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An ecological study of Cueva de los Roques lava tube (Tenerife, Canary Islands)

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Several aspects of the ecology of Cueva de los Roques were studied: the survey initiated by other speleologists was completed; the flora at the entrance to the cave was studied; and the fauna of the whole cave was analysed by sampling on two occasions three months apart, using a combination of visual searching and baited trapping. The most striking result was the difference in both physical conditions and biology between the two branches of the cave. Branch A has several entrances and thus appreciable air movements, with the result that it is inhabited only by trogloxenes and a few troglophiles. In contrast, branch B is a blind tube with constant high humidity and stable temperature, here there is a community of troglobites. We have found a total of 27 species of invertebrates; these include nine troglobites, of which seven are already known from other lava tubes on Tenerife. This suggests the occurrence of dispersal through a network of cracks in the subsoil, as in other volcanic and karst regions.

Introduction

Situation and topography

Cueva de los Roques, at an altitude of 2200 m, is situated in the National Park of Teide in the island of Tenerife, the largest of seven islands which form the Canary Archipelago (Fig. 1).

The entrances to the cave are in an area of pahoehoe lava which flowed down the southern slope of the volcano Pico Viejo, and near a series of dykes and steep rocks know as the Roques de García. The exact age of this lava is not known and estimates range from 3000 to 100,000 years; it is probably closer to the latter figure. On this recent lava, most of the surface is barren; the scarcity of soil has not allowed the establishment of much vegetation. The flow dates from a recent period of volcanic activity, when various eruptions created a number of caves in the north of the island (Cuevas del Viento, Felipe Reventón, San Marcos and Sobrado). An interesting fauna of troglobites has been discovered recently in these caves.

Cueva de los Roques is about 900 m in total length and is made up of two diverging branches (Fig. 2) which join at their upper end, thus forming a V-shaped lay-out with the apex directed towards the saddle between the volcanoes of Pico Viejo and Teide (orientation north north-east). The largest of the three entrances is at the point of convergence and is considered to be a 'jameo' (following the terminology of Montoriol (1973)) of small dimensions; this type of entrance is due to a posterior falling of the roof of the cave, in contrast to the other two which were formed either when the lava solidified and contracted, or perhaps by the force of the flow itself.

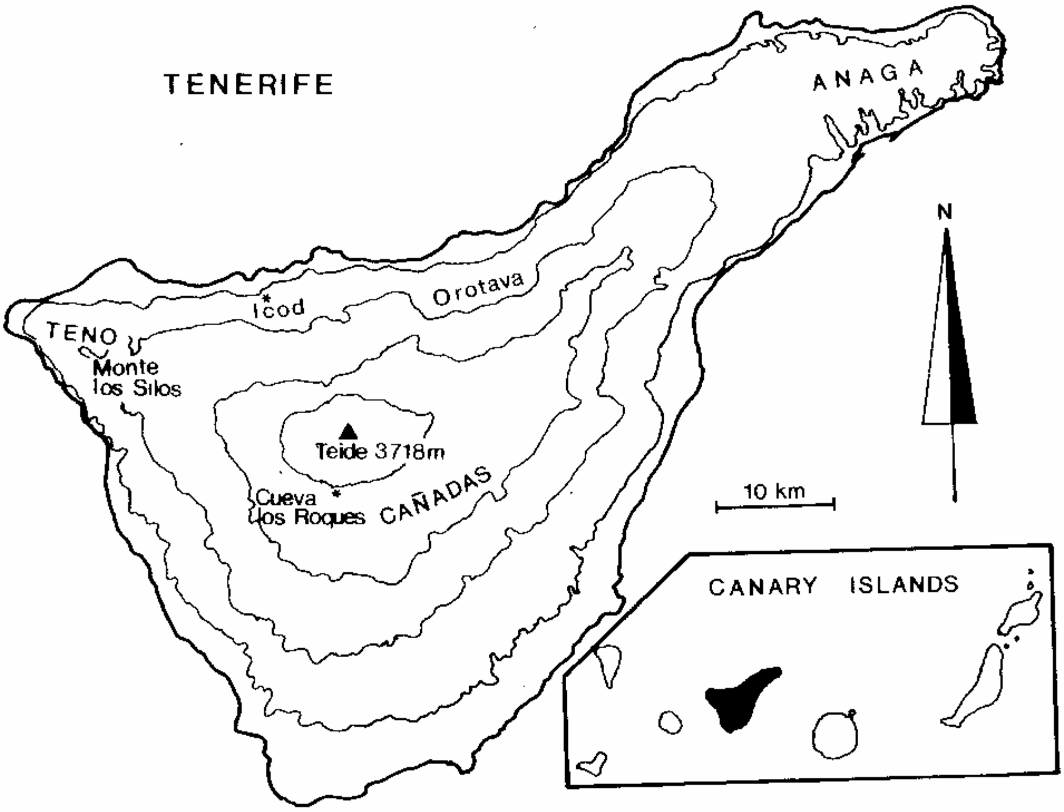

FIG. 1. Situation of Cueva de los Roques in the island of Tenerife.

