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The persistence of an ancient marine fauna in Mediterranean waters: new evidence from misophrioid copepods living in anchihaline caves

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Two new species of misophrioid copepods are described from anchihaline cave habitats. Both sexes of Speleophriopsis canariensis are described from material collected on Lanzarote, Canary Is. Expansophria sarda is described from a single male collected on Sardinia. Both genera have widely disjunct distributions which are broadly Tethyan in character. Species of both genera are stenotopic and appear to be restricted to hypogean habitats of near-marine salinities. The presence of species of both genera on Mediterranean islands is interpreted as evidence of the persistence of marine fauna throughout the Messinian Salinity Crisis.

Keywords: copepods, Speleophriopsis, Expansophria, Tethyan relicts, taxonomy, biogeography.

Introduction

Five and a half million years ago the Mediterranean was dry, according to the widely-accepted theory first proposed by Hsü (1973) to explain the presence of extensive evaporite deposits in the Mediterranean Basin. This so-called Messinian Salinity Crisis would have resulted in the complete extinction of the Mediterranean marine fauna (Hsü, 1973; Por and Dimetman, 1985). Against this background recent faunistic studies of anchihaline habitats (= inland marine habitats, typically caves or lava tubes, lacking direct surface connection with the sea) within the Mediterranean Basin have begun to yield interesting results. Jaume and Boxshall (1995) reported a new genus of misophrioid copepods, Speleophriopsis, in anchihaline caves in Majorca. They recognized other species of the new genus among misophrioids previously described from Bermuda and Palau. This is an extremely disjunct distribution for the genus. Anchihaline organisms with similar disjunct distributions, such as the remipede crustaceans, are commonly described as Tethyan relicts (Stock, 1993).

In this paper we report on a new species of Speleophriopsis from the Canary Is. and on a new species of another misophrioid genus, Expansophria Boxshall and Iliffe (1987) from an anchihaline cave on Sardinia. The latter genus has a similar distribution pattern to that of Speleophriopsis, with three known species occurring on the Canary Is., Palau and the Galapagos. Although we have a single incomplete specimen from Sardinia the biogeographical importance of this discovery is such that we consider its description justified.
Material and methods

The copepods were caught in cave lakes using meat-baited traps placed at different depths and left for several days, and by using a hand-held plankton net with an extensible handle. Two caves were sampled. Dasterru de la Dragunara is a hydrologically fossil cave in fissured Cretaceous limestone, located 200 m inland on the NW coast of Sardinia (Western Mediterranean). The cave has a subaerial entrance 20 m above sea level and harbours an anchialine lake with a maximum depth of 45 m (Mucedda, 1983). The cave fauna includes, in addition to the new Expansophria described below, a stygobiont assemblage comprising the cyclopoids Muceddina multispinosa Jaume and Boxshall, 1996, Halicyclops troglodytes Kiefer, 1954 and Metacyclops subdolus Kiefer, 1958, the calanoid Exumella mediterranea Jaume and Boxshall, 1995, and the amphipod Salentinella angeleri Delamare and Ruffo, 1952 (Grafitti, 1983; Jaume and Boxshall, 1995, 1996 b).

The Jameo de los Lagos cave is a lava tube partially flooded by the sea, located about 1 km inland on the NE coast of Lanzarote (Canary Is). The tube, running perpendicular to the coast, was formed 7000/yBP by the eruption of Volcán de la Corona. The famous Jameo del Agua cave appears to be the near-shore section of the same lava tube (Oromi et al., 1989). The tube contains three lakes with lengths of 60, 88 and 56 m, the latter possibly connected via a submarine passage to Jameo del Agua cave. Tidal oscillations attain > 1 m, with a lag of 30–45 min with respect to the adjacent coastline.

The Jameo de los Lagos tube harbours part of the stygobiont faunistic assemblage characteristic of Jameo del Agua and other anchialine environments on Lanzarote. The fauna of the cave includes the following taxa (Wilkens et al., 1993): Gesiella jameensis (Hartmann-Schröder, 1974) (Polychaeta), Speleoneetes ondinae (Garcia-Valdecasas, 1984) (Remipedia), Heteromysoides cotti (Calman, 1932) (Mysidacea), and the amphipod Speleonicippe buchi (Andres, 1975). Our own surveys can add to this list the misophrioid Expansophria dimorpha Boxshall and Iliffe, 1987, and the cyclopinid Muceddina multispinosa Jaume and Boxshall, in addition to the new Speleophriopsis described below.


