Biospeleology in Macaronesia

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Geographical and speleological background

In the biogeographical sense Macaronesia is a subregion of the Western Palaearctic which includes southwest continental Portugal, part of the coastal zone of south Morocco, and the Atlantic archipelagos of the Azores, Madeira, Selvagens, Canaries and Cape Verde. Since the establishment of the term in the 19th century by the British botanist P.B. Webb, much has been discussed about the validity of Macaronesia as a biogeographic unit, about its appropriate space and boundaries, and about its different meaning for vegetal and animal organisms. Two continental areas and five volcanic archipelagos have generally been identified within Macaronesia. The islands are of oceanic origin with no surface connection with other land since they emerged from the sea bottom. Independently to other biogeographic considerations, in this text we only pay attention to the strictly volcanic Macaronesian archipelagos, which constitute an insular geographic reality very different to that of the continental Macaronesian enclaves. From a political point of view the Azores, Madeira and Selvagens belong to Portugal, the Canary Islands to Spain, and the Cape Verde form an independent country, though with a strong Portuguese character for obvious historical reasons.

The Macaronesian archipelagos have common geological features mainly derived from their volcanic origin. All the islands have been built up from the sea bottom by successive accumulation of volcanic materials that finally emerged over the marine surface along the Tertiary and Quaternary. Actually the volcanism is still active on the Azores, the Canaries and the Cape Verde islands. Almost all the rocks forming these archipelagos are volcanic. However, in some of the Canary Islands (i.e. La Palma, La Gomera and Fuerteventura) there are plutonic rocks that belonged to their original basements, were uplifted over the sea level and are now exposed on the surface by the effects of erosion. On other islands like Santa Maria (Azores) and Porto Santo (Madeira) some limestone rocks of marine origin have been formed and are actually emerged because of eustatic movements of the sea level. These non volcanic rocks are anyway very scarce, and have developed such a slight karstification that true caves are not found at all inside them. Therefore, in the Macaronesian islands the caves enough developed as to be considered of speleological interest occur only in volcanic terrains.

Such particular cavities have a genesis, morphology and a life span very different than limestone caves. The main types of volcanic caves are lava tubes and volcanic pits, each with their variants depending on the type of speleogenesis (see Montoriol, 1973).

The lava tube caves are formed only in fluid basaltic lavas, never occurring in viscous acidic lava flows of trachytic nature. They originate after more or less permanent lava channels that consolidate by cooling of the peripheral layers, and are finally roofed when significant speed differences are established between the inner and the surface flow. The inner temperature of the tube allows the lava to keep flowing inside until the emission stops, the liquid empties totally and the system becomes a hollow tube. These caves are therefore usually shallow and follow parallel to the surface topography at the moment of being formed. Great accumulation of further new lavas on that containing the cave, and changes on the relief by important erosive effects can alter this parallelism between lava tubes and the actual surface upon them.

A particular type of lava tubes are those originated by the emptying of a dyke. They usually have a different morphology and since their origin are located much deeper below surface than the so called rheogenetic lava tube caves (Socorro & Martín, 1992). These dyke caves do not necessarily follow the surface topography, and normally open to outside at cliffs and other steep terrains due to erosion. Some examples of this kina of caves are Gruta dos Anjos (Santa Maria), Gruta do Inferno (Selvagem Grande) or Cueva de la Fajanita (La Palma).

The volcanic pits often derive from the emptying of volcanic chimneys when the eruption stops and the remaining lava contracts. The spatter cones are hollows with limited dimensions, while other volcanic pits can exceed 100 m deep, like Algar do Montoso, in São Jorge (Azores). They are usually bell-shaped, though they often show more complex structures with connected cavities and multiple vents. The geysers and the vents of gaseous phreatomagmatic eruptions can originate remarkable pits, like that of Sima de Tinguatón in Lanzarote. Some times the retraction cracks originated after cooling trachytic, viscous lavas can also originate remarkable pits, like the 70 m deep Sima Vicky (Tenerife).

Also lava tubes can be combined with volcanic pits in a single but complex cavity with several levels at different depths, like it occurs in Sima de Las Palomas (El Hierro) and Cueva del Sobrado (Tenerife).