The eastern branch (B) is a blind gallery, with access only via the jameo. The western branch (A) has, in addition, the other two entrances and for this reason the environmental conditions here are very different. As is characteristic of volcanic tubes, the galleries are very close to the surface, being separated from it by only a thin layer of rock (1–3 m) which allows percolation of water into the cave (Bravo 1954).

Soil is not very abundant in the cave owing to the low level of erosion. A substrate of solid rock (compacted substrate according to the terminology established by Martín (1982)) is very common and that of rubble is rare, the latter being found only at the jameo opening and in a few other places. According to the cycle of geological erosion postulated by Howarth (1973), the cave is in its mature phase, in which it is most suitable for occupation by a specialized fauna.

Physical characteristics of the cave

From the environmental point of view, the two branches of the cave (A and B) present considerable climatic differences, mainly due to the first having three entrances along its length and the second having only one. Thus the temperatures at soil level and at 50 cm above soil level are very different in the two. Most of branch B is stabilized at 12·8°C at 50 cm and a few tenths of a degree less at soil level. In contrast, the temperature in branch A oscillates between 10 and 15°C at 50 cm and is below 10°C at soil level (Fig. 3).

The presence of several entrances in branch A results in the production of air currents of variable strength; hence branch A behaves like a true wind cave (Cigna 1975). Branch B, having only one entrance, has greater environmental stability,

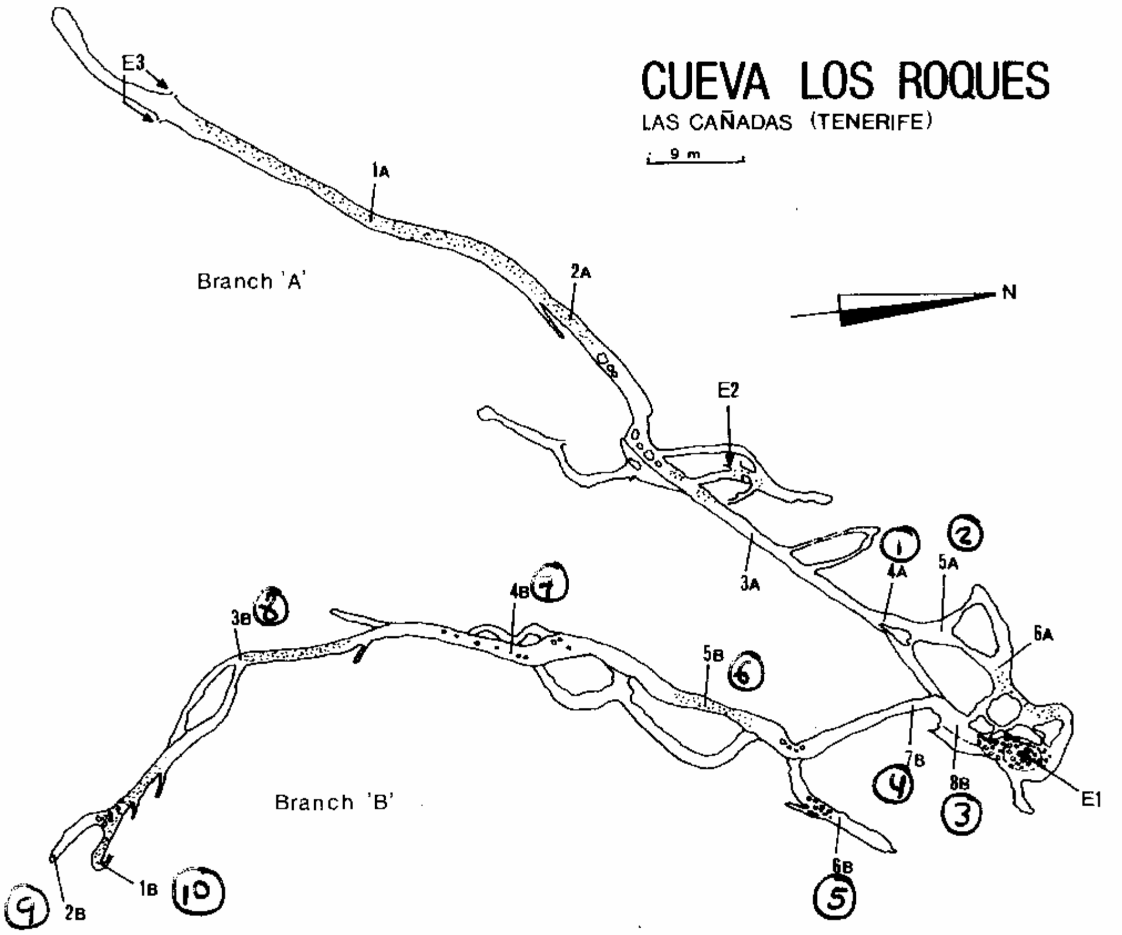

FIG. 2. Topography of Cueva de los Roques. E1, E2 and E3, entrances to the cave.

