

Two new genera of misophrioid copepods (Crustacea) from an anchihaline cave in the Bahamas

D. JAUME¹, G. A. BOXSHALL² and T. M. ILIFFE³

¹*Instituto Mediterráneo de Estudios Avanzados (CSIC-UIB),
Ctra. Valldemossa, km 7'5, 07071 Palma de Mallorca, Spain*

²*Department of Zoology, The Natural History Museum, Cromwell Road,
London SW7 5BD, UK*

³*Department of Marine Biology, Texas A & M University at Galveston,
Galveston, Texas 77553, USA*

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Two new genera of misophrioid copepods are described from an anchihaline cave on the Exuma Cays, Bahamas. Both sexes of *Huysia bahamensis* are characterized by the retention of biramous fifth legs, a character state previously reported only in members of the *Misophria*-lineage. *Protospeleophria lucayae* is described on the basis of a single female. It is closely related to *Speleophria*, but can easily be distinguished by the more plesiomorphic segmentation pattern of the antennules (the lack of fusion between antennular segments IX to XII and XV to XVI) and by the maxillipedal armature. The new taxa belong to a cluster of genera, together with *Speleophria* and *Speleophriopsis*, characterized by: the presence of a long, falcate rostrum; the fusion between genital and first abdominal somites in the female to form a genital double-somite; the presence of enlarged aesthetascs on antennular segments III and VII; the [5,3] armature formula of the maxillary allobasis; the 2-segmented endopod of leg 1; and the 4-segmented fifth legs (comprising coxa, basis and 2-segmented exopod). The unmodified segmentation around the geniculation of the male antennule of *Huysia* and *Speleophriopsis* necessitates some redefinition of the ancestral neocopepodan geniculation.

KEYWORDS: Copepoda, Misophrioida, *Huysia*, *Protospeleophria*, caves, taxonomy, phylogeny, Bahamas.

Introduction

Misophrioid copepods show a curious affinity for marine/anchihaline caves (*sensu* Stock *et al.*, 1986), where more than half of the described taxa occur. Cave-dwelling misophrioids were first reported from Bermuda by Boxshall and Iliffe (1986), who described the new genus and species *Speleophria bivexilla*. Since then the group has proved to be a common component of the crustacean fauna of littoral caves in tropical and subtropical latitudes. Seven of 14 genera and 14 of 26 species are known only from these habitats (Boxshall, 1989; Ohtsuka *et al.*, 1992; Jaume and Boxshall, 1996a,b, 1997; Martínez-Arbizu and Seifried, 1996).

Stygobiont misophrioids typically occur at low population densities and the inaccessibility of their habitats on remote oceanic islands, or in cave chambers that

can be reached only by SCUBA-diving, has precluded repeated sampling programmes, so that little is known of their biology. In addition, they appear not to be readily attracted to baited traps as are many other stygobiont crustaceans. Taxa are often described on the basis of a single or few individuals only, and sometimes only one sex is known but the publication of such descriptions is justified since they have revealed important phylogenetic information.

In this paper we describe two new genera from an anchihaline cave in the Bahamas. The discovery of cave misophrioids in the Bahamas fills an apparent gap in the distribution of the order in Mesoamerica, a region harbouring an otherwise extremely rich anchihaline crustacean fauna (Botosaneanu, 1986; Iliffe, 1992). We also report on the recent discovery in caves on the Yucatan peninsula of Mexico of additional new misophrioid taxa including undescribed species of both *Speleophria* and *Speleophriopsis*, although the state of preservation of this material precludes their formal description.

The cave

The Bahamas consist of a series of broad, shallow-water carbonate platforms rising abruptly from the deep sea. The largest of these platforms is the 100 000 km² Great Bahama Bank containing the major islands of Exuma, Andros, New Providence, Eleuthera, Cat and Long. The Exuma Islands and Cays are situated along the eastern rim of the Great Bahama Bank bordering Exuma Sound, a steep-sided submarine valley reaching oceanic depths to more than 1800 m. The islands, cays and hard grounds consist of Pleistocene limestone covered by a thin veneer of Holocene carbonate reefs and sediments. Underlying these younger limestones is a continuous section of Tertiary and Cretaceous limestones and dolomites exceeding 11 000 m in thickness.

Extensive anchihaline and submarine cave systems are present along the margins of the platform (Sealey, 1994). The development of the caves and sinkholes may be related to joint systems in the Pleistocene bedrock. Viewed from the air, the deep blue colour of these sinkholes in contrast to the lighter bluish-green of the shallow bank has caused them to be named 'blue holes'. Water depths to nearly 100 m have been reported from some blue holes. Their considerable depth, combined with the presence of underwater stalactites and stalagmites which must have formed in air, suggests that these caves developed during Pleistocene glacial periods when sea level was at least 100 m lower than today.

One of the more notable blue holes in the Exumas is Norman's Pond Cave, located near the north end of Norman's Pond Cay. The entrance to this cave is a 2 m wide by 8 m long sinkhole within 2 m of the high tide line. The cave consists of a collapse-floored fissure up to 8 m wide that trends under the island, toward the open waters of the Exuma Sound. The explored horizontal extent of this cave is more than 200 m, while water depths to 86 m have been reported (Dill *et al.*, 1990; B. Kakuk, personal communication). Due to its close proximity to the coast, waters in the cave fluctuate with the tides and are fully marine (35 to 37 ppt salinity). Water temperature, pH and dissolved oxygen drop from 29°C, 7.8 and 6 mg l⁻¹, respectively, at the surface to 26°C, 7.2 and 0.2 mg l⁻¹ at 20 m depth. Below 20 m, temperature, pH and dissolved oxygen tend to remain constant. The upper level of the cave is divided into two larger rooms separated by a narrow chasm at 35 m depth. Calanoid copepods, thermosbaenaceans, cumaceans, tanaidaceans, amphipods, ostracods, and remipedes have been collected from this cave. An undescribed genus of calanoid

copepod belonging to the family Ridgewayiidae from this cave, is being studied in addition to undescribed species of halocyprid ostracods of the genera *Danielopolina* Kornicker & Sohn and *Spelaeoecia* Angel & Iliffe.

Methods

Material was collected with a 93 µm mesh plankton net from the water column in 10–25 m depths in the first room of Norman's Pond Cave, Norman's Pond Cay, Exuma Cays, Bahamas on 4 May 1993. Misophrioids were dissected in lactophenol and examined using a differential interference contrast microscope (Olympus BH-2). The terminology used in descriptions follows Huys and Boxshall (1991). Material is deposited in The Natural History Museum, London (BMNH).

Taxonomic part

Subclass COPEPODA Milne Edwards, 1840

Order MISOPHRIODA Gurney, 1933

Family MISOPHRIIDAE Brady, 1878

Huysia gen. nov.

Diagnosis. Cephalosome not produced posteriorly into carapace-like extension. First pedigerous somite free. Female urosome 5-segmented, with genital and first abdominal somites fused to form genital double-somite; single copulatory pore opening ventrally. Caudal rami armed with 7 setae. Antennules 25-segmented in both sexes, with compound proximal and apical segments derived from ancestral segments I–III and XXVII–XXVIII respectively. Proximal segment (I–III) swollen dorsolaterally, forming lobe; elongate aesthetascs on segments 1 (III) and 5 (VII). Maxillulary basal exite absent. Allobasis of maxilla with armature formula [5,3]. Maxilliped syncoxa lacking praecoxal seta; endopod 6-segmented, setal formula [1,2,2,2,2+1,5]. Swimming legs with segmentation and spine and seta formula as described below for type species. Fifth legs biramous in both sexes, separate coxa and basis, 1-segmented endopod and 2-segmented exopod; narrow intercoxal sclerite present. Armature of fifth legs as follows: coxa unarmed; basis with outer seta, endopod with apical seta, first exopodal segment with outer seta, and second exopodal segment sexually dimorphic, with 3 elements in female and 4 in male.

Type species. *Huysia bahamensis* Jaume, Boxshall and Iliffe sp. nov.

Etymology. The generic name honours our friend and colleague Dr Rony Huys, who has set new standards in copepod systematics.

Huysia bahamensis sp. nov.

(figures 1–6)

Material examined. **Exuma Cays, Bahamas:** Norman's Pond Cave, Norman's Pond Cay. HOLOTYPE adult female 0.60 mm (BMNH reg. no. 1997.986). ALLOTYPE adult male 0.50 mm (BMNH reg. no. 1997.987) with one antennule, fifth legs and urosome dissected on 2 slides and mounted in lactophenol sealed with nail varnish. PARATYPES 1 adult female 0.62 mm and 4 copepodids (BMNH reg. nos. 1997.988–992); adult female dissected on 6 slides and mounted in lactophenol sealed with nail varnish. Collected by T.M. Iliffe, 4 May 1993.

