The Epacteriscidae, a cave-living family of calanoid copepods

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Twelve genera and 20 species of epacteriscids are recorded from marine and anchialine caves in tropical and subtropical waters. Nine genera are new: *Edaxiella* from Jamaica; *Enantronia* from Lanzarote, the Canary Islands; *Balinella*, *Bofuriella*, *Bomburiella*, *Enantronoides*, and *Oinella* from the Bahamas; *Gloinella* from Cuba; *Erebonectes macrochaetus* Fosshagen from the Caicos Islands, West Indies is transferred to a new genus *Erebonectoides*. Six new species of *Enantiosis* Barr are described, one each from Bermuda, Belize, Galapagos, and Fiji, and two from Palau. Two new species of *Epacteriscus* Fosshagen are described from Belize and *E. rapax* Fosshagen is recorded for the first time in Bermuda. New records of *Erebonectes nesioticus* Fosshagen are made in Bermuda and a habitat division between three species of *Epacteriscus, Enantiosis* and *Erebonectes* from Bermuda is suggested. A phylogenetic analysis of described taxa was performed using PAUP. Based on inferences from this analysis two new subfamilies are proposed: the Erebonectinae (to include *Erebonectes* and *Erebonectoides*) and the Epacteriscinae (to include all ten other genera).

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INTRODUCTION

The Epacteriscidae is a relatively recently discovered demersal family within the order Calanoida; most species of which have been obtained from flooded coastal caves in warm temperate to tropical shallow waters. Its members are characterized by a bilobed rostrum bearing filaments, up to 27 segments in the female antennules, raptorial mouthparts and by primitive swimming legs with 3-segmented rami. The first species discovered, *Epacteriscus rapax* Fosshagen, was taken using light dredges on bottom substrates and in washings of coral rubble in Florida and Colombia (Fosshagen 1973). An unnamed species of *Epacteriscus* was obtained in emergence traps in the Indo-Pacific region (Walter 1986). *Epacteriscus* has much reduced and unusual mouthparts, with the enormous paired gnathobases of the mandible extending out from the body as the most characteristic feature.

A second genus, *Enantiosis*, based on the species *E. cavernicola* Barr, was obtained from a cave in San Salvador Island, Bahamas. Subsequently as yet unnamed females of the genus were reported from emergence traps set in the Philippines (Barr 1984). *Enantiosis* has less reduced mouthparts than *Epacteriscus*, however, the fifth legs of the male are considerably more complex. A third genus, *Erebonectes* Fosshagen, formerly with two congeneric species from caves in Bermuda and Caicos Islands but now transferred to separate genera, retains a remarkable combination of some of the most primitive characters known among calanoids. They have 27-segmented antennules and only slightly modified mouthparts (Fosshagen & Iliffe 1985, 1994).

Anchialine caves, from which most of the present specimens were obtained, represent a very interesting habitat for crustaceans and in recent years several groups of high taxonomic status have been discovered. Among the calanoids, the most common families in anchialine habitats are the Ridgewayiidae M.S. Wilson, Stephidae Sars, Arietellidae Sars, Pseudocyclopidae Giesbrecht, Pseudocyclopiidae Sars, and Epacteriscidae Fosshagen (Jaume & Boxshall 1995).

In this investigation several new epacteriscids have been obtained, mostly by cave diving, from Bermuda, Bahamas, Jamaica, Belize, Cuba and Lanzarote in the Atlantic, and from Galapagos, Fiji, and Palau in the Pacific.

Nine new monotypic genera are erected from the Canary Islands, Cuba, Jamaica and the Bahamas. All new genera are based on new material except for *Erebonectes* *macrochaetus* Fosshagen from Caicos Islands (Fosshagen & Iliffe 1994) which now has been transferred to a new genus. In addition, two new species of *Epacteriscus* are described based on material from Belize, and six new species of *Enantiosis* on material from Bermuda, Belize, Galapagos, Fiji and Palau.

MATERIAL AND METHODS

The copepods were mostly obtained using advanced diving techniques, as a rule taken when dragging a fine-mesh hand net (ca. 100 µm) through the water, and a few times in a suction bottle or an open vial. Occasionally, specimens were collected by pumping water through a plankton net, either from the water column or from interstitial water using a Bou-Rouch biophreatic pump (Bou & Rouch 1967). Specimens were also obtained with dip nets, or by leaving a net suspended in a tidal current for a period of time, or in baited traps (Manning 1986).

All type material is kept in The Natural History Museum, London.

The phylogenetic analysis was performed using PAUP 3.1.1, produced by D. Swofford. All characters were treated as *irreversible up* following the analysis of Huys & Boxshall (1991) which demonstrated that oligomerization was the dominant mode of evolutionary transformation with the copepods. This generates longer, less parsimonious trees. A *branch-and-bound* search was initiated but was terminated after 13 days of continuous analysis. Instead a random *heuristic* search was employed. A total of 100 replicates were performed and six equally short trees were generated. The 50 % majority rule consensus tree was calculated and this tree, with bootstrap values shown, is given in Fig. 39. Multiple out-groups were utilised in the analysis. These were Ridgewayiidae (based on *Ridgewayia* sp.), Pseudocyclopiidae (based on *Pseudocyclops bahamensis* Fosshagen) and Metridinidae (based on *Metridia* sp.).

SYSTEMATICS

Family Epacteriscidae Fosshagen, 1973

The family diagnosis is based on the following twelve genera: *Epacteriscus* Fosshagen, 1973; *Enantiosis* Barr, 1984; *Erebonectes* Fosshagen, 1985; *Balinella* gen. n.; *Bofuriella* gen. n.; *Bomburiella* gen. n.; *Edaxiella* gen. n.; *Enantronia* gen. n.; *Enantronoides* gen. n.; *Erebonectoides* gen. n.; *Gloinella* gen. n. and *Oinella* gen. n.

Diagnosis (emend.). Gymnoplea, Calanoida. Body clearly divided into 6-segmented prosome and slender urosome. Prosome oval and robust, comprising cephalosome and 5 free pedigerous somites, rarely with some fusion between cephalosome and first pedigerous somite. Nauplius eye present or absent. Urosome 4-segmented in female; with 3 free abdominal somites; genital double-somite often produced ventrally. Anal somite often extremely small and concealed by being telescoped beneath posterior margin of preceding somite. Genital apparatus comprising paired gonopores located beneath median common genital operculum on ventral surface of genital double-somite; copulatory pores contained within median genital aperture. Urosome 5-segmented in male; comprising genital somite and 4 free abdominal somites, often with reduced anal somite. Single genital aperture located ventrolaterally at posterior rim of genital somite on right side. Caudal rami with up to 7 setae; seta I very small, sometimes absent; seta II spiniform, setiform or absent (in *Erebonectoides*). Caudal setae usually asymmetrical in female with seta V typically elongated on one side only and with left seta VI ornamented with tuft near base in many genera. Caudal setae often symmetrical in male or with elongate seta V on one side only.

Rostrum variable, typically bilobed with paired rostral filaments, sometimes extremely reduced. Antennule 24- to 27-segmented in female. Segments X and XI usually incompletely separated and showing short connection on posterior side; in some species articulations between segments I to IV and between XXVI and XXVII not expressed. Aesthetascs retained on segments I, III to XVIII, XXI, XXVI and XXVII-XXVIII. Antennule geniculate on right side only in male; geniculation present between segments XX and XXI; often with pointed anterior process on second or third segment distal to geniculation (segment XXV); segmental fusions typically XXI-XXIII, (XXII-XXIII in *Erebonectes* and *Erebonectoides*), XXIV-XXV and XXVII-XXVIII.

Antenna biramous; variable with endopod typically shorter than exopod, but longer than exopod in *Erebonectes*, *Erebonectoides* and *Balinella*. Coxa and basis usually separate: coxa with 1 seta or unarmed; basis with 1 or 2 setae, unarmed in *Oinella.* Endopod usually 2-segmented, apparently derived from incompletely 4-segmented ramus with setation formula 2, 9, 5, 2, usually with reductions in number of setae, especially on compound distal segment. Exopod 8-segmented in *Erebonectes*, with segments IX and X fused; setation formula: 1, 1, 1, 1, 1, 1, 1, 4: usually with segments I-IV indistinctly separated, lacking setae or bearing setae of reduced length; additional fusions and setation losses present in other genera.

Mouthparts raptorial. Mandibular gnathobase typically strongly developed, with long and sharp teeth, ventralmost part sometimes enlarged; scythe-like in

Epacteriscus: main axis of palp running through basis and exopod; basis armed with 0 to 4 setae: endopod reduced in size; 2-segmented, 1-segmented or absent according to genus, setation variable: exopod typically 5-segmented, setation formula 1, 1, 1, 1, 2, sometimes reduced.

Maxillule with well developed praecoxal arthrite bearing up to 15 elements; coxa with endite bearing up to 3 setae and 3 to 9 setae on epipodite; basis with outer seta only in *Erebonectes*; maximum number in *Erebonectoides* with proximal and distal groups of 4 and 5 setae, representing endites: endopod elongate, 1 or 2-segmented; setation formula 4+4+7, 3+3+6 or further reduced; exopod 1-segmented, armed with 11 setae. Maxillulary setation often reduced, as in *Epacteriscus*, particularly on coxal and basal endites.

Maxilla strongly built; indistinctly 4-segmented; praecoxa and coxa separate, setation formula of endites 6, 3, 3, 3, or reduced; basis with 4 setae: free endopod unsegmented; armed with up to 11 setae, 4 setae on lobe representing first endopodal segment, distal part of endopod with up to 7 setae. Setation often reduced.

Maxilliped 7-segmented; syncoxa with endite setation formula 1, 2, 4, 4; basis with 3 setae plus 2 setae distally representing incorporated first endopodal segment; free endopod 5-segmented, segmental setation formula 4, 4, 3, 3+1, 4. Setation sometimes reduced, often modified.

Swimming legs 1 to 4 biramous with 3-segmented rami and usually unmodified; some species with modification of third segment of exopod in leg 1. Spine and seta formula typically:

	coxa	basis	exopod segments 1 2 3	endopod segments 1 2 3
leg 1	0-1	0/1-1	I-1; I-1; II,I,4	0-1; 0-2; 1,2,3
leg 2	0-1	0/I-0	I-1; I-1; II,I,5	0-1; 0-2; 2,2,4
leg 3	0-1	0/1/I-0	I-1; I-1; II/III,I,5	0-1; 0-2; 2,2,4
leg 4	0-1	0/1-0	I-1; I-1; II/III,I,5	0-1; 0-2; 2,2,3
leg 5(f)	0-0	1-0	I-0/1;I-1;II/III,I,4	0-1;0-1;1/2,2,2/3

Setation often reduced; outer spine on basis of leg 2 present only in *Erebonectes*. Outer element on basis of leg 3 spiniform in some species. Outer margin of third segment of exopod of all legs with 2 or 3 spines according to genus.

Female fifth leg comprising 3-segmented protopod retaining hoop-like vestige of praecoxa laterally, and 3-segmented rami; setation sometimes reduced.

Male fifth legs asymmetrical; both legs typically with 3-segmented rami; exopod 2-segmented due to fusion of second and third segments on left side in *Epacteriscus*. Endopods similar to those of female with armature 0-1; 0-1; 2,2,2; slightly transformed in some genera (see remarks on *Enantiosis belizensis* sp. nov. below). Exopods usually highly transformed; most complex structures usually present on left exopod; modified with a slender spiniform distal segment, long and curved on right side in *Erebonectes* and *Enantiosis*.

Genus *Edaxiella* gen. nov.

Diagnosis. Female. Body slender, prosome ovoid in dorsal view. Posterior corners of prosome smoothly rounded. Urosome 4-segmented with genital double-somite projecting ventrally and anal somite much reduced. Caudal rami about twice as long as wide, with seta V on left ramus longer than corresponding seta on right. Rostrum bifurcate with strongly pointed corners and bearing pair of long filaments. Antennule reaching slightly beyond posterior end of third pedigerous somite; 27-segmented but with incomplete separation between segments I to III and X and XI; segment XXIV with seta in middle of posterior margin. Antenna compressed, with exopod about twice length of endopod; seta present on first exopod segment and missing on segments two to four; compound distal endopod segment with 5 setae on inner lobe. Mandibular palp with small, 1-segmented endopod carrying 2 setae of unequal length; basis lacking inner setae. Maxillule: praecoxal arthrite with 5 stout spines and 7 long pointed spines; coxal endite with 2 setae; basal endite elongate with 3 setae; endopod well defined and less elongate than typical within family; exopod bearing 7 setae. Maxilliped with basis elongate, longer than syncoxa.

Swimming legs 1 to 4 with spine and seta formula as for family diagnosis; lacking outer basal seta on all legs, with 3 outer spines on third exopod segment of legs 3 to 5. Leg 1 with two outer spines on third exopod segment slender, proximal spine originating near middle of segment and extending slightly beyond base of distal spine. Legs 2-5 with terminal spine on third exopod segment with constriction in proximal half of outer flange, most prominent in legs 4 and 5; leg 5 with small outer seta on posterior surface of basis and stout inner seta on first exopod segment.

Male. Urosome 5-segmented, with last somite very short. Caudal seta V on right ramus longer than corresponding seta on left. Right antennule 23-segmented. Second segment consisting of incompletely separated segments II and III. Fused segments XXIV and XXV bearing one seta on posterior margin in middle of proximal half. Mouthparts and legs 1-4 similar to those of female.

Leg 5 with slightly modified 3-segmented exopods and unmodified endopods. Third segment of right exopod with proximal inner seta and two unequal processes distally. Second segment of left exopod with groove along most of inner margin; third segment short and with three processes of dissimilar shape distally.

Type species. *Edaxiella rubra* gen. et sp. nov.

Etymology. The generic name (gender feminine) refers to the assumed predatory habits of the genus (Latin *edax* meaning greedy). The specific name (Latin fem. *rubra*) refers to the red colour of live specimens.

Edaxiella rubra gen. et sp. nov.
(Figs 1, 2, 14A,F, 15D, 16B,D & 21C)

Material examined. Air Strip Caves, Discovery Bay, Jamaica. 13 June 1990: 6 females, 7 males, 2 copepodids. 30 June 1990: 5 females, 2 males, 3 copepodids.

Types. Holotype: Adult female, total body length 2.04 mm, from Air Strip Caves, Discovery Bay, St. Ann Parish, Jamaica, 30 June 1990, taken at 0-5 m depth. One vial BM(NH) Reg. No. 1998.2232.

Paratypes: Two females and 1 male in 1 vial; 2 females and 1 male dissected and mounted on 11 slides, all with same locality and date of collection as holotype. BM(NH) 1998.2233-2238.

Description. Female. Total body length ranging from 1.96 to 2.06 mm, with mean of 2.00 mm (based on 6 individuals). Body (Fig. 1A,B) red in colour. Ratio of prosome length to urosome length ca. 2.7:1. Rostrum (Figs 1C & 14A) with two large pointed processes meeting in mid line at near right angle; each point with long filament near tip. Rostrum with paired lateral areas of perforated integument, not clearly defined, with perforations of varying size and shape (Fig. 14F). Fifth pedigerous somite with rounded posterolateral margins, reaching about one-third of length along genital double-somite. Urosome 4-segmented. Mid part of genital double-somite produced ventrally, posterior part of produced area pointed. Anal somite minute, being telescoped within preceding somite. Caudal rami with 7 setae; seta I (Fig. 15D) minute, naked; all other setae setose; seta II located near middle of outer margin; seta V on left ramus slightly longer than corresponding seta on right.

Antennules (Fig. 1D) 27-segmented, reaching to posterior end of third pedigerous somite. Segment I (Fig. 21C) with 2 or 3 elements; segments I, II and III, and X and XI incompletely separated, joined on part of posterior margin; segments XVII to XXVI elongate; segment XIX with 2 small setae; segment XX with 1 small and 1 medium-sized seta; segment XXIV with 1 medium-sized seta in middle of posterior margin.

Antenna (Fig. 1E) much compressed; endopod about half length of exopod. Proximal endopod segment with 2 inner setae distally; compound distal segment with inner lobe bearing 1 small and 4 long setae, terminal lobe with 6 long setae. Exopod with small seta on first segment, following three segments not clearly defined, without setae; segments V to VIII expressed but highly compressed, each segment with long setae; apical double segment (IX-X) armed with 1 small and 3 long setae terminally.

Mandible (Fig. 1F) with strong gnathobase, cutting edge with 5 prominent teeth, ventralmost bifid, elongate and clearly set off from others. Palp comprising basis without inner setae, 1-segmented endopod (Fig. 16B) bearing 2 setae of unequal length, and well developed, indistinctly 5-segmented exopod with 6 long setae. Free endopod segment small, apparently carried on lobe representing incorporated proximal endopodal segment.

Maxillule (Fig. 1G): praecoxal arthrite with 12 spines, 6 long, pointed and setose, 6 small and smooth; coxal endite short, with 2 setae of unequal length; basal endite long and slender, with 3 setae of unequal length; endopod with 1 small seta proximally and 1 distally on inner margin, plus 4 long setae terminally; exopod with 7 setae, distal seta small.

Maxilla (Fig. 1H) with endites on partly-fused praecoxa and coxa bearing 4, 3, 3, 3 setae; basis well developed, about equal to combined length of praecoxa and coxa, bearing 4 unequal setae proximally, one particularly strong, curved and spinous. Endopod segmentation typical for family, armed with 5 long and 5 medium-sized strong, curved and spinous setae.

Maxilliped (Fig. 1I,J): syncoxa with endite setal formula 1, 2, 4, 4; setae of differing lengths, surface of inner distal margin spinulate; basis elongate with 3 setae in middle of medial margin, second seta short, bulbous and plumose at base, plus 2 setae on incorporated first endopodal segment. Free endopod 5-segmented, setal formula 4, 4, 3, 3, 4; fourth segment (Fig. 1J) with 3 setae, one fused to segment; apical segment minute with 4 setae, 2 of which minute (Fig. 1J).

Leg 1 (Fig. 2A) with exopod bearing slender outer spines (Fig. 16D), spine on first segment longest, reaching base of spine on second segment; distal exopodal spines flagellate; first segment of endopod with small pointed process at outer distal corner. Legs 2-3 (Fig. 2B,C) with terminal spine on exopod more coarsely serrated on outer margin than corresponding spine on legs 4-5 (Fig. 2D,E).

Leg 5 (Fig. 2E) with small outer seta on basis and short, stout seta on inner margin of first exopod segment.

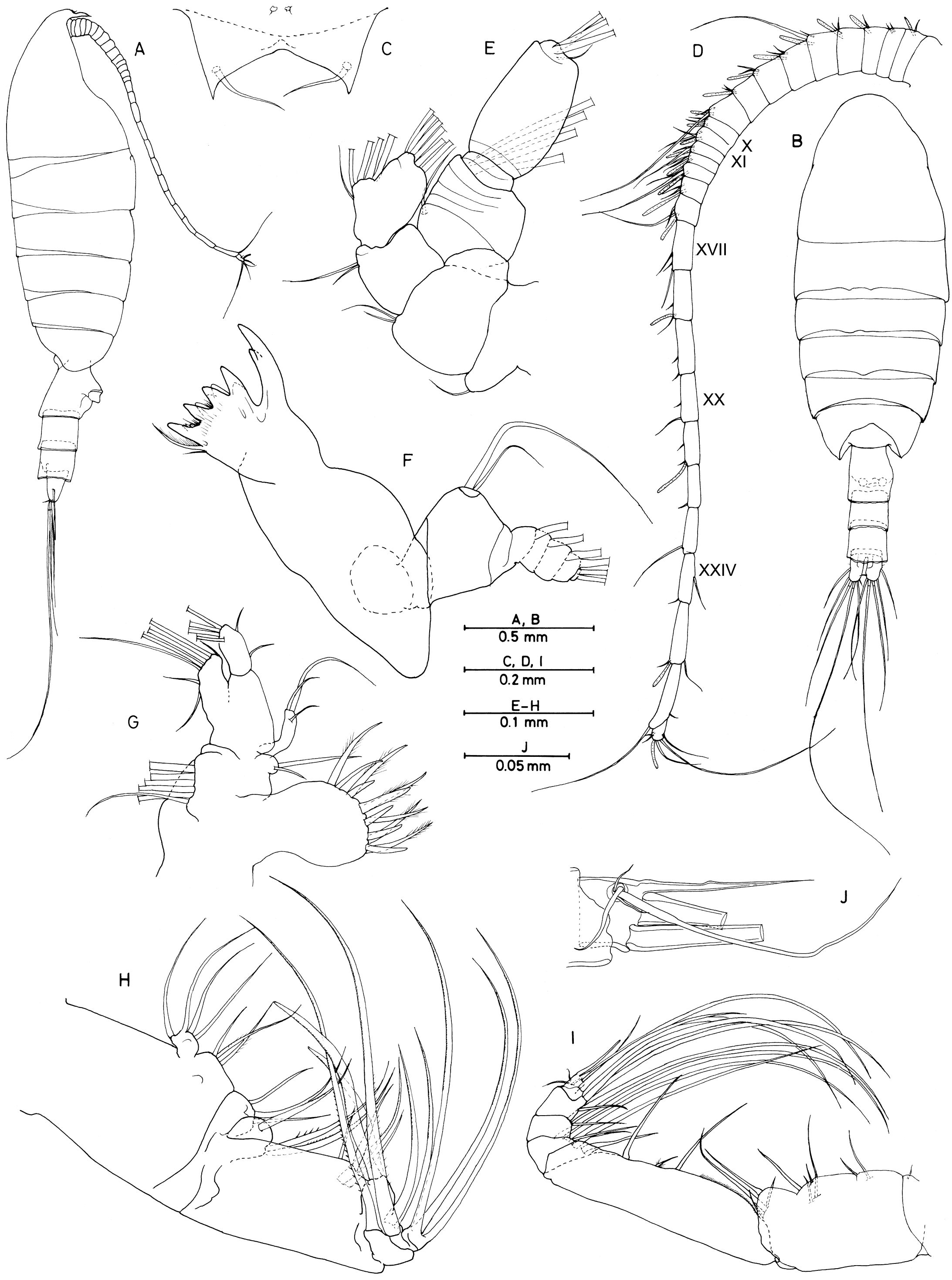

Fig. 1. *Edaxiella rubra* gen. et sp. nov., female. A. Habitus, lateral view. B. Habitus, dorsal view. C. Rostrum. D. Antennule. E. Antenna. F. Mandible. G. Maxillule. H. Maxilla. I. Maxilliped. J. Tip of endopod of maxilliped.

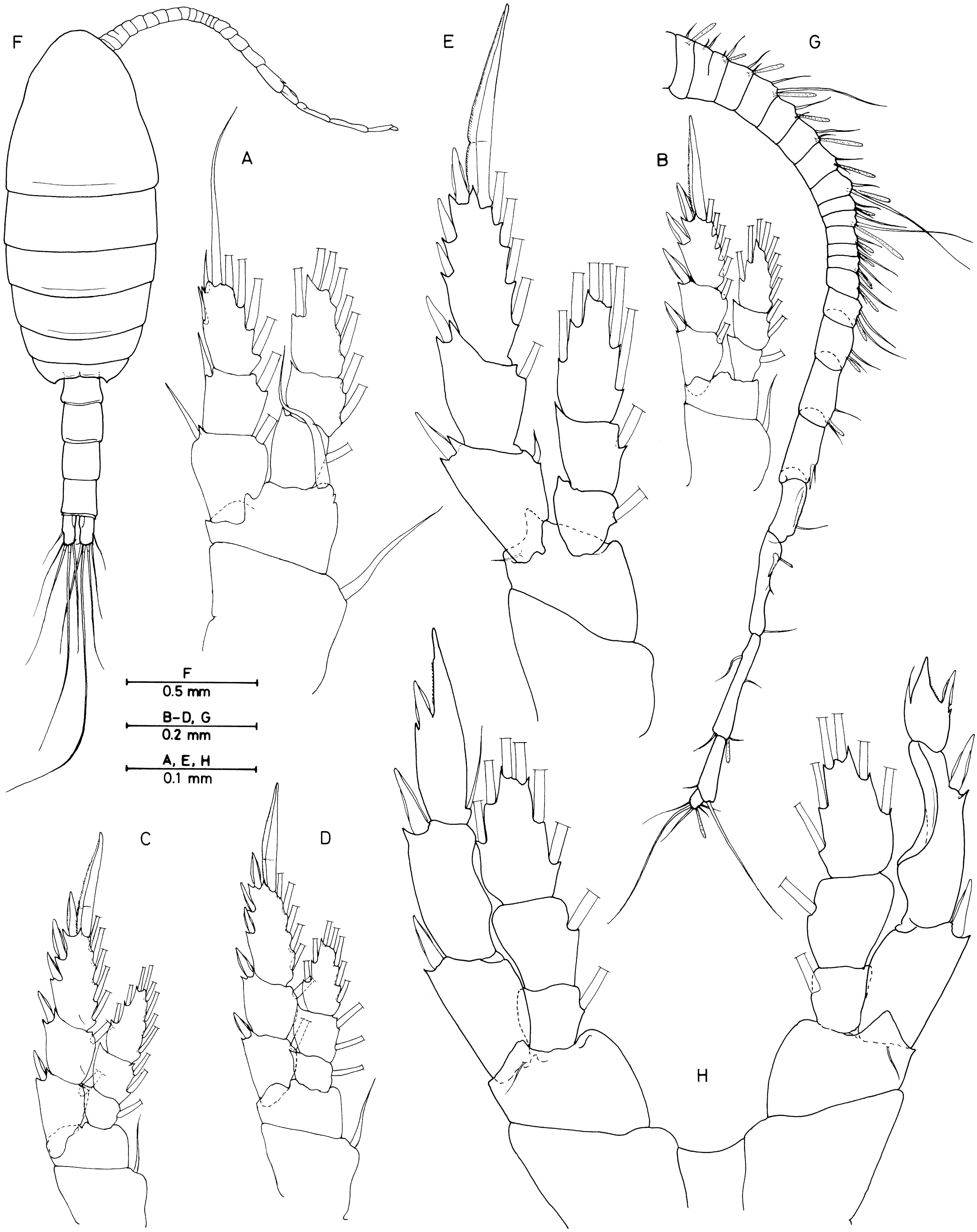

Fig. 2. *Edaxiella rubra* gen. et sp. nov., female (A-E), male (F-H). A. Leg 1. B. Leg 2. C. Leg 3. D. Leg 4. E. Leg 5 . F. Habitus, dorsal view. G. Right antennule. H Leg 5.

Male (Fig. 2F). Total body length ranging between 1.89 and 2.10 mm, mean 2.02 mm (based on 6 individuals). Differing from female in urosome, right antennule and leg 5. Ratio of prosome length to urosome length ca. 2.1:1. Urosome more elongate than that of female; 5-segmented and with much reduced anal somite. Contrary to female, caudal seta V longer on right ramus than on left.

Right antennule (Fig. 2G) 23-segmented; segments II and III incompletely separated, segments X and XI separate; double segment XXIV-XXV with setae derived from segment XXIV located near middle of anterior margin and in proximal quarter of posterior margin.

Fifth legs (Fig. 2H) with 3-segmented rami; endopods symmetrical with outer distal corner of second segment rounded. Exopods asymmetrical and slightly modified: right exopod with first and second segments of equal length, both with strong outer spine; third segment armed with 3 elements: slender seta proximally on inner margin, long pointed terminal process with smooth apex and spinules along most of outer margin, and shorter flanged outer spine fused to segment at base; left exopod with second segment longest, narrowing distally, with sclerotized concave structure running along most of inner margin; strong spine present on outer distal margin; third segment short, with 3 elements: inner seta fused to segment at base, terminal pointed process with spinules along most of outer margin, and flanged outer spine fused to segment at base.

Ecological notes. This species was collected twice, on 13 and 30 June 1990, only from Air Strip Caves, Discovery Bay, Jamaica. These caves are open anchialine limestone sinkholes with rather indirect hydrological connections to the sea. They generally lack the typical open water marine fauna. Other crustaceans found in the caves included typical troglobitic species of *Stygiomysis*, eye-less amphipods and isopods. *Edaxiella rubra* was collected from surface down to 5 m depth, the maximum water depth in these caves, and at salinities of 25-29.5. Live animals were bright red in colour and their body length in excess of 2 mm distinguishes them from most other members of the family, which are colourless and smaller. The coloration indicates that *Edaxiella* is not one of the most extreme troglobitic members of the family.

Remarks. The mouthparts of *Edaxiella rubra*, in particular the powerful mandibular gnathobase and the well-developed, elongate spinous setae on the distal part of maxilla and maxilliped suggest that this species is a predator.

Edaxiella resembles *Enantiosis*, sharing many similarities in the mouthparts and swimming legs, however, they are distinguished by, among other characters, the conspicuous differences in male leg 5 which is simple in *Edaxiella* but complex in *Enantiosis.* The pointed bifid rostrum has long filaments in *E. rubra* whereas in *Enantiosis* species these filaments are short. Long filaments are also present in *Epacteriscus* but here the rostral lobes are rounded (Fig. 14C). Other differences between *Edaxiella* and *Enantiosis* include: better separation of the proximal antennule segments in *Edaxiella*, the number of setae in the proximal part of the antennary exopod and on the terminal lobe of the endopod; the relatively shorter maxillulary endopod in *E. rubra*, the number of setae on the basal endite (1 in *Enantiosis* cf. 3 in *E. rubra*); the more slender spines on the exopod of leg 1 in *E. rubra*, and the relative length of the endopods of legs 2-5, which are shorter in *E. rubra*.

In *E. rubra* the distal seta on segment XX of the female antennule is of moderate size while this seta in other members of the family is usually elongate – the plesiomorphic character state for the Calanoida. *E. rubra* has fewer fusions in segments I-IV of the right antennule in the male than are present in those other genera for which the males are known.

The male leg 5 is reminiscent of that of *Epacteriscus,* with rather simple modifications of the exopods, most marked on the left side. The third segment on the right exopod carries an additional inner seta in *E. rubra*, and on left side the exopod is 3-segmented in *E. rubra* whereas it is 2-segmented in *Epacteriscus*. The third segment of endopod has the same number of setae in both genera but the arrangement differs, with 2 apical elements in *Edaxiella* compared with 3 in *Epacteriscus.*

Genus *Enantronia* gen. nov.

Diagnosis. Female. Prosome oval in dorsal view, widest just posterior to mid length. Last pedigerous somite with short posterolateral margins. Urosome 4-segmented, with genital double-somite produced midventrally. Caudal rami longer than third and fourth urosomites combined. Caudal seta V longer on left ramus than on right; seta VI on left side only with unilateral tuft of setules near base. Rostrum broad, bilobed, slightly pointed, with pair of small filaments near tip. Antennule apparently 26-segmented but with partial fusion of segments II to III and X to XI; modified setae present proximally on segments I to IV.

Antenna with exopod slightly longer than endopod; 3 small setae present on proximal part of exopod; compound distal endopod segment with 3 setae on inner lobe.

Mandibular palp with small 1-segmented endopod carrying 3 setae; large ventral tooth on gnathobase bicuspid and rounded distally. Maxillule: praecoxal arthrite with total of 14 slender spines and setae; coxal endite with 3 setae, basal endites with 3 and 1 setae; exopod with 8 setae. Maxilla and maxilliped generally of similar structure to *Enantiosis* with strong spinous setae distally.

Legs 1-5 with segmentation and setation as in family diagnosis, with outer seta on basis of legs 3 to 5 only, 3 outer spines on third exopod segment of legs 3 and 4, leg 5 with inner seta on first exopod segment.

Male. Unknown.

Type species. *Enantronia canariensis* gen. et sp. nov.

Etymology. The generic name *Enantronia* (Greek *en*, meaning in, and *antron*, meaning cave; gender feminine) refers to the cave habitat of Jameos del Agua, and the specific name refers to the type locality, the Canary Islands.

Enantronia canariensis gen. et sp. nov.
(Figs 3 & 4)

Material examined. Jameos del Agua, Lanzarote, Canary Islands. 24 February 1984: 1 female in 10-24 m depths collected within the first 400 m of flooded section of lava tube. 16 July 1992: 1 female in 9-24 m depth between 10 and 350 m penetration into flooded part. Specimens caught in diver-towed plankton nets.

Types. Holotype: Adult female, body length 1.89 mm, from Jameos del Agua, Lanzarote 16 July 1992 in 9-24 m depth. 1 vial BM(NH) 1997.2239.

Paratype: 1 female, body length 1.85 mm, from same locality as holotype, taken on 24 February 1984. Dissected and mounted on 7 slides, BM(NH) 1997.2240.

Description. Female. Body length 1.85 and 1.89 mm. Ratio of prosome to urosome length ca. 2.5:1. Fifth pedigerous somite (Fig. 3A) with short, rounded posterolateral margins, extending to anterior end of genital double-somite. Urosome 4-segmented; genital double-somite produced midventrally into point (Fig. 3B), double-somite longer than following 3 urosomites combined. Second and third urosomites each with finely striated hyaline membrane along posterior margin. Caudal rami slender, about three times longer than wide. Caudal seta V on left ramus longer than corresponding seta on right; seta VI on left ramus with unilateral tuft of fine setules near base. Rostrum (Fig. 3C) angular, with shallow median indentation; each angle with small filament.

Antennule (Fig. 3D) apparently 26-segmented reaching to end of prosome; segments II and III incompletely separated, segments X and XI almost completely separated; modified setae present on proximal segments I to IV; segment XIX with 2 small setae; segment XX with 1 small and 1 long seta.

Antenna (Fig. 3E) with endopod slightly shorter than exopod; first endopod segment longer than compound distal segment, with 2 inner setae near middle of inner margin; distal segment with inner lobe bearing 3 setae. Exopod with small seta on first segment and 2 small setae on compound second segment; 4 long setae present on defined short segments in mid section; 1 minute and 3 long setae present at apex.

Labrum broad (Fig. 3F); free distal margin ornamented with 2 rounded processes medially, 2 pairs of cylindrical projections and rows of spinules.

Mandible (Fig. 3G) with strongly built gnathobase bearing rounded teeth on cutting edge, ventralmost tooth bifid. Palp slender; endopod reduced to 1-segmented vestige bearing 3 small setae; exopod 5-segmented with 1,1,1,1,2 setae.

Maxillule (Fig. 3H) with coxal and proximal basal endites of equal length, armed with 3 subequal setae and 2 long plus 1 minute seta respectively; distal basal endite represented by 1 seta. Endopod defined from basis, 1-segmented, bearing 2 small setae along inner margin and 4 long setae distally. Exopod slender with 8 setae; distal seta on inner margin minute.

Maxilla (Fig. 4A) syncoxal endite setation 4, 3, 3, 3; endopod with typical family structure, bearing total of 10 long curved spinous setae and 1 short straight seta.

Maxilliped (Fig. 4B,C) basis with 3 basal setae plus 2 distal setae derived from incorporated first endopodal segment; free endopod 5-segmented including minute apical segment; setal formula for endopod segments as for family diagnosis; 2 strong setae on second and third segments, 3 strong inner setae on fourth free segment; 4 small setae on apical segment (Fig. 4C).

Leg 1 (Fig. 4D) with relatively long outer spines on exopod; spines on first and second segments of equal length, slightly longer than 2 equal spines on third segment; all outer spines with flagellate tips.

Legs 2-4 (Fig. 4E,F) with smooth terminal spine on distal exopod segment. Leg 5 (Fig. 4G,H) unmodified, with setation as in family diagnosis, including 3 outer spines on distal exopod segment.

Male. Unknown.

