Mémoires de Biospéologie, Tome XVII, 1990, p. 97-105.

A PRELIMINARY REPORT ON THE CAVERNICOLOUS FAUNA OF THE AZORES

by

P. OROMI[1], J. L. MARTIN[1], N. P. ASHMOLE[2] and M. J. ASHMOLE[2]

[1] Depto. de Biología Animal
Universidad de La Laguna
Canary Islands

[2] Dept. of Zoology
University of Edinburgh
Scotland

I - INTRODUCTION

It has been known for some time that caves in volcanic terrain have a cavernicolous fauna ; during the last 15 years this has been demonstrated in several oceanic archipelagos, some of them very distant from continental land masses. The Hawaiian archipelago was one of the first places where such a fauna was studied (HOWARTH, 1972, 1973), and it has proved to be particularly rich in troglobitic species belonging to diverse taxonomic groups (HOWARTH, 1981, 1987 ; SIMON et al., 1984). Interesting results have also been obtained in the Galápagos (PECK & KUKALOVA-PECK, 1986 a, 1986 b ; PECK & SHEAR, 1987 a, 1987 b), Samoa (HOCH & ASCHE, 1988) and various other volcanic archipelagos in the Pacific. In the Atlantic, however, studies have been fewer. Until now, the Canary Islands have been the only Atlantic volcanic Islands where such a hypogean fauna was known ; this fauna has been demonstrated to be particularly rich and specialized (HERNANDEZ et al., 1986 ; MARTIN et al., in press).

In their geological history and paleoclimatology these oceanic archipelagos are not closely associated with the nearest continental land masses, and the process of biological colonization has depended on a variety of factors. These include their age, the distance from other land, and the winds and oceanic currents that have been dominant for long periods of time. The result has been a generally low diversity of animals, although in some cases the poverty of original stocks has been counteracted by adaptive radiation of some genera in the island environment. It seems impossible for animals highly adapted to hypogean life to colonize oceanic islands. Therefore animals with these characteristics must have evolved on the islands, in some cases from groups not normally found in the subterranean environment (BRINDLE, 1980 ; GAGNÉ & HOWARTH, 1975 ; ESPAÑOL & RIBES, 1983 ; MARTIN & OROMI, 1987, 1988 ; MARTIN & IZQUIERDO, 1988).

In the Canary Islands over 50 species of troglobites have been found in the hypogean environment, either in caves or in the MSS (mesocavernous shallow stratum, or milieu souterrain superficiel : JUBERTHIE, 1983). Up to now only 4 of the 7 islands have been studied, and since the rate of discovery of new species has not decreased in the last two years it seems reasonable to expect that, when investigations extend to the rest of the archipelago, the number of known troglobites will be nearer 100. Many of these troglobites are directly related to epigean endemic species, while others have no close relatives extant and exhibit relict characteristics (MARTIN et al., in press). Although there are some cases of radiation within genera with hypogean species such as *Loboptera* (MARTIN et al., 1986) and *Licinopsis* (OROMI et al., 1989), in general the cavernicolous fauna of the Canaries is taxonomically very diverse, with the 50 or so troglobitic species belonging to about 30 different genera. This diversity can be easily explained, since although the archipelago is oceanic, the distance between the coast of Africa and the nearest island is only 100 km. Although winds from Africa are not dominant, they are fairly frequent, and doubtless transport many animals to the islands.

Furthermore the established dates indicate ages of up to 20 M.A. for subaerial rocks in some of the Canary Islands (CARRACEDO, 1984 ; CANTAGREL, 1985) and it is reckoned that the archipelago has been in existence for a longer time. However, the more westerly islands are relatively young, with La Palma apparently having an age of about 3 M.A. and El Hierro only 1 M.A. (CARRACEDO, 1984).

The Azores are in the same general part of the Atlantic as the Canaries, and - together with Madeira - have closely related flora and fauna. These archipelagos (plus the Cape Verde Islands) are often considered to form a biogeographic unit called Macaronesia. However, the situation of the Azores is very distinct, since they are nearly in the centre of the Atlantic, between 1500 and 2100 km to the west of the Iberian Peninsula and more than 2000 km from the nearest part of North America (Newfoundland). In fact the two western islands, Flores and Corvo, are west of the mid-atlantic ridge. Furthermore the winds and ocean currents are predominantly from the west, and the influence of the European climate is minimal. Finally, the rocks so far dated indicate that the islands of Santa Maria and Sao Miguel, forming the eastern group, have (minimum) ages of only 5.5 and 4 M.A. respectively, while the central and western groups are less than 1 M.A. (FERAUD et al., 1980). All these factors result in the fauna being considerably poorer than those of Madeira and the Canaries. Using the Coleoptera as an example, several genera such as *Calathus*, *Tarphius* and *Laparocerus*, which have a large number of species in the latter two archipelagos (WOLLASTON, 1865), have little representation in the Azores (SERRANO, 1982 ; ISRAELSON, 1984 ; GILLERFORS, 1986).

