



Two new genera of cyclopinid copepods (Crustacea) from anchihaline caves on western Mediterranean and eastern Atlantic islands

DAMIA JAUME and GEOFFREY A. BOXSHALL

Department of Zoology, The Natural History Museum, Cromwell Road, London, SW7 5BD

Received May 1995, accepted for publication August 1995

***Troglocyclopina balearica* gen nov. sp. nov.** and ***Muceddina multispinosa* gen nov. sp. nov.** are described from the flooded coastal karst of the Balearic Islands, and from caves on Sardinia, the Balearics, and Lanzarote (Canaries), respectively. Both taxa seem to prefer anchihaline habitats with water salinities in excess of 18‰, although *Troglocyclopina* has also been found in more reduced salinity cave lakes located some distance from the coast. These new taxa are the first cyclopinids to be reported from caves, all previous citations of cyclopinids from hypogean environments relate only to the marine interstitial. The small clutch-size exhibited by *Troglocyclopina balearica* (two eggs per sac) and the absence of the exopodal seta on the antenna of *Muceddina multispinosa* are interpreted as troglomorphic features, in addition to the absence of the nauplius eye and the lack of body pigmentation in both taxa. The derivation of both taxa from shallow-water, hyperbenthic marine ancestors is proposed.

©1996 The Linnean Society of London

ADDITIONAL KEY WORDS: — Copepoda – Cyclopoida – *Troglocyclopina* – *Muceddina* – taxonomy – Sardinia – Balearic Islands – Canary Islands – stygobionts.

CONTENTS

Introduction	283
The caves	284
Systematics	285
<i>Troglocyclopina</i> gen. nov.	285
<i>Troglocyclopina balearica</i> sp. nov.	285
<i>Muceddina</i> gen. nov.	292
<i>Muceddina multispinosa</i> sp. nov.	293
Discussion	301
Acknowledgements	302
References	302

INTRODUCTION

Cyclopoid copepods were among the most common inhabitants of Mediterranean and Eastern Atlantic anchihaline caves surveyed recently by the authors. Apart from the characteristic assemblage of stygobiont cyclopids, including *Metacyclops subdolos* Kiefer, 1938, *Halicyclops troglodytes* Kiefer, 1954 and *Neocyclops (Protoneocyclops) mediterraneus* (Kiefer, 1960), many cyclopinids were also found. This is remarkable

since members of this family have never been reported from caves before; all previous citations of cyclopinids from hypogean environments relate only to the marine interstitial (Herbst, 1986).

This paper describes two new genera and species of cyclopinids belonging to the subfamily Cyclopininae Kiefer. They were collected from anchihaline caves on Sardinia, the Balearic Islands and Lanzarote (Canary Islands). This raises the number of known genera in the subfamily to 33 (Huys & Boxshall, 1990; Lotufo & da Rocha, 1991), and to 20 the number found in hypogean environments (Herbst, 1986; Lotufo & da Rocha, 1991).

THE CAVES

The copepods were collected from 15 caves, 12 on islands in the Balearic archipelago, two on Sardinia, and one on Lanzarote. The caves in the Balearics (Fig. 1) were located in two different types of substratum. Caves B to I were formed in Tortonian (10 Myr BP), coral reef-derived, porous calcarenites; mixing-zone corrosion processes seem to have played an important role in their development (Ginés & Ginés, 1992), Caves A, J, K and L were formed in Triassic (A, L) or Jurassic (J, K) fissured limestones. The two caves surveyed on Sardinia were also in fissured limestones, although Cretaceous in age. All these caves have subaerial entrances; the difficulty of access can be deduced from their topographies, published elsewhere (see below). The anchihaline lakes they contain are shallower in the Balearics (up to a maximum depth of 6 m) than in Sardinia (up to 45 m). All the caves are hydrologically fossil.

Jameo de los Lagos cave on Lanzarote is a lava tube partially flooded by the sea, located about 1 km inland on the NE coast of the island. The tube, running perpendicular to the coast, was formed 7000 yr BP by the eruption of Volcán de la Corona. The famous Jameo del Agua cave appears to be the near-shore part of the

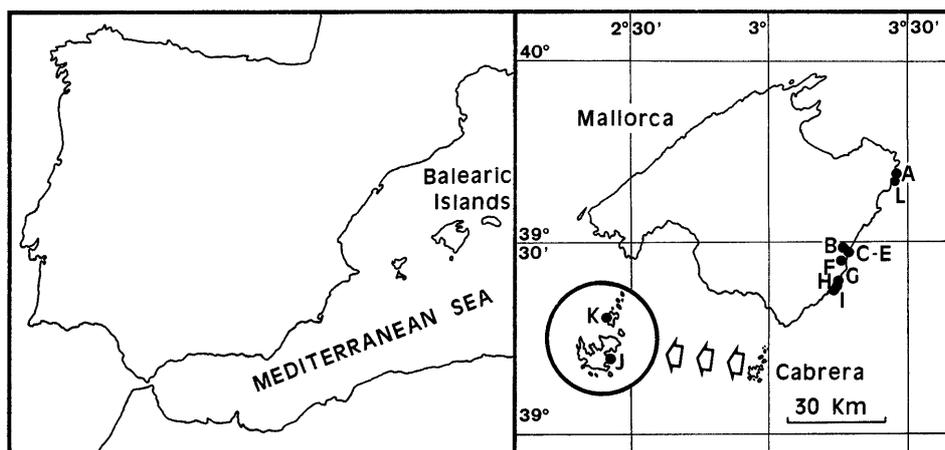


Figure 1. Map showing known localities of *Troglocyclopina balearica*, gen. nov. sp. nov. and *Muceddina multispinosa* gen. nov. sp. nov. on the Balearic Islands. A, Cova de na Barxa; B, Cova des Pont; C, Cova de Cala Falcó; D, Cova 'A' de Cala Varques; E, Cova 'C' de Cala Varques; F, Cova des Serral; G, Es Secret des Moix; H, Cova des Sòtil; I, Cova des Ases; J, Cova des Burri K, Cova de sa Llumeta; L, Cova de na Mitjana.

same lava tube (Oromí *et al.*, 1989). The tube harbours three lakes; tidal oscillations reach more than 1 m with a lag of 30–45 min with respect to the adjacent coastline.

Sampling was undertaken using meat-baited traps placed at different depths in the cave lakes and left for several days, and by using a hand-held plankton net with an extensible (to 3 m) handle. Salinity profiles were determined for some caves with a salinometer ANDERA-3017.

The terminology used in descriptions follows Huys & 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 (BM (NH)).

SYSTEMATICS

Family Cyclopinidae Sars, 1913
Subfamily Cyclopininae Kiefer, 1927
Troglocyclopina **gen. nov.**

Diagnosis. First pedigerous somite free, partially concealed by posterior extension of dorsal cephalic shield of cephalosome. Antennule 10-segmented in female, 16-segmented in male. Exopod of antenna reduced to 2 setae. Mandibular palp with 2-segmented endopod and 4-segmented exopod. Maxillule bearing discrete coxal endite. Endopod of maxilliped 3-segmented. Legs 1 to 4 with 3-segmented rami and armature formula as described below for type species. Leg 5 2-segmented in both sexes, with undivided protopod bearing outer seta; single exopodal segment bearing 3 setae/spines in female and 5 in male. Leg 6 with 3 elements in male.

Etymology. Generic name derived from the Greek Trōglē (= hole), in reference to its hypogean life-style, and *Cyclopina*, a genus which displays a very similar body shape.

Type species. *Troglocyclopina balearica* sp. nov., by monotypy.

***Troglocyclopina balearica* sp. nov.**

(*Figures 2-5*)

Material examined. All collected by D. Jaume. Mallorca (Balearic Islands): Cova de na Barxa (Capdepera). UTM coordinates: 539,30; 4393,10. Topography of the cave published by Andrews *et al.* (1989). HOLOTYPE adult female 0.42 mm (BM(NH) Reg. no. 1995.527); ALLOTYPE adult male 0.39 mm (BM(NH) Reg. no. 1995.538); PARATYPES 74 specimens, both sexes (BM(NH) Reg. no. 528-537). Collected 17 July 1994. — Cova de Cala Falcó (Manacor). Coordinates: 525,63; 4372,78. Topography in Trias & Mir (1977). 8 specimens, both sexes (MNCM-266). Collected 26 February 1994. — Cova 'A' de Cala Varques (Manacor). Coordinates: 525,34; 4372,13. Topography in Trias & Mir (1977). 23 specimens, both sexes (MNCM-268). Collected 10 February 1994. — Cova 'C' de Cala Varques (Manacor). Coordinates: 525,27; 4372,19. Topography in Trias & Mir (1977). 4 specimens, both sexes (MNCM-267). Collected 19 August 1992. — Cova des Pont (Manacor). Coordinates: 525,36; 4373,12. Topography in Trias & Mir (1977). 4 specimens, both sexes (MNCM-273). Collected 14 April 1991. — Cova des Serral (Manacor).

Coordinates: 524,87; 4371,49. 5 specimens, both sexes (MNCM-269). Collected 26 February 1994. — Es Secret des Moix (Manacor). Coordinates: 523,69; 4365,53. Topography in Ginés, Ginés & Pons-Moyà (1975). 27 specimens, both sexes (MNCM-271). Collected 27 May 1994. — Cova des Sòtil (Manacor). Coordinates: 524,66; 4369,54. 19 specimens, both sexes (MNCM-270). Collected 23 April 1994. — Cova dets Ases (Felanitx). Coordinates: 523,31; 4364,82. Topography in Ginés & Ginés (1987). 7 specimens, both sexes (MNCM-272). Collected 21 May 1995. — Cabrera (Balearic Islands): Cova des Burri. Coordinates: 496,60; 4337,35. Topography in Trias (1993). 65 and 30 specimens, both sexes (MNCM-274,323). Collected 19 March 1994 and 13 January 1991, respectively. — Illa dels Conills (Balearic Islands): Cova de sa Llumeta. Coordinates: 496,60; 4337,35. Topography in Trias (1993). 35 and 12 specimens, both sexes (MNCM-324,325). Collected 10 August 1993 and 15 July 1990, respectively.