Adult female. Body (figures 1A, C) cyclopiform, compressed laterally, colourless. Nauplius eye absent. Prosome 5-segmented, with first pedigerous somite not incorporated into cephalothorax and cephalosome not extended posteriorly into

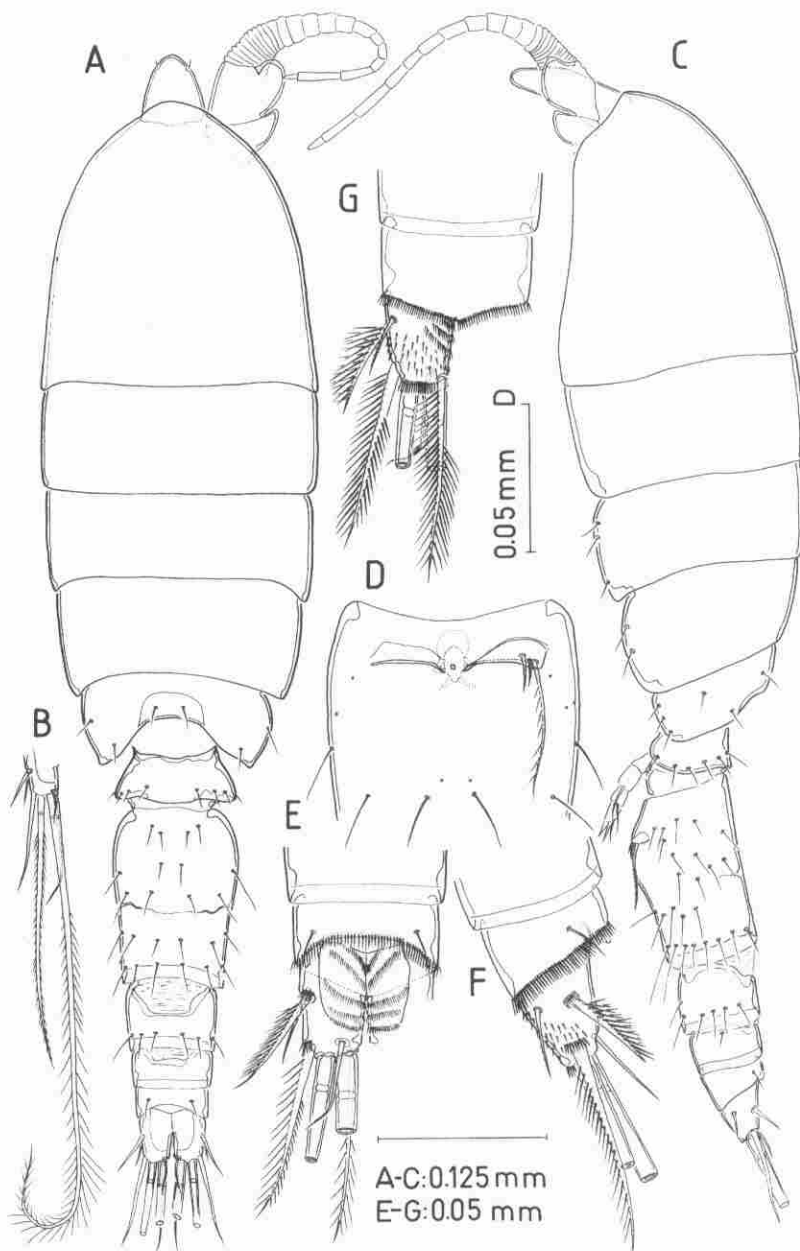


FIG. 1. *Huysia bahamensis* gen. et sp. nov. Adult female. A, body, dorsal; B, detail of armature of left caudal ramus, dorsal; C, body, lateral; D, detail of genital field (right sixth leg removed); E, anal somite and caudal rami, dorsal; F, same, lateral; G, same, ventral.

carapace. Rostrum sickle-shaped, powerfully developed, not fused to cephalic shield. Prosomal pedigerous somites with evenly rounded posterolateral corners.

Urosome 5-segmented, anterior somites richly ornamented with long sensillae (figures 1A,C). Genital and first abdominal somites completely fused to form double-

somite (although internal vestiges of suture between somites visible in dorsal aspect; see figure 1A). Genital field (figure 1D) located anteriorly on double-somite. Single copulatory pore small, located midventrally, communicating with fused seminal receptacles. Gonopores separate, in form of long, narrow slits located ventrally on each side of copulatory pore; each covered by vestigial leg 6 armed with long outer plumose seta plus 2 short inner setae. Second and third free abdominal somites modified, with conspicuous integumental window proximally on dorsal surface adjacent to expansive arthrodial membrane. Anal somite with 2 dorsolateral sensillae; hind margin of somite with continuous row of spinules; anal operculum weak, with smooth rim. Caudal rami (figures 1B, E, F, G) slightly longer than wide, with ventral and ventrolateral surfaces covered with tiny spinules; transverse combs of longer spinules located on inner margin; armed with 7 setae; anterolateral accessory seta (seta I of Huys and Boxshall, 1991) well developed.

Antennules (figure 2A) 25-segmented, short, implanted on segment-like pedestal (arrowed in figure 2A) with outer margin protruding distally into conical process. Segment 1 representing ancestral segments I–III; dorsolateral margin swollen, forming ovoid protuberance distally; apical segment double, XXVII–XXVIII. Segments 2 to 10 densely packed, segment 22 with posterodistal angle produced into pointed process. Segmental armature as follows: segment 1 (I–III), 5 setae + aesthetasc; segments 2 to 4 (IV to VI), 2 setae each; segment 5 (VII), 2 setae + aesthetasc; segments 6 to 13 (VIII to XV), 2 setae each; segment 14 (XVI), 2 setae + aesthetasc; segments 15 to 18 (XVII to XX), 2 setae each; segment 19 (XXI), 2 setae + aesthetasc; segments 20 and 21 (XXII and XXIII), 1 seta each; segment 22 (XXIV), 2 setae; segment 23 (XXV), 2 setae + aesthetasc; segment 24 (XXVI), 2 setae; segment 25 (fused XXVII and XXVIII), 5 setae + aesthetasc. Aesthetascs on segments 1 and 5, and one seta on segment 5 elongate.

Antenna (figure 2B) biramous: coxa unarmed; basis completely fused to proximal endopodal segment forming allobasis armed with 2 unequal setae at two thirds of distance along medial margin. Free endopodal segment double, elongate, with 5 setae proximally and 7 setae on tip; ornamented with 3 transverse rows of setules. Exopod indistinctly segmented, with fusion pattern as follows: I and II completely fused, III partly fused to I–II and also to IV, IV partly fused to V; setal formula of this section 0,1,1,1,1: ancestral segments VI and VII free, bearing 1 seta each: ancestral segments VIII and IX completely fused, latter partly fused to X; setal formula of this section: 1,1,3. Transverse rows of setules present on proximal and distal exopodal segments.

Mandible with stout coxal gnathobase (not figured). Mandibular palp (figure 3A) with basis longer than wide, unarmed but with 2 rows of short spinules. Exopod apparently 3-segmented, but 2 proximal segments partly fused; setal formula [(1 + 1), 4]. Endopod 2-segmented, setal formula [3,8]; ornamented with rows of spinules.

Maxillule (figure 3B) with praecoxa produced into large arthrite bearing 11, some very stout, pectinate spines, plus pair of setae on posterior surface. Coxa with epipodite bearing 8 marginal setae increasing in size distally and with submarginal row of short spinules; endite armed with 5 setae, 2 of them stout. Basis with proximal endite discrete, armed with stout seta plus 3 slender setae subdistally; distal endite represented by 4 setae. Basal exite absent. Articulations of protopodal segments not well defined. Endopod 1-segmented, resulting from partial fusion of ancestral segments I to III; setal formula [3,2,6]. Exopod oar-shaped, with row of 7 distal and 2 lateral setae; medial and lateral margins with setule rows.

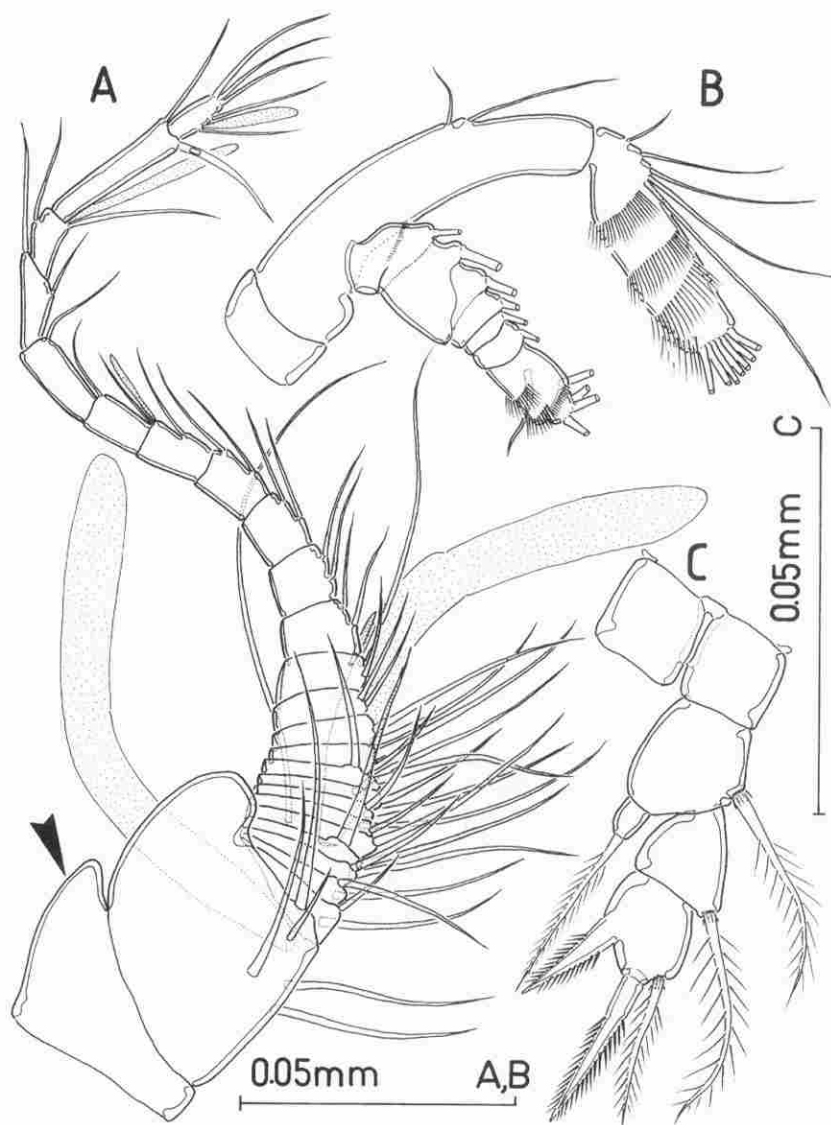


FIG. 2. *Huysia bahamensis* gen. et sp. nov. Adult female. A, antennule with pedestal arrowed, dorsal; B, antenna; C, right fifth leg, reduced intercoxal sclerite and coxa of left leg, posterior.