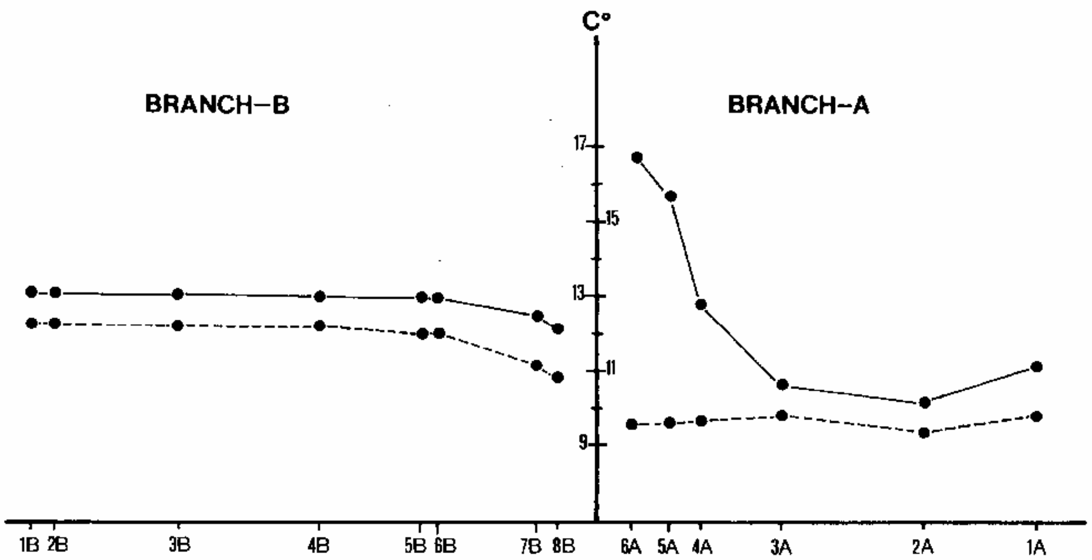

FIG. 3. Temperatures in the cave at soil level and at 50 cm above soil level. The measurements were taken in every station during the second sampling. The relative distances among stations are correlated with that of the cave.

although sometimes one feels a gentle current of air due to connections with the outside via a network of cracks, which behave like a second tiny entrance.

Outside the entrances to the cave the relative humidity is very low, going down to 25% in summer (Ceballos and Ortuño 1976). This is reflected in branch A, where the dry air penetrates from the exterior. However, in branch B the humidity sometimes reaches 100%, resulting in slight dripping from the roof and even the formation of small pools of water.

When there is a thaw, and the snow that covers the principal entrance (E1) melts, the flow of water probably increases and forms temporary subterranean streams along the floors of the tubes, and pools in the lowest parts. Thus we have noticed that in places where the floor of the tube becomes level, there are accumulations of sediment. In some zones, such as the end of branch B, where the floor is completely level for about 10 m before becoming obstructed, there is a large deposit of mud and on the walls there is a band of sediment, about 20 cm high, which includes encrusted animal remains.

Methods

We used pitfall traps, with a solid bait of 2 g of liver soaked in fungicide (Novapim) and a liquid bait of Turquin mixture (Turquin 1973). At the time of setting each trap and also when it was collected we made a visual search around it in a circular area of radius 1·5 m. The traps were in place for 20 days.

We took two samples in the whole cave on 8 December 1982 and 1 March 1983, and in addition made several visits to collect climatological, geological and biological data. In all, we collected at 14 stations in places indicated on the map (Fig. 2), although at four of these (1A, 2A, 3A and 6A) no animals were captured. The characteristics of the cave at each trapping station are shown in Table 1.

In the mathematical treatment applied to the results, we used four types of indices:

Ic—Index of constancy. This expresses the percentage of stations at which a particular species occurred.

Ia—Index of abundance. This is the percentage of all the individuals in the cave that are of a given species. We used the following categories of abundance: very abundant, $Ia > 50\%$; abundant, $50\% > Ia > 25\%$; frequent, $25\% > Ia > 9\%$; rare, $9\% > Ia > 2\%$; very rare, $2\% > Ia$.

H—Index of diversity. We applied the calculation of Shannon–Weaber which takes into account the number of species and the number of individuals of each species.

$$H = -\sum p_i \log p_i$$

where p_i is the probability of finding a particular species in a given sample. There have been many analyses of the validity of this index and there is a full range of

Table 1. Characteristics of the trapping stations.

	Branch A		Branch B	
Substrate	Penumbra	Dark	Penumbra	Dark
Soil	1	2, 4, 6	—	1, 2, 5, 6
Solid rock	—	3, 5	—	3
Rubble	—	—	7, 8	4

opinion in favour (Gibert, Mathieu and Reygrobellet 1975, Bellés 1978, Turquin and Bouvet 1981, Martín 1982) and against (Culver and Poulson 1970).

—We also grouped the different stations using Kulczynski's index of similarity and from the resulting matrix we obtained the corresponding dendrogram using the Lance and Williams' algorithm (in Daget 1976):

$$I_k=\frac{1}{2}\left(\frac{K}{A}+\frac{Y}{A}\right)$$

where K is the total number of individuals of all species from one station, Y is the total from another station and A is the addition of the minimum values of individuals of each species considering the two stations.

Results

Vegetation

We analysed the flora at the jameo entrance to the cave, specifically in the zone where branch B starts; being the largest of the entrances it is the most suitable for a study of this kind.

