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CAVE-DWELLING GROUND BEETLES OF THE AZORES (COL., CARABIDAE)

by

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I - INTRODUCTION

The Azorean archipelago, situated in Mid Atlantic between Portugal and North America, consists of nine volcanic islands geographically arranged in three groups distributed between 36° 55' and 39° 42' N latitude and between 25° and 31° 30' W longitude (see map in fig. 1). The south easterly group comprises São Miguel (4 Ma) and Santa María (8 Ma) with some small but interesting caves, especially the first which has a recently formed region that is still very active (ABDEL-MONEM et al., 1975 ; FERAUD et al., 1980). The central group consists of the younger islands of Faial, Pico, Graciosa, São Jorge and Terceira, all with an age of less than 1 Ma (FERAUD et al., op. cit.) ; all these central islands have lava tubes and pits, some of them very recent. The north westerly group includes Corvo and Flores, islands probably as old as São Miguel (FORJAZ, pers. comm.) but with no lava tubes because of the absence of recent volcanic activity.

As a consequence of the visit of SCHATZMAYR and Prince TORRE-TASSO to the eastern islands in 1935 the first Trechinae from the Azores was collected, this was the scarce forest-living *Trechus torretassoi* Jeannel (JEANNEL, 1937).

The ground-beetle fauna of the Azores has been the subject of several papers, notably by COLAS (1939), MÉQUIGNON (1942) and LINDROTH (1960). However, none of the publications after JEANNEL (op. cit.), including the more recent and comprehensive ones of SERRANO (1982) and ISRAELSON (1984, 1985), include more species of this subfamily.

Several collections of cave beetles have been made during biospeleological expeditions to the Azores : two directed by N. P. ASHMOLE and one of the authors (P. OROMÍ) and supported by the National Geographic Society (USA) in July-August 1987 and 1989 (the latter also with the participation of P. BORGES) (see MACHADO, 1988 ; OROMÍ et al., in press ; OROMÍ and BORGES, in press) ; two more expeditions of the speleological group Os Montanheiros to the island of Pico in May 1989 and March 1990 with the participation of one of the authors (P. BORGES) ; and a visit of one of us (P. BORGES) to S. Miguel in April 1990.

As a result, BORGES (1990) in his catalogue of the Azorean coleoptera refers four more species of *Trechus* (Trechinae) and one of *Thalassophilus* (Trechodinae). Nevertheless, the fauna of the lava tubes in some islands of the Azores remains inadequately known and it is therefore possible that more ground beetles will be found in this habitat in the near future. The lack of records from the older islands where no suitable volcanic tubes have been found (Corvo, Flores and Santa Maria), suggests the importance of investigating the mesocavernous shallow stratum (MSS or "Milieu Souterrain Superficiel" after JUBERTHIE, 1983) on these islands, in order to check whether or not hypogean ground beetles are living there.

In the present paper, the taxonomy of endemic species of *Thalassophilus* and *Trechus* from the Azores is studied, and the ecology, biogeography and possible evolution of these beetles are briefly discussed.

II - TRECHODINAE

Thalassophilus azoricus Oromí and Borges, in press.

The genus *Thalassophilus* Wollaston, 1854, includes seven species, five being endemic to the Macaronesian archipelagos : *T. whitei* Wollaston, an epigean and lucicolous species common to Madeira and the Canaries ; *T. coecus* Jeannel, an eyeless but well pigmented species found under a stone in the laurel forest (JEANNEL, 1938) on Madeira ; *Thalassophilus* n.sp., an undescribed and troglobitic species (ERBER, pers. comm.) also from Madeira ; *T. subterraneus* Machado, another troglobitic species but endemic to the island of La

Palma (Canaries) ; and *T. azoricus* Oromí and Borges, also a troglomorphic species and endemic to the island of São Miguel (Azores).

