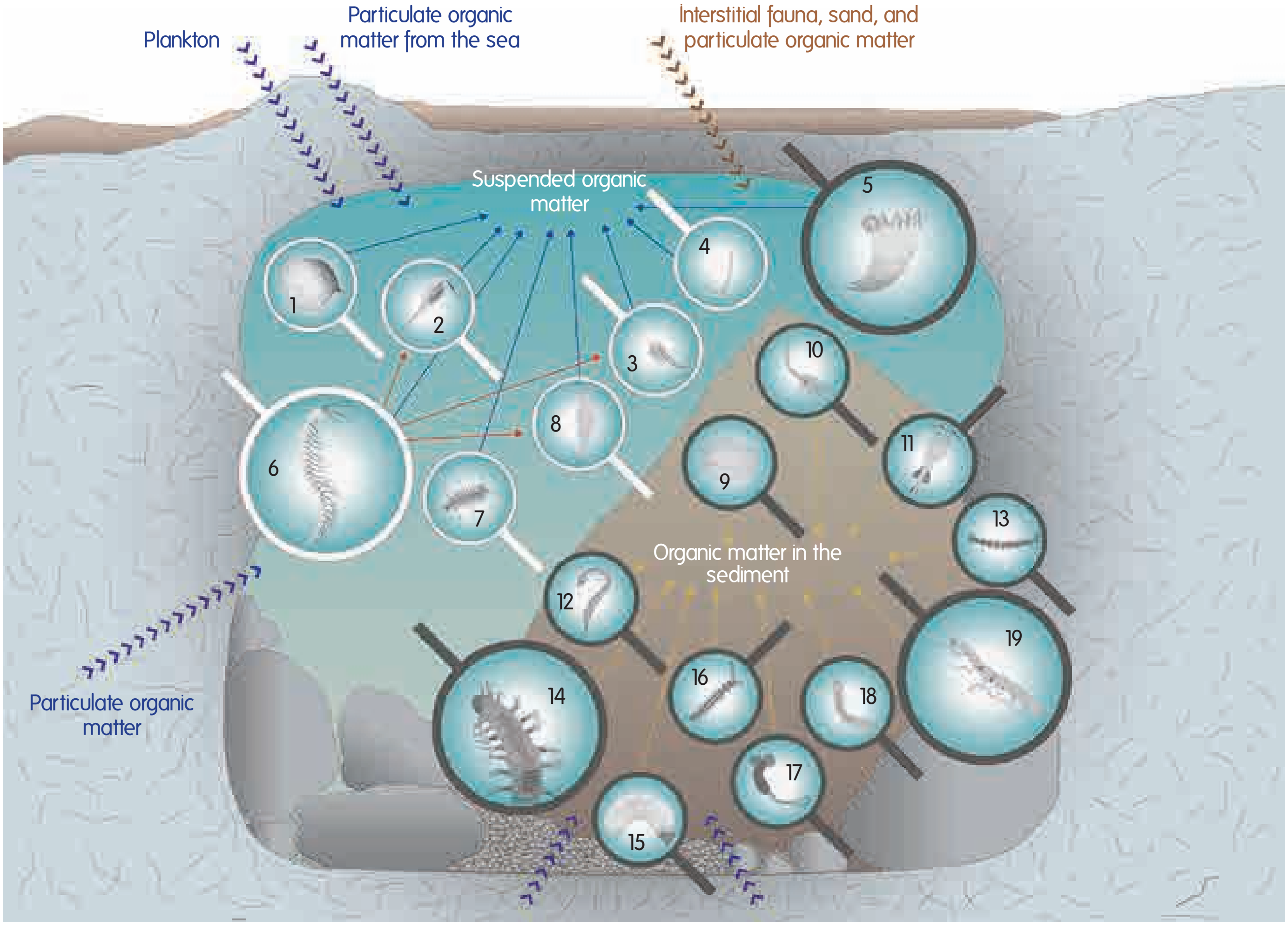


Figure 28. Trophic relationships between Montaña de Arena and the water column of the cave. The species enclosed within the black circles are exclusive from the interstices in Montaña de Arena, while those in the white circles are present in the water column. **1** *Humphreysella*. **2** Misophrioida. **3** *Halosbaena fortunata*. **4** *Megadrilus pelagicus*. **5** *Caryophillia*. **6** *Morlockia*. **7** *Gesiella*. **8** *Neoechinophora*. **9** *Eusarsiella bedoyai*. **10** Cumacea. **11** Cyclopoida. **12** Draconematidae. **13** Nerillidae. **14** Syllidae. **15** *Fauveliopsis jameoaquensis*. **16** *Meganerilla cesari*. **17** *Tubiluchus lemburgi*. **18** Acrocirridae. **19** *Curassanthura canariensis*.

amphipods, and cumaceans. This community is presumably sustained by organic matter of marine origin, coming in with sand from the sea floor above. The relatively lower porosity of the sand grains in the dune facilitates the creation of physicochemical gradients which forms specialized redox layers favored by chemosynthetic bacterial assemblages.

Anchialine Ponds and Wells

Anchialine environments of Lanzarote are not limited to the water filled portions of La Corona lava tube, but also can be found around the island as both natural and manmade anchialine ponds and wells, which have broken into the subterranean anchialine waters. These areas are known to harbor several anchialine endemic and endangered species also present in La Corona lava tube.