In the jameo we found the phanerogams *Nepeta teydea* Webb & Berth and *Scrophularia glabrata* Ait. and, in holes in the walls where a little earth has accumulated, four cryptogams, comprising the bryophytes *Brachytecium* sp. and *Pottia* sp. and two species of lichens of the genus *Lepraria*. *Nepeta teydea* was found only up to 2 or 3 m into the cave, in contrast to *Scrophularia glabrata* which, although less abundant, was found up to about 6 or 7 m from the entrance. The *Scrophularia* found in the interior have a peculiar morphology, showing, apart from the typical phototrophic curvature, some very enlarged leaves which are distinct from those of individuals on the surface.

Near the entrance there are many loose fallen rocks, but at about 7 m further in there are some undisturbed places free of these, and here we found a moss of the genus *Fissidens* and a liverwort of the genus *Clevea*.

Different substrates to be considered in the cave are the walls and the roof. The right-hand wall at the entrance, where there is little light, is without vegetation except for a few green algae in isolated patches. The situation of the roof is similar, at least in its first darkest part. However, in the better-illuminated part (projecting points, etc.) there are two species of moss: *Zygodon* sp. and *Platydyctia* sp. On the left wall there are several species of lichen of the genus *Lepraria*, making the whole wall appear slightly green. The wall is very irregular and the lichens grow on those parts facing the light, so that when the wall is viewed from the other side it appears to have no vegetation.

Finally, in the deeper parts of the entrance, there are green algae which form very well defined circular marks, a very abundant liverwort *Plagiochasma* sp. and the moss mentioned previously (*Fissidens* sp.).

Fauna

In total we collected 27 species of invertebrates and three vertebrates, as shown in Table 2. Comments on the more interesting species are given below.

Chthonius sp. is a species whose adaptation to the cave environment is not known; possibly it should be treated as a troglobite.

Dysdera sp. is a new and very rare species which up to now has been found only in this cave. The other four troglobitic species of this genus which we have collected in other caves of the island also have distributions restricted to single caves.

Table 2. List of species collected in the cave. The species marked with an asterisk were not found at the stations in samples 1 and 2, but were obtained during general collecting.

Pseudoscorpiones			
F. Chthoniidae			
Chthonius sp.	?	Zoophagous	VR
Araneae			
F. Oecobiidae			
Oecobius sp.	Troglophile	Zoophagous	VR
F. Dysderidae			
Dysdera sp.	Troglobite	Zoophagous	VR
F. Pholcidae			
Pholcus sp.	Troglophile	Zoophagous	VR
F. Linyphiidae			
Lepthyphantes sp.	Troglophile	Zoophagous	VR
Isopoda			
F. Armadillidae			
Venezillo tenerifensis Dalens	Troglobite	Rhizosaprophagous	R
Diplopoda			
F. Julidae			
Nesopachyiulus sp.	?	Rhizophagous	R
Chilopoda			
F. Lithobiidae			
Lithobius speleovulcanus Serra*	Troglobite	Zoophagous	
Lithobius crassipes Koch*	Troglophile	Zoophagous	
Collembola			
F. Entomobryidae			
Entomobrya multifasciata (Tullberg)	Acc. trogloxene		A
Pseudosinella octopunctata Borner*	Acc. trogloxene		
Orthoptera			
F. Gryllidae			
Gryllomorpha canariensis Chop.	Acc. trogloxene		A
Dyctioptera			
F. Blatellidae			
Loboptera sp.	Troglobite	Omnivorous	R
Psocoptera			
gen. sp. indet.	Acc. trogloxene		A
Homoptera			
gen. sp. indet.	?	Rhizophagous	R
Coleoptera			
F. Carabidae			
Eutrichopus martini Machado	Troglobite	Zoophagous	F
Wolltinerfia tenerifae (Machado)*	Troglobite	Zoophagous	VR
Platyderus alticola Woll.	Reg. trogloxene	Zoophagous	R
gen. sp. indet.*	Troglobite	Zoophagous	VR
F. Staphylinidae			
Apteranopsis canariensis Oromí and Martín	Troglobite	Zoophagous	F
Domene sp.*	Troglobite	Zoophagous	VR

F. Cucujidae			
Laemophloeus granulatus Woll.	Acc. trogloxene	Zoophagous	R
F. Tenebrionidae			
Pimelia radula ascendens Woll.	Acc. trogloxene		VR
Lepidoptera			
F. Noctuidae			
Pseudocopicucullia syrtana hesperidum Roths.*	Acc. trogloxene		
Euxoa beatissima Rbl.*	Acc. trogloxene		
F. Alucitidae			
Alucita sp.	Reg. trogloxene	?	R
Reptiles			
F. Lacertidae			
Gallotia galloti Dum. & Bibr.*	Acc. trogloxene		
Mammalia			
F. Muridae			
Rattus rattus L.*	Reg. trogloxene		
F. Leporidae			
Oryctolagus cuniculus (L.)*	Acc. trogloxene		

A, Abundant; F, frequent; R, rare; VR, very rare.

Lepthyphantes sp. is a troglophile but belongs to a genus with troglobitic representatives in other caves on the island.

Venezillo tenerifensis belongs to a genus whose species are mainly American (Dalens 1984). In the first sample they were very rare while in the second sample they were much more abundant.

Lithobius speleovulcanus is eyeless and unpigmented, and has also been collected in Cueva del Viento, at 550 m altitude near Icod.

