Journal of Natural History
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tnah20

A new genus and two new species of cave-dwelling Misophrioid copepods from the Balearic Islands (Mediterranean)

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Published online: 17 Feb 2007.

JOURNAL OF NATURAL HISTORY, 1996, **30**, 989–1006

A new genus and two new species of cave-dwelling Misophrioid copepods from the Balearic Islands (Mediterranean)

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(*Accepted 10 May 1995*)

Speleophriopsis balearicus n. gen., n. sp., and *Speleophria gymnesica*, n. sp. are described from the flooded coastal karst of the Balearic Is. Two existing species of *Speleophria* are transferred to the new genus. *Speleophriopsis scottodicarloi* (Boxshall and Iliffe), new combination, occurs on Bermuda (Atlantic) and *S. campaneri* (Boxshall and Iliffe), new combination, in the Palau Archipelago (Indo-West Pacific). The type species of *Speleophria* is known only from caves on Bermuda. Both genera are noteworthy for displaying the most primitive condition known in copepods of the allobasis of maxilla (setal formula 5,3), and of the male antennule which, in *Speleophriopsis* n. gen., is geniculate but exhibits a 27-segmented condition. They inhabit cave waters with salinities in excess of 18‰, avoiding lower salinity inland groundwater habitats. A Tethyan relict status is proposed for both taxa.

KEYWORDS: Misophrioid copepods, *Speleophria*, *Speleophriopsis*, anchihaline caves, Tethyan relicts.

Introduction

The Misophrioida is a small order of copepods comprising 21 species distributed in 11 genera. Their phylogenetic relevance is considerable, as they represent an early branch diverging from the podoplean lineage within the Copepoda (Huys and Boxshall, 1991). They occur in neritic, bathypelagic and hyperbenthic deep-sea waters of all oceans (with the possible exception of Antarctic waters), from where at least five genera and 11 species are known. The remaining six genera and 10 species are restricted to anchihaline environments on oceanic islands of the Atlantic and Pacific (Boxshall, 1989; Ohtsuka *et al.*, 1992).

At present, only *Misophria pallida* Boeck, a neritic species also occurring in the N.W. European and Red Sea coasts has been reported from Mediterranean waters (Giesbrecht, 1892). Citations of cave-dwelling misophrioids, some assigned to the genus *Speleophria* Boxshall and Iliffe, have appeared recently in several publications treating stygobiont crustaceans from the Balearic Islands (Jaume and García, 1992, 1993; Jaume, 1993; Pretus, 1993).

We present descriptions of two new Mediterranean species which are closely related to the three species described by Boxshall and Iliffe (1986, 1990) and placed in the genus *Speleophria*, from anchihaline caves on Bermuda (Atlantic) and the Palau Archipelago (W. Pacific). Detailed comparative study has revealed that these three species represent two distinct genera. *Speleophria s. str.*, comprises *S. bivexilla* Boxshall and Iliffe, 1986

from Bermuda plus one of the new Balearic taxa. A new genus is established based on the other new taxon from the Balearic Is. *Speleophria scottodicarloi* Boxshall and Iliffe, 1990 from Bermuda and *S. campaneri* Boxshall and Iliffe, 1990 from Angaur (Palau Is.) are transferred to the new genus.

Samples were taken using meat-baited traps placed at different depths in the cave lakes and left for several days, and also using a hand-held plankton net. Salinity profiles were determined with a salinometer ANDERA-3017.

The terminology used in the descriptions follows Huys and Boxshall (1991). Material is deposited both in the Museu de la Naturalesa de les Illes Balears, Palma de Mallorca (MNCM), and in The Natural History Museum, London (BMNH).

Taxonomy

Misophrioida Gurney, 1933

Speleophriopsis n. gen.

Speleophria: Boxshall and Iliffe (1990) (*partim*)

Diagnosis. Prosome with first pedigerous somite entirely or partially concealed beneath carapace-like expansion of cephalosome. Female urosome 5-segmented, with genital and first abdominal somites fused forming genital double-somite; single copulatory pore opening ventrally, partly concealed beneath confluent sixth legs. Caudal rami armed with seven setae. Antennules 27-segmented in both sexes. Outer seta on basis of maxillule, representing exite. Swimming legs with segmentation and spine and seta formula as described below for type species. Leg 1 inner margin of basis projecting distally, forming pointed process bearing apical seta or spine. Fifth legs joined by intercoxal sclerite, sexually dimorphic, but maintaining same segmentation pattern, separate coxa and basis, plus 2-segmented exopod, in both sexes.

Type species. *Speleophriopsis balearicus* n. sp., from anchihaline caves on the Balearic Is.

Other species. *Speleophriopsis scottodicarloi* (Boxshall and Iliffe), n. comb., from anchihaline cave on Bermuda, and *S. campaneri* (Boxshall and Iliffe), n. comb., from same environment on Angaur, Palau Is. (Boxshall and Iliffe, 1990).

Etymology. Generic name derived from *Speleophria*, the most closely related genus.

Speleophriopsis balearicus n. sp.

(Figs 1–4)

Material examined. Cabrera Archipelago (Balearic Is.): Cova des Burrí. UTM coordinates: 496, 60; 4337, 35. Topographic profile of cave published by Trias (1993): fossil coastal cave excavated in Jurassic fissured limestone, 30 m from shoreline. Anchihaline lake reaching 6 m maximum depth. HOLOTYPE adult ♀ 1·09 mm (MNCM-262); ALLOTYPE adult ♂ 0·97 mm (MNCM-263); PARATYPES 5 adult ♀♀, 2 adult ♂♂ and 3 copepodids (MNCM-264). Collected by D. Jaume, 13 January 1991. Mallorca (Balearic Is.): Cova 'A' de Cala Varques, Manacor. Coordinates: 525, 34; 4372, 13. Topography in Trias and Mir (1977): fossil coastal cave excavated in Tortonian (10 Myr BP), coral reef-derived, porous calcarenite, about 15 m from shoreline. Anchihaline lake reaching 6 m maximum depth: 2 adult ♂♂, 2 adult ♀♀ and 1 ♂ copepodid (BMNH Reg. no. 1995.147–151). Collected by D. Jaume, 19 August