Taxonomic part

FAMILY MISOPHRIIDAE Brady, 1878
Genus Speleophriopsis Jaume and Boxshall, 1996

Speleophriopsis canariensis n. sp.
(Figs. 1–2)


Adult female. Body (Figs 1A, B) up to 0·68 mm long. Body general outline, tagmosis, and segmentation and armature of all appendages virtually identical to S. balearicus Jaume and Boxshall except genital operculum (Fig. 1C), armed with one long plumose seta, two short, stout spines, plus two tiny denticles (in S. balearicus the
Fig. 1. *Speleophriopsis canariensis* n. sp., adult female: (A), body, lateral; (B), dorsal; (C), detail of genital operculum; (D), leg 5.

Operculum bears two setae only; Jaume and Boxshall, 1996a). Leg 5 (Fig. 1D) with inner margin of basis produced distally into wide, rounded outgrowth; outer spine on first exopodal segment clearly shorter than second exopod segment, its tip not reaching tip of proximal outer spine on that segment (in *S. balearicus* the inner margin of basis is not expanded distally, and the outer spine on the first exopodal segment is as long as the second, its tip reaching clearly the tip of the proximal outer spine on that segment). Ornamentation of distal spine on second exopodal segment of
leg 5 identical in both species (the three transverse rows of spinules on the basal part of this spine in *S. balearicus* illustrated by Jaume and Boxshall (1996a: Fig. 1F) are reinterpreted here as the denticulated rim of the inner distal denticle on this segment; the spine itself is smooth basally in both taxa).

**Adult male.** Body (Figs 2A, B) up to 0.73 mm long, virtually identical to *S. balearicus* in general outline, tagmosis, and segmentation and armature of appendages. Diagnostic differences relate to relative proportions of segments and armature elements of leg 5 (Fig. 2C). In *S. canariensis* inner margin of basis expanded
distally, second spine on inner margin of exopodal segment 2 not reaching tip of distal
spine, the first spine on outer margin of that segment as long as other two spines on
outer margin (in \textit{S. balearicus} inner margin of basis is not expanded distally, the
second spine on the inner margin of the exopod segment 2 clearly extends beyond the
tip of the distal spine, and the first spine on the outer margin of that segment is clearly
longer than the other two marginal spines).

\textit{Etymology.} The species name is derived from its type locality, the Canary Is.

\textit{Remarks.} The genus \textit{Speleophriopsis} includes three other stygobiont, anchihaline
species apart from \textit{S. canariensis} n. sp.; namely, \textit{S. balearicus}, from caves on the
Balearic Is. (Mediterranean), \textit{S. scottodicarloi} (Boxshall and Iliffe, 1990), from a cave
on Bermuda (West Atlantic) and \textit{S. campaneri} (Boxshall and Iliffe, 1990), from a cave
on Angaur, Palau Is. (West Pacific) (Boxshall and Iliffe, 1990; Jaume and Boxshall,
The new species from Lanzarote is very similar to _S. balearicus_, their diagnostic differences having been presented above. Differences from the other two species of the genus are more obvious. In _S. canariensis_ the posterior margin of the cephalosome is only expanded posterolaterally and does not cover the first pedigerous somite dorsally whereas in _S. scottodiaroi_ and _S. campaneri_ it forms a carapace-like structure which completely conceals that somite. In addition, in _S. scottodiaroi_ the female leg 5 lacks an inner spine on the second exopodal segment that is present in _S. canariensis_, and the genital operculum is armed with two setae compared with two spines plus one seta in _S. canariensis_. In _S. campaneri_ the female leg 5 has an inner spine on the second exopodal segment which is elongate, about as long as the segment itself. This spine is very reduced in _S. canariensis_. Also the genital operculum armature carries a single seta in _S. campaneri_.

**Genus _Expansophria_** Boxshall and Iliffe, 1987

*Expansophria sarda* n. sp.