Loboptera sp, is a new species which is completely eyeless; this species may be the most widely distributed in volcanic tubes in Tenerife, occurring in all the caves in parts of the island with recent volcanic rocks. In more ancient rocks in the extreme north of Tenerife (Anaga region) we found another species, also a troglobite, but with eyes in a variety of stages of regression. In addition, this genus is represented in the Canaries by one troglophile species in the caves of the island of Hierro and by three species on the surface, one of which is endemic to Macaronesia.

Eutrichopus martini is an eyeless troglobite which, like *Lithobius speleovulcanus* and *Loboptera* sp., has also been collected in Cueva del Viento. The genus has two other species in Tenerife—*E. gonzalezi* Mateu and *E. fernandezi* Mateu—which live above ground in the humus of the relict laurel forest.

Wolltinerfia tenerifae belongs to a monotypic genus. We did not find it alive but found remains which were easily identifiable by the elytra and abdomen. Similarly, in the laurel forest of Los Silos in a region lacking caves, we found some individuals approximately 1 m below the surface. It also occurs, but is rare, in Cueva del Viento.

Apteranopsis canariensis may be the most interesting troglobite that lives in the cave. It is microphthalmic and has appendages longer than any other known *Apteranopsis*. Its extreme specialization for subterranean life suggests that it is a perfect troglobite. There are representatives of this genus in Tunisia and Algeria, but not in Morocco, where it appears to be replaced by the closely related genus *Apteranillus* (Oromí and Martín 1984). In Tenerife we have also found this species in Cueva del Bucio (Orotava Valley) in the north of the island.

Domene sp., a previously unknown species, belongs to a large genus in which there are only three other troglobitic species in Morocco. In Tenerife we have collected another species in Cueva de Felipe Reventón, making a total of five known troglobites

Table 3. Species and individuals of each species collected in each station during sample 1.

	Stations												
	Branch A		Branch B										
	4A	5A	8B	7B	6B	5B	4B	3B	2B	1B	*T*	*Ic*	*Ia*
Lepthyphantes sp.	—	—	—	—	—	—	—	—	—	1	1	10	1
Pholcus sp.	—	—	1	—	—	—	—	—	—	—	1	10	1
Dysdera sp.	—	—	—	—	—	—	—	—	—	1	1	10	1
Venezillo tenerifensis	—	—	—	—	—	1	—	—	—	—	1	10	1
Nesopachyiulus sp.	—	—	—	—	1	—	1	—	—	1	3	30	3·2
Entomobrya multifasciata	1	—	6	6	—	—	—	—	—	—	13	30	14·1
Loboptera sp.	—	—	—	—	1	1	2	2	2	2	10	60	10·8
Psocoptera indet.	—	—	37	—	—	—	—	—	—	—	37	10	40·2
Eutrichopus martini	—	—	—	—	—	1	—	—	1	2	4	30	4·3
Platyderus alticola	—	—	3	2	1	—	—	—	—	—	6	30	6·5
Apteranopsis canariensis	—	—	—	—	—	—	1	—	—	2	3	20	3·2
Alucita sp.	1	2	—	3	—	—	—	—	—	—	5	40	6·5
Calliphora vicina	—	—	—	—	—	1	1	3	1	—	6	40	6·5

T, Number of individuals; *Ic*, index of constancy; *Ia*, index of abundance.

Table 4. Species and individuals of each species collected in each station during sample 2.

	Stations												
	Branch A		Branch B										
	4A	5A	8B	7B	6B	5B	4B	3B	2B	1B	*T*	*Ia*	*Ia*
Chthonius sp.	—	—	—	—	—	—	—	—	1	—	1	10	1·8
Oecobius sp.	—	—	—	—	—	—	1	—	—	—	1	10	1·8
Venezillo tenerifensis	—	—	—	—	—	—	—	—	1	2	3	20	5·4
Nesopachyiulus sp.	—	—	—	—	—	—	—	—	—	1	1	10	1·8
Entomobrya multifasciata	—	—	21	—	—	—	—	—	—	—	21	10	38·1
Loboptera sp.	—	—	—	—	—	—	—	—	—	1	1	10	1·8
Psocoptera indet	2	2	—	1	—	—	—	—	—	—	5	30	9
Eutrichopus martini	—	—	—	—	—	—	2	5		1	8	30	14·5
Apteranopsis canariensis	—	—	—	—	—	—	2	3	—	1	6	30	10·9
Laemophloeus granulatus	—	—	1	1	—	—	—	—	—	—	2	20	3·6
Pimelia radula ascendens	1	—	—	—	—	—	—	—	—	—	1	10	1·8
Homoptera indet.	—	—	1	—	—	—	2	—	—	—	3	20	5·4
Gryllomorpha canariensis	—	—	—	—	—	—	1	—	—	—	1	10	1·8
Calliphora vicina	—	1	—	—	—	—	—	—	—	1	2	20	3·6

T, Number of individuals; *Ic* index of constancy; *Ia*, index of abundance.

in the genus. This is the only troglobite found in branch A, where there is considerable environmental instability. However, it was collected at the end of the gallery, beyond the three entrances, where the environment is more stable because the gallery is blind.