Anchialine ponds are formed in several places throughout the coastal terrains of Lanzarote in small natural depressions that are lower than the level of the adjacent ocean (Fig. 29). Subterranean anchialine waters emerge within these depressions and fluctuate in response to the marine tides. There are two localities on Lanzarote where several anchialine pools are located: Montaña Bermeja on the southwestern coast, and Órzola on the northeastern tip of the island. While these habitats are considered to be extensions of the subterranean anchialine environment, the abiotic factors acting on open pools are complex and varied, since they are exposed to daily insolation that alters the temperature and salinity in the ponds. In addition, the bottom of these ponds have several layers of fine sediment that are covered by varying degrees of decomposing organic matter including terrestrial leaf litter, green algae (*Ulva muscoides, U. prolifera, Valonia* sp., and *Chaetomorpha* sp.), and cyanobacteria (*Microcoleus lynbyacea, Schizotrix calcicola*). The most common stygobites in these habitats are the amphipod *Parhyale multispinosa* and the calanoid copepod *Stephos canariensis*, both capable of withstanding extreme changes in temperature and salinity. Several other stygobites are common to these exposed anchialine pools but spend much of their time hiding in and amongst small cracks and crevices during the day, with increased activity during the night when temperatures and risk of predation is typically lower. The stygobites commonly observed during evening hours are *Heteromysoides cotti* and *Munidopsis polymorpha* (Fig. 27). Two endemic species from Lanzarote are described solely from these anchialine pools, the misophrioid copepod *Boxshallia bulbantennulata* and the tantulocarid crustacea *Stygotantulus stocki*. Abundant marine intertidal species are also present in these anchialine ponds. This may include include the sea anemone *Aiptasia mutabilis*, several molluscs (*Littorina striata,*