Ecological notes. This species was obtained twice on 24 February 1984 and 16 July 1992, each time only a single female was collected in the first 400 m of the flooded section of the lava tube, Jameos del Agua on Lanzarote. Jameos del Agua is the seaward-most seg-

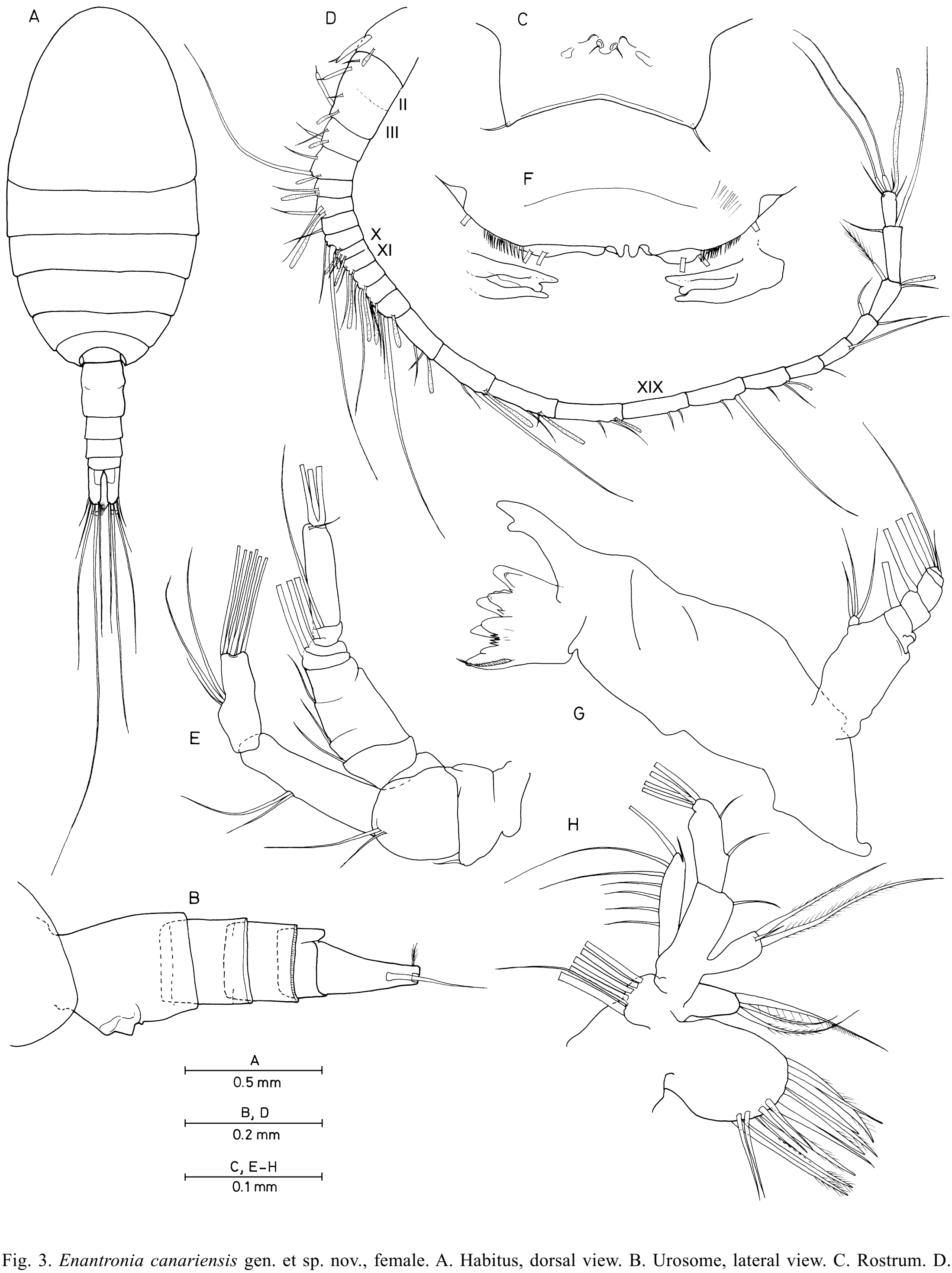

Fig. 3. *Enantronia canariensis* gen. et sp. nov., female. A. Habitus, dorsal view. B. Urosome, lateral view. C. Rostrum. D. Antennule. E. Antenna. F. Labrum and labial lobes, ventral view. G. Mandible. H. Maxillule.

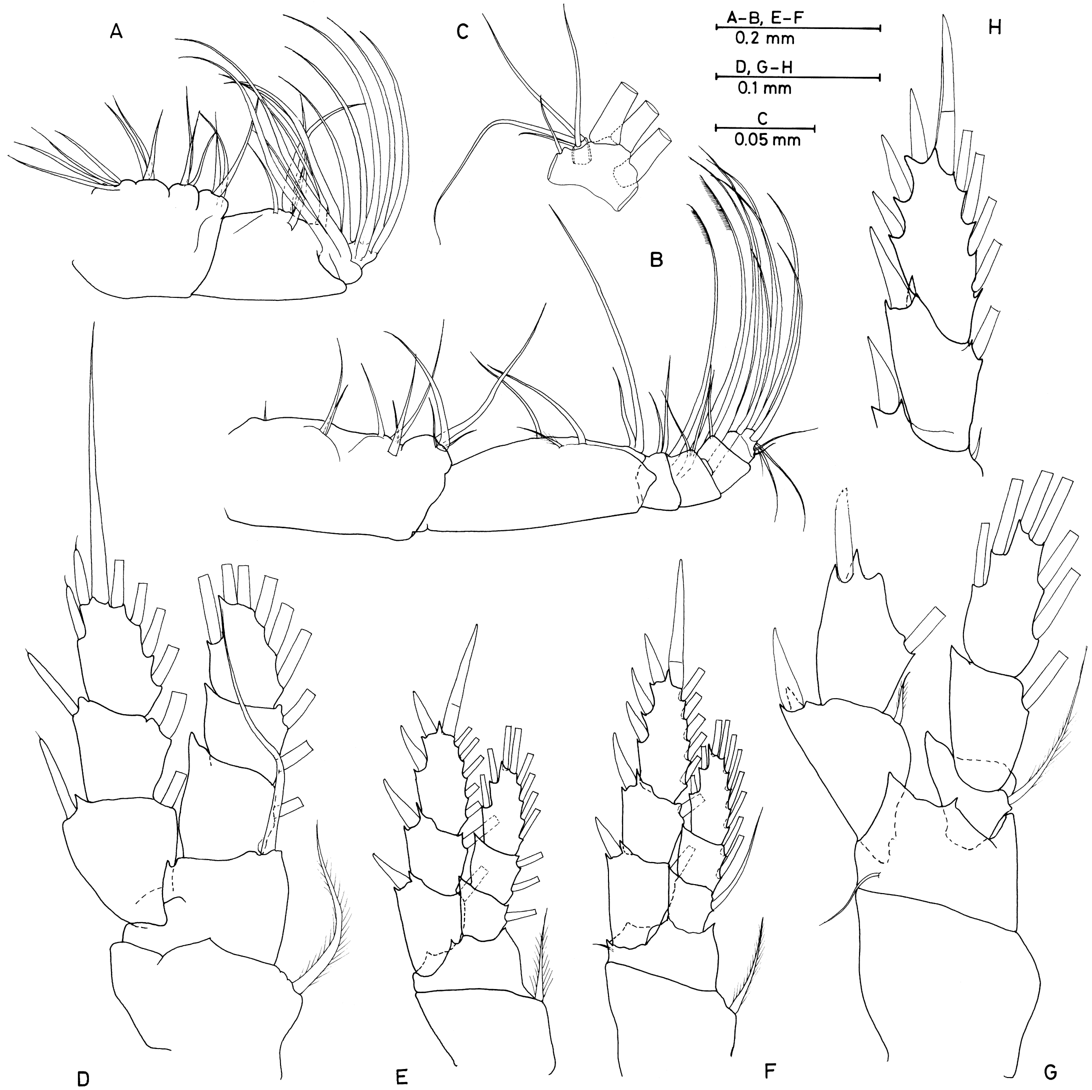

Fig. 4. *Enantronia canariensis* gen. et sp. nov., female. A. Maxilla. B. Maxilliped. C. Tip of endopod of maxilliped. D. Leg 1. E. Leg 2. F. Leg 3. G. Leg 5 (third segment of exopod missing). H. Leg 5, second and third segments of exopod.

ment of an 8 km long lava tube which extends out beneath the sea floor for approximately 1.5 km. This cave contains a particularly rich and varied fauna containing many species of considerable taxonomic and biogeographical interest, including remipedes and thermosbaenaceans (Iliffe & al. 1984; Wilkens, Parzefall & Iliffe 1986; Iliffe, Parzefall & Wilkens 2000).

A remarkably rich fauna of misophrioid copepods has also been discovered in Jameos del Aqua, comprising at least five species in four different genera (Boxshall & Iliffe 1987). Among other calanoids reported from the lava tube are *Stygocyclopia balearica* Jaume & Boxshall (Jaume, Fosshagen & Iliffe 1999) and a species of *Paramisophria* was described from the cave (Ohtsuka, Fosshagen & Iliffe 1993). New species of *Metacalanus* and *Exumella* have also been recovered and descriptions are currently in progress.

Remarks. Despite having only females available *Enantronia* shows close affinities to *Enantiosis* (see below). It shares with *Enantiosis*, the asymmetry of the caudal setae, the form of the rostrum, and the presence of modified setae on the proximal few segments of the antennule. In general *Enantronia* retains more plesiomorphic features than *Enantiosis*, particularly with respect to the urosome, antennule and maxillule. The urosome of the female has a well-developed anal somite whereas this somite is much reduced in *Enantiosis*. The antennule shows incomplete separation of segments II and III in *Enantronia* whereas in *Enantiosis* segments II-IV are not separated; segment XIX bears 2 setae in *Enantronia* but only 1 seta is present in *Enantiosis.* The maxillule bears 3 setae on the coxal endite, 3 on the proximal basal endite, and 8 on the exopod in *Enantronia* but 2, 1, and 7 respectively in *Enantiosis*. In other limbs there are only slight differences between these genera, most often in the relative lengths of setae and rami.

Genus *Enantronoides* gen. nov.

Diagnosis. Male. Last pedigerous somite with short and evenly rounded posterolateral margins. Urosome 5-segmented; caudal rami shorter than fourth and fifth urosomites combined. Caudal seta V on left ramus elongate, more than twice length of corresponding seta on right ramus. Rostrum short and broad, with minute filament at each corner.

Left antennule apparently 26-segmented with partial fusion of segments X to XI; right antennule geniculate and 22-segmented. Antenna as in *Enantronia.* Mandibular palp devoid of inner setae on basis; endopod lacking; exopod indistinctly 4-segmented, bearing 5 setae; ventralmost tooth of gnathobase distinctly enlarged, terminating in single point. Maxillule with 14 elements on praecoxal arthrite and 5 setae on exopod. Maxilla, maxilliped and legs 1-4 as in *Enantronia*, except outer spines on exopod of leg 1 of unequal length. Leg 5 with both rami 3-segmented; endopods unmodified; exopods slightly transformed; distal segment on right exopod with long curved process bearing inner and outer setae proximally; distal segment on left side short with 3 unequal spines.

Type species. *Enantronoides bahamensis* gen. et sp. nov.

Etymology. The generic name (gender masculine) alludes to similarities with the genus *Enantronia*; the specific name refers to the type locality, the Bahama Islands.

Enantronoides bahamensis gen. et sp. nov. (Figs 5 & 6)

Material examined. Oven Rock Cave, Great Guana Cay, Exuma Cays, Bahamas, 22 May 1995: 1 male in 1-22 m depth, collected with towed plankton net or with suction bottle from water column.

Type. Holotype: Adult male body length 2.10 mm, from Oven Rock Cave, Bahamas, 22 May 1995 in 1-22 m depths. Dissected and mounted on 9 slides; BM(NH) 1997.2241.

Description. Male. Holotype body length 2.10 mm. Ratio of prosome to urosome length ca. 2.8:1. Rostrum (Fig. 5C) broad, not prominent; angular with minute filament at each corner. Cephalosome and first pedigerous somite fused dorsally and separated laterally (Fig. 5A); fifth pedigerous somite short, with evenly rounded posterolateral margins. Urosome 5-segmented (Fig. 5B). Caudal rami about twice as long as wide. Caudal seta V asymmetrical, longer on left ramus than on right; narrowing abruptly level with end of seta VI, then flexed slightly inward.

Antennule (Fig. 5D,E) reaching beyond end of first urosomite. Left antennule with segments II and III not separated and segments X and XI partially fused; right antennule with segments II-IV fused; and segment 20 (XXIV-XXV) with long acute process distally.

Mandible (Fig. 5G) with extremely robust gnathobase bearing pointed teeth; ventralmost tooth dominant, simple; palp without trace of endopod; basis unarmed; exopod indistinctly 4-segmented, armed with 5 strong setae. Position of palp in single specimen somewhat uncertain as broken off during dissection.

Maxillule (Fig. 5H) with 14 slender elements on praecoxal arthrite; proximal basal endite slightly longer than coxal endite, each bearing 1 short and 2 long setae. Exopod slender, with 5 setae, distal one strongest.

Maxilla and maxilliped as in *Enantronia* except most proximal spine of endopod of maxilla with few coarse spinules in proximal half.

Leg 1 (Fig. 6A) with outer spines of exopod of unequal length; spine on first segment longest, spine on second segment and proximal spine on third segment short and stout; all outer spines flagellate at tip.

Legs 2-4 (Fig. 6B-D) with outer spines on third segment of exopod increasing in length distally more clearly than in *Enantronia*.

Leg 5 (Fig. 6E) with 3-segmented rami: exopods asymmetrical, with greatest modifications in distal segment. Right exopod with first and second segments of equal length, third segment elongate, curved medially and tapering to blunt point; bearing outer seta near middle of proximal half and stronger inner seta near proximal corner. Left exopod with first and second segments of equal length, but first broader; first with strong outer spine reaching end of third segment, second segment with slender outer spine; third segment short, about as broad as long, with 3 unequal slender spines pointing obliquely medially, innermost spine about twice length of outer.

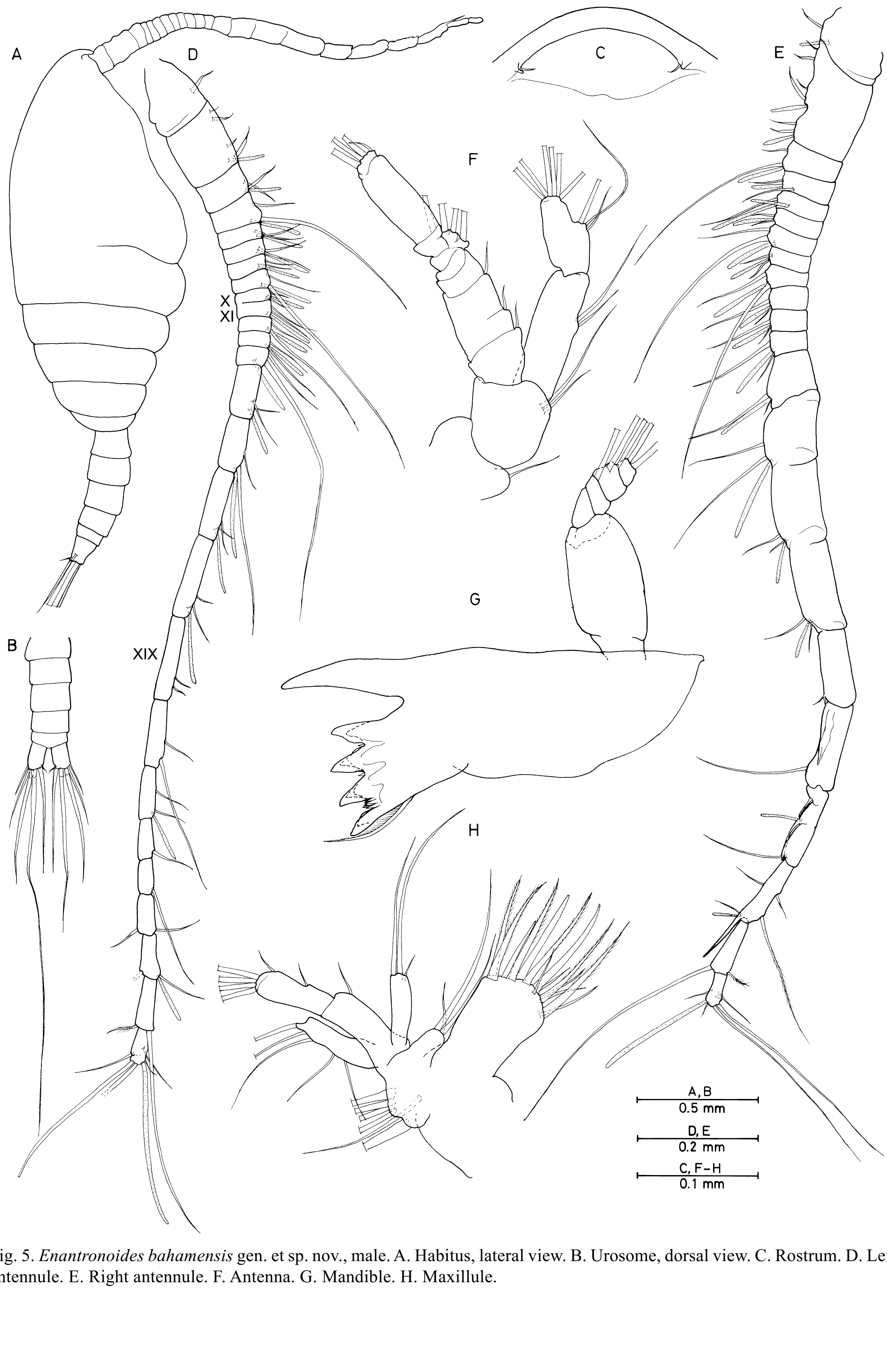

Fig. 5. *Enantronoides bahamensis* gen. et sp. nov., male. A. Habitus, lateral view. B. Urosome, dorsal view. C. Rostrum. D. Left antennule. E. Right antennule. F. Antenna. G. Mandible. H. Maxillule.

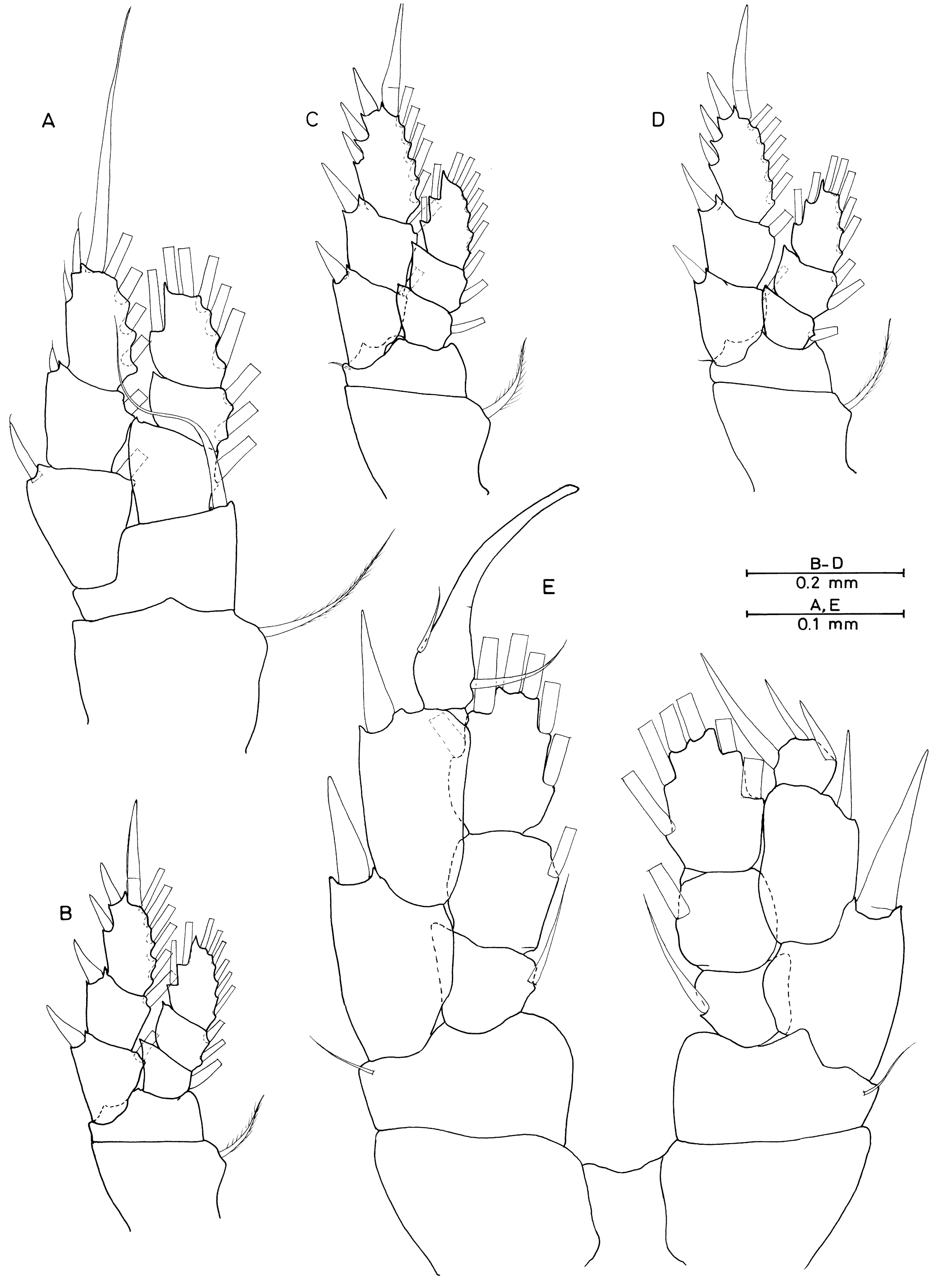

Fig. 6. *Enantronoides bahamensis* gen. et sp. nov., male. A. Leg 1. B. Leg 2. C Leg 3. D. Leg 4. E. Leg 5.

Female. Unknown.

Ecological notes. This species was collected only once on 22 May 1995, as a single male from Oven Rock Cave, Bahamas, from the water column in 1-22 m depth. The cave is anchialine and surface salinity on the day of sampling was 35. It is not known whether the specimen was taken in a towed plankton net or from a suction bottle since samples were mixed.

The cave is one of the more notable inland caves in the Exumas. Its entrance is situated in a hillside about 1 km from the southern tip of the island. A large dry chamber descends over breakdown from the entrance to a tidal anchialine lake. The first underwater chamber of the cave is decorated with large stalactites and stalagmites at depths down to 5 m. A second chamber has a small air bell at one end but dips to 10 m depth at the far end where a submerged passage extends down to 24 m.

The cave is the type locality of four of the new monotypic genera *Bomburiella, Bofuriella, Oinella* and *Enantronoides* described in this paper. Of these only *Bomburiella* has been recorded from another cave, Stargate Cave on South Andros, located directly across Tongue of the Ocean. In addition to the new copepods, other fauna in Oven Rock Cave includes remipedes, amphipods, halocyprid ostracods, thermosbaenaceans and polychaetes. The isopod *Cirolana troglexuma* was described from the same sample as *E. bahamensis* (Botosaneanu & Iliffe 1997).

Remarks. Although only the male is known, this species shows many similarities to *Enantronia canariensis*, which is known only from the female. The left antennule, antenna, maxilla, maxilliped, and legs 2-4 are all similar. The most conspicuous differences between these species are the mandibular palp, with no trace of an endopod in *E. bahamensis*, the exopod of the maxillule which is more reduced in *E. bahamensis*, and the relative lengths of the outer spines on the exopod of leg 1. These characters support the placement of the two species in separate genera, as indicated by the phylogenetic analysis (see below).

The elongation of seta V on the left caudal ramus, as in *Enantronoides*, is somewhat unusual in males. This particular asymmetry is commonly found in females of other genera of the family and in both sexes of *Gloinella*.

Compared with other known males within the family, *Enantronoides* has, like *Epacteriscus* and *Edaxiella*, relatively weakly transformed fifth legs. The right leg 5 is reminiscent of that of *Enantiosis*, but that genus has a highly transformed left leg.

Genus *Enantiosis* Barr, 1984

Diagnosis (emend.). Female. Body robust, with broad prosome; posterolateral margins of prosome extending to middle of genital double-somite. Urosome 4-segmented; anal somite extremely small and concealed beneath posterior margin of preceding somite. Caudal rami about as long as wide; seta V on left ramus longer than corresponding seta on right; seta VI on left ramus only with conspicuous unilateral tuft of long setules on inner margin near base. Rostrum bifurcate with pointed corners and pair of small filaments.

Antennule varying in length from reaching end of second pedigerous somite to end of prosome; 25-segmented; with modified setae on proximal segments I to V; segments II-IV not separated; segments X-XI with partial fusion; segment XIX with 1 seta.

Antenna with endopod about two thirds of length of exopod; distal endopod segment with 3 setae on inner lobe; exopod indistinctly 7-segmented, first segment with short seta, second segment double with 2 short setae; third to sixth segments defined, each with long seta; apical segment double, with 1 short and 3 long apical setae. Mandibular palp with well-developed exopod and reduced 1-segmented endopod carrying 2 or 3 setae, one of which minute; gnathobase with strong teeth, ventralmost tooth bicuspid and clearly offset from others. Maxillule with reduced setation; coxal endite and basal endites with 2, 1 and 1 setae respectively; exopod with 7 setae. Maxilla with typical compressed endopod, bearing strong, spinous setae. Maxilliped syncoxa about same length as basis; free endopod 5-segmented with minute terminal segment carrying 4 reduced setae.

Leg 1 with two outer stout spines on third exopod segment, first originating in distal half of segment and extending to about middle of second spine.

Male. Urosome 5-segmented, with first four somites of equal length, anal somite minute. Caudal setae unmodified, with seta V on right ramus slightly longer than corresponding seta on left. Right antennule 22-segmented; segments X and XI separate; compound segment XXI-XXIII with or without distal process on anterior margin. Fifth legs complex, with all rami 3-segmented. Exopods highly transformed on left leg and on third segment of right leg; endopod on left leg with modified outer margin. Strong process usually present on inner side of right basis and strong, irregularly-shaped spine situated on outer margin of first exopod segment of left leg.

Type species. *Enantiosis cavernicola* Barr, 1984.

Enantiosis bermudensis sp. nov.
(Figs 7, 8 & 9A-C)

Material examined. The species was collected at 11 different localities around Bermuda (see sites 3, 4, and 8-16 in Fig. 37). Unless otherwise mentioned, specimens were taken with a hand-held, fine-mesh net.

Cripplegate Cave: 9 October 1981, 1 female in plankton net suspended at Harrington Sound entrance of this tidal spring for 6 hours; 7 October 1984, 5 females, 3 males and 6 copepodids in Bou-Rouch pump sample from 1 m depth in gravel and shell at the tidal spring entrance.

Double Pond Cave: 7 October 1984, 2 females, 2 males and 3 copepodids in Bou-Rouch pump sample from 1 m depth in gravel at small pond under rock bluff.

Emerald Sink Cave: 17 January 1982, 1 male from near-bottom sediments in 11 m depth.

Green Bay Cave: 31 January 1984, 1 female in 12 m depth near roof of Trunk Passage.

Red Bay Cave: 5 November 1981, 1 female and 1 male in plankton net suspended across Harrington Sound entrance of this tidal spring for 6 h and 25 min.

Shop Cave: 4 September 1984, 2 females and 1 copepodid in 3-6 m in layer of turbid, oligoxic water in this polluted cave pool.

Small Fish Pond Cave: 15 November 1981, 1 copepodid in 12 m depth around rotting wood.

Tucker's Town Cave: 26 November 1981, 2 females and 1 male in 14 m depth at base of sand slope in entrance pool.

Walsingham Cave: 12 December 1978, 1 male in 3-6 m, from walls and bottom sediments of Round Room; 28 May 1980, 1 female in surface 0.5 m from rocks in west corner of entrance pool; 10 June 1982, 2 copepodids from same locality; 11 September 1986, 1 copepodid in 3-5 m from near roof and walls at back of entrance pool; 10 October 1986, 1 copepodid from same locality.

Walsingham Sink Cave: 8 September 1978, 2 females in surface 1 m from soil slope of main pool; 13 August 1982, 8 copepodids in surface 1.5 m from same locality.

Wonderland Cave: 4 October 1984, 1 female in 15 m depth from surface of silty rocks in main pool.

Types. Holotype: Adult male, body length 1.17 mm, from Cripplegate Cave, Bermuda, 7 October 1984, collected with Bou-Rouch pump from 1 m depth in gravel and shell at tidal spring entrance. One vial BM(NH) 1998.2251.

Paratypes: One adult male and 1 adult female with same locality and collection date as holotype, mounted on 5 slides. One male and 1 female from Tucker's Town Cave, 26 November 1981 mounted on 8 slides, and 2 females and 2 males from Double Pond Cave, 7 October 1984 in 1 vial. BM(NH) 1998.2252-2255.

Etymology. The specific name refers to Bermuda.

Description. A detailed description of this species is provided as a basis for comparison with the other species of the genus treated later in this work.

Female. Body (Fig. 7A) length with mean of 1.26 mm, range 1.13 to 1.50 mm (based on 9 individuals). Colourless when alive, with faint, whitish nauplius eye.

Antennule (Fig. 7B) reaching slightly beyond third pedigerous somite; five proximal segments (I to VII) with modified setae, flattened with slender flagellate apex; segments V, IX, XIV, XVI, XXVI and XXVII each with one extra long seta.

Antenna (Fig. 7C): endopod short, with 2 subequal segments; proximal with 2 inner setae in middle of inner margin; distal with 3 setae on indistinct inner lobe; exopod with small seta on first segment and 2 small setae on compound second segment; 4 long setae present on defined short segments in mid section; 1 minute and 3 long setae present at apex.

Mandible (Fig. 7D): gnathobase with following elements (from dorsal to ventral): 1 seta, 1 long pointed tooth, 2-3 slender spines, 3 unequal teeth in group, 2-3 slender spines, 3 teeth in group, 2 bicuspid teeth; exopod indistinctly 5-segmented; endopod represented by tiny vestigial segment bearing 1 minute and 2 long setae.

Maxillule (Fig. 7E): praecoxal arthrite with 13 spinous setae; coxal epipodite with 6 setae; coxal endite with 2 setae; proximal basal endite with thickened seta; distal endite represented by single seta; endopod elongate with 2 small setae along inner margin and 4 long terminal setae; exopod slender with 7 setae, terminal seta longest.

Maxilla (Fig. 7F): endites along syncoxa bearing 4, 3, 3, and 3 setae; basis with 4 medial setae; compressed endopod with 9 strong and spinous setae and 1 small, slender seta.

Maxilliped (Fig. 8A): syncoxal setation 1, 2, 4, 4; parts of distal endite bearing dense cover of setule-like ornamentation; basis with 3 basal setae, middle one short and bulbous at base, plus 2 distal setae derived from incorporated first endopodal segment. Free endopod indistinctly 5-segmented with setal formula 4, 4, 3, 3+1, 4; 2 of setae on second to fourth free segments and 3 on fifth segment, strong and spiniform.

Leg 1 (Fig. 8B): outer spine on second exopodal segment extending to base of proximal outer spine on third segment. Legs 2-5 (Fig. 8C-F) with segmentation and setation as in family diagnosis. Basis of legs 3-5 with

Fig. 7. *Enantiosis bermudensis* sp. nov., female. A. Habitus, lateral view. B. Antennule. C. Antenna. D. Mandible. E. Maxillule. F. Maxilla.

Fig. 8. *Enantiosis bermudensis* sp. nov., female (A-F), male (G). A. Maxilliped. B. Leg 1. C. Leg 2. D. Leg 3. E. Leg 4. F. Leg 5. G. Distal part of right antennule.

Fig. 9. *Enantiosis bermudensis* sp. nov., male (A-C); *E. galapagensis* sp. nov., female (D, E) , male (F-I). A. Leg 5, anterior view. B. Second and third segments of left exopod of leg 5. C. Right leg 5, posterior view. D. Leg 1. E. Leg 5. F. Distal part of right antennule. G. Leg 5, anterior view. H. Left exopod leg 5. I. Right exopod and basis of leg 5.

small outer seta on posterior side. Leg 5 with small seta on inner margin of first exopodal segment.

Male. Body length ranging between 1.13 and 1.31 mm, mean 1.22 mm (based on 7 individuals). Differing from female in urosome, right antennule and fifth legs.

Urosome 5-segmented with anal somite much reduced; hyaline frill on penultimate somite with sculptured margin dorsally, with 2 prominent lobes middorsally.

Antennule with segments X and XI separate on right side, incompletely separated on left side; segments XIX, XX and XXI-XXIII on right side (Fig. 8G) with modified setal elements, each fused to segment and ornamented with ridges (cf. Fig. 16C); modified element on segment XIX and distal element on XXI-XXIII projecting beyond end of segment giving appearance of small process.

Right leg 5 (Fig. 9C): basis bearing small rounded process proximally on inner margin and discrete patch of fine setules distally on inner margin. Endopod unmodified. First and second exopod segments lacking inner setae; third segment forming long outer process tapering to flexible tip, armed with inner seta proximally, extending more than halfway along outer process. Left leg 5 (Fig. 9A,B) endopod with modified outer margins of first and second segments; first segment produced into slender, curved process, evenly rounded at tip; second segment with bulbous expansion proximally ornamented with tuft of long setules, and with 2 unequal, pointed processes distally; third segment unmodified. Exopod first segment with long, irregular outer spine, thickened proximally and reaching well beyond second segment; second segment with elongate outer spine, thickest at base and tapering gradually to fine point; third segment inserting near middle of inner margin of second segment, irregular in outline and complex in structure (Fig. 9B), with small outer seta near middle, produced into array of styliform and membranous distal processes.

Ecological notes. This species occurs in a variety of caves ranging from coastal tidal springs to apparently hydrologically isolated caves in the interior of the island (Fig. 37). The greatest numbers of individuals were taken interstitially near cave openings at Cripplegate and Double Pond Caves. These two caves and Emerald Sink Cave are likely to be interconnected via the Palm Cave System. Moderate tidal currents pass through these caves and a direct connection to the sea exists via Harrington Sound. Walsingham, Walsingham Sink and Wonderland Caves are merely separate entrances to another long flooded cave, the Walsingham Cave System. This system may be hydrologically connected with Palm Cave System but has less direct communication with the sea, with some sections being quite isolated.

Green Bay and Red Bay Caves are long caves on the northern side of Harrington Sound with strong tidal currents flushing through them. Green Bay Cave is the largest cave in Bermuda with more than 2 km of mapped passages at depths averaging 18 m. Shop Cave on the grounds of Government Quarry suffers from anoxic pollution, apparently resulting from seepage from an adjacent cave into which organic waste was dumped (Iliffe & al. 1984). Small Fish Pond Cave is situated in an isolated tract of older, Walsingham age limestone at the western tip of Bermuda. Tucker's Town Cave, on the Tucker's Town Peninsula, contains one of the largest underwater cave chambers in Bermuda. All three of these caves appear to be relatively isolated from the sea with no noticeable water currents.

This species has been collected from interstitial waters in gravel sediments outside caves, as well as from the interior caves both in plankton and near bottom. It occurs close to the opening and in the dark interior parts of caves. It is suggested here that when the species is transported outside caves it seeks shelter at the bottom, among shells and gravel, and when the current turns it may emerge into the water column to be eventually returned into the cave. It is colourless and undoubtedly troglobitic. Its mouthparts speak for a predatory life style. It has been observed swimming rapidly holding its antennules out at right angles to the longitudinal axis of the body.

Remarks. This species is very similar to the only known species until now, *Enantiosis cavernicola* from San Salvador Island, Bahamas (Barr 1984). Compared with *E. cavernicola*, the antennule is considerably shorter in *E. bermudensis*, and the single seta on the proximal basal endite of the maxillule is thicker in *E. bermudensis* than in any other species of the genus including *E. cavernicola*. The male leg 5 in *E. bermudensis* possesses a small rounded process proximally on the inner margin of the basis of the right leg, whereas most species of *Enantiosis* have a strong, recurved process in this position. Details of the complex structure of the male left leg 5, in particular of the third segment of exopod and of the outer margin of second segment of endopod distinguish this species from its congeners.

Enantiosis belizensis sp. nov.
(Figs 10, 11, 14E, 15A,C, 16A & 21E)

Material examined. The species was collected in three cave localities along the Belize Barrier Reef and was taken both with a hand-held plankton net and in baited traps.

Giant Cave, Caye Caulker: between 15 January 1989 and 24 February 1989 14 samples containing ca. 250 specimens were obtained at 16-30 m depth and at penetrations of 40 to 500 m from the entrance. Rich samples of ca. 50 specimens were also obtained 19 January 1989 in a plankton net at 25 m depth, at a penetration of 250 m, and on 27 January 1989 with 22 specimens in baited traps at 23-25 m depth at a penetration of 40 to 60 m.

Caye Chapel Cave, Caye Chapel: 22 January 1989, 1 female and 4 copepodids in plankton net at 12-34 m depth at 150 m penetration; 18 February 1989, 11 specimens in plankton net at 20-35 m depths at 150 m penetration; 1 copepodid in plankton net and 1 female in baited trap at 8-10 m depth at 40 to 60 m penetration.

Columbus Caye Blue Hole, Columbus Caye: 28 February 1989, 10 females in plankton net at 30-45 m depth.

Types. Holotype: Adult male body length 1.24 mm, from Giant Cave, Caye Caulker, Belize, 19 January 1989 collected with plankton net in 25 m depth at a penetration to 250 m from the cave entrance. One vial BM(NH) 1998.2399.

Paratypes: Two adult males and 1 adult female with same locality and collection data as holotype, mounted on 6 slides, and 1 female from same cave, 29 January 1989 in 16-24 m depth at a penetration of 400 m, mounted on 1 slide. Seven males and 3 females from cave, 17 January 1989, in 25 m depth at a penetration of 150 m, in 1 vial. BM(NH) 1998.2400-2409.

Etymology. The specific name refers to Belize.

Description. Female (Fig. 10A,B). Body length of 7 individuals from Giant Cave 14 February 1989 ranging between 1.21 and 1.31 mm, with mean of 1.28 mm. Very similar to *E. bermudensis*, differing only in minor details. Description supplemented with SEM-photographs of central rostral sensillae (Fig. 14E), genital double-somite with asymmetrical operculum (Fig. 15A), caudal rami (Fig. 15C), and modified seta on first segment of antennule (Fig. 21E), and exopod of antenna (Fig. 16A).