Description

Adult female. Body (Fig 2A,B) cyclopiform, up to 0.42 mm long, colourless. Nauplius eye absent. Prosome 5-segmented, about 1.4 times longer than urosome. Rostrum developed, oval. Lateral margins of cephalosome vaulted. Second to fourth prosomal pedigerous somites with evenly rounded posterolateral corners. First pedigerous somite free, with weakly sclerotized lateral margins completely concealed by paired, carapace-like extensions from posterolateral corners of cephalosome. Urosome 5-segmented, with genital and first abdominal somites fused to form genital double-somite. Double-somite and free abdominal somites ornamented with hyaline frill on posterior margin; frill entire dorsally, but deeply serrated ventrally. Genital double-somite (Fig 2C,D) symmetrical, 1.5 times longer than wide, slightly expanded anteriorly. Single copulatory pore opening mid-ventrally about one third of distance along somite, connected via copulatory duct with small, fused seminal receptacles. Paired gonopores located dorso-laterally, connected to receptacle by long receptacle ducts. Gonopores covered by opercula derived from sixth legs, each armed with 2 unequal setae, dorsal-most longest, lying along surface of somite. Paired egg sacs containing 2 eggs each. Anal somite (Fig. 2E) as long as preceding abdominal somite, bearing operculum ornamented with tiny, serrated hyaline frill and flanked by pair of dorsal sensillae. Caudal rami (Fig. 2E) longer than anal somite, about 3.3 times longer than wide, symmetrical. Armature consisting of 6 setae and subdistal row of spinules on ventral surface; seta II as long as seta III, implanted two fifths of distance along lateral margin of ramus; relative lengths of distal setae as in Figure 2A.

Antennules (Fig. 2F) symmetrical, 10-segmented, not reaching distal end of prosome. Armature as follows: segment 1 (corresponding to fused ancestral segments I and II), 2 setae; segment 2 (ancestral segments III to V), 5 setae; segment 3 (ancestral segments VI to IX), 8 setae; segment 4 (ancestral segments X and XI), 4 setae; segment 5 (ancestral segments XII to XIV), 6 setae; segment 6 (ancestral segments XV to XX), 6 setae; segment 7 (ancestral segments XXI to XXIII), 3 setae + aesthetasc; segment 8 (ancestral segment XXIV), 2 setae; segment 9 (ancestral segment XXV), 2 setae + aesthetasc; apical segment (ancestral segments XXVI to XXVIII), 6 setae + aesthetasc, the latter fused at base to adjacent seta. Fusion pattern of ancestral segments deduced after comparison with antennular segmentation pattern displayed by *Euryte robusta* Giesbrecht (see Huys & Boxshall,

1991), and also from variations in thickness of integument which represent traces of original segmental sclerotizations.

Antenna (Fig. 3A) 4-segmented. First segment comprising fused coxa and basis,

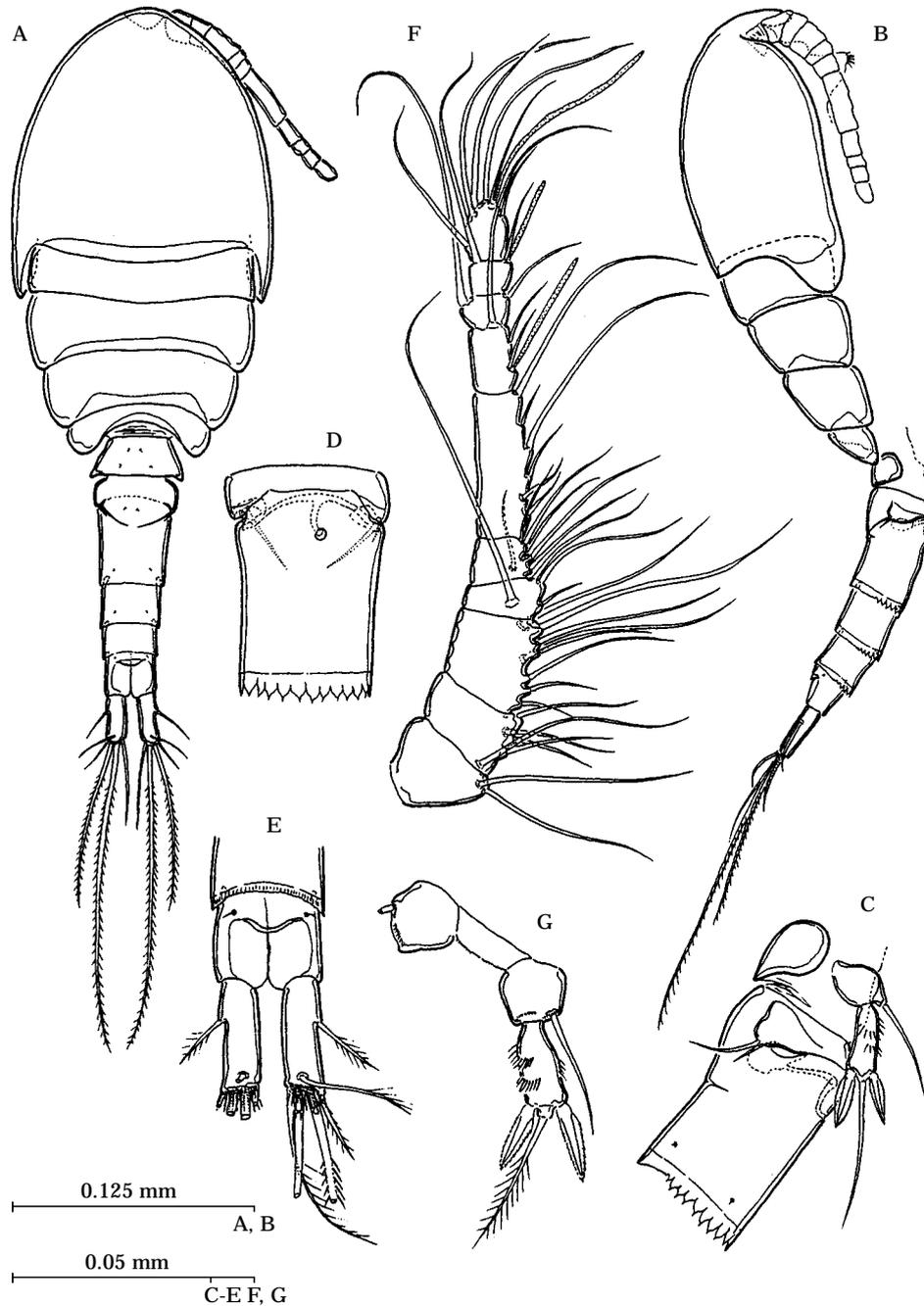


Figure 2. *Troglodyclopina balearica*, gen. nov., sp. nov.; Adult female. A, habitus, dorsal; B, lateral; C, first urosomal somite and genital double-somite, lateral; D, genital double-somite, ventral; E, anal segment and caudal rami, dorsal; F, antennule; G, leg 5.

armed with 1 inner basal seta distally, and 2 outer setae representing exopod. Endopodal setal formula 1,5,7; segments ornamented with several rows of spinules, as figured.

Mandible (Fig. 3B) comprising small coxa, with gnathobase bearing 9 sharp, deeply-incised unequal blades plus 1 marginal spine, and large palp. Palp basis as long as coxa, bearing single seta; endopod 2-segmented, with setal formula 3,6; exopod small, about as long as endopod, 4-segmented, with setal formula 1,1,1,2; apical seta shorter, naked proximally and bearing brush of 7 tiny setules distally.

Maxillule (Fig. 3C) with well developed praecoxal arthrite, armed with 10 thick, unequal spines plus 1 isolated seta on posterior surface. Coxal epipodite with



Figure 3. *Troglodyclopina balearica*, gen. nov., sp. nov.; Adult female. A, antenna; B, mandible; C, maxillule; D, maxilla; E, maxilliped.

armature reduced to 2 unequal setae; coxal endite discrete, armed with 1 seta. Proximal and distal endites of basis discrete, bearing 3 and 2 setae respectively. Endopod 1-segmented, bearing 7 setae. Exopod 1-segmented, about same size as endopod, armed with 4 distal setae and marginal row of long setules.

Maxilla (Fig. 3D) powerfully developed, 5-segmented. Praecoxa and coxa fused, with syncoxal endite formula 3,1,3,3. Basis with large endite bearing claw-like spine plus 2 unequal setae. Endopod 3-segmented, proximal segment double, representing fused first and second ancestral endopodal segments; setal formula (2 + 2), 2,4.

Maxilliped (Fig. 3E) slender, 5-segmented. Praecoxa and coxa fused forming syncoxal, bearing 3 endites with setal formula 1,3,2. Basis with medial margin swollen, ornamented with marginal row of long setules and submarginal row of short spinules; 2 setae distally on medial margin. Endopod 3-segmented, setal formula 0,0,4.

Swimming legs 1 to 4 (Fig. 4) biramous, both rami 3-segmented. Coxae of leg pairs joined by intercoxal sclerite; that of leg 1 with conspicuous forked outgrowth; those of legs 2 to 4 ornamented with 3 rows of spinules, as figured. Armature as follows:

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

Transverse row of long spinules present near inner margin of basis of each leg. Other ornamentation as figured. Distal segment of endopod of leg 4 bearing 3 stout spinules on posterior surface.