Maxilla (figure 3C) powerfully developed, 6-segmented. Praecoxa and coxa discrete; endites with setal formula [6,3,3,3]; row of short spinules along lateral margin of praecoxa. Allobasis ornamented with 2 rows of short spinules, as figured; proximal (= basal) endite powerfully developed, drawn out distally into stout, non-articulating curved medial claw with 4 unequal setae implanted around its base; distal (= endopodal) endite hardly developed, represented by 3 long setae. Free endopod 3-segmented, with setal formula [2,2,4].

Maxilliped (figure 4A) slender, 8-segmented. Syncoxa ornamented with 2 rows of setules as figured; praecoxal endite absent; coxal endites with setal formula [2,4,3].

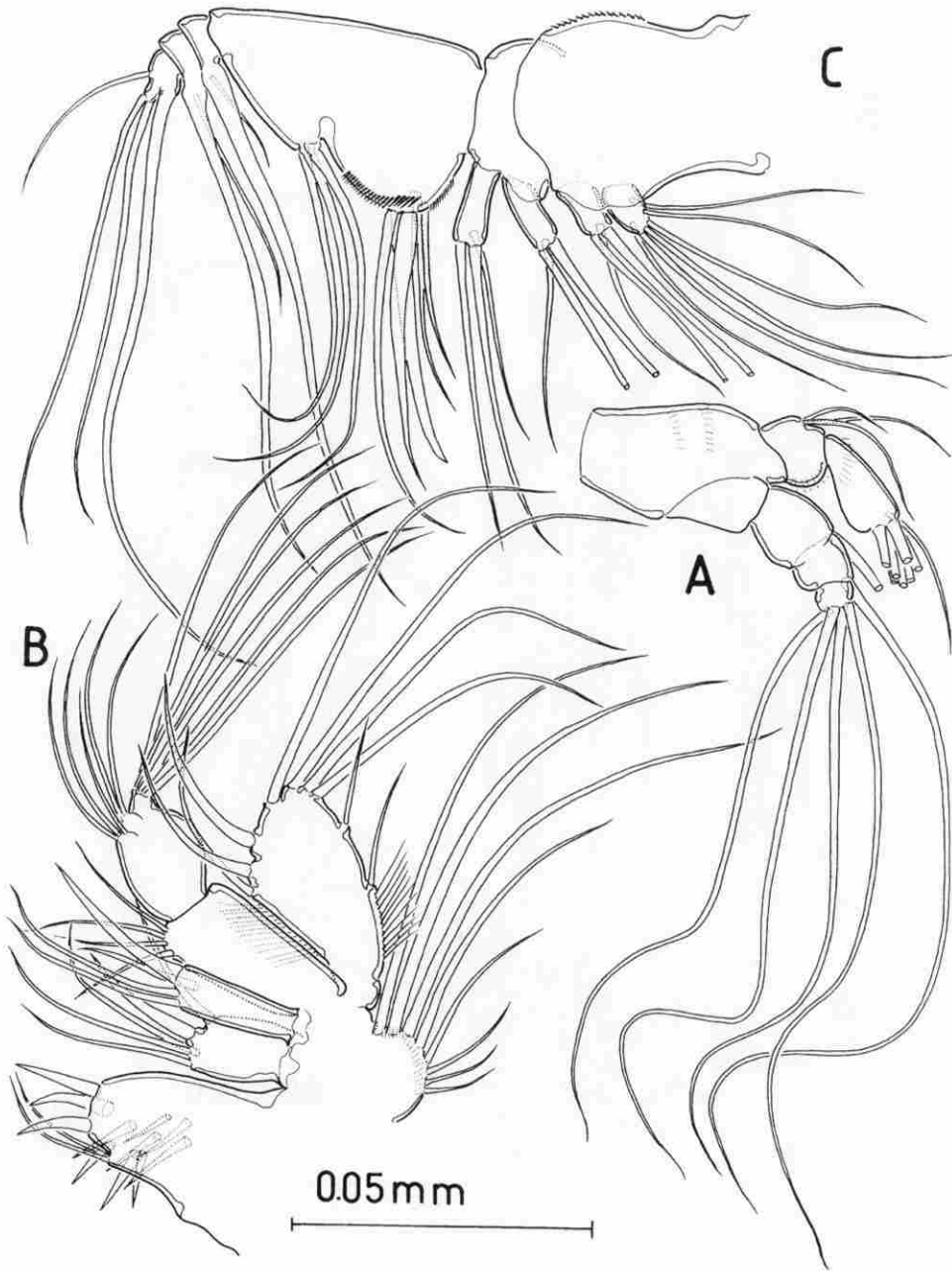


FIG. 3. *Huysia bahamensis* gen. et sp. nov. Adult female. A, mandibular palp; B, maxillule; C, maxilla.

Basis triangular, armed with 3 setae. Endopod 6-segmented, with setal formula [1,2,2,2,2+1,5]; distal segment elongate.

Swimming legs (figures 4B, C; 5) with 3-segmented rami except for 2-segmented endopod of leg 1. Legs similar in size except leg 1 somewhat smaller. Praecoxa retained on each leg. Acute spinous process on inner margin of basis of leg 2 smaller

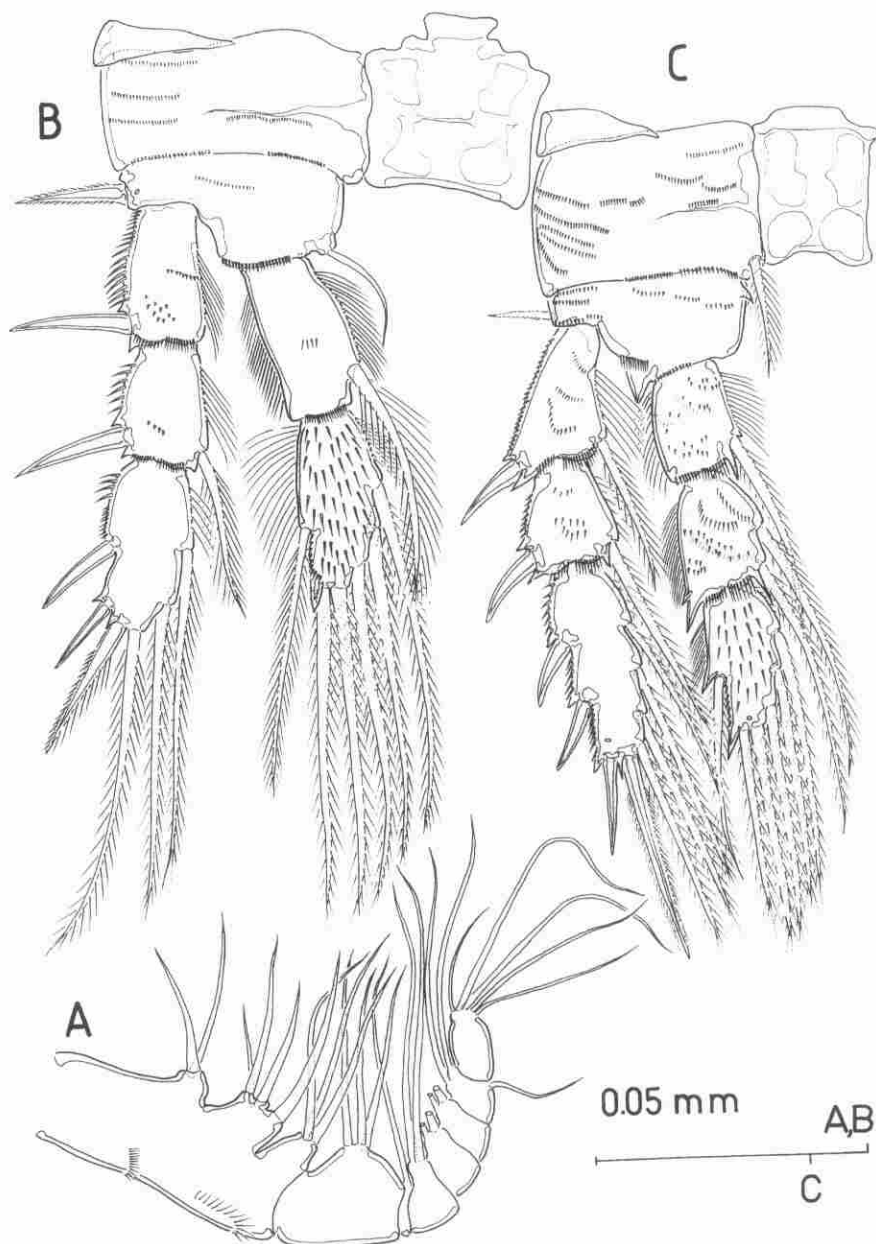


FIG. 4. *Huysia bahamensis* gen. et sp. nov. Adult female. A, maxilliped; B, leg 1, anterior; C, leg 2, anterior.