Speleogenesis and ecological succession on volcanic terrains

Besides their peculiar speleogenesis when compared to karstic caves, lava tube caves have a geological cycle and an ecological succession also very different (see Howarth, 1996). The formation of a lava tube is very quick, sometimes just a few days, and immediately starts its evolution towards definitive destruction as a cave, which will take place within a period of 100,000 to 500,000 years depending on the local climate and erosion (Howarth, 1973). Volcanic pits, however, can last longer time. The cycle of lava tubes is very short in geological terms, compared to that of limestone caves (millions of years) which needed at least 100,000 years to initiate its formation. On the other hand, lava tube caves usually have much less permanent water than limestone caves (which need it for their formation and is only absent in fossil, inactive caves), and are in general much shallower so that the roots of surface plants often reach and invade the cave.

A recently formed lava tube starts with a juvenile phase characterized by its dependence on the outside climate due to the network of cracks of the lava, easily connecting the cave to the exterior. As ecological succession goes on over the lava, the soil seals the surface, shallower passages retain moisture and the cave enters in a mature phase with the subsequent climatic isolation (temperature and humidity). Thus, there is a simultaneous ecological succession inside and outside the cave, which is very important to determine the living community inhabiting this environment (Ashmole *et al*., 1992). There is a particular way to accelerate this process when a thick layer of small-sized pyroclasts (cinder and lapilli) are deposited upon the recent lavas, which isolate the cave from outside temperatures, keep the moisture and allow many plants to grow up and provide roots to the cave. Many caves in recent or very dry areas of the Canary and the Cape Verde islands have good conditions for troglobites thanks to be covered by ash fields. As time goes by the erosion leads the cave to a senile stage, in which silting of the network of cracks and voids in the surrounding lava isolates the system, the inner space of the cave can be even stuffed up by clay deposits, and internal collapses finally destroy the cavity. Volcanic pits usually have a much longer senile stage due to their larger volume and their vertical shape and more solid architecture. Thus volcanic pits last much longer than lava tube caves, reaching a few million years and being the only caves in the oldest terrains of the islands (Oromí *et al*., 1985).

In the lava tube caves ecological succession typically progresses upwards (Howarth, 1996) in such way that deep levels reach maturity before the upper levels, which need better soil cover on the surface to maintain ideal conditions for troglobites. For example Cueva de Todoque (La Palma, Canary Is.) formed in the lavas of San Juan eruption (1949) some troglobites have been found in the deepest passages, while lavicolous species are the only inhabitants in the rest of the cave (Ashmole et al., 1992; Martín, 1992). In limestone caves instead, the oldest habitats are closer to the surface and ecological succession progresses downwards.

The older is a lava tube, the higher probability to be covered by further lava flows, which keep the cave away from surface. In such conditions the roots do not reach the cave, and provision of organic matter by percolating water is more difficult. Consequently, lava tubes occurring under many lava flows hold a poor fauna or are even abiotic, as it also happens in dyke caves.

Animal communities in volcanic caves

When a lava tube has attained maturity, its environmental conditions are similar to that of limestone caves: absence of light, temperature stability, humidity close to saturation. Scarcity of organic matter is also severe, with lesser provision by water than in limestone caves but frequently compensated by the presence of roots (if there are). In the Macaronesian islands bat colonies are very few inside the caves, therefore the guano is negligible.

Volcanic pits are usually richer in food because they operate as pitfall traps for many organisms; on the contrary, in lava tubes the input of energy through the entrance only affects a few metres inside, and hardly progresses into the cave.

Adaptations to cave life are the same for volcanic and limestone troglobites: depigmentation, eye reduction, elongation of body and appendages, slow metabolism, starving resistance, longer life span, inability to live outside the cave, *k* reproductive strategies (more limited but successful offspring), etc. Higher tolerance to temperature changes has been observed in island troglobites with respect to temperate continental species, both in the nature and in laboratory experiences (Izquierdo, 1997); this could be related to the shallower lava tubes to which they are adapted, and maybe also to the less marked seasonal differences in oceanic islands.