Fifth legs (Fig. 2G) uniramous, 2-segmented, joined by intercoxal sclerite ornamented with row of tiny denticles. Coxa and basis fused forming subquadrangular protopodal segment armed with long, smooth outer seta. Distal segment (exopod) longer than proximal, about twice as long as wide, produced distally into median process bearing 1 long, feathered seta; 1 subdistal, stout flanged spine present on each side of process. Some setular ornamentation on both segments, as figured.

Adult male. Body (Fig. 5A) up to 0.39 mm long, resembling female. Urosome 6-segmented, with genital somite (Fig. 5B) symmetrical, laterally expanded; pair of gonopores opening ventrolaterally at posterior border of somite. Sixth legs reduced to paired opercular flaps, each armed with 2 long outer setae and short inner seta.

Antennules (Fig. 5C–E) 16-segmented, symmetrical, digeniculate. Geniculations between segments homologous with ancestral segments XV and XVI, and between XX and XXI. Segment XV cup-shaped, forming sheath around proximal half of segment XVI. Articulations between ancestral segments XII and XIII, and XIII and XIV provided with extensive arthrodistal membrane. Armature as follows: segment 1 (corresponding to fused ancestral segments I and II), 2 setae; segment 2 (segments III to V), 5 setae; segment 3 (VI and VIII), 4 setae; segment 4 (ancestral segment VIII), 2 setae; segment 5 (partially fused ancestral segments IX and X), 4 setae; segments 6 to 10 (ancestral segments XI to XV, 2 setae each; segment 11 (ancestral segment XVI), 2 spines; segment 12 (ancestral segment XVII), 2 spines plus 1 seta-like

element; segment 13 (ancestral segment XVIII); 1 spine, 1 seta plus 1 seta-like element; segment 14 (ancestral segments XIX and XX), 1 spine, 2 setae plus 1 spine-like process; segment 15 (ancestral segments XXI to XXIII), 1 seta plus 2 spine-like processes; distal segment (ancestral segments XXIV to XXVIII), 9 setae plus 1 aesthetasc.

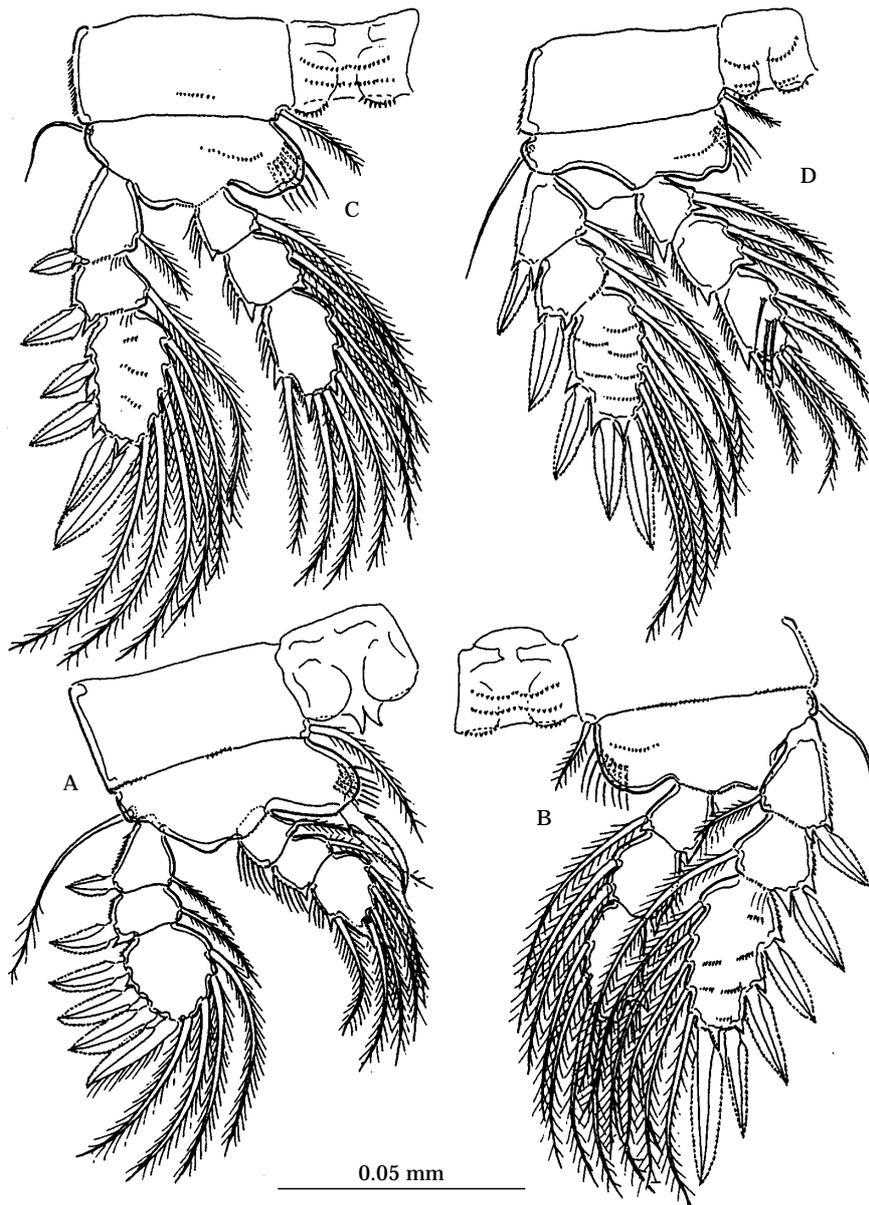


Figure 4. *Troglodyclopinia balearica* gen. nov., sp. nov.; Adult female. A, leg 1; B, leg 2; C, leg 3; D, leg 4.

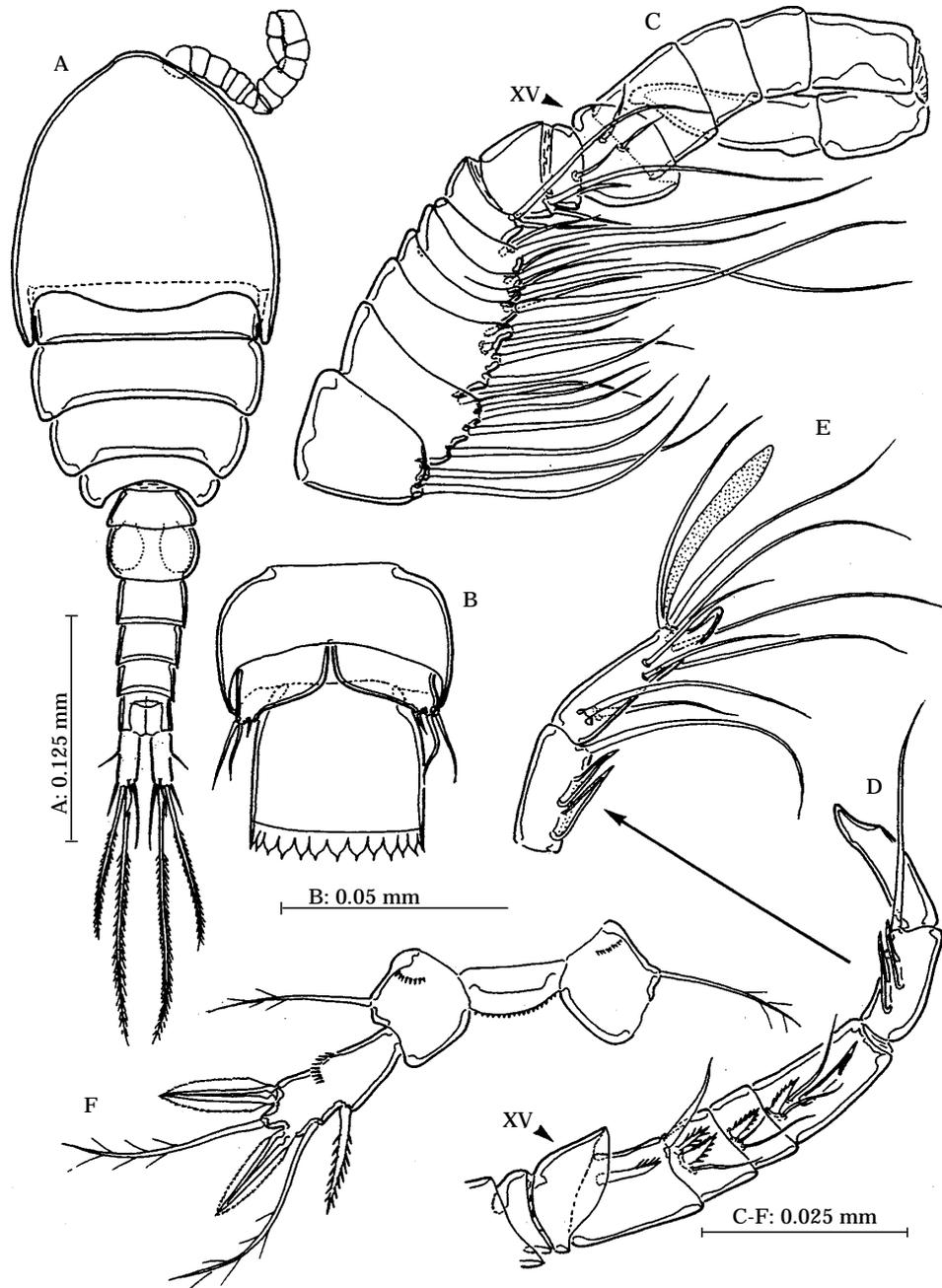


Figure 5. *Troglodyclopina balearica* gen. nov., sp. nov.; Adult male. A, habitus, dorsal; B, genital and first abdominal somites, ventral; C, antennule, with armature of ancestral segment XVI onwards omitted; D, detail of armature of segments XVI onwards, armature of distal segment omitted; E, detail of distal segments of antennule; F, leg 5.