Antennule extending to end of third pedigerous somite. Maxillule with seta on proximal basal endite tapering evenly, not thickened at base as in *E. bermudensis*.

Male. Body length of 7 individuals ranging between 1.17 and 1.29 mm, with mean of 1.21 mm. Caudal seta V on right ramus slightly longer than corresponding seta on left ramus. Right antennule with segments X and XI separate; compound segment XXI-XXIII (Fig. 10C) with distal process extending as far beyond end of segment as that of *E. bermudensis*, but more pointed.

Right leg 5 (Fig. 10E, 11A): basis bearing strong curved process and large patch of fine setules on inner proximal margin (Fig. 11B); third segment of exopod (Fig. 11D) with inner seta extending less than halfway along outer process; third segment of endopod typically with 6, sometimes with 7 setae (Fig. 10D). Left leg 5 (Figs 10F,G; 11A,C,D): outer margin of first endopod segment extended into irregularly rounded process, bulbous at base; outer margin of second segment ornamented with 2 tufts of setules, produced into 2 distal processes, one pointed, other saw-toothed with strong inner tooth (Fig. 11C); first segment of exopod with strong curved outer spine, reaching beyond second segment, ornamented with 2 long setules near base of spine; second exopod segment with styliform spine and small process on outer margin; third segment relatively narrow, with complex structure (Fig. 10F), inner distal margin more extended than that of *E. bermudensis.*

Ecological notes. *Enantiosis belizensis* was abundant in Giant Cave, one of the world's largest submarine caves in terms of volume. The cave can be classified as anchialine since much of the cave lies directly beneath the island of Caye Caulker. The single known entrance is located 15 m offshore from the mangroves fringing the western coast of this low, sandy island.

Over 3 km of passage in the cave has been surveyed. Its major passageways lie primarily between 22 and 25 m below sea level and the depth in the cave ranges from a minimum of 8 m in ceiling domes to over 30 m in depressions in the cave floor. Strong tidal currents have been observed in passageways and on 3 and 9 February 1989 salinities of 34-36 and temperatures of 27.5-29.1 °C were recorded in the cave.

E. belizensis was obtained in plankton tows and in baited traps from all sections of the cave interior, but not from the entrance or outside the cave. It was the second most abundant of the calanoid copepods in the cave, always co-occurring with the dominant species, the ridgewayiid *Brattstromia longicaudata* Fosshagen & Iliffe, first recorded from this cave (Fosshagen & Iliffe 1991). As both species were obtained in baited traps they may be regarded as scavengers. A small number of *E. belizensis* was also obtained from the interior of the less well investigated Caye Chapel Cave and Columbus Caye Blue Hole. These two caves extend below the sea floor and are considered marine rather than anchialine.

Caye Chapel Cave is the type locality for the two new species of *Epacteriscus* described below and for the harpacticoid *Novocrinia trifida*, the type of a new family established by Huys & Iliffe (1998). The copepod fauna of this cave also includes species of *Ridgewayia* and some stephids.

Remarks. The females of *E. belizensis* and *E. bermudensis* are of the same size and are hardly distinguishable from each other using morphological characters, except for the more slender seta on proximal basal endite of maxillule in *E. belizensis*. In males, the differences between the two species are more apparent, especially

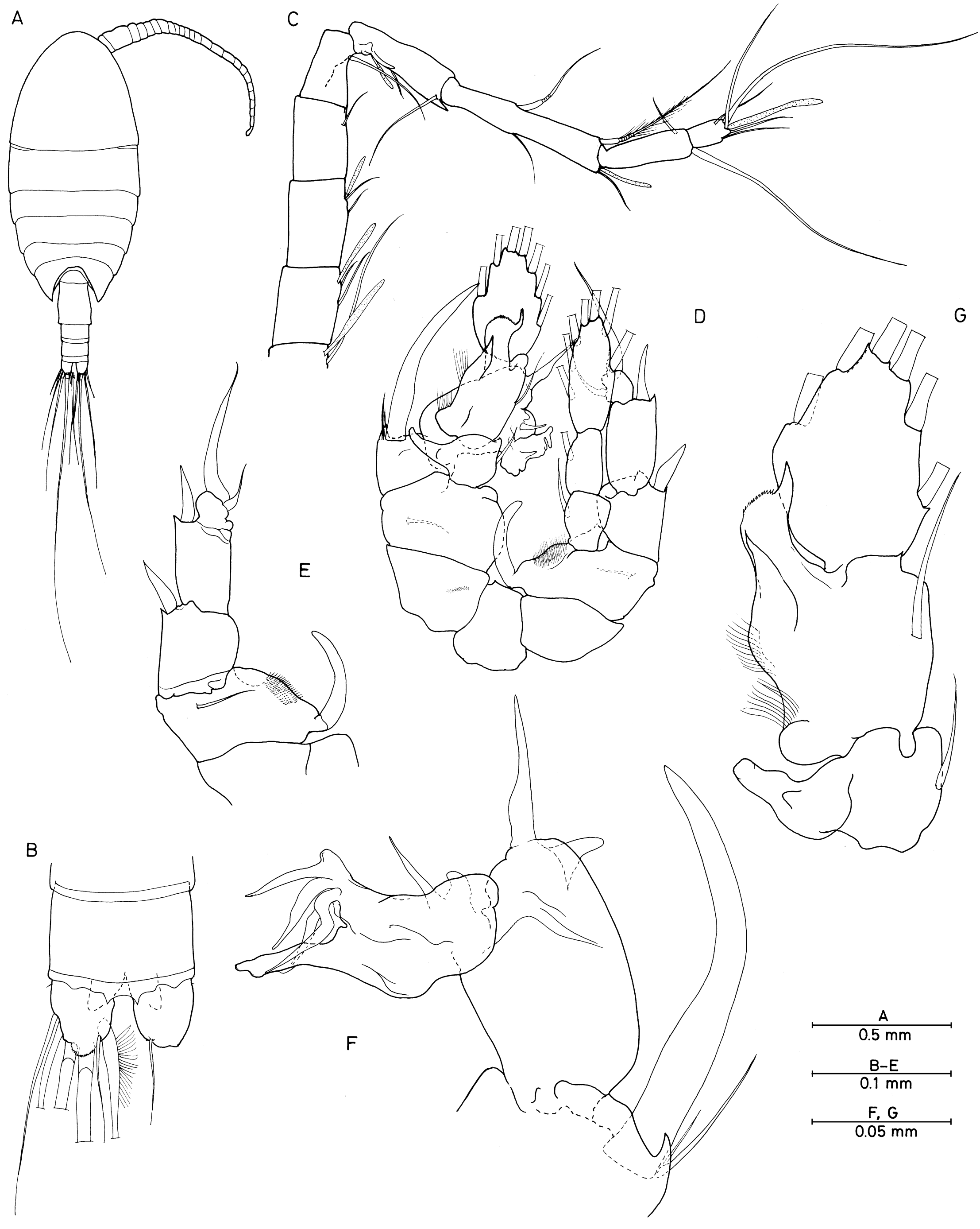

Fig. 10. *Enantiosis belizensis* sp. nov., female (A, B), male (C-G). A. Habitus, dorsal view. B. Urosome, distal part. C. Distal part of right antennule. D. Leg 5, anterior view. E. Right exopod and basis leg 5. F. Left exopod leg 5. G. Left endopod leg 5.

in leg 5 where the significant differences include the basis of the right leg, the left exopod, and the outer margin of first and second endopod segments of the left leg.

The occurrence of 7 setae on third segment of endopod of leg 5 in some males is remarkable. The maximum number of setae known to occur on this segment

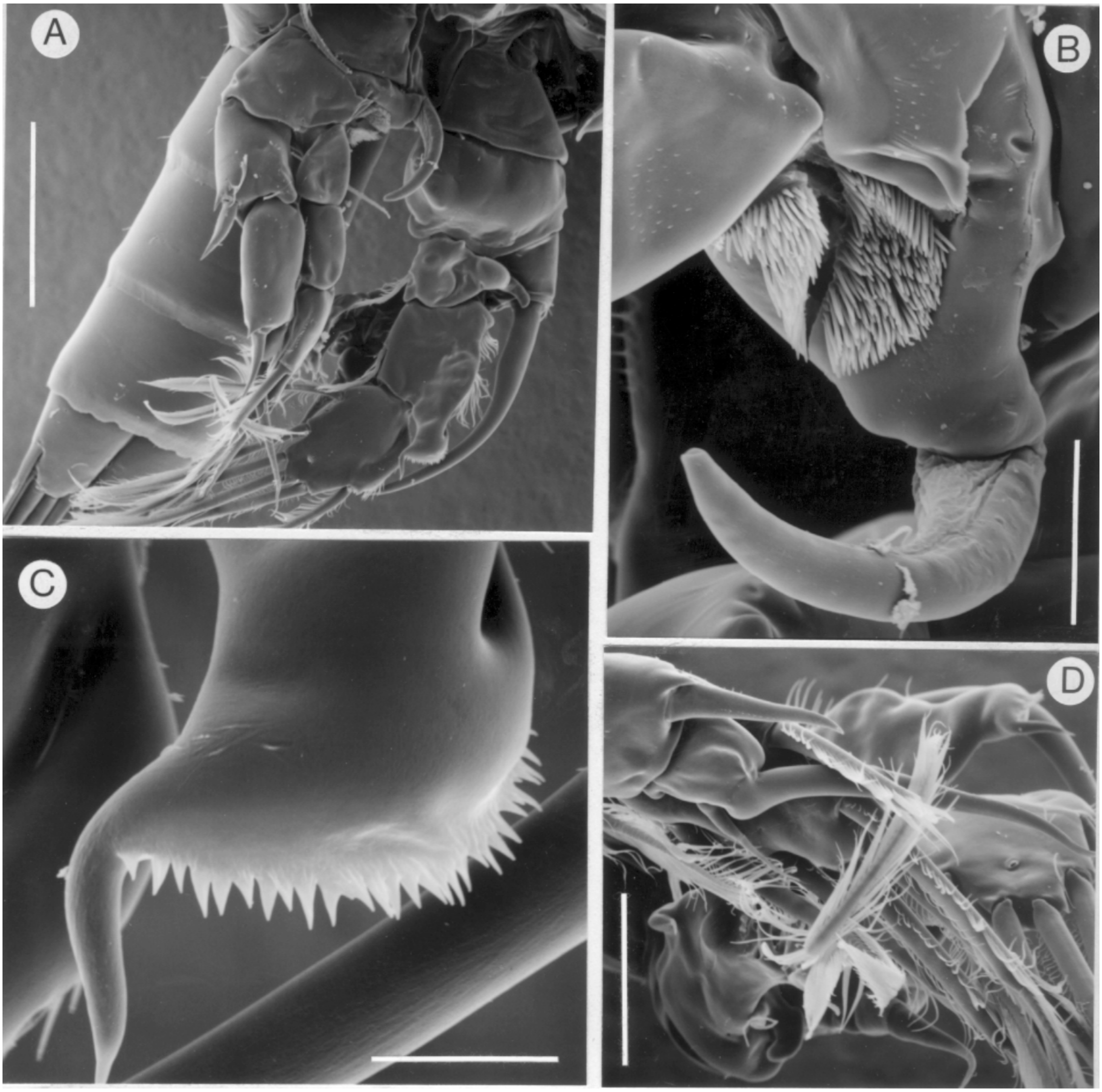

Fig. 11. *Enantiosis belizensis* sp. nov., male fifth legs. A. Anterior view; scale bar = 100 µm. B. Basis of right leg; scale bar = 20 µm. C. Outer process distally on second segment of left endopod; scale bar = 10 µm. D. Posterior view; scale bar = 40 µm.

among the Calanoida is 6 (Huys & Boxshall 1991). This polymorphic character may be interpreted either as a newly discovered extreme plesiomorphy for the order Calanoida (and the Copepoda as a whole), or as a secondary condition. Our preferred interpretation is the latter.

Enantiosis cavernicola Barr, 1984

Material examined. Additional material of the type species was obtained from the type locality and was re-examined to confirm particular morphological details. Lighthouse Cave, San Salvador, Bahamas; 2 females and 1 male were taken on 10 June 1986, with a plankton net in the surface 0.5 m of the shallow pool in the cave. On the date of sampling the surface salinity was 32.5 and the temperature 24.7 °C; at 0.7 m depth the salinity was 33.5 and the temperature 24.4 °C.

Description. The following characters of the female were not shown in the original description (Barr 1984) but agree with those of *E. bermudensis*: segments X and XI of antennule partly fused, terminal segment of antenna exopod with 3 long and 1 small setae, distalmost coxal endite of maxilliped armed with group of 4 setae, small outer seta present on basis of leg 3, and small inner seta on first exopodal segment of leg 5.

In male seta V on right caudal ramus slightly longer than corresponding seta on left.

Remarks. *E. cavernicola* closely resembles *E. belizensis.* They have a similar seta on the proximal basal endite of the maxillule and exhibit similar modifications to the basis of the right male leg 5. They differ in that *E. cavernicola* is slightly larger and lacks the distal process on compound segment XXI-XXIII of the male right antennule, as well as in the form of the modifications along the outer margin of male left endopod of leg 5.

Enantiosis galapagensis sp. nov.
(Fig. 9D-I)

Enantiosis sp. (Iliffe 1991).

Material examined. This species was obtained from four cave localities in the Galapagos, using a fine mesh plankton net towed in the open water column.

Deep Grieta at Tortuga Bay, Isla Santa Cruz: 3 May 1987, 2 females, 8 males and 4 copepodids in 6-12 m depth.

Grieta de Caleta la Torta, Isla Santa Cruz: 8 June 1987, 1 female in 17-29 m depth in large underwater chamber.

Grieta north of trail to Tortuga Bay, Isla Santa Cruz: 18 June 1987, 1 female, 4 males and 1 copepodid in 9-10 m depth, below halocline.

Post Office Bay Cave, Isla Floreana: 20 June 1987, 1 female, 15 males and 2 copepodids in 1.5-2 m depth, below halocline.

Types. Holotype: Adult male total length 1.39 mm from Post Office Bay Cave, Isla Floreana 20 June 1987 in 1.5-2 m depth. One vial BM(NH) 1998.2414.

Paratypes: Two adult males and one adult female mounted on 3, 2 and 2 slides respectively, and 6 males in 1 vial, all from same locality as holotype. BM(NH) 1998.2415-2423. One male from Deep Grieta at Tortuga Bay, Isla Santa Cruz, 3 May 1987 6-12 m depth, mounted on 3 slides, and 1 female and 4 males in 1 vial from same locality. BM(NH) 1998.2424-2429.

Etymology. The specific name refers to the Galapagos Islands.

Description. Female. Body length of four individuals ranging from 1.25 to 1.45 mm, with mean of 1.36 mm. Body morphology and appendages very similar to *E. bermudensis*, differing only in minor details as follows: antennule reaching slightly beyond last prosome somite; maxillule with seta on proximal basal endite tapering evenly, not thickened at base. Legs 1 and 5 (Fig. 9D,E) as in *E. bermudensis.*

Male. Body length ranging between 1.21 and 1.39 mm, with mean of 1.30 mm (based on 22 individuals). Right antennule (Fig. 9F) with long pointed extension on compound segment XXI-XXIII reaching midway along next segment. Right leg 5 (Fig. 9G, I) without inner process on basis, but with patch of fine setules. Left leg 5 (Fig. 9G, H) with outer margin of first endopod segment produced laterally into irregular club-like process; outer margin of second segment ornamented with tuft of setules, produced into 2 pointed distal processes. First exopod segment of left leg bearing long slightly recurved spine reaching end of third segment; second segment with outer spine elongate, straight; third segment with various styliform and membranous structures distally, inner process spatulate and narrower than corresponding process in *E. bermudensis.*

Ecological notes. A detailed description of the caves on the Galapagos and their fauna is given by Iliffe (1991). *Enantiosis galapagensis* was recorded from four caves, three on Isla Santa Cruz and one on Floreana.

The Deep Grieta at Tortuga Bay is an anchialine tectonic fissure in volcanic rock running parallel to the south coast of Isla Santa Cruz. On 3 May 1987 the surface salinity was 8 and the temperature 25 °C, and at 12 m depth the values were salinity 22 and temperature 23 °C.

Grieta de Caleta la Torta is another tectonic fissure on the same coast. It consists of three large anchialine pools separated by collapse barriers. The first pool contains a spacious underwater chamber in total darkness, reached by passing through a narrow slot between breakdown blocks at 12 m depth. On 8 June 1987 the surface salinity was 9 and the temperature 23 °C, and at 17 m the values were salinity 29 and temperature 22 °C.

The Grieta north of trail to Tortuga Bay is an extension of the tectonic cliff forming Academy Bay on Isla Santa Cruz. A pool about 30 m long by 2 m wide occupies the bottom of this steep-walled crack. On 18 June 1987 the surface salinity was 1.5 and the temperature 23 °C, and at 9 m depth the values were salinity 13 and temperature 23 °C.

Post Office Bay Cave is a lava tube on Isla Floreana. This 200 m long cave slopes down to an anchialine pool with a maximum depth of 2 m. On 20 June 1987 the surface salinity was 17 increasing to 22 at 2 m. The temperature at both depths was 20 °C.

The species is present on these two isolated islands, Santa Cruz and Floreana, which have never had any

Fig. 12. *Enantiosis dicerata* sp. nov., female (A, B), male (C-H). A. Leg 1. B. Leg 5. C. Distal part of right antennule. D. Leg 5, anterior view. E. Left exopod of leg 5. F. Second and third segments of left exopod of leg 5. G. Left endopod of leg 5. H. Right exopod and basis of leg 5.

shallow-water connections. Collection depths of the species ranged from 1.5 to 29 m. The preferred habitat seems to be brackish water since most of the specimens were collected at salinities of 22 or less. Other newly described troglobitic copepods from three of these caves are the misophrioid *Expansophria galapagensis* Boxshall & Iliffe from the two grietas near Tortuga Bay, Santa Cruz (Boxshall and Iliffe 1990) and the calanoid *Paramisophria galapagensis* Ohtsuka, Fosshagen & Iliffe from Grieta de Caleta la Torta, Santa Cruz (Ohtsuka & al. 1993).

Remarks. The species most closely resembles *E. bermudensis* in its morphology. The antennule is slightly longer and the seta on proximal basal endite of maxillule is more slender in *E. galapagensis* than in *E. bermudensis.* The prominent pointed process present on compound segment XXI-XXIII of right antennule in male *E. galapagensis*, plus minor details of the male leg 5, such as the lack of any inner process on the right basis of *E. galapagensis*, and the shape of the strong outer spine on first exopodal segment of the left leg serve to distinguish these two species.

Enantiosis dicerata sp. nov.
(Figs 12, 13, 14B, 16C & 21D)

Material examined. The species was obtained from a single locality in Fiji using a plankton net in 0.5-1 m depth in Naurambuta Cave, Vatulele: 9 May 1988, 14 females, 18 males, collected by Serban Sarbu.

Types. Holotype: Adult male body length 1.19 mm, from Naurambuta Cave, Vatulele, 9 May 1988 in 0.5-1 m depth. One vial BM(NH) 1998.2430.

Paratypes: Two males and 2 females dissected and mounted on 8 slides, and 5 males and 5 females in one vial from same locality as holotype. BM(NH) 1998.2431-2444.

Etymology. The specific name (Greek *dikeratos*, meaning two-horned) alludes to the prominent bifid spine on the exopod of the male left leg 5.

Description. Female. Body length ranging between 1.29 and 1.41 mm, with mean of 1.34 mm (based on 13 individuals). Antennule reaching slightly beyond third pedigerous somite; modified setae on proximal segments with distal flagellate displaced laterally (Fig. 21D). Endopod of mandible 1-segmented, bearing 2 setae.

Leg 1 (Fig. 12A) with 2 outer spines on third exopod segment slightly different in form; distal spine larger and with inner serrated flange. Leg 5 (Fig. 12B) with terminal spine on third exopod segment coarsely serrated along outer margin.

Male. Body length ranging between 1.19 and 1.37 mm, with mean of 1.23 mm (based on 14 individuals). Rostrum pointed with minute filaments (Fig. 14B). Right antennule (Figs 12C & 16C) with modified fused setal element not extending beyond distal margin of compound segment XXI-XXIII.

Right leg 5 (Fig. 12D,H) with strong curved inner process on basis, without patch of setules; third exopod segment with outer and terminal slightly curved processes (Fig. 13D) and inner seta (arrowed in Fig. 13D). Left leg 5 (Fig. 12D-G) highly complex in structure. Outer margin of first endopod segment produced into two irregular rounded processes distally (Fig. 12G); second segment modified into irregular process proximally and tapering process distally; third segment very broad. First segment of exopod with strong, bifid outer spine, main (outer) branch of spine ornamented with row of spinules (Fig. 13A); [secondary (inner) branch of spine concealed in Fig. 13A]; second exopod segment with proximal lappet and distal styliform spine (arrowed in Fig 13A) set between outer pointed and inner rounded processes; third segment broad with several membranous and styliform or flagellate processes (Fig. 13B,C) originating around outer and distal surfaces; long stylet-like element proximally on inner margin (Fig. 13D).

Ecological notes. Naurambuta Cave on the island of Vatulele, off the south coast of the main island of Viti Levu, is a large anchialine cave famous for the sacred red prawn, *Parhippolyte uveae* Borradaile, which occurs there (Choy 1987). A species of amphipod, *Liagoceradocus unciferus* Stock & Iliffe has been described from material collected in this cave (Stock & Iliffe 1991). Although part of the cave is open to daylight through ceiling collapse, other sections are in darkness. On 9 May 1988 the salinity was 26.5 at the surface and 30 at 3 m depth, the water temperature was 25 °C. In the sample together with *Enantiosis dicerata* sp. nov., were representatives of a calanoid belonging to the family Stephidae.

Remarks. The species has many features in common with *E. belizensis*. The females are morphologically very similar but exhibit some slight differences in the third exopod segments of legs 1 and 5. In leg 1 of *E. belizensis* the two outer spines are smooth and of equal length while they are subequal and with a serrated inner margin in *E. dicerata*. In leg 5 the terminal exopodal spine of *E. belizensis* is smooth along outer margin and serrated in *E. dicerata*. In the male right antennule a proc-

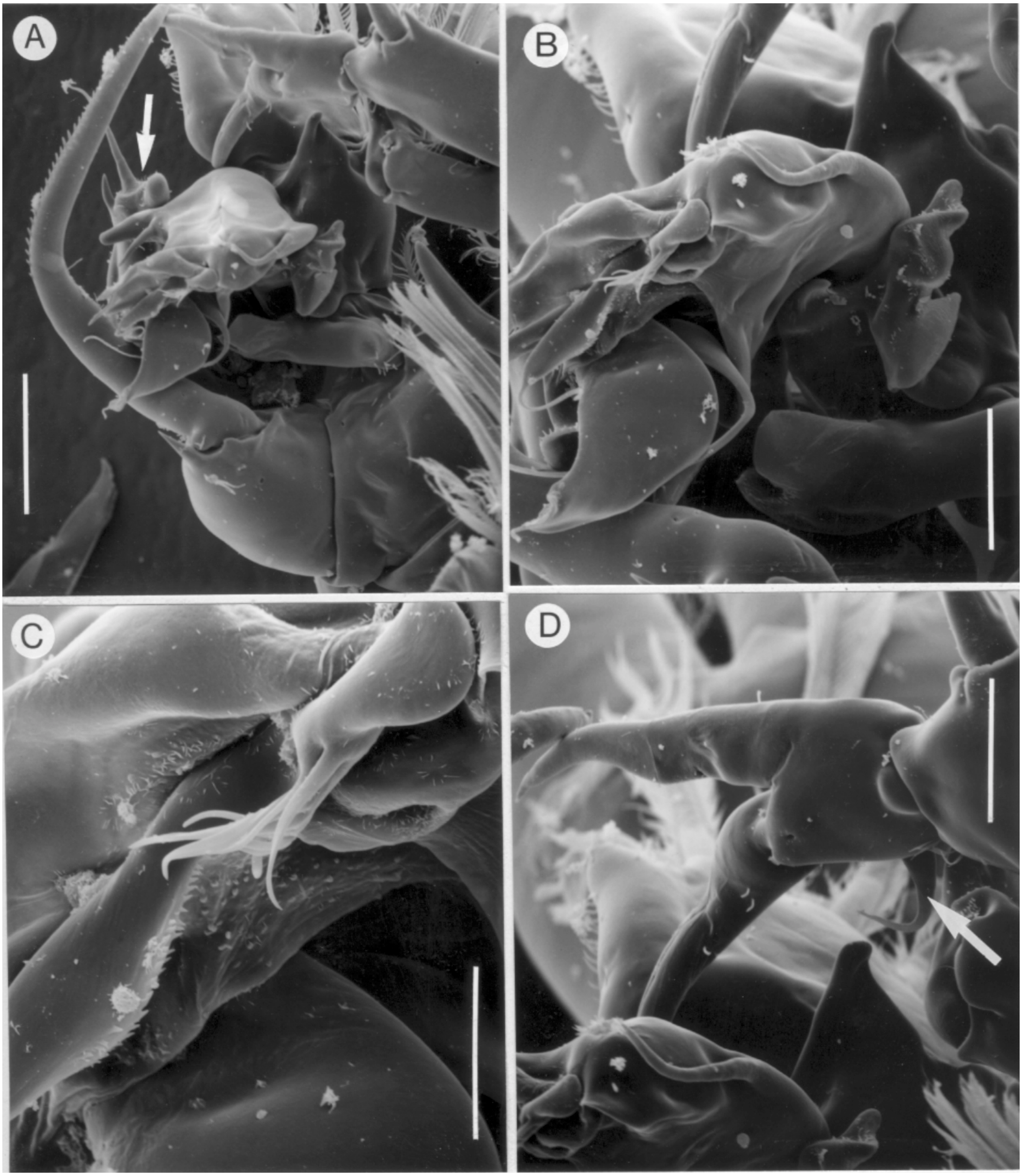

Fig. 13. *Enantiosis dicerata* sp. nov., male leg 5. A. Left exopod; scale bar = 50 µm. Arrow indicates distal corner of second segment. B. Third segment of left exopod; scale bar = 25 µm. C. Details of third segment of left exopod; scale bar = 10 µm. D. Third segment of right exopod with parts of left exopod below; scale bar = 25 µm. Arrow indicates inner seta on third segment of right exopod.

ess formed by the distal extension of the fused modified setal element is present on compound segment XXI-XXIII of *E. belizensis* but *E. dicerata* lacks such a process.

The distinctive characters of the male leg 5 also serve to separate these two species. The right basis lacks a patch of setules in *E. dicerata*, and the right third exopod segment of *E. belizensis* has a single terminal process while that of *E. dicerata* has two subequal processes. The first segment of the left exopod has a strongly curved spine in *E. belizensis* whereas *E. dicerata* has a conspicuous bifid spine. The two species also differ in

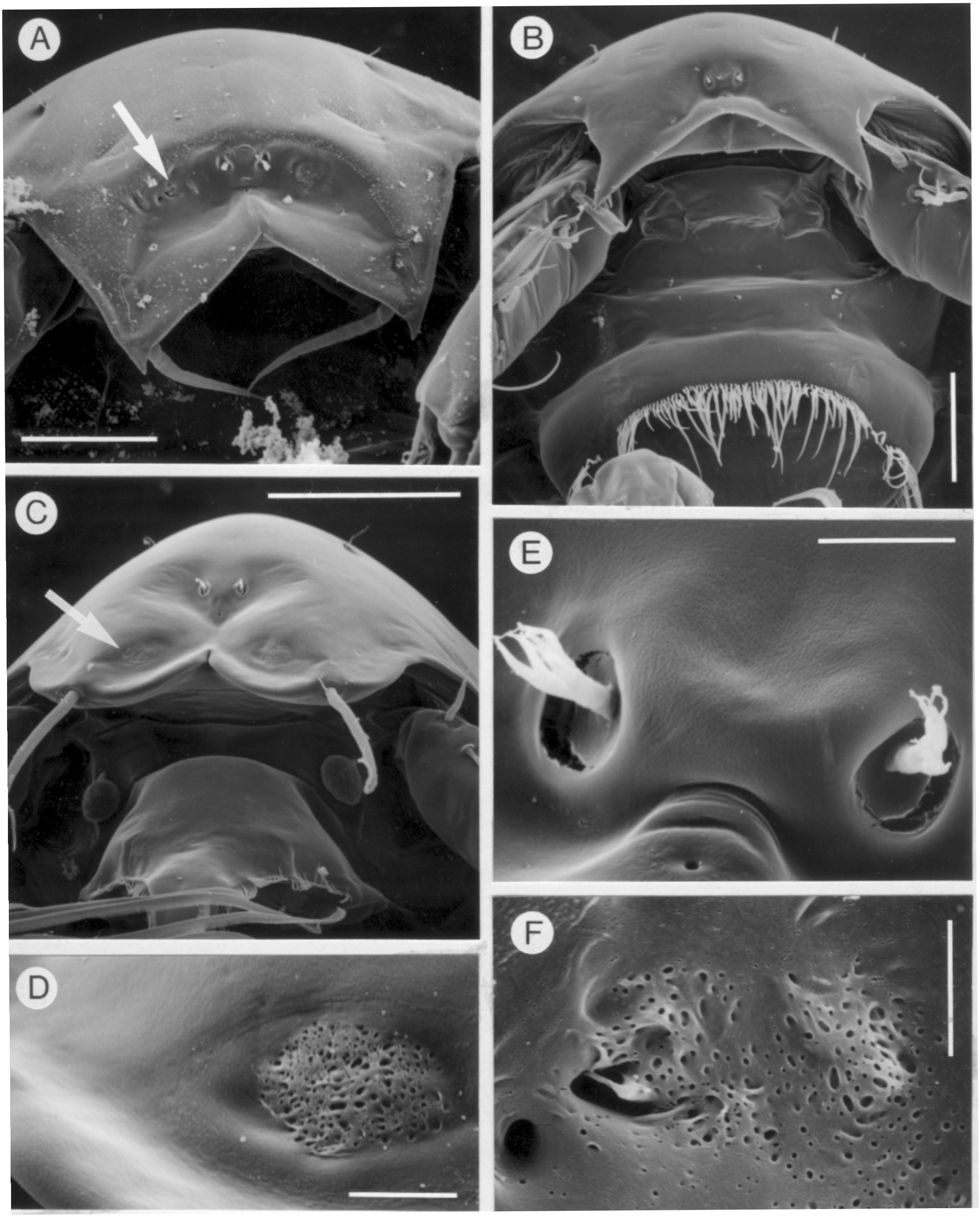

Fig. 14. A. *Edaxiella rubra* gen. et sp. nov., female. Rostrum; scale bar = 50 µm. Arrow indicates surface structures shown in F. B. *Enantiosis dicerata* sp. nov., male. Rostrum and labrum; scale bar = 50 µm. C. *Epacteriscus cuspidantennula* sp. nov., female. Rostrum and labrum; scale bar = 50 µm. Arrow indicates surface structures shown in D. D. *Epacteriscus cuspidantennula*, female. Rostral surface structures; scale bar = 5 µm. E. *Enantiosis belizensis* sp. nov., female. Rostral sensillae; scale bar = 5 µm. F. *Edaxiella rubra,* female. Rostral surface structures; scale bar = 5 µm.

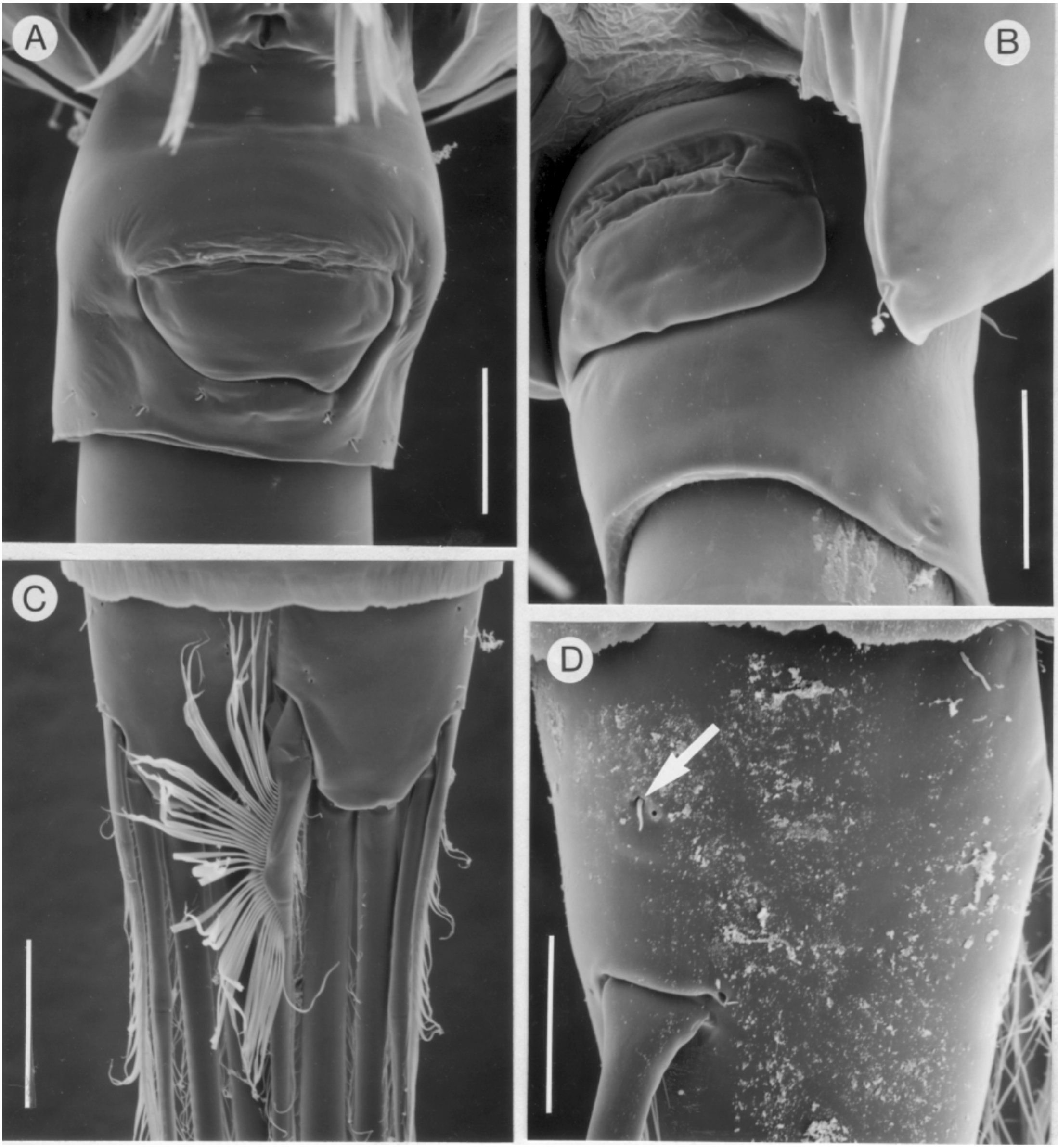

Fig. 15. A. *Enantiosis belizensis* sp. nov., female. Genital double-somite; scale bar = 50 µm. B. *Epacteriscus dentipes* sp. nov., female. Genital double-somite; scale bar = 20 µm. C. *Enantiosis belizensis* , female. Caudal rami, ventral view; scale bar = 40 µm. D. *Edaxiella rubra* gen. et sp. nov., female. Caudal ramus with arrow showing seta I; scale bar = 25 µm.

the precise form of the complex processes on third segment of left exopod.

Enantiosis conspinulata sp. nov.
(Fig. 17)

Material examined. This species was collected in a single locality in Palau, the Western Caroline Islands, using a plankton net in 0-3 m depth, in the cenote on Ngeruktabel Island, 9 February 1985: 1 female, 2 males and 1 copepodid. Collected by T.M. Iliffe and D. Williams.

Types. Holotype: Adult male total length 1.23 mm from the cenote on Ngeruktabel Island, 9 February 1985. One vial deposited in BM(NH) 1999.2445.