_(Figs 3, 4A–E)_


**Adult male.** Body (Figs 3A, B) incomplete. First pedigerous somite not incorporated into cephalosome. Second and third pedigerous somites with lateral margins slightly produced posteriorly. Urosome 6-segmented. Fifth pedigerous somite with pointed posterolateral edges. Genital somite symmetrical, expanded laterally; opercular flaps (Fig. 3C) located ventrolaterally close to posterior margin of somite, each armed with three setae. Genital somite with dorsal posterior margin, and first to third abdominal somites with posterior margin all around, fringed with continuous hyaline frill. Anal somite (Fig. 3D) bearing hyaline operculum ornamented with row of about 20 large marginal denticles. Caudal rami (Fig. 3D) symmetrical, about twice as long as wide, with inner margin ornamented proximally with two transverse rows of tiny setules; armature consisting of seven setae, seta I very reduced, seta VII displaced medially.

Swimming legs 1–4 (Fig. 4A–D) biramous, slender, with both rami 3-segmented. Legs subsimilar in size although first slightly smaller. Coxae of leg pairs joined by intercoxal sclerite; intercoxal sclerites lacking ornamentation, first considerably larger, fourth narrowest. Outer margin of first endopodal segment of first leg produced distally into strong spinous process not reaching distal margin of second
Fig. 4. *Expansophria sarda* n. sp., adult male: (A), swimming leg 1; (B), leg 2; (C), leg 3; (D), leg 4; (E), leg 5. *E. galapagensis* Boxshall and Iliffe, 1990, adult male. (F), leg 5. *E. dimorpha* Boxshall and Iliffe, 1987, adult male: (G), leg 5.
endopodal segment. Armature as follows:

<table>
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<th></th>
<th>Coxa</th>
<th>Basis</th>
<th>Exopod</th>
<th>Endopod</th>
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<tr>
<td>Leg 1</td>
<td>0-1</td>
<td>0-1</td>
<td>I-1;I-1;III,1,3</td>
<td>0-1;0-1;1,2,3</td>
</tr>
<tr>
<td>Leg 2</td>
<td>0-1</td>
<td>0-0</td>
<td>I-1;I-1;III,1,4</td>
<td>0-1;0-2;1,2,3</td>
</tr>
<tr>
<td>Leg 3</td>
<td>0-1</td>
<td>1-0</td>
<td>I-1;I-1;III,1,4</td>
<td>0-1;0-2;1,2,3</td>
</tr>
<tr>
<td>Leg 4</td>
<td>0-1</td>
<td>1-0</td>
<td>I-1;I-1;III,1,4</td>
<td>0-1;0-2;1,2,2</td>
</tr>
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Lateral spines on leg segments fringed with faint, serrate hyaline frill; distal spine on third exopodal segment of each leg furnished with hyaline frill on outer margin and row of pinnules on inner margin. Setae on rami of characteristic spatulate form, fringed with stout pinnules, except inner seta of endopodal segments 1 and 2 and exopod segment 1 of first leg, and of endopodal segment 1 of leg 3, which have the normal, tapering form.

Leg 5 (Fig. 4E) positioned adjacent to ventral midline, 5-segmented. Intercoxal sclerite absent. Coxa and basis separate, former unarmed, latter bearing outer, thick plumose seta not reaching distal margin of exopod segment 2. Exopod 3-segmented, segment 1 unarmed; segment 2 bearing short and thick plumose spine reaching insertion point of medial spine on segment 3; segment 3 with one distal spine, one subdistal spine, and one short and thick plumose spine located medially; distal and subdistal spines subequal, medial spine not reaching tip of these spines.

Etymology. The species name is derived from its type locality, the island of Sardinia.

Remarks. Although common practice in palaeontological studies it is highly unusual in zoology to establish a new species of extant animal on the basis of a single incomplete individual. We do not recommend this practice but we consider it justified in this case because the discovery of this unique specimen provides new insights into the biogeography of the group and the history of the region. Despite its condition the specimen can be placed unequivocally in the genus Expansophria and recognized as a new species.

Expansophria was established by Boxshall and Iliffe (1987) to accommodate two species found in anchialine caves from oceanic islands, viz. E. dimorpha from Jameo del Agua lava tube in Lanzarote (Canary Is.), and E. apoda from a cenote in Ngeruktabel (Palau, Caroline Archipelago). The same authors later added a third species, E. galapagensis, from anchialine caves in Santa Cruz, Galápagos Is. (Boxshall and Iliffe, 1990). The genus is characterized by a modification of the integument between the cephalosome and the first pedigerous somite, which is extensively folded and allows distension of the prosome, and by the minimal posterior extension of the dorsal cephalic shield, a feature which contrasts sharply with the deep carapace displayed by the majority of misophrioids. The 26-segmented condition of the female antennule, the reduced setation of the maxillule, the modified setae on the swimming legs, the prolongation of the outer distal angle of the first endopodal segment of leg 1 into a slender spinous process, and the medial displacement of seta VII on the caudal ramus are also diagnostic features at the generic level.