Caves of volcanic origin are abundant in the Azores (HALLIDAY, 1981 ; ANON., 1988 ; OROMI et al., in press), and some have been studied from the point of view of geomorphology (FORJAZ, 1963 ; MOTTET, 1972, 1974 ; MONTSERRAT & ROMERO, 1983). Although there are groups of local speleologists - Os Montanheiros in Terceira and Os Amigos da Terra in Sao Miguel - who know a large number of the caves, and several scientists have been consulted by them, there has never been a biospeological investigation of this archipelago. We therefore decided to make such a study, to confirm the existence of cave-dwelling animals and to see to what extent the adverse biogeographic factors (in comparison with the Canaries) have limited the development of a cavernicolous fauna. The expedition, in July-August 1987, also included a study of the surface fauna of recent volcanic terrain, which in the Canaries shows interesting relationships with the subterranean fauna (MARTIN et al., 1987 ; OROMI et al., in prep.).

II - METHODS

Work was restricted to four of the central group of islands-Terceira, Sao Jorge, Pico and Faial. Most of the caves were known previously, and the newly discovered ones have now been described (OROMI et al., in press). Inevitably the shortage of time limited the number of caves that we could study, and in most cases we chose caves that were in or close to recent lava flows, since comparison of the fauna of these two habitats was an essential part of our study. We carried out systematic trapping in the following lava tubes : Gruta dos Balcoes, Gruta do Coelho and Gruta das Agulhas in Terceira ; Furna do Soldao, Furna da Agostina and Furna dos Montanheiros in Pico ; and Gruta da Beira in Sao Jorge. We also visited the volcanic pits of Algar do Carvao (Terceira), Furna das Bocas do Fogo (Sao Jorge) and Furna Ruim (Faial), but we could not fully explore them due to shortage of time (and of rope).

We made our collections by both trapping and searching. Eight pairs of traps were placed deep in each cave and eight pairs in the cave threshold. Visual searching was for three hours in the deep cave zone and three hours in threshold. Within the threshold one quarter of the effort (2 pairs of traps and 45 minutes searching) was in the "entrance" (where there were some green plants) and three quarters (6 pairs of traps and 135 mins searching) was in the true twilight zone. Each pair of traps comprised : a) one pitfall (Barber trap) consisting of a polyethylene jar with internal diameter 47 mm, containing modified Turquin's liquid (ASHMOLE et al., in press) ; and b) one 330 ml pvc bottle with the same liquid, but also with a small piece of "Danish Blue" cheese, supported above the level of the liquid in order to keep it dry : the bottle was set at an angle of 45 degrees. All the traps were left in place for four days. Visual searching was carried out in the vicinity of the traps, and was split between the day when the traps were put out and the day when they were collected ; at least two members of the team participated in the search at each site.

III - RESULTS

Altogether we found more than 60 species of invertebrates in the lava tubes that we studied. Eleven of these, all of them probably new species, can be considered to be cavernicolous, because of their morphological adaptations or because they are new taxa found only in caves ; one more species has two distinct forms, one occuring in caves and the other on the surface. The aim of this paper is to demonstrate the presence in the Azores of a fauna adapted to the subterranean environment, and we therefore concentrate on these 12 species.

	Close Azorean species	Close Macaronesian species	Hypogean adaptations	Islands
Pseudoblothrus vulcanus	no	no	few	T
Pseudoblothrus oromii	no	no	few	J
Theridion pico	yes	yes	yes	P
Talitridae indet.	no	no	few	T
Trichoniscidae indet.	no	no	few	J
Lithobius obscurus	yes	yes	few	TP
Onychiurus sp.	yes	yes	few	TP
Pseudosinella ashmoleorum	yes	yes	yes	TP
Pseudosinella azorica	yes	yes	no	TP
Cixius sp.	yes	yes	yes	P
Trechus terceiranus	yes	yes	yes	T
Trechus picoensis	yes	yes	yes	P

Table 1 - Azorean arthropods collected exclusively in caves. T : Terceira ; J : Sao Jorge ; P : Pico.

PSEUDOSCORPIONES
Syarinidae

Pseudoblothrus vulcanus Mahnert. This species was found only in Gruta das Agulhas, Terceira. It belongs to a European genus which is exclusively cavernicolous, and the implications of this record are considered later. The only species of this family known from the Azores is *Microcreagrina hispanica* (Ellingsen), which seems not to be closely related to *Pseudoblothrus* (Mahnert, in press).