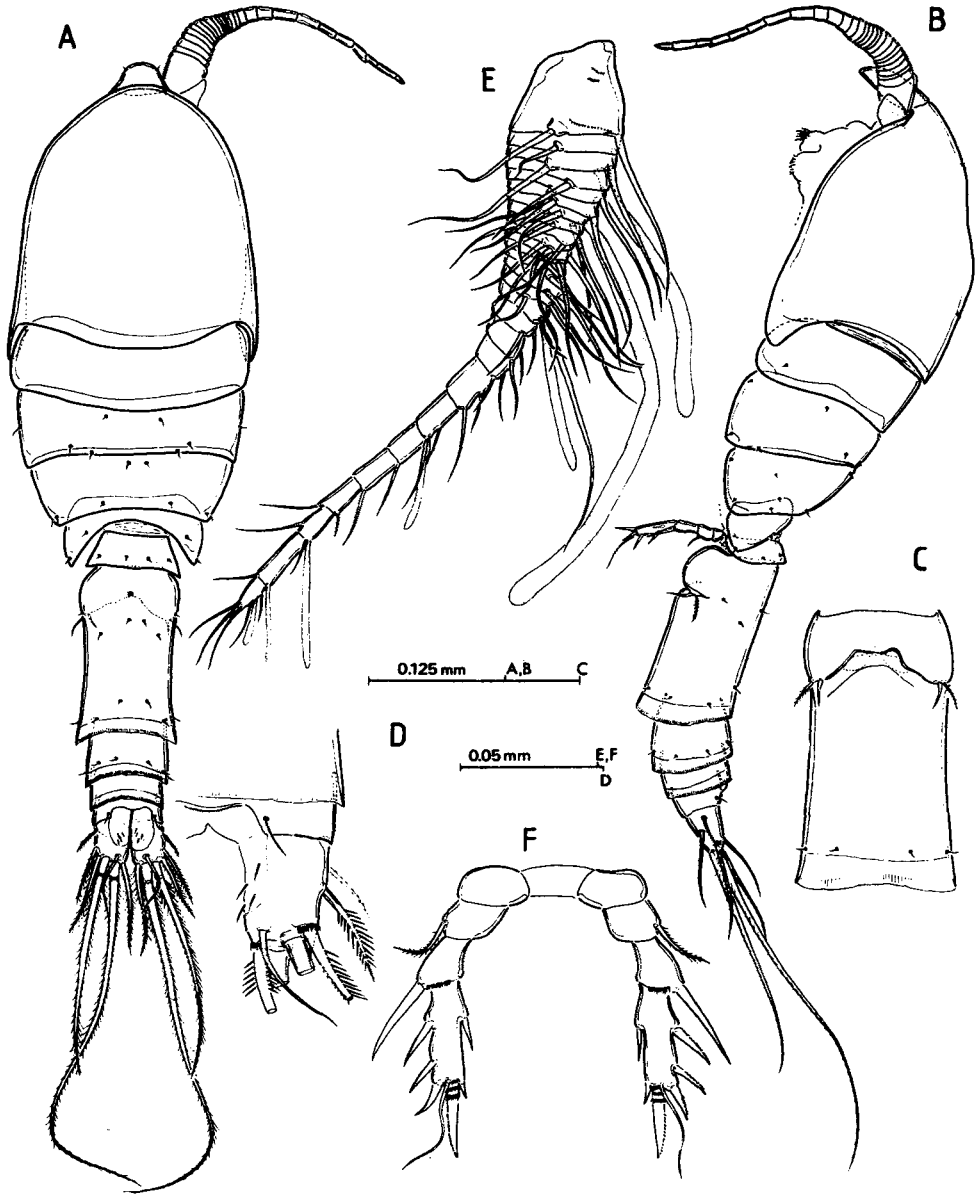

FIG. 1. *Speleophriopsis balearicus* n. gen., n. sp., female: (A) dorsal aspect; (B) lateral; (C) genital double-somite, ventral; (D) anal somite and right caudal ramus, dorsal; (E) right antennule; (F) fifth legs.

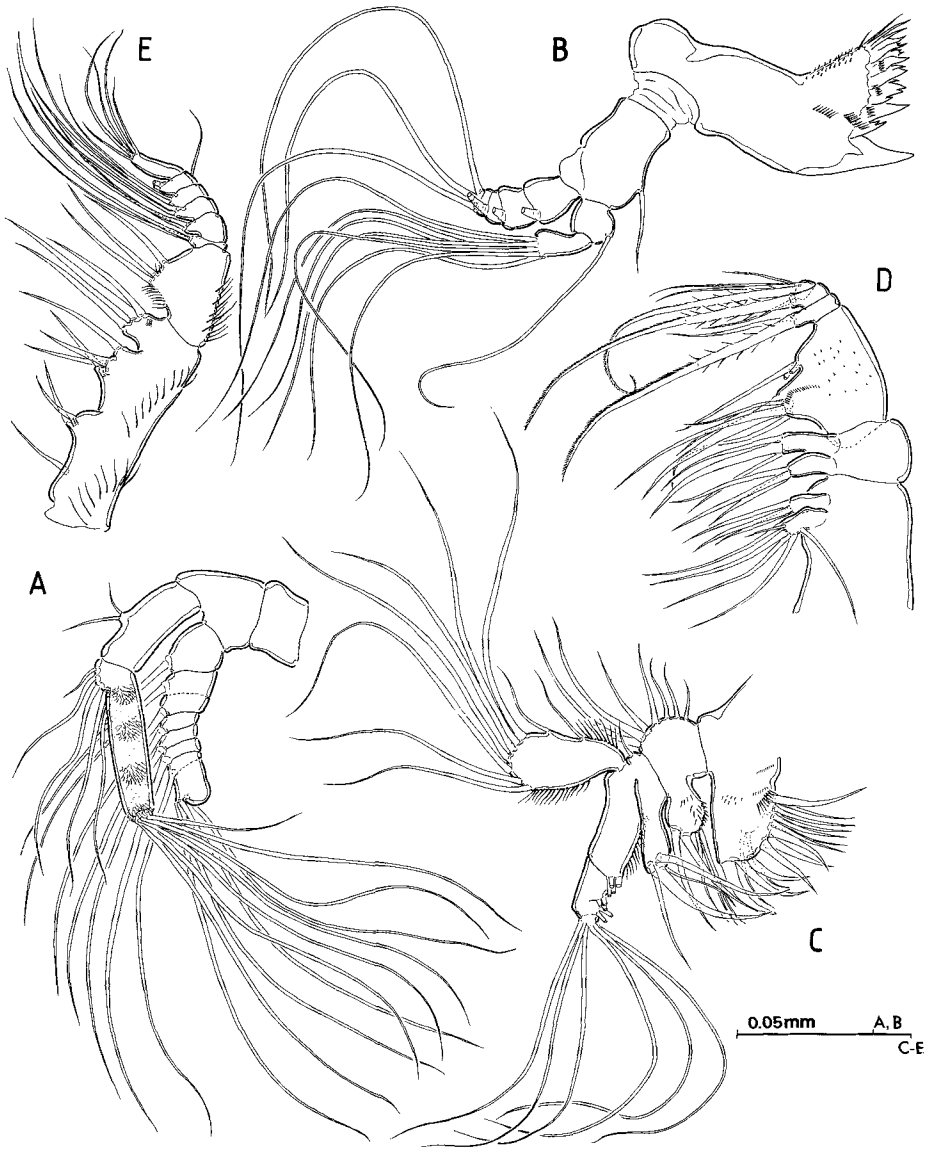

FIG. 2. *Speleophriopsis balearicus*, n. gen., n. sp., female: (A) antenna; (B) mandible; (C) maxillule; (D) maxilla; (E) maxilliped.

1992. Cova de Cala Falcó, Manacor. Coordinates: 525, 63; 4372, 78. Excavated in the same substratum as preceding cave, 10 m from shoreline. Topography also in Trias and Mir (1977). Anchihaline lake reaching 1·5 m maximum depth. 1 adult ♂ and 2 ♀ copepodids (MNCM-265). Collected by D. Jaume, 26 February 1994.

Comparative material examined. Speleophriopsis scottodicarloi. Chalk Cave, Smith's Parish, Bermuda. Female holotype (BMNH Reg. no. 1989.963).