In addition, we detected the presence of another troglobitic coleoptera, a dead specimen of carabid with its appendages missing. It is probably a new species of the subfamily *Trechinae*, but this cannot be confirmed until a complete specimen is found.

Analysis of the fauna

It can be seen that the categories 'very rare' and 'rare' predominate, and this gives an idea of the low density of the fauna in this habitat. The most abundant species are *Collembola* and *Psocoptera* which live around the entrance and can be considered accidental trogloxenes. However, the abundance of each species shows considerable variation from one sample to the other.

The diversity, which was not calculated for each station, but for the cave as a whole, turned out to be very low in both samples (0·8 in sample 1 and 0·9 in sample 2). Similarly, in other lava tubes in Tenerife where we have calculated diversity (Martín 1984) this has always been lower than 1.

On the basis of the catch at each station we have calculated the similarity between it and all the other stations in each sample. In the resulting dendrogram for sample 1 (fig. 4), two groups of stations are differentiated: one composed of the six deep in branch B and the other of those near the entrance and those in branch A. In sample 2 (fig. 4), slight differences can be observed, which may be due to the dynamics of the cave community or to sampling error. Although the two main groups are maintained, stations 5 and 6 of branch B lie outside them.

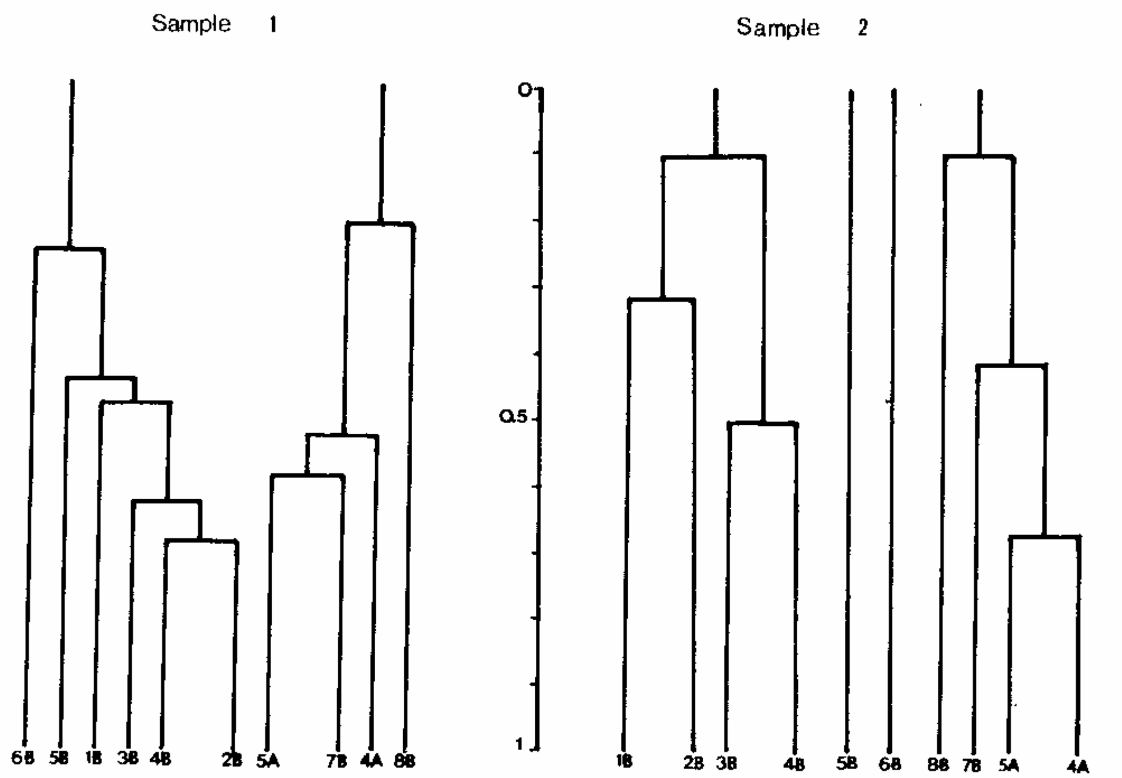

FIG. 4. Dendrogram of similarities among the stations in the cave, according to the results of the first and the second samples. 4A and 5A, Stations in branch A; 1B...8B, stations in branch B.

The first group of stations (in the deepest part of the branch B) are characterized by a set of species almost all well adapted for subterranean life, consisting of *Chthonius* sp., *Lepthyphantes* sp., *Dysdera* sp., *Oecobius* sp., *Loboptera* sp., *Venezillo tenerifensis*, *Nesopachyiulus* sp., *Eutrichopus martini*, *Apteranopsis canariensis* and *Calliphora vicina*. We must include in this set some species captured outside of samples 1 and 2—*Wolltinerfia tenerifae* and *Lithobius speleovulcanus*. Typical of the second group of stations is a set of species less adapted to subterranean life: *Pholcus* sp., *Alucita* sp., *Platyderus alticola* and *Calliphora vicina* as well.

Discussion

Cueva de los Roques presents, from a biologist's point of view, certain advantages over other lava tubes in Tenerife. It is little visited except by people aware of the need to conserve it, and it is at an altitude of 2200 m in a climatic and biological situation distinct from the other cave systems. These characteristics result in differences from other caves in some respects and similarities in others.

