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Three new genera and five new species of misophrioid copepods (Crustacea) from anchialine caves on Indo-West Pacific and North Atlantic Islands

GEOFFREY A. BOXSHALL

Department of Zoology, British Museum (Natural History), Cromwell Road, London SW7 5BD

AND

THOMAS M. ILIFFE

Bermuda Biological Station for Research, Ferry Reach 1–15, Bermuda

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Misophrioid copepods are described from anchialine caves on Palau, Western Caroline Islands and on Lanzarote, Canary Islands. A new species of *Misophria,* **M. kororiensis sp. nov.**, is described, based on material found in a submerged cave on Koror Island, Palau. A new genus, **Expansophria gen. nov.**, characterized by a distensible but unenclosed first pedigerous somite, is established for two new species. The type species, **E. dimorpha sp. nov.**, was collected from a flooded lava tube (Jameos del Agua) on Lanzarote and the second species, **E. apoda sp. nov.**, from a sinkhole on Ngeruktabel Island, Palau. Two other new genera are erected for new species collected in Jameos del Agua on Lanzarote, **Palpophria gen. nov.** and **Dimisophria gen. nov.** The former is characterized by extremely long, uniramous mandibular palps, the latter by the reduced number of spines on the swimming legs. In addition, a fourth genus and species, represented only by an unnamed copepodid IV stage, was recorded from Jameos del Agua. It is suggested that at least some of the cave-dwelling misophrioids represent descendants of deep-sea forms which became separated by vertical vicariance events.

KEY WORDS:—Copepoda – Misophrioida – cave-dwelling – anchialine caves – taxonomy.

CONTENTS

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INTRODUCTION

Anchialine habitats have recently been defined as 'bodies of haline water, usually with a restricted exposure to open air, always with more or less extensive subterranean connections to the sea, and showing noticeable marine as well as terrestrial influences' (Stock, Iliffe & Williams, 1986). Anchialine caves are known to harbour many interesting crustaceans, including a new class, Remipedia (Yager, 1981), a representative of the new peracaridan order, Mictacea (Bowman & Iliffe, 1985) and one of a new order of copepods, Platycopioida (Fosshagen & Iliffe, 1985). The discovery of a new genus and two new species of misophrioid copepods from anchialine caves on Bermuda (Boxshall & Iliffe, 1986) revealed that this habitat was also exploited by the Misophrioida, previously considered to be essentially a deep-sea taxon (Boxshall, 1984).

This paper describes three new genera and five new species of misophrioids from anchialine caves on Indo-West Pacific and North Atlantic islands. The collections also contained a copepodid IV stage of a further species which is not named. This raises the number of known misophrioids to 15, eight of which occur in anchialine caves, six in the deep-sea plankton, and one in shallow European coastal waters, from Norway through to the Mediterranean and the Red Sea.

THE CAVES

The misophrioids were collected in three anchialine caves, two on islands in Palau in the Western Caroline Islands and one on Lanzarote in the Canary Islands. South Point Cave on Koror (Oreor) Island, Palau, is entered via a small, immediately subtidal, opening on the coast at the southernmost tip of the island. This limestone cave consists of three completely submerged chambers angling down to a maximum depth of 18 m and can only be explored by diving. The first chamber, which receives a shaft of sunlight from the entrance opening, contains many sponges and hydroids, plus numerous fish taking refuge in the cave. The second and third chambers are in total darkness, have fewer encrusting organisms on the walls and have a fine silt covering the floor. Salinity in the cave is at or very close to open ocean levels. A slight reversing tidal current was noted at the entrance. Other animals collected from the cave and still being identified include sponges, polychaetes, calanoids, mysids, isopods, amphipods, shrimps and fishes.

The Cenote on Ngeruktabel Island, Palau, was named for its resemblance to the cenotes or sheer-walled limestone sinkholes of the Yucatan Peninsula. It is located inland, about 75 m from the coast, in a saddle between two highly karstified limestone hills. The cave consists of a pit about 20 m deep and 15 m in

diameter that was descended with ropes. A large pool at the base of the drop extends back under an overhanging roof to a section of the cave receiving only very dim and indirect illumination. Underwater the Cenote ends in an impassable jumble of collapse blocks at a depth of 11 m. Salinity at the surface was 26‰, while at 11 m it reached 29‰. Several large logs and three to four human skeletons, probably of considerable age, were present in the back section of the pool. The walls of the underwater cave were bare with no encrusting organisms. Polychaetes, calanoids, ostracods, isopods, amphipods, shrimps and ophiuroids were also collected here and are being identified.

The Jameos del Agua Cave on Lanzarote is a lava tube formed by an eruption of the volcano La Corona about 3000–5000 years ago (Wilkens & Parzefall, 1974). This cave is the type-locality of a remipede, *Speleonectes ondinae* (Valdecasas), (Iliffe, Wilkens, Parzefall & Williams, 1984; Valdecasas, 1984). The cave begins at the base of the volcano, extends 6 km to the coast as an unbranching but sometimes multi-level passage and continues for an additional explored distance of 1.4 km underwater, beneath the sea floor. At the limit of exploration the cave was at a depth of 53 m and still continuing. Although a number of collapse entrances to the cave exist inland, only a single tiny hole in the ceiling, 700 m into the underwater cave, is known to connect directly with the open sea. The water in the cave is very clear, with a salinity nearly identical to that of the open sea. Moderate reversing currents, producing a tidal range of about 2 m in inland cave pools, sweep through the underwater passages.

Several of the troglobitic species inhabiting the Jameos del Agua, including the galatheid crab *Munidopsis polymorpha* Koelbel and the polynoid polychaete *Gesiella jameensis* (Hartmann-Schroder), show affinities to deep sea species. Other endemic taxa present, such as the remipede *Speleonectes ondinae*, the paranthurid isopod *Currassanthura canariensis* Wagele, the mysid *Heteromysidoides cotti* (Calman), the gammaridean amphipod *Hadzia acutus* (Andres), the oniscoid isopod *Halophiloscia canariensis* Dalens, and the thermosbaenacean *Halasbaena fortunata* Bowman & Iliffe, have closely related forms occupying similar habitats in the Western Atlantic. Two additional endemic species, the pardaliscid amphipod *Spelaeonicippe buchi* (Andres) and the thaumatocyprid ostracod *Danielopolina wilkensi* Hartmann, show both deep sea and amphi-Atlantic distributions.

SYSTEMATICS

Family Misophriidae

Genus *Misophria* Boeck

***Misophria kororiensis* sp. nov.**

(Figs 1–3)

Description

Adult female (Fig. 1A): length 685 μm. Prosome large, apparently 4-segmented but with first pedigerous somite free and entirely concealed beneath a carapace-like extension from the posterior margin of the maxilliped-bearing somite. Nauplius eye absent. Rostrum small, posteroventrally directed, not fused to

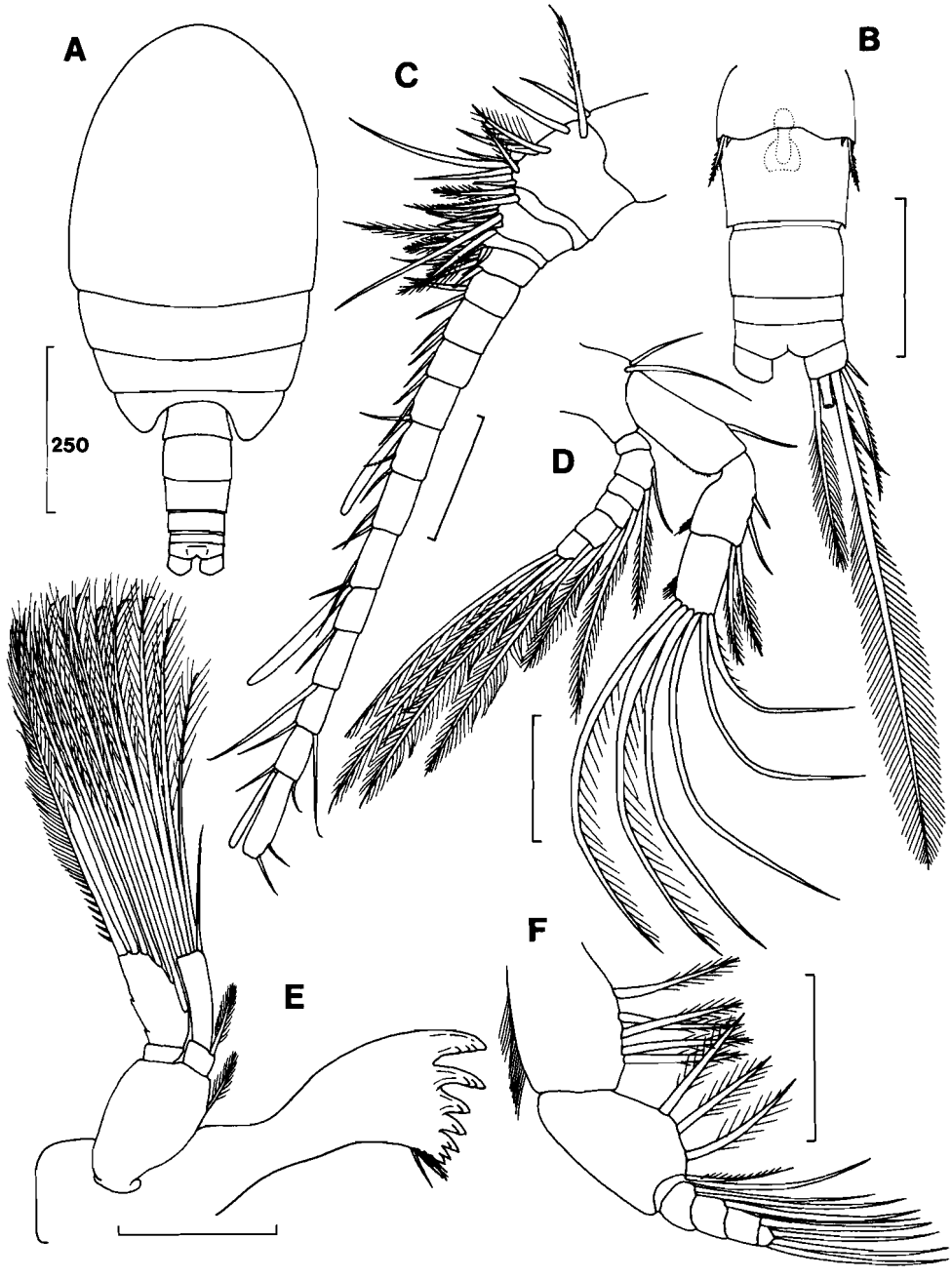

Figure 1. ***Misophria kororiensis* sp. nov.** Holotype female. A, dorsal; B, urosome excluding fifth *pedigerous somite, ventral; C, antennule, dorsal; D, antenna, posterior; E, mandible, posterior; F,* maxilliped, posterior. Scale bars = 50 μm, except for A (250 μm).

labrum. Urosome (Fig. 1B) 6-segmented. Prosome and urosome somites 1 to 5 ornamented with a reticulum of fine lamellae. Urosome somite 6 without such ornamentation. Caudal rami wider than long; armed with 2 long distal margin

setae, 2 medium-length distal angle setae, a dorsal seta near the midposterior margin and a short seta located subapically on the lateral margin.

Antennule (Fig. 1C) 18-segmented; segments armed as follows: I-1, II-9, III-2, IV-6, V-3, VI-3, VII-2, VIII-2, IX-2, X-2 + 1 aesthetasc, XI-2, XII-2, XIII-2+1 aesthetasc, XIV-1, XV-1, XVI-2, XVII-2+1 aesthetasc, XVIII-2 (incomplete).

Antenna (Fig. 1D) sympod with 2 distomedial setae; endopod 3-segmented, exopod 6-segmented. Endopod segment 1 with 1 distomedial seta; segment 2 with 2 short setae on medial margin and 2 longer setae at distomedial angle, lateral margin with patch of setules; segment 3 with 6 long, curved apical setae and a patch of lateral margin setules. First exopod segment unarmed, second armed with 2 medial setae, third to fifth each with 1 plumose seta on medial margin, sixth bearing 3 plumose setae around apex.

Mandible (Fig. 1E) with well-developed gnathobase bearing distally a row of 5 multicusped blades, 2 simple blades and some spinules. Mandibular palp comprising basis bearing a medial plumose seta, 2-segmented endopod and an indistinctly segmented exopod. Endopod segment 1 with 1 short plumose seta, segment 2 with 1 short and 5 long plumose setae apically. Exopod segment 1 distinct and unarmed, remaining part of exopod with 2 partial sutures, bearing 6 long plumose setae.

Maxillule (Fig. 2A), praecoxal arthrite with 14 distal elements; coxal and basal endites each with 4 setae. Outer lobe rudimentary, represented by 6 plumose setae on outer surface of segment. Maxillulary palp biramous with 2-segmented endopod and 1-segmented exopod. Endopod segment 1 fused to basis, with 3 distal angle setae; segment 2 with 3 setae on midmedial margin, 2 subapical and 3 apical setae. Exopod with a proximal fringe of pinnules and 10 plumose setae around medial and distal margins.