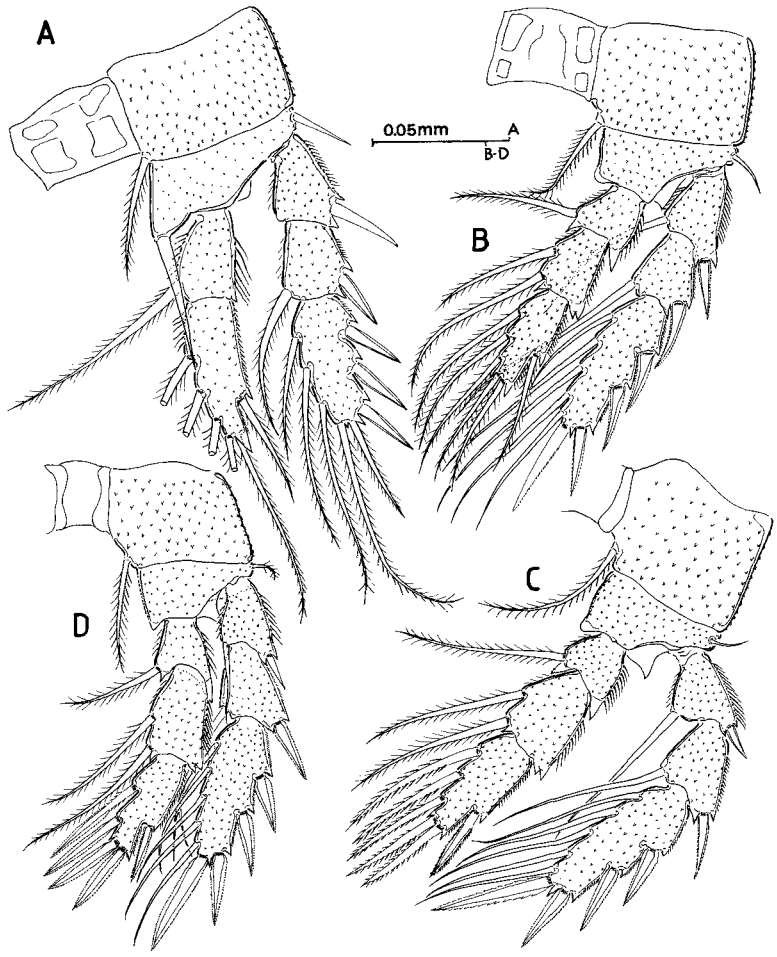

FIG. 3. *Speleophriopsis balearicus*, n. gen., n. sp., female: (A) swimming leg 1; (B) leg 2; (C) leg 3; (D) leg 4.

Adult female. Body (Figs 1 A, B) colourless and slender, up to 1·09 mm long. Eye absent. Prosome 5-segmented, about 1·5 × longer than urosome. Rostrum powerfully developed, free from labrum, about 2·8 × as long as wide, tapering and directed anteroventrally; sensillae implanted about midway along lateral margins. Prosomal pedigerous somites with evenly rounded posterolateral corners. First pedigerous somite free, with lateral margins partially concealed by carapace-like extension from posterolateral corners of cephalosome. Urosome 5-segmented. Fifth pedigerous somite partly concealed laterally by posterolateral corners of fourth somite. Urosome somites two (genital double-somite) to four with hyaline frill adorning posterior margin. Genital double-somite (Fig. 1 C) elongate, symmetrical, with single gonopore opening ventrally about one quarter of distance along somite. Genital operculum consisting of paired plates located either side of gonopore; each armed with spine and seta. Anal somite (Fig. 1 D) short, operculum ornamented with tiny, serrated hyaline frill; pair of long sensillae implanted dorsally; tiny, serrated hyaline frill present laterally on posterior margin. Caudal rami (Fig. 1 D) short, symmetrical, about 1·4 × longer than wide.

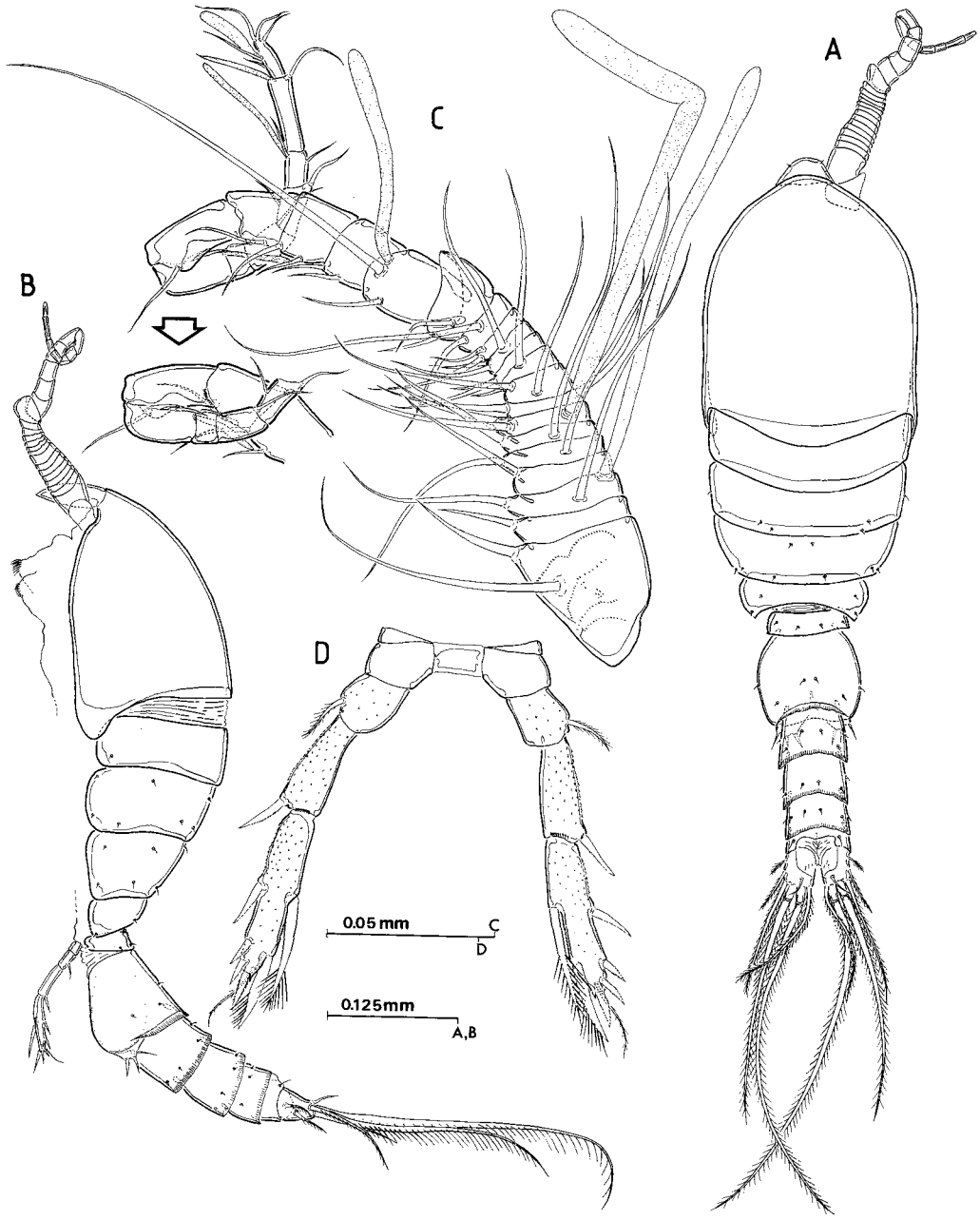

FIG. 4. *Speleophriopsis balearicus*, n. gen., n. sp., male: (A) dorsal aspect; (B) lateral; (C) right antennule; (D) fifth legs.

Armature consisting of seven setae; row of short setules around bases of setae III and VI; some sparse spinules implanted on inner margin of rami.