Other mouthparts and swimming legs 1 to 4 as in female in segmentation and setation.

Fifth legs (Fig. 5F) as in female, but bearing 2 additional armature elements on inner margin of exopodal segment, *viz.*, 1 short pectinate spine midway, and 1 smooth seta about two-thirds of distance along margin.

Etymology. The new species is named after its known distribution, limited to the Balearic Islands.

Remarks. *Troglocyclopina balearica* gen. nov., sp. nov. displays a carapace-like extension of the posterolateral margin of the dorsal cephalic shield which partially conceals the first pedigerous somite. The latter is not incorporated into the cephalosome. Both features are considered to be the ancestral condition among cyclopinid copepods (Huys & Boxshall, 1991) and are displayed by a relatively low number of taxa, namely *Pterinopsyllus* Brady, 1880, *Cyclopina* Claus, 1862, *Metacyclopina* Lindberg, 1953, *Procylopina* Herbst, 1955, *Cyclopinodes* Wilson, 1932, *Cyclopinoides* Lindberg, 1953 and *Cuipora* Lotufo & da Rocha, 1991 (Huys & Boxshall, 1991; Lotufo & da Rocha, 1991; da Rocha & Iliffe, 1994). They have also been reported recently from the cyclopid *Troglocyclops* da Rocha & Iliffe, 1994. A free first pedigerous somite is also exhibited by the cyclopid *Euryte* Philippi, 1843 (da Rocha & Iliffe, 1994) and by the cyclopinid *Muceddina* gen. nov., described below.

Troglocyclopina is the second cyclopinid, after *Cyclopinodes elegans* (T. Scott, 1894) known to possess a discrete coxal endite on the maxillule. Huys & Boxshall (1991), after discovering the presence of the coxal endite in *Cyclopinodes*, already commented on the significance of this feature in leading to rejection of their proposal (Huys & Boxshall, 1990) that its putative absence in cyclopinids and cyclopids might represent a synapomorphy between these two families.

According to the generic key provided by Huys & Boxshall (1990) for the Cyclopininae, the new taxon from the Balearic Islands falls close to *Procylopina* Herbst except for the presence of 2 setae representing the exopod of the antenna. Nevertheless *Troglocyclopina* gen. nov. differs sharply from *Procylopina* in other character states, such as the 10-segmented condition of the female antennule instead of 19-segmented, the 3-segmented endopod of maxilliped instead of 4-segmented, and in the armature of the proximal segment of the exopod of swimming leg 1, which bears an inner seta in the new genus and none in *Procylopina*. In addition, *Procylopina* lacks a coxal endite on the maxillule.

Muceddina gen. nov.

Diagnosis. Carapace-like extension of dorsal cephalic shield of cephalosome absent. First pedigerous somite free. Genital double-somite of female almost completely subdivided. Caudal rami bearing 7 setae. Antennule 15-segmented in female, 17-segmented in male. Antenna displaying 2 pointed processes flanged with bristles on outer margin of 2 distal endopodal segments; exopod absent. Mandibular palp slender, with 2-segmented endopod and 4-segmented exopod; endopod longer than exopod, with proximal segment unusually elongate. Maxillule lacking coxal endite. Maxilla with completely separated praecoxa and coxa, enditic setation formula 4,1,3,3. Endopod of maxilliped 5-segmented. Legs 1 to 4 with 3-segmented rami and armature formula as described below for type species. Fifth leg 3-segmented in

female, 4-segmented in male; coxa and basis separated in both sexes; exopod 1-segmented in female, 2-segmented in male. Leg 6 with 3 elements in male.

Etymology. The new genus is dedicated to the Sardinian speleologist Mauro Mucedda, who guided us across the caves of Cape Caccia, where this new taxon was initially found.

Type species. *Muceddina multispinosa* sp. nov., by monotypy.

***Muceddina multispinosa* sp. nov.**

(Figures 6–9)

Material examined. SARDINIA: Capo Caccia, Alghero. Grotta Verde. IGM coordinates: Lat. 40° 33' 51"; Long. 4° 17' 12". Topography of the cave published by Mucedda (1988). HOLOTYPE adult female 0.71 mm (BM(NH) Reg.no. 1995.517); ALLOTYPE adult male 0.52 mm (BM(NH) Reg.no. 1995.518); PARATYPES 4 adult males, 2 adult females and 2 copepodids (BM(NH) Reg.no. 1995.519-526). Other 3 adult females and 2 adult males not preserved. Collected by D. Jaume and G. Pons, 19 June 1991. — Dasterru de la Draganara. Coordinates: Lat. 40° 34' 29"; Long. 4° 17' 30". Topography in Mucedda (1983). One adult female and 2 copepodids (BM(NH) Reg.no. 1995. 514-516). Collected by D. Jaume and G. Pons, 19 June 1991.

BALEARIC ISLANDS: Capdepera, Mallorca. Cova de na Mitjana. UTM coordinates: 539.10; 4390.95. Topography of the cave published by Ginés *et al.* (1975). One adult male (MNCM-326). Collected by the authors, 1 April 1995. — Illa dels Conills, Cabrera. Cova de sa Llumeta. 1 adult male and 1 adult female (MNCM-327). Collected by D. Jaume, 17 June 1994.

CANARY ISLANDS: Lanzarote. Jameo de los Lagos. UTM coordinates: 652.20; 3226.40. Nine adult males and 4 adult females (MNCM-328). Collected by D. Jaume and G. Pons, 24 September 1992.

Description

Adult female. Body (Fig. 6A,B) cyclopiform, up to 0.71 mm long, colourless, densely ornamented with faint, tiny tubercles. Nauplius eye absent. Prosome 5-segmented, wide and rounded, about as long as urosome. Rostrum developed, oval. Pedigerous somites with evenly rounded posterolateral corners. Urosome 5-segmented, with genital and first abdominal somites partially fused to form genital double-somite; fusion incomplete laterally. Genital double-somite (Fig. 6A–C) symmetrical, 1.7 times longer than wide, subdivided by almost completely continuous suture line except for short lateral sections just above genital opercula; patches of setules located subdistally on both sides of somite. Single copulatory pore opening mid-ventrally about midway along somite, connected via long copulatory duct with fused seminal receptacles. Paired gonopores located laterally, connected to receptacle by long receptacle ducts. Gonopores covered by opercula derived from sixth legs, each armed with long plumose seta plus 2 short spines. Double-somite and free abdominal somites ornamented with entire hyaline frill around posterior margin. Free abdominal somites ornamented proximally with transverse series of short rows of tiny setules. Anal somite deeply incised (Fig. 6D), about 1.5 times longer than preceding abdominal somite; operculum ornamented with tiny hyaline frill and flanked by pair

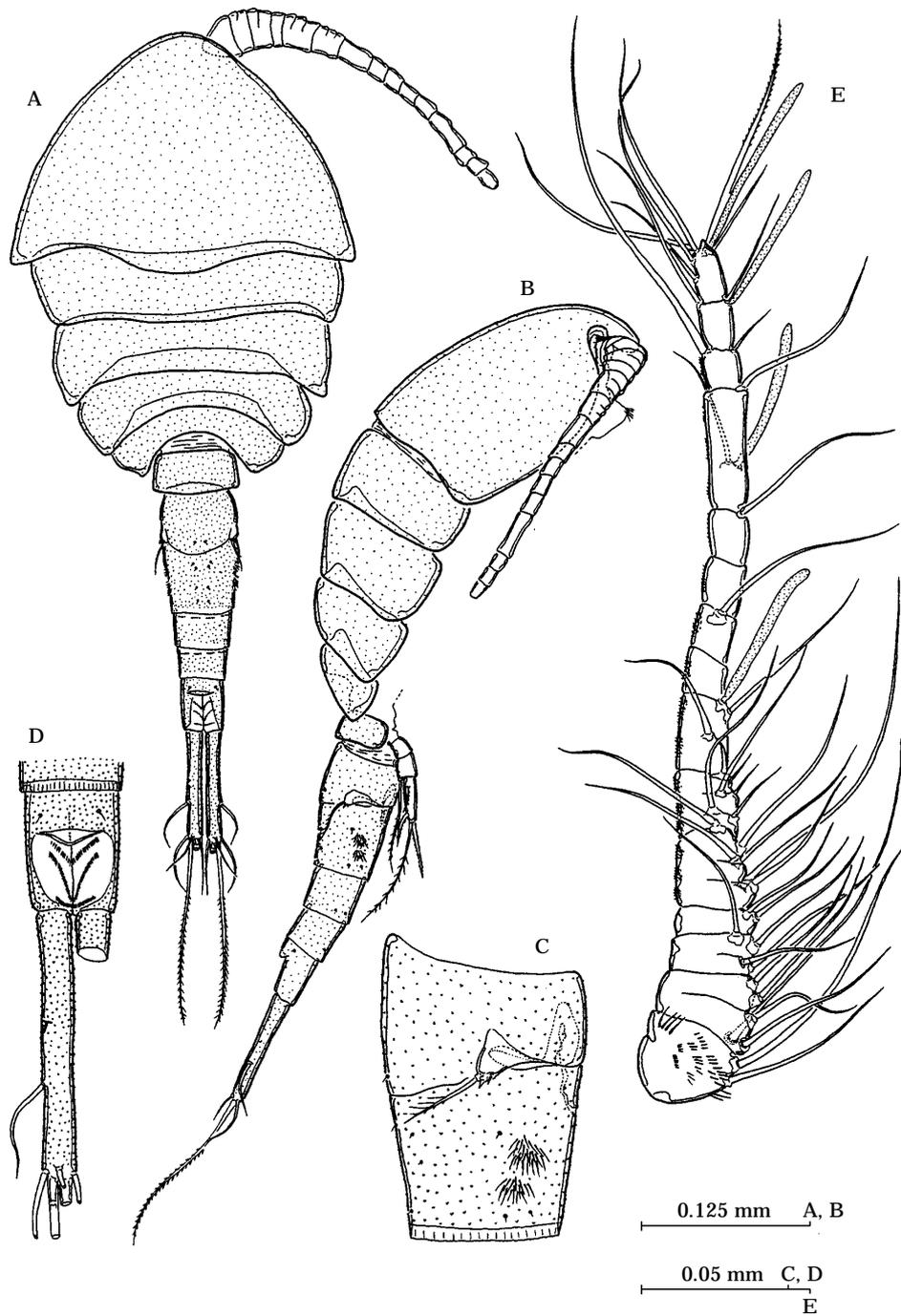


Figure 6. *Muceddina multispinosa*, gen. nov., sp. nov., Adult female. A, habitus, dorsal; B, ventral; C, genital double-somite, lateral; D, anal segment and caudal rami, dorsal; E, antennule.