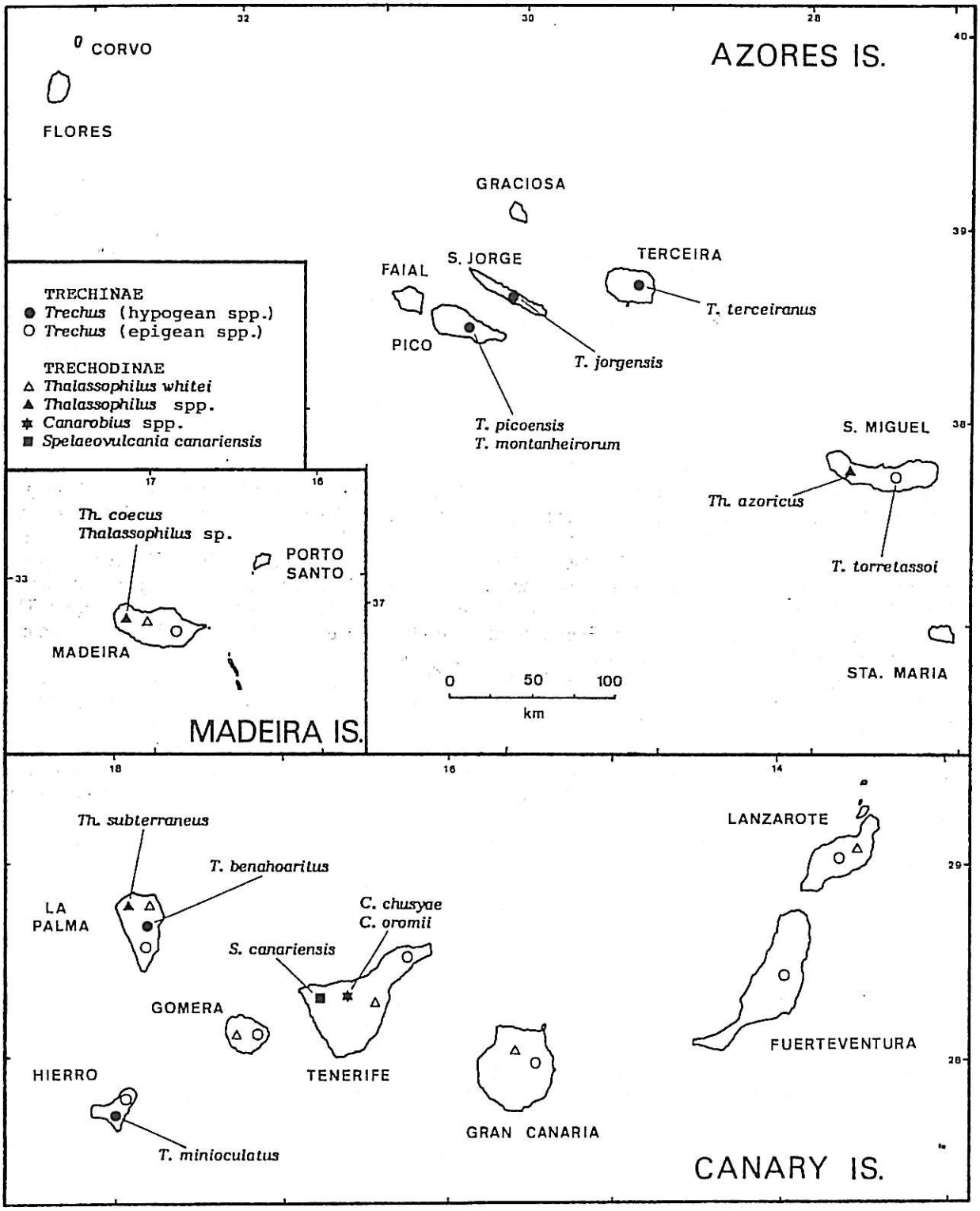

Fig. 1 - Distribution of Macaronesian Trechinae and Trechodinae belonging to genera with hypogean species in these archipelagos (the epigean *Trechus* are not specified). Black symbols : hypogean or endogean species ; open symbols : epigean species.