and arising more proximally than in legs 3 and 4. Distal corners of endopodal segments of legs 2 to 4 typically produced into conspicuous spinous processes. Spines on outer margin of exopod of leg 4 hirsute, not serrate. Surface of rami of legs adorned with spinules and setules as figured; ornamentation especially rich on posterior surface of leg 4 (figure 5C). Spine and seta formula as follows:

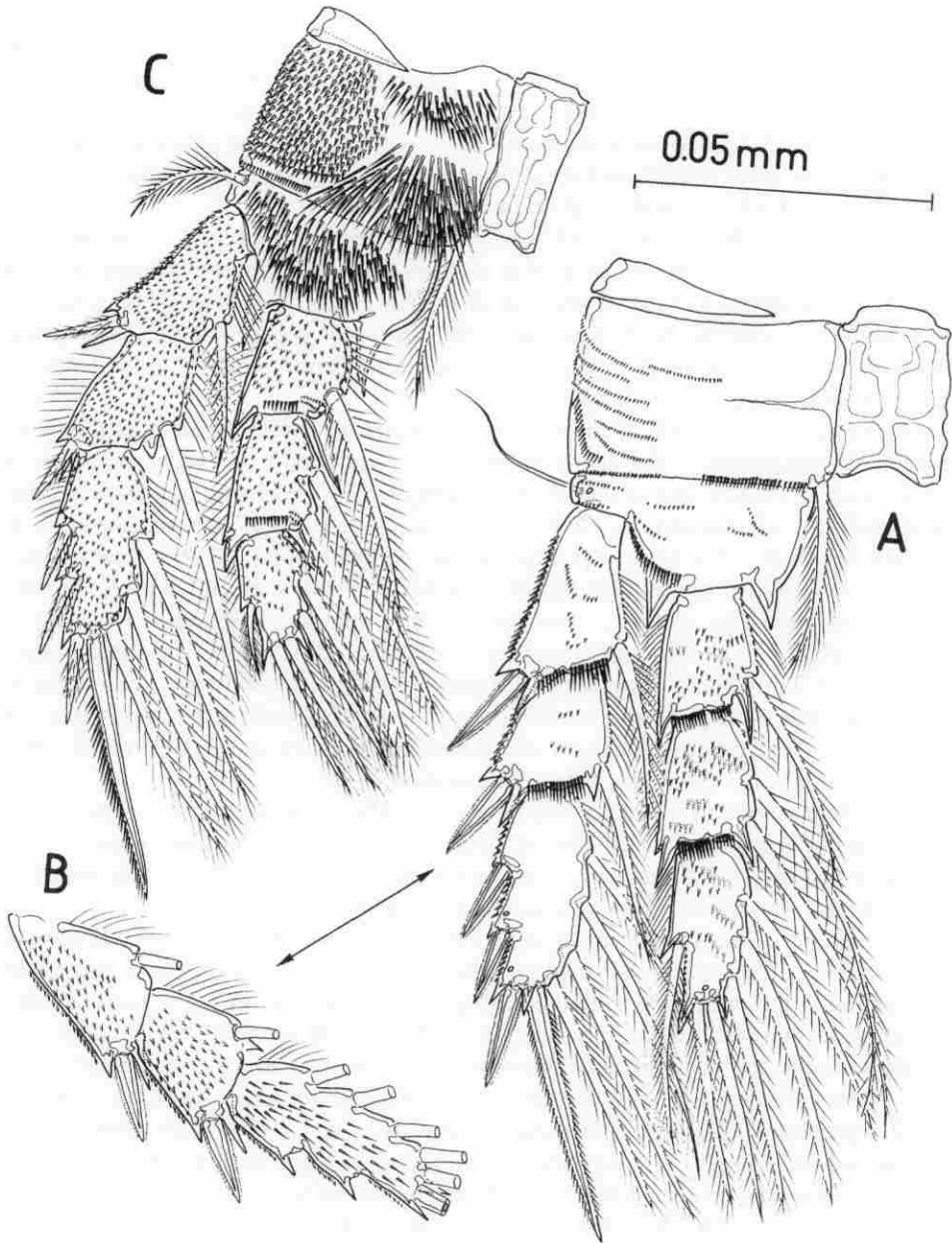


FIG. 5. *Hysia bahamensis* gen. et sp. nov. Adult female. A, leg 3, anterior; B, detail of posterior surface of leg 3 exopod, with outer spines of third segment omitted; C, leg 4, posterior.

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

Fifth legs (figure 2C) positioned adjacent to ventral midline; minute intercoxal sclerite present. Leg biramous comprising coxa, basis, 2-segmented exopod and 1-segmented endopod. Tiny lateral sclerite present, possibly representing praecoxa. Coxa unarmed; basis and proximal exopodal segment each with plumose seta on outer margin. Distal exopodal segment armed with distal spine articulated at base, stout spine on inner margin lacking articulation with segment, and plumose seta on outer margin. Endopod with single plumose seta apically.

Adult male. Body (figure 6A) resembling female, sexually dimorphic in antennules, legs 5 and 6 and in genital segmentation. Urosome 6-segmented, with genital somite about as long as wide, slightly larger than following somites; surface with abundant sensillae. Sixth legs (figure 6E) represented by opercular flaps articulated to somite; bearing 3 unequal plumose setae and patch of tiny denticles. Spermatophores paired, elongate.

Antennules (figures 6B, C) bilaterally symmetrical, similar to female in general aspect; 25-segmented; differing in presence of geniculation between segments 18 (XX) and 19 (XXI) and in cup-shaped segment 13 (XV) forming sheath around proximal half of segment 14 (XVI). Segmental armature as in female except as follows: segment 1 (I–III), 4 setae + aesthetasc; segment 9 (XI), 2 setae + aesthetasc; segment 17 (XIX) 1 seta plus modified plate-like element; segment 18 (XX), 1 seta, 1 modified plate-like element, plus row of tiny spinules; segment 19 (XXI), 2 modified plate-like elements plus aesthetasc; segment 20 (XXII), 1 modified plate-like element. Differences in number of elements between sexes involve only segment 1 (2 setae less in males) and segment 9 (1 aesthetasc present in males but not in females). Remaining differences are transformations of setae to form modified plate-like spines in segments around geniculation.

Fifth legs (figure 6D) general aspect as in female, differing only in armature of distal exopodal segment, consisting of distal spine articulated at base, plumose seta on outer margin, and 2 unequal, stout spines lacking articulation with segment on inner margin; innermost spine pinnate only along inner margin.

Etymology. The new species is named after its known distribution, the Bahamas.

Remarks. *Huysia* can be distinguished from all other misophrioid genera by the unique combination of a derived 2-segmented endopod in leg 1 and a plesiomorphic 1-segmented endopod in leg 5 of both sexes. Boxshall (1989) recognized 2 lineages among the misophrioids known at that time. A distinct 1-segmented endopod on the fifth leg was known only in the *Misophria*-lineage, with the endopod being represented by at most an isolated seta, as in *Boxshallia* Huys, 1988, in the *Archimisophria*-lineage. The 2-segmented endopod in leg 1 occurs only in the relatively apomorphic genera within the *Archimisophria*-lineage, such as *Speleophria* Boxshall & Iliffe, 1986, *Speleophriopsis* Jaume & Boxshall, 1996, *Palpophria* Boxshall & Iliffe, 1987 and *Dimisophria* Boxshall & Iliffe, 1987.

This new genus shares with *Protospeleophria* gen. nov. (described below) the general body form, the form of the rostrum, the segmentation and armature of all the cephalic appendages except the maxilliped, the segmentation of the swimming legs and the armature of the swimming legs except leg 1. The fifth legs of both sexes of *Huysia* are distinctive in the retention of the discrete endopod and in the armature of the distal exopodal segment in the female, in which the inner, non-articulating element is a typical bipinnate spine rather than a heavily-sclerotized, dentate plate. The tiny sclerite located laterally at the base of the coxa of the fifth leg in both sexes of *Huysia* (and in *Protospeleophria* described below) may represent a vestige of the

