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New epacteriscids (Copepoda, Calanoida) from anchialine caves in the Bahamas

Audun Fosshagen & Thomas M. Iliffe

SARSIA

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Three new monotypic genera, *Azygonectes*, *Cryptonectes* and *Minnonectes*, and the male of *Oinella longiseta* Fosshagen, Boxshall & Iliffe are described. New records are made of *Balinella ornata* Fosshagen, Boxshall & Iliffe, *Bofuriella vorata* Fosshagen, Boxshall & Iliffe and *Bomburiella gigas* Fosshagen, Boxshall & Iliffe. *Azygonectes* is considered pelagic, with many plesiomorphic features and in an intermediate position with characters of swimming legs reminiscent of both Erebonectinae and Epacteriscinae. *Cryptonectes* is considered benthic, with several apomorphic features, and reductions of mouthparts, but for characters of the swimming legs it is included in the Erebonectinae. *Minnonectes*, bearing some unique modifications of setae in maxilla and maxilliped, is included in the Epacteriscinae. The Epacteriscidae and Ridgewayiidae are considered fairly closely related.

Audun Fosshagen, Department of Fisheries and Marine Biology, University of Bergen, P.O. Box 7800, NO-5020 Bergen, Norway.
E-mail: audun.fosshagen@bio.uib.no
Thomas M. Iliffe, Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX 77553-1675, USA.
E-mail: iliffet@tamug.tamu.edu

Keywords: Calanoida; Epacteriscidae; taxonomy; anchialine caves; Bahamas.

INTRODUCTION

In a recent paper (Fosshagen & al. 2001), the family Epacteriscidae with a total of 20 species distributed in 12 genera, most of them new, is reviewed. Since then two new monotypic genera have been described from Western Australia (Jaume & Humphreys 2001) and Cuba (Boxshall & Jaume 2003), bringing the number of described genera up to 14 with 22 species. Nearly all species are cave-living, and no other family of calanoids yet has as many stygobionts as the Epacteriscidae. Other cave-living calanoids have representatives among mainly hyperbenthic families (Jaume & Boxshall 1995). Most epacteriscids are obtained from net hauls in anchialine caves in tropical and subtropical waters, mainly from the Caribbean area, others from Bermuda, the Canary Islands, Western Australia, the Philippines, Palau, Fiji, and the Galapagos Islands. Some species of *Epacteriscus* Fosshagen and *Enantiosis* Barr have also been found in cryptic environments outside caves (Fosshagen 1973; Fosshagen & al. 2001) and from emergence traps in shallow water among corals in the Philippines (Walter & al. 1982). One species, *Enantiosis belizensis* Fosshagen, Boxshall & Iliffe, has been obtained from baited traps; from Giant Cave in Belize and also from plankton hauls in the same cave (Fosshagen & al. 2001).

Epacteriscid taxa are extremely disjunct and typically have a Tethyan distribution and often co-occur with remipedes. The family is one of the most primitive of the Calanoida and there are few synapomorphies. Important characteristics include the stout body, usually with a broad, bilobed rostrum with filaments, the dominance of the exopod and reduction of the endopod of the mandible, raptorial mouthparts with a strong gnathobase of the mandible with long sharp teeth, modified spines of the maxilla and maxilliped, and swimming legs with three-segmented rami.

Other copepods might be a possible prey as has been observed in *Bunderia misophaga* from Western Australia where Jaume & Humphreys (2001) found remnants of a misophrioid in the gut of the copepod. Few specimens of epacteriscids have usually been obtained, as may be expected of a predator, and they were often present when there were great numbers of stephids, ridgewayiids and other small copepods in the sample (Fosshagen & Iliffe 1991, 1998, 2003).

The family has been divided into two subfamilies, the Erebonectinae (*Erebonectes* and *Erebonectoides*) and the Epacteriscinae (12 genera) mainly on account of the armature of the swimming legs and the state of the mandible.