Antennules (Fig. 1 E) symmetrical, 27-segmented, not reaching distal end of prosome. Segment I with several rows of denticles dorsally. Segments II to XV condensed, wider than long; segments XVI onwards progressively longer than wide. Suture between segments XXIV and XXV transverse. Segment XXIV with distolateral angle produced into pointed outgrowth. Armature elements as follows: I, 2 setae; II, 1 seta; III, 2 setae + aesthetasc; IV, 1 seta; V and VI, 2 setae; VII, 2 + aesthetasc; VIII to XV, 2 setae; XVI, 2 + aesthetasc; XVII to XX, 2 setae; XXI, 2 + aesthetasc; XXII and XXIII, 1 seta; XXIV, 2 setae; XXV, 2 + aesthetasc; XXVI, 1 + aesthetasc; apical segment (corresponding to fused ancestral segments XXVII and XXVIII), 5 + aesthetasc.

Antenna (Fig. 2 A) biramous. Coxa and basis naked. Endopod 2-segmented, longer than exopod; both segments elongate, proximal shorter, armed with two short setae midway along medial margin; distal with row of five setae implanted proximally and seven setae on tip; four patches of short setules distributed at regular intervals along segment. Exopod 6-segmented, with complete fusion of ancestral segments I–II and IX–X; ancestral segments III and IV partially fused; ancestral segment VIII partially fused to IX–X (fusion pattern deduced from number of setal elements on segments and from partial fusion pattern displayed by the exopod of *Speleophria* n. sp.; see below). Distal segment with broad, rounded apex; setal formula: 1, 2, 1, 1, 1, 5.

Mandible (Fig. 2 B) with stout coxal gnathobase, ornamented with several rows and patches of denticles and setules; cutting blade well developed, with nine deeply incised, irregular teeth, and four spines on inner margin. Mandibular palp with basis longer than wide, stout, with short seta implanted on two thirds of distance along inner margin; both rami shorter than basis, exopod longer, 5-segmented, with setal formula 1, 1, 1, 1, 2. Endopod 2-segmented, setal formula 1, 7.

Maxillule (Fig. 2 C) with well-defined praecoxa produced medially into arthrite bearing 10, some very stout, pectinate spines, plus submarginal row of three setae and isolated pair of setae on posterior surface; several rows of short setules on anterior surface, distributed as figured. Coxa with epipodite armed with seven marginal setae; endite bearing two stout setae distally, three slender setae subdistally, and patch of short setules. Basis with proximal endite discrete, armed distally with stout claw-like seta plus three slender setae; distal endite elongate, armed with four distal setae plus row of setules along medial margin; basal exite represented by short slender seta. Endopod 1-segmented, resulting from partial fusion of ancestral segments I–III; setal formula 3, 2, 6. Exopod with row of nine distal and lateral setae, row of setules along medial margin, and row of setules along lateral margin.

Maxilla (Fig. 2 D) heavily developed, 6-segmented. Praecoxa and coxa discrete; endites with setal formula 6, 3, 3, 3. Allobasis ornamented with sparse denticles; proximal (= basal) endite powerfully developed, with transverse row of short setules, drawn out distally into stout, curved medial claw bearing four basal setae; distal (= endopodal) endite hardly developed, bearing three long setae. Free endopod 3-segmented, with setal formula 2, 2, 4.

Maxilliped (Fig. 2 E) slender, 8-segmented. Syncoxa ornamented with two rows of long setules as figured, and armed with isolated seta proximally (representing praecoxal endite) and three (coxal) endites with setal formula 2, 4, 3; row of three minute denticles on each coxal endite. Basis triangular in shape, armed with three setae and three clusters

of setules, as in figure. Endopod 6-segmented, with setal formula 2, 2, 2, 2, 2 + 1, 5; distal segment elongate.

Swimming legs (Fig. 3) covered by minute denticles; each with 3-segmented rami; legs similar in size except leg 1, somewhat reduced and with 2-segmented endopod. Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–1	I–I	I–0; I–1; III,1,4	0–1; 1,2,3
Leg 2	0–1	1–0	I–1; I–1; III,I,5	0–1; 0–2; 1,2,3
Leg 3	0–1	1–0	I–1; I–1; III,I,5	0–1; 0–2; I,II,3
Leg 4	0–1	1–0	I–1; I–1; III,I,5	0–1; 0–2; I,II,II

Inner spine on basis of leg 1 straight and powerfully developed, implanted on conspicuous outgrowth. Armature of third endopod segment with setae progressively replaced by spines, from leg 2 to leg 4.

Fifth legs (Fig. 1 F) symmetrical, slender, uniramous, comprising coxa, basis and 2-segmented exopod. Coxa and basis similar in size, wider than long; coxa unarmed; basis bearing plumose seta on outer margin. Proximal exopod segment approximately equal in size to coxa and basis, armed with stout spine on outer margin and with row of short spinules along posterior distal margin; distal exopod segment elongate, twice as long as proximal segment; armature consisting of three short, denticulate spines along outer margin, thin spine on inner margin, stout, distal denticulate spine plus long seta located subdistally on posterior side of segment; inner margin of segment produced distally into acute, spine-like process.

Adult male. Body (Figs 4 A, B) up to 0·97 mm long, resembling female. Urosome 6-segmented, with genital somite symmetrical, laterally expanded, containing two pear-shaped spermatophores; pair of gonopores opening ventrolaterally; genital operculum as in female, but armed with two spines and one seta; hyaline frill only along posterodorsal margin of somite.

Antennules (Fig. 4 C) 27-segmented, symmetrical, geniculate, reflexed distally. Segments I to XIV densely packed, as in female; segment XV cup-shaped, forming a sheath around proximal half of segment XVI; segments XVI onwards longer than wide except reduced segment XXII; geniculation between segments XX and XXI. Segments XIX onwards very sclerotized. Setal formula as follows: I, 2 setae; II, 1 seta; III, 2 setae + aesthetasc; IV, 1 seta; V and VI, 2 setae; VII, 2 + aesthetasc; VIII to XI, 2 setae; XII, 3 setae; XIII to XV, 2 setae; XVI, 2 + aesthetasc; XVII and XVIII, 2 setae; XIX and XX, 1 seta; XXI, 2 spines + aesthetasc; XXII, 1 spine; XXIII, 1 seta; XXIV, 2 setae; XXV, 2 setae + aesthetasc; XXVI, 1 + aesthetasc; distal segment, 5 + aesthetasc.

Other mouth parts and swimming legs 1–4 as in female in segmentation and setation.

Fifth legs (Fig. 1 D) symmetrical, slender and uniramous, more elongate than in female. Coxa and basis subquadrangular; coxa unarmed; basis with plumose seta on outer margin; exopod segments elongate; proximal armed with short, denticulate spine on outer margin and row of short denticles on distal margin; distal segment with three short, denticulate spines along outer margin; one short, denticulate spine distally, and one slender seta located subdistally on posterior side of segment; two stout spines,

ornamented with long spinules, along inner margin. Surfaces of all segments except coxae ornamented with small denticles.

Etymology. Named after its known distribution, limited to the Balearic Islands.

Remarks. *Speleophriopsis* n. gen displays a series of primitive features which place it very close to the putative ancestral misophrioid. Thus, the female antennule is 27-segmented. This is the maximum number detected in extant copepods, although it is also found in other misophrioids and calanoids (*viz.*, *Archimisophria* Boxshall, *Boxshallia* Huys, *Dimisophria* Boxshall and Iliffe, *Erebonectes* Fosshagen). It approximates closely the 28-segmented state postulated for the ancestral copepod (Boxshall *et al.*, 1984). Most surprisingly, there are no additional fusions associated with the presence of a geniculation in the male antennule, which is also 27-segmented. This represents the maximum number of segments expressed in any extant male copepod.