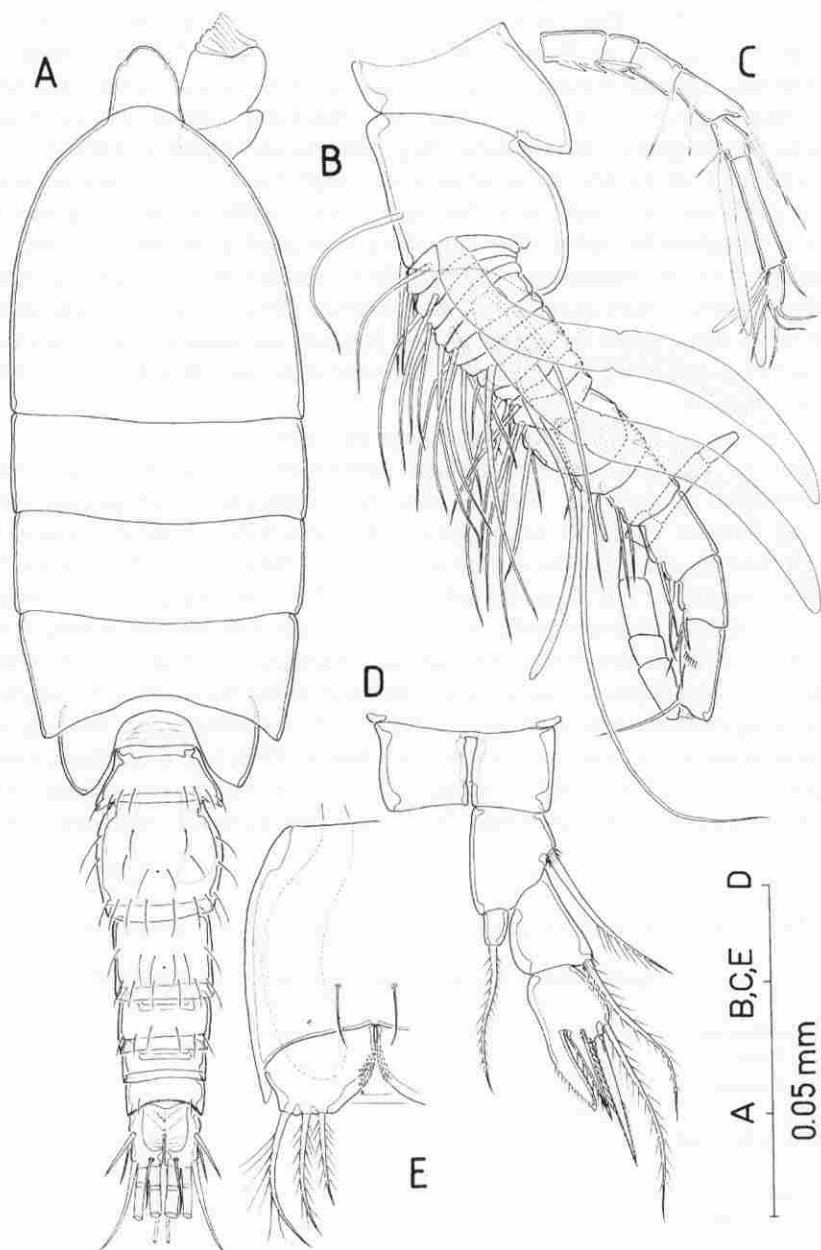


FIG. 6. *Huysia bahamensis* gen. et sp. nov. Adult male. A, body, dorsal; B, antennule, ventral (armature of segments distal to geniculation omitted); C, antennule, detail of segments distal to geniculation (19 to 25); D, right fifth leg, reduced intercoxal sclerite and coxa of left leg, posterior; E, detail of genital somite, ventral.

praecoxal segment. If this interpretation were correct, this would be the first report of any praecoxal vestige on the fifth leg in any podoplean copepod.

The maxillipeds of these genera differ in the loss of the praecoxal seta in *Huysia* and in the setation formula of the endopod, [1,2,2,2,2+1,5] in *Huysia* compared

with [1,3,3,2,2+1,5] in *Protospeleophria*. The differences in leg 1 include the absence of the inner coxal seta in *Huysia* and the presence of only 2 outer spines on the third exopodal segment instead of the 3 displayed by *Protospeleophria*. The lobe on the proximal segment of the antennules is remarkably similar to that found in *Boxshallia* and suggests a close relationship between these genera (table 1).

Even though all the *Huysia* material was gathered in open cave waters with the aid of a plankton net, some morphological traits exhibited by the genus might indicate a hyperbenthic habit. The laterally compressed prosome, the lobe on the proximal part of the antennules, the modified articulations between the posterior abdominal somites (permitting strong dorsoventral flexure between these somites), and the stout distal setae on the swimming legs are all features previously noticed in taxa which temporarily burrow into loose sediments (see Ohtsuka *et al.*, 1996 and references therein).

***Protospeleophria* gen. nov.**

Diagnosis. Cephalosome not produced posteriorly into carapace-like extension. First pedigerous somite free. Female urosome 5-segmented, with genital and first abdominal somites fused to form genital double-somite; single copulatory pore opening ventrally. Caudal rami armed with 7 setae. Antennules 25-segmented, with compound proximal (I–III) and apical (XXVII–XXVIII) segments. Proximal segment slightly swollen dorsolaterally; elongate aesthetascs present on segments 1 (III) and 5 (VII). Maxillary basal exite absent. Allobasis of maxilla with armature formula [5,3]. Maxilliped syncoxa with praecoxal endite represented by single seta; endopod 6-segmented, setal formula [1,3,3,2,2+1,5]. Swimming legs with segmentation and setation as for type species described below. Fifth legs uniramous, comprising separate coxa, basis and 2-segmented exopod; intercoxal sclerite present. Armature as follows: coxa unarmed; basis and first exopodal segment each with

Table 1. Main distinguishing features between genera in the *Speleophria* group.

	<i>Speleophria</i>	<i>Huysia</i>	<i>Speleophriopsis</i>	<i>Boxshallia</i>	<i>Protospeleophria</i>
Proximal antennule segment lobate	+	++	—	++	—
Maxillary allobasis setation	5+3	5+3	5+3	5+1	5+3
Maxilliped praecoxal seta	—	—	+	+	+
Leg 1 endopod, segment number	2	2	2	3	2
Leg 4, inner setae on third exopodal segment	4	3	5	3	3
Female leg 5, endopod state	—	1-segment + 1 seta	—	1 seta	—
Female leg 5, distal segment mid-outer margin spine	—	—	+	—	—
Female leg 5, distal segment mid-inner margin seta	—	—	+	—	—

outer seta; second exopodal segment with 3 elements, innermost modified as a broad sclerotized plate denticulated distally. Male unknown.

Type species. *Protospeleophria lucayae* Jaume, Boxshall and Iliffe sp.nov.

Etymology. The generic name alludes to the relatively plesiomorphic state of some characters of the new taxon with respect to *Speleophria*.

Protospeleophria lucayae sp. nov.

(figures 7–11)

Material examined. **Exuma Cays, Bahamas:** Norman's Pond Cave, Norman's Pond Cay. HOLOTYPE adult female 0.74 mm (BMNH reg. no. 1997.993) dissected on 8 slides and mounted in lactophenol sealed with nail varnish. Collected by T.M. Iliffe, 4 May 1993.

Adult female. Body (figures 7A, B) cyclopiform, ovoid, colourless. Nauplius eye absent. Prosome 5-segmented, with first pedigerous somite not incorporated into cephalothorax. Cephalosome not extended posteriorly into carapace. Rostrum sickle-shaped, powerfully developed, fused to dorsal cephalic shield. Prosomal pedigerous somites with evenly rounded posterolateral corners.

Urosome 5-segmented; genital and first abdominal somites completely fused to form genital double-somite, with internal vestige of suture between somites visible in dorsal aspect (figure 7A). Genital field (figures 7C, D) located anteriorly on double-somite. Single copulatory pore small, located midventrally, communicating with fused seminal receptacles. Gonopores separate, in form of narrow slits located ventrally on each side of copulatory pore; each covered by vestigial leg 6 armed with long outer plumose seta plus 2 short inner spines. Ventral surface of genital double-somite and sixth legs ornamented with patches of spinules as figured. Anal somite and caudal rami with surface uniformly covered by tiny spinules, as figured (figures 7E, F); anal operculum faint, with smooth rim. Caudal rami with 7 setae (figures 7F, G); anterolateral accessory seta (seta I of Huys and Boxshall, 1991) reduced.

Antennules (figures 8A, B) 25-segmented, similar to *Huysia* except dorsolateral protuberance on proximal segment only weakly developed and presence of tiny aesthetasc on segment 9 (XI), apparently absent in female *Huysia*.

Antenna (figure 9A) biramous, identical in segmentation and armature to *Huysia*, although combs of setules ornamenting proximal and distal exopodal segments apparently lacking. Compound second exopodal segment expanded laterally. Mandible with stout coxal gnathobase (not figured); mandibular palp (figure 8C) identical in segmentation and setation to *Huysia*, but exopod medially expanded proximal to first seta. Maxillule (figure 9B) with general aspect similar to *Huysia* but differing in armature of endopod, displaying only 2 groups of setae, with setal formula [5,6], rather than 3 groups (formula [3,2,6]).

Maxilla (figure 9C) powerfully developed, 6-segmented. Praecoxa and coxa partially fused; endites with setal formula [6,3,3,3]. Allobasis with proximal (=basal) endite powerfully developed, drawn out distally into stout, medial claw articulated at base; claw pinnate along one side only; 4 unequal setae implanted around claw base; endite ornamented with patch of tiny spinules and row of fine setules, as figured; distal (=endopodal) endite represented by 3 long setae. Free endopod 3-segmented, with setal formula [2,2,4].