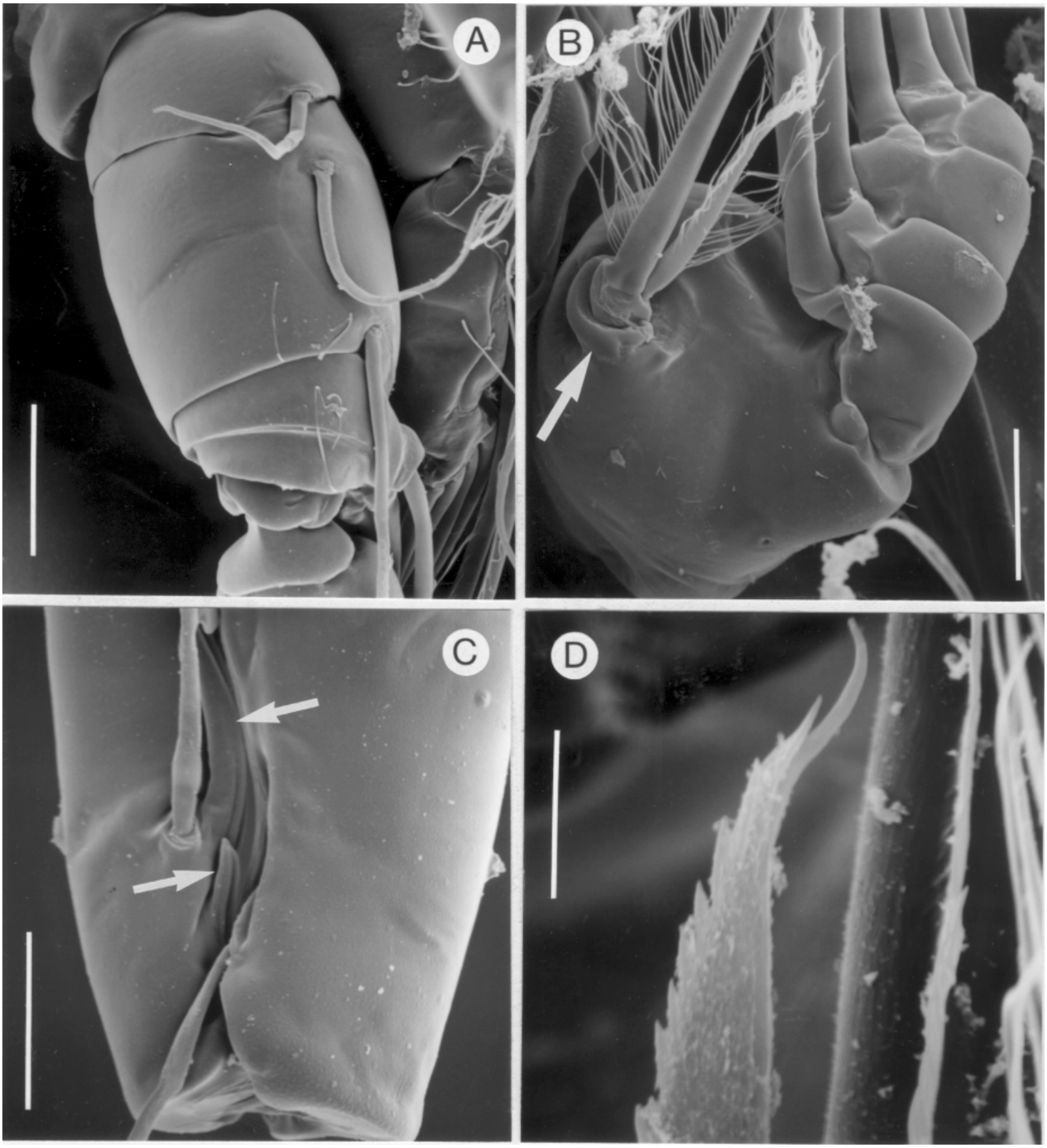

Fig. 16. A. *Enantiosis belizensis* sp. nov., male. Antennal exopod; scale bar = 25 µm. B. *Edaxiella rubra* gen. et sp. nov., female. Mandibular palp with endopod indicated by arrow; scale bar = 25 µm. C. *Enantiosis dicerata* sp. nov., male. Right antennule at geniculation; scale bar = 20 µm. Arrows indicate spines on compound segment XXI-XXIII. D. *Edaxiella rubra,* female. Tip of distal outer spine on third exopodal segment leg 1; scale bar = 4 µm.

Paratypes: One male and 1 female dissected and mounted on 6 slides from the same locality and date as the holotype. Deposited in BM(NH) 1999.2446-2447.

Etymology. The specific name refers to the row of spinules present on the basis of leg 1.

Description. Female. Body length of single female 1.31 mm. Antennule reaching slightly beyond third pedigerous somite. Leg 1 (Fig. 17A) with transverse row of few spinules distally on inner margin of basis. Leg 5 (Fig. 17B) with terminal spine on third exopod segment finely serrated along outer margin.

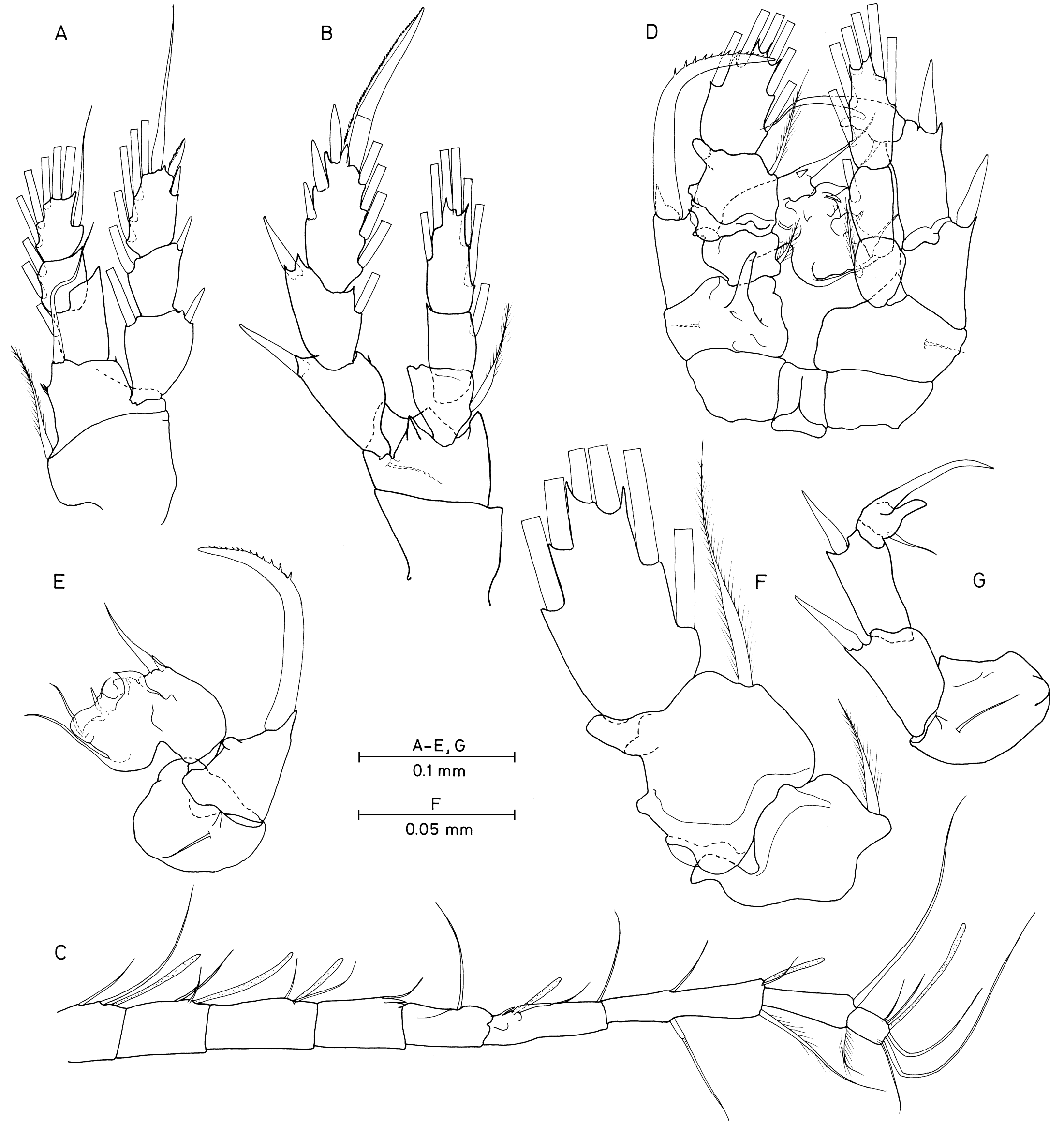

Fig. 17. *Enantiosis conspinulata* sp. nov., female (A, B), male (C-G). A. Leg 1. B. Leg 5. C. Distal part of right antennule. D. Leg 5, anterior view. E. Left exopod and basis of leg 5. F. Left endopod of leg 5. G. Right exopod and basis of leg 5.

Male. Body length of two males 1.23 and 1.25 mm. Right antennule (Fig. 17C) without distal extension on compound segment XXI-XXIII formed by modified fused setal element. Right leg 5 (Fig. 17D, G) with rounded process near inner margin of basis, without patch of setules; third exopod segment with long outer process tapering into slender flexible tip and short, blunt medial process about same length as inner seta. Left leg 5 (Fig. 17D-F) with slender process arising on anterior surface of basis, process directed along endopod. First endopod segment (Fig. 17F) with outer margin produced into slender process, blunt and constricted near tip; second segment with short, irregular, rounded processes along outer margin. First exopod segment (Fig. 17E) with strongly curved outer spine, distal part of which ornamented with coarse spinules laterally; second segment with strong and styliform spine distally; third segment of complex structure with two long subequal seta-like projections on inner margin.

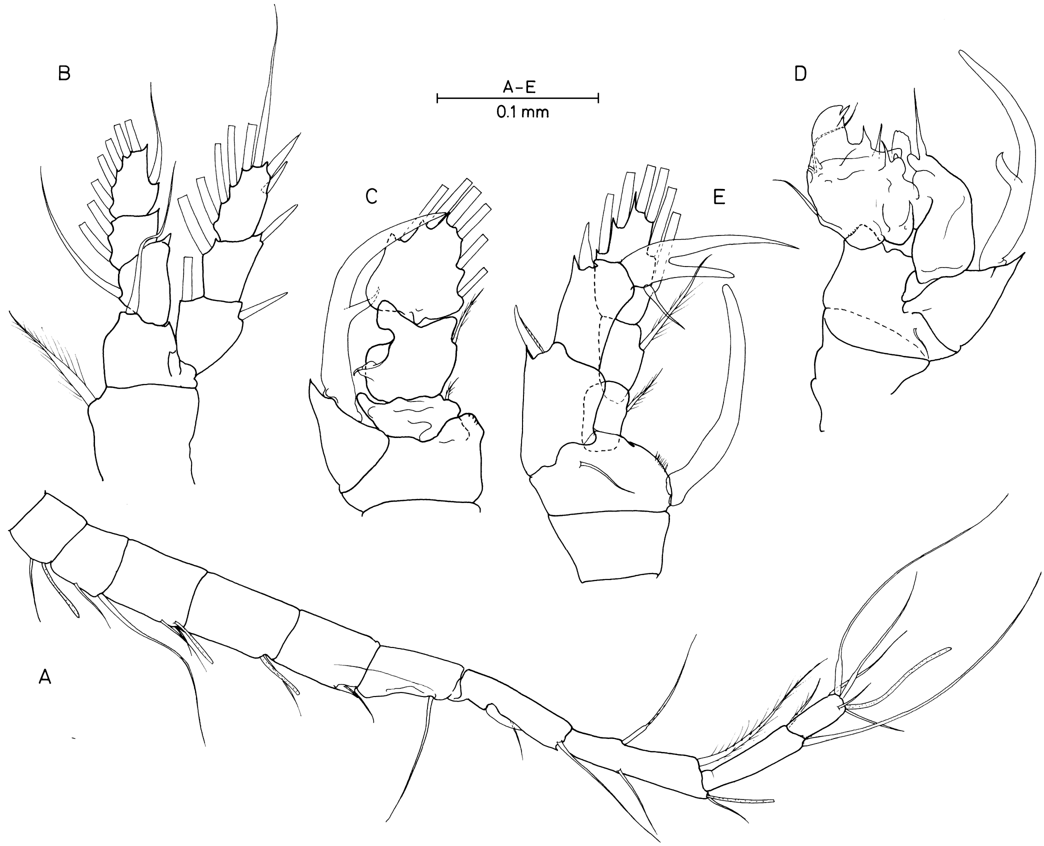

Fig. 18. *Enantiosis longiprocessa* sp. nov., male. A. Distal part of right antennule. B. Leg 1. C. Left leg 5, anterior view (second and third segments of exopod omitted). D. Left leg 5, posterior view (second and third segments of endopod omitted). E. Right leg 5, posterior view.

Ecological notes. The Cenote on Ngeruktabel Island is a 15 m deep, collapse sinkhole with an anchialine pool at the bottom extending back under a ledge into darkness. Logs and other debris from the surface are present on the bottom of the pool. The water in this cave is clear and with no noticeable currents present. In the sample together with *E. conspinulata* sp. nov. were several specimens of a calanoid belonging to the family Stephidae. This site is also the type locality of the misophrioid *Expansophria apoda* Boxshall and Iliffe, 1987.

Remarks. The structure of leg 5 in male *E. conspinulata* differs from that of its congeners, particularly in the absence of a strong process on right basis in combination with the presence of an anterior process on left basis. There are similarities with the female of *E. dicerata* sp. nov. from Fiji; both have a serrated flange on the two outer spines of third exopod segment of leg 1, and on the terminal spine of third exopod segment of leg 5. The males of both species lack any process-like extension on compound segment XXI-XXIII of the right antennule and both have a medial process on the third exopod segment of right leg 5.

Enantiosis longiprocessa sp. nov.
(Fig. 18)

Material examined. A single male was obtained in Palau, Western Caroline Islands using a suction bottle in 15 m depth, from the surface of silty sediments at Lake 2a Cave, Ngermeuangel Island: 7 February 1985. Collected by T.M. Iliffe and D. Williams.

Types. Holotype: Adult male body length 1.13 mm, from Ngermeuangel Island, 7 February 1985. Dissected and mounted on 3 slides. BM(NH) 1998.2448.

Etymology. The specific name refers to the very long process on the basis of the right leg 5 of the male.

Description. Male. In dorsal view posterior margin of urosomites coarsely serrated. Right antennule (Fig. 18A) without distal extension of modified fused setal element on compound segment XXI-XXIII. Left antennule reaching slightly beyond third pedigerous somite. Leg 1 (Fig. 18B) with 2 subequal outer spines on third exopod segment, distal spine slightly longer; both with smooth flange on inner side.

Right leg 5 (Fig. 18E) with long curved inner process on basis, reaching beyond second exopod segment, patch of spinules present in middle of inner margin of basis; third exopod segment with two distal processes and inner seta, inner process half length of outer. Left leg 5 (Fig. 18C, D) with outer margin of first endopod segment produced into short, evenly rounded process; second segment with outer medial lappet or process, and distal rounded process. First exopod segment (Fig. 18D) with strong, bifid, curved outer spine, inner branch shorter, originating near middle of spine, with curved tip; third exopod segment of complex structure, with several processes including prominent distal lappet, divided at tip, and long slender seta.

Ecological notes. Lake 2a Cave on Ngermeuangel Island is a totally underwater cave draining an anchialine lake. The cave consists of a large, elongated chamber with depths to over 30 m through which moderate tidal currents pass. Sponges and other encrusting organisms are plentiful on the walls and ceiling.

Remarks. The male of *E. longiprocessa* sp. nov. is clearly distinguished from the other species from Palau, *E. conspinulata* sp. nov., by the presence of the strong process on right basis of the leg 5 and the bifid spine on the first segment of the left exopod. These two characters are shared with *E. dicerata* sp. nov. from Fiji, indicating a possible closer relationship between these two more distant species rather than between the two from Palau and is supported by the phylogenetic analysis (Fig. 39). Characters in common for the three species from the western Pacific are the lack of a process on compound segment XXI-XXIII of the male right antennule and the presence of a prominent medial process on the third exopod segment of the male right leg 5.

Genus *Epacteriscus* Fosshagen, 1973

Diagnosis (emend.). Female. Body compact; oval in dorsal view. Urosome 4-segmented with minute anal somite. Caudal rami about twice as long as broad; caudal setae asymmetrical, seta V elongate on left ramus only; seta VI with small unilateral tuft of setules near base on left ramus only. Rostrum bilobed, with broad, rounded lobes, carrying pair of filaments.

Antennule 24-segmented, extending backwards to end of prosome; segments I-IV not separated. Antenna with endopod about half length of exopod; inner lobe on second endopodal segment not present, represented by single seta. Labrum large, directed frontally, forming beak-like structure. Mandibular palp without endopod; gnathobase strongly developed, projecting ventrally forming saw-toothed, grasping organ. Maxillule weakly developed with reduced number of elements and lobes; exopod absent. Maxilla with relatively long setae on protopodal segments; endopod compressed, with short spinous setae. Maxilliped with reduced setation on syncoxa; free endopod compact, setae varying in length and strength.

Leg 1 with modified rami: third exopod segment broad, outer margin produced into row of pointed processes; outer spines on exopod strongly developed, flagellate; third endopod segment terminating in curved process. Legs 2 and 3 with strong pointed processes along outer margin of last endopodal segment; basis of leg 3 with strong outer spine. Leg 5 lacking inner seta on first exopodal segment.

Male. Urosome 5-segmented with minute anal somite. Antennule with extra long aesthetascs in proximal half; right geniculate antennule with incomplete separation between segments IX-XI and XII-XIV. Leg 5 with 2-segmented exopod on left leg; both legs only slightly modified, with some transformations of distal exopod segments.

Type species. *Epacteriscus rapax* Fosshagen, 1973.

Epacteriscus rapax Fosshagen, 1973

The species was the first recorded member of the family and is a rather atypical member of the family, now that a wider range of taxa is known. It was originally taken in bottom samples from shallow water in Florida and in Colombia (Fosshagen 1973). This species has now been recorded from 9 caves in Bermuda (1-9 in Fig. 37). Unless otherwise mentioned, the samples were taken with a fine-mesh hand held net.

Cherry Pit Cave, 26 January 1982, 16 females, 3 males and 8 copepodids by pumping 7.4 m^3 of water from 2.5 m depth through plankton net; 23 June 1982, 1 copepodid from near bottom sediments in 1-7 m depth; 12 January 1984, 3 females from bottom sediments in 3-12 m.

Deep Blue Cave: 3 September 1984, 1 female and 1 copepodid in water column in 15 m of main underwater chamber.

Emerald Sink Cave: 17 January 1982, 1 female and 2 males from near bottom sediments in 11 m.

Green Bay Cave: 31 January 1984, 2 females, 1 male and 1 copepodid in 12 m from near roof of Trunk Passage; 13 March 1984, 1 male, same data.

Myrtle Bank Cave: 31 January 1982, 3 females and 2 males in 5 m from near roof, walls and ledges in entrance pool.

Palm Cave: 29 January 1984, 2 females in 8-16 m from base of entrance slope.

Straw Market Cave: 12 January 1984, 3 females in 10-12 m from area below entrance at which water flow emerges from breakdown choke.

Walsingham Cave: 28 May 1980, 1 male in surface 0.5 m, from rocks in west corner of entrance pool; 18 February 1982, 2 females and 1 copepodid with a suction bottle and fine-mesh net in 6-8 m from near bottom sediments in back portion of entrance pool; 10 June 1982, 2 copepodids in surface 0.5 m from rocks in west corner of entrance pool; 11 September 1986, 2 specimens in 3-5 m from near roof at back of entrance pool.

Walsingham Sink Cave: 7 February 1982, 1 male by pumping 5 m^3 of water from 5 m through a plankton net.

The specimens from Bermuda are slightly larger than the few specimens obtained from Florida and Colombia. The body length of 7 adult females ranged between 0.80 and 0.87 mm, with a mean of 0.85 mm, compared to 0.73 and 0.74 mm of the two females from the type localities. Three males from Bermuda measured 0.75, 0.77 and 0.78 mm, whereas the single male from Florida was only 0.63 mm. The abundant material from Bermuda allowed us to check some characters that were overlooked or missing from the original material. Differences in morphology between specimens from Bermuda, Florida and Colombia are so slight that they are considered to belong to the same species. The minute anal somite in both sexes is completely concealed beneath the posterior margin of the preceding somite and was overlooked in previous descriptions.

There is asymmetry in the caudal setae of the female with seta V on the left ramus being elongated and the left seta VI possessing a unilateral tuft of fine setules proximally. The female antennule and the left antennule of the male have segments X and XI incompletely separated over part of the posterior surface; a feature that is easily overlooked. Segment XIX has only one seta distally and not an aesthetasc and seta, as indicated in Fosshagen (1973). The terminal part of the reduced maxillule is most probably the endopod and not the exopod as originally interpreted. This reinterpretation is based on comparisons with the less reduced limb of *Enantiosis.* The single seta on the outer margin of the maxillule in *E. rapax* is probably the only remnant of the exopod.

In the male no discernible differences could be found in the right antennule and leg 5 between the specimens. A small process located distally on third from last segment of the right antennule, indicated in the male from Florida, was also present in the specimens from Bermuda.

Ecological notes. This species has mostly been taken in the Palm Cave System and in caves likely to be connected with it. Myrtle Bank, Palm, and Straw Market Caves are all segments of an interconnected system and Cherry Pit and Emerald Sink Caves are also situated close by. All these caves (Fig. 37) have moderate tidal currents and a direct connection to the sea in Harrington Sound. Deep Blue, Walsingham and Walsingham Sink Caves may be hydrologically connected to the system but they have a less direct communication to the sea. Green Bay Cave on the northern side of Harrington Sound is distinct from this system and is influenced by strong tidal currents in the entrance section.

The greatest numbers of *E. rapax* were obtained from Cherry Pit Cave where *Miostephos leamingtonensis* Yeatman was abundant and a few specimens of a *Metacalanus* species were also taken. *E. rapax* co-occurred with large numbers of *Ridgewayia marki* (Esterly) and some *M. leamingtonensis* in Emerald Sink Cave; in Walsingham and Green Bay Caves with *M. leamingtonensis* and a species of *Calanopia*, and in Myrtle Bank Cave with large numbers of an *Acartia* species.

E. rapax has primarily been collected in areas with moderate tidal currents and from the deeper, more saline waters of the caves. A live female from Deep Blue Cave had a distinct red eyespot surrounded by some white pigment; the body had a light brownish tinge. The animal was observed swimming slowly along the bottom in a petri dish with the exopod of the antenna and the mandibular palp vibrating very rapidly. This observation of a pigmented specimen and previous records of the species in bottom samples outside caves (Fosshagen 1973) suggests that the species is not exclusively troglobitic, as are most others in the family Epacteriscidae.

Epacteriscus cuspidantennula sp. nov.
(Figs 14C,D, 19A-F, 20A,C,E & 21A)

Material examined. The species was taken in two samples from Caye Chapel Cave, Caye Chapel, Belize, using a hand-held plankton net on 18 February 1989; 1 female and 2 males in 20-35 m depth at a penetration of 150 m; and 2 females and 2 males in 8-10 m depth at a penetration of 40-60 m.

Types. Holotype: Adult male body length 0.58 mm, from Caye Chapel Cave, Caye Chapel, Belize, 18 February

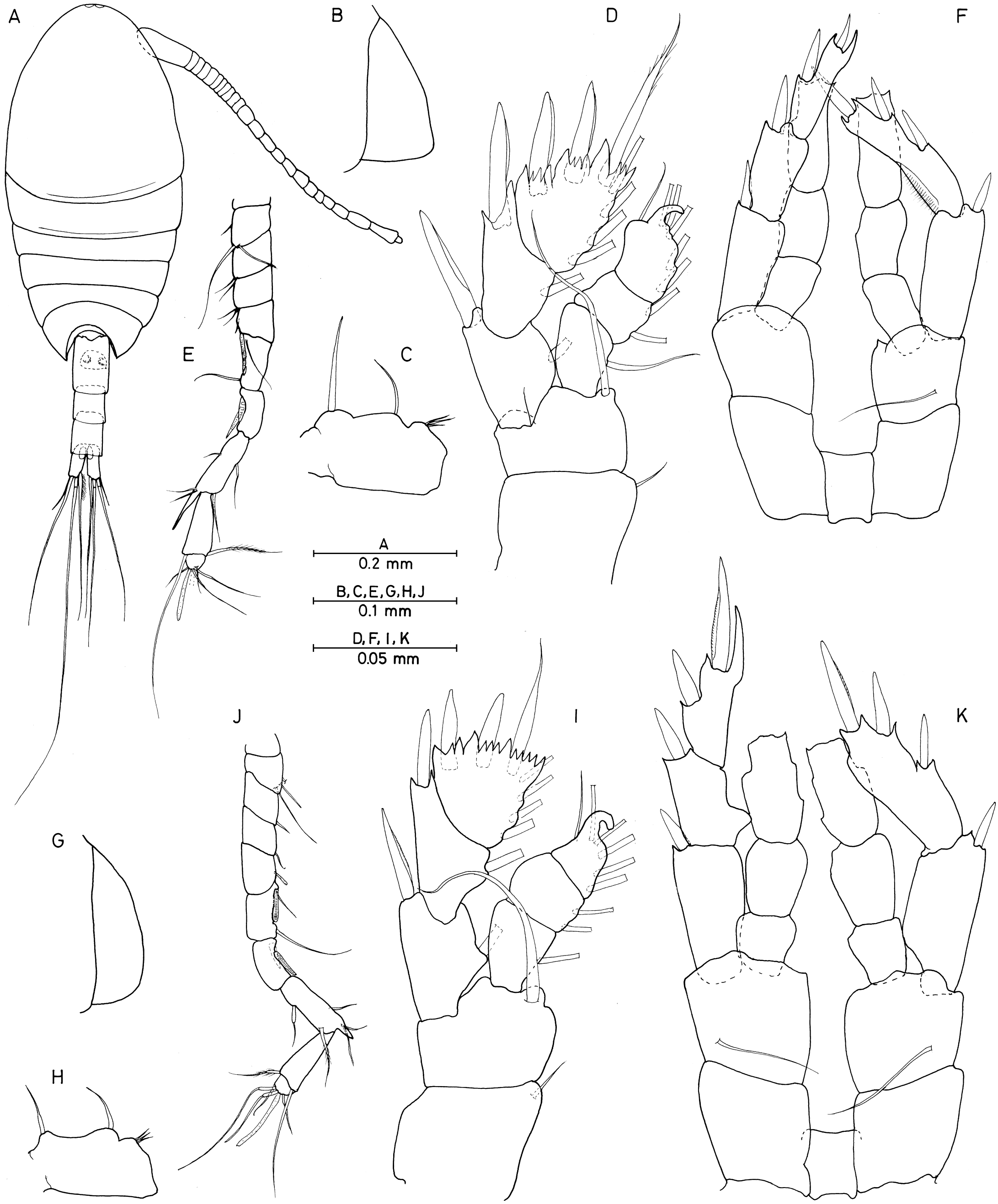

Fig. 19. *Epacteriscus cuspidantennula* sp. nov., female (A-D), male (E, F). *Epacteriscus dentipes* sp. nov. female (G-I), male (J, K). A. Habitus, dorsal view. B. Last somite of prosome, lateral view. C. Syncoxa of maxilliped. D. Leg 1. E. Distal part of right antennule. F. Leg 5, posterior view (setae on endopod omitted). G. Last somite of prosome, lateral view. H. Syncoxa of maxilliped. I. Leg 1. J. Distal part of right antennule. K. Leg 5, posterior view (setae on endopod omitted).

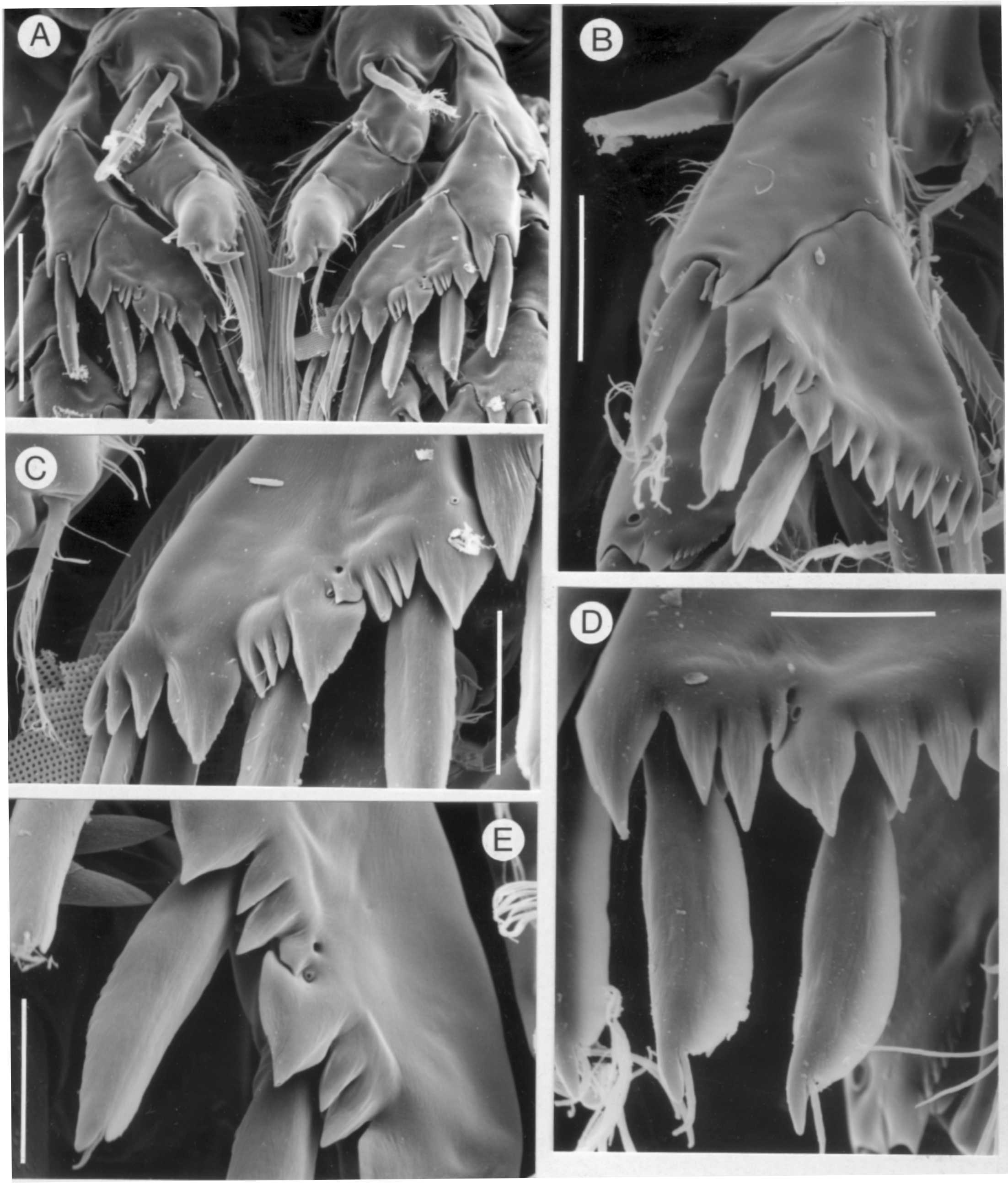

Fig. 20. A. *Epacteriscus cuspidantennula* sp. nov., female. Leg 1, anterior view; scale bar = 43 µm. B. *Epacteriscus dentipes* sp. nov., male. Right exopod of leg 1, anterior view; scale bar = 15 µm. C. *E. cuspidantennula,* female. Third segment of left exopod leg 1, anterior view; scale bar = 15 µm. D. *E. dentipes*, male. Detail of third segment of right exopod leg 1, anterior view; scale bar = 7.5 µm. E. *E. cuspidantennula,* female. Detail of third segment of right exopod leg 1, anterior view; scale bar = 10 µm.

1989, taken with a plankton net in 20-35 m depths at a penetration to 150 m. One vial BM(NH) 1998.2449.

Paratypes: Two adult females and 2 adult males dissected and mounted on 10 slides from same locality and on same date as holotype in 8-10 m depth at a penetration to 40-60 m. BM(NH) 1998.2450-2453.

Etymology. The specific name refers to the prominent process on the right antennule of the male (*cuspis* Latin meaning point).

Description. Female. Body lengths of two adults, 0.61 and 0.65 mm. Body relatively slender (Fig. 19A) with ventral part of last prosomal somite somewhat produced posteriorly (Fig. 19B). Caudal seta V on left ramus longer than corresponding seta on right. Rostrum bilobed with pair of long terminal filaments and paired areas of well defined perforated integument, in middle of inner half of lobes (Fig. 14C, D). Labrum and gnathobase of mandible extremely strongly developed (Fig. 21A). Endopod of maxillule with 3 long setae and 1 short seta distally. Syncoxa of maxilliped with 2 unequal setae (Fig. 19C). Leg 1 (Figs 19D, 20A) with hook-like process distally on apical segment of endopod. Outer margin of third exopod segment with array of primary and secondary pointed processes (Fig. 20C); with 3 processes extending medial to terminal seta; outer margin spines flagellate (Fig. 20E).

Male. Body length of four males ranging from 0.54 to 0.60 mm, with mean of 0.57 mm. Caudal seta V on left ramus longer than corresponding seta on right, but not as asymmetrically elongate as in female.

Right antennule (Fig. 19E) with segment XXI-XXIII distal to geniculation with 2 modified fused setal elements of unequal length; long pointed process distally on anterior margin of double segment XXIV-XXV reaching halfway along segment XXVI.

Leg 5 with unmodified endopods (Fig. 19F); distal part of both exopods slightly transformed; 3-segmented on right side and 2-segmented on left. Distal segment of right exopod with outer medial spine longer than terminal spine; terminal spine about one third length of segment and longer than adjacent inner process; distal segment of left exopod with patch of setules proximally on concave inner margin; terminal spine adjacent to short inner process.

Ecological notes. Caye Chapel Cave is located ca. 500 m east of the southern tip of Caye Chapel. Its entrance is in a seagrass bed in 3 m depth and the entire cave extends beneath the sea floor. It is therefore considered as a marine cave. At the time of sampling the water was quite clear with a visibility about 20 to 30 m.

E. cuspidantennula was obtained using a hand-held plankton net in Caye Chapel Cave at two sites, at 8-10 m depth at 40-60 m penetration, and at 20-35 m depth at 150 m penetration, at both localities it co-occurred with its newly discovered congener *Epacteriscus dentipes* sp. nov. (see below), and at the innermost location also with *Enantiosis belizensis* sp. nov.

Remarks. This species is closely related to *E. rapax*; the females are best distinguished by details of the tips of exopod and endopod of leg 1. Males can be separated by the long process located distally on double segment XXIV-XXV of the geniculate right antennule of *E. cuspidantennula*, and by differences in morphology of the tips of both exopods of leg 5.

Epacteriscus dentipes sp. nov.
(Figs 15B, 19G-K, 20B,D & 21B)

Material examined. This species was obtained in three samples from Caye Chapel Cave, Caye Chapel, Belize, taken using a hand held net; 22 January 1989, 2 females, 1 male in 12-34 m depth at a penetration of 150 m; twice on 18 February 1989, 1 female and 2 males in 20-35 m depth at a penetration of 150 m, and 13 females and 5 males in 8-10 m depth at a penetration of 40-60 m.

Types. Holotype: Adult female, body length 0.68 mm, from Caye Chapel Cave, Caye Chapel, Belize, 18 February 1989, collected using a plankton net in 8-10 m depths close to entrance at 40-60 m penetration. One vial BM(NH) 1998.2454.

Paratypes: Two adult males and 1 adult female dissected and mounted on 7 slides; 4 females and 3 males in one vial, all from same locality and date as holotype. BM(NH) 1998.2455-2464.

Etymology. The specific name refers to the toothed distal part of the exopod of leg 1.