of dorsal sensillae; 3 transverse rows of setules adorning inner side of both distal lobes of somite. Caudal rami (Fig. 6D) elongate, about equal in length to 3 preceding somites together, symmetrical, 7.6 times longer than wide. Armature consisting of 7 setae and subdistal row of spinules (not figured) on ventral surface. Seta I vestigial, implanted about two fifths of distance along lateral margin of ramus; seta II implanted about two thirds of distance. Relative lengths of distal setae (except seta VI, which was lacking in all the individuals examined) as in Fig. 6D.

Antennules (Fig. 6E) symmetrical, 15-segmented, extending beyond posterior margin of prosome. Armature as follows: segment 1 (corresponding to fused ancestral segments I and II), 2 setae; segment 2 (ancestral segments III to V), 5 setae; segment 3 (ancestral segments VI and VII), 4 setae; segment 4 (ancestral segment VIII), 2 setae; segment 5 (ancestral segments IX to XI), 6 setae; segment 6 (ancestral segments XII to XIV), 6 setae; segment 7 (ancestral segments XV and XVI), 2 setae + aesthetasc; segment 8 (ancestral segment XVII), naked; segment 9 (ancestral segment XVIII), 1 seta; segment 10 (ancestral segment XIX), naked; segment 11 (ancestral segment XX), 1 seta; segment 12 (ancestral segments XXI to XXIII), 2 setae + aesthetasc; segment 13 (ancestral segment XXIV), 2 setae; segment 14 (ancestral segment XXV), 2 setae + aesthetasc; segment 15 (ancestral segments XXVI to XXVIII), 6 setae + aesthetasc. Posterior side of almost every segment bearing patch of short setules; ornamentation on compound segments representing several ancestral segments displaying 1 patch per incorporated ancestral segment, thus helping to clarify homologies between segments. Segment 1 ornamented with several rows of setules.

Antenna (Fig. 7A) 4-segmented. First segment comprising fused coxa and basis, armed with inner basal seta distally; outer margin covered by dense patch of setules; several transverse rows of tiny denticles ornamenting segment, as figured. Endopodal setal formula 1,5,7. Outer margin of first endopodal segment covered by dense patch of spinules. Outer margin of second endopodal segment produced distally into pointed process bearing row of long bristles on inner margin. Third segment of endopod with pointed process midway along outer margin, plus marginal row of setules in distal half.

Mandible (Fig. 7B) with coxal gnathobase bearing 5 sharp, serrated blades, plus 1 marginal spine, 1 marginal pointed process, and row of tiny denticles. Palp biramous, with endopod much longer than exopod. Basis with single seta. Endopod about as long as basis, 2-segmented, with proximal segment twice as long as distal; setal formula 3,5. Exopod reduced in size, 4-segmented, with setal formula 1,1,1,2. Several patches of tiny spinules on palp segments, distributed as figured.

Maxillule (Fig. 7C) with well developed praecoxal arthrite, armed with 9 thick, unequal spines plus 1 isolated seta on posterior surface. Coxal epipodite with 3 marginal setae; coxal endite absent. Proximal and distal endites of basis discrete, bearing 3 and 1 setae. Endopod 1-segmented, bearing 6 setae. Exopod 1-segmented, with 4 distal setae. Several marginal and transverse rows of tiny denticles and setules adorning segments, as figured.

Maxilla (Fig. 7D) powerfully developed, 6-segmented. Praecoxa and coxa completely separate, with endite formula 4,1,3,3; distal part of praecoxa covered by tiny denticles, few sparse rows of spinules on coxa. Basis with large endite bearing claw-like spine plus 2 unequal setae; row of 3 long spinules on endite. Endopod 3-segmented, proximal segment representing fused first and second ancestral endopodal segments, setal formula (2 + 2), 2,4.

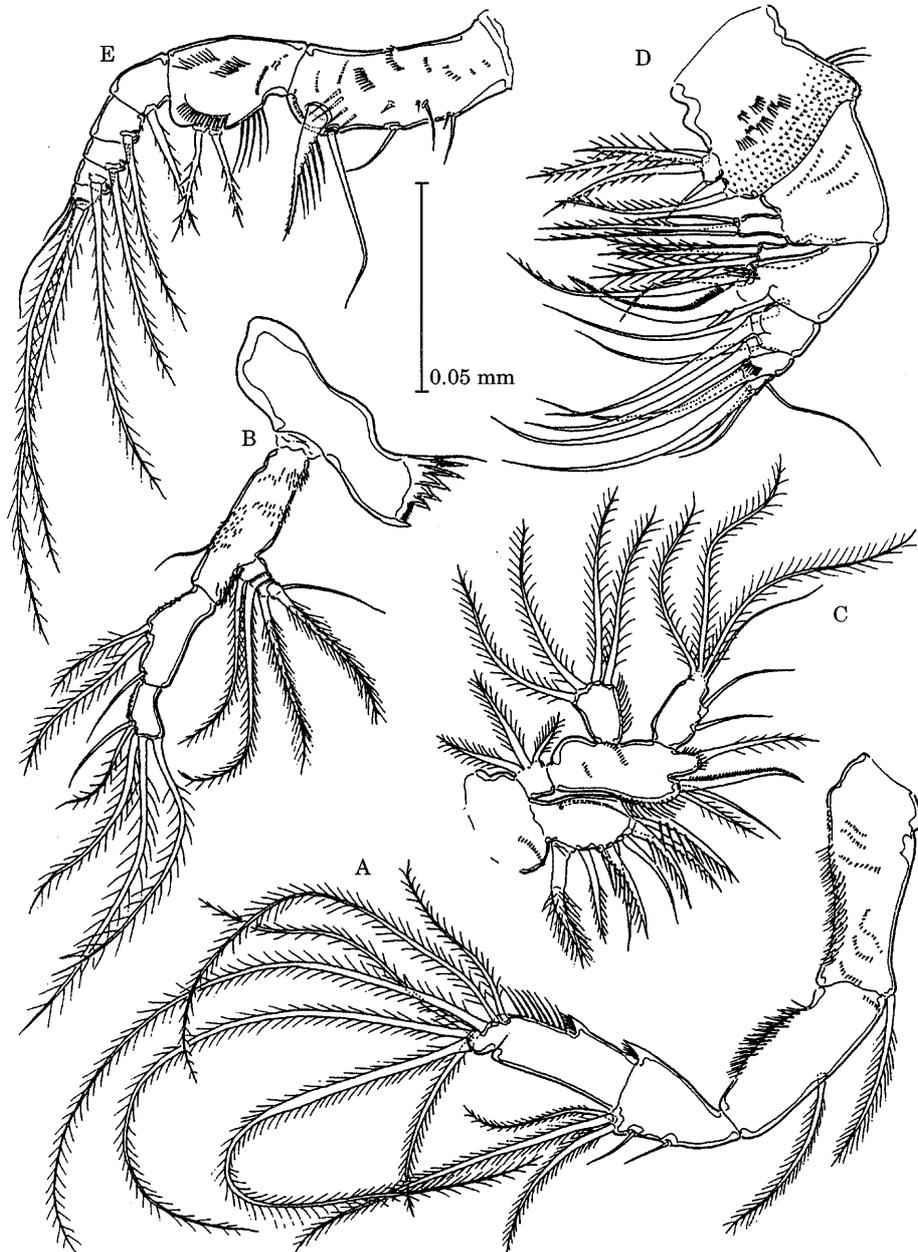


Figure 7. *Muceddina multispinosa* gen. nov., sp. nov.; Adult female. A, antenna; B, mandible (palp has been rotated during preparation so exopod appears on inner side of basis); C, maxillule; D, maxilla; E, maxilliped.