Maxilliped (figures 11A, B) slender, 8-segmented. Syncoxa ornamented distally

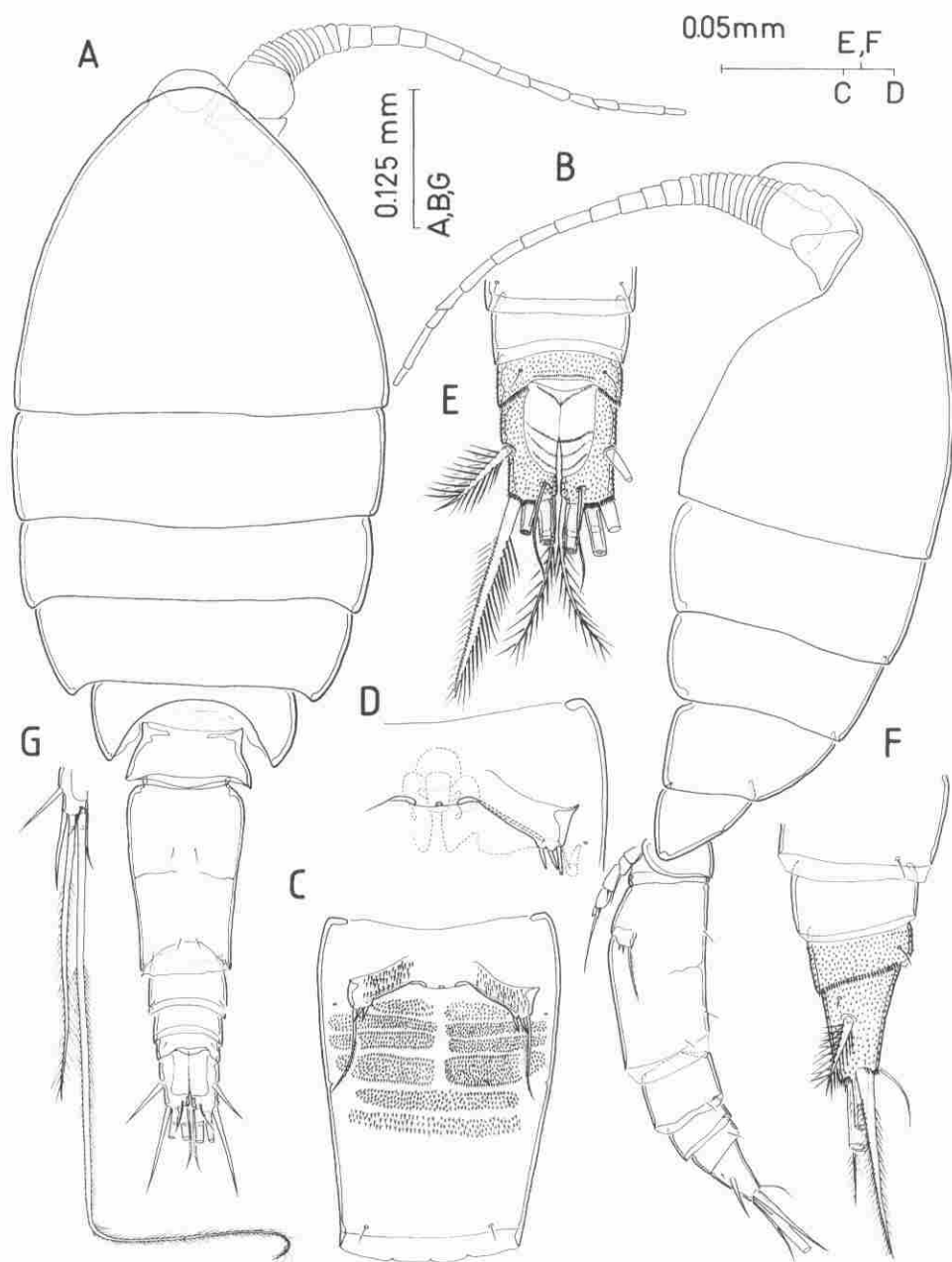


FIG. 7. *Protospeleophria lucayae* gen. et sp. nov. Adult female. A, body, dorsal; B, same, lateral; C, genital double-somite, ventral; D, detail of genital field; E, anal somite and caudal rami, dorsal; F, same, lateral; G, detail of setae on left caudal ramus, dorsal.

with row of setules; praecoxal endite represented by 1 seta; coxal endites with setal formula [2,4,3]. Basis triangular, armed with 3 setae and ornamented with 4 rows of setules. Endopod 6-segmented, with setal formula [1,3,3,2,2+1,5]; distal segment elongate.

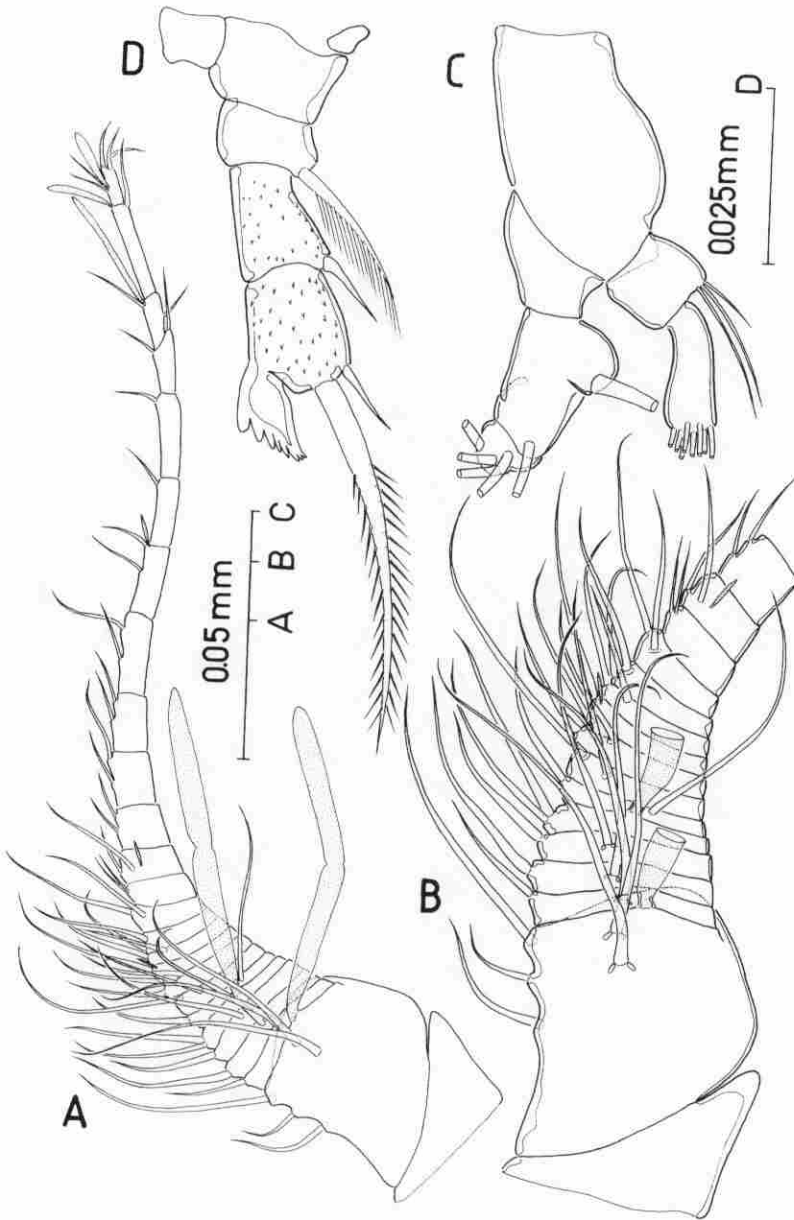


FIG. 8. *Protospeleophria lucayae* gen. et sp. nov. Adult female. A, antennule, ventral; B, detail of antennular segments 1 to 15, ventral; C, mandibular palp; D, left fifth leg and intercoxal sclerite, anterior.

Swimming legs (figures 10A,B; 11C, D) with 3-segmented rami except 2-segmented endopod of leg 1. Legs similar in size except leg 1 somewhat smaller. Vestige of praecoxa retained on each leg. Leg 1 with inner coxal seta reduced; inner basal seta implanted subdistally on spinous process. Apical setae on both rami of legs 2 to 4 short and robust. Surfaces of legs ornamented with spinules as figured. Spine and seta formula as follows:

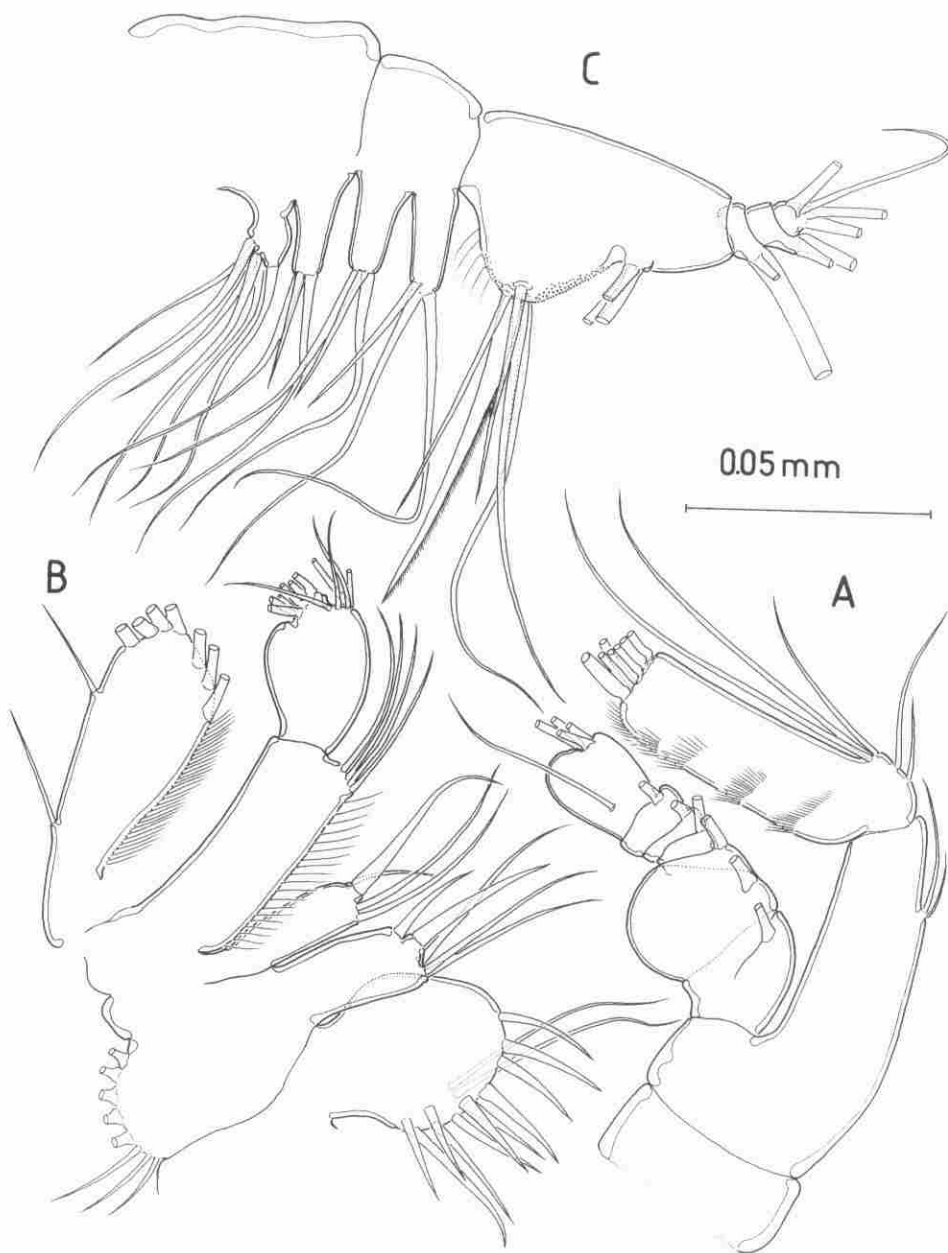


FIG. 9. *Protospeleophria lucayae* gen. et sp. nov. Adult female. A, antenna; B, maxillule (exopod disarticulated); C, maxilla.