Description. Female. Body length of 8 adults ranging between 0.60 and 0.69 mm, with mean of 0.64 mm. Genital double-somite with operculum evenly rounded on left posterior corner (Fig. 15B). Differing from *E. cuspidantennula* in following characters. Last somite of prosome evenly rounded and not extending as far posteriorly (Fig. 19G). Maxilliped with seta on proximal endite of coxa weak, about same length as seta on second endite (Fig. 19H). Leg 1 with relatively weaker outer spines on exopod and with different arrangement of primary and secondary processes along outer margin of third exopod segment (Fig. 20B and D show male leg 1 exopod, identical with that of female); with 5 pointed processes medial to terminal seta, in contrast to 3 in *E. cuspidantennula.*

Male. Body length of 5 males ranging between 0.54 and 0.60 mm, with mean of 0.55 mm. Right antennule (Fig. 19J) with short pointed process distally on anterior margin of double segment XXIV-XXV. Leg 5 (Fig. 19K) with distal segment of right exopod bearing outer

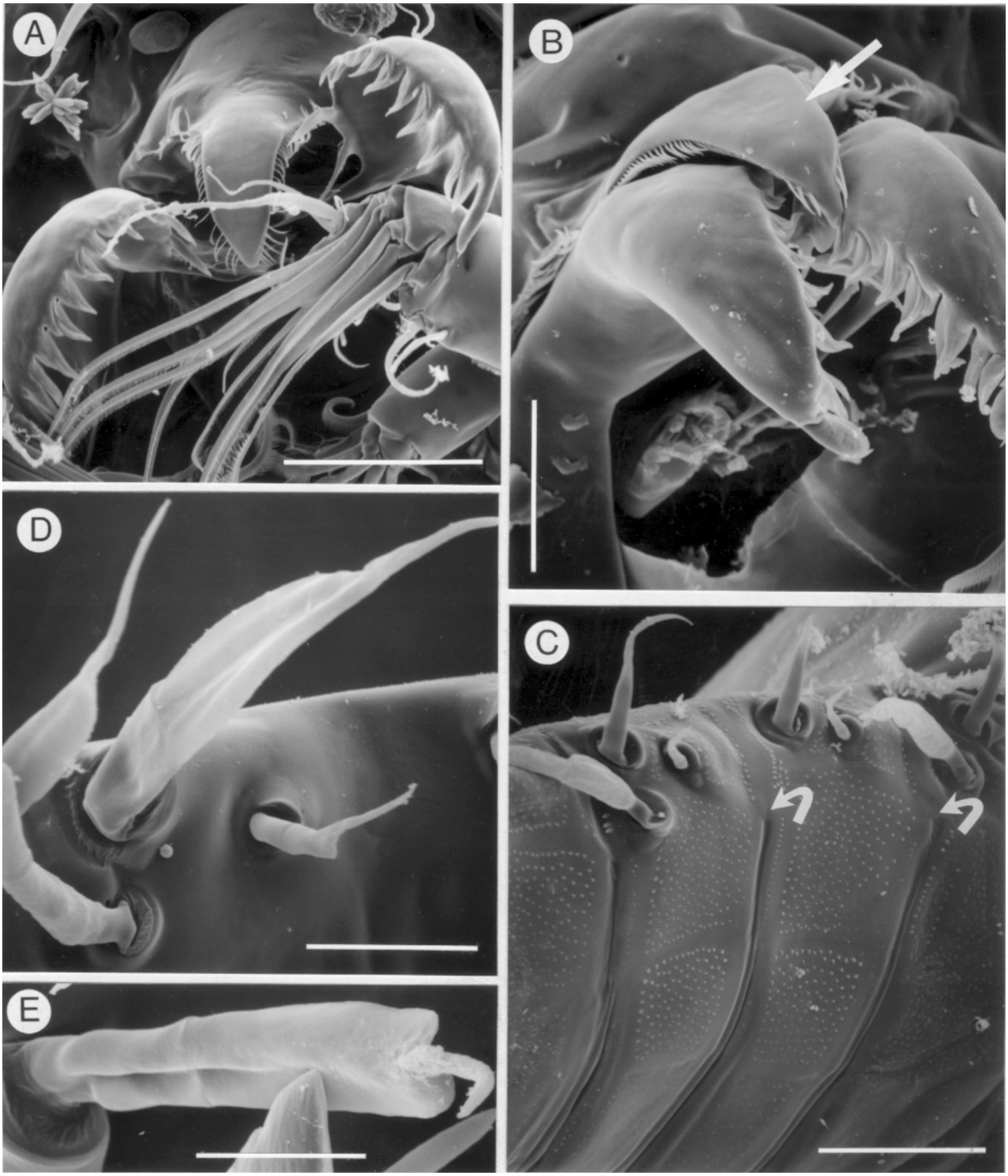

Fig. 21. A. *Epacteriscus cuspidantennula* sp. nov., female. Labrum, gnathobase mandible and maxilliped, ventral view; scale bar = 50 µm. B. *Epacteriscus dentipes* sp. nov., male. Labrum and gnathobase mandible; scale bar = 20 µm. C. *Edaxiella rubra* gen. et sp. nov., female. Segments I-III antennule; scale bar = 15 µm. Arrows indicate fusion between segments. D. *Enantiosis dicerata* sp. nov., female. Elements on segment III of antennule; scale bar = 25 µm. E. *Enantiosis belizensis* sp. nov., female. Modified seta on segment I antennule and point of rostrum; scale bar = 10 µm.

medial spine shorter than terminal spine; terminal spine about equal in length to segment excluding terminal process; second segment of right exopod with medial expansion proximally on inner margin.

Ecological notes. The species was obtained using a plankton net in two samples from Caye Chapel Cave where it co-occurred with *E. cuspidantennula* sp. nov. In addition, a single specimen was recorded in one sample at the innermost penetration of 150 m. Of the two species, *E. dentipes* was the more abundant and was caught in greatest numbers closest to the entrance of the cave. In all samples copepodids of *Epacteriscus* were present, but no attempts were made to distinguish between the species.

In all samples with *Epacteriscus* one or more species of *Ridgewayia* was abundant, and in the sample closest to the entrance, a small stephid was also present in large numbers. This shows faunal similarities to the situation in the Bermuda caves where *E. rapax* often co-occurred with *Ridgewayia marki* and *Miostephos leamingtonensis*. It may indicate that proximity to open sea and moderate currents are the preferred habitat for *Epacteriscus* as well as for species of *Ridgewayia* and stephids.

Baited traps were used in Caye Chapel Cave but no *Epacteriscus* were caught.

Remarks. With two closely related species of nearly equal size present in the same locality, they may easily be confused. The main distinguishing features are in leg 1 and in the male secondary sexual characters of fifth legs.

Genus *Bomburiella* gen. nov.

Diagnosis. Female. Prosome oval in dorsal view, dividing line between cephalosome and first pedigerous somite well defined. Urosome 4-segmented, genital double-somite with aperture on left side; anal somite very short. Caudal rami short, with plumose setae; caudal seta V on left ramus only elongate. Rostral lobes weakly developed with small filaments.

Antennule 26-segmented with apical segment incorporating XXVI and XXVII-XXVIII. Antenna with short endopod, about two thirds length of exopod, distal segment with well developed inner lobe; last segment of exopod elongate, comprising about half of length of ramus. Mandibular palp with minute 2-segmented endopod carrying 2 small terminal setae; gnathobase with strongly projecting ventralmost tooth. Coxal and basal endites of maxillule each with 1 seta; coxal epipodite with 4 long setae. Maxilla with reduced praecoxal endites; endopod compressed as typical for family. Maxilliped strongly developed; syncoxa with reduced enditic setation; basis elongate with group of 3 setae distally plus 2 setae from incorporated first endopodal segment; free endopod with 4 very long flexible setae, 2 each on two proximal segments; apical segment minute, with 3 setae. Legs 1-5 with 3-segmented rami and following seta and spine formula:

	coxa	basis	exopod segments 1 2 3	endopod segments 1 2 3
leg 1	0-1	1-1	I-1; I-1; II,I,4	0-1; 0-2; 1,2,3
leg 2	0-1	0-0	I-1; I-1; II,I,5	0-1; 0-2; 2,2,4
leg 3	0-1	I-0	I-1; I-1; III,I,5	0-1; 0-2; 2,2,4
leg 4	0-1	1-0	I-1; I-1; III,I,5	0-1; 0-2; 2,2,3
leg 5	0-0	1-0	I-1; I-1; III,I,4	0-1; 0-1; 2,2,2

Outer spines on second and third exopod segments of leg 1 relatively longer and more slender than in *Bofuriella* gen. nov. (see below).

Male. Urosome 5-segmented with anal somite very short. Leg 5 with highly transformed exopods and slight modifications on first segment of left endopod and second segment of right endopod. Inner margin of basis evenly rounded on both legs. Left leg first exopod segment with stout outward-curved outer spine; second segment bearing curved slender outer spine; third segment short and broad with 2 subterminal straight spines. Second exopod segment of right leg with long inner process in mid-medial margin; third segment elongate and curved with 3 straight spines proximally on inner margin.

Type species. *Bomburiella gigas* gen. et sp. nov.

Etymology. The generic name (gender feminine) is a diminutive of Bombur, one of the dwarfs mentioned in The Edda as often living underground. The specific name (Greek - a giant) refers to the large size of this copepod.

Bomburiella gigas gen. et sp. nov.
(Figs 22 & 23)

Material examined. Oven Rock Cave, Great Guana Cay, Bahamas, 22 May 1995: 1 male from water column in 1-22 m depth, collected using a plankton net or a suction bottle. August 1996: 1 female and 1 male from about 18 m depth, collected with a suction bottle. 13 September 1996: 5 females, 2 males and 1 copepodid from 0-18 m depth, with a plankton net or a vial. 4 January 1998: 2 females, 1 male and 4 copepodids stage V collected using vials in 0-18 m depth.

Stargate Blue Hole, South Andros, Bahamas, 22 August 1997: 1 female from 30 m depth of North Passage collected with a vial. 25 August 1997: 1 copepodid from 33-36 m depth in North Passage, collected with plankton net or a vial.

Types. Holotype: Adult female, body length 3.16 mm,

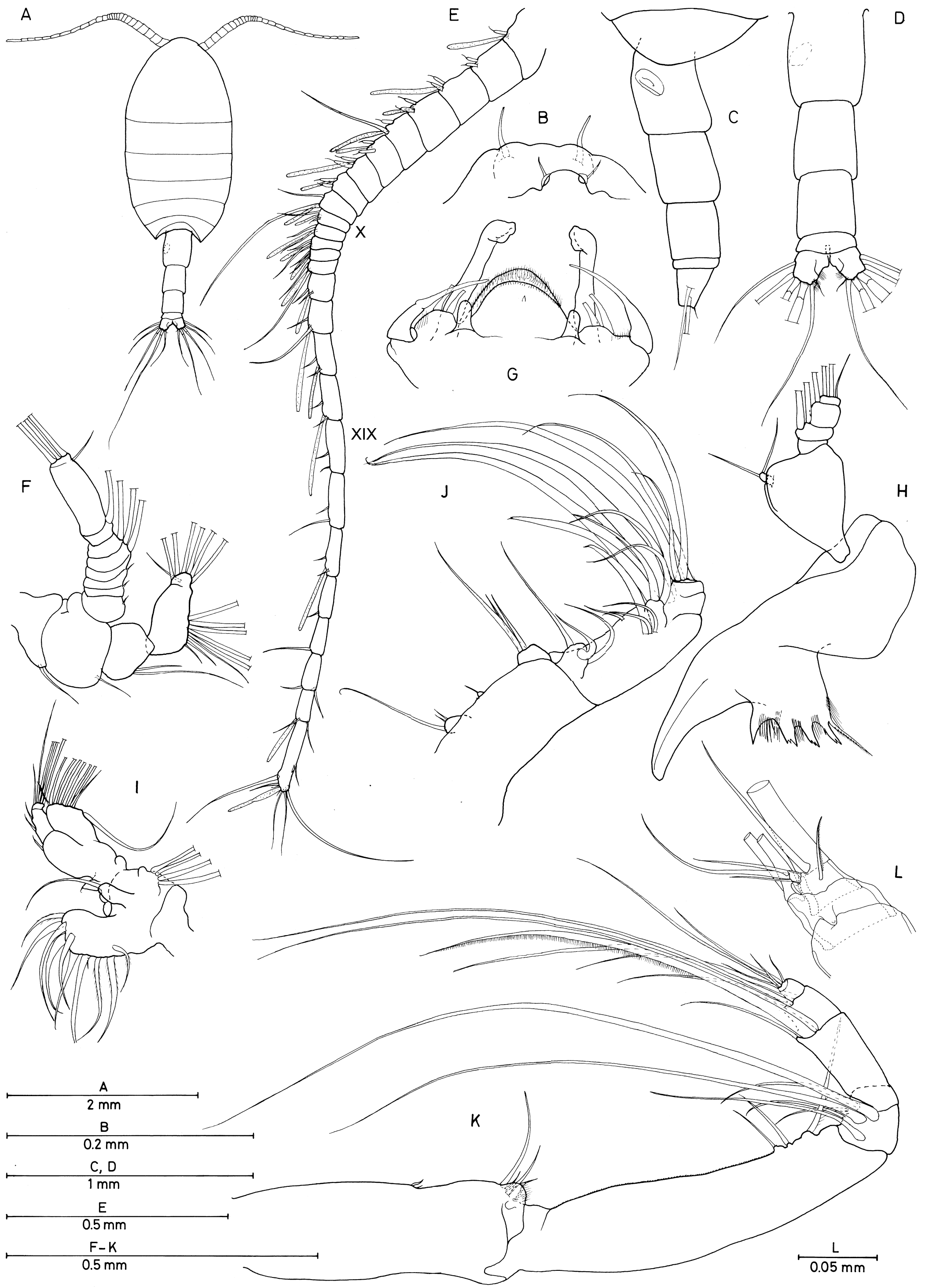

Fig. 22. *Bomburiella gigas* gen. et sp. nov., female. A. Habitus, dorsal view. B. Rostrum, dorsal view. C. Urosome and last prosomal somite, left side. D. Urosome, dorsal view. E. Antennule. F. Antenna. G. Labrum and labial lobes, ventral view. H. Mandible. I. Maxillule. J. Maxilla. K. Maxilliped. L. Tip of endopod of maxilliped.

from Oven Rock Cave, Bahamas, 13 September 1996, 0-18 m depth. In vial BM(NH) 1998.2245.

Paratypes: 1 male, total length 2.82 mm, and 1 female total length 3.31 mm, in one vial; 1 male, total length 2.90 mm, dissected and mounted on 2 slides; 2 females, 3.20 and 3.27 mm, dissected and mounted on 2 slides respectively. All paratypes from same locality and date as holotype, BM(NH) 1998.2246-2250.

Non-type Copepodid V from same locality, in vial BM(NH) 1998.2770.

Description. Female. Body length of 5 females ranging from 2.95 to 3.31 mm, with mean of 3.17 mm. Ratio of prosome to urosome length ca. 2:1. Pedigerous somites well defined (Fig. 22A), last somite with rounded posterolateral margins. Urosome (Fig. 22C,D) 4-segmented; anal somite short, about 1/6 length of preceding somite. Genital double-somite (Fig. 22C) with aperture located obliquely on left side. One specimen with spermatophore attached to left side. Length of spermatophore equal to length of urosome. Caudal rami about as long as broad; seta V on left ramus considerably longer than corresponding seta on right; seta VI on left ramus with dense unilateral tuft of small setules near base. Rostrum (Fig. 22B) reduced, represented by two ill-defined, rounded lobes, each with short filament.

Antennule (Fig. 22E) 26-segmented, reaching end of third pedigerous somite; small setae modified at tip present on segments I-VIII and X, segments X and XI separate, segment XIX with 2 small setae; segment XXVI incorporated into apical double segment XXVII-XXVIII.

Antenna (Fig. 22F) with endopod about two thirds length of exopod. First endopod segment with 2 inner setae in mid medial margin; second segment with inner lobe bearing 3 small and 5 long setae, terminal lobe with 1 small and 6 long setae. Exopod with minute seta on first, second and third segments, terminal segment about half length of ramus.

Labrum complex (Fig. 22G), with hirsute medial lobe and long lateral processes; paragnaths (= labial palps?) elongate, bulbous distally.

Mandible (Fig. 22H) with strongly developed gnathobase bearing massive ventralmost tooth, directed ventrally from body and separated by distinct gap from other 4 strong teeth, which bear stiff spinules at bases. Palp with reduced 2-segmented endopod, carrying 2 small terminal setae of equal length; exopod well-developed, with 1 small and 5 long setae.

Maxillule (Fig. 22I) with praecoxal arthrite bearing 10 long seta-like spines and 1 short spine, all tapering to thin points; coxal endite with 1 seta and coxal epipodite with 4 long setae; proximal basal endite short, with minute seta at tip, distal endite represented by short seta. Endopod with 2 small setae along inner margin and 5 terminal setae. Exopod with 9 setae, proximal one long and curved.

Maxilla (Fig. 22J): endites on partly fused praecoxa and coxa reduced, formula 3, 1, 3, 3; two of setae on distal coxal endite curved and claw-like. Basis with 4 setae, 3 of which relatively small and flexible, 1 strong and stout. Endopod compressed as typical for family, bearing total of 11 elements of various length, most of which spiniform.

Maxilliped (Fig. 22K) powerfully developed, with syncoxal endites reduced; distal coxal endite represented by 4 unequal setae, one plumose and bulbous at base. Basis elongate, with group of 3 basal setae in distal part. Endopod with group of 6 setae, two of which very long and flexible at tip, derived from partially fused first and second segments; third segment elongate with 3 setae, one long and smooth, one strong with row of fine setules, and one short; fifth segment with 3 setae, lacking outer margin seta; minute apical segment (Fig. 22L) with 3 setae.

Leg 1 (Fig. 23A): basis with small outer seta; exopod with slender outer spines, that of first segment longest; first endopodal segment with row of setules along distal anterior margin.

Leg 2 (Fig. 23B) typical for family; leg 3 (Fig. 23C) with outer spine on basis; leg 4 (Fig. 23D) with small outer seta on basis. Leg 5 (Fig. 23E) with slightly asymmetrical inner distal corner of basis, produced into point on right side, with point and rounded process on left side; slender inner seta on first exopod segment; outer corner of first segment of endopod minutely bifid.

Male. Body length of 3 males 2.82, 2.90 and 3.05 mm, with mean of 2.92 mm. Differing from female in urosome, right antennule and leg 5. Ratio of prosome to urosome length ca. 2.2:1. Urosome (Fig. 23F) 5-segmented, genital somite swollen on left side, about equal in length to second urosomite. Caudal rami and setae symmetrical.

Right antennule (Fig. 23G) 22-segmented; small portion of compound second segment not fused in middle of posterior margin, anterodistal corner of segment 21 with pointed process reaching halfway along segment 22.

Fifth legs (Fig. 23H, I) with 3-segmented rami; exopods much modified, endopods only slightly modified. Inner margin of basis evenly rounded, devoid of processes on both legs. First exopod segment of right leg with strong spine on outer distal corner. Second segment with outer spine situated distally on posterior surface in distal half, and mid inner margin bearing strong medial process. Third segment with long inward-curved, tapering process plus 3 strong spines proximally on in-

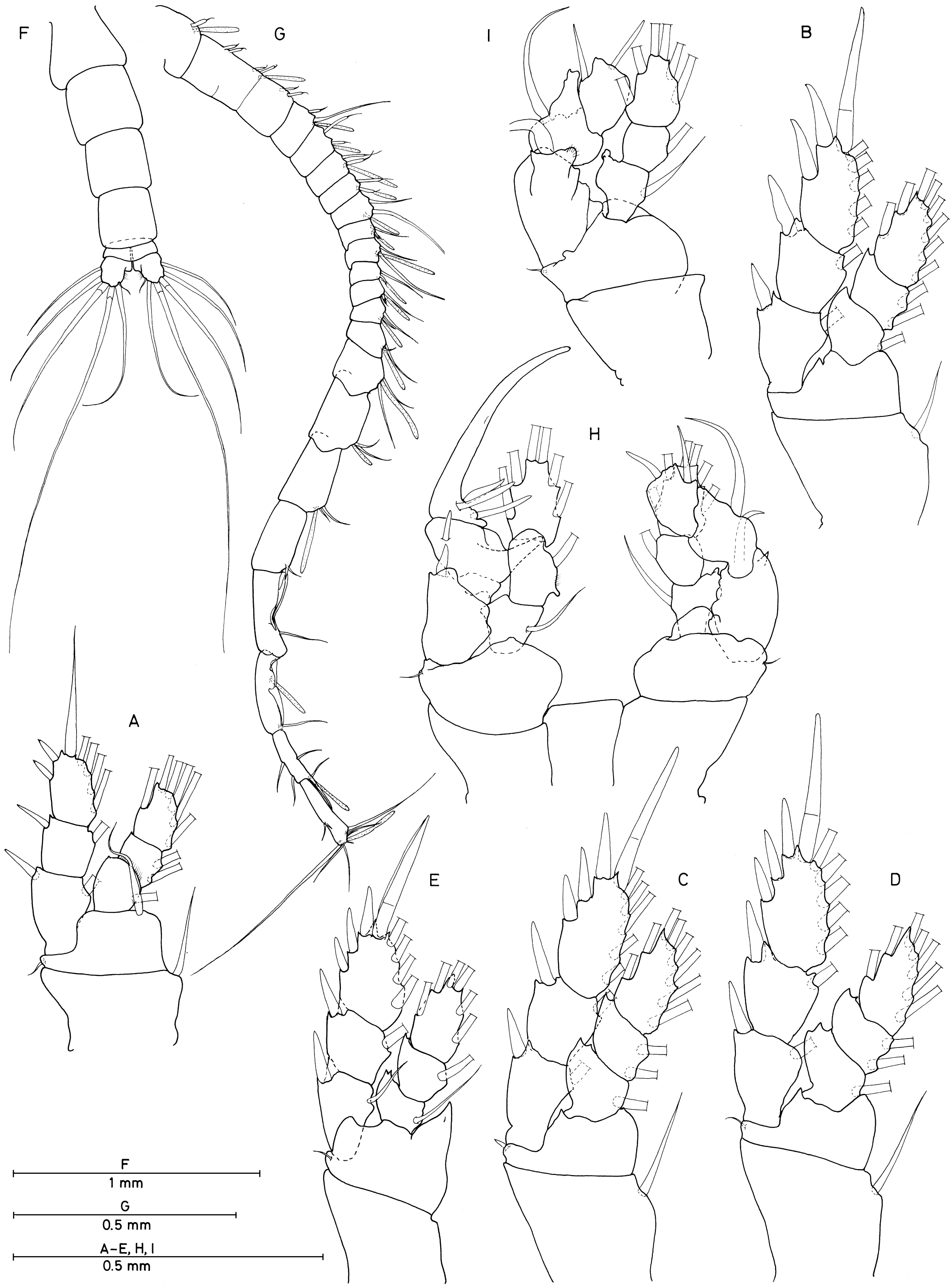

Fig. 23. *Bomburiella gigas* gen. et sp. nov., female (A-E), male (F-I). A. Leg 1. B. Leg 2. C. Leg 3. D. Leg 4. E. Right Leg 5. F. Urosome, dorsal view. G. Right antennule. H. Leg 5, posterior view. I. Left leg 5, anterior view.

ner margin. Second endopod segment of right leg with small process proximally on inner margin. First segment of left exopod with strong, curved outer spine and rounded hirsute inner process distally on anterior margin. Second segment with long curved spine in middle of outer margin and with outer distal corner extended into long blunt irregular process; third segment with terminal process, notched at tip, and 2 subequal slender spines, one either side of process. First endopod segment of left leg extended at outer distal corner into rounded process.

Ecological notes. *Bomburiella gigas* was obtained in plankton hauls and taken from the water column in vials from depths of 22 m to the surface in Oven Rock Cave, Exumas at four dates in the years 1995, 1996 and 1998. It co-occurred with *Enantronoides bahamensis* sp. nov. on 22 May 1995, and with *Bofuriella vorata* sp. nov. (see below) in August and 13 September 1996. For a description of Oven Rock Cave see *E. bahamensis* (above).

This species was collected twice from Stargate Blue Hole, Andros at depths between 30 and 36 m. This cave is located about 500 m inland from the eastern coast of South Andros Island in an extensive fracture zone running north to south. The restricted nature of the entrance limits organic input into the cave. The cave has a vertical shaft down to ca. 80 m depth and large horizontal passages around 30 m depth. Two water layers, each several metres thick, characterized by reduced clarity and by abundance of copepods, were present at 16-20 m and at 43 m depths. The salinity at 30 m was close to 37 and the temperature 26 °C. Ostracods, thermosbaenaceans, archiannelids and polychaetes were collected from the same locations within the cave.

Remarks. This is the largest species of epacteriscid known. The morphology of the urosome with asymmetrical caudal setae in female, the modifications of the labrum and paragnaths around the oral opening, the powerfully developed mandibular gnathobase, the elongate maxilliped with some very long setae, together with the characteristic leg 5 of the male, are all distinguishing characters of the species. The robust structure of the mandible and the maxilla suggest a raptorial feeding habit. Unlike most other epacteriscids, which are well equipped with spinous setae along the maxilliped, the long and flexible setae of the maxillipedal endopod of *B. gigas* suggest an unusual and specialised feeding behaviour. The other extreme of maxilliped development is exhibited in *Bofuriella vorata*, in which the endopod bears curved claw-like spines apparently well suited for catching and holding prey.

Legs 1-5 of the female are very similar to those of *Enantiosis*, although the retention of an outer seta on the basis of leg 1 and an outer spine on the basis of leg 3 are plesiomorphic characters that are shared with *Erebonectes nesioticus*, and, for the latter character only, also with *Epacteriscus rapax*, *Erebonectoides macrochaetus* and *Bofuriella vorata.*

Genus *Bofuriella* gen. nov.

Diagnosis. Female. Prosome oval in dorsal view, widest anterior to middle; separation of cephalosome and first pedigerous somite not clearly visible. Urosome 4-segmented, with third and fourth urosomites of subequal length. Caudal rami with seta II spiniform; setae V of subequal length on both rami; seta VI on left ramus ornamented with small unilateral tuft of long setules proximally. Rostral lobes weakly developed, each with 1 minute filament. Antennule 26-segmented with segment XXVI incorporated into apical double segment XXVII-XXVIII. Endopod of antenna about two thirds length of exopod, and with well-developed inner lobe. Mandibular palp with small, 2-segmented endopod carrying 2 setae; gnathobase with strong, bicuspid ventralmost tooth. Maxillule with coxal and proximal basal endites each armed with 2 unequal setae; coxal epipodite with 5 long setae. Maxilla with well-developed endites on praecoxa and coxa; endopod compressed as typical for family, armed with very strong spines distally. Maxilliped strongly developed, endopod short, carrying 5 claw-like spines, two of which coarsely serrated.

Legs 1-5 generally with same segmentation and setation as in *Bomburiella* although lacking outer seta on basis of leg 1, with reduced length of outer spines on second and third segments of exopod leg 1, and with stronger spine on outer margin of basis of leg 3.

Male. Urosome 5-segmented with anal somite slightly shorter than preceding somite. Leg 5 with transformed exopods and modifications on anterior surface of third endopod segment of left leg. Inner margin of basis extended into club-shaped processes on both legs. First exopod segment of left leg with strong curved outer spine; second segment with outer margin extended into pointed process reaching beyond third segment; third segment slender with rounded apex and distal slender inner process. Second exopod segment of right leg with long outer spine; third segment tapering into pointed tip, bearing proximal inner seta and small process on outer margin.

Type species. *Bofuriella vorata* gen. et sp. nov.

Etymology. The generic name (gender feminine) is a diminutive of Bofur, one of the dwarfs mentioned in

The Edda as often living underground. The specific name (Latin *voratus* meaning the devouring one) refers to its assumed predatory habits.

Bofuriella vorata gen. et sp. nov.
(Figs 24, 25 & 26A-C)

Material examined. Oven Rock Cave, Great Guana Cay, Exuma Cays, Bahamas. 8 May 1993: 1 female from water column in 3-15 m depth, collected with plankton net. 16 May 1994: 1 male copepodid V from water column in 0.5-6 m depth of entrance pool collected with plankton net. August 1996: 1 female from about 18 m depth collected with suction bottle. 13 September 1996: 1 male from 0-18 m collected with plankton net or vial.

Types. Holotype: Adult female, body length 1.65 mm, from Oven Rock Cave, Bahamas 8 May 1993, 3-15 m depth. Dissected and mounted on 2 slides, BM(NH) 1998.2242.

Paratypes: 1 male, body length 1.53 mm, dissected and mounted on 2 slides, and 1 female, body length 1.71 mm, in one vial from same locality as holotype, BM(NH) 1988.2243-2244.

Description. Female. Body length of 2 females 1.65 and 1.71 mm. Ratio of prosome to urosome length ca. 2.2:1. Cephalosome and first pedigerous somite mostly fused; last prosome somite with rounded posterolateral margins (Fig. 24A, B). Urosome (Fig. 24D) 4-segmented; anal somite only slightly shorter than preceding somite. Genital double-somite produced ventrally, broadest in middle and genital aperture located posteroventrally. Caudal rami slightly longer than broad; seta II spinous; seta V on each side subequal; seta VI on left side broadened at base with small unilateral tuft of setules. Rostrum (Fig. 24C) weakly defined, with two small lobes each with short filament.

Antennule (Fig. 24E) 26-segmented, reaching slightly beyond second pedigerous somite; very similar to that of *Bomburiella gigas*.

Antenna (Fig. 24F) with endopod about two thirds length of exopod; with well-developed inner lobe; basis with 2 small setae; exopod with minute seta on first and second segments and with medium-sized seta on third segment, terminal exopod segment about one third length of exopod.

Mandible (Fig. 24G) with ventralmost tooth on gnathobase strong and bicuspid; endopod small, 2-segmented and with 2 equal terminal setae; exopod well-developed.

Maxillule (Fig. 24H) with praecoxal arthrite bearing 12 long spinous or flexible setae and 1 short spine; coxal endite with 1 strong spinous seta and 1 small seta; coxal epipodite with 5 long setae. Proximal basal endite with 2 unequal setae, distal endite represented by short seta; endopod with 2 setae along inner margin and 5 terminal setae of unequal length. Exopod with 9 setae, proximal seta long and plumose.

Maxilla (Fig. 24I) with well-developed endites on praecoxa and coxa, setal formula 5 (plus minute process), 3, 3, 3. Basis with 4 setae, 3 long and 1 half length of others. Endopod compressed, armed with 11 elements, 1 weak seta, other elements long, spinous with pointed tips.

Maxilliped (Fig. 25A) with syncoxal endite formula 2, 4, 4; setae unequal, second longest element on distal endite rigid and spinous. Basis compressed and broad, armed with 3 basal setae in mid margin plus 2 distal setae derived from incorporated first endopodal segment; medial margin ornamented with spinule row proximally. Free endopod 5-segmented; first free segment with 4 setae of various lengths, distal one longest and strongest, curved and with row of fine setules. Second free segment with 2 massive, spinulate claws plus 2 small slender setae; third free segment with 1 small and 2 long slender setae with row of very fine spinules. Fourth free segment with 2 strong spinulate claws, although less strong and with finer spinules than those on second free segment; apical segment minute bearing 3 unequal slender setae.

Leg 1 (Fig. 24J): outer spine on first exopodal segment strong, outer spines on second and third segments much reduced in length; outer distal corner of first endopodal segment gradually tapering into point.

Legs 2 and 3 (Fig. 25B, C) with paired projections on intercoxal sclerite; leg 3 with outer spine and leg 4 (Fig. 25D) with small outer seta on basis.

Leg 5 (Fig. 25E) with inner distal corner of basis slightly produced, with rounded tip. First exopod segment with short, stout inner seta; outer spine on second exopodal segment strong; outer margin of third exopodal segment produced into slender processes between bases of outer spines, distalmost process reaching beyond tip of middle outer spine.

Male. Body length of damaged specimen 1.53 mm. Urosome (Fig. 26A) 5-segmented; genital somite shorter than second urosomite; anal somite about two thirds length of preceding somite.

Right antennule (Fig. 26B) 21-segmented with segments II-IV not separated; segments 18 (XIX-XX) and 19 (XXI-XXIII), either side of geniculation, bearing obvious modified, fused setal elements; segment 18 with apparently serrated anterior margin, segment 19 with serrated anterior margin and with 2 conspicuous modified fused spines. Anterodistal corner of segment 20 (XXIV-XXV) with thin pointed process.

Fig. 24. *Bofuriella vorata* gen. et sp. nov., female. A. Habitus, dorsal view. B. Habitus, lateral view. C. Rostrum. D. Urosome, dorsal view. E. Antennule. F. Antenna. G. Mandible. H. Maxillule. I. Maxilla. J. Leg 1.

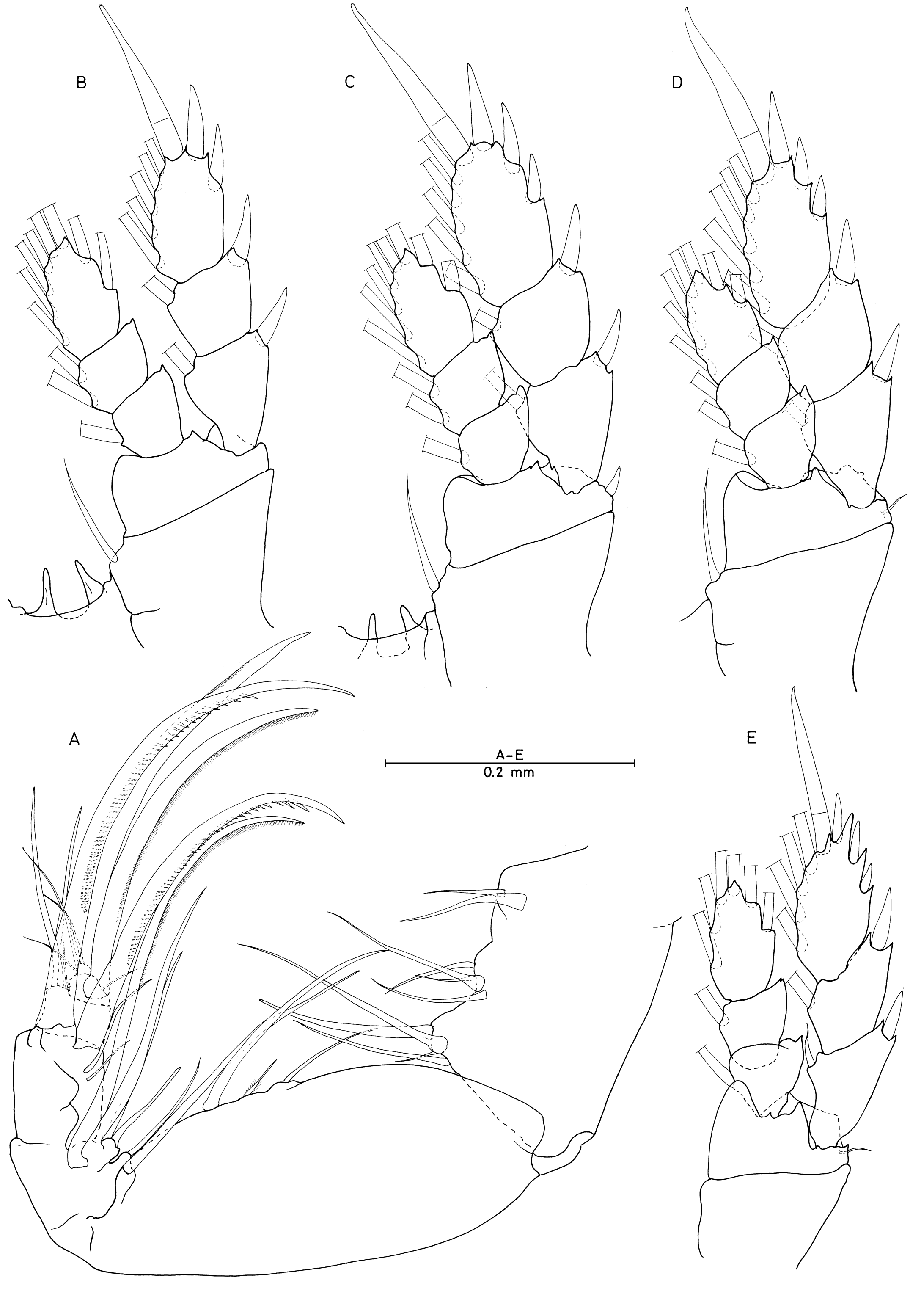

Fig. 25. *Bofuriella vorata* gen. et sp. nov., female. A. Maxilliped. B. Leg 2. C. Leg 3. D. Leg 4. E. Leg 5.