With the exception of *T. whitei*, all the other species have reduced or absent eyes, but only *T. azoricus* (Azores), *Thalassophilus* n.sp. (Madeira) and *T. subterraneus* (Canaries) are truely hypogean species. The Madeiran *T. coecus*, in spite of being anophthalmous (according to JEANNEL, 1938 ; but MACHADO, 1989 considers it microphthalmic) is probably an endogean species (LANEYRIE, 1979).

The single Azorean species of *Thalassophilus* is well adapted to subterranean life. It is the only eyeless ground beetle so far known from this archipelago, and is a relict and paleoendemic species. It was found in a lava tube (Água de Pau, S. Miguel) only 5 or 6 meters a.s.l. and covered by some 70 m of overburden (OROMÍ and BORGES, in press). The type material consited of fourteen specimens but two more individuals were recently collected in the same cave by the speleological group Os Montanheiros. All the specimens were collected after periods of intensive searching and not a single one fell into the pitfall traps.

III - TRECHINAE

Trechus torretassoi Jeannel, 1937

This neoendemic species (sensu LINDROTH, 1960) is closely related to certain Madeiran species around *flavomarginatus* Wollaston, belonging to the *tingitanus* group (JEANNEL, 1937). It is the only epigean *Trechus* known from the Azores, and is a scarce species restricted to the forests around Sete Cidades (JEANNEL, op. cit.) and Furnas (GILLERFORS, 1986) on the island of S. Miguel.

Trechus terceiranus Machado, 1988

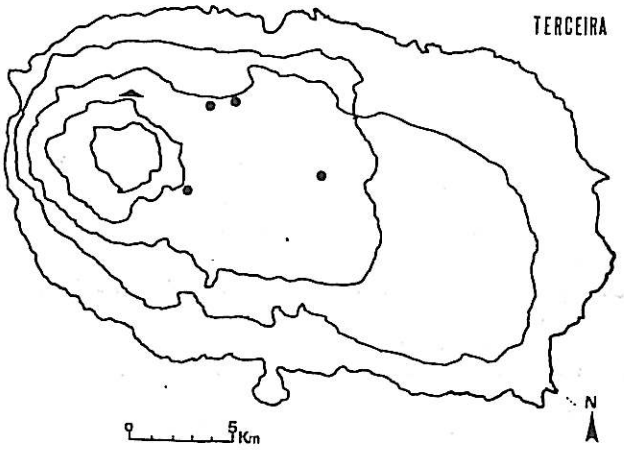

Fig. 2 - Localities where *Trechus terceiranus* have so far been collected. Dots indicate the caves and triangles the MSS stations.

This is the first cavernicolous *Trechus* collected in the Azores, being an endemic from Terceira Island. Previously known from only Gruta do Coelho and Gruta dos Balcões (OROMÍ et al., 1990) is now reported also from Algar do Carvão and Gruta do Caldeira. In 1990 the first author also collected several specimens in the MSS on Terceira, this being the first record of a troglobite from the MSS in the Azores (see map in fig; 2). The plant community at this MSS station (Pico Rachado) is the natural laurel forest.

Trechus jorgensis Oromí and Borges, in press

This species is endemic to the island of São Jorge, and is apparently rare in the cave where it was found, Algar das Bocas do Fogo, a 50 m deep volcanic pit. Only a single specimen (a female) has so far been collected.

Trechus picoensis Machado, 1988, and *Trechus montanheirorum* Oromí and Borges, in press

The most interesting aspect of the Azorean *Trechus* is the peculiar distribution of these two species, both apparently endemic to the island of Pico. The two species were collected in the lava tube Gruta dos Montanheiros and occur in sympatry at the entrance of the cave (OROMÍ and BORGES, in press). The troglobitic *T. picoensis* is the only one occuring in the darker parts of the cave and it has also been found in another cave, Gruta do Henrique Maciel, during our visit to Pico in 1989. During a pitfall survey in several epigean habitats of Pico (March 1990) no specimens of *T. montanheirorum* were found. Although we cannot affirm that *montanheirorum* is a cave-limited (i.e. troglobitic) trechine ground beetle, it seems that it is restricted to the skylight entrances of the cave, since no specimens were collected in a large series of pitfall traps set in the epigean environment around the cave, similar to those installed inside.