Pseudoblothrus oromii Mahnert. This species was collected only from Gruta da Beira, in Sao Jorge. As with the previous species, the record is very difficult to explain from the biogeographic point of view. Both species have adaptations to subterranean life, but less than some cavernicolous pseudoscorpions in nearby regions. MAHNERT (in press) indicates several morphological differences between *vulcanus* and *oromii*, but considers that they indicate relatively recent separation from a common ancestor.

ARANEAE
Theridiidae

Theridion pico Merrett & Ashmole. This species was found in Furna da Agostina and Furna do Soldao, both in Pico. This is a sedentary species and all the examples were collected on webs. MERRETT & ASHMOLE (1989) believe that this species has evolved from a stock closely related to *T. bellicosum* Simon, cited from Sao Miguel by DENIS (1963, 1964). *T. pico* is a true troglobite, with clear adaptations such as the elongation of the legs, pale colour and extreme reduction of the eyes.

AMPHIPODA
Talitridae

Gen. sp. indet. The Talitridae that we collected in the threshold zone of Gruta das Agulhas on Terceira have reduced eyes, and are considered to represent a new species and a new genus doubtless with terrestrial ancestors (J. STOCK, pers. comm.). Talitridae are very abundant in the Azores, occuring in nearly all habitats because of the prevailing high humidity. There were many in the lava tubes on Pico, but these belonged to two epigean species already known from the island. The

geographically closest known troglobitic talitrid is *Palmorchestia hypogaea* Stock & Martin from La Palma (Canary Islands) and none are known from the nearest continents of Europe and Africa.

ISOPODA

Trichoniscidae

Gen. sp. indet. This new species, found only in Gruta da Beira, Sao Jorge, may represent a new genus (H. SCHMALFUSS, pers. comm.). It has somewhat reduced eyes, showing adaptation to hypogean life. The family Trichoniscidae is the isopod group with the largest number of troglobitic representatives on the Iberian Peninsula (BELLES, 1987), whilst in the Canaries there is only a single troglobite (*Miktoniscus* sp.) and one troglophile (*Trichoniscus bassoti* Vandel), the latter occurring in Madeira too.

LITHOBIOMORPHA

Lithobiidae

Lithobius obscurus Meinert. This species, originally from the western Mediterranean region, has spread to many parts of the world with the aid of humans, but has not previously been found in the Azores (EASON, 1985). We recorded the species from several caves : Gruta dos Balcoes on Terceira, and Furna da Agostina and Furna do Soldao on Pico. However, we also obtained specimens on the Mistério Negro, an unvegetated dome of lava on Terceira dating from 1761, and a single damaged individual at Cabeço do Fogo, the vent of an eruption on Faial in 1672. Dr. E. H. EASON, who studied the material, found that the specimens from the Mistério Negro agreed with the Mediterranean form except for a tendency to have more antennal articles. The individuals from the caves, however, are quite distinct, exhibiting a number of adaptations to subterranean life, including elongated appendages (especially antennae) and pale colour (E. H. EASON, pers. comm.). The three species of Lithobiidae previously recorded from the Azores were considered to have been introduced by humans (EASON, 1985), but the presence of the cave-adapted form of *L. obscurus* implies that this species colonized the islands naturally. We also obtained specimens of a fifth species of *Lithobius*, an epigean form similar to *L. melanops orotavae* Latzel (EASON, 1985 and pers. comm.).

COLLEMBOLA

Onychiuridae

Onychiurus sp. Specimens collected in Gruta dos Balcoes and Gruta do Coelho on Terceira, and in Furna dos Montanheiros on Pico, apparently represent a new species (M. M. da GAMA, pers. comm.). Study of the material has not been completed, but Dr. Gama informs us that the specimens show one adaptive character to cavernicolous life. It is worth pointing out that neither the *Onychiurus* species from the Canaries nor those from continental Europe are morphologically adapted to caves (GAMA and THIBAUD, pers. comm.).

Entomobryidae

Pseudosinella ashmoleorum Gama. Specimens collected in Gruta dos Balcoes, Gruta do Coelho and Gruta das Agulhas on Terceira, and in Furna do Soldao and Furna da Agostina on Pico, represent a new cavernicolous species with one morphological character (the lack of the unpaired tooth of the unguis) that may represent an adaptation to cave life (GAMA, 1988 and pers. comm. ; CHRISTIANSEN & CULVER, 1987) ; it is closely related to the epigean *Ps. gamae* (GAMA, 1988).

Pseudosinella azorica Gama. This is a second new species, with a distribution very similar to the previous one : we found it in Gruta das Agulhas on Terceira, and in Furna do Soldao, Furna da Agostina and Furna dos Montanheiros in Pico (GAMA, 1988). However, *Ps. azorica* does not show any obvious adaptation to cave life (GAMA, 1988). The significance of the pattern of distribution shown by this species and *ashmoleorum* is considered in the discussion.