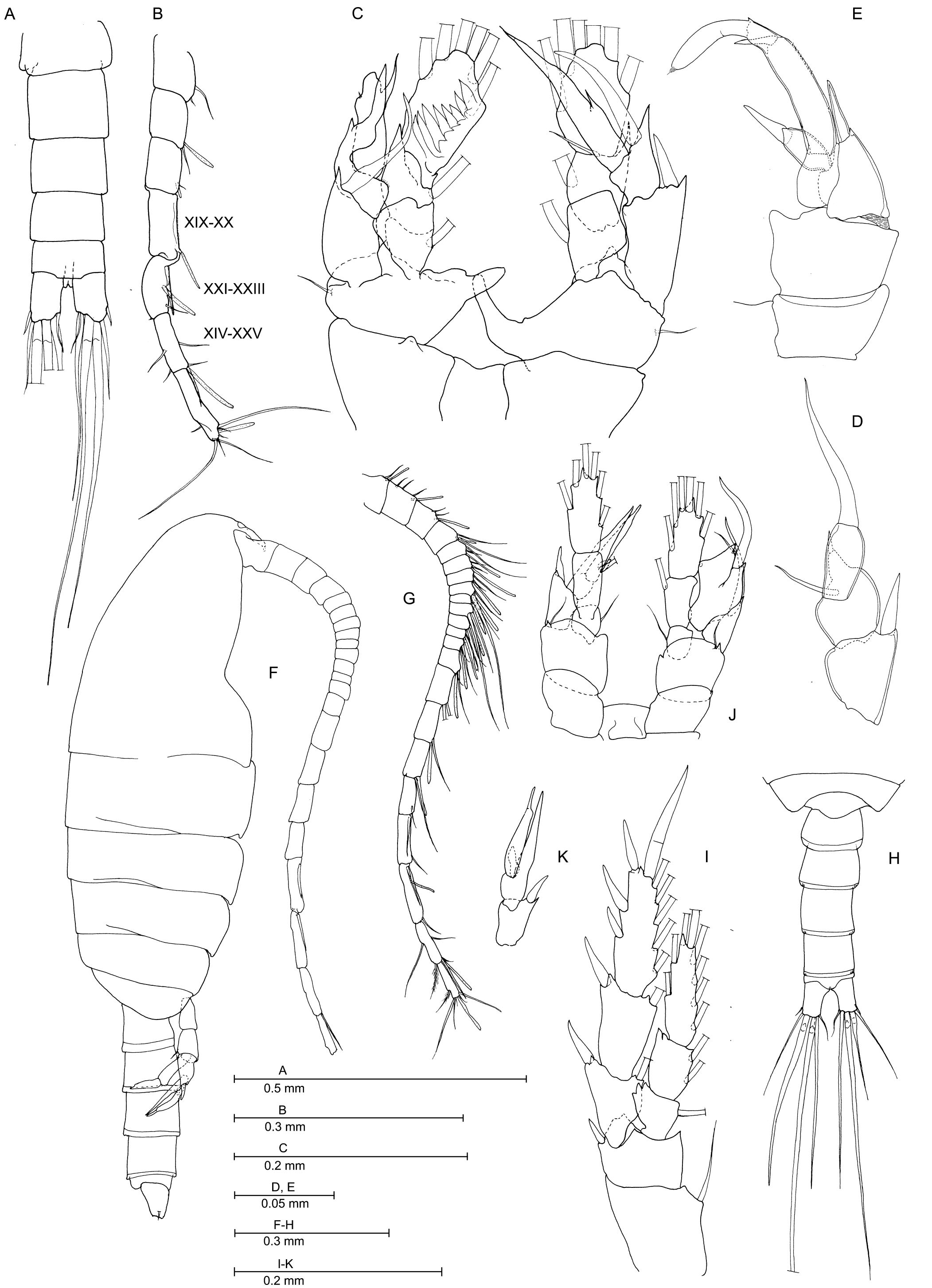

Fig. 26. *Bofuriella vorata* gen. et sp. nov., male (A-C); *Erebonectoides macrochaetus* (Fosshagen) male (D, E). *Balinella ornata* gen. et sp. nov., male paratype (F-K). A. Urosome, dorsal view. B. Right antennule, distal part. C. Fifth legs, anterior view. D. Exopod of right leg 5, anterior view. E. Exopod and protopod of left leg 5, posterior view. F. Habitus, lateral view. G. Right antennule. H. Urosome, dorsal view. I. Leg 3. J. Legs 5, posterior view. K. Leg 5, right exopod anterior view.

Fifth legs (Fig. 26C) with left basis produced into process at inner distal corner, right basis produced proximally into long, club-shaped structure; exopod of both legs and left endopod third segment strongly modified, right endopod only slightly modified. First segment of right exopod with strong regular spine at outer distal corner; second segment with outer distal corner forming acute extension; outer spine long, inwardly-curved; third segment gradually tapering into pointed tip, bearing inner seta proximally and, near middle on outer margin, small pointed process. First exopod segment of left leg with long outwardly-curved outer spine reaching nearly to end of third segment; outer margin of second segment greatly elongate, bulbous initially, with outer notch in mid section, tapering into pointed tip; third segment slender, with small outer process distally, rounded apex and long slender inner process. Third endopod segment of left leg with row of 8 unequal flattened spinous processes on anterior surface; outer distal corner of second endopodal segment on both sides extended into point.

Ecological notes. Four specimens only were obtained from the four different samples taken in Oven Rock Cave, Exumas at depths of 0-18 m. On 16 May 1994 it cooccurred with *Oinella longiseta* sp. nov. and in August and on 13 September 1996 with *Bomburiella gigas.* The cave is described above (see *Enantronoides bahamensis*).

Remarks. The structure of the urosome, the arrangement of the caudal setae, the powerfully developed maxilliped with its massive claw-like spines, together with the male leg 5, are the best distinguishing characters of this species. Among epacteriscids this species has the most powerfully developed maxilliped. The form of the maxilliped, together with the long spinous setae on the maxilla and the powerful mandibular gnathobase, suggests that this species is a raptorial feeder.

Characters of the antennule, such as the complete separation of segments X and XI and the incorporation of segment XXVI into the apical XXVII-XXVIII, are shared with *Bomburiella gigas*, and are not found among other epacteriscids. Legs 1-5 of the female agree closely with the family diagnosis in basic structure and resemble those of *Enantiosis* except for the relatively shorter outer spines on exopod leg 1 and the retention of an outer spine on basis of leg 3. The latter, plesiomorphic, character is shared with all *Epacteriscus* species, *Erebonectes nesioticus, Erebonectoides macrochaetus* and *Bomburiella gigas.*

Genus *Erebonectes* Fosshagen, 1985

Diagnosis (emend.). Female. Prosome oval, broadest in middle; last prosome somite short and with evenly rounded posterolateral margins. Caudal rami symmetrical and with 6 plumose terminal setae. Rostrum with two closely set points, with filaments. Antenna with endopod about twice length of exopod. Mandibular palp with 2-segmented endopod carrying 10 setae. Maxillule with 7 setae on coxal epipodite and outer seta representing basal exite. Endopod of maxilliped about two thirds length of basis and with relatively short spinous setae. All legs with 2 outer spines on third exopodal segment. Leg 1 with outer seta on basis; legs 2 and 3 each with strong outer spine on basis.

Male. Caudal setae symmetrical. Leg 5 with highly transformed exopods and unmodified endopods. Left leg first exopod segment with large and irregular outer spine; second segment small, with short outer spine; third segment fused to distal process, bearing small inner and outer spines proximally. Right leg with outer spines on first and second segments, third segment forming long curved claw-like process bearing outer spine proximally and tiny inner seta carried on proximal tubercle.

Type species. *Erebonectes nesioticus* Fosshagen, 1985.

Erebonectes nesioticus Fosshagen, 1985

This species has been collected from 5 caves in Bermuda (Fig. 37). Since its initial discovery from Christie's and Devonshire Caves (Fosshagen & Iliffe 1985), it has been collected from Jane's Cave on 28 July 1986 (1 copepodid stage I) in 3-12 m from the water column and peaty bottom sediments of west pool; from Church Cave on 15 December 1995 in 1-20 m from the water column (1 female, 1 copepodid stage V); and from Bitumen Cave on 16 December 1995 in 1-25 m from the water column (1 damaged female).

Christie's Cave is located about 130 m northeast of Bitumen Cave and these two caves together with Church Cave may all be interconnected hydrologically. All caves inhabited by *E. nesioticus* are quite isolated from the sea. The water is still and clear, with no perceptible currents.

The female, total length 1.99 mm, from Church Cave had complete caudal setae. These were symmetrical, all plumose and lacking the characteristic tuft commonly found on left seta VI among many other epacteriscids. It has a prominent labrum furnished with a patch of long, stiff spinules distally.

Genus *Erebonectoides* gen. nov.

Diagnosis. Female. Prosome slender, posterolateral margins of last somite tapering to rounded point extending to middle of genital double-somite. Only five caudal setae present, all distal; seta V on left side extremely elongate, outermost element modified as flattened scale-like spine. Rostrum comprising two closely set lobes, with filaments. Antenna with endopod slightly longer than exopod. Mandibular palp with 2-segmented endopod carrying 5 setae. Maxillule with 9 setae on coxal epipodite; outer basal seta absent. Endopod of maxilliped compressed and less than half length of basis; setae of endopod weaker than those of *Erebonectes* and each with flexible tip. All legs with 2 outer spines on third segment of exopod; leg 3 with strong outer spine on basis.

Male. Caudal seta V on left side elongate. Leg 5 with highly transformed exopods; first segment of left leg with regular outer spine, terminal part of left exopod curved inward.

Type species. *Erebonectes macrochaetus* Fosshagen, 1994.

Etymology. The generic name (gender masculine) alludes to the close similarity of the new genus to *Erebonectes* Fosshagen, 1985.

Erebonectoides macrochaetus (Fosshagen, 1994) comb. nov.
(Fig. 26D, E)

This species has been recorded from only two caves on the Caicos Islands, West Indies (Fosshagen & Iliffe 1994). It was originally included in the genus *Erebonectes*, which had only been found in Bermuda. Both species had similar rostrum, an antenna with the endopod longer than the exopod, raptorial mouthparts, and all legs in the female had 2 outer spines on the third exopodal segment. During the course of this revision of the family it became apparent that this species from the Caicos Islands should be placed in a separate genus. It shows a different arrangement of caudal rami with fewer setae and with one seta transformed into a scale-like spine. Setae I and, possibly, II appear to be lacking. The mandible has a reduced number of setae on the endopod and the maxilliped has a more compressed endopod and weaker setae than in *Erebonectes*. In addition, leg 1 has a projection on outer distal corner of the first endopodal segment and leg 2 has no outer element on the basis.

The male leg 5 has been reexamined and left exopod (Fig. 26E) is reinterpreted as 3-segmented, with the small second segment articulating with the elongate third segment at an oblique joint located proximally on its posterior surface. The first exopod segment bears an unmodified outer spine, the small second segment bears a similar spine, and the elongate third segment bears an outer spine and a modified apical element. The right exopod (Fig. 26D) bears an outer spine on the first and second segments; the third segment bears a long distal spine and an inner seta, as found in other genera such as *Edaxiella* and *Enantronoides*. The inner spine is not on the second segment as stated in the original description.

Genus *Balinella* gen. nov.

Diagnosis. Female. Prosome oval, with short last pedigerous somite with rounded posterolateral margins. Caudal rami shorter than third and fourth urosomites combined, slightly asymmetrical, with seta V on right ramus elongate. Rostrum with two closely-set lobes and pair of short stout filaments. Antennule 26-segmented, with segments XXVI and XXVII-XXVIII incompletely separated. Antenna with endopod slightly longer than exopod; exopod 9-segmented with 7 long setae on inner margin: compound distal endopodal segment with 8 setae on inner lobe. Mandibular palp with 2-segmented endopod bearing 5 setae; basis with 2 unequal setae. Maxillule well developed; coxal and basal endites with setal formula 3, 4, 4; exopod with 9 setae. Maxilla and maxilliped generally of same structure as those of *Erebonectes*, with strong spinous setae distally, but with rows of spinules on distal praecoxal endite and on coxal endites of maxilla. Legs 1 and 2 very similar to those of *Erebonectoides*. Legs 4 and 5 and (probably) leg 3 with 3 outer spines on distal exopodal segment; basis of leg 3 with strong outer spine.

Male. Urosome 5-segmented. Seta V on left caudal ramus elongate. Right antennule geniculate, 22-segmented with segments II and III fused, segment 21 (XXIV-XXV) with long pointed process distally, reaching beyond distal segment of antennule. Legs 5 with modified exopods and unmodified endopods; distal part of right exopod slender, ending in 2 points; distal part of left exopod irregular, broad and flattened, bearing outer strong curved spine.

Type species. *Balinella ornata* gen. et sp. nov.

Etymology. The generic name (gender feminine) is a diminutive of Balin, one of the dwarfs mentioned in The Edda as often living underground. The specific name refers to the ornamentation of the praecoxal arthrite of the maxillule.

Balinella ornata gen. et sp. nov.
(Figs 26F-K, 27-29)

Material examined. Norman's Pond Cave, Norman's Pond Cay, Exuma Cays, Bahamas, 18 May 1994: 1 fe-

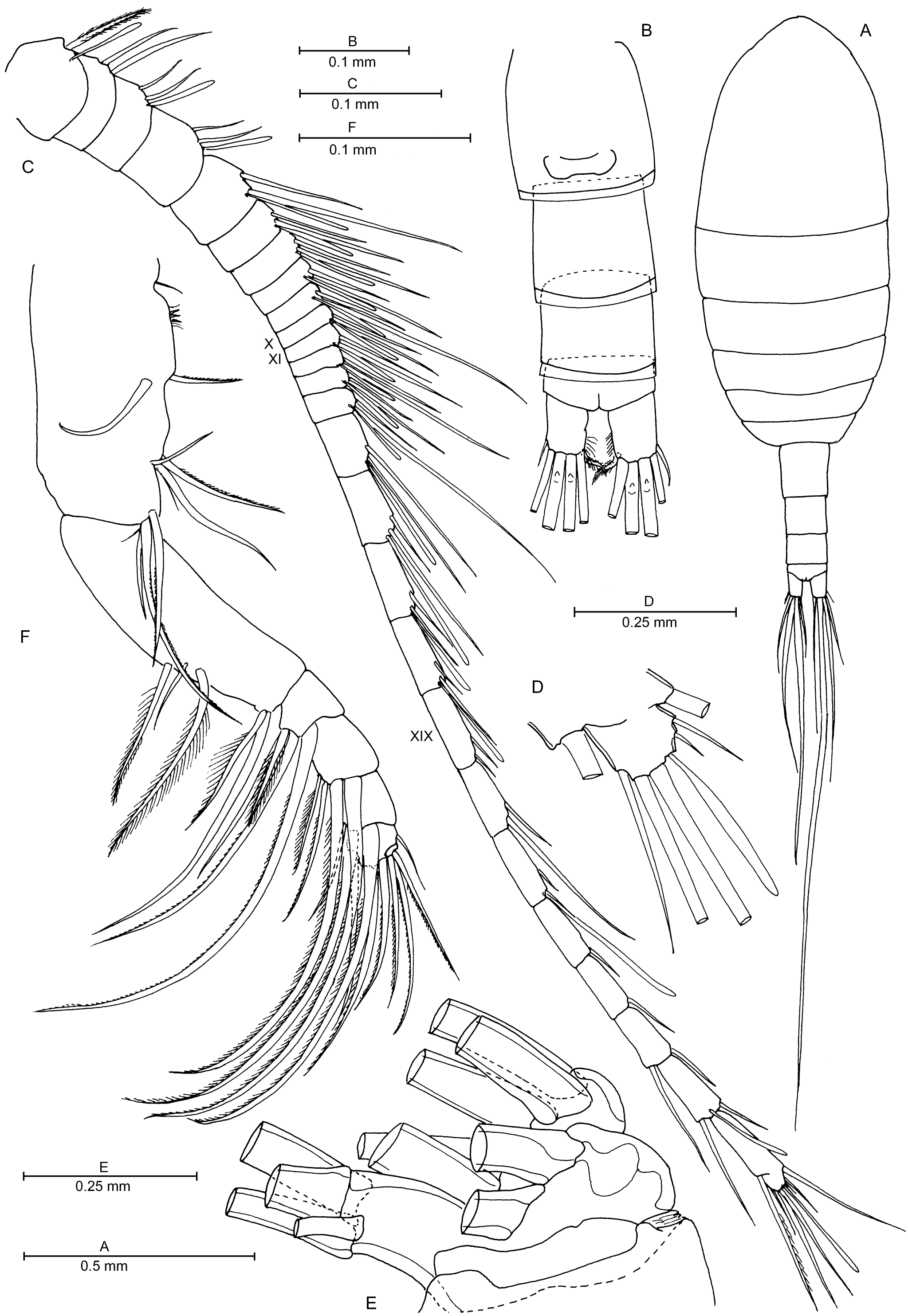

Fig. 27. *Balinella ornata* gen. et sp. nov., female. A. Habitus, dorsal view. B. Urosome, ventral view. C. Antennule. D. Apex of antennule. E. Endopod of maxilla. F. Maxilliped.

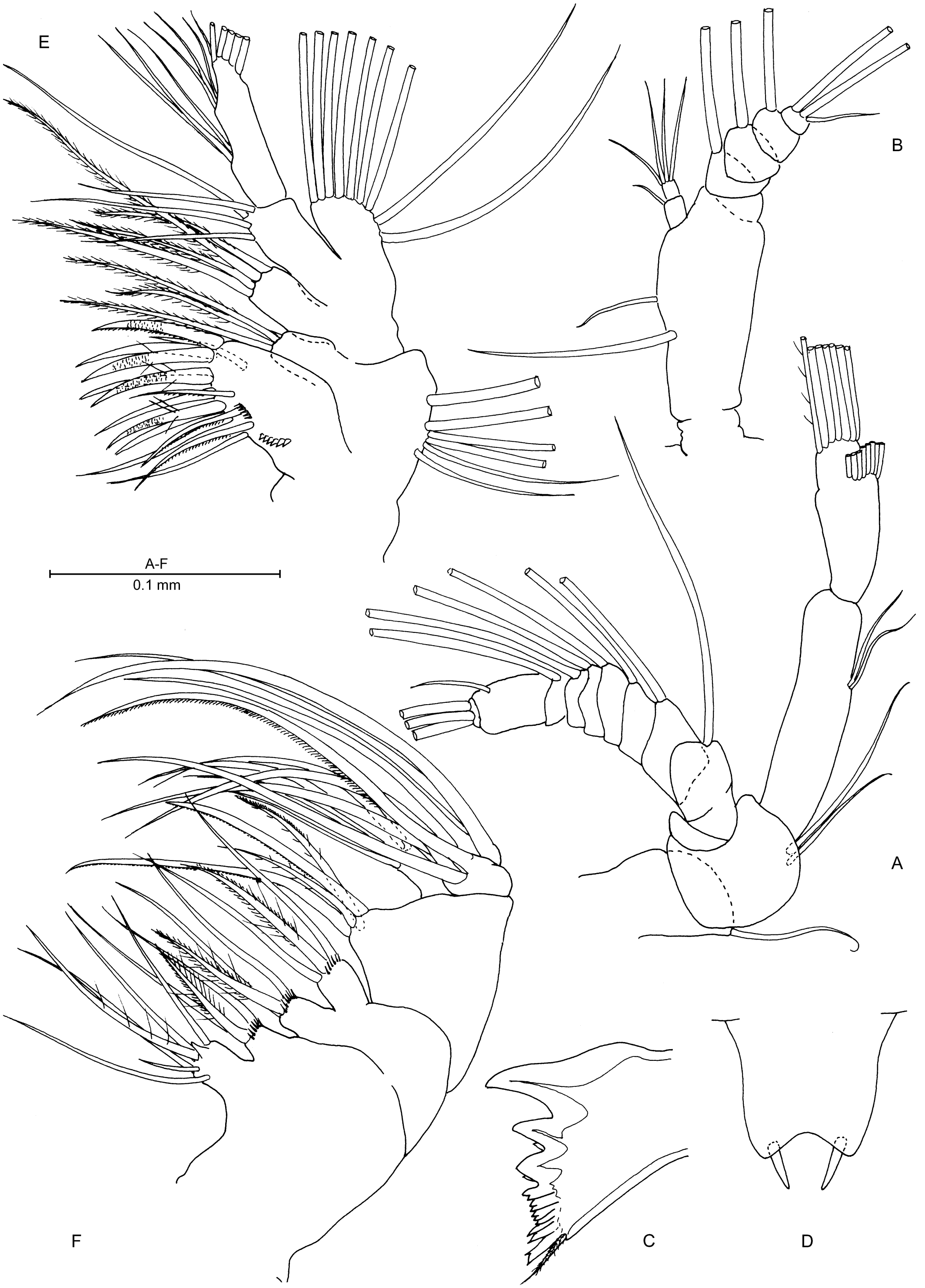

Fig. 28. *Balinella ornata* gen. et sp. nov., female. A. Antenna. B. Mandibular palp. C. Mandibular gnathobase. D. Rostrum, frontal view. E. Maxillule. F. Maxilla.

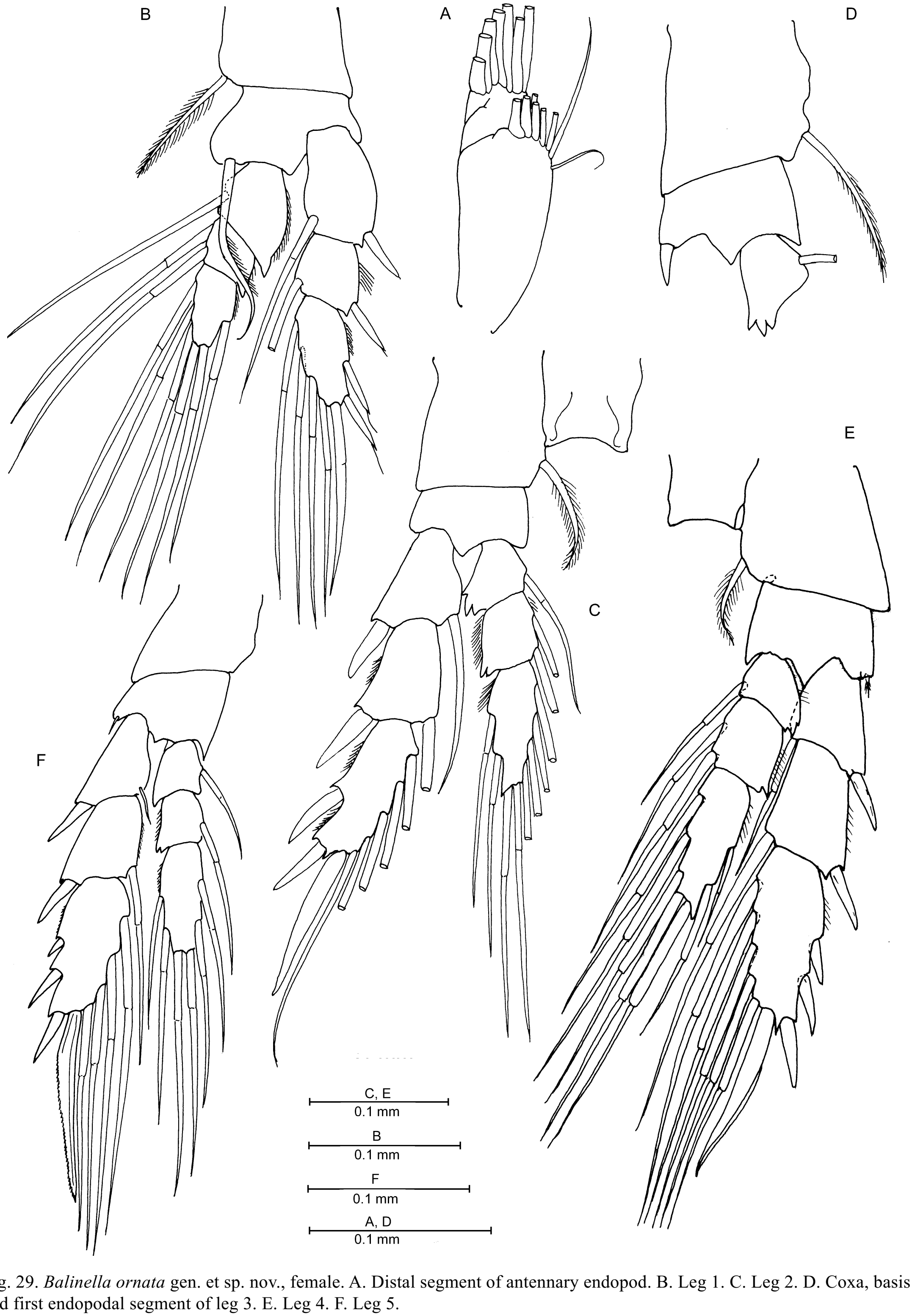

Fig. 29. *Balinella ornata* gen. et sp. nov., female. A. Distal segment of antennary endopod. B. Leg 1. C. Leg 2. D. Coxa, basis and first endopodal segment of leg 3. E. Leg 4. F. Leg 5.

male in 10-18 m depth, collected with 93 µm mesh plankton net from water column and from silt on ledges of first room. 6 May 1993: 1 male in 15-35 m depth, collected with plankton net from the water column.

Types. Holotype: Adult female body length 1.20 mm from Norman's Pond Cave, Bahamas, 18 May 1994, in 10-18 m depth. Dissected and mounted on 11 slides. BM(NH) 1998.2773.

Paratype: Adult male, body length 1.33 mm from the same cave, 6 May 1993 in 15-35 m depth. Dissected and mounted on 4 slides. BM(NH) 2001.392.

Description. Female. Ratio of prosome to urosome length ca. 2.8:1. Fifth pedigerous somite (Fig. 27A) short, with rounded posterolateral margins extending to anterior part of genital double-somite. Urosome (Fig. 27B) 4-segmented; genital double-somite shorter than following two somites combined; anal somite very short. Caudal rami longer than wide; slightly asymmetrical, with seta V on right ramus about twice length of corresponding seta on left. Rostrum (Fig. 28D) with two closely-set, rounded lobes bearing pair of stout filaments.

Antennule (Fig. 27C) 26-segmented; segments I-IV clearly expressed; segment XIX with 2 small setae; segment XX with 1 small and 1 medium length seta. Segment XXVI incompletely separated from apical double segment XXVII-XXVIII (Fig. 27D).

Antenna (Fig. 28A) with endopod just longer than exopod; proximal endopodal segment elongate with 2 setae on inner margin about at two thirds of length of segment; compound distal segment (Fig. 29A) with inner lobe bearing 8 setae and distal lobe, 7 setae; exopod with 7 long setae on inner margin.

Mandibular palp (Fig. 28B) with small, 2-segmented endopod; armature comprising 1 seta on first segment, 4 setae on second segment; basis with 2 unequal setae. Gnathobase (Fig. 28C) with simple ventralmost tooth.

Maxillule (Fig. 28E) with coxal and basal endites bearing 3, 4, 4 setae; endopod with 3 setae in two groups along inner margin, and 1 short and 5 long setae distally; exopod compressed, with 9 long setae.

Maxilla (Fig. 28F) with proximal praecoxal endite bearing 1 short and 5 long setae, second praecoxal endite and coxal endites each with 3 setae and row of spinules distally; endopod (Fig. 27E) much compressed with long and strong spinous setae; setal formula originally corresponding to 4, 3, 2, 2 pattern.

Maxilliped (Fig. 27F) well developed; basis with 3 basal setae and 2 distal setae from incorporated first endopodal segment; free endopod 5-segmented bearing relatively stout and spinous setae; formula 4, 4, 3, 3 + 1; 3.

Leg 1 (Fig. 29B) with outer spines on exopodal segments long, flagellate, and of equal length. Leg 2 (Fig. 29C) without outer setal element on basis. Leg 3 incomplete in holotype (Fig. 29D), with strong outer spine on basis. Leg 4 (Fig. 29E) and leg 5 (Fig. 29F) each with 3 outer spines on third exopodal segment, first outer spine of leg 5 about half length of following 2 spines.

Male. Urosome (Fig. 26H) 5-segmented. Caudal rami asymmetrical with seta V on left ramus elongate.

Antennule extending back to middle of urosome (Fig. 26F); geniculate right antennule (Fig. 26G) 22-segmented with segments II and III fused and segment 21 (XXIV-XXV) with distal process extending beyond apex of limb.

Maxillule (partly damaged along basal margin in female) with 9 setae on coxal epipodite.

Leg 3 (Fig. 26I) (damaged in female) with 3 outer spines on third exopodal segment.

Legs 5 (Fig. 26J, K) with moderately modified exopods and unmodified 3-segmented endopods. First segment of right exopod (Fig. 26K) with strong short outer spine; distal part of exopod with outer long regularly tapering process bearing small lappet proximally on inner margin, and in same site irregularly tapering element reaching end of process. First segment of left exopod with long outer curved spine reaching beyond distal segment; distal segment partly divided in middle of outer margin, bearing outer strong spine in middle; flattened distal part with rounded inner corner, and pointed outer corner with adjacent small seta.

Ecological notes. The 2 specimens were collected in the upper levels of Norman's Pond Cave, one of the more notable blue holes in the Exumas. The cave is close to the coast and the water is fully marine (for further description of the cave see Fosshagen & Iliffe (1998)). The locality is also the type locality of the ridgewayiid calanoid *Exumellina bucculenta* Fosshagen, which was abundant together with a stephid calanoid belonging to the genus *Miostephos*. In addition to copepods, thermosbaenaceans, cumaceans, tanaidaceans, amphipods, halocyprid ostracods and remipedes have been reported from this cave.

Remarks. In common with both *Erebonectes* and *Erebonectoides*, this species retains numerous plesiomorphic characters, combined with relatively few reductions and modifications of mouthparts. The rostrum also resembles that of *Erebonectes*. The antenna has elongate endopod like that of *Erebonectes* and *Erebonectoides*, and the mandible is very similar to that of *Erebonectoides*. The maxillule of *Balinella* shows some reductions in numbers of setae along its outer margin, but the maxilla and maxilliped are both very similar and only slightly modified in all three genera. The possession of three outer spines on the third exopodal segment of legs 3 to 5, is a character shared with most genera of the family, except for *Erebonectes* and *Erebonectoides.* The presence of a strong outer spine on the basis of leg 3 is shared with *Bofuriella, Bomburiella, Epacteriscus, Erebonectes* and *Erebonectoides.*

An autapomorphic character of *Balinella* is the elongate caudal seta V on the right ramus of the female and left ramus of the male; usually seta V in females is elongate on left side, as in *Bomburiella, Edaxiella, Enantiosis, Enantronia, Epacteriscus* and *Erebonectoides.* Another unique character is the presence of rows of spinules on the praecoxal and coxal endites of the maxilla.

Genus *Oinella* gen. nov.

Diagnosis. Female. Urosome 4-segmented,with anal somite minute. Antennule with digitiform process on segment IX; segments XXVI and XXVII-XXVIII fully separate. Antenna lacking setae on protopodal segments and on proximal segments of both rami; endopod about half length of exopod; exopod with 3 long setae on inner distal margin and 3 setae distally. Mandibular palp lacking any vestige of endopod; basis unarmed; exopod with 6 setae, seta on penultimate segment extremely long. Maxillule with reduced number of elements; coxal and basal endites with 2, 2, 0 setae; exopod with 6 setae. Maxilla and maxilliped well-developed, with long, strong spinous setae distally; praecoxa and coxa of maxilla with fewer and weaker setae than in *Balinella.* Leg 1 with outer spines on exopod minutely flagellate and of unequal length. Leg 5 with 3 outer spines on third exopodal segment.

Male. One copepodid stage V known. Urosome 4-segmented. Caudal rami symmetrical. Rostrum broad with small filaments set far apart.

Type species. *Oinella longiseta* gen. et sp. nov.

Etymology. The generic name (gender feminine) is a diminutive of Oin, one of the dwarfs mentioned in The Edda as often living underground. The specific name refers to the elongate seta on the exopod of the mandibular palp.

Oinella longiseta gen. et sp. nov.
(Figs 30-32)

Material examined. Oven Rock Cave, Great Guana Cay, Exuma Cays, Bahamas, 16 May 1994: 1 adult female and 1 male copepodid stage V in 0.5-6 m depth, in entrance pool, collected with plankton net from water column.

Types. Holotype: Adult female body length 1.05 mm from Oven Rock Cave, Bahamas, 16 May 1994 in 0.5-6 m depth. Dissected and mounted on 11 slides. BM(NH) 1998.2771.

Paratype: 1 male copepodid stage V from same locality as holotype. BM(NH) 1998.2772.

Description. Female. Only 1 incomplete adult female known. Urosome (Fig. 30A) 4-segmented with genital double-somite about equal to length of following two somites combined; anal somite telescoped within preceding somite. Caudal rami missing in damaged specimen.

Antennule (Fig. 31A, B) 25-segmented; segments II-IV incompletely separated; segment IX (Fig. 31B) with rounded process in middle of anterior margin and extra long anterior seta; segment XIV also bearing extra long seta; segment XIX possessing trithek; segment XX with only 1 long seta; segments XXVI and XXVII-XXVIII separate.

Antenna (Fig. 32A) with endopod about half length of exopod; first endopodal segment very short, devoid of elements; second segment with 4 setae on inner lobe and 6 setae distally; exopod with 3 setae along inner margin and 3 distally.

Mandible with ventralmost tooth of gnathobase (Fig. 32B) offset as strong simple blade; basis unarmed. Mandibular palp (Fig. 32C) with 6 setae on exopod, seta on penultimate segment extremely long; lacking any trace of endopod.

Maxillule (Fig. 31C) with reduced setation; coxal and basal endites bearing 2, 2, 0 setae; endopod without setae along inner margin and with only 4 setae distally; exopod slender, with 6 relatively short setae.

Maxilla (Fig. 32D) with reduced enditic setation: formula 3, 1, 2, 3; basis elongate, with 4 inner setae; endopod compressed, with 3 strong spinulate setae, plus other finer setae.

Maxilliped (Fig. 31D) very similar to that of *Balinella ornata*, but endopod with relatively longer, spinous setae.

Leg 1 (Fig. 30E) with outer spines on exopodal segments of unequal length, spine on first segment longest; all outer spines minutely flagellate at tip. Leg 5 (Fig. 30F) very similar to that of *Balinella ornata,* with somewhat longer inner seta on first exopodal segment and lacking outer seta on basis.

Male. Only 1 copepodid stage V known. Prosome (Fig. 30B) with 5 pedigerous somites, last prosomite extend-

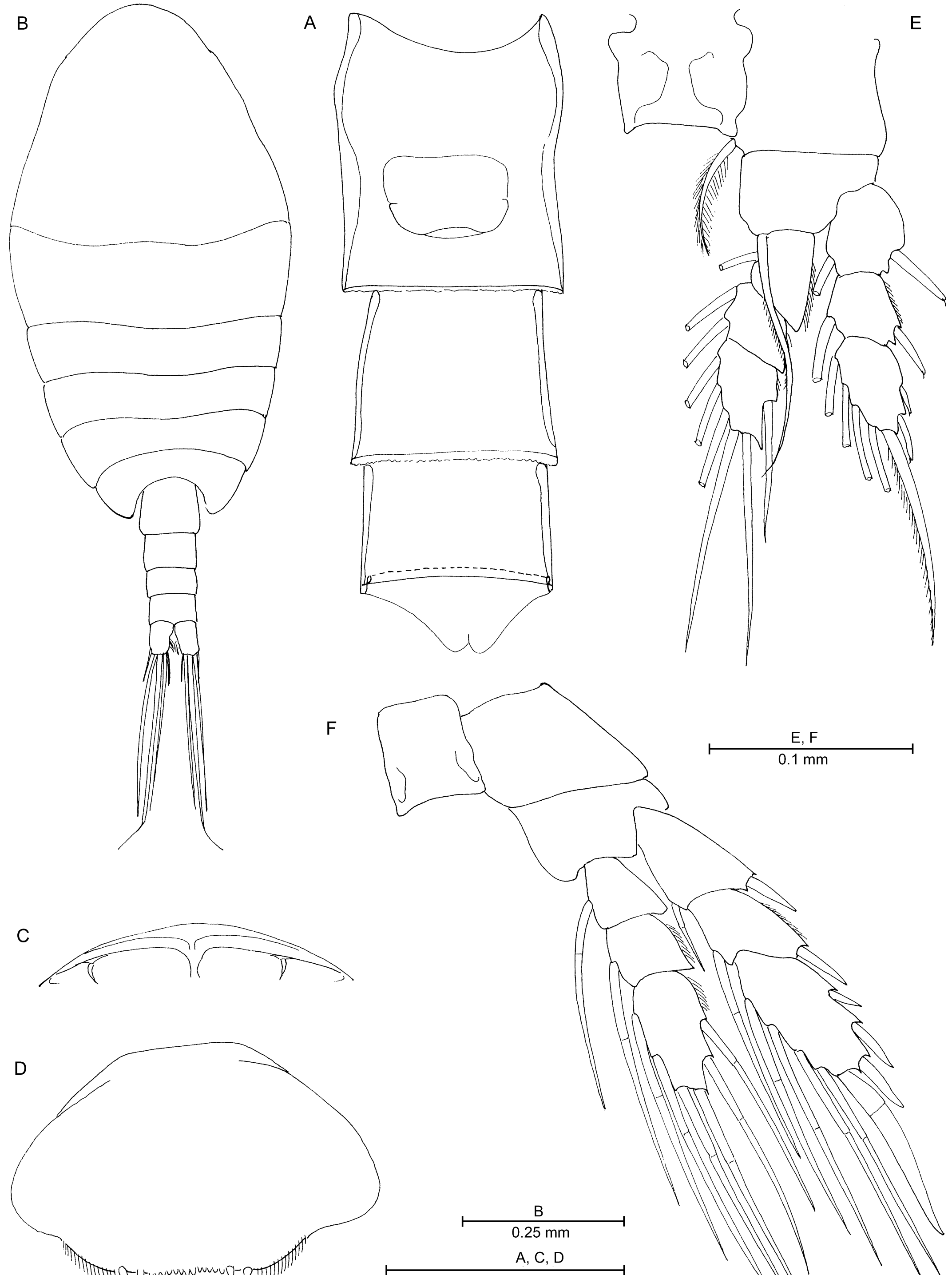

Fig. 30. *Oinella longiseta* gen. et sp. nov. A. Female holotype urosome, ventral view (lacking caudal rami). B. Male copepodid V paratype, dorsal view. C. Male copepodid V, rostrum. D. Male copepodid V, labrum. E. Female holotype, leg 1. F. Female leg 5.