Maxilla (Fig. 2B) 6-segmented; praecoxa with 5 setae on proximal endite and 3 on distal endite; coxa with 2 setae on proximal endite and 3 on distal endite; basis produced into curved medial claw bearing 3 setae around its base; ramus of 3 short segments bearing a total of 8 spines and setae.

Maxilliped (Fig. 1F) 7-segmented, with 2-segmented protopod comprising syncoxa and basis, and 5-segmented ramus. Syncoxa with 5 medial margin setae, basis with 3 similar setae. Ramus segments 1 to 3 each with 2, segment 4 with 1 and segment 5 with 3 setae.

Legs 1 to 4 (Figs 2C-D, 3A-B) biramous with 3-segmented rami; spine and seta formula as follows:

	coxa	basis	endopod	exopod
leg 1	0–1	I–I	0–1; 0–2; missing	I–1; I–1; III, I, 3
leg 2	0–1	I–0	0–1; 0–2; 2, 2, 3	I–1; I–1; III, I, 4
leg 3	0–1	1–0	0–1; 0–2; 1, 2, 3	I–1; I–1; missing
leg 4	0–1	1–0	0–1; 0–2; 1, 2, 2	I–1; I–1; III, I, 4

Pinnule rows present on medial and lateral margins of all endopod segments and on medial margins of exopod segments except segments 2 and 3 of leg 1. Lateral margins of exopod segments armed with rows of small denticles. Lateral spines on exopod armed with strips of fine membrane on leg 1 and with strips of serrated membrane on legs 2 to 4. Apical spine on exopod armed with pinnules medially and serrate membrane laterally, except on leg 1 which has fine

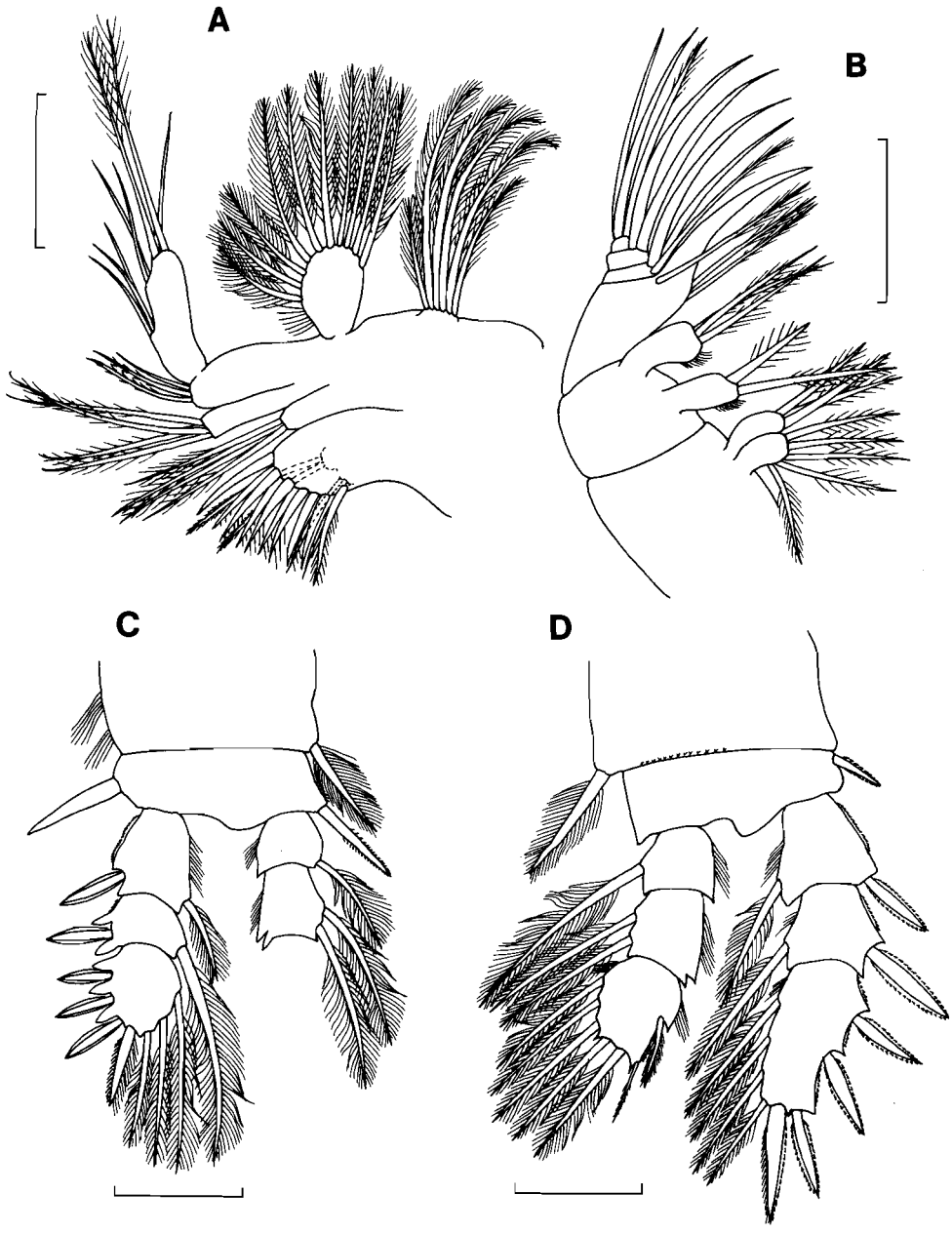

Figure 2. ***Misophria kororiensis* sp. nov.** Holotype female. A, maxillule, posterior; B, maxilla, posterior; C, leg 1, anterior; D, leg 2, anterior. Scale bars = 50 μm.

pinnules laterally as well. Distolateral angle of second endopod segment bifid in all legs.

Leg 5 (Fig. 3C) uniramous, comprising a small unarmed coxa joined to the other coxa of the pair by a rod-like intercoxal sclerite, a basis armed with inner and outer angle setae, and a 2-segmented exopod. Exopod segment 1 with a

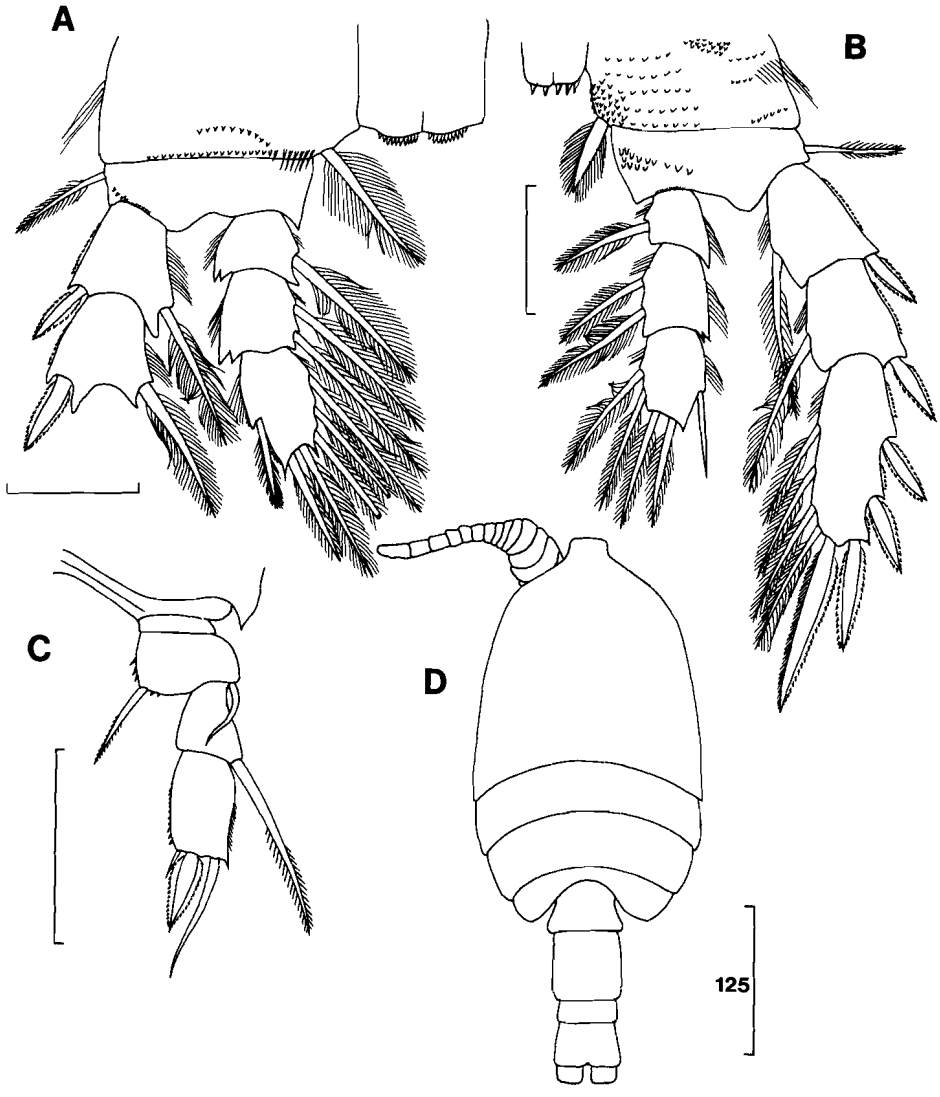

Figure 3. ***Misophria kororiensis* sp. nov.** Holotype female. A, leg 3, anterior; B, leg 4, anterior; C, leg 5, anterior. D, unidentified Copepodid IV stage from Jameos del Agua Cave, Lanzarote. Scale bars = 50 μm except for D (125 μm).

long lateral seta. segment 2 with a lateral seta, a serrate spine and a short medial seta along its distal margin.

Leg 6 (Fig. 1B) represented by a plate overlying the genital opening, bearing an outer seta and inner spinule.

Material Examined

Holotype ♀ collected from South Point Cave, Koror (Oreor) Island, Palau, 3 March 1985, caught with a plankton net towed by a diver in 10–15 m water depths of the second and third chambers; leg. T. M. Iliffe, D. Williams and J. Bozanic. BM(NH) Registration no. 1986.335.

Etymology

The new species is named after the type locality, Koror Island.

Remarks

The new species is placed in the genus *Misophria* Boeck and closely resembles the type and only species, *M. pallida* Boeck, in general morphology, limb segmentation and armature. The fifth legs of *M. kororiensis* and of *M. pallida* are similar in structure and in the number and relative sizes of spines and setae although Sars (1903) interprets the basal part of this leg in *M. pallida* as 1-segmented. The segmentation at the base of this limb is difficult to observe clearly but there appear to be two distinct segments in *M. kororiensis*. The inner angle seta on the basis of both species may represent the endopod which is present, though reduced to a single segment, in *Misophriopsis* Boxshall. Both species of *Misophria* possess a well developed carapace-like extension of the posterior margin of the maxilliped-bearing somite which encloses, dorsally and laterally, the free thoracic somite beneath.

The new species differs from *M. pallida* most noticeably in the segmentation of the antennule, having 18 segments in the female compared to 16 in female *M. pallida*. The other difference is the presence of a very fine seta near the apex of the lateral margin of endopod segment 3 of leg 2. Only the single midmargin lateral seta is present in *M. pallida*, although it is possible that Sars (1903) may have overlooked the additional fine seta.

Genus *Expansophria* nov.

Diagnosis: Misophrioida; first pedigerous somite with areas of folded flexible integument anteriorly but not entirely enclosed by carapace-like extension of maxilliped-bearing somite; lateral margins of dorsal shield incised at level of reflexed antennae and mandibular palps; female antennule 26-segmented, with large aesthetascs on segments VII, XI and XVI; male antennule unigeniculate, 23-segmented; mandibular exopod indistinctly segmented; swimming legs 1 to 4 with 3-segmented rami; leg 5 present or absent.

Type species: ***Expansophria dimorpha* gen. et sp. nov.**

Expansophria dimorpha sp. nov.

(Figs 4–7)

Description

Adult female (Fig. 4A): body length 557–580 μm, based on 2 specimens. Prosome large, 5-segmented. Lateral margins of dorsal cephalic shield with notch (arrowed in Fig. 4B) at level of reflexed antennae and mandibular palps. Cone organs not observed in area beneath reflexed appendages. First pedigerous somite capable of some distension as it possesses areas of folded, flexible integument anteriorly (Fig. 4B). Some ventrolateral distension also occurs to accommodate lateral caecae of midgut. Posterior margin of maxilliped-bearing somite slightly overlapping flexible area of first pedigerous somite (Fig. 4A). Nauplius eye absent. Rostrum small, posteroventrally directed, not fused to labrum. Urosome 6-segmented (Fig. 4C). Caudal rami slightly more than twice as long as wide; armed with 6 setae as in male (Fig. 7A).