Maxilliped (Fig. 7E) well developed, 7-segmented. Praecoxa and coxa fused forming syncoxa; syncoxal endites weakly discernible; distal endite with thick spinulate seta plus long slender seta, proximal endites comprising 3 medium length setae, possibly plus 2 smaller elements although these possibly ornamentation

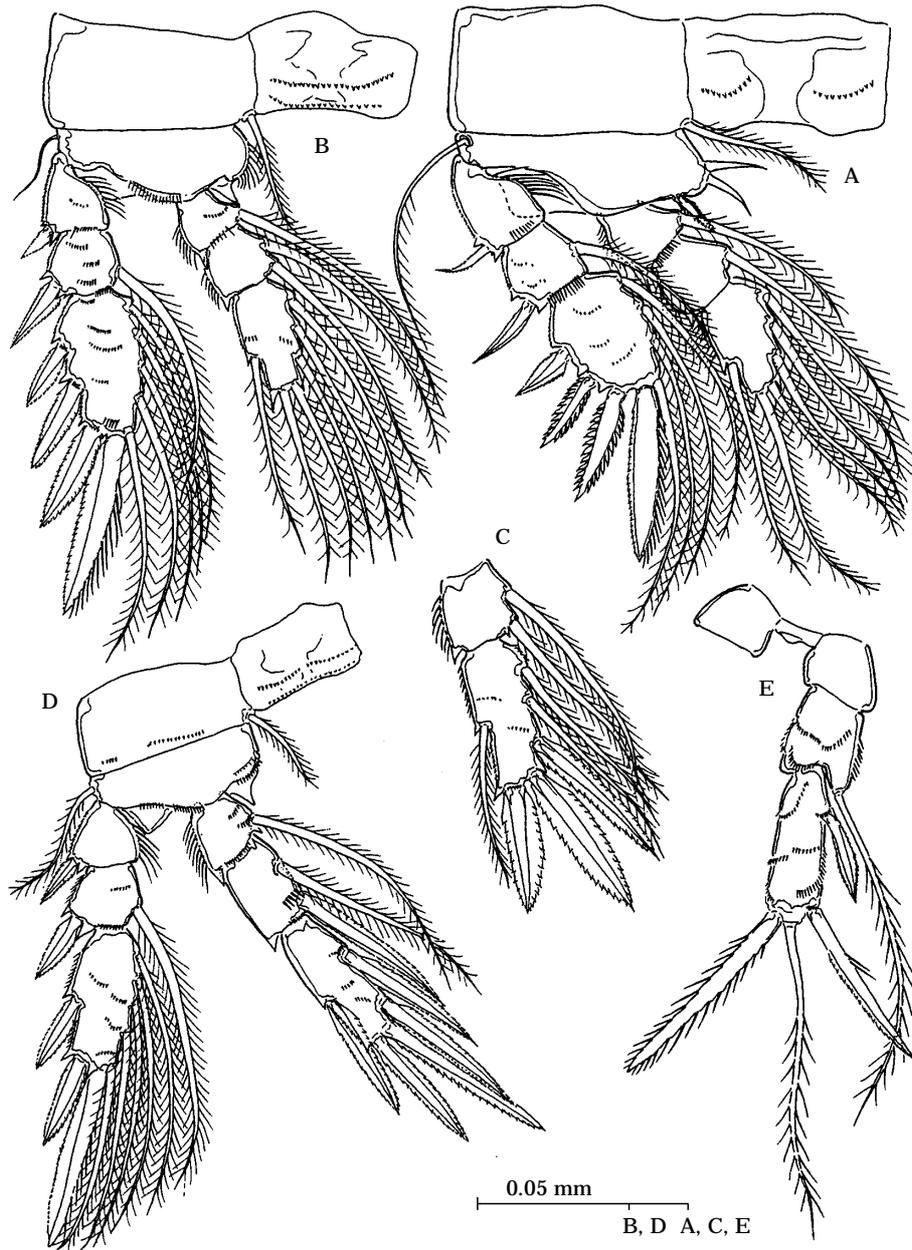


Figure 8. *Muceddina multispinosa* gen. nov., sp. nov.; Adult female. A, leg 1; B, leg 2; C, second and third endopodal segments of leg 3; D, leg 4; E, leg 5.

elements; ornamentation as figured. Basis with medial margin swollen, ornamented with marginal row of long setules proximally and submarginal row of short spinules distally; 2 setae about midway of margin; other oblique rows of tiny setules and denticles as figured. Endopod 5-segmented, setal formula 1,1,1,1,4.

Swimming legs 1 to 4 (Figs 8A-D) biramous, both rami 3-segmented, endopods longer than exopods except in leg 4. Coxae of leg pairs joined by intercoxal sclerite; intercoxal sclerites of legs 2 to 4 ornamented with 2 parallel rows of tiny denticles; short row of denticles on each side of sclerite of leg 1. Armature as follows:

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

Inner margin of basis of leg 1 bearing 2 or 3 thick, spine-like processes; true inner basal spine with serrated marginal flanges and with integumental interruption apparent at its origin on segment; also small row of denticles close to its origin on segment. Other secondary ornamentation as represented in figures.

Fifth legs (Fig. 8E), uniramous, 3-segmented, joined by intercoxal sclerite. Coxa and basis separate, former unarmed, latter with distal long seta on outer margin. Distal segment (exopod) as long as preceding 2 segments together, about 3 times as long as wide, produced distally into median process bearing long seta; 1 subdistal, stout spine present on each side of process, inner stouter; spine ornamented with serrated flanges located in proximal third of outer margin of segment. Ornamentation on segments as figured.

Adult male. Body (Fig. 9A,B) up to 0.52 mm long, resembling female except with a slightly more laterally compressed prosome and somewhat shorter caudal rami. Urosome 6-segmented, with genital somite (Fig. 9A-C) symmetrical, laterally expanded; pair of gonopores opening ventrally at posterior border of somite. Sixth legs reduced to paired opercular flaps, each armed with 3 long, subequal setae; inner margin of flaps produced into pointed process distally. Ventral surface of first abdominal somite adorned with 3 transverse series of short rows of setules.

Antennules (Fig. 9D) 17-segmented, symmetrical, digeniculate. Genuculations between segments homologous with ancestral segments XV and XVI, and between XX and XXI. Segment 11 (XV) cup-shaped, forming sheath around proximal half of segment 12 (XVI). Armature as follows: segment 1 (corresponding to fused ancestral segments I and II), 2 setae + aesthetasc; segment 2 (partially fused ancestral segments III to V), 5 + aesthetasc; segment 3 (partially fused ancestral segments VI and VII), 4 setae; segment 4 (ancestral segment VIII), 2 setae; segment 5 (ancestral segment IX), 2 + aesthetasc; segments 6 to 9 (ancestral segments X to XIII), 2 setae each; segment 10 (ancestral segment XIV), 2 + aesthetasc; segment 11 (ancestral segment XV), 2 setae; segment 12 (ancestral segment XVI), 2 + aesthetasc; segment 13 (ancestral segment XVII), 2 setae; segment 14 (ancestral segment XVIII), 2 setae + aesthetasc; segment 15 (partially fused ancestral segments XIX and XX), 2 setae plus 1 spine-like process; segment 16 (ancestral segments XXI to XXIII), 1 seta,

2 spine-like processes + aesthetasc; distal segment (ancestral segments XXIV to XXVIII), 10 + 2 aesthetascs. Ornamentation on segments as in female.

Other mouthparts and swimming legs 1 to 4 as in female in segmentation and setation.

Fifth legs (Fig. 9E) 4-segmented, coxa, basis and intercoxal sclerite as in female. Exopod 2-segmented; proximal segment armed with long seta distally on inner

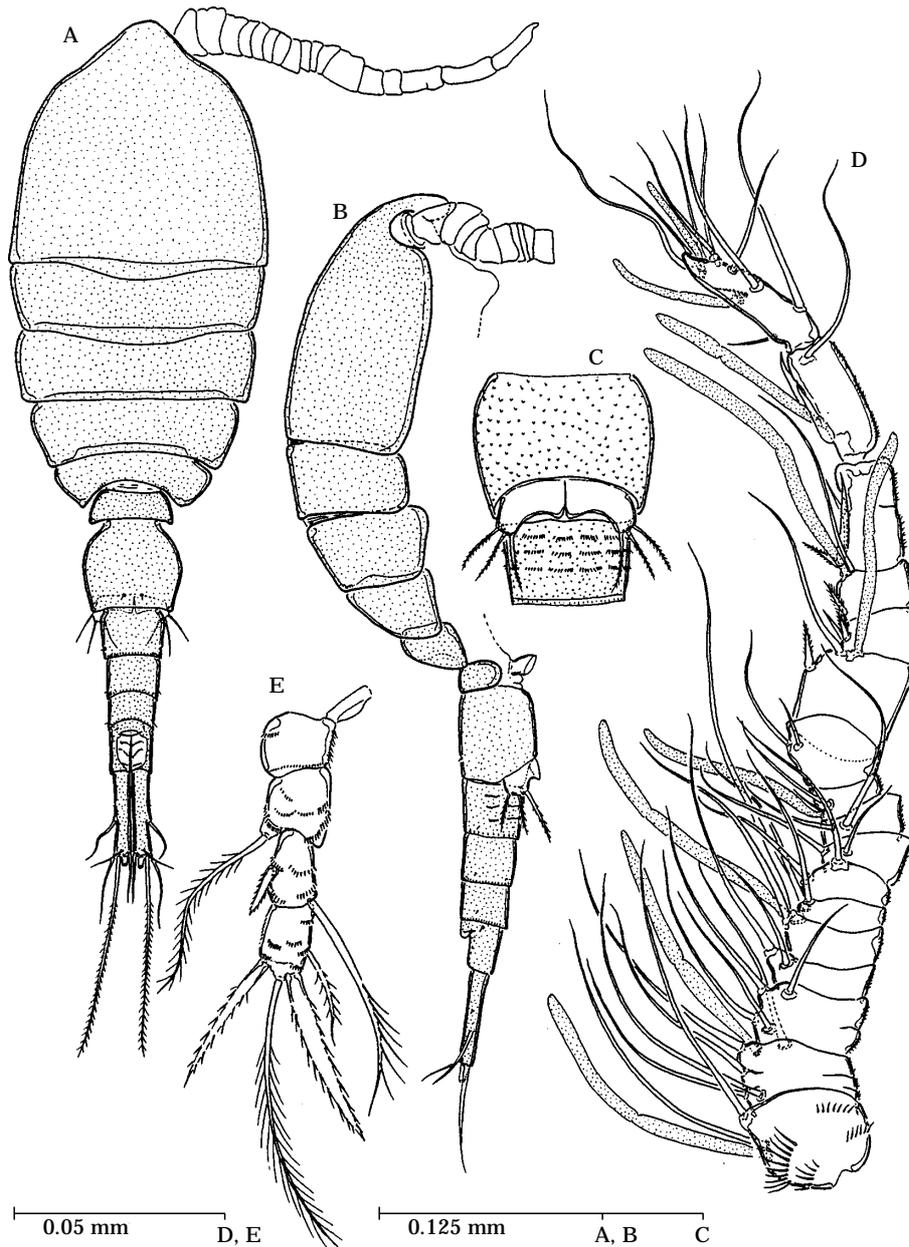


Figure 9. *Muceddina multispinosa* gen. nov., sp. nov.; Adult male. A, habitus, dorsal; B, lateral; C, genital and first abdominal somites, ventral; D, antennule; E, leg 5.

margin and short spine ornamented with serrated flange, located midway along outer margin; distal segment with apex armed with 3 elements as in female, plus short seta implanted about two thirds of distance along inner margin. Ornamentation on segments as figured.