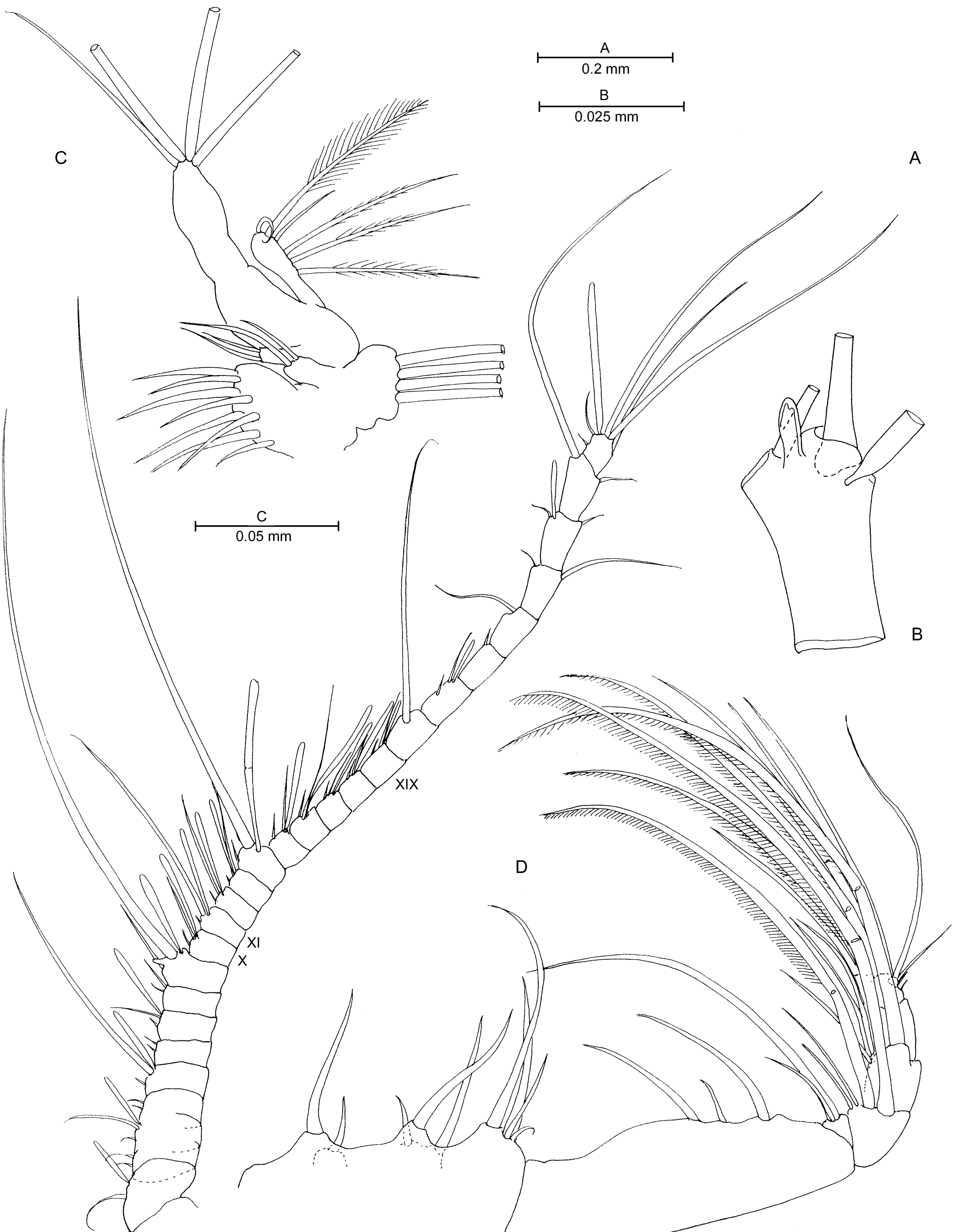

Fig. 31. *Oinella longiseta* gen. et sp. nov., female holotype. A. Antennule. B. Detail of antennulary segment IX showing digitiform process. C. Maxillule. D. Maxilliped.

Fig. 32. *Oinella longiseta* gen. et sp. nov., female holotype. A. Antenna. B. Mandibular gnathobase. C. Mandibular palp. D. Maxilla.

ing to middle of first urosomite. Urosome 4-segmented, with symmetrical caudal rami. Rostrum (Fig. 30C) broad, with pair of small filaments set far apart. Labrum (Fig. 30D) with free distomedial margin bearing row of teeth; on each side with pair of 2 strong teeth and row of fine marginal setules.

Ecological notes. *Oinella longiseta* was obtained only once, on 16 May 1994, from Oven Rock Cave, Bahamas, from the water column in 0.5-6 m depth in the entrance pool. In the same sample there was a single specimen of *Bofuriella vorata* sp. nov. plus large numbers of a small stephid. For the cave description and details of other species from the same locality see notes on *Enantronoides bahamensis* (above).

Remarks. Although known only as one incomplete female and one male copepodid V, this new species shows sufficient specific characters to justify the erection of a new genus. Most conspicuous are the reductions of the mouthparts, through loss of setae, and the peculiar condition of having a very long seta on the mandibular exopod. Although parts are missing, the swimming legs seem to be essentially similar to those of other epacteriscid genera bearing 3 outer spines on the third exopodal segments of legs 3-5, except for *Epacteriscus.*

The reduced setation of the antenna, the complete lack of an endopod on the mandibular palp, the presence of one extremely long seta on the exopod of mandible, the loss of setal elements from the maxillule, and the long spinous setae on endopod of the maxilla and of the maxilliped, distinguish this species from others in the family. It seems likely that this animal is a specialised predator.

Genus *Gloinella* gen. nov.

Diagnosis. Female. Prosome oval, with last prosomite extending laterally to middle of genital double-somite. Urosome 4-segmented; anal somite concealed. Caudal rami asymmetrical; right ramus elongate, with seta V longer than corresponding seta on left; seta VI on left ramus with unilateral tuft of setules near base. Rostrum elongate, with two closely-set lobes bearing pair of short, thick filaments. Antennule 25-segmented with segments I-III fused. Antenna with exopod longer than endopod; exopod bearing 7 setae on inner margin. Mandibular palp with 1-segmented endopod, basis with 1 small seta. Maxillule with reduced setation; coxal and basal endites with 3, 3, 1 setae; exopod with 7 setae. Maxilla with unusually elongate basis, longer than praecoxa and coxa combined; setae on endopod not as strong and spinous as commonly found within family. Leg 1 with outer spines of exopod flagellate, subequal in length. Legs 3-5 each with 3 outer spines on last exopodal segment.

Male. Urosome 5-segmented; anal somite concealed. Caudal rami asymmetrical with left ramus elongate. Right antennule geniculate, 22-segmented, with segments II-IV only partially separated; segment 20 (XXIV-XXV) with long pointed process distally. Legs 5 with both rami 3-segmented, only slightly asymmetrical, with small differences in endopods and last segments of exopods.

Type species. *Gloinella yagerae* gen. et sp. nov.

Etymology. The generic name (gender feminine) is a diminutive of Gloin, one of the dwarfs mentioned in The Edda as often living underground. The specific name is in honour of Jill Yager and her many contributions to the study of anchialine crustaceans.

Gloinella yagerae gen. et sp. nov.
(Figs 33-36)

Material examined. Cueva de los Carboneros, Playa Girón, Matanzas, Cuba, collected 14 September 1992: 3 adult females, 1 adult male, and 1 male copepodid stage V.

Types. Holotype: Adult female body length 1.24 mm, from Cueva de los Carboneros, Cuba, 14 September 1992. BM(NH) 1998.2765.

Paratypes: 1 adult male length 1.12 mm. BM(NH) 1998.2766. 2 adult females, both with body lengths of 1.14 mm, BM(NH) 1998.2767-2768. 1 male copepodid stage V, body length 1.08 mm, BM(NH) 1998.2769. All paratypes from same locality as holotype.

Description. Female. Ratio of prosome to urosome length ca. 2.0:1. Fifth pedigerous somite (Fig. 33A) with rounded posterolateral margins, extending to middle of genital double-somite. Urosome (Fig. 33B) 4-segmented; genital double-somite slightly longer than following two somites combined; anal somite telescoped within preceding somite. Caudal rami asymmetrical; right ramus longer, with seta V greatly elongate; left side with seta VI bearing unilateral tuft of setules proximally. Rostrum (Fig. 33C, D) elongate, with two closely-set rounded lobes, each with short, thick filament, rounded at tip.

Antennule (Fig. 33E) 25-segmented; segments I-III fused; segment XIX with 2 small setae; segment XX with trithek; articulation separating segments XXVI and XXVII-XXVIII clearly expressed.

Antenna (Fig. 33F) with endopod distinctly shorter

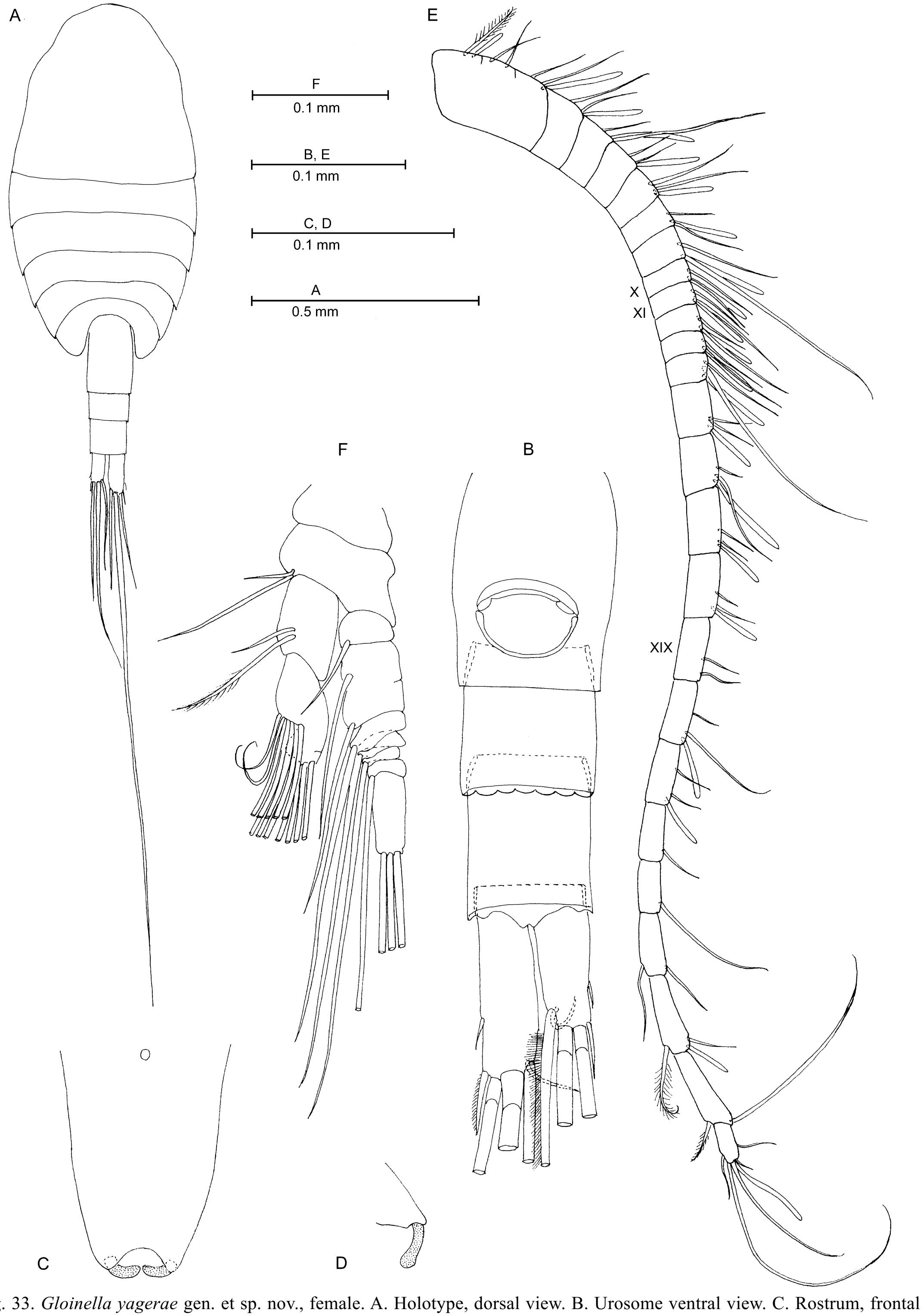

Fig. 33. *Gloinella yagerae* gen. et sp. nov., female. A. Holotype, dorsal view. B. Urosome ventral view. C. Rostrum, frontal view. D. Tip of rostrum, lateral view. E. Antennule. F. Antenna.

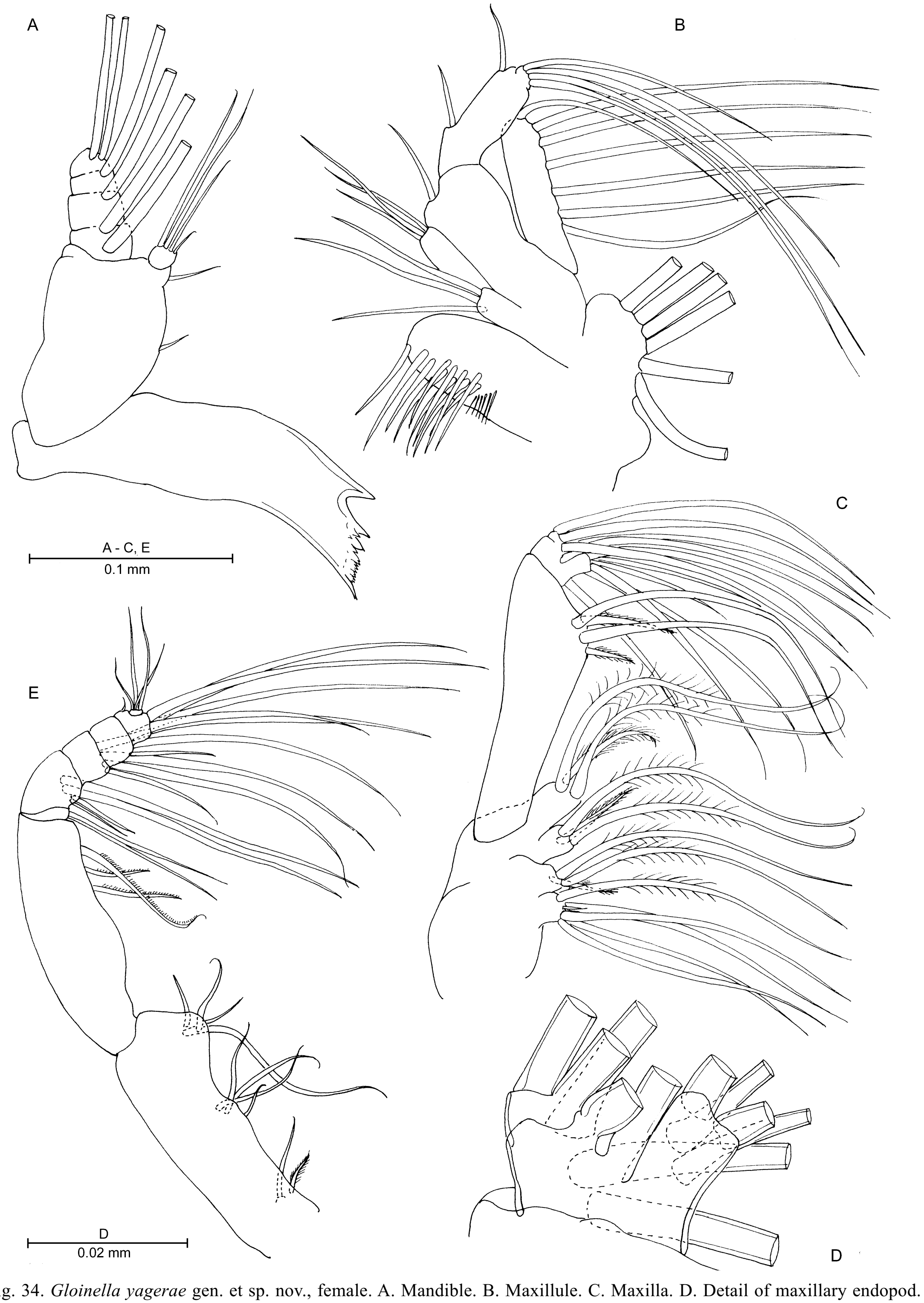

Fig. 34. *Gloinella yagerae* gen. et sp. nov., female. A. Mandible. B. Maxillule. C. Maxilla. D. Detail of maxillary endopod. E. Maxilliped.

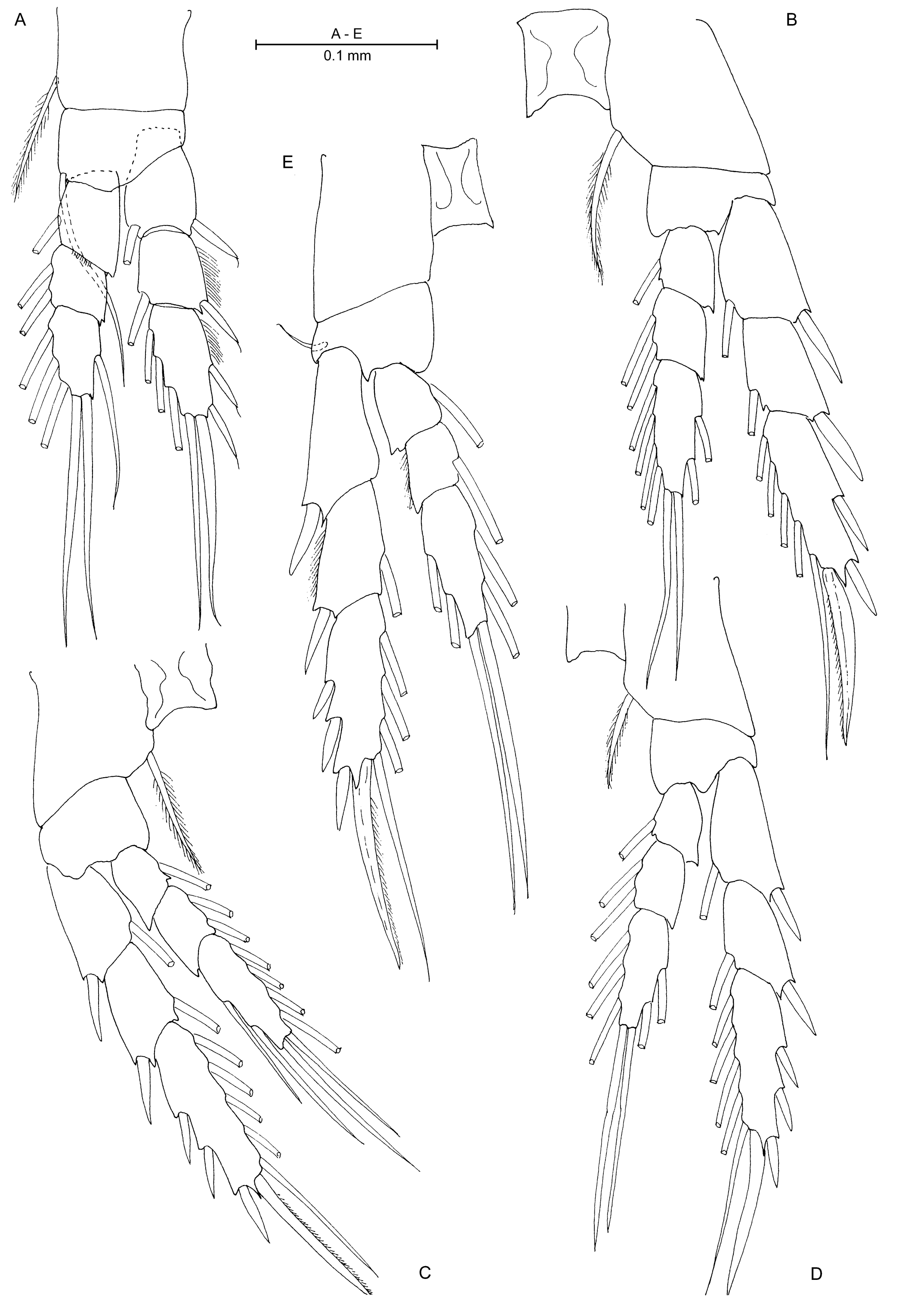

Fig. 35. *Gloinella yagerae* gen. et sp. nov., female. A. Leg 1. B. Leg 2. C. Leg 3. D. Leg 4. E. Leg 5.

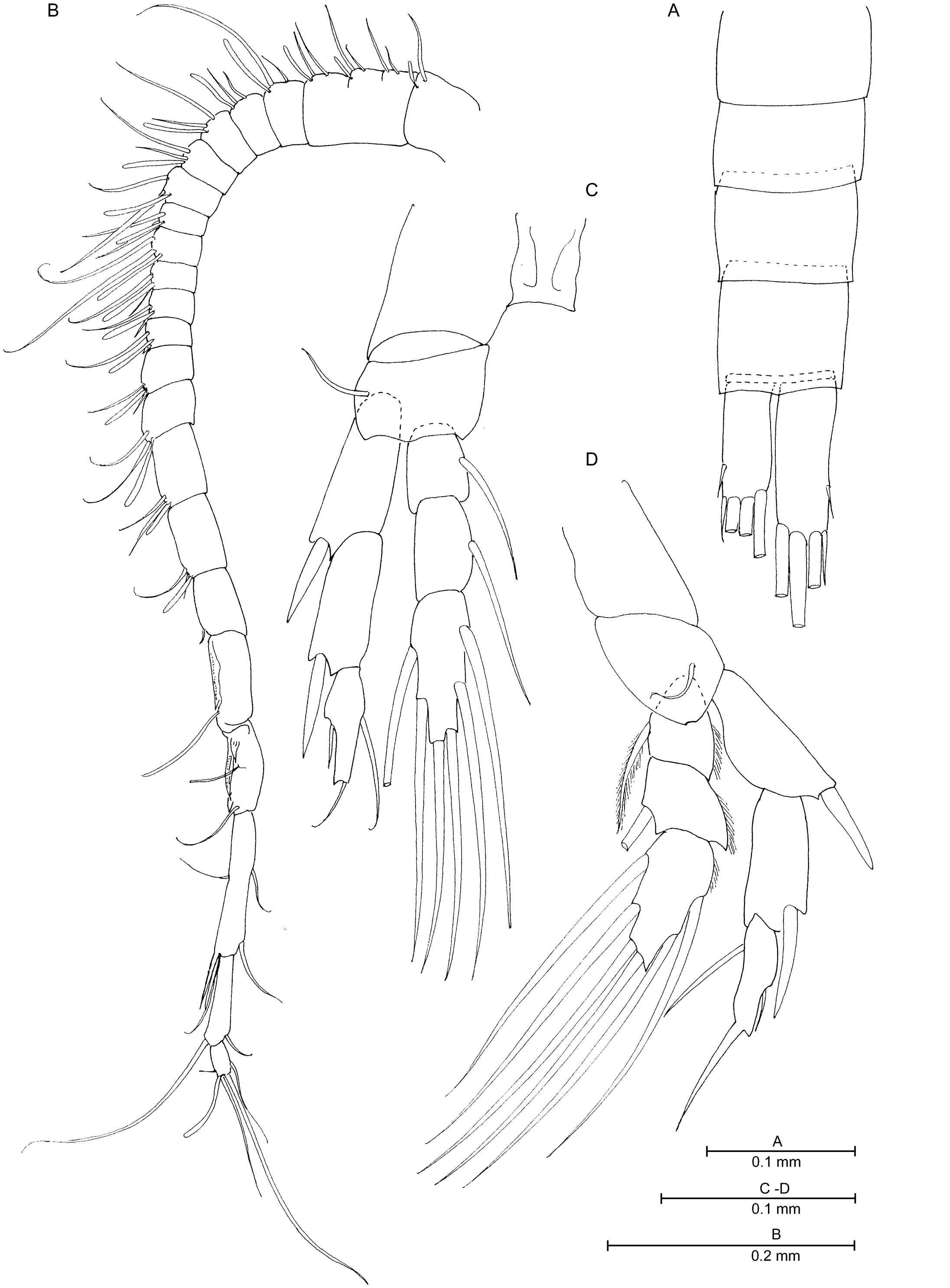

Fig. 36. *Gloinella yagerae* gen. et sp. nov., male paratype. A. Urosome, ventral view. B. Right antennule. C. Left leg 5, posterior view. D. Right leg 5.

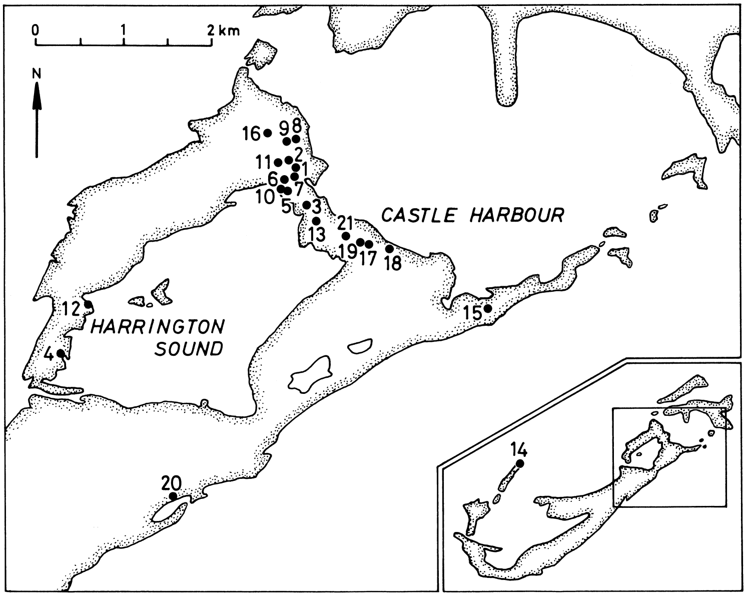

Fig. 37. Map of Bermuda showing caves (1-21) where *Epacteriscus rapax* (1-9), *Enantiosis bermudensis* sp. nov. (3, 4, 8-16), and *Erebonectes nesioticus* (17-21) have been collected. 1. Cherry Pit. 2. Deep Blue. 3. Emerald Sink. 4. Green Bay. 5. Myrtle Bank. 6. Palm. 7. Straw Market. 8. Walsingham. 9. Walsingham Sink. 10. Cripplegate. 11. Double Pond. 12. Red Bay. 13. Shop. 14. Small Fish Pond. 15. Tucker's Town. 16. Wonderland. 17. Bitumen. 18. Christie's. 19. Church. 20. Devonshire. 21. Jane's.

than exopod; first endopodal segment about length of second, bearing 2 setae distally; distal segment with 7 setae both on inner and distal lobes; exopod second segment armed with 2 setae; ramus bearing 7 setae along inner margin and 3 long setae distally.

Mandibular palp (Fig. 34A) with proximal segment of endopod incorporated into basis and bearing 1 seta; defined distal endopodal segment with 4 setae; basis with 1 small seta; exopod with 6 long setae.

Maxillule (Fig. 34B) with coxal and basal endites bearing 3, 3, 1 seta; unsegmented endopod with 2 setae along inner margin and 4 setae distally; exopod elongate with 7 long setae; coxal epipodite represented by 6 long setae.

Maxilla (Fig. 34C, D) with proximal praecoxal endite bearing 1 short and 5 long setae; distal praecoxal and coxal endites each with 2 long spinulate setae and 1 short seta; basis elongate; long setae on basis and endopod of about same length as those on proximal half of limb; endopodal setation 4, 3, 2, 2.

Maxilliped (Fig. 34E) well developed, with weaker and less spinous setae on endopod than those of *Oinella longiseta.* Setal formula of free endopod 4, 4, 3, 3 + 1, 4.

Leg 1 (Fig. 35A) with outer spines on exopodal segments long, flagellate and subequal in length. Leg 2 (Fig. 35B) with unarmed basis. Legs 3-5 (Fig. 35C-E) each with 3 outer spines on third exopodal segment; on leg 5 proximal outer spine on same segment slightly shorter than following 2 spines; first exopodal segment lacking inner seta.

Male. Urosome (Fig. 36A) 5-segmented. Caudal rami asymmetrical, in contrast to female, with left ramus longer than right. Geniculate right antennule (Fig. 36B) 22-segmented; segments II-IV fused and segment 20 (XXIV-XXV) with pointed process distally. Legs 5 (Fig. 36C, D) only slightly modified; asymmetrical with most differences in third exopodal segment; segment slender with 3 elements, on right side with pointed process distally, on left side with weak seta in same position.

Ecological notes. *Gloinella yagerae* was obtained from Cueva de los Carboneros on Cuba, which is an anchialine cave with its surface opening located about 3 km from the open Caribbean Sea (Yager 1994). At time of collecting, the cave had a density interface at a depth of about 12-14 m and the copepod was taken directly below this layer in low oxygenated marine waters, at a site which Yager (1994) characterizes as a typical remipede locality. Together with the remipede *Speleonectes*

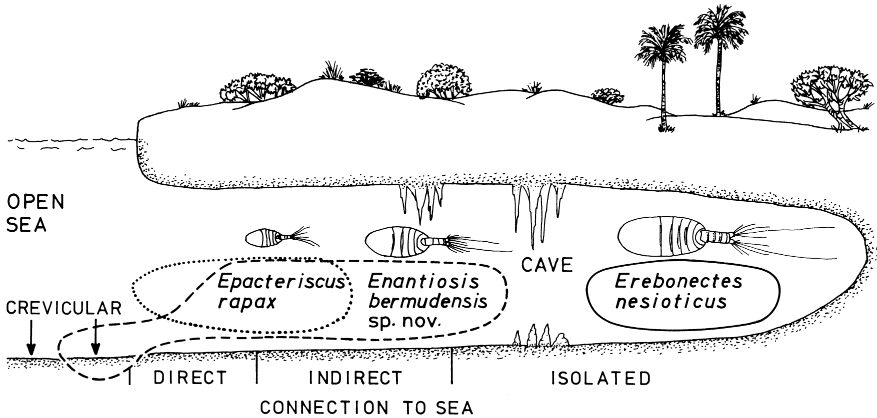

Fig. 38. Vertical section through a stylized marine cave in Bermuda showing distribution of the three epacteriscid copepods: *Epacteriscus rapax, Enantiosis bermudensis* sp. nov., and *Erebonectes nesioticus.* The correct relative body length of the species is indicated.

gironensis Yager, there was an accompanying crustacean assemblage including ostracods, amphipods, thermosbaenaceans, cirolanid isopods, and decapod shrimps.

Remarks. Characters unique to this species include the elongate rostrum, the strong asymmetry of the caudal rami in both sexes, and the elongation of the basis of the maxilla. In addition, there are reductions in numbers of setae on some mouthparts, such as the basis and endopod of the mandibular palp and the maxillule.

Primitive features retained in the female antennule include the trithek on segment XX, a character not observed in any other members of the family. Other plesiomorphic characters are the presence of 3 outer spines on the third exopodal segment in legs 3 to 5, and the nearly symmetrical and only slightly modified fifth legs of the male. The male fifth legs are the least modified in the family and are most reminiscent of those of *Edaxiella* and *Enantronoides.*

The presence of a unilateral tuft of setules proximally on caudal seta VI of the left ramus only, in the female, is shared with *Bofuriella, Bomburiella, Enantiosis, Enantronia,* and *Epacteriscus.*

DISCUSSION

Most of the epacteriscids described here were obtained from caves. They typically have a bilobed rostrum with filaments, 26- or 27-segmented antennules in the female, 25-segmented in *Enantiosis*, more-or-less raptorial mouthparts as especially expressed in the form of the mandible, and plesiomorphic 3-segmented swimming legs. In the fifth legs both rami are usually 3-segmented, but often with highly modified exopods in males.

Epacteriscus has the smallest body length of the known genera, usually between 0.60 and 0.80 mm, and there are now three described species. *Epacteriscus rapax* is the most widely distributed species, found in Bermuda, Florida and Colombia, *E. dentipes* and *E. cuspidantennula* both inhabit a single cave in Belize. Specimens of the two species from Belize were taken as far as 150 m into this cave, but the cave is considered marine as it is entirely beneath the sea floor. All three species were obtained in caves with hand-held nets or suction bottles, never in baited traps. Outside caves in Florida and Colombia, *E. rapax* was also taken in washings of corals and in bottom samples (Fosshagen 1973) and in the Philippines an undescribed *Epacteriscus* species appeared in emergence traps (Barr 1984). Pigmented specimens, records from caves with direct connections to the outside and coexistence with species of stephids, *Ridgewayia* and *Acartia* all indicate a marine rather than an anchialine environment as the habitat for the genus.

In the caves of Bermuda which have been most thoroughly investigated, there seems to be a habitat division between the three epacteriscids: *Epacteriscus rapax, Enantiosis bermudensis* and *Erebonectes nesioticus* (Fig. 38). *Epacteriscus rapax*, the smallest of the species, prefers outer parts of caves with direct connection to open sea, whereas *Enantiosis bermudensis*, of intermediate size, lives in habitats with more indirect connection to sea and, in addition, in crevicular environments outside of caves. *Erebonectes nesioticus*, the largest of the species, was only obtained from the most isolated inner parts of caves.

Epacteriscus exhibits the most reduced, apomorphic states of the mouthparts within the family and is the only epacteriscid genus found routinely outside of caves. The peculiar modifications of leg 1 and the strong outer spines on the exopods of the swimming legs suggest a mode of life in close contact with the substrate. It seems possible that this is a cave-adapted genus that is in the process of exploiting habitats outside caves, by reverse colonization.

Enantiosis seems to be successful in colonizing caves. It is rich in species with seven described from Bermuda, Bahamas, Belize, Galapagos, Fiji, and Palau. A single species is known from each of these areas except for Palau, which has two species. *Enantiosis* was obtained in caves in plankton tows, for *E. belizensis* also in baited traps, but never in great numbers and mostly from the cave interior. The exceptions are *E. bermudensis* from Bermuda, which was obtained in gravel outside one cave, and an as yet undescribed *Enantiosis* species reported from emergence traps in the Philippines by Barr (1984). The body lengths of *Enantiosis* species vary between 1.15 and 1.40 mm. The females of different species of *Enantiosis* are extremely similar, being distinguishable only by minor differences in the relative length of antennules and in the shapes of spines on leg 5. The males, however, differ greatly in the form of their highly complex fifth legs, particularly in the exopods.

In contrast to *Epacteriscus* and *Enantiosis* all the other ten genera are monotypic. Most are known from a few specimens only and in some only one sex is known. They are caught in anchialine environments and are considered troglobitic. Except for *Edaxiella rubra* which lives close to an inland cave opening and has a uniform red colour, all other species appear to be unpigmented.

There are considerable differences in body length; most epacteriscids are from 1 to 1.5 mm but *Bomburiella gigas* attains a length of 3.3 mm. Mouthparts are raptorial in all species and there are great differences in structure between the genera. This may indicate that different genera exploit different prey types and, as other copepods were sometimes abundant in the samples, they represent a possible food source. For example; in Oven Rock Cave in the Bahamas, *Bofuriella* and *Oinella* were obtained together with large numbers of a small stephid and in Norman's Pond Cave, Bahamas, *Balinella* co-occurred with swarms of *Exumellina bucculenta.* The presence of the four genera *Bomburiella, Bofuriella, Enantronoides,* and *Oinella* in Oven Rock Cave, the last three endemic to this cave, raises several interesting questions concerning niche separation. The epacteriscids belong to an ancient lineage of calanoid copepods which has undergone evolutionary radiation, with different genera exhibiting different degrees of adaptation to predatory life. Given the more or less exclusively anchialine habitat it is most probable that this adaptive radiation took place after the epacteriscid ancestral stock invaded caves. The most plesiomorphic mouthpart character states are present in *Erebonectes* which inhabits the remote inner parts of caves, and the most apomorphic states are in *Epacteriscus* which inhabits cryptic habitats outside caves. It is possible that the caves are acting as refugia for the extremely primitive copepods and that the presence of *Epacteriscus* outside of caves represents a secondary re-emergence.

We consider that the family Ridgewayiidae is the sister group of the Epacteriscidae and belongs in the superfamily Epacteriscoidea, rather than in the Pseudocyclopoidea where it was placed by Andronov (1974). The Ridgewayiidae includes cave-adapted species as well as species living outside caves (Fosshagen & Iliffe 1998), however, we consider that the generally looser association of ridgewayiids with caves indicates an independent, perhaps several, invasion of cave habitats by ridgewayiids. The common ancestor of the Epacteriscidae and Ridgewayiidae probably inhabited the shallow water hyperbenthic layers.

The copepod order Misophrioida also contains stygobionts and hyperbenthic forms, as well as two bathypelagic species (Boxshall & Jaume 2000). Within the order, members of family Misophriidae are primarily hyperbenthic in marine habitats and those of the Palpophriidae and Speleophriidae are primarily cavernicolous in anchialine habitats. Boxshall & Jaume (2000) interpreted the occurrence of misophriids in littoral and submarine caves as evidence of a relatively recent landward extension of habitat range, from the shallow-water hyperbenthic community. In contrast they interpreted the presence of speleophriids in anchialine caves as evidence of a dispersal and colonization episode prior to the closure of the Tethys Sea. The distribution and habitat exploitation of epacteriscids is most similar to that of speleophriids and it is suggested here that the original colonization of caves by the Epacteriscidae is a similarly ancient event.