In these volcanic hypogean communities the root-feeding species are particularly abundant with respect to other trophic categories. It is remarkable the richness of sap-sucking plant-hoppers (Cixiidae and Meenoplidae) on three of the archipelagos, while in Europe and North Africa these groups are unknown in the caves. It is also peculiar of these island cave-dwelling communities the presence of troglobitic species belonging to taxonomical groups absent in caves of the nearby mainland, and even very rare all over the world. This is the case for landhoppers (Amphipoda: Talitridae), earwigs (Dermaptera) and thread-legged bugs (Hemiptera: Reduviidae) which have troglomorphic species only in the Canary Islands and in Hawaii. The diversity and abundance of troglobitic cockroaches (Blattaria) in the Canaries contrasts with the absence of these insects in caves of the whole Palaearctic.

Troglobitic species are unable to survive outside their hypogean environment, and therefore they cannot colonize other islands. This implies that all troglobites in Macaronesia are always endemic to a single island. The presence of a troglobite in two islands could only be explained when these islands had been connected in relatively recent past times due to regressions of the sea level (for example Pico and Faial in the Azores; Fuerteventura and Lanzarote in the Canaries).

Types of caves and biological richness

It is very common to find a troglobitic species in different, distant caves formed in separated lava flows within an island. This is due to the existence of the so called Mesovoid Shallow Substratum (MSS: Juberthie, 1983; Culver, 2001), an extensive network of cracks and voids connecting large areas, which is suitable to be occupied by many troglobites. There is a particular type of MSS in volcanic islands made up by the lava clinker covered by a thin soil (Oromí et al., 1986), which has provided a rich adapted fauna in places without caves on the Canary and the Azores islands (Medina & Oromí, 1990 and 1991; Borges, 1993).

Actually troglobites occupy the extensive network of spaces in the appropriate underground, either good caves, crevices or MSS. In general they often prefer small tubes and cracks than proper "caves" that are for us just windows to reach the hypogean habitat. But in

Table I. Types of caves and animal richness.

Type of cave	Troglobites	Other species
Lava tubes	rich	moderate
Chimney pits	moderate	rich
Big crevices	poor	poor
Drained dykes	poor	poor
Erosion caves	none	poor

general the abundance of cavities is a good indicator to the richness of well adapted fauna in an area, especially lava tube caves which are found in basaltic terrain, the best for a good network of spaces.

Besides the stage of ecological succession and the geographic situation of a cave, the animal communities occurring in it also depends on its morphology and depth. Mature lava tubes are more isolated from the surface than volcanic pits concerning direct input through the entrance. Thus the pits can hold a richer fauna with many epigean species, while in the tubes the community is poorer but with much higher proportion of troglobites. The dyke caves are usually very poor because of their location very deep underground, where neither roots nor percolating water with organic matter arrive easily. Most of the dyke caves we have studied had a scarce fauna and always close to the entrance. Other pits like big crevices are also poor because they are usually formed in acidic lavas, which are more impermeable and unconnected to the Mesovoid shallow substratum (MSS), an important reservoir of the hypogean fauna in volcanic terrains without lava tubes. The erosion caves generally formed close to the sea shore are very often also dyke caves, and lack an adapted hypogean fauna.

Main features of the terrestrial cave fauna in Macaronesia

Island faunas are always peculiar because of their disharmony, with many absent animal groups that are found in the continent. This is also the same concerning to cave animals, in such way that these lacking species are partially replaced by other species preadapted to hypogean life, very often belonging to unusual taxonomic groups in the continental cave faunas. This is due to the inability for some of these groups to colonize oceanic islands, being their potential hypogean niches occupied by other groups that commonly don't do it in the mainland.