Etymology. The new species is named after the unusual number of spiniform processes displayed on the inner margin of basis of the first leg.

Remarks. The most outstanding feature of *Muceddina multispinosa* gen. nov., sp. nov. is the group of spines displayed on the inner margin of the basis of the first swimming leg, since a single spine or seta in this position is the typical condition in copepods. Cases of secondary multiplication of the armature elements on this segment of leg 1 have been reported from 3 species of the harpacticoid genus *Scottopsyllus* Kunz, 1962, where 5 setae are present at the inner angle (Huys & Boxshall, 1991). In *Muceddina*, as stated above, close examination of the additional 'spines' reveals that they are ornamentation elements because they lack the connection through the integument that is present in all true setation elements.

Another remarkable feature of *Muceddina* gen. nov. is the almost completely subdivided genital double-somite of the female. In the great majority of cyclopoids the genital and first abdominal somites are fused to form a genital double-somite, as is the case for all other members of the Cyclopinidae, the Oithonidae Dana, 1853 and the Archinotodelphyidae Lang, 1949. Separate somites are retained only in some members of the Notodelphyidae Dana, 1853, such as *Notodelphys* Allman, 1847. In the Thaumatopsyllidae Sars, 1913 the fusion is, as in *Muceddina*, incomplete.

Muceddina multispinosa displays also an unusual, slender mandibular palp, bearing a small 4-segmented exopod, and an elongate endopod. This contrasts with the typical palp which displays an endopod which is subequal to or shorter than the exopod.

Other character states displayed by the new taxon are considered as primitive for the Cyclopoida: namely, the first pedigerous somite not integrated into the cephalosome, the presence of 7 setae on the caudal rami, the 17-segmented condition of male antennule (only exceeded by the 18-segmented condition of the male antennule of *Cyclopinoides longicornis* (Boeck, 1872); see Huys & Boxshall, 1991; fig. 2.8.4B), the maxilla with completely separate praecoxa and coxa and the ancestral setation pattern of 4,1,3,3 on endites, the 5-segmented endopod of maxilliped and the segmentation of fifth leg of both sexes, 3-segmented in female, 4-segmented in male.

According to the generic key provided by Huys & Boxshall (1990) for the Cyclopininae, *Muceddina* gen. nov. falls close to *Cyclopinoides* Lindberg, 1953, although the differences between these taxa are noteworthy. Thus, *Cyclopinoides* exhibits a carapace-like extension of the lateral margins of the dorsal cephalic shield (absent in *Muceddina*), the segmentation of the antennules is different (18/20-segmented in the female, 18-segmented in male, compared to 15 in the female and 17 in the male of *Muceddina*), the armature formula of the swimming legs also differs, with each leg lacking the seta on inner margin of the first exopodal segment (present in *Muceddina*). In addition, *Cyclopinoides* exhibits a completely fused genital double-somite and a normal mandibular palp, in contrast to those of *Muceddina*.

DISCUSSION

The two new genera of cyclopinid copepods described above are restricted to caves located very close to the sea, and are absent from more inland, freshwater environments. Most of the caves containing *Troglocyclopina balearica* in the Balearic archipelago are less than 20 m from the seashore, and their waters display salinities in excess of 18‰. Only three localities (Fig. 1:E,F,I) are located more inland, one of them (F) is a cenote 200 m from the coast and has a salinity in excess of 18‰. The other two (E, I) are located 400–500 m inland and have more diluted waters, but precise salinities are not available. Caves inhabited by *Muceddina multispinosa* are also located near the shoreline; precise salinities are not available for the Sardinian cave lakes or the lava tube on Lanzarote, but the Balearic habitats had salinities in excess of 18‰.

Cyclopinids are a wholly marine group typical of the shallow water hyperbenthic and the littoral interstitial environments. The strong link to the coast displayed by the new cave taxa described above is in accordance with these features, and thus with the hypothesis of Stock (1986), who regarded the ancestors of the anchihaline cave fauna as shallow water preadapted lineages rather than deep-sea lineages.

Among copepods troglomorphic features are weakly expressed, apart from the reduction of the visual apparatus and body pigmentation. Lescher-Moutoué (1986) has also pointed to the reduction of clutch size in stygobiont cyclopinids, and the absence of the exopodal seta from the antenna of several *Diacyclops* Kiefer, 1927 from European groundwaters and from the interstitial of Lake Baikal has been also interpreted as a troglomorphic feature (Pesce & Galassi, 1985; Boxshall, Evstigneeva & Clark, 1993). The small clutch-size displayed by *Troglocyclopina balearica* (2 eggs per sac) and the absence of the exopodal seta on the antenna of *Muceddina multispinosa* may, therefore, represent troglomorphic features.

From a biogeographic point of view the discovery of *Muceddina multispinosa* in hypogean stations on islands that are so remote from each other is interesting. The reduced dispersal abilities of cave organisms and the presumed reduction in survivalship outside the cave environment of these blind and unpigmented taxa tend to result in vicariant distribution patterns (Stock, 1993). Several marine, or freshwater with an immediate marine ancestor, stygobiont crustaceans exhibit distributions embracing both the Canary Islands and the Mediterranean region, including the amphipods *Pseudoniphargus* Chevreux, 1901, *Psammogammarus* Karaman, 1955, *Metacrangonyx* Chevreux, 1909 and *Rhipidogammarus* Stock, 1971, the isopod *Caecostenetroides* Fresi & Schiecke, 1968, and the copepods *Speleophriopsis* Jaume & Boxshall, 1995 and *Expansophria* Boxshall & Iliffe, 1987 (Sánchez, 1990; Jaume & García, 1992; Boutin, 1994; Stock, 1988; Stock & Vonk, 1992; Jaume and Boxshall, pers. obs.). All these genera have the Canary Island populations differentiated at the species level from the Mediterranean populations. Stock (1993) interpreted the correspondence between the present distribution of these taxa and the former limits of the Tethys Sea as indicative of an ancient origin. The opening of the Atlantic (*c.* 120 Myr BP) and the breakup of the Tethys Sea (*c.* 20 Myr BP) may have provided the vicariant events reflected in such differentiation.

Detailed comparison of *Muceddina* from the Canary Islands population with the Mediterranean populations has revealed no significant morphological differences. The main interpopulation variability observed was in the number of false spines on the inner margin of the basis of the first swimming leg: 2 false spines are present in

the population from Sardinia, 3 in the Balearic Islands and 2 or 3 in the Canary Islands. Only a small sample of 3 individuals was available from the Balearics. Variability was even observed from left and right legs of some individuals in the Canary Islands population. Variability was also noted for minor features of ornamentation such as the shape of the serrations on the hyaline margins of exopodal spines of the fifth legs, and the degree of microtuberculation of the body integument. Microscopic differences of this nature are rarely reported and are not regarded as significant.

The lack of morphological differentiation between *Muceddina* populations is reminiscent of other stygobionts which have wide but disjunct distributions in the coastal environments around the Mediterranean Basin. Other similar crustacean stygobionts include: (1) copepods such as the formerly mentioned *Halicyclops troglodytes*, *Neocyclops mediterraneus* and *Metacyclops subdolos*, or *Exumella mediterranea* Jaume & Boxshall, 1995, (2) amphipods such as *Salentinella angelieri* Ruffo & Delamare Deboutteville, 1952, *Pseudoniphargus adriaticus* Karaman, 1955 or *Rhipidogammarus rhipidiophorus* (Catta, 1878). The lack of morphological differentiation might indicate that these taxa are more widely distributed (and less isolated) than previously reported, or that their morphology is highly conservative over evolutionary time. We favour the latter interpretation in view of the wide, deep-water separation of the Canary Islands from the Mediterranean Basin.

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 our visits to the Archipelago, and also J. Ginés, A. Ginés, M. Fiol, G. Pons, J.A. Alcover, and J. Damians for their help during fieldwork on Mallorca. A. Martínez and G. Moyà (UIB) provided the salinity data. The support of Mauro Mucedda and other members of 'Gruppo Speleologico Sassarese' (Sassari) during fieldwork on Sardinia is also greatly appreciated. In the Canaries, A. Lainez and F. Pérez Rijo ('Grupo Espeleológico Benisahare', Sta. Cruz de Tenerife), and our colleagues J.L. Martín-Esquivel, E. Sánchez and P. Oromí (Universidad de La Laguna, Tenerife) facilitated the fieldwork there in many ways. This work is supported by the EC Training Research Contract ERBCHBICT941306.