HOMOPTERA

Cixiidae

Cixius sp. We collected several nymphs of this species in the Furna do Soldao and Furna da Agostina, both on Pico. Their adaptations to subterranean life are clear, and they certainly belong to a new species (HOCH & ASCHE, pers. comm.) but they cannot be described because of the lack of adult individuals. There are several species of epigean *Cixius* on the Azores, all of them endemic

(REMANE & ASCHE, 1979). No troglobitic cixiids have been found in continental Europe, but there are several species in the Canaries, where there are also cavernicolous Meenoplidae (HOCH & ASCHE, 1988 ; REMANE & HOCH, 1988).

COLEOPTERA
Carabidae

Trechus terceiranus Machado. This new species was very common in Gruta do Coelho, and less common in Gruta dos Balcoes, both caves in the central plateau of Terceira. It has small eyes and reduced pigmentation, but is clearly related to *T. torretassoi* Jeannel from the island of Sao Miguel, the only member of this genus previously found in the archipelago (MACHADO, 1988). No epigean species of *Trechus* are recorded from Terceira, but the fauna is not yet well studied, as is shown by the recent discovery of a *Calathus* on this island (SERRANO & BORGES, 1986) and our own finding of a new epigean species of *Trechus* on Pico (see below).

Trechus picoensis Machado. We found this cavernicolous species only in the Furna dos Montanheiros, on Pico. It is larger than and quite distinct from *T. terceiranus*, but it is closely related to this species and also to *T. torretassoi* (MACHADO, 1988). The reduced pigmentation of the integument, reduction of the eyes and the long legs and bristles, all indicate good adaptation to hypogean life. Although this adaptation is not so marked as in some troglobitic carabids of Europe and the Canaries, we have to bear in mind that the species of the genus *Trechus* do not become highly modified even in the Iberian Peninsula (BELLES, 1987) or the Canaries (MACHADO, 1987). In the entrance of the same cave we found an example of an epigean species of *Trechus*, which has not yet been described because we have only a female. According to MACHADO (1988) it is very similar to *T. torretassoi*, and may well turn out to be the ancestral form of *T. picoensis*. Its presence in the cave is clearly accidental, since the entrance is, in effect, a pitfall trap.

IV - DISCUSSION

We carried out detailed biological investigations of the caves that we visited, but these seven caves were on only three islands. Thus, although the results are not sufficiently broad to reach definitive conclusions, we can offer preliminary observations on the similarities and differences of the cave fauna of the Azores and the Canaries. We are using the Canary Islands for comparison because they constitute another oceanic archipelago of volcanic origin, situated in the same biogeographic area and with lava tubes similar to those of the Azores. However, the climate and paleogeography are quite distinct.

Many of the cave species that we found in the Azores belong to genera that have representatives in the troglobitic fauna of the Canaries. This is so in the case of *Trechus terceiranus* and *T. picoensis*, in the *T. tingitanus* species group. This has two troglobitic representatives in the Canaries : *T. minioculatus* Machado from El Hierro, and a species from La Palma which is still being studied (A. MACHADO, pers. comm.). The collembolan genus *Pseudosinella* has cavernicolous species in the Canaries (GAMA, 1988), and the same is true for *Lithobius*, represented in lava tubes of the Canaries by *L. speleovulcanus* Serra and by another species not yet described.

The family Trichoniscidae (Isopoda) is represented in the hypogean environment of the two archipelagos, although by species belonging to distinct genera and with different degrees of adaptation. *Miktoniscus* sp. from the Canaries is a troglomorphic species (in the sense of BARR & HOLSINGER, 1985), while the new genus found in Sao Jorge has less pronounced adaptations to hypogean life. *Trichoniscus bassoti* has been considered to be cavernicolous (VANDEL, 1960), but its degree of adaptation to that habitat is not great when compared with *Miktoniscus* sp. or with the armadillid *Venezillo tenerifensis* Dalens, which are true troglobites of the Canaries (DALENS, 1984).

It is interesting that troglobitic Talitridae (Amphipoda) and Cixiidae (Homoptera) occur in both archipelagos, although there are no troglobitic representatives of these families in continental Europe. These are not the only cases, since there are some more families with cavernicolous species in the Canaries but not in the Western Palaearctic, such as Schizomidae, Blattellidae and Reduviidae.

On the other hand, the cavernicolous arachnids of the Azores belong to families that do not have troglobitic representatives in the fauna of the Canaries. Although spiders are well represented in the lava tubes of the Canaries (RIBERA et al., 1985 ; RIBERA & BLASCO, 1986), no troglobitic

Theridiidae have been described from there (although a juvenile that we collected in a cave on La Palma may represent a troglobitic species). Furthermore, on the Iberian Peninsula only one strictly cavernicolous species is known (BELLES, 1987) and it is not closely related to *Theridion* ; in fact the only other troglobitic species known in this genus is *T. strepitus* recently described from lava tubes in the Galápagos Islands (PECK & SHEAR, 1987 a).