All Macaronesian troglobites have evolved locally, in such way that all species are endemic to a single island with the exceptions above mentioned. This implies allopatric speciation and many independent colonisations of the underground. However, some genera include various related troglobitic species in one island (3 *Trechus* spp. in Pico, 5 *Cixius* spp. in La Palma, 11 *Loboptera* spp. and 8 *Dysdera* spp. in Tenerife, etc.) In some of these cases two or more congeneric species are found together, but they have different epigean sister species, which also implies independent invasions of the underground. Moreover, many of the epigean sister species are actually occurring on the surface in the same area to their corresponding hypogean sister species, what means that the latter have evolved by parapatric speciation. This is a common situation in Macaronesian islands and agrees with the adaptive shift hypothesis for the origin of troglobites (Rouch & Danielopol, 1987; Howarth, 1987). However, there are also troglobites with no epigean relatives at all on their island and even on the whole archipelago. This is the case for the thread-legged bugs *Collartida anophthalma* (from El Hierro) and *Collartida tanausu* (from La Palma), several species of the pseudoscorpion genus *Tyrannochthonius* and the planthopper genus *Meenoplus*. Some of the species belong to endemic genera, like the harvestman *Maiorerus randoi* from Fuerteventura, the ground beetles *Spelaeovulcania canariensis* from Tenerife and *Pseudoplatyderus amblyops* from La Gomera, with no related species elsewhere in the world. It is difficult to say that these species evolved according to the classical climatic relict hypothesis proposed for the troglobites from Europe and North America (Vandel, 1964; Barr, 1968), since glaciations didn't affect these islands of the mid Atlantic. Maybe their relict condition was due to secondary climatic changes derived from glaciations (drought, forest withdrawal).

Azores Islands

This is the western and northernmost archipelago, being located on the Midatlantic ridge. This implies interesting geologic consequences, with predominance of Hawaiian type volcanism and therefore basaltic rocks, very suitable for the formation of lava tubes. Its geographical situation divides the archipelago in two groups of islands, one at west (Flores and Corvo) and the other at east (rest of the islands) of this ridge, in such way that the former shift westwards together with the ocean floor, and the second group move eastwards towards Europe. The age of each island varies depending on the distance to the ridge, the youngest being those of the central group (Faial, Pico and São Jorge) and the oldest one Santa Maria. The greatest abundance on lava tube caves is in general in the youngest islands, though older islands can be also rich in such caves whenever recent volcanism (in geological terms) have took place and have modern terrains, like for instance São Miguel. On the contrary, modern islands like Flores (2.16 Ma) but lacking recent eruptions, are poor in such caves. All the Azores islands are rather rich in lava tube caves except Corvo, Flores and Santa Maria, and at least some troglobitic species are so far known from all the rest except Graciosa (see Table II).

The studies on cave biology had been very sporadic before the 1980's, and only a few freshwater species occurring in pools at the bottom of pits were known. The knowledge on the terrestrial fauna started in 1987, when an expedition by researchers from Edinburgh University (UK) and La Laguna University (Canary Islands) financed by National Geographic Society and with the valuable collaboration of Os Montanheiros members (Angra do Heroísmo) studied the cave fauna from Terceira, Pico, and São Jorge, and discovered the first cave-dwelling species (see Oromí *et al*., 1990). The same team visited again the archipelago in 1989, also joining the first Azorean biospeleologist (Paulo Borges)

Table II. Islands of the Azorean archipelago. Ages in million years (after França et al., 2004). Presence or absence of volcanic caves with apparent conditions to hold troglobitic fauna. Presence or absence of troglobites.

	Corvo	Flores	Faial	Pico	Graciosa	S.Jorge	Terceira	S.Miguel	S.Maria
age	0.7	2.1	0.7	0.2	2.5	0.5	3.5	4.0	8.1
caves	-	-	+	+	+	+	+	+	-
troglobites	-	-	+	+	+	+	+	+	-

for the study of caves in São Miguel, where they also were helped by the local caver Teófilo Braga (Amigos dos Açores). They also visited Pico, São Jorge, Faial and Graciosa, and found new troglobitic species in all except Graciosa (Oromí *et al*., 1990; Oromí & Borges, 1991; Mahnert, 1990; Merrett & Ashmole, 1989). Since then the biospeleologist team created in Universidade dos Açores at Terceira, has continued the research on cave fauna from the different islands, and now they have an advanced knowledge on the Azorean hypogean fauna, both from caves and from the MSS. The BALA Project carried out in 1998-2001 and directed by Prof. Paulo Borges provided a remarkable improve on the knowledge of the Azorean fauna (Borges *et al*., 2005a, 2005b).