Antennule (Fig. 4D) 26-segmented, reaching to posterior margin of second

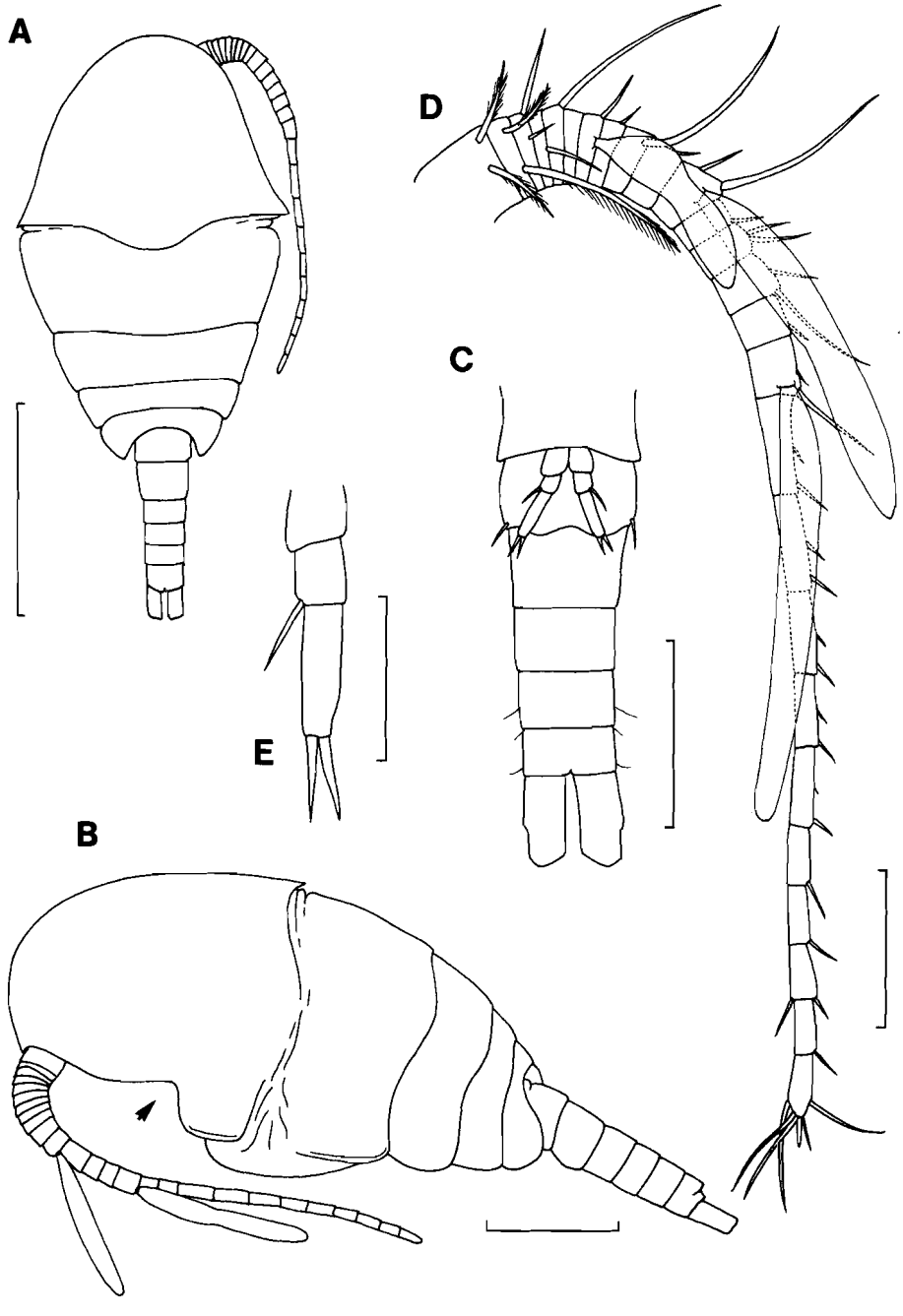

Figure 4. ***Expansophria dimorpha* gen. et sp. nov.** Female. A, dorsal, scale bar = 200 μm; B, lateral, scale bar = 100 μm; C, urosome, ventral, scale bar = 50 μm; D, antennule, ventral, scale bar = 50 μm; E, leg 5, ventral, scale bar = 25 μm.

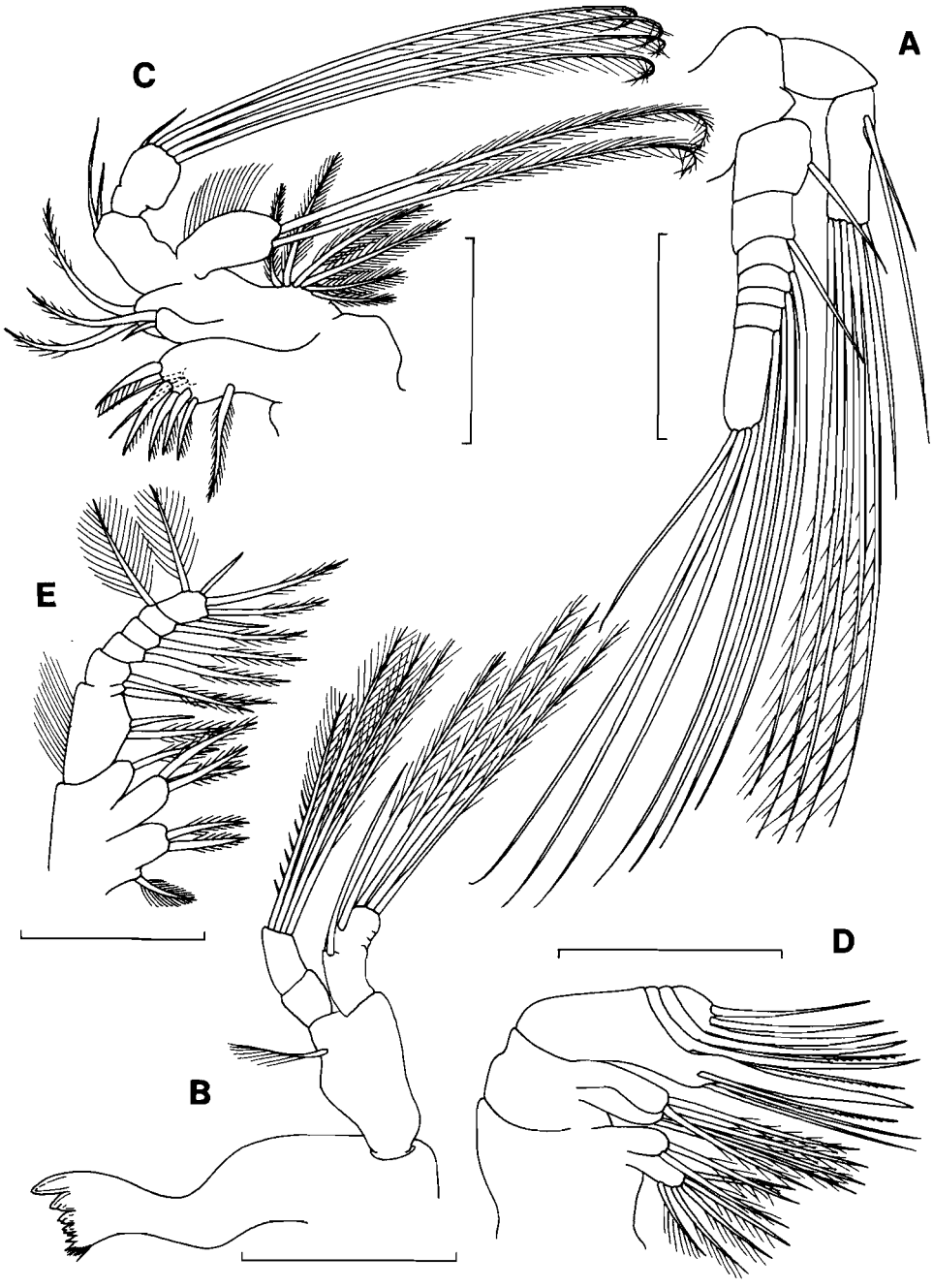

Figure 5. ***Expansophria dimorpha* gen. et sp. nov.** Female. A, antenna, posterior; B, mandible, posterior; C, maxillule, anterior; D, maxilla, posterior; E, maxilliped, posterior. Scale bars = 50 μm.

pedigerous somite; armed as follows: I-2, II-2, III-2, IV-1, V-1, VI-0, VII-1 + 1 aesthetasc, VIII-1, IX-1, X-1, XI-2 + 1 aesthetasc, XII-1, XIII-2, XIV-2, XV-1, XVI-2 + 1 aesthetasc, XVII-2, XVIII-2, XIX-2, XX-2, XXI-2, XXII-

1, XXIII-1, XXIV-2, XXV-1, XXVI-5 + 1 aesthetasc. Aesthetascs on segments XI and XVI very long.

Antenna (Fig. 5A) biramous, with unarmed protopod. First endopod segment unarmed, second with 2 medial margin setae located proximally and 1 short and 5 long plumose setae on distal margin. Exopod 7-segmented, segments 1 to 6 with a single medial margin seta each, segment 7 with 4 apical setae.

Mandibular gnathobase (Fig. 5B) with 1 large simple blade, 3 multicusped blades and 3 small teeth plus a patch of pinnules. Palp comprising basis armed with a medial plumose seta, indistinctly segmented exopod and 2-segmented endopod. Exopod armed with 2 medial and 3 distal setae; endopod segment 1 unarmed, segment 2 with 4 plumose apical setae.

Maxillule (Fig. 5C) of typical structure but with reduced armament; praecoxal arthrite with 8 spines and setae, coxal endite with 1 short and 1 long seta, basal endite with 2 long setae. Outer coxal lobe represented by 6 plumose setae. Endopod with first segment fused to basis, armed with 2 naked setae distally; second segment constricted proximally, bearing 1 short and 4 long plumose apical setae. Exopod with fringe of long pinnules along medial margin and 2 long plumose apical setae.

Maxilla (Fig. 5D) 6-segmented: praecoxa with 5 and 2 setae on proximal and distal endites respectively; coxa with 3 and 2 setae on proximal and distal endites respectively. Basis produced into curved medial claw bearing 3 setae proximally. Ramus 3-segmented, bearing a total of 7 setae.

Maxilliped (Fig. 5E) indistinctly 8-segmented. Syncoxa bearing 3 endites and a single proximal seta representing the proximal praecoxal endite. Basis with 2 medial margin setae. Ramus 6-segmented, first segment partly fused to basis, bearing 1 seta; segments 2 to 4 each with a medial seta; segment 5 with a medial seta and a lateral plumose seta; segment 6 with 1 lateral plumose seta and 4 medial and distal setae.

Legs 1 to 4 (Figs 6A–D) biramous, with 3-segmented rami; spine and seta formula as follows:

	coxa	basis	endopod	exopod
leg 1	0–1	0-I	0–1; 0–1; I, 2, 3	I–1; I–1; III, I, 3
leg 2	0–1	0–0	0–1; 0–2; I, 2, 3	I–1; I–1; III, I, 4
leg 3	0–1	0–0	0–1; 0–2; I, 2, 3	I–1; I–1; III, I, 4
leg 4	0–1	0–0	0–1; 0–2; I, 2, 2	I–1; I–1; III, I, 4

Medial margins of exopods and lateral margins of endopods all with rows of pinnules. All setae on both rami of unusual form, with swollen shafts and shorter pinnules than in *M. kororiensis* (cf. for example, Fig. 2D). Medial setae on coxae typical, with narrow shafts and long pinnules. Lateral spines on exopods armed with strips of smooth membrane, apical spines with lateral membranes and medial rows of pinnules. Tip of apical segment of exopod of legs 2 to 4 produced into a bifid process. Leg 1 with first endopod segment drawn out into a long spiniform process at distolateral angle (Fig. 6A).

Leg 5 (Fig. 4E) uniramous and 3-segmented, positioned adjacent to ventral midline with bases touching (Fig. 4C). First segment unarmed, second with a lateral seta, third with 2 apical setae. Leg 6 (Fig. 4C) represented by the single seta on the plate closing off the genital opening on each side.