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

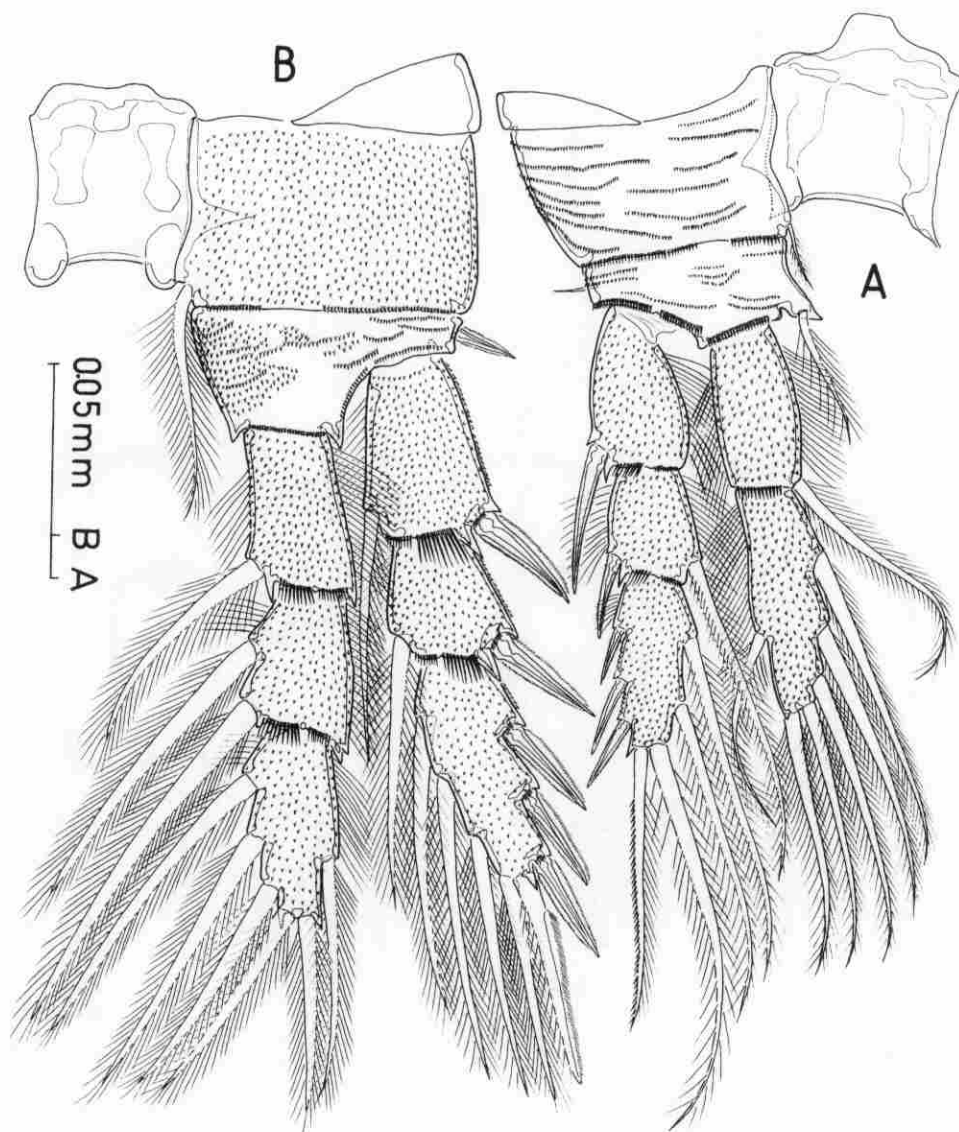


FIG. 10. *Protospeleophria lucayae* gen. et sp. nov. Adult female. A, leg 1, anterior; B, leg 2, anterior.

Fifth legs (figure 8D) positioned adjacent to ventral midline, intercoxal sclerite well developed. Legs uniramous, comprising tiny lateral sclerite, coxa, basis and 2-segmented exopod. Coxa unarmed; basis with thick, plumose seta on outer distal margin. Proximal exopodal segment with short, smooth seta on outer margin; distal exopodal segment armed with long pectinate seta distally; stout, powerfully sclerotized dentate plate lacking articulation to segment on inner margin and short smooth seta on outer margin.

Adult male. Unknown.

Etymology. The species name is derived from Lucayo, the indigenous people of the Bahamas.

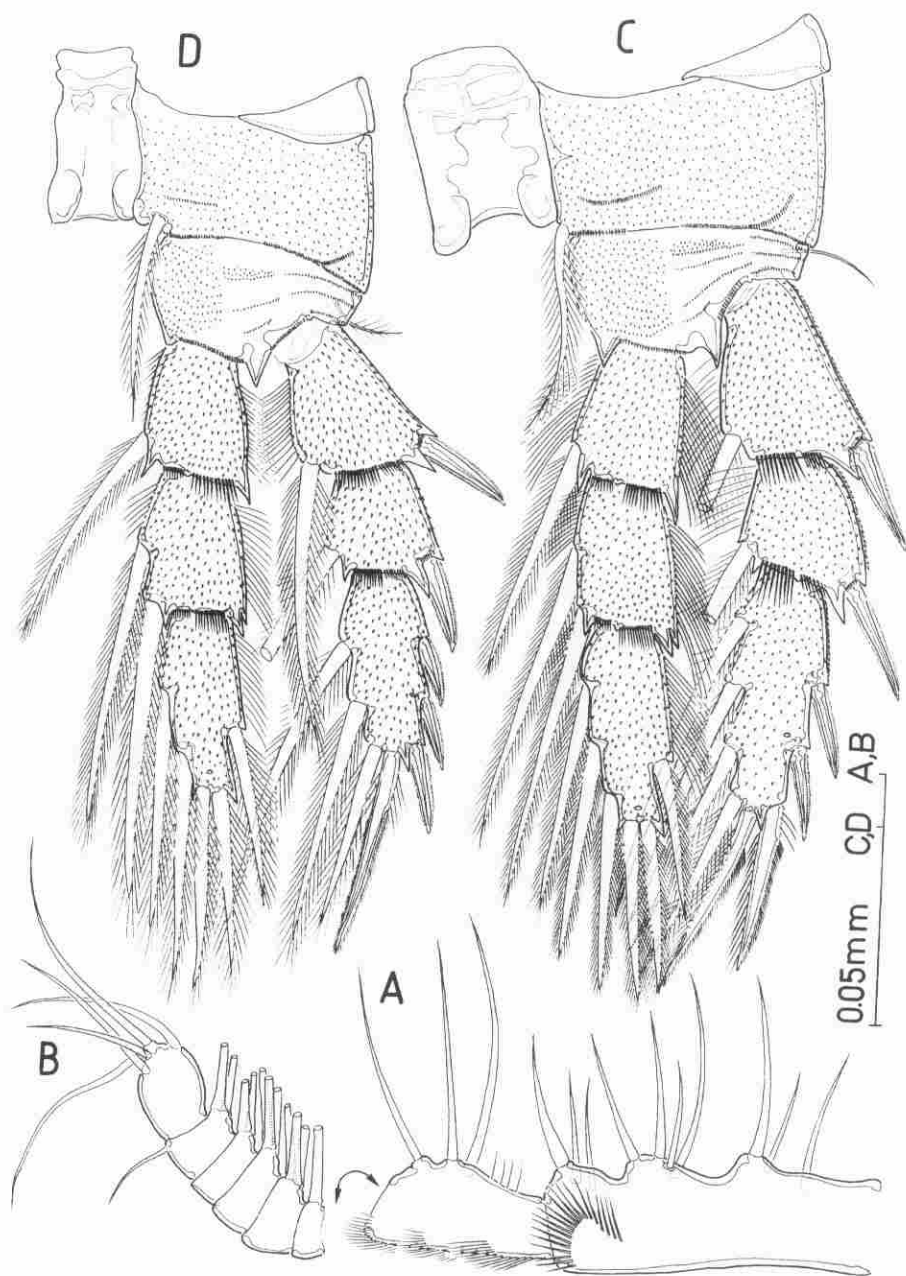


FIG. 11. *Protospeleophria lucayae* gen. et sp. nov. Adult female. A., syncoxa and basis of maxilliped; B, endopod of maxilliped; C, leg 3, anterior; D, leg 4, anterior.