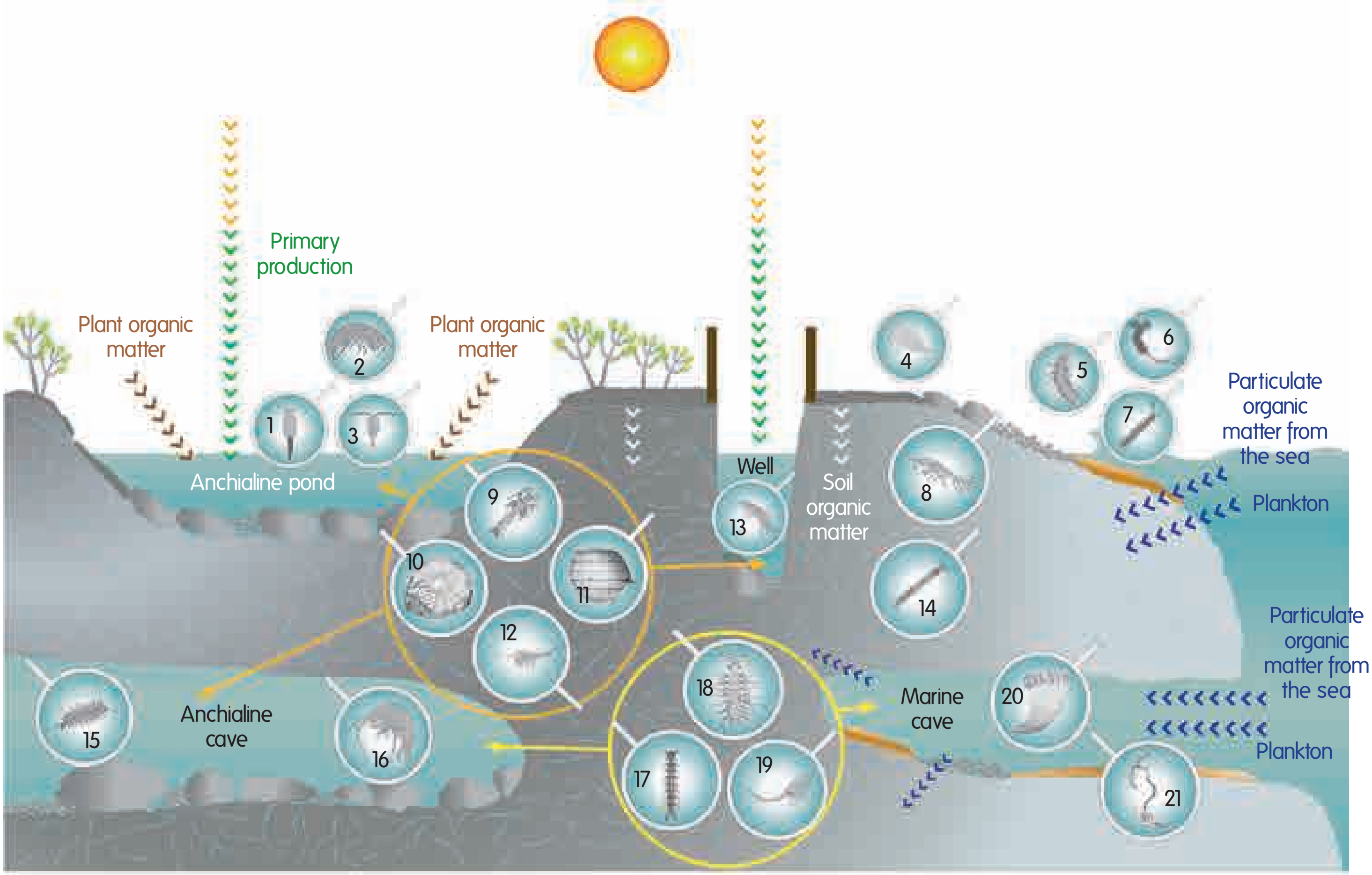


Figure 29. Anchialine environment of Lanzarote. Particulate organic matter penetrates from the sea towards the different anchialine habitats occupied by various specific assemblages of animals. **1** *Boxshallia bulbantennulata*. **2** *Parhyale multispinosa*. **3** Calanoida. **4** *Halosphiloscia*. **5** Syllidae. **6** *Tubiluchus lemburgi*. **7** *Meganerilla cesari*. **8** *Bogidiella uniramosa*. **9** *Heteromysoides cotti*. **10** *Munidopsis polymorpha*. **11** *Humphreysella*. **12** *Halosbaena fortunata*. **13** *Liagoceradocus acutus*. **14** Harpacticoida. **15** *Gesiella jameensis*. **16** *Spelaeonicippe buchi*. **17** *Mesonerilla* sp. **18** *Leptonerilla diatomeophaga*. **19** Cumacea. **20** *Caryophyllia smithii*. **21** *Bonellia viridis*.