Other primitive features can be found in the oral appendages. The exopod of the mandibular palp displays the 5-segmented ancestral condition, with setal formula 1, 1, 1, 1, 2; this state is found only in *Speleophria* among the Misophrioida. The maxillule in the new genus, together with *Speleophria* and the harpacticoid genus *Longipedia* Claus, is unique among podoplean copepods in retaining a vestige of the basal exite.

The maxillary allobasis displays an unusual armature, with one claw-like spine plus four setae on the proximal (= basal) endite, and three setae on the distal (= endopodal) endite. According to Huys and Boxshall (1991), the ancestral copepod setation was 4,4 for the basal endite and first endopod segment. The 5,3 pattern displayed by *Speleophriopsis* n. gen. could be explained either by migration of one of the endopodal elements to the basis or by its derivation from a 5,4 condition of the ancestral copepod. There is insufficient evidence to determine which of these possibilities is correct. The new genus also retains, as does *Archimisophria*, the maximum setation pattern of the free maxillary endopod (2,2,4) among misophrioids.

The maxilliped of *Speleophriopsis* n. gen. is also the most primitive within the Misophrioida in the following respects: the conservation of the praecoxal seta, the 2,4,3 setal formula of the coxal endites, the 6-segmented condition of the endopod, and the retention of the ancestral setation 2, 2, 2, 2, 2 + 1, 5.

Swimming legs of the new genus, with the exception of the first, retain the segmentation and armature postulated for the ancestral misophrioid (Huys and Boxshall, 1991). Another primitive character state displayed is the retention of the intercoxal sclerite between the fifth legs although it is combined with a derived character, loss of the endopod, in the same limb.

The retention of the ancestral seven caudal setae is also a primitive misophrioid condition displayed by the new taxon, although it is shown as well by *Speleophria*.

Speleophriopsis balearicus differs from the other two species here transferred to the new genus by, among other characters, the degree of development of the carapace, which in the former is reduced to two posterolateral lappets whereas in the latter two species it covers the first pedigerous somite. It differs from *S. scottodicarloi* in the armature of female fifth leg, which bears a plumose seta on the outer margin of basis and a spine on the inner margin of the distal segment of the endopod. Differences from *S. campaneri* are less marked, relating to the armature of the genital operculum (reduced to one seta in *S. campaneri*), and to the relative lengths of the spines plus the absence of the subdistal seta in *S. campaneri*, on the endopod of leg 5.

The armature of the oral appendages has not been used in the generic and specific differential diagnoses presented here because of the inaccuracies in the original description of Boxshall and Iliffe (1990). The type material of the taxa described by these authors consisted of only one individual per species, and is so severely damaged by dissection as to preclude the checking of all appendages. In *S. scottodicarloi* the complete maxillule, maxilla and maxilliped, the mandibular basis and exopod, and antennulary segments XIV onwards have been successfully re-examined. The armature of each appendage is identical to that of the new taxon from the Balearics. The coxa, basis and endopod of the antenna of *S. scottodicarloi* displayed differences in the armature of the distal endopod segment, which is armed with 4 + 6, instead of the 5 + 7 displayed by the Balearic taxon.

Speleophria Boxshall and Iliffe, 1986 (emend.)

Diagnosis. Cephalosome not produced posteriorly into carapace-like expansion. First pedigerous somite free. Female urosome 5-segmented, displaying full genital double-somite; single copulatory pore opening ventrally, partly concealed beneath confluent sixth legs. Caudal rami armed with seven setae. Antennules 21-segmented, with characteristic fusions involving ancestral segments I–III, IX–XII and XV–XVI. Outer seta on basis of maxillule representing exite. Swimming legs with segmentation and spine and seta formula as those of new species described below. Inner margin of coxa of leg 1 not produced distally into pointed process. Fifth legs joined by intercoxal sclerite, with segmentation consisting of separate coxa and basis, plus 2-segmented exopod; characteristic barbed, spine-like plate on distal segment of exopod. Male unknown.

Type species. *Speleophria bivexilla* Boxshall and Iliffe, from the flooded coastal karst of Bermuda (Boxshall and Iliffe, 1986).

Other species. *Speleophria gymnesica* n. sp., from similar habitats on the Balearic Is., described below.

Etymology. Generic name derived from the Greek 'spelaion', meaning a cave.

Speleophria gymnesica n. sp.
(Figs 5–7)

Material examined. Mallorca (Balearic Is.): Cova 'C' de Cala Varques, Manacor. UTM coordinates: 525, 27; 4372, 19. Topography of the cave published by Trias and Mir (1977); fossil coastal cave excavated in Tortonian (10 Myr BP) coral reef-derived, porous calcarenite, about 10 m from shoreline. Anchihaline lake reaching 2 m maximum depth. HOLOTYPE adult ♀ 0·57 mm (BMNH Reg. no. 1995.145). PARATYPE adult ♀ 0·60 mm (BMNH Reg. no. 1995.146). Other 2 adult ♀♀ not preserved. Collected by D. Jaume, 19 August 1992. Cova 'A' de Cala Varques, Manacor. A single adult ♀, not preserved. Collected by D. Jaume, 19 August 1992.

Comparative material examined. *Speleophria bivexilla*. Roadside Cave, Bermuda. Holotype and 9 paratypes (BMNH Reg. no. 1985.116–126).

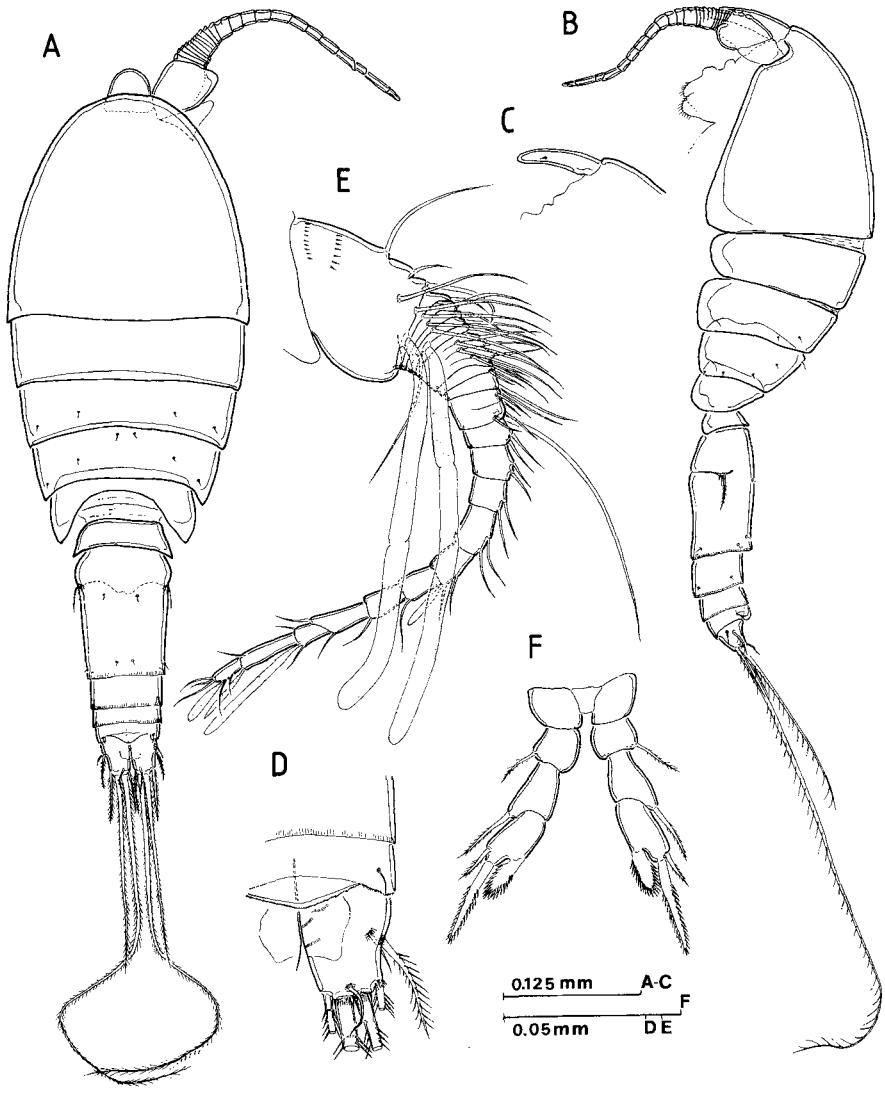

FIG. 5. *Speleophria gymnesica* n. sp., female: (A) dorsal; (B) lateral; (C) rostrum, lateral; (D) anal somite and right caudal ramus, dorsal; (E) antennnule, ventral; (F) fifth legs.