Three new genera are established in this paper; some show unusual characters in the armature of the

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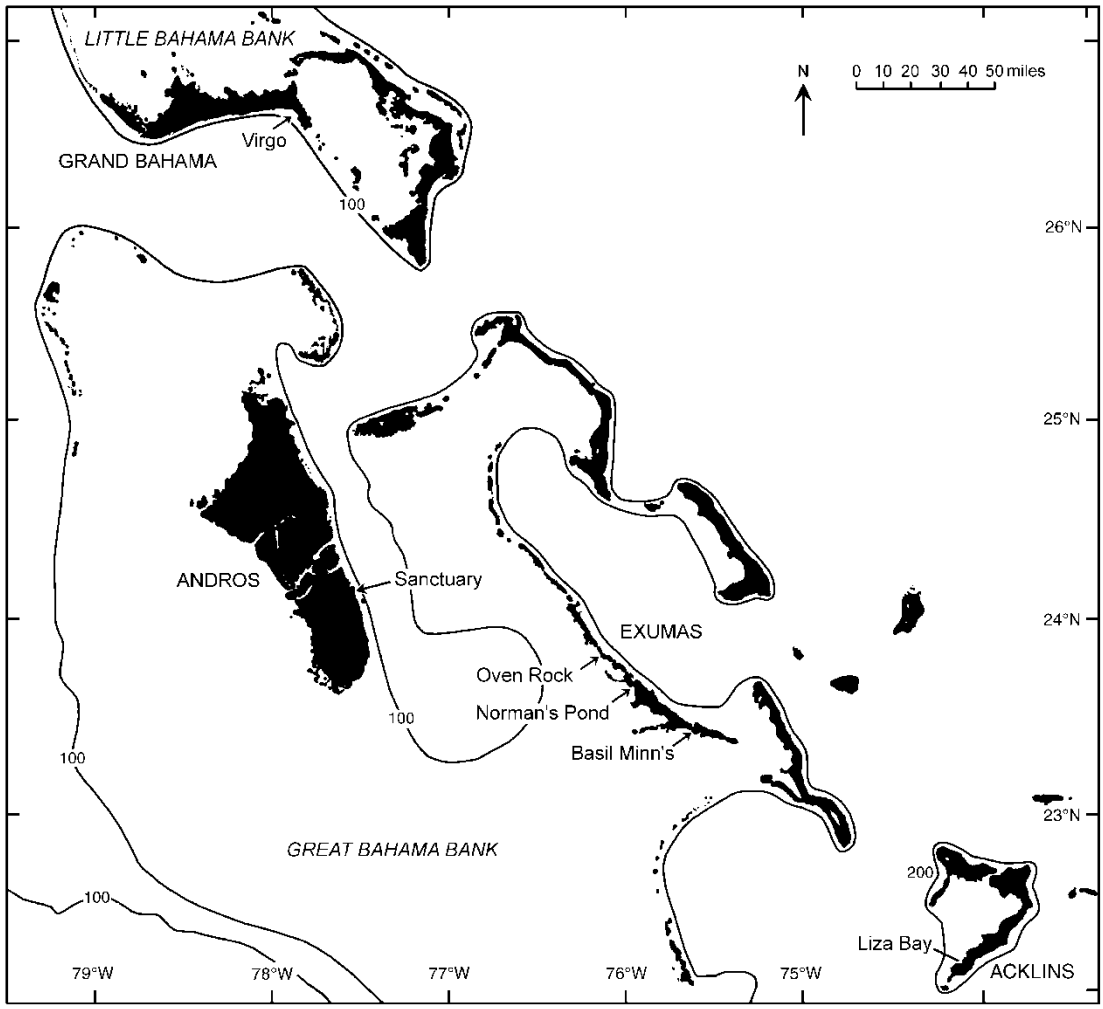

Fig. 1. A map of central and northern Bahamas showing the locations of the principal caves from which new epacteriscids were collected: Liza Bay Cave, Basil Minn's Blue Hole, Norman's Pond Cave, Oven Rock Cave, Sanctuary Blue Hole (Stargate Blue Hole is adjacent to Sanctuary Blue Hole), Virgo Blue Hole (Lucy's Cave and Sagittarius Blue Hole are within a few kilometres of Virgo Blue Hole). Depth curves in fathoms.

swimming legs and in mouthparts, some characters are in conflict with the systematic arrangement of the family into two subfamilies. New records of four previously known species are added, including the description of the hitherto unknown male of *Oinella longiseta* Fosshagen, Boxshall & Iliffe.