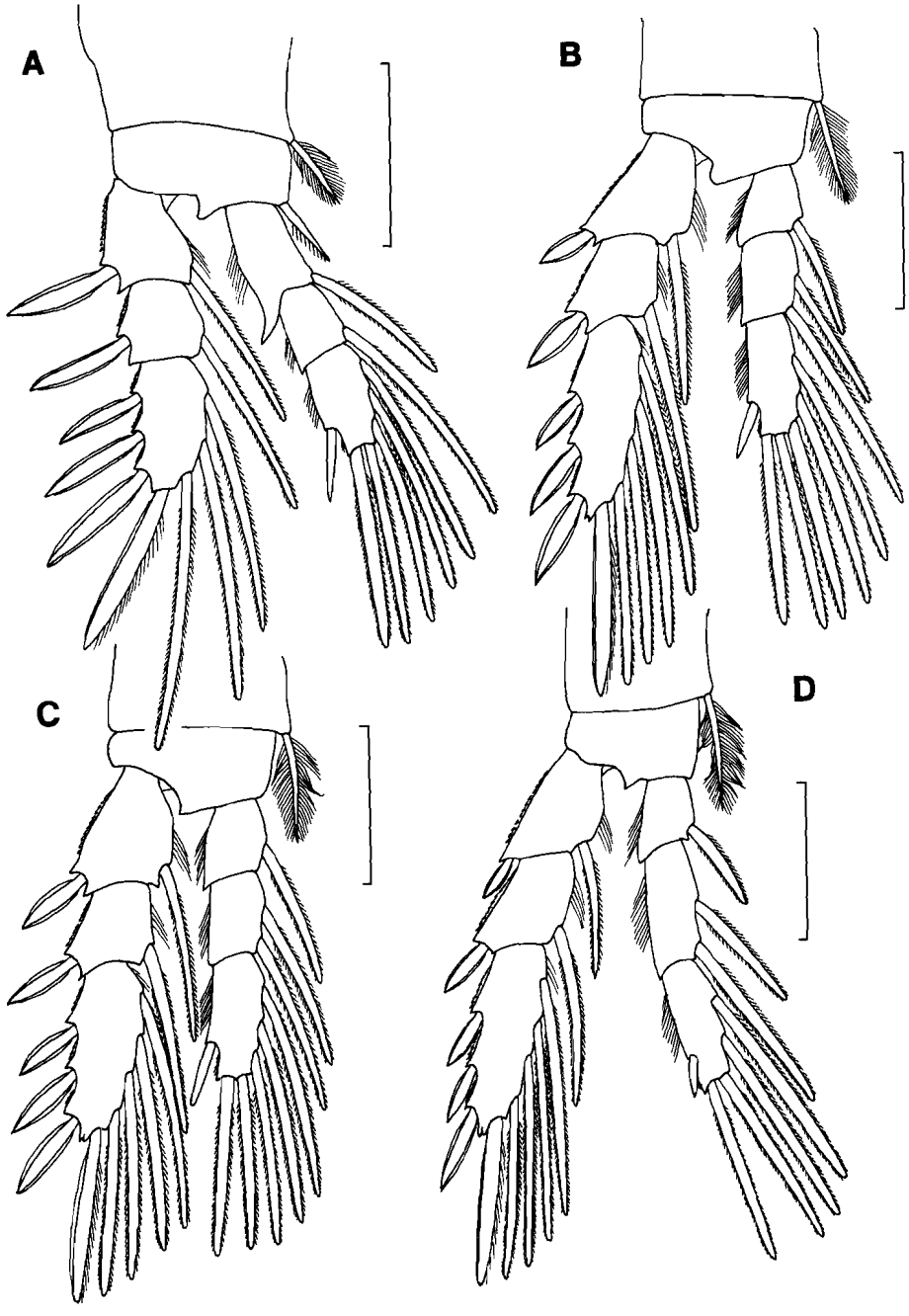

Figure 6. ***Expansophria dimorpha* gen. et sp. nov.** Female. A, leg 1, anterior; B, leg 2, anterior; C, leg 3, anterior; D, leg 4, anterior. Scale bars = 50 μm.

Adult male (Fig. 7A): body form as in female; length 450–510 μm, mean 487 μm (based on 3 specimens). Genital somite wider than long, containing 2 oval spermatophores visible through integument, on either side of midline. Caudal rami (Fig. 7A) about twice as long as wide, armed with a midlateral

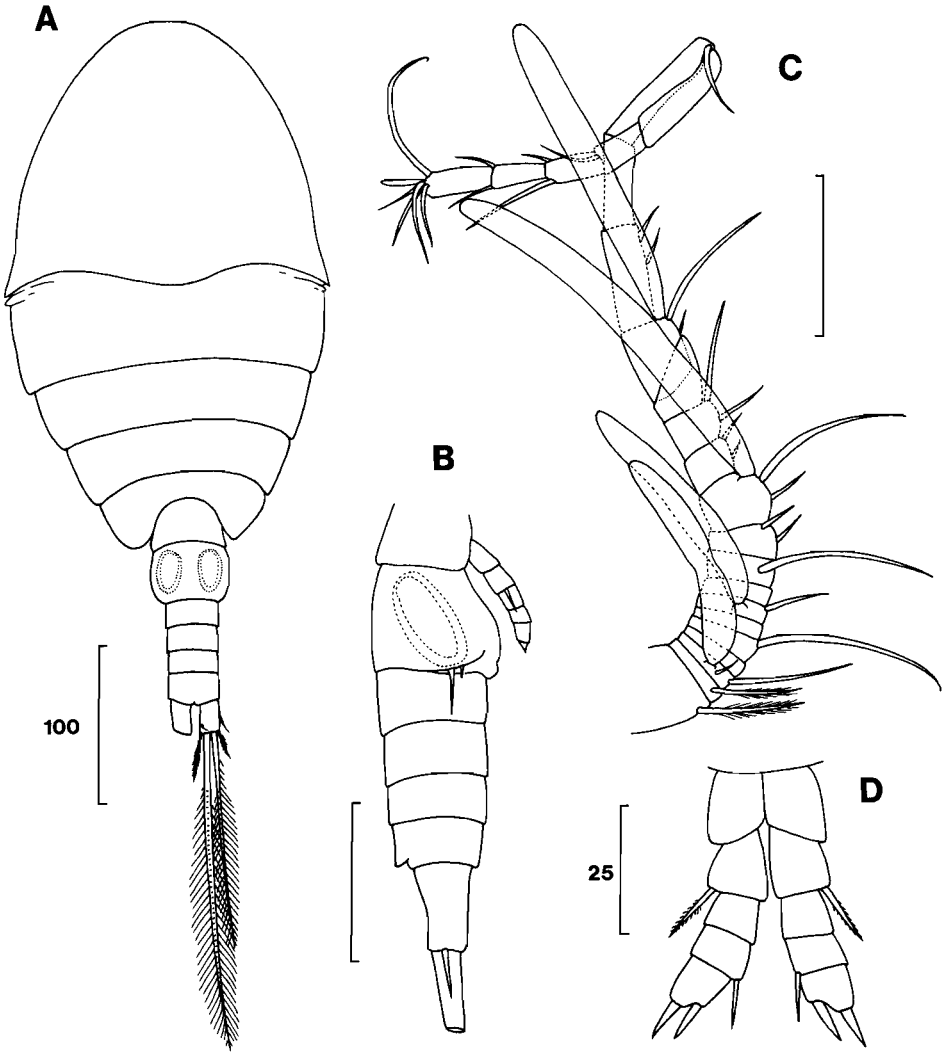

Figure 7. ***Expansophria dimorpha* gen. et sp. nov.** Male. A, dorsal; B, urosome, lateral; C, fifth legs, ventral; D, antennule, ventral. Scale bars = 50 μm except for A (100 μm) and D (25 μm).

margin seta, a small dorsal seta situated near the distomedial angle, an inner and an outer distal angle set and 2 long distal setae, both of which appear to have articulated shafts. Appendages as for female except for antennules and legs 5 and 6.

Antennules (Fig. 7C) 23-segmented, unigeniculate on both sides with geniculation located between segments XVIII and XIX. Segment XIV produced anteriorly into a sheath overlapping much of segment XV. Segments armed as follows: I-1, II-1, III-2 + 1 aesthetasc, IV-0, V-1, VI-0, VII-1 + 1 aesthetasc, VIII-0, IX-1, X-2, XI-2 + 1 aesthetasc, XII-2, XIII-2, XIV-0, XV-2 + 1 aesthetasc, XVI-2, XVII-0, XVIII-1, XIX-0, XX-1, XXI-2, XXII-2, XXIII-5 + 1 aesthetasc.

Leg 5 (Fig. 7D) uniramous, 5-segmented, positioned adjacent to ventral midline as in female. Coxa unarmed, basis with a lateral spine, exopod segment 1 unarmed, segment 2 with a medial seta, segment 3 with 2 apical spines.

Leg 6 (Fig. 7B) represented by the plate closing off the genital opening, armed with 1 long and 1 short spine.

Material Examined

Holotype ♀; 1♀, 3 ♂♂ and 6 copepodid paratypes all collected in the Jameos del Agua, Lanzarote. Material collected on: 2 March 1983 (2 paratypes) by divers using a hand held net or suction bottle in 1–25 m water depths in the first 250 m of the seaward extension of the tube, leg. T. M. Iliffe & D. Williams; 24 February 1984 (5 paratypes) by plankton net towed by a diver in 10–25 m water depths in the first 400 m of the seaward tube, leg. T. M. Iliffe, P. Hobbs, D. Williams and J. Bozanic; 25 February 1984 (holotype and 1 paratype) using a plankton net towed by a diver in 10–28 m water depths of the first 500 m of the seaward tube, leg. T. M. Iliffe, P. Hobbs, J. Bozanic and D. Williams. Two additional paratypes collected by H. Wilkens in March 1985. BM(NH) Reg. nos: 1986.336 (holotype) and 1986.337–346 (paratypes).

Etymology

The generic name is derived from the Latin *expansus* meaning expanded and refers to the distensibility of the first pedigerous somite. Gender—feminine. The specific name is based on the sexual dimorphism exhibited by this species in structure of the fifth legs.

Remarks

In the new genus the anterior part of the first pedigerous somite is thinner than the posterior part and is flexible. It is usually folded but, as there is only a narrow strip of integument extending back from the preceding somite, the folds are exposed. They are not completely enclosed by a carapace-like extension of the maxilliped-bearing somite, such as is present in *Misophria* and the deep-sea genera *Benthomisophria*, *Archimisophria*, *Misophriopsis* and *Misophriella* (Boxshall, 1983). This arrangement allows some limited distension to take place during feeding but the system is not as well developed as in *Benthomisophria palliata* Sars which is profoundly modified for an opportunistic gorging strategy (Boxshall, 1984). Viewed from the side (Fig. 4B) it is apparent that limited ventrolateral distension of the first pedigerous somite is also possible. The narrow lip of integument along the posterior margin of the maxilliped-bearing somite may represent a vestige of the typical misophrioid carapace.

The new genus differs from *Misophria* and the deep-sea genera listed above in the absence of a full carapace enclosing the first pedigerous somite. It is similar to *Speleophria* in possessing a very reduced strip of integument which may be homologous with the carapace of other misophrioids. It may represent a stage through which the new genera described below, *Palpophria* and *Dimisophria*, have passed as both these genera show no trace of a carapace. The new genus can be distinguished from *Speleophria* as it possesses a 6-segmented urosome in the female, lacking the fused genital complex of *Speleophria*. Also the combination of 26 and 23 segments in the female and male antennules respectively serves to separate *Expansophria* from other known genera.

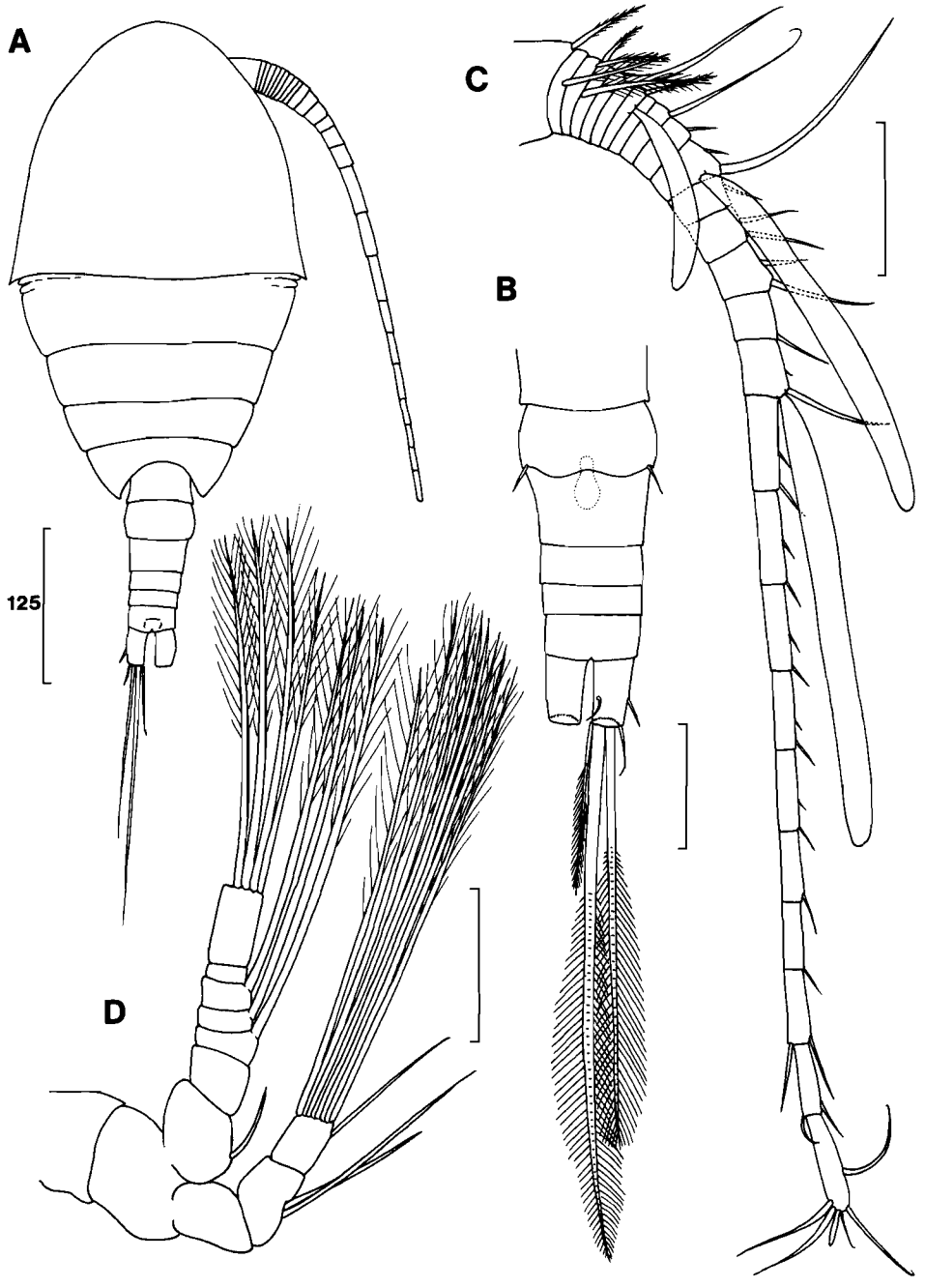

Figure 8. ***Expansophria apoda* sp. nov.** Female. A, dorsal; B, urosome, ventral; C, antennule, anteroventral; D, antenna, posterior. Scale bars = 50 μm except for A (125 μm).