Adult female. Body (Figs 5 A, B) colourless, up to 0·64 mm long. Eye absent. Prosome 5-segmented, about 1·7 × longer than urosome. Rostrum (Fig. 5 C) powerfully developed, narrow, sickle-shaped and free from labrum, about 3·7 × as long as wide; sensillae implanted about midway along lateral margins. Cephalosome not extended posteriorly into carapace. Prosomal pedigerous somites with evenly rounded posterolateral corners. First pedigerous somite free. Urosome 5-segmented. Urosome somites 2 (genital double-somite)–4 with hyaline frill along posterior margin. Genital double-somite elongate, symmetrical, with single gonopore opening ventrally about 0·33 of distance along somite. Genital operculum consisting of paired simple plates located on either side of gonopore, armed with spine and two setae. Anal somite (Fig. 5 D) short, with operculum ornamented with tiny, serrated hyaline frill; pair of long

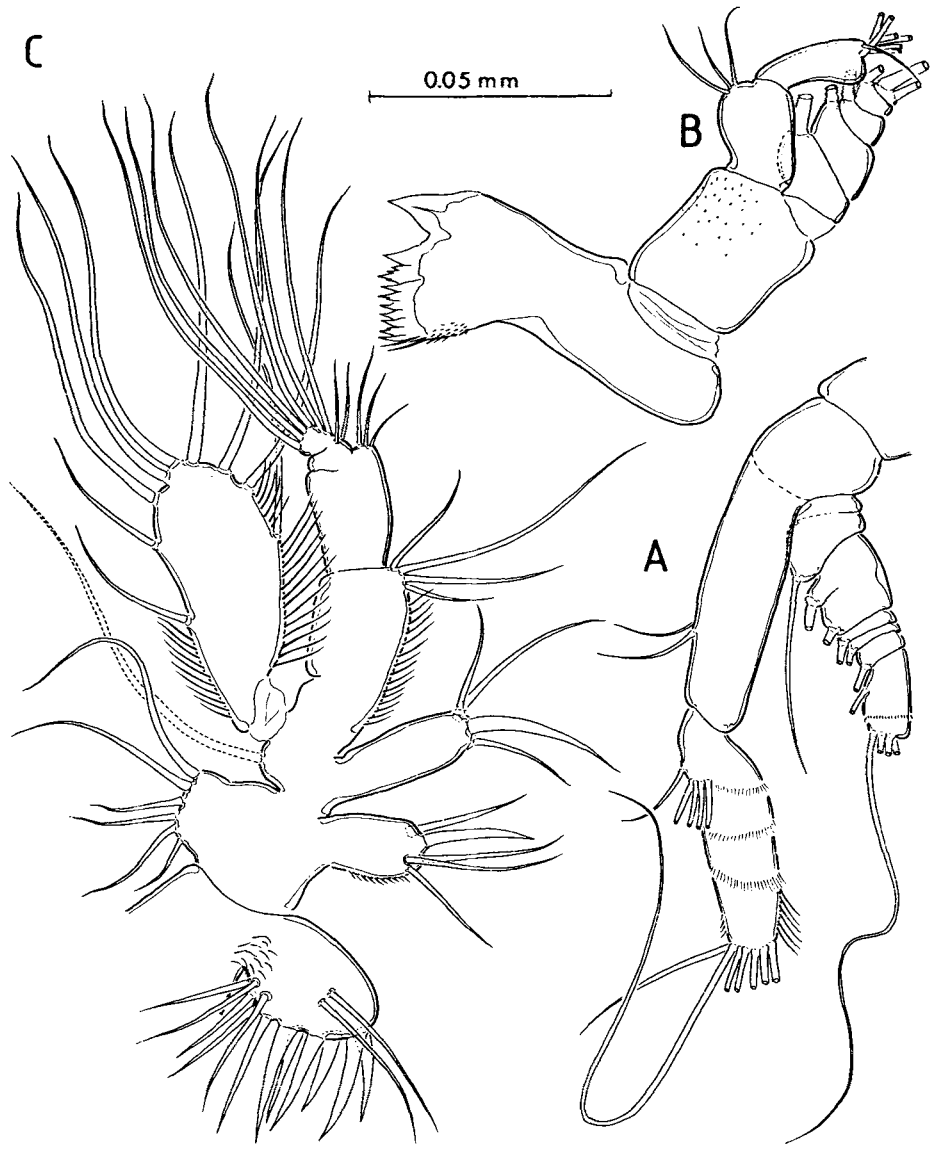

FIG. 6. *Speleophria gymnesica.* n. sp., female: (A) antenna; (B) mandible; (C) maxillule.

sensillae implanted dorsally; tiny, serrated hyaline frill also present along lateral half of posterior margin of somite. Caudal rami (Fig. 5 D) short, symmetrical, bearing seven setae; some rows of tiny setules implanted on inner margin.

Antennules (Fig. 5 E) symmetrical, 21-segmented, not reaching end of prosome. Segment 1 resulting from fusion of ancestral segments I–III, ornamented with two transverse rows of spinules proximally; outer margin swollen, forming ovoid protuberance. Segment 7 resulting from partial fusion of ancestal segments IX–XII. Segment 10 resulting from partial fusion of ancestral segments XV and XVI; long seta-like element on latter homologous with the aesthetasc present on this segment in other misophrioids. Suture between segments 18 and 19 oblique. Segment 18 with