Actually 20 species of troglobites have been found on the archipelago, belonging to eight different orders of arthropods (Borges & Oromí, 1994 and in press). All of them are endemic to a single island, except a few which are found both in Pico and Faial, This is difficult to explain unless a land connection existed between the two islands in the past allowing troglobites to move to each other, separated by less than 50 m depths (see Eason & Ashmole, 1992); however, this hypothesis is controversial since the western part of Pico is extremely recent, probably younger than the descent of sea level during the last glaciation (João C. Nunes, pers. comm.). The hypogean species from the Azores have a moderated degree of troglomorphism, with an obvious reduction of eyes but never reaching the eyeless condition, and never with a very marked lengthening of appendages. The most remarkable case of splitting is found in the genus *Trechus* which includes seven different cave-dwelling species in the archipelago (see Oromí & Borges, 1991; Borges & Oromí, 1991 and in press; Borges *et al*., 2004).

Madeira Islands

The archipelago of Madeira is located at latitude of 33ºN and is formed by two main islands, Madeira and Porto Santo, and the Desertas islets. Porto Santo is an old island (15 Ma), without lava tube caves and troglobitic fauna known so far. Madeira is younger (5.5 Ma) but with scarce recent volcanism, and therefore with few caves. However, the island had often been visited by entomologists which sporadically entered the caves and discovered a few troglobitic species of woodlice (Vandel, 1960), spiders (Wunderlich, 1992) and beetles (Erber, 1990; Serrano & Borges, 1995). In 2000 the GIET team from the University of La Laguna organized a research expedition to Madeira and visited Grutas do Cavalum (Machico) and Grutas de São Vicente, but it has been after 2002 when Dora Aguín and Elvio Nunes, from Universidade da Madeira, who carried about for the first time an accurate study of Machico caves, and discovered several unknown troglobites (Nunes *et al*., 2003).

The cave-dwelling fauna from Madeira is not very rich in species, which have a little marked degree of troglomorphism (Serrano & Borges, in press). This is the only archipelago in Macaronesia where no cave-adapted planthoppers have ever been found. Not a single genus of arthropods includes various troglobitic species, which probable indicates that its limited underground environment has not promoted the radiative evolution in this habitat.

Selvagens Islands

This very small and isolated archipelago is between Madeira and the Canaries, at 30° N. It originated some 24 Ma but it after remained under the sea level for a long time, when new eruptions emerged again the islands between 12 and 8 Ma. They are low islands (less than 150 m) and only Selvagem Grande has one cave, formed in a dyke by marine erosion when it was at the sea level (now the cave is higher up). It was recently visited by a biologist from La Laguna who was looking for cave fauna. The conditions are not good for trogobites, and just a troglophilic spider was collected (*Spermopohorides selvagensis* Wunderlich) (Arechavaleta *et al*., 2001).

Canary Islands

This is the larger archipelago and the closest to the mainland (110 km from Fuerteventura to the Sahara coast), being situated between 27° and 29° N. Their ages rank from 21 Ma (Fuerteventura) to less than 1 Ma (El Hierro), in such way that the age decreases from east to west (see Table III). The origin of the Canaries is not related to the mid-Atlantic ridge like the Azores but to a hotspot model with the peculiarity that the older islands still continue with volcanic activity (Carracedo *et al*., 1998). This has allowed the presence of modern lavas on all the islands except La Gomera where no eruptions have occurred along the last 3 Ma (Cantagrel *et al*., 1984). The islands with more volcanic caves are Lanzarote, Tenerife, La Palma and El Hierro. The lava tube caves in Lanzarote are large and abundant, but the aridity of the climate and the scarce soil covering the lavas prevents the existence of the necessary humidity for the existence of a true troglobitic fauna. The islands containing more troglobites are Tenerife, La Palma and El Hierro. In Fuerteventura they are also rare because of the dry climate, but there are two species. In Gran Canaria there are few caves, but recent research points to the presence of an adapted fauna. A similar situation occurs on La Gomera, where there are no caves at all but a few hypogean species inhabit the MSS in the humid forest.