The most surprising case is that of the pseudoscorpions *Pseudoblothrus vulcanus* and *P. oromii*, belonging to a European genus which is strictly cavernicolous and recorded from Switzerland, France, Italy and the Crimea (MAHNERT, in press). A number of non-Mediterranean European faunal elements present in the Azores are absent from the Canaries (SERRANO, 1982), but this appears to be the only case involving cavernicolous species whose only close relatives are cavernicolous and continental. As previously mentioned, troglobites are not likely to be able to colonize oceanic islands, so there seem to be only two possible explanations of this situation : either the cavernicolous forms are relicts whose epigean ancestors have become extinct, or the taxonomy is misleading and the genus *Pseudoblothrus* is not monophyletic (MAHNERT, in press).

Somewhat similar problems are presented by the two new species of *Pseudosinella* - especially by the more adapted *Ps. ashmoleorum* - that we found on two different islands, but only in caves. Since these islands (Terceira and Pico) are separated by deep sea (MUECKE et al., 1974) it is unlikely that they have been connected in the past, even at times of marine regression. It seems possible that the species concerned are not entirely restricted to caves, and that over-water colonization from one island to the other has occurred at some stage. Alternatively, cavernicolous populations on the two islands may be a result of parallel evolution from a common ancestral epigean stock (cf. CHRISTIANSEN & CULVER, 1968).

The degree of adaptation to cavernicolous life is, in general, less in the species that we found in the Azores than in related troglobites from the Canaries. For instance, although belonging to different families, the morphological adaptations of *Tyrannochthonius superstes* Mahnert of Tenerife are considerably greater than those of the *Pseudoblothrus* species of the Azores. The same can be said of *Lithobius speleovulcanus* and *Trechus minioculatus* of the Canaries, which are all more specialized than the vicariant species in the Azores. Perhaps the most advanced troglobite that we found in the archipelago was *Theridion pico*, with vestigial eyes (MERRETT & ASHMOLE, 1989). However, in the Canaries there are spiders even more strongly adapted to cave life, such as *Leptyphantes oromii* Rib. & Blasco, *Dysdera unguimannis* Rib., Ferr. & Blasco and several other species (RIBERA et al., 1985 ; RIBERA & BLASCO, 1986).

It should be pointed out that considerable differences in degree of adaptation are frequently encountered between troglobitic species on islands of different ages within the same archipelago (MARTIN et al., 1986 ; HOWARTH, pers. comm.). The islands of Sao Miguel and Santa Maria, the most eastern of the Azores, are much older than the central islands where we made our studies (ABDEL-MONEM et al., 1975 ; FERAUD et al., 1980). Since it appears that Sao Miguel has many volcanic caves suitable for cavernicoles (ANON., 1988 ; T. BRAGA, pers. comm.), until we have been able to study this island we cannot be sure that we have found the most advanced troglobites of the archipelago. We are hoping to rectify this soon, and not only visit Sao Miguel but also Faial and Graciosa which lack lava tubes but have deep volcanic pits.

ACKNOWLEDGEMENTS - We were enabled to carry out the field work by the support of the National Geographic Society (USA). We would also like to express our gratitude for the help that we received from the Camara Municipal da Madalena (Pico), Eng. Sr. Taveira (Sao Jorge), Prof. Avila Martins (Faial) and especially to Os Montanheiros (Angra do Heroismo, Terceira), and to L. Sánchez-Pinto, who accompanied us on the expedition. In this study, the species were studied in collaboration with M. Asche (Marburg), E. H. Eason (Moreton-in-Marsh), M. M. da Gama (Coimbra), H. Hoch (Marburg), A. Machado (La Laguna), V. Mahnert (Genève), P. Merrett (Dorset), H. Schmalfuss (Stuttgart) and J. Stock (Amsterdam) ; we are very grateful to all these people.

ABSTRACT

The Azores archipelago consists of nine oceanic islands of volcanic origin, with estimated ages ranging from less than one million to more than five million years. At least six of the islands possess caves, either in the form of lava tubes or of volcanic pits. In 1987 intensive sampling of arthropods was carried out in caves on Terceira, Pico and Sao Jorge, which form part of the central - and probably youngest - group of islands.

Apart from a number of epigean or at most troglophilous species, 12 of the species of arthropods obtained were apparently restricted to hypogean environments ; almost all of these possessed some degree of morphological adaptation to subterranean life. The species concerned belong to the orders Amphipoda, Isopoda, Pseudoscorpiones, Araneae, Lithobiomorpha, Collembola, Homoptera and Coleoptera. Some of these species have close relatives in the epigean environments of the islands, while others apparently do not. In general the cavernicolous fauna seems to be less rich than that of the Canary Islands, although we have not yet investigated three of the Azorean islands that possess caves, including one considerably older than any of those studied.