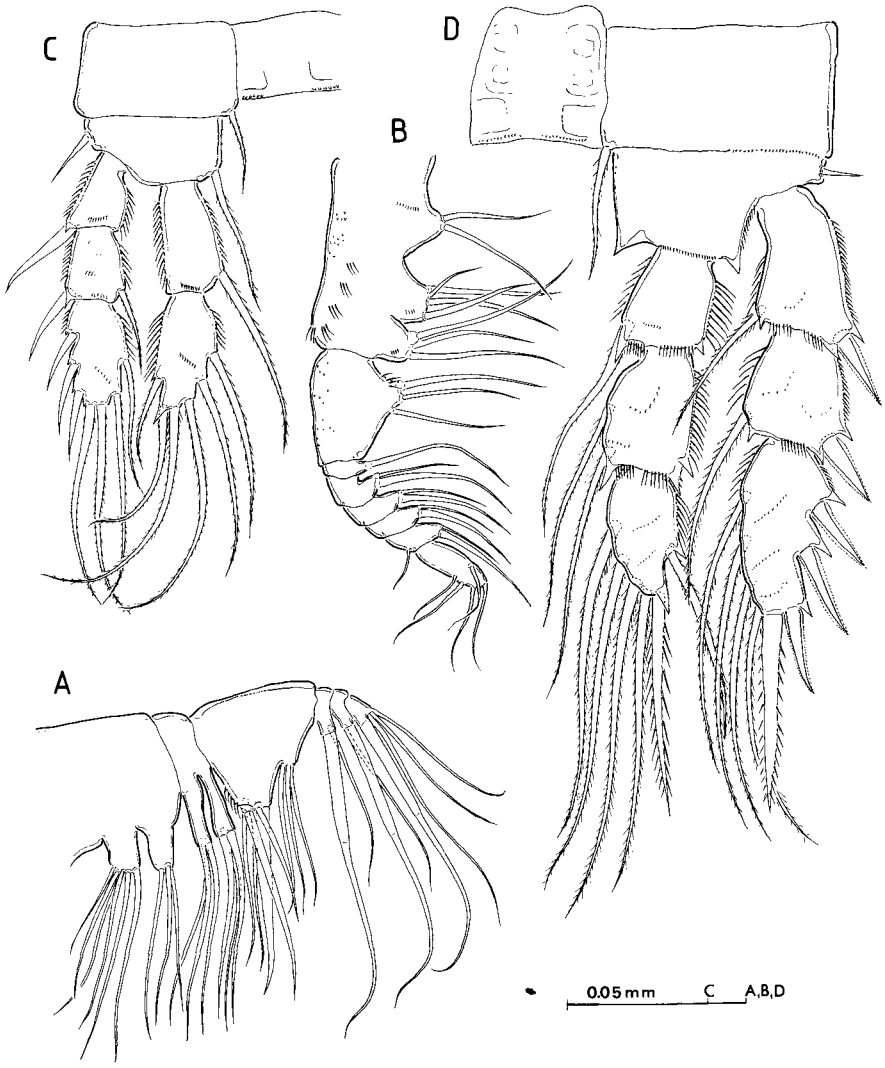

FIG. 7. *Speleophria gymnesica* n. sp., female: (A) maxilla; (B) maxilliped; (C) first leg; (D) second leg.

distolateral corner protruding in pointed outgrowth. Armature as follows: I, 1 seta; II, 2 setae; III, 2 setae + aesthetasc; IV to VI, 2 setae; VII, 2 + aesthetasc; VIII, 1 seta; IX to XV, 2 setae; XVI, 3 setae; XVII to XX, 2 setae; XXI, 2 + aesthetasc; XXII and XXIII, 1 seta; XXIV, 2 setae; XXV, 2 + aesthetasc; XXVI, 1 + aesthetasc; apical segment, 5 + aesthetasc.

Antenna (Fig. 6 A) biramous. Coxa and basis naked. Endopod 2-segmented, about 2 × as long as exopod. Proximal segment partly fused to basis, elongate (about equal to entire exopod), armed with two short setae at about 0·66 of distance along medial margin. Distal segment with five setae implanted proximally and seven apically; for transverse rows of short setules distributed at regular intervals along segment; row of long setules along distal part of lateral margin. Exopod 6-segmented, with complete fusion of ancestral segments VIII–X; segments I and II, and III and IV partially fused.

Distal segment with broad, rounded apex, ornamented with subdistal transverse row of tiny denticles. Setal formula: 1, 2, 1, 1, 1, 5.

Mandible (Fig. 6 B) stout, with coxal gnathobase armed with 10 irregularly incised, sharp teeth, and with two distal spines on inner margin. Some patches and rows of short setules distributed as figured. Mandibular palp with quadrangular basis, ornamented only with tiny denticles. Both rami longer than basis. Endopod well developed, longer than exopod, with setal formula 3,7. Exopod 5-segmented, with setal formula 1, 1, 1, 1, 2.

Maxillule (Fig. 6 C) with well-defined praecoxa produced medially into arthrite bearing nine, some very stout, pectinate marginal spines, plus submarginal row of three setae and isolated pair of setae on posterior surface; patch of short setules located as in figure. Coxa with epipodite armed with row of six (or possibly seven, see below) marginal setae; endite bearing two stout setae distally, three slender setae subdistally, and row of short setules. Basis with proximal endite discrete, armed with stout claw-like seta plus three slender setae; distal endite elongate, armed with 4 distal setae plus row of setules along medial margin; basal exite apparently represented by isolated long seta (but see below). Endopod 1-segmented, resulting from fusion of ancestral segments I–III, with setal formula 3, 2, 6. Exopod with nine distal and lateral setae, row of setules along medial margin, and row of setules along lateral margin.

Maxilla (Fig. 7 A) 6-segmented. Praecoxa and coxa discrete; endites with setal formula 6, 3, 3, 3. Allobasis with proximal (= basal) endite powerfully developed, with row of short, marginal setules and drawn out distally into stout, curved medial claw bearing four basal setae; distal (= endopodal) endite hardly developed, bearing three long setae. Free endopod 3-segmented, with setal formula 2, 2, 4.

Maxilliped (Fig. 7 B) slender, 8-segmented. Syncoxa ornamented with setules and tiny denticles as figured; coxal endites with setal formula 2, 4, 3; row of minute denticles on each coxal endite; no trace of praecoxal endite. Basis triangular in shape, armed with three setae, ornamented with denticles and setules, as figured. Endopod 6-segmented, with setal formula 1, 2, 2, 2, 2 + 1, 5; distal segment elongate.

Swimming legs (Figs 7 C and 7 D; legs 3 and 4 not figured) each with 3-segmented rami and similar in size except leg 1 somewhat reduced and with 2-segmented endopod. Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0–1	I–1	I–0; I–1, III,1,3	0–1; 1,2,3
Leg 2	0–1	1–0	I–1; I–1; III,I,4	0–1; 0–2; 1,2,3
Leg 3	0–1	1–0	I–1; I–1; III,I,4	0–1; 0–2; I,II,3
Leg 4	0–1	1–0	I–1; I–1; III,I,4	0–1; 0–2; 1,II,II

Armature of third endopod segment with setae progressively replaced by spines from leg 2 to leg 4.

Fifth legs (Fig. 5F) symmetrical, slender, uniramous, comprising coxa, basis and 2-segmented exopod. Coxa and basis subquadrangular; coxa unarmed; basis bearing plumose seta on outer margin. Proximal exopod segment longer than wide, armed with spine on outer margin; distal exopod segment about the same size as proximal, armed with one long, distal spine, subdistal spine on outer margin, and broad barbed, spiniform plate subdistally on inner margin. Intercoxal sclerite very narrow.

Etymology. Name derived from the Gymnesic Is., the ancient Greek name for Mallorca and Menorca (Balearic Is.).

Remarks. Re-examination of the type material of *S. bivexilla* has revealed that the patterns of segmentation and armature described for some oral appendages in the original description were wrong. The antennules are 19-segmented, with fusions involving ancestral segments I–III, IX–XII, and XV–XVI, and not 22-segmented as proposed Boxshall and Iliffe (1986), who did not observe the partial fusions of segments IX–XII, and who represented ancestral segments XXIV and XXV as fused, and segment XXVI as fused to the apical segment.

The antenna drawn by Boxshall and Iliffe (1986) showed the coxa and basis as partly fused, the proximal endopodal segment bearing three setae, and the proximal row of setae on the distal segment as comprising three elements. Re-examination of *S. bivexilla* reveals that the coxa and basis are completely separate, and the endopodal armature of the antenna is two and four, respectively. Additionally, Boxshall and Iliffe's (1986) interpretation of the exopod of the antenna is completely wrong. The exopod of *S. bivexilla* corresponds exactly to the pattern described above for *S. gymnesica* n. sp., except that ancestral segments I–II are completely fused and the second segment carries only one seta instead of two.