Remarks. Even though the structure and armature of the fifth legs of *Protospeleophria* gen. nov. is almost identical to that of *Speleophria*, other important characters indicate that these taxa are distinct at the generic level (table 1). *Protospeleophria* differs from *Speleophria* in the separate expression of antennular segments IX to XII and XV to XVI, the absence of the basal exite seta on the

maxillule, the retention of a seta representing the praecoxal endite of the maxilliped, the setal formula of the maxilliped [1,3,3,2,2+1,5] (compared to [1,2,2,2,2+1,5] in *Speleophria*) and in the loss of 1 inner seta from the third exopodal segment of leg 4. An additional difference between these genera is the structure of the inner armature element on the distal segment of leg 5. It is a plate-like spine fused basally to the segment in both genera, but in *Protospeleophria* it is powerfully sclerotized and provided with large, rounded denticles decreasing in size distally whereas in *Speleophria* it is less sclerotized and is barbed along both margins.

Discussion

The two new genera can be placed in the *Archimisophria*-lineage as defined by Boxshall (1989) since they share two of the diagnostic synapomorphies: loss of the aesthetasc from ancestral antennular segment XVIII, and the loss of 1 inner seta from the second endopodal segment of leg 1. In his phylogenetic analysis, Boxshall (1989) coded this latter character as missing data in those misophrioid genera with a 2-segmented endopod in leg 1 but it is suggested here that one of the inner setae originally derived from the second endopodal segment is lost in all the genera with a 2-segmented ramus, including *Huysia* and *Protospeleophria*. The absence of the proximal seta from the inner margin of the second endopodal segment of leg 1 of *Archimisophria* and *Boxshallia* suggests that this seta might be absent from the entire *Archimisophria*-lineage. According to our interpretation the proximal inner seta of the original second endopodal segment is one of those lost.

A close relationship between the new genera described above and *Speleophria* and *Speleophriopsis* is indicated by the following shared characters: the presence of a long, falcate rostrum, the fusion of genital and first abdominal somites of the female to form a double-somite, the presence of elongate aesthetascs on antennular segments 1 (III) and 5 (VII), the [5,3] armature formula of the allobasis of the maxilla, the 2-segmented endopod of leg 1 and the 4-segmented fifth legs (with coxa, basis and 2-segmented exopod). Many of these characters are shared with less closely-related genera, such as *Boxshallia* and *Expansophria* Boxshall & Iliffe, 1987, but the unusual form and armature of the maxillary allobasis is an important synapomorphy linking only these four genera (table 1). The large triangular allobasis is unique to these genera and the presence of eight setation elements is the maximum recorded on the allobasis of any copepod. The presumed ancestral copepod setation proposed by Huys and Boxshall (1991) was [4,4] for the basal endite and the first endopodal segment of maxilla. The pattern displayed by this group of genera of five proximal and three distal elements could be derived either by migration of one element from the endopodal endite to the basal endite after the formation of the allobasis, or by reduction from a [5,4] condition of the ancestral copepod (with the loss of one endopodal seta in all other copepods). At present there is insufficient evidence to choose between these alternative hypotheses.

Another outstanding characteristic of this group of genera is the segmentation pattern exhibited in the region around the geniculation in the male antennule. The males of *Speleophria* and *Protospeleophria* are unknown but in *Huysia* and *Speleophriopsis* there are no complete fusions between the segments separated by the geniculation and the adjacent segments. This necessitates some refinement of the concept of the neocopepodan geniculation of Huys and Boxshall (1991). The neocopepodan geniculation is a modified articulation between ancestral segments XX and XXI, with an area of arthrodial membrane posteriorly and an anteriorly-located

hinge line about which adduction of the distal part takes place. This adduction is effected by opposing muscles which originate proximally in the antennule and insert on the rim of segment XXI. The modified type of articulation differs from the telescopic articulation present in the female at this position in the restriction of flexure to a single plane only by the presence of a hinge line, and in the reduction of the extent of arthrodial membrane present. Typically there are segmental fusions either side of the geniculation (XIX to XX and XXI to XXII) but these are apparently absent in *Speleophriopsis* (Jaume and Boxshall, 1996a) and in *Huysia*. Such fusions can be difficult to interpret since, in some taxa, a suture line apparently separates segments that are functionally fused (i.e. unable to articulate against each other). Fused segments should be considered as a subsequent addition to the complex of character states that comprises the neocopepodan articulation.

An additional aspect of the neocopepodan geniculation that has not been considered is the modification of setation elements on segments near the geniculation. In adult males of misophrioids, setae on segments XIX, XX, XXI and XXII are modified into fused, plate-like structures, usually with a pore and often with surface ridges. Modified elements occur on these segments in males of other orders, including cyclopoids, harpacticoids and calanoids, and their presence may be yet another facet of the neocopepodan geniculation.

The third character used by Boxshall (1989) in defining the *Archimisophria*-lineage was the state of the fifth leg. The fullest expression of leg 5 previously known in this lineage was the retention of a single endopodal seta in *Boxshallia*. A more plesiomorphic state, a defined endopodal segment bearing a single apical seta, is retained in *Huysia* although the presence of a single endopodal seta remains a synapomorphy of the *Archimisophria*-lineage since two endopodal setae are retained only in members of the *Misophria*-lineage, such as the genera *Misophria* Boeck, 1865, *Arcticomisophria* Martinez-Arbizu & Seifried, 1996 and *Fosshageniella* Jaume & Boxshall, 1997. A single endopodal seta is also found in the *Misophria*-lineage in the following genera, *Misophriopsis* Boxshall, 1983, *Stygomisophria* Ohtsuka, Huys, Boxshall & Itô, 1992 and *Benthomisophria* Sars, 1909.

Central American Misophrioida

New misophrioid taxa were collected by T. M. Iliffe during two expeditions to the Yucatan Peninsula in Mexico. The records are as follows:
1993 biospeleological expedition to the Yucatan Peninsula

Locality:

Noc Ac Cenote, Noc Ac	4 misophrioids
Cenote Mucuyché, Mucuyché	1 misophrioid copepodid

1994 biospeleological expedition to the Yucatan Peninsula

Locality:

Mayan Blue Cenote, Tulum, Quintana Roo	3 misophrioids
Temple of Doom Cenote, Tulum, Quintana Roo	1 misophrioid

Among these samples were representatives of an undescribed species of *Speleophriopsis*, a new species of *Speleophria* and a possible new genus. Unfortunately the material was not in a suitable state for full taxonomic description, but the presence of these taxa is noted here.

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References

- BOTOSANEANU, L. (ed.), 1986, *Stygofauna Mundi*, (Leiden: E. J. Brill), 740 pp.
- BOXSHALL, G. A., 1989, Colonization of inland marine caves by misophrioid copepods, *Journal of Zoology*, **219**, 521–526.
- BOXSHALL, G. A. and ILIFFE, T. M., 1986, New cave-dwelling misophrioids (Crustacea: Copepoda) from Bermuda, *Sarsia*, **71**, 55–64.
- DILL, R. F., WILKENS, R. and CURRAN, H. A., 1990, Caves and Blue Holes, in Christopher G. St. C. Kendall, Robert F. Dill and Eugene A. Shinn, *Guidebook to the Marine Geology and Tropical Environments of Lee Stocking Island, the Southern Exumas, Bahamas*, (San Diego, CA: Ken Dill Publishers) 5th edition, pp. 59–60.
- HUYS, R. and BOXSHALL, G. A., 1991, *Copepod Evolution*, (London: The Ray Society), 468 pp.
- ILIFFE, T. M., 1992, Anchialine cave biology, in A. I. Camacho (ed.), *The Natural History of Biospeleology*, (Madrid: Monografías del Museo Nacional de Ciencias Naturales), pp. 613–636.
- JAUME, D. and BOXSHALL, G. A., 1996a, A new genus and two new species of cave-dwelling misophrioid copepods from the Balearic Islands (Mediterranean), *Journal of Natural History*, **30**, 989–1006.
- JAUME, D. and BOXSHALL, G. A., 1996b, The persistence of an ancient marine fauna in Mediterranean waters: new evidence from misophrioid copepods living in anchialine caves, *Journal of Natural History*, **30**, 1583–1595.
- JAUME, D. and BOXSHALL, G. A., 1997, A new genus and two new species of misophrioid copepods (Crustacea) from the North Atlantic hyperbenthos, *Sarsia*, **82**, 39–54.
- MARTÍNEZ-ARBIZU, P. and SEIFRIED, S., 1996, The phylogenetic position of *Arcticomisophria bathylaptevensis* gen. et sp. n. (Crustacea: Copepoda) a new misophrioid from hyperbenthic deep-sea waters in the Laptev Sea (Arctic Ocean), *Sarsia*, **81**, 285–295.
- OHTSUKA, S., FOSSHAGEN, A. and SOH, H. Y., 1996, Three new species of the demersal calanoid copepod *Placocalanus* (Ridgewayiidae) from Okinawa, southern Japan, *Sarsia*, **81**, 247–263.
- OHTSUKA, S., HUYS, R., BOXSHALL, G. A. and ITÔ, T., 1992, *Misophriopsis okinawensis* sp. nov. (Crustacea: Copepoda) from hyperbenthic waters off Okinawa, South Japan, with definitions of related genera *Misophria* Boeck, 1864 and *Stygomisophria* gen. nov., *Zoological Science*, **9**, 859–874.
- SEALEY, N. E., 1994, *Bahamian Landscapes*. (Nassau, Bahamas: Media Publ.) 2nd edition, 128 pp.
- STOCK, J. H., ILIFFE, T. M. and WILLIAMS, D. 1986 The concept 'anchialine' reconsidered, *Stygologia*, **2**, 90–92.