The new taxon from Sardinia conforms completely with the diagnosis of Expansophria in all the non-cephalosomal character states listed above. These are the only available characters observable in the incomplete holotype. The structure
and armature of the male fifth legs is identical to that exhibited by the other representatives of the genus (with the exception of E. apoda, whose male is unknown). All available characters indicate that this specimen belongs to the genus Expansophria.

The new species differs from E. dimorpha and E. galapagensis in the armature of the third exopodal segment of leg 3, which bears only two outer spines instead of three. There are other differences in the anal operculum. In the new species, it is evenly rounded and its margin carries about 20 large triangular denticles. In E. dimorpha and E. galapagensis the anal operculum is also evenly rounded, but the marginal denticles are tiny and much more numerous (up to 44; Fig. 3F). Additional differences from E. dimorpha include the smaller body size of the latter, especially the urosome (compare Fig 3A and E). Re-examination of E. dimorpha males has revealed errors in the original description of Boxshall and Iliffe (1987); the genital operculum of the species bears the three setae characteristic of the genus, and the third exopodal segment of leg 5 bears an inner medial spine (Fig. 4G).

The male leg 5 of all three species shares the same segmentation pattern, and the same number and position of armature elements. They can, however, be differentiated by the relative lengths of the armature elements. In E. sarda n. sp. the other seta on basis does not reach the distal margin of exopodal segment 2, the distal spines on the third segment are subequal and about the same length as the segment itself, and the medial spine on this segment does not reach the tip of the distal spines. In E. galapagensis (Fig. 4F) the outer seta on basis clearly exceeds the distal margin of exopod segment 2, and the distal spines of segment 3 are unequal, the distalmost being longer than the segment; as in E. sarda, the medial spine on segment 3 clearly does not reach the tip of the distal spines. In E. dimorpha the outer seta on basis does not reach the distal margin of exopod segment 2 (as in E. sarda), and the distal spines on segment 3 are also subequal, but they are clearly shorter than the segment itself; in addition, the medial spine on this segment is well developed, reaching the tip of the distal spines, a feature not displayed by the other two species.

Comparisons with E. apoda, only the female of which is known, are limited to characters known not to be sexually dimorphic in the other representatives of the genus. The third exopod segment of leg 3 is armed with only two outer spines in E. sarda compared with three in E. apoda. Also the anal operculum is completely smooth in E. apoda (Fig. 3G) instead of serrate. Finally, the spinous process on the outer distal angle of the first endopod segment of leg 1 is longer and more slender in E. apoda, reaching the distal margin of the second endopod segment, whereas in E. sarda it does not reach the distal margin of the second segment.

Discussion

The biogeography of these two new cave-dwelling species is remarkable. Both belong to genera which display the so-called ‘full Tethyan’ distribution (Stock, 1993), i.e. they are circumtropical in the entire region occupied by the former Tethys Sea (see maps in Smith et al., 1994). Each of the four Expansoporia species exists on only one island, one in the Atlantic (Lanzarote) two at opposite sides of the Pacific (Palau Is. and Galapagos) and the fourth on Sardinia (Mediterranean) (Boxshall and Iliffe, 1987; 1990). The known distribution of Speleophriopsis embraces both sides of the Atlantic (Bermuda and Lanzarote), the Pacific (Palau Is), the Yucatán Peninsula of Mexico (undescribed new species) and the Balearic
Expansophria and Speleophriopsis are strictly limited to hypogean habitats. Some traits of their natural history, such as their blindness, restriction to shallow, coastal hypogean waters and to life closely tied to the substratum suggest that their dispersal abilities across areas of open waters are limited. This leads us to infer that their distribution pattern is more likely a result of vicariance events than of dispersal.