Expansophria apoda sp. nov.

(Figs 8, 9)

Description

Adult female (Fig. 8A): body length 496–540 μm, mean 527 μm (based on 8 specimens). Prosome 5-segmented, with area of folded, flexible integument as in *E. dimorpha*. Nauplius eye absent. Rostrum small, posteroventrally directed and free from labrum. Urosome (Fig. 8B) 6-segmented. Caudal rami about twice as long as wide; armed with a midlateral margin spine, a small dorsal seta situated near the medial margin, an inner and an outer distal angle seta and 2 long distal setae, both of which appear to have articulated shafts.

Antennules (Fig. 8C) 26-segmented, reaching beyond posterior margin of prosome; armed as follows: I-1, II-1, III-2, IV-1, V-1, VI-0, VII-1 + 1 aesthetasc, VIII-0, IX-1, X-1, XI-2 + 1 aesthetasc, XII-1, XIII-2, XIV-2, XV-1, XVI-2 + 1 aesthetasc, XVII-2, XVIII-2, XIX-2, XX-2, XXI-2, XXII-1, XXIII-1, XXIV-2, XV-2, XVI-5 + 1 aesthetasc. Aesthetascs on segments XI and XVI very long.

Antenna (Fig. 8D) biramous, with unarmed protopod. First endopod segment unarmed, second with 2 setae midway along medial margin, third segment with 8 long plumose setae and a shorter naked seta along distal margin. Exopod 7-segmented: first segment with a short medial seta, second unarmed, third to fifth each with a medial plumose seta, sixth unarmed, apical segment with 4 plumose setae on distal margin.

Mandible (Fig. 9A) with 5 main blades on gnathobase, 2 of them bicusped; also with a small denticle and a patch of spinules. Palp comprising basis, armed with a medial plumose seta, indistinctly segmented exopod and 2-segmented endopod. Exopod with 6 plumose setae around medial and distal margins. Endopod segment 1 with a small spine, segment 2 with 4 plumose setae on distal margin.

Maxillule (Fig. 9B) with reduced armament, similar to that of *E. dimorpha*. Praecoxal arthrite with 8 spines and setae, coxal and basal endites each with 2 setae. Outer coxal lobe represented by 4 plumose setae. Endopod with first segment fused to basis, armed with a single naked seta distally; second segment with 1 short and 5 long plumose setae distally. Exopod with fringe of long pinnules along medial margin, and with 1 short and 2 long plumose setae apically.

Maxilla (Fig. 9C) 6-segmented; praecoxa with 4 and 2 setae on proximal and distal endites respectively; coxa with 2 setae on each endit. Basis produced into a curved medial claw bearing 3 setae proximally. Ramus 3-segmented, bearing a total of 7 setae.

Maxilliped (Fig. 9D) 6-segmented. Syncoxa bearing 3 endites and a single proximal seta representing the proximal praecoxal endite. Basis with 2 medial margin setae. Ramus 4-segmented, segments 1 to 3 each with a single medial seta, segment 4 with 2 lateral plumose setae and 4 medial and distal setae.

Swimming legs 1 to 4 with same segmentation and spine and seta formula as for *E. dimorpha*. Leg 1 (Fig. 9E) with the first endopod segment drawn out into a long spiniform process at the distolateral angle. Distal setae on rami of all legs modified, with swollen shafts and short pinnules, as in *E. dimorpha*, but setae on proximal segments of rami unmodified.

Leg 5 absent. No vestige of this appendage remains on the first urosome

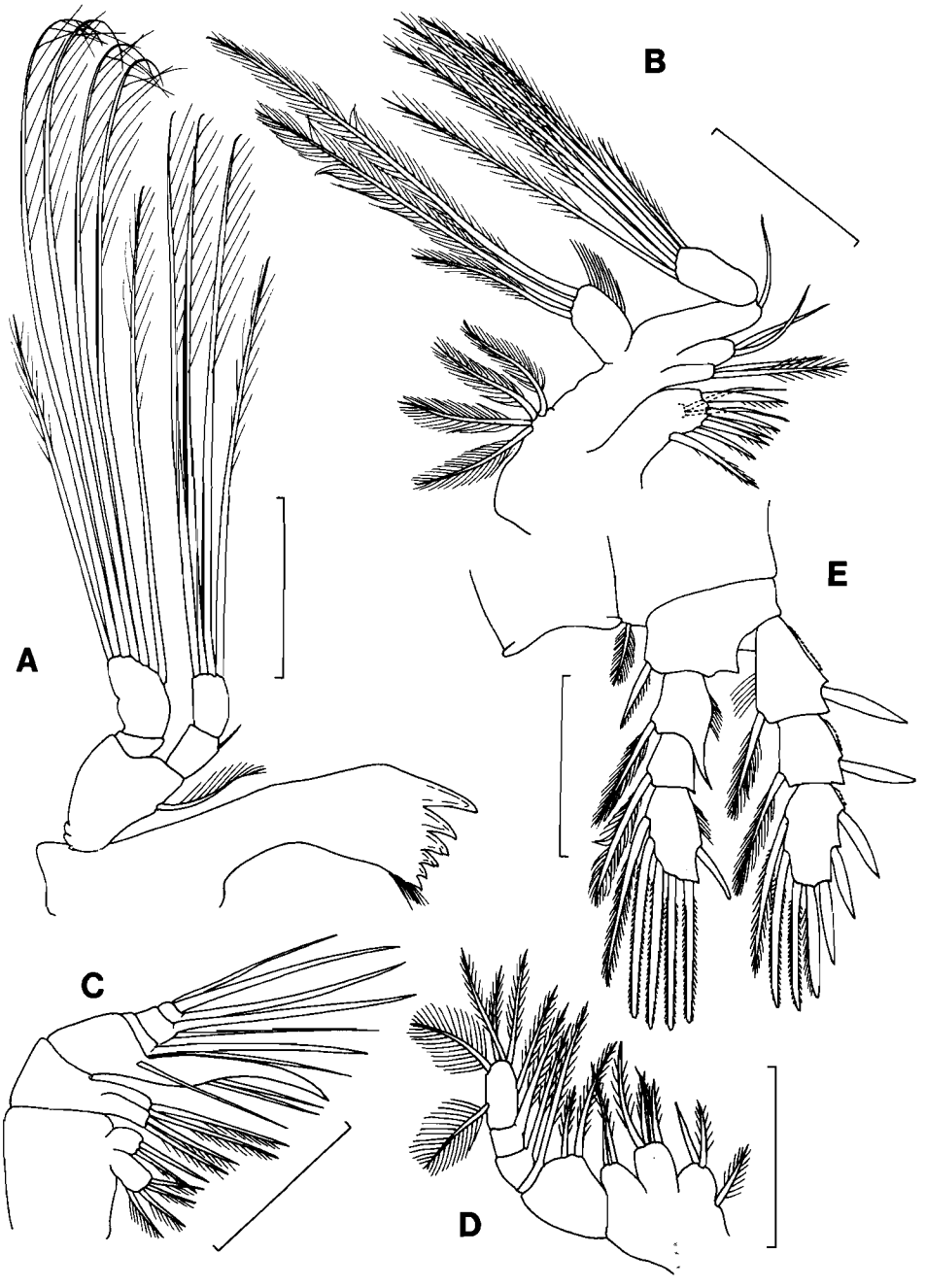

Figure 9. ***Expansophria apoda* sp. nov.** Female. A, mandible, anterior; B, maxillule, anterior; C, maxilla, posterior; D, maxilliped, posterior; E, leg 1, anterior. Scale bars = 50 μm.

somite (Fig. 8B). Leg 6 represented by a single seta on each of the plates closing off the genital openings.

Material Examined

Holotype ♀. 7 ♀♀ paratypes, and 1 stage III, 1 stage IV and 3 stage V copepodids from the Cenote, Ngeruktabel Island, Palau, on 9 February 1985, collected with a plankton net towed by a diver in 0–3 m water depths around old logs in the back portion of the pool; leg. T. M. Iliffe and D. Williams. BM(NH) Registration nos: 1986.347 (holotype) and 1986.348–359 (paratypes).

Etymology

The specific name refers to the absence of the fifth legs.

Remarks

The new species is unique amongst misophrioids in lacking a fifth leg, at least in the adult female. This also serves to distinguish it from *E. dimorpha* which has a well developed, and sexually dimorphic, fifth leg in the adult. Despite this major difference between the two species they share a large number of derived characters; 26-segmented antennules in the females with aesthetascs on segments VII, XI, XVI and XXVI, unusual prosome structure, reduced setation of the maxillule, the modified setae on the swimming legs and the prolongation of the inner margin of the first endopod segment of leg 1 into a spiniform process. On the basis of these similarities the new species is placed in *Expansophria*.

Genus *Palpophria* nov.

Diagnosis: Misophrioida; posterior margin of maxilliped-bearing somite not produced into carapace-like expansion; first pedigerous somite exposed; female antennule 25-segmented; mandibular palp uniramous, 3-segmented and extremely long, reaching almost to posterior border of prosome; praecoxal arthrite of maxillule strongly developed; endopod of first leg 2-segmented; leg 5 reduced to a conical lobe bearing an apical seta.

Type species: ***Palpophria aestheta* gen. et sp. nov.**

Palpophria aestheta sp. nov.

(Figs 10–12)

Description

Adult female (Fig. 10A): body length 395–440 μm, based on 2 specimens. Prosome 5-segmented; no carapace-like extension present on maxilliped-bearing somite so first pedigerous somite completely exposed. Nauplius eye absent. Rostrum (Fig. 11A) bilobed, ventrally directed and just visible in dorsal aspect. Urosome 5-segmented, with genital and first abdominal somites fused although a partial suture is present ventrally (Fig. 10B). Caudal rami about 1.4 times longer than wide, tapering distally from level of lateral seta; armed with a long inner seta on distal margin, a short distal seta, a lateral seta and a dorsal seta.

Antennule (Fig. 10C) 25-segmented; armed as follows: I-1, II-2, III-1, IV-1, V-2, VI-1, VII-2 + 1 aesthetasc, VIII-1 + 1 aesthetasc, IX-2, X-1 aesthetasc, XI-2, XII-2, XIII-1 + 1 aesthetasc, XIV-2, XV-1 + 1 aesthetasc, XVI-2,

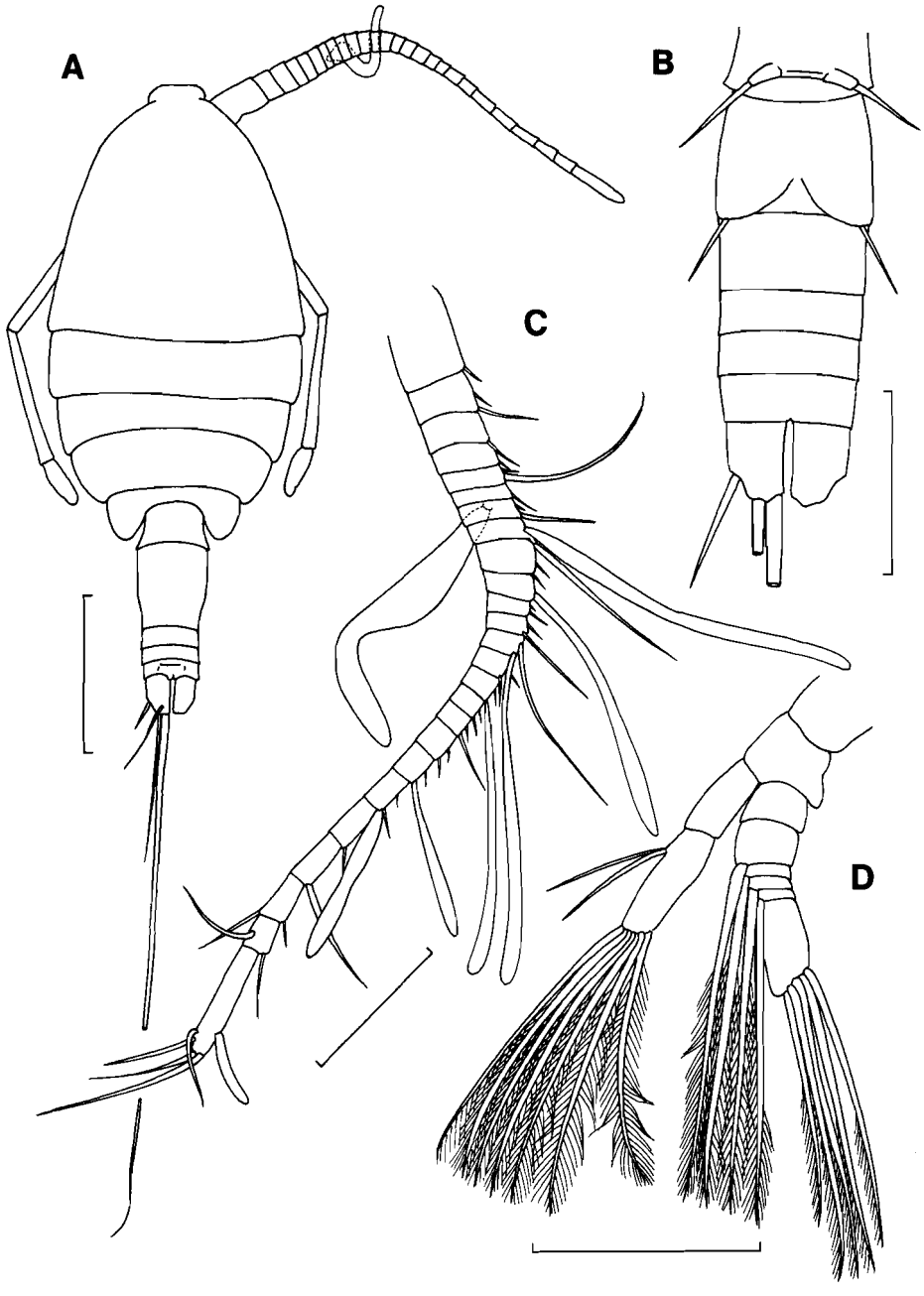

Figure 10. ***Palpophria aestheta* gen. et sp. nov.** Female. A, dorsal; B, urosome, ventral; C, antenna, posterior; D, antennule, dorsal. Scale bars = 50 μm except for A (100 μm).