As OROMÍ and BORGES (in press) pointed out, some of the more evident differences between the two species are those relating to adaptation to cave life (eye reduction, depigmentation) which are more marked in *picoensis* ; some other differences such as those concerning to male genitalia, are presumably not related to degree of adaptation to hypogean life, but some of them may be significant with respect to reproductive isolation between the two species.

T. montanheirorum shows some intermediate features between a true troglobite and an epigean *Trechus*. In fact, pigmentation is not uniform, some parts being darker than others, but always darker than *picoensis* ; and the eyes are larger than those of the troglobitic *picoensis* but clearly smaller that in the epigean *torretassoi*.

These two cave-dwelling *Trechus* are almost certainly sister species, whose origin can be interpreted in two different ways (fig. 3) : a) classical allopatric speciation on the surface, followed by two separate invasions of the underground environment and eventual sympatry ; or b) radiation after an underground colonization with the divergence as a consequence of adaptation to two different habitats, and leading to parapatric speciation (sensu BUSH, 1975).

We consider the first alternative to be more plausible, the two hypogean taxa representing successive isolations from a shared surface-living ancestor (cf. KANE and BRUNNER, 1986) now probably extinct. The

that vulcanism could have played in this phenomenon should not be neglected. The two speciation processes probably occured during a breakdown of the ecological equilibrium related to volcanic events, with the destruction of the natural laurel forest and consequent potential isolation of cave and surface populations.

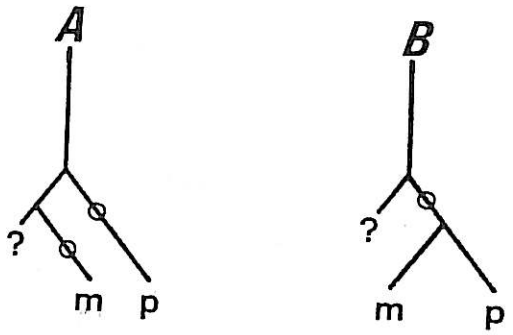

Fig. 3 - Possible ways of speciation of the two species of *Trechus* from Pico, *T. picoensis* (p) and *T. montanheirorum* (m). A : allopatric speciation on the surface and two separate invasions of the underground environment. B : parapatric speciation after a single invasion of the subsoil. Circles : colonization of the subsoil.

Lava flows are very common in Pico, a young and still active volcanic island, and they might have destroyed some small populations and isolated others in which genetic drift facilitated differentiation. In this case the allopatric speciation would have been of Type Ib of BUSH (1975), speciation by the "founder effect". A more precise model of the speciation of these two beetles could only arise from future genetic, ethological, ecophysiological, biometric and ecological studies.

IV - DISCUSSION

The hypogean *Trechus* from the Azores have retained remnants of eyes, but show marked adaptations in other characters, such as depigmentation, elongate appendages, incipinet physogastry, etc. ; but *Thalassophilus azoricus* is still more troglomorphic, with no eyes at all and less pigmented.

We could easily conclude that this difference in troglomorphy is due to the age of the islands, since *Th. azoricus* occurs in São Miguel (4 Ma) while the hypogean *Trechus* are in the youngest, central islands (1 Ma), but it is always difficult to make this kind of comparison among species of different genera. We have to point out that, in general, all but one hypogean Trechodinae in Macaronesia are eyeless, while all the hypogean *Trechus* from these archipelagos have small eyes (MACHADO, 1987 and 1989). However, the situation in the relatively young island of La Palma, Canary Is. (see fig. 1), where *Trechus benahoaritus* Machado, *Thalassophilus subterraneus* Machado are found together and both are microphthalmic (MACHADO, 1989), could be in agreement with the first idea of correlation between age and troglomorphism.