RESUME

L'archipel des Açores est formé par neuf îles d'origine volcanique, avec un âge estimé de moins d'un million jusqu'à plus de cinq millions d'années. Au moins six de ces îles ont des grottes, aussi bien des tubes de lave que des gouffres volcaniques. On a effectué en 1987 un échantillonnage intensif d'arthropodes dans les grottes de Terceira, Pico et Sao Jorge, trois îles du groupe central, probablement le plus jeune.

Outre de nombreuses espèces épigées ou tout au plus troglophiles, 12 des espèces obtenues sont apparemment limitées au milieu hypogé et présentent des adaptations à la vie souterraine plus ou moins accentuées. Ces espèces appartiennent aux Amphipoda, Isopoda, Pseudoscorpiones, Araneae, Lithobiomorpha, Collembola, Homoptera et Coleoptera. Parmi les espèces mentionnées, certaines ont des formes proches dans le milieu épigé de ces îles, tandis que d'autres n'en ont pas. En général cette faune cavernicole semble moins riche que celle des Iles Canaries, bien que l'on n'en ait pas encore collecté dans trois autres Iles des Açores, l'une d'elles considérablement plus ancienne que les autres déjà étudiées.

BIBLIOGRAPHY

ABDEL-MONEM, A. A., FERNANDEZ, L. A. and G. M. BOONE - 1975 - K-Ar ages from the eastern Azores group (Santa Maria, Sao Miguel and the Formigas Islands). **Lithos**, 8, p. 247-254.

ANONYMOUS - 1988 - Algumas grutas. **Zimbro, Bol. Amigos da Terra**, 20, p. 5-8.

ASHMOLE, N. P., ASHMOLE, M. J. and P. OROMI - in press - Arthropods of recent lava flows on Lanzarote. **Vieraea**, 18.

BARR, T. C. and J. R. HOLSINGER - 1985 - Speciation in cave faunas. **Ann. Rev. Ecol. Syst.**, 16, p. 313-337.

BELLES, X. - 1987 - *Fauna cavernícola i intersticial de la Península Ibérica i les Illes Balears.* C.S.IC. Ed. Moll., Madrid y Palma de Mallorca. 207 pp.

BRINDLE, A. - 1980 - The cavernicolous fauna of Hawaiian lava tubes. 12. A new species of blind troglobitic earwig (Dermaptera : Carcinophoridae) with a revision of the related surface-living earwigs of the Hawaiian Islands. **Pacific Insects**, 21, 4, p. 261-274.

CANTAGREL, J. M. - 1985 - Cual es la edad de las Islas Canarias ? Datos cronológicos actuales. In : Seminario sobre "*Evolución vulcanológica del Atlántico Central (Canarias, Madeira, Azores)*". Santa Cruz de Tenerife, Marzo 1985, 7 pp.

CARRACEDO, J. C. - 1984 - Etapas en la formacion de las Canarias. In : "*Geografía de Canarias. Geografía Fisica*", vol. 1, p. 40-55.

CHRISTIANSEN, K. and D. CULVER - 1968 - Geographic variation and evolution in *Pseudosinella hirsuta*. **Evolution**, 22, p. 237-255.

CHRISTIANSEN, K. and D. CULVER - 1987 - Biogeography and the distribution of cave collembola. **J. Biogeog.**, 14, p. 459-477.

DALENS, H. - 1984 - Isopodes terrestres rencontrés dans les cavités volcaniques de l'île de Tenerife. **Trav. Lab. Ecobiol. Arthrop. Edaph., Toulouse**, 5, 1, p. 12-19.

DENIS, J. - 1963 - Spiders from the Madeira and Salvage Islands. **Bol. Mus. Mun. Funchal**, 17, 61, p. 29-48.

DENIS, J. - 1964 - Spiders from the Azores and Madeira. **Bol. Mus. Mun. Funchal**, 18, 68, p. 68-102.

EASON, E. H. - 1985 - The Lithobiomorpha (Chilopoda) of the Macaronesian Islands. **Entomol. Scand.**, 15, p. 387-400.

ESPANOL, F. y J. RIBES - 1983 - Una nueva especie troglobia de Emesinae (Heteroptera, Reduviidae) de las Islas Canarias. **Speleon**, 26-27, p. 57-60.

FERAUD, G., KANEOKA, I. and C. J. ALLEGRE - 1980 - K/Ar ages and stress pattern in the Azores : geodynamic implications. **Earth Planet. Sci. Lett.**, 46, p. 275-286.