Botryphallus epidauricus, Cerithium lividulum, Ovatella myosotis, Lasaea rubra, and *Cardita calyculata),* annelids (*Perinereis cultrifera, Perinereis olivarae, Ophryotrocha* sp., *Cirriformia cirrifera,* and *Jauna pagersteni),* marine amphipods (*Amphitoe rubricata* and *Aora typica*), the shrimp *Palaemon elegans*, and the starfish *Coscinasteria tenuispina*. This list of marine intertidal organisms inhabiting anchialine pools is not exhaustive, and may often include several fish, most commonly the bleniid *Mauligobius madeirensis,* and the endangered European eel *Anguilla anguilla*.

Throughout the 19th and early 20th centuries, hand dug wells, approximately 2-3 meters in diameter and averaging 10 m in depth, were constructed along the coastline of Lanzarote in order to pump the subterranean marine water into saltpans for salt production. While most of these original wells are now unused, they still remain near the northeastern towns of Arrecife, Los Mármoles, Costa Teguise, Guatiza, Mala, Punta Mujeres, Arrieta, and Órzola (Figs. 30 and 31). The water inside the wells is similarly affected by tides from the surrounding marine waters, although protected by by their steep walls from direct sunlight and temperature extremes of the day. The bottom of most wells is highly variable; consisting of mostly gravel and mud, since each well was only excavated until enough water was present to install a wind driven pump. Several stygobites are present in the wells, the most abundant being the stygobitic amphipod *Liagoceradocus acutus*. Baited traps placed in wells revealed other stygobites attracted out of the cracks and crevices by the presence of food. From such traps, several crustaceans have been found including the ostracod *Humphreysella wilkensi*, the thermosbaenacean *Halosbaena fortunata*, the mysid *Heteromysoides cotti*, and the squat lobster *Munidopsis polymorpha*. Occasionally, non-stygobitic marine species can also be found in the wells in low densities and mostly consisting of oculate harpacticoid copepods and podocopid ostracods.

-BOX 1- The life amongst sand and cinder grains

Interstitial environments exist in the spaces between the sand grains, both in La Corona lava tube as well as surrounding marine environments. Due to the small size of these spaces, water does not flow freely amongst the grains, but instead is acted upon by capillary forces. The intensity of these capillary forces depends on the size of the grains, with larger spaces leading to greater flow. The angularity of the sand grains also plays an important role in water flow through interstitial environments, with increased angularity of the sand grains yielding a heightened compactness of the sand. Due to these flow conditions, interstitial habitats can be compared to porous media, whereby limited water exchange between the interstices and the overlying water leads to the formation of vertical gradients throughout the sediment. This limited circulation facilitates the deposition of organic matter atop and within interstitial habitats, often becoming anoxic a few centimeters below the surface of the sand. These redox gradients limit the distribution of fauna to the upper few centimeters where they feed on the decomposing organic matter and bacterial communities. The rich communities of microscopic animals collectively living within the interstitial spaces are known as interstitial meiofauna. These habitats harbor deposit feeders, grazers, and even predators, all with small vermiform bodies designed to move within the spaces between the sand.

Throughout La Corona lava tube, unconsolidated particles of varying porosity are present and consist mostly of cinder grains, which are significantly larger than sand grains. The larger grains are less compact and permit water flow more freely throughout. Because of the large grain size, the role of capillary forces among cinder grains is negligible, and instead, water flow is mostly dominated by inertial forces. The inertial flow facilitates water exchange between the water column and the cinder grains more readily, preventing the formation of redox gradients. Animals living within cinders will experience abiotic conditions similar to those of the water column throughout La Corona lava tube rather than of true interstitial habitats among the sand grains.