XVII-2, XVIII-2, XIX-1 + 1 aesthetasc, XX-2 + 1 aesthetasc, XXI-1, XXII-1, XXIII-2, XXIV-2, XXV-4 + 1 aesthetasc. Aesthetasc on ventral surface of segment VII rigid, with a right angled bend between the swollen, ventrally directed, proximal part and the anteriorly directed distal part.

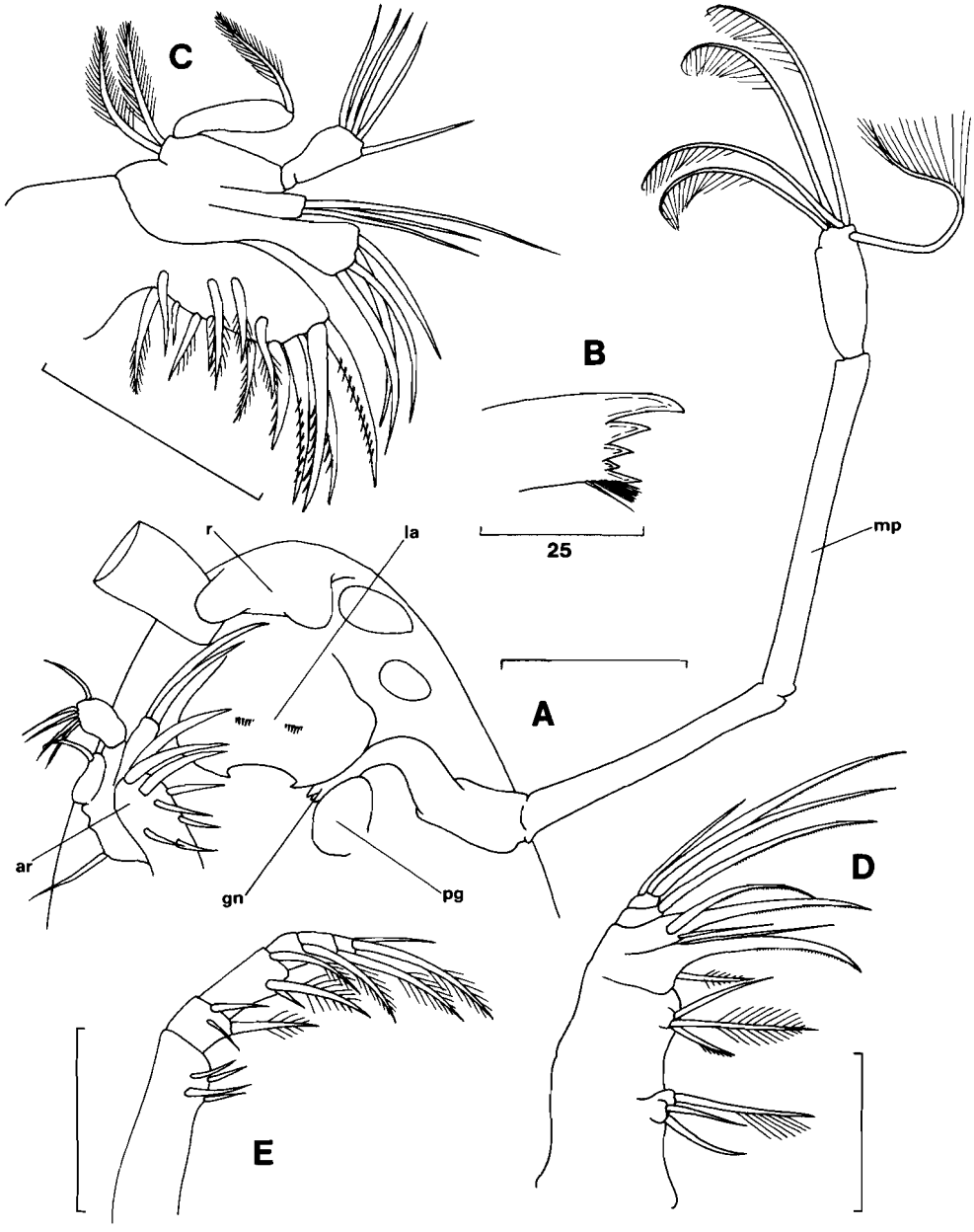

Figure 11. ***Palpophria aestheta* gen. et sp. nov.** Female. A, ventral view of oral area, showing labrum (la), rostrum (r), paragnath (pg) maxillulary arthrite (ar), mandibular gnathobase (gn) and mandibular palp (mp); B, distal margin of mandibular gnathobase, anterior; C, maxillule, anterior; D, maxilla, posterior; E, maxilliped, posterior. Scale bars = 50 μm except for B (25 μm).

Antenna (Fig. 10D) biramous, with unarmed coxa and basis. First endopod segment unarmed, second with 2 naked medial margin setae and 7 plumose setae distally. Exopod 6-segmented, segment 1 unarmed, segment 2 to 5 each with a medial margin plumose seta, segment 6 with 5 plumose setae along oblique distal margin.

Labrum (Fig. 11A) a large lobe with a medially incised posterior margin.

Mandible with a slender gnathobase (Fig. 11B) bearing 5 simple blades and a patch of spinules distally. Palp (Fig. 11A) uniramous, 3-segmented and armed with 5 plumose setae on apical segment. Palp extremely long, reaching almost to posterior margin of prosome, and is capable of considerable rotation around its articulation with the coxa; in one specimen it was directed forwards (Fig. 11A) but in another, backwards (Fig. 10A)

Maxillule (Fig. 11C) with strongly developed praecoxal arthrite and coxal endite but weakly developed palp. Praecoxal arthrite produced medially, armed with 5 strong spinulate spines distally and 9 setose elements along dorsal margin. Coxal-praecoxal articulation well developed. Coxal endite produced medially, with expanded apex bearing 4 spiniform setae; outer lobe represented by 2 plumose setae on outer surface of segment. Basal endite short, armed with 3 setae. First endopod segment fused to basis, unarmed; free segment of endopod bearing 5 setae on distal margin. Exopod narrow, with naked margins, bearing a single plumose apical seta.

Maxilla (Fig. 11D) indistinctly 5-segmented; first segment representing syncoxa. Praecoxal endites situated close together, bearing 1 or 2 setae; single coxal endite with 3 setae. Basis produced into a curved claw-like process armed with 2 basal setae. Ramus 3-segmented; first segment produced into a curved medial claw bearing 2 setae proximally, second bearing a long curved seta, third a short seta and 2 long, curved setae.

Maxilliped (Fig. 11E) slender, 6-segmented. First segment armed with 4 short spines distally, second with 2 short spines and a long spinulate seta, third with 2 spinulate setae, fourth and fifth with 1 each, sixth with 1 naked and 1 spinulate seta.

Legs 1 to 4 (Figs 12A–D) biramous; leg 1 with 2-segmented endopod, all other rami 3-segmented; spine and seta formula as follows:

	coxa	basis	endopod	exopod
leg 1	0–1	1–I	0–1; 1, 2, 5	I–1; I–1; III, I, 4
leg 2	0–1	1–0	0–1; 0–2; 1, 2, 3	I–1; I–1; III, I, 5
leg 3	0–1	1–0	0–1; 0–2; 1, 2, 3	I–1; I–1; III, I, 5
leg 4	0–1	1–0	0–1; 0–2; 0, 2, 2	I–1; I–1; III, I, 5

Lateral margins of all endopod segments with rows of pinnules. Setae on first endopod segments of legs 2 to 4 swollen with short pinnules, all other setae typical. Lateral spines on exopods apparently unarmed.

Leg 5 (Fig. 10B) reduced to a ventrolaterally directed, conical lobe bearing a single apical seta. Legs connected medially by bar representing intercoxal sclerite.

Leg 6 represented by a single seta on each of the plates closing off the genital openings.

Material Examined

Holotype ♀; 1♀ and 1 copepodid V paratypes all collected in the Jameos del Agua, Lanzarote: 2 March 1983, paratypes collected with hand net and suction bottle by divers in 1–25 m water depths of the first 250 m of the seaward tube, leg. T. M. Iliffe & D. Williams; 25 February 1984, holotype collected with plankton net towed by diver in 10–28 m of the first 500 m of the seaward tube,

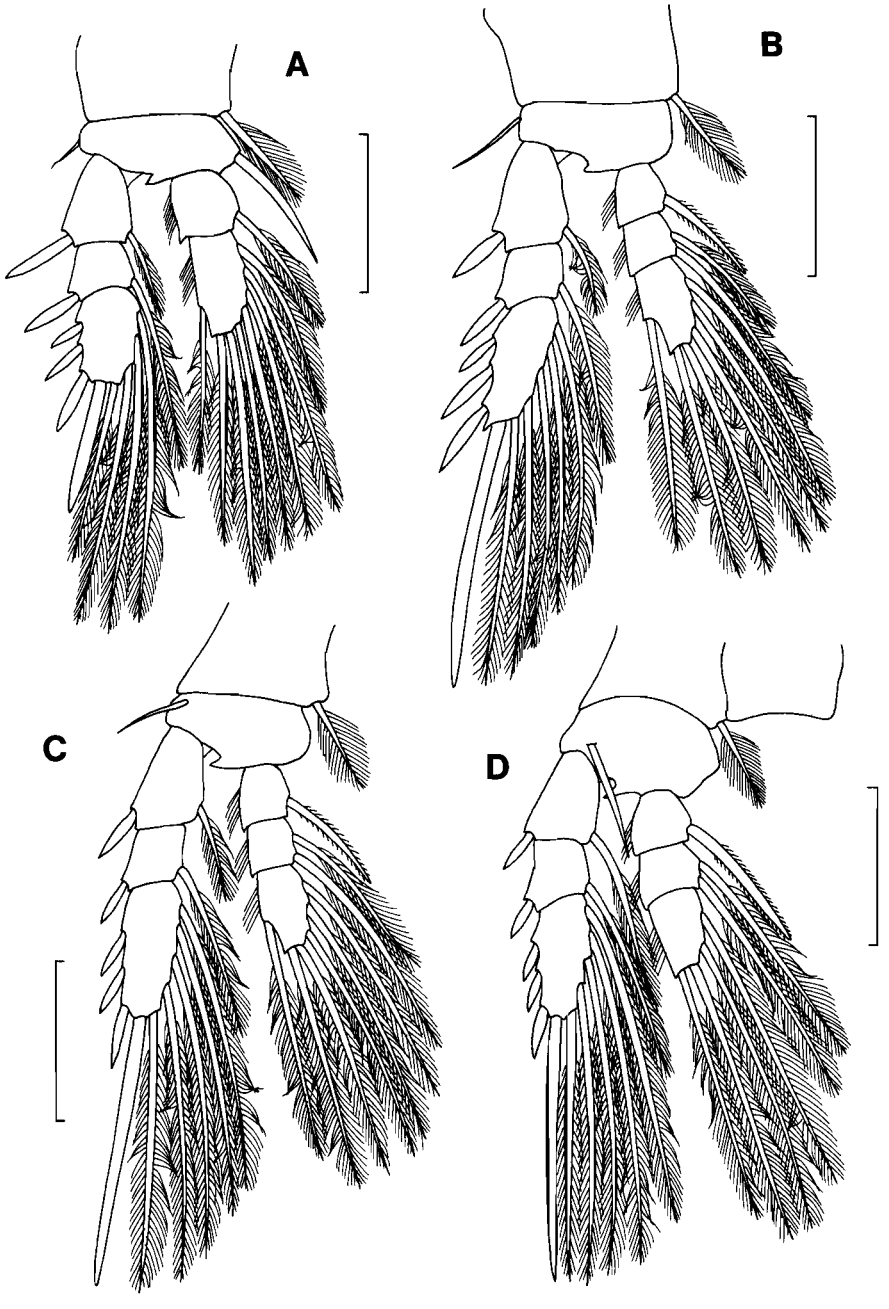

Figure 12. ***Palpophria aestheta* gen. et sp. nov.** Female. A, leg 1, anterior; B, leg 2, anterior; C, leg 3, anterior; D, leg 4, anterior. Scale bars = 50 μm.

leg. T. M. Iliffe, P. Hobbs, D. Williams and J. Bozanic. BM(NH) Registration nos: 1986.360 (holotype) and 1986.361–362 (paratypes).