FORJAZ, V. H. - 1963 - Notas sobre a "Furna de Henrique Maciel" (Pico, Açores). **Bol. Soc. port.**

Ciências Naturais, 2 ser., 9, p. 159-165.
GAGNE, W. C. and F. G. HOWARTH - 1975 - The cavernicolous fauna of Hawaiian lava tubes. 6. Mesoveliidae or water treaders (Heteroptera). **Pacific Insects**, 16, 4, p. 399-413.
GAMA, M. M. da - 1988 - Systématique évolutive des *Pseudosinella*. XIV. Deux espèces nouvelles provenant des Açores (Ins., Collembola). **Rev. Suisse Zool.**, 95, 2, p. 607-611.
GAMA, M. M. da - 1988 - Colêmbolos das Canarias. **Act. III Congr. Ibér. Entomol.**, Granada 1987, p. 73-89.
GILLERFORS, G. - 1986 - Two new species of *Tarphius* Erichson (Col., Colydiidae) and a new species of *Mniophilosoma* Wollaston (Col., Chrysomelidae) from the Azores. **Bocagiana**, 98, p. 1-10.
HALLIDAY, W. R. - 1981 - Caves of the Açores. An initial reconnaissance. **NWRA Symp. Cave Sci. & Technol.**, Seattle.
HERNANDEZ, J. J., MARTIN, J. L. y A. L. MEDINA - 1986 - La fauna de las cuevas volcanicas en Tenerife (Islas Canarias). **Act. IX Congr. Int. Espeleol., Barcelona**, 2, p. 139-142.
HOCH, H. and M. ASCHE - 1988 - On the track of cave-adapted Fulgoroidea in lava tubes on the Canary Islands. **Tymbal Auchenor. Newsletter**, 11, p. 11-14.
HOWARTH, F. G. - 1972 - Cavernicoles in lava tubes on the island of Hawaii. **Science**, 175, p. 325-326.
HOWARTH, F. G. - 1973 - The cavernicolous fauna of Hawaiian lava tubes. I. Introduction. **Pacific Insects**, 15, 1, p. 139-151.
HOWARTH, F. G. - 1981 - Community structure and niche differentiation in Hawaiian lava tubes. In Mueller-Dombois, Bridges & Carson *"Island Ecosystems. Biological organization in selected Hawaiian communities"*. Hutchinson Ross Publ. Co., Stroudsburg., pp. 318-336.
HOWARTH, F. G. - 1987 - Evolutionary ecology of aeolian and subterranean habitats in Hawai'i. **TREE**, 2, 7, p. 220-223.
ISRAELSON, G. - 1984 - Coleoptera from the Azores. **Bol. Mus. Mun. Funchal**, 36, p. 142-161.
JUBERTHIE, C. - 1983 - Le milieu souterrain : étendue et composition. **Mém. Biospéol.**, 10, p. 17-65.
MACHADO, A. - 1987 - Nuevos Trechodinae y Trechinae de las Islas Canarias. **Fragmenta entomologica**, 19, 2, p. 323-338.
MACHADO, A. - 1988 - Two new cavernicolous *Trechus* Clairv. species from Azores (Coleoptera, Carabidae). **Bocagiana**, 119, p. 1-8.
MAHNERT, V. - in press - Deux nouvelles espèces du genre *Pseudoblothrus* Beier, 1931 (Pseudoscorpiones, Syarinidae) des Açores (Portugal). **Vieraea**, 18, 6 p.
MARTIN, J. L. y I. IZQUIERDO - 1988 - Dos nuevas formas hipogeas de *Loboptera* Brunn. W. (Blattaria, Blattellidae) de la isla de El Hierro (Islas Canarias). **Fragmenta entomologica**, 19, 2, p. 301-310.
MARTIN, J. L., IZQUIERDO, I. and P. OROMI - 1986 - The genus *Loboptera* Brunn. W. (Blattaria, Blattellidae) in the Canary Islands and its distribution in the underground compartment. **Act. IX Congr. Int. Espeleol. Barcelona**, 2, p. 142-145.
MARTIN, J. L., IZQUIERDO, I. et P. OROMI - 1989 - Sur les relations entre les troglobies et les espèces épigées des Iles Canaries. **Mém. Biospéol.**, 16, p. 25-34.
MARTIN, J. L. y P. OROMI - 1987 - Tres nuevas especies hipogeas de *Loboptera* Brunn. W. (Blattaria, Blattellidae) y consideraciones sobre el medio subterraneo en Tenerife (Islas Canarias). **Annls. Soc. Ent. Fr. (N.S.)**, 23, 3, p. 315-326.
MARTIN, J. L. y P. OROMI - 1988 - Dos nuevas especies de *Anataelia* Bol. (Dermaptera, Pygidicranidae) de cuevas y lavas recientes del Hierro y La Palma (Islas Canarias). **Mém. Biospéol.**, 15, p. 49-59.
MARTIN, J. L., OROMI, P. y I. IZQUIERDO - 1987 - El ecosistema eolico de la colada volcanica de Lomo Negro en la isla de El Hierro (Islas Canarias). **Vieraea**, 17, p. 261-270.
MERRETT, P. and N. P. ASHMOLE - 1989 - A new troglobitic *Theridion* (Araneae : Theridiidae) from the Azores. **Bull. Brit. Arach. Soc.**, 8, p. 51-54.
MONTSERRAT I NEBOT, A. y M. ROMERO I RECTORET - 1983 - Noves dades sobre el coneixement vulcanoespeleologic de l'illa de Terceira (Açores, Portugal). **Speleon**, 26-27, p. 93-104.
MOTTET, G. - 1972 - Observations géomorphologiques à l'île volcanique de Terceira (Açores). **Finisterra**, 7, 14.
MOTTET, G. - 1974 - Les tunnels dans les coulées de lave de Terceira (Açores). Note de morphologie volcanique. **Finisterra**, 9, 17.