The differences between these two environments may explain why many anchialine stygobites of La Corona lava tube that are common among cinders, are absent from the sandy sediments of Montaña de Arena. (Figs. 29 and 30).

Brett C. Gonzalez

Figura 30. Salinas de Los Agujeros, near the settlement of Mala, is one of the few, still functional saltworks in Lanzarote.

Brett C. Gonzalez

Figura 31. A windmill at Salinas de Los Agujeros.

Concluding Remarks:

the biological treasure under Lanzarote

There are 32 stygobites in La Corona lava tube (five of these species still undescribed) including 21 crustaceans and 11 annelids, most of them restricted to the flooded sections of La Corona lava tube. *Heteromysoides cotti, Munidopsis polymorpha, Halosbaena fortunata, Humphreysella wilkensi, Humphreysella phalanx, Liagoceradocus acutus*, and *Bogidiella uniramosa*, also occur in anchialine wells or pools along the coast of Lanzarote. *Leptonerilla diatomeophaga, Muceddina multispinosa,* and *Stygocyclopia balearica* can also be found in caves elsewhere, including Tenerife and throughout the Mediterranean respectively. İn addition, there are three stygophilic endemics from La Corona lava tube, *Mesonerilla* n. sp. 1, *Mesonerilla* n. sp. 2, and *Parhyale multispinosa.*

Biodiversity in La Corona lava tube appears low when compared to other major anchialine areas of the Atlantic, including the Bahamas (107 crustaceans and 2 annelids), Bermuda (70 crustaceans and 1 annelid), and the Yucatan Peninsula (39 crustaceans and 2 annelids). İn comparison, the diversity in these regions is represented in numerous caves and islands whereas in Lanzarote, the diversity is solely from a single locality. The only other known anchialine cave in the world with a higher biodiversity of stygobites than that of La Corona lava tube is Walshingham cave system in Bermuda, having 37 known stygobites.

The biogeographic affinities of the stygobites in Lanzarote are highly diverse. Six genera and one family are exclusively represented here. The annelids *Gesiella jameensis* and *Speleobregma lanzaroteum*, and the copepods *Enantronia canariensis* (Calanoida), *Oromiina fortunata* (Cyclopoida), *Dimisophria cavernicola*, and *Palpophria aestheta* (Misophrioida) represent monotypic genera. *Palpophria aestheta* is in fact the only known representative of the family Palpophriidae.

Other endemics of La Corona belong to genera which display interesting disjunt distribution patterns from groups that exclusively inhabit caves. An amphiatlantic distribution (occurring on both sides of the Atlantic Ocean) can be seen in 15 genera. The nerillid annelid genus *Longipalpa* is known from the Yucatan Peninsula, the Bahamas, and Bermuda. Similarly, the amphipod genus *Spelaeonicippe* is found in the Bahamas and Turks and Caicos, and the harpacticoid copepod genus *Neoechinophora* is present in Bermuda and the Mediterranean. The ancestor of these genera may have colonized caves or similar habitats before the opening of the Atlantic Ocean, speciating by tectonic vicariance. A species of *Macrochaeta* is also found in a single cave in the Yucatan Peninsula, although otherwise the genus is found in the ocean at shallow waters, suggesting independent colonization events. Full Tethyan distribution patterns are found in several genera from La Corona lava tube including *Speleophriopsis, Curassanthura, Halosbaena, Humphreysella, Morlockia,* and a clade within *Prionospio*. All these lineages have been proposed as Tethyan relicts colonizing caves from shallow water marine ancestors during the Mesozoic, diverging by vicariance driven by plate tectonics during the opening of the Atlantic Ocean. The stygobitic genera *Liagoceradocus* and *Stygocyclopia* occur in caves in the Indopacific, representing a partial Tethyan distribution.