Remipedians, an exclusively stygobiont and ancient group of crustaceans, often co-occur with epacteriscids, such as in Oven Rock Cave and Norman's Pond Cave, Bahamas (T. Iliffe pers. obs.), in Cueva de los Carboneros, Cuba (Yager 1994) and in Jameos del Agua, Lanzarote (Yager 1991). In addition a new genus of epacteriscid has just been recorded from Western Australia (Jaume & Humphreys 2001) from the same cave as a new remipede (Yager & Humphreys 1996). These co-occurrences, often as part of a typical anchialine faunal suite, further support the ancient status of epacteriscids.

KEY TO GENERA OF THE FAMILY EPACTERISCIDAE

1 Legs 3 and 4 with 2 outer spines on third exopodal segment 2
Legs 3 and 4 with 3 outer spines on third exopodal segment 3

2 Leg 2 with strong outer spine on basis .... *Erebonectes*
Leg 2 without outer spine on basis .... *Erebonectoides*

3 Gnathobase of mandible projecting frontally, with tip modified into coarse rake-like blade; labrum elongate, tapering to single point .... *Epacteriscus*
Gnathobase not projecting frontally and not of this form; labrum typically rounded with bifid tip, not as above 4

4 Mandibular palp lacking endopod and with 1 extremely long seta distally on exopod; female antennule with rounded process on segment IX; first endopodal segment of antenna markedly shorter than second ... *Oinella*
These characters not combined 5

5 Mandibular palp with 2 setae on basis; endopod clearly 2-segmented with setal formula 1, 4; antenna with endopod just longer than exopod; seta V on right caudal ramus elongate in female .... *Balinella*
These characters not combined 6

6 Mandibular palp uniramous, lacking trace of endopod .... *Enantronoides*
Mandibular palp biramous, with endopod represented at least by 1 or more setae on vestigial segment 7

7 Segments I to V of female antennule with modified setae (somewhat flattened with thinner filament-like distal section) 8
These segments carrying unmodified setae 10

8 Mandibular gnathobase with very powerfully developed, simple ventral-most tooth; setal formula of syncoxa of maxilliped 0,0,2,4 .... *Bomburiella*
Mandibular gnathobase with ventralmost tooth typically bifid and slightly larger than other teeth; setal formula of syncoxa of maxilliped 1,2,4,4 9

9 First endopodal segment of antenna distinctly longer than compound distal segment; anal somite well developed, conspicuous .... *Enantronia*
First endopodal segment of antenna about equal in length to compound distal segment; anal somite minute, completely concealed beneath posterior rim of preceding somite .... *Enantiosis*

10 Rostrum elongate with 2 closely set rounded lobes at tip; maxillary basis elongate, mandibular palp with 1 seta on basis .... *Gloinella*
Rostrum not elongate, either bifid with pointed branches or barely produced, almost vestigial; maxillary basis stout; mandibular palp lacking setae on basis (except for setae representing vestigial endopod) 11

11 Rostrum bifid with pointed branches; anal somite minute, completely concealed beneath posterior rim of preceding somite .... *Edaxiella*
Rostrum vestigial, represented by weak rounded lobes on frontal margin; anal somite well developed, conspicuous .... *Bofuriella*

ANALYSIS OF PHYLOGENETIC RELATIONSHIPS

Characters

The phylogenetic analysis is based on a character matrix of 56 characters and 23 taxa (Table 1). The taxa include all described species of the Epacteriscidae plus 3 outgroups, the families Ridgewayiidae, Pseudocyclopidae and Metridinidae. The characters used are listed in Table 2 and the interpretation of certain character states is discussed below.

Data on male *Balinella ornata* were added in proof and are not included in the matrix for the analysis. Nor does the matrix include the new epacteriscid genus *Bunderia* from Western Australia (Jaume & Humphreys 2001).

1. Rostrum. The form of the rostrum varies from genus to genus. It may be well developed, even elongate, as in *Gloinella*, or it may be broad and protruding only slightly, as in *Enantiosis*, *Enantronia* and *Edaxiella*. In all genera with a defined rostrum it is bilobed. The lobes may be rounded and carry the frontal filaments apically, as in *Epacteriscus*, but usually they are pointed and carry the frontal filaments ventrally near the medial margins of the lobes. In *Enantronoides*, *Oinella*, *Bofuriella* and *Bomburiella* the rostrum is virtually absent, being reduced to the slightly thickened frontal rim of the dorsal cephalic shield. Paired frontal filaments are present in these genera. The rostrum typically carries a pair of conspicuous sensillae proximally and, in some genera, carries paired areas of modified cuticle, here termed "rostral windows". They appear as areas of thinner cuticle under the light microscope but SEM shows them as patches of pores or pits in the integument (Fig. 14A, C-D, F). Rostral windows are present in *Epacteriscus* and *Edaxiella* but their absence from other genera, such as *Enantronia*, should be confirmed as additional material becomes available.

2. Caudal rami. The caudal rami are typically asymmetrical. This asymmetry may involve a marked difference in size, as in *Gloinella* in which the right ramus is considerably larger than the left in the female, but the left larger than the right in the male. More typically the size difference between the rami is slight or the rami are equal in size and the asymmetry involves the length or ornamentation of the setal elements. *Erebonectes* has symmetrical caudal rami. The only adult specimen of *Oinella* was damaged and lacked caudal rami. Although the CoV stage of *Oinella* has symmetrical rami, it is possible that the asymmetry appears only at the last moult.

The presence on the caudal ramus on one side only of a markedly enlarged inner terminal seta (seta V) is typical for the family. Seta V is enlarged on the left side in females of *Enantiosis*, *Edaxiella*, *Enantronia*, *Epacteriscus*, *Erebonectoides* and *Bomburiella*, and in males of *Enantronoides*, *Epacteriscus* (in *E. cuspidantennula*), *Erebonectoides* and *Gloinella*. It is enlarged on the right side in females of *Balinella* and *Gloinella*, and in males of *Enantiosis* and *Edaxiella*. In those genera where both sexes are known the elongate seta V is usually on different rami in the two sexes, with the exceptions of *Epacteriscus* and *Erebonectoides*. Seta V is symmetrical in males of *Bomburiella* and *Bofuriella* and in both sexes of *Erebonectes*.

The full ancestral complement of 7 setae (setae I to VII) is retained in most epacteriscids, although the anterolateral accessory seta (seta I) is usually minute and may be lacking in some genera. The anterolateral seta (seta II) is usually setiform. The caudal ramus of *Erebonectoides* is unusual: it lacks both seta I and seta II, and seta III is rather flattened and scale-like when viewed laterally. In females of *Enantiosis, Enantronia, Epacteriscus, Bomburiella*, *Bofuriella* and *Gloinella* the terminal accessory seta (seta VI) on the left caudal ramus is slightly swollen near its base and carries a unilateral tuft of long setules. This seta is unmodified in females of other genera and in males.

3. Female antennule. Primitively all 27 antennulary segments are expressed in epacteriscids, as in *Erebonectes*, *Erebonectoides* and *Edaxiella*. Due to the failure of expression of the original articulation II/III the antennule may be 26-segmented, as in *Enantronia*, and due to the partial failure of expression of both articulations II/III and III/IV, the antennule is 25-segmented in *Enantiosis* and *Oinella*. It is 26-segmented in *Bomburiella*, *Bofuriella* and *Balinella* due to incorporation of segment XXVI into the apical double-segment XXVII-XXVIII. There are other instances of incomplete segmental expression, for example, in the region of segments X and XI in *Enantiosis* and *Epacteriscus*.

The setae on the proximal segments (I to V) of the antennule are modified in *Enantiosis*, *Enantronia* and *Bomburiella*. Modified setae are somewhat flattened proximally and have a thinner, filament-like distal section. The aesthetasc on segment XIX is retained only in *Erebonectoides* and *Oinella*. All other genera in which the female is known, lack this aesthetasc. The female of *Enantronoides* is unknown but scores have been placed in the matrix (characters 10 to 13) on the assumption that the female state is identical to that of the left, non-geniculate antennule of the male.

4. Male antennule. Adult male antennules display secondary segmental fusions distal to the neocopepodan geniculation, typically generating the compound segments XXI-XXIII and XXIV-XXV, XXII-XXIII in males of *Erebonectes* and *Erebonectoides*. The anterodistal angle of double-segment XXIV-XXV carries a long spinous process in *Epacteriscus*, *Erebonectes*, *Gloinella*, *Enantronoides, Bofuriella* and *Bomburiella*.

5. Labrum. *Epacteriscus* has an elongate, tapering labrum with setulose lateral margins. It is anteroventrally directed and, at rest, the enormous mandibular gnathobases so characteristic of this genus lie immediately posterior to, and either side of, the labrum. The typical epacteriscid labrum is a broad muscular lobe, often bearing transverse rows of spinules or setules.

6. Antenna. There is gross variation in the relative size of the rami of the antenna. In *Erebonectes* the endopod is considerably longer than the exopod, whereas in *Oinella* the exopod is markedly longer than the endopod. The remaining genera fall between these two extremes. In the phylogenetic analysis, the length of the first endopodal segment is used to define this character: an elongate endopod being retained in *Erebonectes*, *Erebonectoides*, *Enantronia*, *Enantronoides*, and *Balinella*. The loss of setae from both exopodal segments II and III, is shared by *Epacteriscus* and *Oinella*. The seta is lost from segment III only in *Edaxiella*. All other genera retain both setae. The number of setae retained on the inner lobe of the compound distal endopodal segment is also used in the analysis even though the homology of the lost setae cannot be confirmed.

7. Mandible. The mandible of *Epacteriscus*, with its enormous, anteriorly-directed gnathobases, is unique within the family and within the Copepoda. The trend towards reduction of the endopod and the dominance of the exopod, which forms the main axis of the mandibular palp, is diagnostic of the Epacteriscidae. The primitive state within the family, as found in *Erebonectes*, is a 2-segmented endopod, bearing a maximum of 2 and 8 setae on the first and second segments respectively. The most derived state is a uniramous palp, lacking any trace of the endopod, as found in *Enantronoides* and *Oinella*. *Oinella* is remarkable in the elongation of the seta on the penultimate exopodal segment. The segmentation and setation of the endopod provide several characters used in the phylogenetic analysis. The reduction of the endopodal segmentation is here interpreted to proceed by incorporation of the proximal segment into the basis, due to failure of expression of the proximal basis-endopod articulation. The evidence supporting this interpretation is based on comparison of *Balinella* and *Gloinella.* In the former (Fig. 28B) the endopod is 2-segmented with a setal formula of 1, 4, whereas in the latter (Fig. 34A) it is 1-segmented but the expressed segment carries 4 setae and 1 seta is located on a pedestal-like area immediately proximal to the free segment. An attempt has been made to define characters relating to the setation of the mandibular basis in terms of their homology. The primitive array of 4 setae is retained on the basis in *Erebonectes*. Three are retained in *Erebonectoides,* 2 in *Balinella* and 1 in *Gloinella*. All other genera lack any setae on the basis. Loss is assumed to proceed from distal to proximal in scoring these characters for the character matrix.

8. Maxillule. The distal segmentation of the endopod is used as a character in the analysis. The articulation separating endopodal segments 2 and 3 is expressed in *Erebonectoides*, *Bomburiella* and *Bofuriella*. In all other genera the maxillulary endopod is unsegmented. All other maxillulary characters used are setal counts. Apart from the presence and absence of the outer basal exite seta, which is retained only in *Erebonectes*, all setation characters rely on a key assumption concerning homology, namely that the sequence of loss of elements is the same in all genera. This assumption has not been tested.

9. Maxilla. In the typical epacteriscid maxilla the praecoxa and coxa are incompletely separated. The first praecoxal endite has at most 6 setae, 1 of which is reduced in all genera except *Erebonectes*. The remaining praecoxal and the coxal endites have the setal formula 3: 3: 3, except in *Oinella* which has 1: 2: 3, *Bomburiella* which has 1: 3: 3, and *Epacteriscus* with 1, 3, 2. Spinule rows are present on the endites only in *Balinella*. The basis is typically triangular in shape but in *Gloinella* has become elongate. It carries 4 setae. Epacteriscids typically have a condensed endopod bearing a well defined endite derived from the incorporated first endopodal segment. This endite bears 4 setae. The distal three endopodal segments carry 7 setae in total, arranged in a 3: 2: 2 formula.

10. Maxilliped. The maxilliped is usually a powerfully developed limb. It comprises syncoxa, basis and endopod. The proximal endopodal segment is usually partly incorporated into the basis. The maximum syncoxal setal formula in the family is 1: 2: 4: 4, but the proximal endites commonly exhibit reduced setation. The basis carries 3 setae plus 2 distal setae on the inner lobe of the partly incorporated first endopodal segment. The free endopod is 5-segmented and the distal segment is characteristically reduced in epacteriscids. The ancestral setal formula is 4: 4: 3: 3 + 1: 4. The appearance of the maxilliped, in terms of the robustness and orientation of the basis, and the state of particular endopodal setae varies from genus to genus but is not readily usable in the analysis. For example, the 2 distal setae on the second free endopodal segment are spinulate and extremely powerfully developed in *Bofuriella* but long, slender and naked in *Bomburiella*. However, the precise state of the setal elements appears to be unique for each genus and cannot, therefore, be used in the phylogenetic analysis.

11. Swimming legs 1 to 4. The swimming legs have 3-segmented rami throughout the family. *Epacteriscus* has unusual first legs: the exopod has highly dentate outer and distal margins and the endopod is produced into a hooked distal process. Most genera have flagellate outer spines on the exopodal segments of leg 1.

Bofuriella and *Bomburiella* appear to lack such subapical flagellae. Other characters used in the analysis relate either to the presence or absence of particular setal elements, or to the form of a particular element. The proximal spine on the outer margin of the third exopodal segment of legs 3 to 4 is lost only in *Erebonectes* and *Erebonectoides*.

12. Female fifth legs. The fifth legs also have 3-segmented rami. Characters used relate to the presence/absence of particular setal elements. The inner seta from the first exopodal segment is usually small but is lost only in *Epacteriscus* and *Gloinella*. The proximal spine on the outer margin of the third exopodal segment is lost only in *Erebonectes* and *Erebonectoides*.

13. Male fifth legs. The basis may be modified by the possession of an inner process on either the left leg (in *Erebonectes*, *Erebonectoides*, *Enantiosis galapagensis* and *Enantiosis conspinulata*), or the right leg (in *Enantiosis cavernicola*, *E. belizensis*, *E. dicerata*, and *E. longiprocessa*) or on both legs (in *Bofuriella* and *Enantiosis bermudensis*). On the basis of the right leg, just distal to the inner process if present, some species

Table 1. Character matrix used as basis for the phylogenetic analysis.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	Ridgewayiidae	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
2	Pseudocyclopidae	1	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0
3	Metridinidae	1	0	0	0	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	*Epacteriscus rapax*	0	0	0	1	1	1	0	0	1	1	1	1	1	1	6	1	1	1	2	1	1	3	5	1	1	4	4	3
5	*Epacteriscus cuspidantennula*	0	0	0	1	1	1	0	0	1	1	1	1	1	1	6	1	1	1	2	1	1	3	5	1	1	4	4	3
6	*Epacteriscus dentipes*	0	0	0	1	1	1	0	0	1	1	1	1	1	1	6	1	1	1	2	1	1	3	5	1	1	4	4	3
7	*Erebonectes nesioticus*	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	1	0	1	1	1
8	*Erebonectoides macrochaetus*	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	2	2	1	0	1	1	0
9	*Enantiosis cavernicola*	1	1	0	1	1	0	1	1	1	1	1	0	0	0	5	1	1	1	2	1	0	3	3	1	1	2	4	2
10	*Enantiosis bermudensis*	1	1	0	1	1	0	1	1	1	1	1	0	0	0	5	1	1	1	2	1	0	3	3	1	1	2	4	2
11	*Enantiosis belizensis*	1	1	0	1	1	0	1	1	1	1	1	0	0	0	5	1	1	1	2	1	0	3	3	1	1	2	4	2
12	*Enantiosis galapagensis*	1	1	0	1	1	0	1	1	1	1	1	0	0	0	5	1	1	1	2	1	0	3	3	1	1	2	4	2
13	*Enantiosis dicerata*	1	1	0	1	1	0	1	1	1	1	1	0	0	0	5	1	1	1	2	1	0	3	3	1	1	2	4	2
14	*Enantiosis conspinulata*	1	1	0	1	1	0	1	1	1	1	1	0	0	0	5	1	1	1	2	1	0	3	3	1	1	2	4	2
15	*Enantiosis longiprocessa*	1	1	0	1	1	0	1	1	1	1	1	0	0	0	5	1	1	1	2	1	0	3	3	1	1	2	4	2
16	*Edaxiella rubra*	0	1	0	0	1	0	1	0	0	0	1	0	0	1	3	1	1	1	2	1	0	3	4	1	1	2	2	3
17	*Enantronia canariensis*	1	1	0	1	1	?	?	1	1	0	1	?	0	0	5	0	1	1	2	1	0	3	3	1	1	1	2	2
18	*Enantronoides bahamensis*	1	2	?	?	?	1	0	1	1	0	0	1	0	0	5	0	1	1	2	1	1	3	6	1	1	1	2	2
19	*Oinella longiseta*	1	2	?	?	?	?	?	0	1	1	0	?	1	1	4	1	1	1	2	1	1	3	6	1	1	2	4	3
20	*Bofuriella vorata*	1	2	0	1	0	0	0	0	0	0	1	1	0	0	1	1	1	1	2	0	0	3	4	1	0	2	3	2
21	*Bomburiella gigas*	1	2	0	1	1	0	0	1	0	0	1	1	0	0	1	1	1	1	2	0	0	3	4	1	0	3	4	2
22	*Gloinella yagerae*	1	0	1	1	0	1	0	0	1	0	1	1	0	0	2	1	0	1	2	1	0	2	2	1	1	1	2	2
23	*Balinella ornata*	1	0	1	0	0	?	?	0	0	0	1	?	0	0	1	0	0	0	2	0	0	2	2	1	1	1	1	1

		29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56
1	Ridgewayiidae	1	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0	2	2	1	0	0	0	0	0	1
2	Pseudocyclopidae	1	1	1	0	0	0	0	1	?	1	1	0	0	0	0	0	1	1	2	1	1	?	?	?	?	0	0	0
3	Metridinidae	0	0	1	0	0	0	0	0	0	1	0	2	0	0	0	0	0	?	1	2	1	1	?	?	?	0	0	0
4	*Epacteriscus rapax*	3	4	3	6	1	5	1	1	0	1	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	1
5	*Epacteriscus cuspidantennula*	3	4	3	6	1	5	1	1	0	1	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	1
6	*Epacteriscus dentipes*	3	4	3	6	1	5	1	1	0	1	1	0	0	0	1	0	0	0	0	2	0	1	0	0	0	0	0	1
7	*Erebonectes nesioticus*	1	2	1	0	0	1	0	0	0	0	1	0	1	1	0	1	1	1	0	0	1	0	0	0	0	0	0	1
8	*Erebonectoides macrochaetus*	1	1	0	0	1	0	0	1	0	1	1	0	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	1
9	*Enantiosis cavernicola*	2	3	3	3	1	2	0	1	0	1	1	1	0	0	0	0	0	1	0	1	2	0	1	1	0	1	1	1
10	*Enantiosis bermudensis*	2	3	3	3	1	2	0	1	0	1	1	1	0	0	0	0	1	1	1	1	2	0	1	1	0	1	1	1
11	*Enantiosis belizensis*	2	3	3	3	1	2	0	1	0	1	1	1	0	0	0	0	0	1	1	1	2	0	1	1	0	1	1	1
12	*Enantiosis galapagensis*	2	3	3	3	1	2	0	1	0	1	1	1	0	0	0	0	1	1	1	1	2	0	1	1	0	1	0	1
13	*Enantiosis dicerata*	2	3	3	3	1	2	0	1	0	1	1	1	0	0	0	0	0	2	0	1	2	0	1	2	1	0	1	1
14	*Enantiosis conspinulata*	2	3	3	3	1	2	0	1	0	1	1	1	0	0	0	0	1	1	0	1	2	0	1	2	0	0	0	1
15	*Enantiosis longiprocessa*	2	3	3	3	1	2	0	1	0	1	1	1	0	0	0	0	0	2	0	1	2	0	1	2	1	1	1	1
16	*Edaxiella rubra*	2	3	3	3	1	2	0	1	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
17	*Enantronia canariensis*	2	3	3	2	1	2	0	1	0	1	1	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	1
18	*Enantronoides bahamensis*	2	3	3	5	1	2	0	1	0	1	1	1	0	0	?	?	0	1	0	0	0	0	0	0	0	0	0	?
19	*Oinella longiseta*	3	4	3	4	1	4	1	1	0	1	1	1	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	1
20	*Bofuriella vorata*	2	3	2	1	1	3	0	1	1	1	1	0	0	0	0	0	1	1	1	0	0	0	1	1	0	0	1	1
21	*Bomburiella gigas*	2	3	2	1	1	4	1	0	1	1	1	0	0	0	0	0	0	1	1	2	0	0	1	0	0	0	0	1
22	*Gloinella yagerae*	2	3	3	3	1	2	0	1	0	1	1	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
23	*Balinella ornata*	1	2	2	1	1	2	0	1	0	1	1	0	0	0	0	0	?	?	?	?	?	?	?	?	?	?	?	1

of *Enantiosis* bear a conspicuous patch of spinules (*E. cavernicola*, *E. bermudensis*, *E. belizensis*, *E. galapagensis* and *E. longiprocessa*). The endopods are 3-segmented and, typically, relatively unmodified on both legs. In *Enantiosis* species the outer margins of the first and second endopodal segments are modified on the left leg. The outer margin of the first is often produced into an irregular, laterally-directed process and similar modifications are found in *Bomburiella* and *Bofuriella*. The second is produced into one or more irregular process in some *Enantiosis* species. The outer distal angle of this segment can be drawn out into a conspicuous pointed or rounded process, which may be ornamented as in *Enantiosis belizensis*.

The exopods are typically 3-segmented but in *Epacteriscus* males the articulation between the second and third ancestral segments is not expressed and the left exopod is only 2-segmented The first and second exopodal segments of the left leg both lack inner setae but retain outer spines, which may be modified as processes. The third exopodal segment typically carries three setal elements: an outer spine, distal seta and inner seta. The inner seta can be modified or lost. This segment may also form a single lobate process, as in *Erebonectes* and *Erebonectoides*, or it may carry numerous irregular processes, as in *Enantiosis* species.

Analysis

The phylogenetic analysis was based on 100 replicate searches and generated eight equally short trees, all with a branch length of 233. The strict consensus tree (Fig. 39) indicates that the Epacteriscidae is a monophyletic group (clade 1 on Fig. 39). One key synapomorphy of the family is the dominance of the mandibular exopod, which forms the main axis of the palp, and the reduction of the endopod. The first endopodal segment of *Erebonectes* carries 2 setae and the second carries 8 setae. These are the most plesiomorphic states within the Epacteriscidae and constitute apomorphies, relative to the outgroups, which exhibit an endopodal setal formula of 4, 10. There are few other synapomorphies for the family, but this is perhaps to be expected since the *Erebonectes*-lineage within the Epacteriscidae exhibits many of the most extreme plesiomorphic character states for the entire Calanoida.

The first subdivision within the family is the separation from the main lineage, of the *Erebonectes* group (clade 2) comprising just two genera, *Erebonectes* and *Erebonectoides*. These two genera retain many plesiomorphic character states but share the following derived states: legs 3 and 4 in both sexes bear only 2 spines on the outer margin of the third exopodal segment; the female fifth leg carries only 2 spines on the outer margin of the third exopodal segment; and inner margin of the basis of the male left fifth leg is produced into a small process. The *Erebonectes* group is here treated as a distinct new subfamily, the Erebonectinae, diagnosed formally below.

The main lineage (clade 3) within the family becomes the nominate subfamily, the Epacteriscinae, and is also formally diagnosed below. It is characterized by the following synapomorphies: the retention of at most 8 setae on the inner lobe of the compound distal endopodal segment of the antenna; the loss of at least 2 setae from the mandibular basis, and the reduction of the maxillulary setation, including the retention of at most 9 setae on the exopod, at most 5 setae on the tip of the endopod and at most 6 setae on the epipodite.

The first offshoot within the subfamily Epacteriscinae is *Balinella*, which does not share the following synapomorphies that link all other taxa (clade 4) within the subfamily: seta V on the left caudal ramus is elongate; the loss of at least 3 setae from the mandibular basis; the relatively short first endopodal segment of the antenna; the fusion of the proximal endopodal segment to the basis on the mandibular palp and the reduction in setation on this palp (loss of all setae on basis and on first endopodal segment, and retention of at most 2 setae on second endopodal segment); and the reduction in setation of the maxillulary basis and endopod (retention of at most 3 setae on the first basal endite and 1 on the second, maximum endopodal setation 1, 1, 4). *Balinella* retains relatively plesiomorphic states of all these characters except that it displays the alternative apomorphic state of having an elongate seta V on the right caudal ramus in the female, rather than on the left ramus.

After the separation of *Bofuriella* and *Bomburiella*, then *Gloinella*, the remaining taxa cluster into two main groups: the *Epacteriscus*-group comprising *Epacteriscus* species, *Oinella* and *Edaxiella*, and the *Enantiosis*-group comprising *Enantiosis* species, *Enantronia* and *Enantronoides*. The establishment of new genera proposed above and their placement into two new subfamilies are fully supported by the results of the phylogenetic analysis, i.e. by inference from Fig. 39.

Subfamily Erebonectinae nov. Epacteriscidae with spine and seta formula for legs 1 to 4, and female leg 5:

	coxa	basis	exopodal segments	endopodal segments
leg 1	0-1	0/1-1	I-1; I-1; II,I,4	0-1; 0-2; 1,2,3
leg 2	0-1	0/I-0	I-1; I-1; II,I,5	0-1; 0-2; 2,2,4
leg 3	0-1	I-0	I-1; I-1; II,I,5	0-1; 0-2; 2,2,4
leg 4	0-1	1-0	I-1; I-1; II,I,5	0-1; 0-2; 2,2,3
leg 5(f)	0-0	1-0	I-1; I-1; II,I,4	0-1; 0-1; 2,2,2

Type genus *Erebonectes* Fosshagen, 1985; other included genus: *Erebonectoides* gen. n.

Subfamily Epacteriscinae Fosshagen, 1973. Epacteriscidae with spine and seta formula for legs 1 to 4, and female leg 5:

	coxa	basis	exopodal segments	endopodal segments
leg 1	0-1	0/1-1	I-1; I-1; II,I,4	0-1; 0-2; 1,2,3
leg 2	0-1	0-0	I-1; I-1; II,I,5	0-1; 0-2; 2,2,4
leg 3	0-1	0/1/I-0	I-1; I-1; III,I,5	0-1; 0-2; 2,2,4
leg 4	0-1	0/1-0	I-1; I-1; III,I,5	0-1; 0-2; 2,2,3
leg 5(f)	0-0	1-0	I-0/1; I-1; III,I,4	0-1; 0-1; 1/2,2,2/3

Type genus *Epacteriscus* Fosshagen, 1973; other included genera: *Enantiosis* Barr, 1984; *Balinella* gen. n.; *Bofuriella* gen. n.; *Bomburiella* gen. n.; *Edaxiella* gen. n.; *Enantronia* gen. n.; *Enantronoides* gen. n.; *Gloinella* gen. n. and *Oinella* gen. n.

BIOGEOGRAPHY

As with other anchialine taxa, such as remipedes (Yager 1994) and misophrioid copepods (Boxshall & Jaume

Table 2. Characters and character states used in phylogenetic analysis (PAUP).

Ch. No.	Character	States and scores applied
1	rostral windows	present/absent = 0/1
2	rostrum	well-developed, protruding markedly = 0 broad, protruding slightly = 1 virtually absent = 2
3	female right caudal seta V	normal length/elongate = 0/1
4	female left caudal seta VI	without/with unilateral tuft = 0/1
5	female left caudal seta V	normal length/elongate = 0/1
6	male left caudal seta V	normal length/elongate = 0/1
7	male right caudal seta V	normal length/elongate = 0/1
Female antennule		
8	setae on segments I-V	normal/modified = 0/1
9	articulation II-III	expressed/not expressed = 0/1
10	articulation III-IV	expressed/not expressed = 0/1
11	aesthetasc on segment XIX	present/absent = 0/1
Male antennule		
12	segment XXV process	absent/present = 0/1
Antenna		
13	exopod segment II seta	present/absent = 0/1
14	exopod segment III seta	present/absent = 0/1
15	inner setae on endopod	9/8/7/5/4/3/1 = 0/1/2/3/4/5/6
16	length endopod segment I	elongate/short = 0/1
Mandible		
17	proximal seta on basis	present/absent = 0/1
18	adjacent seta on basis	present/absent = 0/1
19	distal setae on basis	present/1 absent/2 absent = 0/1/2
20	endopod	defined proximally/fused to basis = 0/1
21	endopod articulation I-II	expressed/not expressed = 0/1
22	endopod segment I setae	4/2/1/0 = 0/1/2/3
23	endopod segment II setae	10/8/4/3/2/1/0 = 0/1/2/3/4/5/6
24	main axis of palp	endopod/exopod = 0/1
Maxillule		
25	endopod articulation II-III	expressed/not expressed = 0/1
26	coxal endite setae	5/3/2/1/0 = 0/1/2/3/4
27	basal endite 1 setae	5/4/3/2/1 = 0/1/2/3/4
28	basal endite 2 setae	5/4//1/0 = 0/1/2/3/
29	endopod segment I setae	6/4/1/0 = 0/1/2/3
30	endopod segment II setae	5/4/3/1/0 = 0/1/2/3/4
31	endopod segment III setae	7/6/5/4 = 0/1/2/3
32	exopod setae	11/9/8/7/6/5/1 = 0/1/2/3/4/5/6
33	basal exite	present/absent = 0/1
34	epipod setae	9/7/6/5/4/3 = 0/1/2/3/4/5

2000), the distribution patterns of epacteriscid taxa are extremely disjunct. The family appears to have originated in the Central American/Caribbean region and has undergone only four expansions. One resulted in the colonization of Lanzarote in the Canary Islands by *Enantronia*, two in the independent colonization of Indo-west Pacific islands by *Enantiosis* and by *Epacteriscus*, and a fourth by *Enantiosis* in the Galapagos Islands. The discovery of a new genus of epacteriscid from an anchialine sinkhole in Northwestern Australia (Jaume & Humphreys 2001) may indicate another independent colonization of the Pacific. As discussed above, it is postulated here that these colonizations occurred prior to the closure of the Tethys Sea.

The genus *Enantiosis* contains species from the Bahamas, Bermuda, Belize, Galapagos, Fiji and Palau (two species). Superimposing modern distribution patterns on Fig. 39 provides a simple indication of their historical biogeography. Two lineages are apparent within the genus *Enantiosis*: the *dicerata*-group comprising three species from the Indo-Pacific, and the *cavernicola*-group comprising four species, one from Bermuda, two from Caribbean islands, and the fourth from the Galapagos. The affinity of *E. galapagensis* with the Caribbean species rather than the Indo-Pacific species is interesting and undoubtedly reflects the complex tectonic history of the Central American region.

Table 2. (continued)

Ch. No.	Character	States and scores applied
Maxilla		
35	praecoxal endite 2 setae	3/1 = 0/1
Swimming legs		
37	P1 exopod spines	flagellate tips/simple = 0/1
36	P1 outer basal seta	present/absent = 0/1
38	P2 outer basal spine	present/absent = 0/1
39	P2 exopod segment III outer spines	3/2 = 0/1
40	P3 outer basal element	spine/seta/absent = 0/1/2
41	P3 exopod segment III outer spines	3/2 = 0/1
42	P4 exopod segment III outer spines	3/2 = 0/1
Female P5		
43	exopod segment I inner seta	present/absent = 0/1
44	exopod segment III outer spines	3/2 = 0/1
Male left P5		
45	inner basal process	absent/present = 0/1
46	exopod segment I spine	unmodified/enlarged/bifid = 0/1/2
47	exopod segment II spine	unmodified/enlarged = 0/1
48	exopod seg. III inner seta	present/modified/absent = 0/1/2
49	exopod segment III	without processes/forming single lobate process/with many processes = 0/1/2
50	exopod II/III articulation	expressed/not expressed = 0/1
51	endopod segment I margin	smooth/modified = 0/1
52	endopod segment II margin	smooth/drawn out to modified tapering tip/modified with rounded tip = 0/1/2
53	endopod segment III shape	significantly longer than wide/ laterally expanded = 0/1
Male right P5		
54	inner margin basis	without spinule patch/with spinule patch = 0/1
55	basal process	absent/present = 0/1
Gonopores		
56	female gonopores	paired/single = 0/1

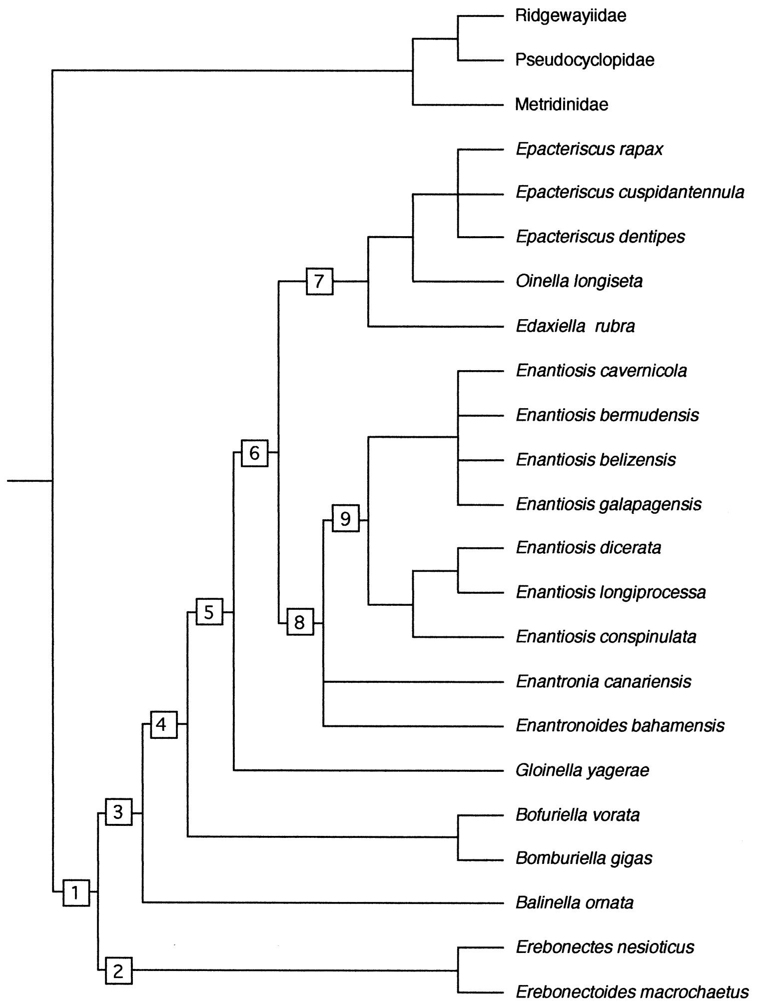

Fig. 39. Strict consensus tree showing inferred relationships between described taxa of the family Epacteriscidae. Apomorphy lists defining clades 1 to 9: Clade 1 - character 22 (0>1), 23 (0>1), 24 (0>1), 26 (0>1), 27 (0>1), 29 (0>1), 30 (0>1), 39 (0>1), 56 (0>1); Clade 2 - character 1 (0>1), 41 (0>1), 42 (0>1), 44 (0>1), 45 (0>1), 49 (0>1); Clade 3 - character 15 (0>1), 19 (0>2), 22 (1>2), 23 (1>2), 28 (0>1), 30 (1>2), 31 (0>2), 32 (0>1), 33 (0>1), 34 (0>2), 38 (0>1); Clade 4 - character 18 (0>1), 27 (1>2), 28 (1>2), 9 (1>2), 30 (2>3); Clade 5 - character 15 (1>2), 20 (0>1), 25 (0>1), 31 (2>3), 32 (1>2), 36 (0>1); Clade 6 - character 5 (0>1), 15 (2>3), 17 (0>1), 22 (2>3), 23 (2>3); Clade 7 - character 14 (0>1), 16 (0>1), 23 (3>4), 26 (1>2), 28 (2>3), 32 (2>3); Clade 8 - character 1 (0>1), 2 (0>1), 8 (0>1), 9 (0>1), 15 (3>5), 40 (0>1), 46 (0>1); Clade 9 - character 7 (0>1), 10 (0>1), 16 (0>1), 26 (1>2), 27 (2>4), 32 (2>3), 48 (0>1), 49 (0>2), 51 (0>1), 52 (0>1).

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NOTE ADDED IN PROOF

Recently we have recorded three new genera of the Epacteriscidae and the male of *Oinella longiseta* from caves in the Bahamas.