MUECKE, G. K., ADE-HALL, J. M., AUMENTO, F., MACDONALD, A., REYNOLDS, P. H., HYNDMAN, R. D., QUINTINO, J., OPDYKE, N. and W. LOWRIE - 1974 - Deep drilling in an active geothermal area in the Azores. **Nature**, 252 (Nov. 22), p. 281-285.

OROMI, P., ASHMOLE, N. P., ASHMOLE, M. J. and J. L. MARTIN - in preparation - Faunal succession on lava flows and in caves of the Canary Islands.

OROMI, P., MEDINA, A. L. and J. L. MARTIN - 1989 - The genus *Licinopsis* Bedel (Col., Caraboidea) in the Canary Islands and its distribution in the underground compartment. **Mém. Biospéol.**, XVI, p. 35-40.

OROMI, P., MARTIN, J. L. y N. P. ASHMOLE - in press - Las cavidades volcánicas en las Islas Azores. **I Congr. Atlant. Meio Ambiente, Angra do Heroismo.**

PECK, S. B. and J. KUKALOVA-PECK - 1986 a - Preliminary summary of the subterranean fauna of the Galapagos Islands, Ecuador. Part I. Introduction and non-insect invertebrates.; **IX Congr. Int. Espeleol., Barcelona**, 2, p. 164-166.

PECK, S. B. and J. KUKALOVA-PECK - 1986 b - Preliminary summary of the subterranean fauna of the Galapagos Islands, Ecuador. Part II. The Insects, evolution and biogeography. **IX Congr. Int. Espeleol., Barcelona**, 2, p. 166-169.

PECK, S. B. and W. A. SHEAR - 1987 a - A new eyeless, stridulating *Theridion* spider from caves in the Galapagos Islands (Araneae, Theridiidae). **Can. Ent.**, 119, p. 881-885.

PECK, S. B. and W. A. SHEAR - 1987 b - A new blind *Lygromma* (Araneae, Gnaphosidae) from the Galapagos Islands. **Can. Entomol.**, 119, p. 105-108.

REMANE, R. & M. ASCHE - 1979 - Evolution und Speziation der Gattung *Cixius* Latreille, 1804 (Homoptera, Auchenorrhyncha, Fulgoromorpha, Cixiidae) auf den Azorischen Inseln. **Marburger Ent. Publ.**, 1, 2, p. 1-264.

REMANE, R. and H. HOCH - 1988 - Cave-dwelling Fulgoroidea (Homoptera : Auchenorrhyncha) from the Canary Islands. **J. Nat. Hist.**, 22, p. 403-412.

RIBERA, C. y A. BLASCO - 1986 - Araneidos cavernicolas de Canarias. I. **Vieraea**, 16, p. 41-48.

RIBERA, C., FERRANDEZ, M. A. y A. BLASCO - 1985 - Araneidos cavernícolas de Canarias. II. **Mém. Biospéol.**, 12, p. 51-66.

SERRANO, A. M. - 1982 - Contribuiçao para o conhecimento do povoamento, distribuiçao e origem dos coleopteros do arquipélago dos Açores (Insecta, Coleoptera). **Bol. Mus. Mun. Funchal**, 34, p. 67-104.

SERRANO, A. M. and P. V. BORGES - 1986 - A new *Calathus* Bonelli from the Azores (Coleoptera, Carabidae). **Bolm. Soc. port. Ent.**, 78, p. 1-6.

SIMON, C. M., GAGNE, W. C., HOWARTH, F. G. and F. J. RADOVSKY - 1984 - Hawai'i : a natural entomological laboratory. **Bull. Ent. Soc. Amer.**, 30, 3, p. 8-17.

VANDEL, A. - 1960 - Les Isopodes terrestres de l'archipel madérien. **Mém. Mus. nat. Hist. nat.**, sér. A, Zool., 22, 1, p. 1-155.

WOLLASTON, T. V. - 1865 - *Coleoptera Atlantidum.* John van Voorst, London, 526 pp., App. 140 pp.