The mandibular palp of *S. bivexilla* has a setal formula of the exopod 1, 1, 1, 1, 2, as indicated by Huys and Boxshall (1991), and the distal endopodal segment bears seven rather than four setae as previously reported.

Following re-examination of *S. bivexilla*, the maxillule has been shown to bear 14 elements on the praecoxal arthrite instead of only 10, seven on the coxal epipodite instead of six, four on the distal basal endite instead of three, and the endopod is identical to that of *S. gymnesica*. The presence of the basal exite seta in *S. bivexilla* has already been documented by Huys and Boxshall (1991).

The armature of the maxilla was correctly figured in Huys and Boxshall (1991) except for the proximal praecoxal endite which carries seven setae rather than six, as previously reported.

The armature of the maxilliped was also misinterpreted by Boxshall and Iliffe but was corrected in Huys and Boxshall (1991), except that two setae rather than only one are present on the proximal segment of the endopod.

Taking all these corrections into account, the major differences between the two representatives of the genus are as follows: in *Speleophria gymnesica* n. sp. the outer margin of the first segment of the antennule is conspicuously swollen. A long seta-like element is present on ancestral segment XVI instead of an aesthetasc. The proximal antennal endopod segment is elongate and partly fused to the basis, and there are five proximal setae on distal segment. The exopod bears 11 setae. In *S. bivexilla* the proximal antennal endopod segment is much shorter than the exopod (which carries 10 setae instead of 11) and is completely separate from the basis. Also only four setae are present in the proximal row of setae on the distal segment. In *S. bivexilla* the mandibular palp has one seta on the basis and the exopod is longer than the endopod, which bears only one seta on the proximal segment. In contrast, the new taxon displays an unarmed basis and an endopod that is longer than the exopod, and which bears three setae on the proximal segment. The maxillule of the new taxon differs from *S. bivexilla* in the presence of two setae, instead of only one, on the lateral margin of the exopod, and of five elements instead of four on the coxal endite. The low number and poor state of preservation of the specimens available have prevented confirmation that the exite seta

represented was in fact as long and robust as figured. Due to damage to the material the possibility remains that this seta was really a seventh marginal seta of coxal epipodite. However, a basal exite seta is present in the new species described here. The maxillae differ only in the presence of six setae instead of seven on the proximal praecoxal endite of the new species. The presence of one seta instead of two on the proximal segment of the maxillipedal endopod is also diagnostic of the new species. In the fifth legs, differences relate mainly to the presence of only two spines instead of three on the distal segment of the new taxon, the most distal being enlarged and fringed with denticles.

Discussion

The genus *Speleophria* was erected by Boxshall and Iliffe (1986) for the first misophrioid to be discovered from an anchihaline cave environment, *viz. S. bivexilla* from Bermuda. Later, Boxshall and Iliffe (1990) placed in the same genus two additional species found in anchihaline caves on Bermuda and the Palau Is., *S. scottodicarloi* and *S. campaneri*. Although there is a close relationship between *S. bivexilla* and the latter two taxa, the discovery of new misophrioid genera and the re-examination of existing taxa has revealed differences which are now considered to be significant at the generic level. Boxshall and Iliffe (1990) realized that 'in many respects *S. scottodicarloi* is more closely related to *S. campaneri* than the latter is to *S. bivexilla* which is found in a separate cave on the same island' (Bermuda).

Speleophria and *Speleophriopsis* n. gen. appear to be closely related, although much of the resemblance is due to shared primitive character states. Among these, the following are specially noteworthy: the 5-segmented condition of the exopod of the mandibular palp; the retention of the basal exite of maxillule, a feature unknown in other misophrioids; the maxilla with its allobasis bearing the maximum armature recorded for any copepod, *viz.* five setae on the proximal (= basal) endite and three on the distal (= endopodal) endite; the maxillary endopod retaining the maximum setation (2, 2, 4) recorded for the misophrioids; the maxilliped displaying a setal formula for the coxal endites of 2, 4, 3, and a 6-segmented endopod. To these characters can be added the retention of seven setae on caudal rami, and of the intercoxal sclerite joining the fifth legs.

Shared derived characters, apart from their similar habitus, include the loss of the endopod in the female fifth legs, and the presence of an elongate genital double-somite in female, with a single copulatory pore opening ventrally. The 2-segmented condition of the endopod of leg 1, although displayed also by other misophrioid genera (i.e., *Dimisophria* Boxshall and Iliffe, *Palpophria* Boxshall and Iliffe) is also significant.

One of the diagnostic differences between *Speleophria and Speleophriopsis* n. gen. is the segmentation of the antennules, 27-segmented in the latter compared to 21-segmented in the former, with fusions between segments I–III, IX–XII and XV–XVI. Other diagnostic differences relate to the armature of the swimming legs, with *Speleophriopsis* exhibiting 1 seta more on the distal segment of the exopod in legs 1–4. The pointed process on distal inner margin of the basis of leg 1, the presence of a carapace-like extension of the cephalosome, and of two setae instead of only one on the proximal endopod segment of the maxilliped, are also diagnostic characteristics of the latter genus. *Speleophria*, on the other hand, exhibits a characteristic barbed, spine-like element on the distal segment of the fifth leg, that is absent in *Speleophriopsis*.

Speleophria and *Speleophriopsis* n. gen. display a circumtropical distribution which fits within the ancient limits of the Early Tertiary Tethys Sea. This large scale pattern

consists of local distributions that are restricted to anchihaline habitats in close proximity to the sea and with salinities close to that of seawater. The Balearic taxa were always found in waters with salinities in excess of 18‰, and appeared unable to survive in the more inland, reduced salinity habitats.

The combination of a Tethyan distributional pattern with the apparent restriction to waters close to marine salinities is remarkable since these taxa display a life cycle that is closely linked to the hypogean environment and, thus, their potential for dispersal seems to be extremely limited. It appears therefore to be highly likely that they survived *in situ* during the Upper Tertiary, a period of dramatic environmental change in the Mediterranean region, and which apparently included the complete desiccation of the Sea and the consequent annihilation of its marine biota (Hsü, 1973; Por and Dimentman, 1985).

The discovery of stygobiont misophrioids on continental, non-volcanic islands also casts doubt on the validity of the hypothesis advanced by Boxshall (1989), whose analysis of phylogenetic relationships between known misophrioid genera indicated a deep-sea origin of the anchihaline lineages. The 'crevicular corridor' concept postulated by Hart *et al.* (1985), in which a continuum of crevicular habitats connect the deep-sea oceanic crust with seamounts and oceanic islands, and which could have provided a route used by deep-sea misophrioids to colonize shallow-water habitats, cannot be claimed as a pathway in this case. In addition, the discovery of primitive characters in *Speleophriopsis* n. gen. and the description of other new misophrioid taxa since 1989 both suggest that a new and comprehensive phylogenetic analysis of the order Misophrioida is required before the biogeographical patterns can be interpreted.

Acknowledgements

The fieldwork was sponsored by ICONA-CSIC project 'Estudio de la Fauna Endémica y Singular del Parque Nacional Marítimo-Terrestre del Archipiélago de Cabrera', and DGICYT project PB91-0055. We thank the staff of Cabrera National Park for logistical support during visits to the Archipelago, and also J. Ginés, A. Ginés, M. Fiol, M. Trias, G. Pons, J. A. Alcover, and J. Damians for their help during fieldwork on Mallorca. A. Martínez and G. Moyà (UIB) determined the salinity profiles. This work is supported by EC Training Research Contract ERBCHBICT941306.

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