The distribution of the fauna of the cave is not uniform and obviously depends on the conditions of light, temperature, humidity and substrate. The troglobitic species inhabit the deepest parts of the cave where it is completely dark, the temperature is relatively constant and the humidity close to saturation. These conditions, together with the scarcity of food, result in a very specialized habitat in which troglobites, with their special adaptations, are competitively superior to the troglophiles and trogloxenes which are thus confined to the zones closer to the entrance.

The type of substrate is also relevant, as where sediments are abundant the energy reserve for the animals is relatively great, as we demonstrated by the presence of seeds of *Echium wildpreti* Pears ex Hook.fil. and *Argyranthemum teneriffae* Humphr., along with various fungi; Howarth (1981) also found several fungi in similar conditions in Hawaiian lava tubes, as well as abundant spores. Moreover, considerable quantities of organic particles occur in the sediments; these enter from the exterior via cracks and are carried inwards by percolating water. On the other hand, where the substrate is solid rock, it is completely sterile and crossed by numerous shrinkage cracks formed during the cooling of the lava; it is these spaces that are often penetrated by roots, but in this cave are very scarce due to the poverty of the surface vegetation.

The differentiation of the two groups of stations by their fauna is related to their microclimatic conditions. The first group, in the deepest part of branch B, presents ideal conditions for the establishment of a community of troglobites, with a stable temperature around 13°C, relative humidity close to 100%, complete darkness and absence of air currents of sufficient strength to have any drying effect. Naturally the species that colonize this zone show a high level of adaptation to subterranean life; it is here that we found all the troglobites of the cave, together with a few troglophiles (e.g., *Dolichoiulus* sp.) and one regular trogloxene (*Calliphora vicina*) which is commonly found throughout the interior of the lava tube.

The second group of stations includes all those in branch A and also those near the entrance of branch B; they are characterized by a fauna of low abundance and low diversity, which is composed of trogloxenes. The explanation for this lies in the particular microclimatic conditions of these zones, with more varied temperature and much lower relative humidity than in the deep parts of branch B. These conditions in the parts close to the entrances—both in branch A and branch B—are due to the 'winter effect', a phenomenon well studied in karst caves (Barr 1968) as well as in lava tubes (Howarth 1980, 1982). Due to the abrupt diurnal changes in temperature above ground, the night temperature outside the cave is much lower than that within it and moist air diffuses outwards; during the day the exterior temperature is much higher, but for most of the year the humidity is lower than that in the cave, and for this reason the moist air still diffuses outwards.

In branch A, moreover, the presence of various entrances permits the free circulation of currents of air throughout its length, these being stronger when the temperature difference between the interior and exterior is greater. Both phenomena are thus responsible for the high rate of evaporation at the second group of stations, with the result that troglobites cannot live there.

The considerable faunal elements in common with the cave systems of Icod (situated between 1500 and 2000 m lower) are somewhat surprising, especially since animals like *Eutrichopus martini* and *Wolltinerfia tenerifae* are from genera closely related to the complex *Paraeutrichopus/Pseudoplatyderus/Gomerina*/etc., typical of moist wooded habitats at relatively low altitude (Machado 1984). We must bear in mind, however, that the subterranean environment (sensu lato not exclusively in caves) present physical conditions which are very stable and similar to those at lower levels, so that the differences in temperature and humidity between Cueva de los Roques and the lower caves are much less than the differences between the corresponding surface habitats.

Similarly, the cockroach *Loboptera* sp. occurs in various caves both at sea level (in the north and south of Tenerife) and in Cueva de los Roques. The staphylinid *Apteranopsis canariensis* also occurs in two widely separated caves. It seems probable that migration from one cave to another cannot occur on the surface, with conditions totally unsuitable for these arthropods, but presumably occurs underground, by means of the innumerable cracks which vary in size but are normally smaller than a lava tube. This is one more demonstration that the subterranean environment consists largely of networks of cracks connecting the few cave systems where we can gain access.

Several studies in recent years support this hypothesis. In karst regions Juberthie, Delay and Bouillon (1980) discovered that the level above the soil horizon C was occupied by troglobites, thus considerably enlarging their habitat. In the Canaries, we have caught at this level examples of *Loboptera* sp. and *Wolltinerfia tenerifae*. However, it is not at this level that the troglobites of Cueva de los Roques have dispersed, since this cave is in a region of recent lava flows where no soil has formed. Dispersal must have occurred at deeper levels, probably in the region which Howarth (1983) calls the mesocavernose—and perhaps also via the macrocavernose—where the conditions of temperature, humidity and light are like those of the deep part of branch B, or even more stable. Neverthless, there are some species (Table 5) exclusively found in Cueva de los Roques. It is noteworthy than the level of adaptation to the cave environment is particularly high in Cueva de los Roques; there are many more species of troglobites (Table 5) than of troglophiles, a phenomenon not seen in the other caves that we have studied in the Canaries.