An alternative deep sea affinity is seen in several groups from La Corona lava tube. This accounts for genera exclusively found in the deep sea and caves. Genera in La Corona lava tube with this pattern include *Humphreysella, Munidopsis, Paramisophria, Gesiella, Fauveliopsis, Speleobregma*, and the misophrioid genera *Palpophria, Speleophriopsis, Dimisophria*, and *Expansophria*. This affinity, however, does not necessarily indicate a deep sea origin, i.e., colonization of caves from deep sea ancestors. Independent phylogenetic analyses performed on misophrioid (*Palpophria, Speleophriopsis, Dimisophria*, and *Expansophria*) and calanoid copepods (*Paramisophria*), ostracods (*Humphreysella*), and annelids (*Speleobregma*) have favored a shallow water origin for the cave species in these clades. The two stygobites *Gesiella jameensis* and *Munidopsis polymorpha* are the only cases in which phylogenetic analyses cannot reject a deep sea origin.

It is important to note that there is no single biogeographical model that can explain the complex patterns and affinities seen in La Corona lava tube. The fauna currently present in La Corona lava tube is most likely the result of multiple independent colonization events occurring throughout the complex geological history of Lanzarote.

From an evolutionary perspective, stygobites in La Corona lava tube are the result of many thousands to millions of years of adaptation to the unique characteristics of the subterranean environment. Numerous groups, including *Gesiella, Munidopsis, Spelaeonicippe,* and *Heteromysoides* have undergone loss of features, including eyes and pigmentation, to save energy and cope with lack of resources within the cave. In contrast, other genera including *Megadrilus, Longipalpa, Speleobregma*, and *Palpophria*, have invested in the development of features with new unique adaptations to access the few resources available within the water column of the cave. The study of these various evolutionary responses and mechanisms may help elucidate general evolutionary processes in other environments.

The conservation of the subterranean ecosystems of Lanzarote is essential as it represents the only known habitat for these endemic species. These animals are not only a part of the natural heritage of Lanzarote, but also a source of knowledge to all. The benefits of cave studies, like all others, are far more than scientific or applied knowledge, but serve as an outlet to our natural curiosity and wonder.

Summary of the Stygobitic Species Recorded in La Corona Lava Tube

🟥 Stygobitic species

🟦 Marine species

	Distribution					Habitat				Affinities		Congeners					Origin			
	Cueva de los Lagos	Jameos del Agua	Túnel de la Atlántida	Montaña de Arena	Other anchialine environments in Lanzarote	Cinder	Water column	Epibenthic	Sand	Species in the genus	Stygobites in the genus	Caribbean	Atlantic Ocean	Mediterranean	Pacific Ocean	Indian Ocean	Tethyan	Deep sea	Shallow waters	Interstitial
Annelida, Aphroditiformia																				
Gesiella jameensis	🟥	🟥	🟥				🟥			1	1	🟥					🟥	🟦		
Annelida, Terebelliformia																				
Fauveliopsis jameoaquensis		🟥	🟥			🟥			🟥	17	3	🟥	🟦	🟥	🟦	🟦		🟦		
Annelida, Scolecida																				
Speleobregma lanzaroteum			🟥				🟥			1	1							🟦		
Prionospio **n. sp.**			🟥				🟥			1000	5	🟥	🟦	🟦	🟦	🟥	🟦			
Annelida, Protodrilida																				
Megadrilus pelagicus	🟥		🟥				🟥			7	1	🟦	🟦	🟦	🟦	🟦			🟥	🟦
Annelida, Terebellida																				
Macrochaeta **n. sp**		🟥	🟥			🟥				13	2	🟥	🟦	🟦	🟦	🟦			🟥	🟦
Annelida, Polychaeta incertae sedis																				
Mesonerilla **n. sp**	🟥	🟥	🟥			🟥				10	1	🟥	🟥	🟦	🟦	🟦			🟥	🟦
Leptonerilla diatomeophaga		🟥	🟥			🟥				9	5	🟥	🟥	🟥			🟥	🟦 ?		🟦 ?
Longipalpa **n. sp**	🟥		🟥				🟥			5	5	🟥					🟥			🟦
Annelida, Phyllodocida																				
Sphaerosyllis iliffei				🟥					🟥	68	1	🟦	🟦	🟦	🟦	🟦			🟦	
Ostracoda, Halocyprida																				
Eupolycope pnyx	🟥	🟥	🟥				🟥			7	1	🟦	🟥	🟦	🟦	🟦	🟥		🟦	
Humphreysella wilkensi	🟥	🟥	🟥		🟥		🟥			11	11	🟥	🟥		🟥	🟥	🟥	🟦		
Humphreysella phalanx	🟥	🟥	🟥		🟥		🟥			11	11	🟥	🟥		🟥	🟥	🟥	🟦		