Boxshall (1989) attempted to explain the distributions of anchihaline misophrioid genera through a complicated series of vicariant events in three dimensions generated by a combination of tectonic and volcanic activity. This vicariant process would have affected taxa originally inhabiting deep-water crevicular habitats associated with the world-wide system of oceanic spreading zones. The cavernicolous species of genera, such as Expansophria and Speleophriopsis, would thus represent only a sample of the deep-water crevicular fauna from which they became isolated.

The possibility that Expansophria and Speleophriopsis were widely distributed on the ocean floor cannot be excluded, as faunistic knowledge of the deep-sea hyperbenthic misophrioids is still extremely fragmentary (Boxshall, 1983; Alvarez, 1985). However, the discovery of representatives of both genera in non-oceanic, Mediterranean islands which have never been directly connected to the global oceanic ridge system does not accord with the colonization route proposed by Boxshall (1989).

The most parsimonious interpretation of the current known distributions of Expansophria and Speleophriopsis appears to be as relicts of an ancient (late Mesozoic), once widely distributed tropical/subtropical shallow-water fauna. This is manifested by plotting their known localities on a late Mesozoic palaeocoastline map (Fig. 5). This reveals a remarkable continuity between localities which are today separated by large distances and by continental land-masses. The coincidence with the borders of the former Tethys Sea is remarkable.

The distribution of both taxa appears to be the result of a vicariant processes associated with tectonic plate motion, with the opening of the Atlantic (ca. 120 Myr BP) and the closure of the Tethys Sea (ca. 20 Myr BP) as the major vicariant events. This conforms exactly with the explanation currently offered for similarly disjunct modern distributions displayed by numerous stygobiont malacostracan genera with limited dispersal abilities (Stock, 1993).

The presence of Expansophria and Speleophriopsis in Mediterranean waters is especially noteworthy, as it apparently contradicts the widely held view that this sea does not harbour an ancient marine fauna. Such a fauna would have vanished during the Messinian Salinity Crisis—a putative complete desiccation event of approximately 5.5 Myr BP (Hsü, 1973; Pérès, 1985; Por and Dimentman, 1985). Both taxa are tightly associated with coastal, hypogean waters and their potential for dispersal is limited. These characteristics indicate that it is unlikely that they could have invaded the Mediterranean Sea only after its reflooding during the Pliocene. These taxa inhabit waters with salinities only marginally reduced from the normal marine waters and never penetrate into brackish or fresh inland waters. Thus, it appears that they could not have survived the desiccation event in continental waters, as can be proposed to explain the presence on Mediterranean shores of stygobiont thalassoid (i.e. freshwater, but directly derived from marine relatives) crustaceans exhibiting both Tethyan or amphi-Atlantic distributions (many examples listed in Botosaneanu, 1986).
Expansophria and Speleophriopsis are not the only stygobiont genera in Mediterranean waters displaying these characteristics. The list of similar taxa includes the melitid amphipods Psammogammarus S. Karaman, 1955 and Pseudoniphargus Chevreux, 1901, the isopods Angeliera Chappuis and Delamare, 1952 and Caecostenetroides Fresi and Schiecke, 1968, and, among the copepods, the misophrioid Speleophria Boxshall and Iliffe, 1986, the calanoid Exumella Fosshagen, 1970, and the cyclopoid Neocyclops (Protoneocyclops) Petkovski, 1986 (Coineau, 1986; Stock, 1986; Jaume and Garcia, 1992; Stock and Vonk, 1992; Jaume and Boxshall, 1995, 1996a, in press). Taken together these constitute a 'Generalized track' (sensu Croizat, 1958) which should stimulate marine biogeographers to consider alternative paleogeographic scenarios for the massive deposition of salts on the Mediterranean floor during the Messinian. Sonnenfeld (1985) and Sonnenfeld and Finetti (1985) postulated the deposition of salts on the Mediterranean sea floor without resorting to
either the total dessication of the Sea or to its isolation from the World Ocean. Although harsh conditions for marine life are implicit in their model, these are far from the arid tomb postulated by the desiccation model of Hsü (1973), and could permit the survival of an ancient marine biota in Mediterranean waters.

We infer from the presence of highly stenotopic anchialine taxa such as *Expansophria* and *Speleophriopsis*, that anchialine habitats with near marine salinities have been continuously available within the Mediterranean Basin from Tethyan to recent times. Such habitats would also have served as refuges during the Quaternary glaciations.

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