The studies on the underground fauna in the Canaries early started in 1892 when the crab *Munidopsis polymorpha* was described from the anchialine cave Jameos del Agua (Lanzarote), together with some other adapted species (Koelbel, 1892). The animal community of this cave and the neighbouring Túnel de la Atlántida has been intensively studied along the last century, and as much as 25 species adapted to this particular habitat are so far known (Oromí & Izquierdo, 1994, in press). It is remarkable the existence of *Speleonectes ondinae*, the only Remipede crustacean known from the oriental part of the Atlantic.

The first terrestrial troglobite to be described was *Collartida anophthalma*, discovered in the early 80's by catalan cavers in El Hierro (Español & Ribes, 1983). At this time was created the Grupo de Investigaciones Espeleológicas de Tenerife (GIET) from the University of La Laguna (Tenerife), which has been regularly studying the hypogean fauna with a remarkable success (Oromí & Izquierdo, 1994, in press). In the Museo de Ciencias Naturales de Tenerife also the late J.J. Hernández Pacheco was active on cave research up to his death in 1993 (Hernández Pacheco *et al*., 1995), and in La Palma island members of the G.E. Benisahare caving club also studied many caves with discoveries of many interesting hypogean species (García & Oromí, 1996; Machado, 1998).

The organization in 1992 of the 10th Int. Symposium of Biospeleology in Tenerife by the GIET team, and the 7th Int. Symposium on Vulcanospeleology in 1994 in La Palma by Junonia and GIET groups, show the intense activity and the relevance of their studies. Between 1999 and 2001 this team from La Laguna carried out a research LIFE-Nature project on the cave fauna from the Canary Islands and its conservation.

Table III. The islands of the Canary archipelago set from west to east according to their geographic position. Ages in million years. Presence of caves apparently suitable to hold terrestrial adapted fauna. Number of troglobitic species.

	Hierro	LaPalma	Gomera	Tenerife	G.Canaria	Fuerteventura	Lanzarote
age	0.8	2	12	12	14	21	15.5
caves	+	+	-	+	+	+	-
troglobites	19	31	8	64	4	2	-

The hypogean fauna from the Canaries is the richest in Macaronesia, 132 of terrestrial troglobitic and 57 aquatic stygobiont (either freshwater or anchialine) species having been found so far. This is also the fauna with the most advanced degree of troglomorphism among these Atlantic islands, including some species such as the thread-legged bug *Collartida anophthalma* (Hemiptera, Reduviidae) and the rove-beetle *Domene vulcanica* (Coleoptera, Staphylinidae) easily comparable to the most troglomorphic species from the Palaearctic. The most adapted fauna to the underground occurs in the modern terrains of Tenerife, while the hypogean species from the western islands (La Palma and El Hierro) are usually more ambimorphic with some exceptions.

Various genera having undergone radiative evolution on the Canaries are also represented in the underground fauna, like the spiders *Dysdera* (9 spp.) and *Spermophora* (5 spp.). In other genera such as the cockroaches *Loboptera* (Blattaria), the planthoppers *Meenoplus* (Hemiptera) and the beetles Domene and *Wolltinerfia* (Coleoptera) this radiation has originated only troglobitic species(see Table IV). There are also hypogean species with no relatives on the surface, neither belonging to the same nor to close genera, for which they can be considered as relict species whose epigean ancestors disappeared from the islands after originating the actual hypogean forms. In this sense they are remarkable the cases of *Tyrannochthonius* and *Lagynochthonius* (Pseudoscorpiones

Table IV. Arthropod polyspecific genera with troglobites in the Canary Islands. The islands where each species occurs are indicated (H: El Hierro; P: La Palma; G: La Gomera; T: Tenerife; F: Fuerteventura).

GENERA	TOTAL NO. SPECIES	HYPOGEAN SPECIES	ISLANDS
Dysdera (Araneae)	44	9	P, T
Spermophora (Araneae)	24	5	H, P, T, F
Porcellio (Isopoda)	19	1	T
Dolichoiulus (Diplopoda)	43	4	H, P, T
Lithobius (Chilopoda)	11	4	H, P, G, T
Loboptera (Blattaria)	12	11	H, P, T
Cixius (Hemiptera)	7	6	H, P
Meenoplus (Hemiptera)	3	3	H, P
Trechus (Coleoptera)	12	2	H, P
Wolltinerfia (Coleoptera)	3	3	T
Licinopsis (Coleoptera)	6	2	H, P
Alevonota (Coleoptera)	10	6	P, T
Ocypus (Coleoptera)	7	2	T
Domene (Coleoptera)	5	5	T, G, P
Laparocerus (Coleoptera)	>100	4	H, P, G

Chthoniidae), *Maiorerus* (Opiliones Laniatores), *Collartida* (Hemiptera Reduviidae) or *Spelaeovulcania* and *Canarobius* (Coleoptera Carabidae).