🟥 Stygobitic species
🟦 Marine species

	Distribution					Habitat				Affinities		Congeners					Origin			
	Cueva de los Lagos	Jameos del Agua	Túnel de la Atlántida	Montaña de Arena	Other anchialine environments in Lanzarote	Cinder	Water column	Epibenthic	Sand	Species in the genus	Stygobites in the genus	Caribbean	Atlantic Ocean	Mediterranean	Pacific Ocean	Indian Ocean	Tethyan	Deep sea	Shallow waters	Interstitial
Copepoda, Cyclopoida																				
Oromiina fortunata		🟥				🟥				1	1								?	
Muceddina multispinosa			🟥				🟥			1	1			🟦					🟦	
Copepoda, Calanoida																				
Enantronia canariensis			🟥				🟥			1	1								?	
Paramisophria reducta			🟥				🟥			18	6	🟥	🟥	🟥	🟦		🟥		🟦	
Stygocyclopia balearica	🟥		🟥				🟥			3	3						🟥		?	
Copepoda, Harpacticoida																				
Neoechinophora karaytugi		🟥					🟥			5	5		🟥	🟥			🟥		?	?
Copepoda, Misophrioida																				
Expansophria dimorpha			🟥				🟥			3	3		🟥	🟥	🟥		🟥		🟦	
Dimisophria cavernicola			🟥				🟥			1	1								🟦	
Speleophriopsis canariensis	🟥	🟥	🟥				🟥			3	3		🟥	🟥	🟥		🟥			
Palpophria aestheta	🟥	🟥	🟥				🟥			1	1								🟦	
Pericarida, Mysida																				
Heteromysoides cotti	🟥	🟥	🟥		🟥		🟥			4	4	🟥			🟥		🟥		🟦	
Pericarida, Thermosbaenacea																				
Halosbaena fortunata	🟥	🟥	🟥		🟥		🟥			4	4	🟥			🟥	🟥	🟥			
Amphipoda, Gammaridea																				
Bogidiella uniramosa		🟥				🟥				110	110	🟥	🟥	🟥	🟥	🟥			🟦	
Liagoceradocus acutus	🟥	🟥	🟥		🟥	🟥	🟥			6	6				🟥	🟥	🟥		🟦	
Spelaeonicippe buchi	🟥	🟥	🟥				🟥			2	2	🟥					🟥	🟦		
Isopoda, Anthuroidea																				
Curassanthura canariensis	🟥	🟥	🟥			🟥				4	4	🟥	🟥				🟥		🟥	🟥
Decapoda, Anomura																				
Munidopsis polymorpha	🟥	🟥	🟥		🟥			🟥		300	1	🟦	🟦	🟦	🟦	🟦		🟦		
Remipedia, Nectiopoda																				
Morlockia atlantida	🟥		🟥				🟥			4	4	🟥	🟥				🟥			
Morlockia ondinae	🟥		🟥				🟥			4	4	🟥	🟥				🟥			

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Chapter 2

Outlook on Subterranean Fauna

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