Etymology

The generic name alludes to the extreme development of the mandibular palp. Gender—feminine. The specific name refers to the rigid, curved aesthetasc on the seventh antennulary segment.

Remarks

This new genus is remarkable for the length of the uniramous mandibular palp. All known misophrioids have biramous mandibular palps and no other copepod exhibits such extreme development of the palp. The palp appears to be relatively mobile and might be used in grooming behaviour.

The new species is probably a raptorial predator. The maxillules, maxillae and maxillipeds are adapted for grasping and manipulating prey. In particular, the long praecoxal arthrite and coxal endite of the maxillule are held in such a way as to be able to grip prey and hold it near to the mouth (Fig. 11A). This arrangement is similar to that found in some cyclopoids, and the maxillules may be used as in the predatory *Macrocyclops albidus* studied by Fryer (1957). The robust, spinous nature of the armature of the maxillae and maxillipeds also resembles that of *Macrocyclops albidus* and the feeding mechanism as a whole is probably the same as that described by Fryer (1957) for that species.

Genus *Dimisophria* nov.

Diagnosis: Misophrioida; posterior margin of maxilliped-bearing somite not produced into carapace-like expansion; first pedigerous somite exposed; urosome 5-segmented; female antennule 27-segmented; outer lobe of maxillule represented by single plumose seta; maxilliped 4-segmented; endopod of first leg 2-segmented; third exopod segments of legs 1 to 4 with 2, 2, 2 and 1 lateral spines respectively; leg 5 comprising a large basal segment and small distal segment.

Type species: ***Dimisophria cavernicola* gen. et sp. nov.**

Dimisophria cavernicola sp. nov.

(Figs 13, 14)

Description

Holotype female (Fig. 13A) body length 327 μm. Prosome 5-segmented; no carapace-like extension present on maxilliped-bearing somite so first pedigerous somite completely exposed. Nauplius eye absent. Rostrum small, posteroventrally directed, not fused to labrum. Urosome 5-segmented; first urosome somite bearing fifth legs, second with paired genital openings either side of ventral midline; third fused to second but line of fusion marked by a complete suture. Caudal rami about twice as long as wide; armed with a long inner seta on distal margin, a short distal seta, a lateral seta and dorsal seta.

Antennule (Fig. 13C) 27-segmented; armed as follows: I-1, II-1, III-1, IV-1, V-1, VI-0, VII-1 + 1 aesthetasc, VIII-0, IX-0, X-1, XI-1, XII-1, XIII-1,

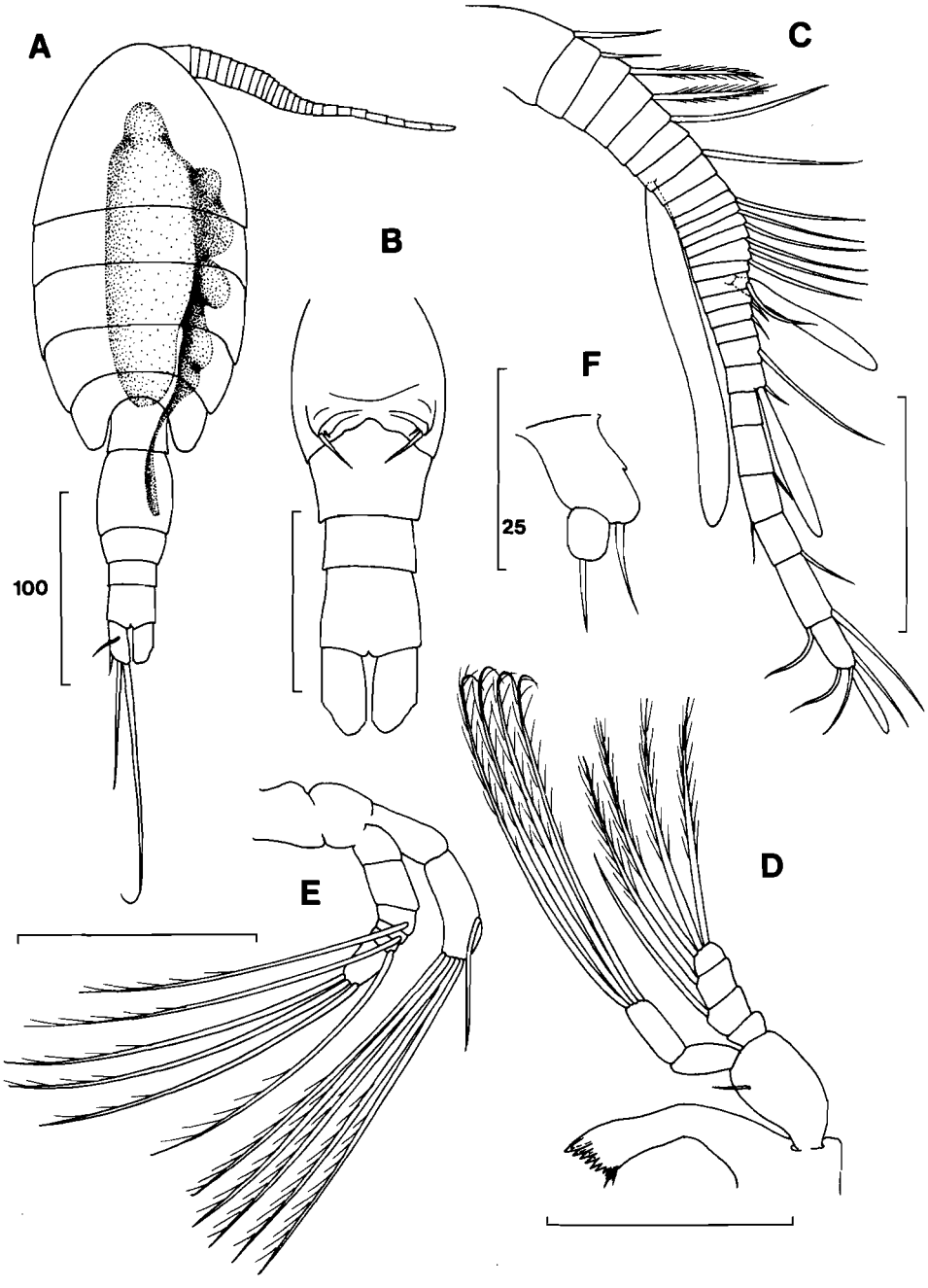

Figure 13. ***Dimisophria cavernicola* gen. et. sp. nov.** Female. A, dorsal, showing median ovary and asymmetrical oviduct as visible through integument; B, urosome, ventral; C, antennule, dorsal; D, mandible, posterior; E, antenna, posterior; F, leg 5, ventral. Scale bars = 50 μm except A (100 μm) and F (25 μm).

XIV-2, XV-0, XVI-1 + 1 aesthetasc, XVII-1, XVIII-1, XIX-0, XX-1, XXI-1 + 1 aesthetasc, XXII-0, XXIII-1, XXIV-1, XXV-1, XXVI-2, XXVII-3 + 1 aesthetasc. Aesthetasc on segment VII very long.

Antenna (Fig. 13E) biramous, with unarmed coxa and basis. First endopod segment unarmed, second with 1 naked medial margin seta and 5 plumose setae distally. Exopod 6-segmented; segments 1 and 2 unarmed, segments 3 to 5 each with a medial margin plumose seta, segment 6 with 3 plumose setae on distal margin.

Mandible (Fig. 13D) with about 6 simple blades and a patch of spinules on the gnathobase. Palp comprising basis, armed with a single seta, 4-segmented exopod and 2-segmented endopod. First endopod segment unarmed, second bearing 4 plumose setae distally. First exopod segment unarmed, second and third each with a medial plumose seta, fourth bearing 3 plumose setae apically.

Maxillule (Fig. 14A) of typical form, but segments poorly defined. Praecoxal arthrite armed with 8 spines and setae around distal margin; coxal endite with 3 setae. Outer lobe represented by a single, medially directed, plumose seta. Basal endite small, with a single apical seta. Endopod fused to basis, bearing a naked seta proximally and 1 naked and 5 plumose setae distally. Exopod lying almost parallel to medially directed endopod, carrying 1 short and 3 long plumose setae at its apex.

Maxilla (Fig. 14B) 6-segmented. Praecoxa bearing 5 and 3 setae on its proximal and distal endites respectively. Coxal endites both with 2 setae. Basis produced into a strong medial claw armed with a row of 7 denticles along its concave margin, and bearing 3 setae near its base. Ramus 3-segmented, armed with 3 curved claw-like setae and 2 slender setae.

Maxilliped (Fig. 14C) 4-segmented. First segment bearing 3 setae, 1 on each of 3 medial margin swellings. Second segment with 3 setae proximally and 2 distally on medial margin. Third segment with 2 claw-like medial setae. Fourth segment tiny, bearing 4 slender, naked setae.

Legs 1 to 4 (Figs 14D–G) biramous; leg 1 with a 2-segmented endopod, all other rami 3-segmented; spine and seta formula as follows:

	coxa	basis	endopod	exopod
leg 1	0–1	0–I	0–1; 1, 2, 3	I–0; I–1; II, I, 3
leg 2	0–1	0–0	0–1; 0–2; 1, 2, 3	I–1; I–1; II, I, 4
leg 3	0–1	0–0	0–1; 0–2; 1, 2, 3	0–1; I–1; II; I, 4
leg 4	0–1	0–0	0–1; 0–2; 1, 2, 2	0–1; 0–1; I, I, 4

Lateral margins of endopods all with rows of pinnules. Setae on first endopod segments of legs 3 and 4 swollen with short pinnules, all other setae typical. Lateral spines on exopods blade-like, with smooth margins; apical spines plumose on medial margins.

Leg 5 (Fig. 13F) comprising a large basal segment armed with an outer distal seta, and an oval terminal segment bearing an apical seta.

Leg 6 (Fig. 13B) represented by the seta and spinule present on the plate closing off the genital openings.

Material Examined

Holotype collected in Jameos del Agua, Lanzarote, 25 February 1984, collected with plankton net towed by a diver in 10–28 m water depths in the

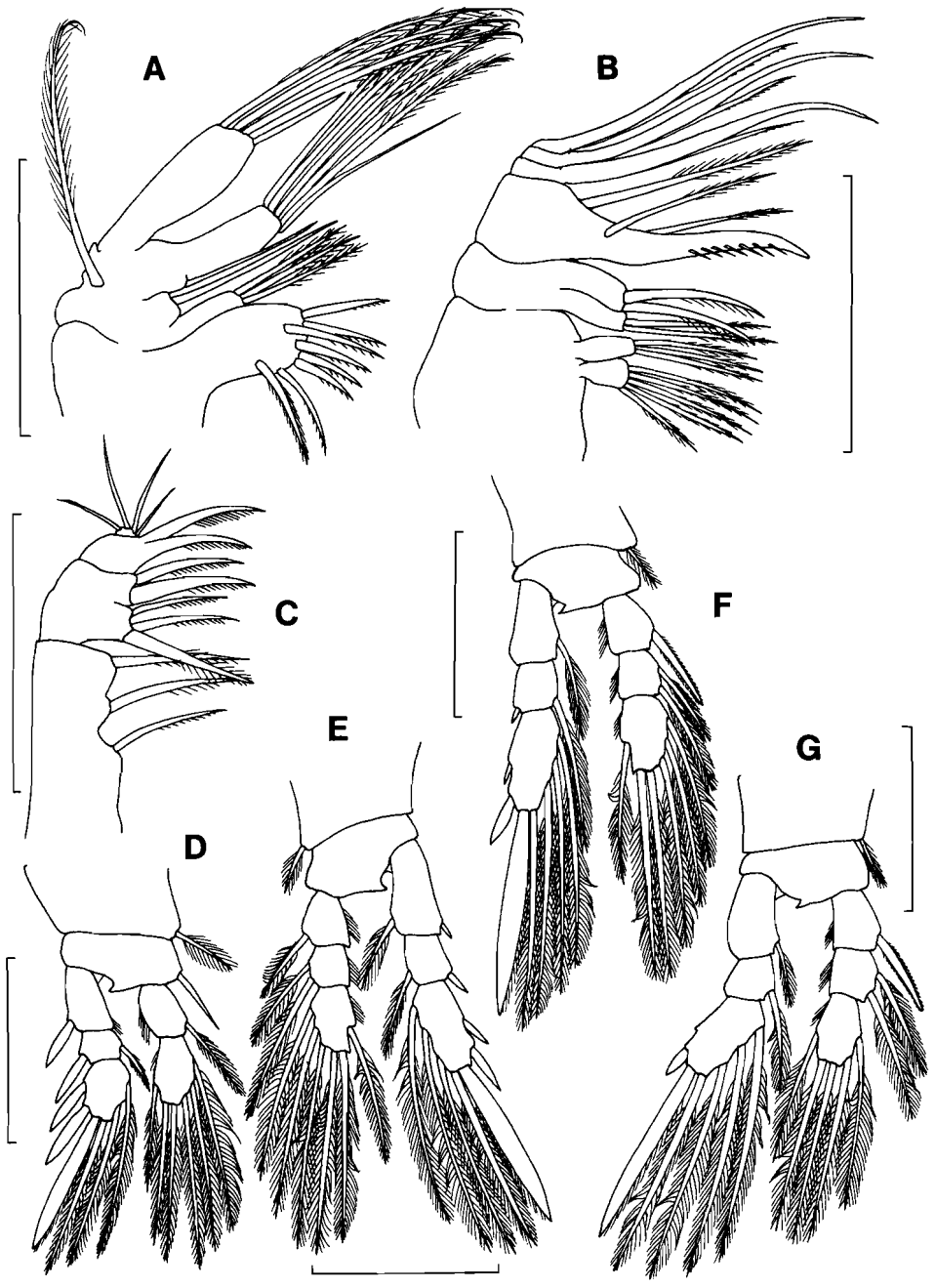

Figure 14. ***Dimisophria cavernicola* gen. et sp. nov.** Female. A, maxillule, anterior; B, maxilla, posterior; C, maxilliped, posterior; D, leg 1, anterior; E, leg 2, anterior; F, leg 3, anterior; G, leg 4, anterior. Scale bars = 50 μm.

first 500 m of the seaward tube, leg. T. M. Iliffe, P. Hobbs, D. Williams and J. Bozanic. BM(NH) Registration no: 1986.363.