On the other hand, Pico shows a certain faunistic disharmony in comparison to the other islands : in spite of being among the youngest, it has two endemic cave-dwelling *Trechus*. This provides a clear indication that evolution in this genus was very rapid. LANEYRIE (1979) argued that the presence of small eyes in *Thalassophilus breuili* Jeannel, a cavernicolous species from Spain, while the endogean *T. coecus* from Madeira is eyeless, could be explained by accelerated evolution in the latter as a consequence of insular isolation.

Cave colonization in the Azores can not be explained by the Pleistocene-effect theory (BARR, 1985) since this Atlantic archipelago remained out of the direct influence of the last glaciations. It is believed (BRADLEY, 1989) that surface temperatures in the North Atlantic, in a zone about 40° to 50° N, were the subject of dynamic changes, more marked than in southern latitudes which were more stable (ISRAELSON, 1990) ; but probably this is far from being the reason of the underground colonization. However, massive volcanic eruptions could have been responsible for environmental changes facilitating the appearance of terrestrial troglobites. Another hypothesis is the adaptive-shift theory (HOWARTH, 1973 and 1981) first applied to the Hawaiian fauna. This theory does not invoke isolation during climatic (or volcanic ?) changes but instead proposes that the partly adapted ancestors shifted into newly developing niches (HOLSINGER, 1988).

Like many other endemic groups of very similar forms, the *Trechus* species from the Azores (belonging to the *tingitanus* group) probably derive from a common ancestor which once colonized the archipelago. The particular characters of the various species certainly evolved during a prolonged isolation.

The extreme poverty of epigean Trechinae on the Azores is an intriguing problem, and contrasts with the abundance of striking epigean species swarms in Madeira and the Canaries (see table 1). In Madeira there are 21 different epigean *Trechus* (LUNDBLAD, 1958 ; FRANZ, 1981) and in the Canaries 16, of which 9 are in Tenerife (MACHADO, 1976 ; ISRAELSON and PALM, 1979). Possible relevant factors in the Azores are :

a) unfavourable climate for many species : constant high humidity causes a general levelling of abiotic conditions, with a resulting pronounced poverty of biotopes (LINDROTH, 1960),

b) the age of the Azores is much less and they lie much farther from the mainland than the other archipelagos,

c) volcanic activity with the destruction of local faunas (LINDROTH, op. cit.),

d) the influence of human activity with the loss of natural habitats,

e) insufficient exploration, with some species still to be discovered.

In contrast, the number of hypogean Trechinae from the Azores is greater than in Madeira or the Canaries, where a high number of epigean froms occur. The reason for this could be the competition caused by the presence of a number of species of troglobitic ground beetles belonging to this and other subfamilies, at least in the Canaries (see MARTIN et al., 1989 ; MACHADO, 1989 ; OROMÍ and MEDINA, in press).

Tab. 1 - List of Macaronesian Trechinae and Trechodinae belonging to genera with hypogean species in these archipelagos. * : hypogean species. + : endogean species. AZORES. S : São Miguel ; T : Terceira ; S : São Jorge ; P : Pico. MADEIRA. M : Madeira ; P : Porto Santo. CANARIES. H : Hierro ; P : La Palma ; G : Gomera ; T : Tenerife ; C : Gran Canaria ; F : Fuerteventura ; L : Lanzarote.