One of the most interesting features of the Canary hypogean fauna is the presence of unexpected groups in such faunas of the neighbouring mainland. The cave-adapted cockroaches are unknown in the whole Palaearctic, while landhoppers (Amphipoda Talitridae), earwigs (Dermaptera) and thread-legged bugs (Hemiptera Reduviidae) have troglobitic species only in the Canary Islands and in Hawaii.

Cape Verde Islands

The Cape Verde Islands are the southernmost in Macaronesia, being located some 500 km west of Dakar, in Senegal. They form a double arch of islands, the windward islands (Ilhas de Barlavento) and the leeward islands (Ilhas de Sotavento) with ages decreasing from east to west. The easternmost islands (Sal, Boavista and Maio) are low and rather flat, with an arid climate and very few caves due to erosion in such old terrains. Santo Antão, São Vicente, São Nicolau, and Santiago are mountainous but with hardly any recent volcanism for which lava tubes are also scarce: only a few unexplored caves in Santo Antão and the clay-silted Gruta do Lázaro in Santiago are known. But in Fogo island there is an active recent volcanism (last eruption in 1995) with abundant basaltic lavas which have originated abundant caves, though never as large as those from the Azores and the Canary Islands. The relatively recent lava tube caves related to the main volcano (both in Chã das Caldeiras and on the eastern slopes of the island) are better preserved than those in older terrains of the rest of the island.

Knowledge and popularization of caves has been scarce in Cape Verde. Besides some popular believes (the so called "grutas de Lázaro" on Santiago, where supposedly this Robin Hood like bandit hid his treasures) and a few references in modern tourist guides (Schleich & Schleich, 1995), very little is published about this subject. The serious surveying of lava tubes started with the Espeleo Clube de Torres Vedras expedition in 1997, and in 1999 the GIET team from La Laguna University carried out a biological study in eight caves, discovering for the first time the presence of an adapted fauna on this archipelago. Troglobites were found only in caves above 2000 m from the sea level, being remarkable for their adaptations the planthopper *Nysia subfogo* (Hemiptera, Meenoplidae), a Cryptopidae centipede and two still undescribed spiders (Hoch *et al*., 1999).

The aridity of Cape Verde prevents most of its caves to be inhabited by troglobites, since the inner environment is highly influenced by the climate outside. Only in Fogo the Chã das Caldeiras caves covered by a thick layer of cinders are isolated and keep humidity enough for the development of true cave-dwelling species. More visits and research are needed to better know this adapted fauna, which is probably richer than the few species so far discovered.

The hypogean fauna from Macaronesia is abundant in spite of being recently studied, it is varied and has a special interest for the peculiarities due to the insular condition. All troglobitic species are endemic to reduced areas, since they are almost always exclusive to a single island. They are the result of local processes of speciation, with the appearance of troglomorphic characters in groups often unexpected in other parts of the world. But they are often threatened species as well, since the fragility of their environment is remarkable. Many caves on the Azores are silting up due to transformation of forest in pastureland, the few caves in Madeira are absolutely spoiled for tourist use without any sensibility by the owners (case of Grutas de São Vicente) or very damaged by uncontrolled visits and vandalism (case of Grutas do Cavalum); and many caves on the Canary Islands are more and more severely polluted by sewage (case of Cueva del Viento and other lava tubes in Icod de los Vinos), stupidly transformed as show-caves in spite of the presence of protected species (case of Cueva del Llano in Fuerteventura and the endangered *Maiorerus randoi*), or spoiled by uncontrolled visits. The troglobitic fauna has a low resistance to environmental changes and they can easily disappear from the caves.

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