Etymology

The generic name is derived from the Greek '*di-*' meaning two and *Misophria,* and is based on the presence of only two outer spines on the third exopod segment of legs 1 to 3 compared with the usual three. Gender—feminine. The specific name refers to the habitat of this species.

Remarks

It is difficult to determine the precise sexual status of the only specimen. The 5-segmented urosome can be interpreted either as that of a copepodid V stage or as that of an adult female in which the genital and first abdominal somites are fused into a genital complex, as in *Speleophria* (Boxshall & Iliffe, 1986). In the latter case the genital openings are usually situated near the middle of the genital complex, as their original position is at the posterior margin of the genital somite. The position of the genital openings of this specimen, at the posterior margin of the second urosome somite, suggests that it is a copepodid V stage. In this case the telson (last division of the urosome) will probably subdivide at the final moult to give a 6-segmented urosome in the adult female. However, the ovary and a single oviduct, on the right side of the body (Fig. 13A), are visible through the integument of this specimen. The well-developed state of the female reproductive system suggest that the specimen should be regarded as a mature adult.

Even though there is uncertainty regarding the sexual state of the holotype there is no difficulty in establishing a new genus to accommodate it. The new genus resembles *Speleophria* and *Palpophria* in possessing a 2-segmented endopod on the first leg but differs from them both in a number of characters, including antennule segmentation and the spine and seta formula of the swimming leg. It has antennules of 27 segments compared to 22 in *Speleophria* and 25 in *Palpophria.* The reduced number of spines on the exopods of legs 1 to 4 separates the new genus from all other misophrioid genera which, where known, have three outer margin spines on the third exopod segment of their legs. In addition it can be easily distinguished from *Speleophria* by the different rostrum configuration, and from *Palpophria* by its biramous mandibular palp.

Misophrioid copepodid IV

A single copepodid IV (Fig. 3D) was also collected from Jameos del Agua, Lanzarote on 25 February 1984 with a plankton net towed by a diver in 10–28 m water depths in the first 500 m of the seaward tube. It is not described in full and is not named as it is too immature to be placed in a genus at present. However, it clearly represents a fourth misophrioid genus from that same cave because it possesses an apparently 4-segmented prosome, with the first pedigerous somite entirely concealed beneath a typical carapace-like extention from the maxilliped-bearing somite. This distinguishes it from the other three misophrioids known from this cave, *Expansophria dimorpha, Palpophria aestheta* and *Dimisophria cavernicola,* all of which lack a carapace.

DISCUSSION

The first misophrioid, *M. pallida* was described by Boeck in 1864. A century later the number of known species had only increased to three, by the addition of the deep-sea species *Benthomisophria palliata* Sars in 1909 and *B. cornuta* Hulsemann & Grice in 1964. Since 1983 however, 12 new misophrioid species have been discovered, four in the deep-sea plankton (Boxshall, 1983; Alvarez, 1985) and eight in anchialine caves (Boxshall & Iliffe, 1986; present account). The discovery of this latter group of species has greatly increased the known range of morphological diversity of the group. Two new genera, *Palpophria* and *Dimisophria*, lack any trace of the carapace and it is greatly reduced in *Speleophria* and *Expansophria*. In the latter, however, the prosome is still modified to allow distension of the midgut and this may represent an intermediate evolutionary phase in the loss of the gorging feeeding strategy for which the carapace system is adapted. Not all cave-dwelling misophrioids lack a carapace. *Misophria kororiensis*, the unnamed copepodid III from Bermuda and the copepodid IV from Lanzarote all possess a full carapace enclosing the first pedigerous somite.

Other derived characters are shown by some of the cave-dwelling forms including partial or complete fusion of the genital and first abdominal somites in females, a 2-segmented endopod on the first pair of swimming legs, reduced setation of the maxillule and a uniramous mandibular palp. The characters exhibited by the cavernicolous taxa are generally more advanced compared to those of the deep-sea forms, although some primitive characters are retained, such as 26 or 27 segments in the antennules.

A preliminary analysis of the biogeography of the Misophrioida can be attempted but this will be very open to reassessment as new taxa are discovered. The deep-sea misophrioids exhibit a complex suite of unique and plesiomorphic characters, the former collectively viewed as adaptations to an opportunistic gorging feeding strategy (Boxshall, 1984), the latter as features retained from those present in the common ancestor of the Copepoda as a whole (Boxshall, Ferrari & Tiemann, 1984). The character set of the deep-sea genera *Benthomisophria, Archimisophria, Misophriella* and *Misophriopsis* may be interpreted as evidence of a bathypelagic origin and evolutionary radiation of the group as opportunistic gorgers of the near-bottom plankton community (Boxshall, 1983). Assuming a deep-sea origin of the group it is necessary to explain the distribution of the other taxa.

The absence of the nauplius eye and the presence of a carapace covering a non-distensible first pedigerous somite in the shallow neritic species *M pallida* was regarded as evidence that this species had secondarily emerged from the deep sea (Boxshall, 1984); a situation analogous to that reported from some deep-sea asellote isopods (Hessler, Wilson & Thistle, 1979). The new *Misophria* from the Indo-West Pacific might be the sister species of *M. pallida*, which is primarily northeastern Atlantic in distribution though extending into the Mediterranean and the Red Sea. Their common ancestor may have emerged from the deep sea and dispersed in shallow waters, possibly by way of caves as had been suggested for the oligochaete *Phallodrilus* (Erséus, 1986). Subsequent splitting into the two allopatric species could then have occurred.

It was suggested that the Bermudan cave-dwelling misophrioids may have been derived from deep-sea taxa which were associated with this volcanic

seamount, perhaps in crevicular microhabitats or even lava tubes, subsequent to its formation on the Mid-Atlantic Ridge (Boxshall & Iliffe, 1986). This was one of four possible routes of colonization of Bermuda's marine caves put forwards by Iliffe, Hart & Manning (1983) and expanded upon by Hart, Manning & Iliffe (1985). The recent discovery of five endemic species, previously known only from the Jameos del Agua cave, in near-coastal wells around the island of Lanzarote (Wilkens, Parzefall & Iliffe, 1986) further suggests that marine caves may also be considered an extension of the crevicular groundwater habitat. The process of emergence from the deep sea, through interior voids in submerged seamounts, to shallow cavernicolous habitats may be equally applicable to misophrioids found in anchialine caves on other islands, whether in the North Atlantic or in the Indo-West Pacific. The cave-dwelling taxa would thus represent descendants of deep-sea forms which became separated by vertical vicariance events. Other routes may also be important for the misophrioids. The distribution of *Expansophria*, with one Atlantic and one Indo-West Pacific species, is difficult to explain by the deep-sea emergence route unless the genus was widespread in the deep sea.

The coexistence of four genera of misophrioids in the Jameos del Agua Cave system on Lanzarote is remarkable. These genera differ considerably in morphology but it is possible that they represent a group of taxa derived from the common ancestor that first colonized separate and older cavernicolous habitats on the island. Speciation and subsequent generic separation could have occurred allopatrically in isolated caves followed by dispersal of the resulting taxa, with raising sea levels, into the newly formed Jameos del Agua cave.

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REFERENCES

ALVAREZ, M. P. J., 1985 A new species of misophrioid copepod from the near-bottom waters off Brazil. *Journal of Natural History, 19:* 953–959.

BOWMAN, T. E. & ILIFFE, T. M., 1985 *Mictocaris halope*, a new unusual peracaridan crustacean from marine caves on Bermuda. *Journal of Crustacean Biology, 5:* 58–73.

BOXSHALL, G. A., 1983 Three new genera of misophrioid copepods from the near-bottom plankton

community in the North Atlantic Ocean. *Bulletin of the British Museum (Natural History), Zoology, 44:* 103–124.

BOXSHALL, G. A., 1984 The functional morphology of *Benthomisophria palliata* Sars, with a consideration of the evolution of the Misophrioida. *Crustaceana, Suppl. 7:* 32–46.

BOXSHALL, G. A. & ILIFFE, T. M., 1986 New cave-dwelling misophrioids (Crustacea: Copepoda) from Bermuda. *Sarsia, 71:* 54–64.

BOXSHALL, G. A., FERRARI, F. D. & TIEMANN, H., 1984 The ancestral copepod: towards a consensus of opinion at the First International Conference on Copepoda 1981. *Crustaceana, Suppl. 7:* 68–84.

ERSÉUS, C., 1986 A new species of *Phallodrilus* (Oligochaeta, Tubificidae) from a limestone cave in Bermuda. *Sarsia, 71:* 7–9.

FOSSHAGEN, A. & ILIFFE, T. M., 1985 Two new genera of Calanoida and a new order of Copepoda, Platycopioida, from marine caves on Bermuda. *Sarsia. 70:* 345–358.

FRYER, G. 1957 The feeding mechanism of some freshwater cyclopoid copepods. *Proceedings of the Zoological Society of London, 129:* 1–25.

HART, C. W., JR. MANNING, R. B. & ILIFFE, T. M. 1985 The fauna of Atlantic marine caves: Evidence of dispersal by sea floor spreading while maintaining ties to deep waters. *Proceedings of the Biological Society of Washington, 98:* 288–292.

HARTMANN, G. 1985 *Danielopolina wilkensi* n. sp. (Halocyprida, Thaumatocyprididae), ein neuer Ostracode aus einem marinen Lava-Tunnel auf Lanzarote (Kanarische Inseln). *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut, 82:* 255–261.

HESSLER, R. R., WILSON, G. D. & THISTLE, D. 1979 The deep-sea isopods: A biogeographic and phylogenetic overview. *Sarsia, 64:* 67–75.

HULSEMANN, K. & GRICE, G. D., 1964 A new bathypelagic species of *Benthomisophria* (Copepoda: Misophriidae) from the North Atlantic. *Zoologischer Anzeiger, 173:* 259–264.

ILIFFE, T. M., HART, C. W., JR. & MANNING, R. B., 1983 Biogeography and the caves of Bermuda. *Nature (London), 302:* 141–142

ILIFFE, T. M., WILKENS, H., PARZEFALL, J. & WILLIAMS, D., 1984 Marine lava cave fauna: Composition, biogeography and origins. *Science, 225:* 309–311.

SARS, G. O., 1903 *An account of the Crustacea of Norway. V. Copepoda Harpacticoida.* Bergen Museum. Pts. I–II: 1–28.

SARS, G. O., 1909 Note préliminaire sur trois formes rémarquables de copépodes provenant des Campagnes de S.A.S. Le Prince Albert de Monaco. *Bulletin d'Institute Océanographique de Monaco. 147:* 1–8.

STOCK, J. H., ILIFFE, T. M. & WILLIAMS, D., 1986 The concept "anchialine" reconsidered. *Stygologia 2:* 90–92.

VALDECASAS, A. G., 1984 Morlockiidae new family of Remipedia (Crustacea) from Lanzarote (Canary Islands). *Eos, 60:* 329–333.

WILKENS, H. & PARZEFALL, J., 1974 Die Oekologie der Jameos del Agua (Lanzarote). Zur Entwicklung limnischer Hoehlentiere aus marinen Vorfahren. *Annales de Spéléologie, 29:* 419–434.

WILKENS, H., PARZEFALL, J. & ILIFFE, T. M., 1986 Origin and age of the marine stygofauna of Lanzarote, Canary Islands. *Mitteilungen aus dem Hamburgischen Zoologischen Museum and Institut. 83:* 223–230.

YAGER, J. 1981 Remipedia, a new class of Crustacea from a marine cave in the Bahamas. *Journal of Crustacean Biology, 1:* 328–333.