	AZORES	MADEIRA	CANARIES
TRECHINAE			
Trechus torretassoi Jeannel	S		
* *T. terceiranus* Machado	T		
* *T. picoensis* Machado	P		
* *T. montanheirorum* Oromí and Borges	P		
* *T. jorgensis* Oromí and Borges	J		
T. umbricola Wollaston		M	
T. nigrocruciatus Wollaston		M	
T. laevis Wollaston		M	
T. flavomarginatus Wollaston		M	
T. signatus Wollaston		M	
T. dilutus Wollaston		M	
T. quadricollis Wollaston		M	
T. custos Wollaston		M	
T. alticola Wollaston		M	
T. minyops Wollaston		M	
T. lundbladi Jeannel		M	
T. debilis Wollaston		M	
T. wollastoni Jeannel		M	
T. obtusus Erichson		M	
T. obtusus pecoudianus Jeannel		M	
T. lindbergi Colas		M	
T. maderae Franz		M	
T. alecrinensis Franz		M	
T. laurisilvae Franz		M	
T. ribeiranus Franz		M	
T. rabacalensis Franz		M	
T. cautus Wollaston		P	
T. machadoensis Franz			P
T. flavicircumdatus Woll.			P
* *T. benahoaritus* Machado			P
* *T. minioculatus* Machado			H
T. laureticola Jeannel			G
T. gomerensis Franz			G
T. flavocinctus Jeannel			T
T. flavocinctus gomerae Jeannel			HG
T. uyttenboogaarti Jeannel			T
T. fortunatus Jeannel			T
T. flavolimbatus Wollaston			C
T. detersus Wollaston			FL
T. canoi Franz			T
T. felix Jeannel			T
T. felix tahodiensis Jeannel			T
T. felix faustus Jeannel			T
T. antonii Jeannel			T
T. tenoensis Israelson and Palm			T
TRECHODINAE			
Thalassophilus whitei Woll.		M	PGTCL
* *Th. azoricus* Oromí and Borges	S		
+ *Th. coecus* Jeannel		M	
**Thalassophilus* sp.		M	
* *Th. subterraneus* Machado			P
* *Canarobius chusyae* Machado			T
* *Canarobius oromii* Machado			T
* *Spelaeovulcania canariensis* Machado			T

All the hypogean species of *Trechus* inhabiting the Azorean caves are relicts, since there are no epigean species recorded from the islands where the troglobites live. This contrasts with the situation on Hawaii, where many of the troglobites are closely related to species living on the surface near the caves. It is not surprising that the troglobitic species of *Trechus* from the Azores are relicts, in spite of being not very old. The epigean environment has been strongly modified by volcanic eruptions and human alteration, so the extinction of surface ancestors in recent times is not unlikely.

SUMMARY

Four species of *Trechus* and one of *Thalassophilus* are known from volcanic caves on the Azores. Three of the *Trechus* (*T. picoensis* Machado, *T. terceiranus* Machado and *T. jorgensis* Oromí and Borges) are troglomorphic, and occur in the islands of Pico, Terceira and São Jorge respectively. The fourth species (*T. montanheirorum* Oromí and Borges) shows very slight adaptations to hypogean life, and has been collected only in a cave also inhabited by *T. picoensis* ; however, each species tends to occupy different parts of the cave. The only epigean *Trechus* known from the Azores is *T. torretassoi* Jeannel ; this scarce, forest-living species is endemic to São Miguel, an older island where no cave-dwelling *Trechus* have ever been found. Instead, a troglobitic *Thalassophilus* occurs here, and is considered as a relict because of its advanced adaptations to underground life and the absence of close relatives in the archipelago. The significance of the hypogean ground beetle fauna of the archipelago is assessed.

RESUME

Quatre espèces de *Trechus* et une de *Thalassophilus* sont connues des grottes volcaniques des Açores. Trois de ces *Trechus* (*T. picoensis* Machado, *T. terceiranus* Machado et *T. jorgensis* Oromí et Borges) sont troglomorphes, et sont connus respectivement des îles de Pico, Terceira et São Jorge. La quatrième espèce (*T. montanheirorum* Oromí et Borges) montre de très légères adaptations à la vie hypogée, et a été récolté seulement dans une grotte où vit également *T. picoensis* ; cependant, chaque espèce tend à occuper des zones différentes dans la grotte. Le seul *Trechus* épigé connu des Açores est *T. torretassoi* Jeannel ; cette espèce rare des forêts est endémique à l'île São Miguel, une vieille île où aucun *Trechus* cavernicole n'a jamais été trouvé. Au lieu de cela, un *Thalassophilus* vit dans cette île, et il est considéré comme une relicte en raison de son degré élevé d'adaptation à la vie souterraine et de l'absence de relations étroites dans l'archipel. La signification de la faune de coléoptères hypogés de l'archipel est discutée.

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