REFERENCES

- Allman GJ, 1847.** Biological Contribution. No. III. Description of a new genus and species of Entomostraca. *Annals and Magazine of Natural History* **20**: 1–9.
- Andrews JN, Ginés A, Pons-Moyà J, Smart PL, Trias M. 1989.** Noves dades sobre el jaciment paleontològic de la Cova de na Barxa (Capdepera, Mallorca). *Endins* **14/15**: 17–26.
- Boeck A. 1872.** Nye Slaegter og Arter af Saltvands-Copepoder. *Forhandlingar i Videnskabselskabet i Kristiania*, **1872**: 35–60.
- Boutin C. 1994.** Phylogeny and biogeography of metacrangonyctid amphipods in North Africa. *Hydrobiologia* **287**: 49–64.
- Boxshall GA, Evstigneeva TD, Clark PF. 1993.** A new interstitial cyclopoid copepod from a sandy beach on the western shore of Lake Baikal, Siberia. *Hydrobiologia* **268**: 99–107.

- Boxshall GA, Iliffe, TM. 1987.** Three new genera and five new species of misophrioid copepods (Crustacea) from anchialine caves on Indo-West Pacific and North Atlantic Islands. *Zoological Journal of the Linnean Society* **91**: 223–252.
- Brady GS. 1880.** *A Monograph of the free and semi-parasitic Copepoda of the British Isles*. London: The Ray Society.
- Catta J-D. 1878.** Sur un amphipode nouveau, le *Gammarus rhipidophorus*. *Actes de la Société Helvétique des Sciences Naturelles Reunie a Bex les 20, 21 et 22 Aout 1877, Compte-Rendu 1876/1877, 60^e Session*. 256–263.
- Chevreaux E. 1901.** Amphipodes des eaux souterraines de France et s'Algerie. *Bulletin de la Société Zoologique de France* **26**: 168–179, 197–205, 216–239.
- Chevreaux E. 1909.** Amphipodes. *Archives de Zoologie* **2**: 27–42.
- Claus C. 1862.** Untersuchungen über die Organisation und Verwandtschaft der Copepoden *Verhandlungen der Physikalisch-Medizinischen Gesellschaft zu Würzburg* **3**: 51–103.
- Dana JD. 1853.** Crustacea. In. *United States exploring expedition during the years 1838–1842 under the command of Charles Wilkes*. **13**(1,2): 1–1618).
- Fresi E, Schiecke U. 1968.** *Caecostenetrioides ischitanum* (Isopoda: Parastenetriidae) a new genus and species from the Bay of Naples. *Publicazioni della Stazione Zoologica di Napoli* **36**: 427–436.
- Ginés A, Ginés J. 1987.** Características espeleológicas del karst de Mallorca. *Endins* **13**: 3–19.
- Ginés A, Ginés J. 1992.** Las Coves del Drac (Manacor, Mallorca). Apuntes históricos y espeleogenéticos. *Endins* **17/18**: 5–20.
- Ginés A, Ginés J, Pons-Moyà J. 1975.** Nuevas aportaciones al conocimiento morfológico y cronológico de las cavernas costeras mallorquinas. *Speleon* (Monografía 1): 49–56.
- Herbst H-V. 1955.** Cyclopoida Gnathostoma (Crustacea Copepoda) von der brasilianischen Atlantikküste. *Kieler Meeresforschungen* **11**: 214–229.
- Herbst H-V. 1986.** Copepoda: Cyclopoida aus dem Meeres- und Brackwasser-Interstitial. In. Botosaneanu L, ed. *Stygofauna Mundi*. Leiden: EJ Brill, 313–320.
- Huys R, Boxshall GA. 1990.** The rediscovery of *Cyclopicina longifurcata* (Scott)(Copepoda: Cyclopinidae) in deep water in the North Atlantic, with a key to genera of the subfamily Cyclopininae. *Sarsia* **75**: 17–32.
- Huys R, Boxshall GA. 1991.** *Copepod Evolution*. London: The Ray Society.
- Jaume D, Boxshall GA.** in press. A new genus and two new species of cave-dwelling Misophrioid copepods from the Balearic islands (Mediterranean). *Journal of Natural History*.
- Jaume D, García L. 1992.** A new *Psammogammarus* (Amphipoda: Melitidae) from Cabrera (Balearic Islands). *Stygologia* **7**: 107–115.
- Karaman SL. 1955.** Über einige Amphipoden des grundwassers des jugoslaviaschen Meeresküste. *Acta Musei Macedonici Scientiarum Naturalium* **2**: 223–242.
- Keifer F. 1927.** Versuch eines Systems der Cyclopiden. *Zoologischer Anzeiger* **73**:302–308.
- Keifer F. 1938.** Cyclopiden (Crus. Cop.) aus süditalienschen Brunnen und Höhlen. *Zoologischer Anzeiger* **123**: 1–12.
- Keifer F. 1954.** Einige Cyclopiden aus Südfanzosische Höhlen. *Notes Biospéologiques* **9**: 157–165.
- Keifer F. 1960.** Beiträge zur Copepodenkunde (XX). *Zoologischer Anzeiger* **23**: 147–159.
- Kunz H. 1962.** Revision der Paramesochrideae (Crust. Copepoda). *Kieler Meeresforschungen* **18**: 245–257.
- Lang K. 1949.** On a new copepod family related to Notodelphyidae and on two new copepod species from South-Georgia. *Arkiv för Zoologi* **42**: 1–7.
- Lescher-Moutoué F. 1986.** Copepoda Cyclopoida Cyclopidae des eaux douces souterraines continentales. In: Botosaneanu L, ed. *Stygofauna Mundi*. Leiden: EJ Brill, 299–312.
- Lindberg K. 1953.** La sous-famille des Cyclopininae Kiefer (Crustacés Copépodes). *Arkiv för Zoologi* **4**: 311–325.
- Lotufo GR, da Rocha CEF. 1991.** Copepods from interstitial water of Salvador, Brazil. I. *Cuipora janaina* gen. n., sp. n. & *Cyclopina caiala* sp. n. (Cyclopoida: Cyclopinidae). *Bijdragen tot de Dierkunde* **61**: 107–118.
- Mucedda M. 1983.** L'Inghiottoio della Dragunara (Alghero, Capo Caccia). *Bollettino del Gruppo Speleologico Sassarese* **7**: 41–43.
- Mucedda M. 1988.** La Grotta Verde di Capo Caccia (Alghero). *Bollettino del Gruppo Speleologico Sassarese* **11**: 19–27.
- Oromí P, Hernández JJ, Izquierdo I, Martín JL, Medina AL. 1989.** *Catálogo de las cavidades volcánicas de Canarias. II. Lanzarote*. Unpublished report, Consejería Territorial del Gobierno de Canarias.
- Pesce GL, Galassi DP. 1985.** Due nuovi *Diacyclops* del complesso 'languidoidei' (Copepoda: Cyclopidae) di acque sotteranee di Sardegna e considerazioni sul significato evolutivo dell'antenna nei copepodi stigobionti. *Bollettino del Museo Civico di Storia Naturale di Verona* **12**: 411–418.
- Philippi 1843.** Fernere Beobachtungen über die Copepoden. *Archiv für Naturgeschichte* **9**: 54–71.
- Rocha CEF da, Iliffe T. 1994.** *Troglocyclops janstocki*, new genus new species, a very primitive cyclopid (Copepoda: Cyclopoida) from an anchialine cave in the Bahamas. *Hydrobiologia* **292/293**: 105–111.
- Ruffo S, Delamare Deboutteville C. 1952.** Deux nouveaux Amphipodes souterrains de France. *Salentiella angelieri* n.sp. et *Bogidiella chappuisi* n.sp. *Comptes Rendu de l'Académie des Sciences, Paris* **234**: 1636–1638.
- Sánchez E. 1990.** A new species of *Pseudoniphargus* (Amphipoda) from subterranean waters in Tenerife (Canary Islands). *Hydrobiologia* **196**: 51–63.
- Sars GO. 1913.** *An Account of the Crustacea of Norway. Copepoda Cyclopoida. Parts I & II*. Bergen.
- Scott T. 1894.** Additions to the fauna of the Firth of Forth. *Report of the Fishery Board for Scotland* **12**: 231–271.

- Stock JH. 1971.** A revision of the *Sarathrogammarus*-group (Crustacea, Amphipoda). *Bijdragen tot de Dierkunde* **41**: 94–129.
- Stock JH. 1986.** Deep sea origin of cave faunas: an unlikely supposition *Stygologia* **2**: 105–111.
- Stock JH. 1988.** A new *Rhipidogammarus* (Crustacea, Amphipoda) from Tenerife: first record of the genus outside the Mediterranean region and its biogeographic implications. *Hydrobiologia* **169**: 279–292.
- Stock JH. 1993.** Some remarkable distribution patterns in stygobiont Amphipoda. *Journal of Natural History* **27**: 807–819.
- Stock JH, Vonk R. 1992.** Marine interstitial Amphipoda and Isopoda (Crustacea) from Santiago, Cape Verde Islands. *Bijdragen tot de Dierkunde* **62**: 21–36.
- Trias M. 1993.** Catàleg espeleològic. In: Alcover JA, Ballesteros E, Fornós JJ, eds. *Història Natural de l'Arxipèlag de Cabrera*. Palma de Mallorca: Ed. Moll — CSIC, 131–152.
- Trias M, Mir F. 1977.** Les coves de la zona de C'an Frasquet — Cala Varques. *Endins* **4**: 21–42.
- Wilson CB. 1932.** The Copepoda of the Woods Hole region, Massachusetts. *Bulletin of the United States National Museum* **158**: 1–635.