As can be deduced from fig. 5, secondary consumers are more abundant than primary consumers, as is also the case in lava tubes in Hawaii (Howarth 1981) and in other caves studied in the Canaries (Martín, Oromí and Barquín 1985), so long as the detritivores are ignored. This result is of course due to one of the principal characteristics of subterranean ecosystems—the primary production is not *in situ* (Juberthie 1983) and the intermediate links in the trophic chain consist of detritivores, which can act as both primary and secondary consumers. Nevertheless, in Cueva de los Roques the detritivores are not abundant, probably owing to the scarcity of

Table 5. Adaptations to cave life including all the species of invertebrates known from Cueva de los Roques.

Adaptation	Branch A	Branch B	Whole cave	%	Exclusive†
Troglobites	1	8	9	33·3	3
Troglophiles	—	4	4	14·8	—
Regular trogloxenes	2	3	4	14·8	—
Accidental trogloxenes	3	7	8	29·6	—
Unknown adaptation	—	3	3	7·4	—
Total	6	25	27	100	3

† Species only known from this cave.

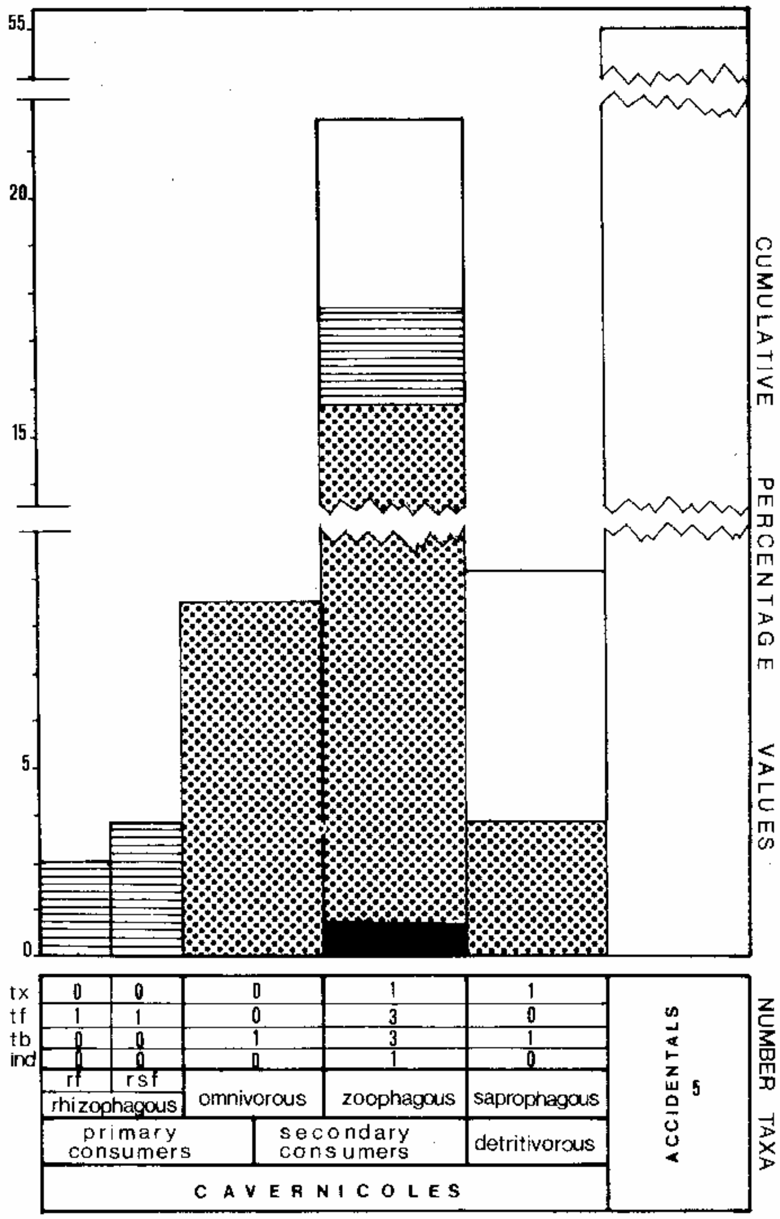

FIG. 5. Life-form spectrum of the invertebrate community in Cueva de los Roques. Only the species and individuals collected in samples 1 and 2 are included; those with unknown diet are also excluded. □, trogloxenes (tx); ⊟, troglophiles (tf); □, troglobites (tb); ■, undetermined (ind); rf, rhizophagous; rsf, rhizosaprophagous.

decomposing autochthonous vegetable matter (roots); on the other hand accidentals are abundant, especially in terms of numbers of individuals. This is partly due to many species using the cave as a refuge from the sharp changes in the local climate which occur above ground between day and night. In addition, the previously described phenomenon of sporadic increase in water flow due to rain facilitates the ingress of animals, alive and dead, together with other types of organic material of external origin. Thus it is clear that the accidentals represent an important trophic contribution to the cave ecosystem, but in absolute terms the energy flow is not of great magnitude. This explains the low diversity observed, and we can deduce that the ecosystem is particularly fragile and depends to a great extent on the sporadic input of organic material from outside.

In conclusion, the study of Cueva de los Roques has shown that its fauna is of great interest and demonstrates the contrast that can exist between two branches of a single cave, in spite of their closeness and the connections between them. Branch A remains practically devoid of life because of its openings to the exterior, with the exception of its deepest part; this is a blind gallery where the physical environment is more stable, and rather similar to that of branch B, and hence permits the occurrence of the occasional troglobites in its fauna.

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