These discoveries bring the total for the family to 17 genera and 25 species, of which 15 genera and 19 species are obtained from the Caribbean region and Bermuda.

MATERIAL AND METHODS

The material was collected from anchialine caves in central and northern Bahamas (Fig. 1). The copepods were mostly obtained using advanced diving techniques, when dragging a fine-mesh hand net (*Ca* 100 μm) through the water. The terminology used in descriptions follows Huys & Boxshall (1991).

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

SYSTEMATICS

Genus *Azygonectes* gen. nov.

Diagnosis

Female. Prosome with five well-defined pedigerous somites. Urosome four-segmented with second and third urosomites of subequal length. Caudal rami slightly asymmetrical, caudal seta II short and spinous, seta V on left side extremely elongate. Rostrum elongate with two closely set filaments at tip. Antennule indistinctly 27-segmented, with segments 10 and 11 partially fused, reaching beyond caudal rami. Antenna with endopod slightly longer than exopod, second endopodal segment with nine setae on inner lobe. Gnathobase of mandible ventrally with two strong multicuspid teeth; palp with two-segmented endopod and with three setae on basis. Maxillule well developed but with some reduction in number and length of setae along inner margin of endopod. Maxilla with well-defined articulation between praecoxa and coxa, long and flexible setae on praecoxal and coxal endites. Maxilliped with long and flexible setae along syncoxa; endopod unmodified with flexible setae, third segment slightly elongate. Leg 1 with two outer spines on third exopod segment, slender and with a filament at tip. Legs 2 and 3 with two outer spines on third exopod segment, proximal one short and stout; leg 3 with outer stout spine on basis. Legs 4 and 5 with outer seta on basis and three outer spines on third exopod segment.

Type species

Azygonectes intermedius gen. et sp. nov.

Etymology

The generic name refers to two single specimens obtained from caves far apart (from Greek *azygos* meaning solitary, and *nectos* meaning swimming). Gender masculine. The specific name alludes to the intermediate state of the swimming legs 3 and 4, in conflict with the former definition of the two subfamilies.

Azygonectes intermedius gen. et sp. nov.

Material examined

Sanctuary Blue Hole (24°7′N 77°35′W), The Bluffs, South Andros Island, Bahamas. 15 October 1999: one female. Basil Minn's Blue Hole (23°29′N 75°46′W), Great Exuma, Bahamas. 9 August 2002: one female.

Type

Holotype. Adult female, total body length 1.77 mm, from Sanctuary Blue Hole, South Andros, Bahamas, 15 October 1999, collected from water column in 50–35 m depth. Six slides BM(NH) reg. no. 2003.581.

Paratype. Adult female (antennule and caudal setae broken off), total body length 1.69 mm from Basil Minn's Blue Hole, Great Exuma, Bahamas, 9 August 2002, collected from water column at 20–36 m depth. One vial BM(NH) reg. no. 2003.582.

Description

Female. Total body length 1.69 and 1.77 mm. Body (Fig. 2A) with ratio of prosome length to urosome length *Ca* 3:1. Fifth pedigerous somite with evenly rounded posterolateral margin. Urosome (Fig. 2B) four-segmented; genital double somite about length of following three somites combined. Caudal rami asymmetrical; left ramus slightly longer and broader than right one, seta II on left ramus with flexible tip, spinous on right side, seta V on left ramus greatly elongate, longer than body length although with broken tip.

Rostrum (Fig. 2C) elongate with two long filaments at tip.

Antennule (Fig. 2D) 27-segmented reaching beyond caudal rami. Segments X and XI incompletely separated, joined on part of posterior margin, segments XV–XXVII elongate, segment XIX with two small setae, terminal segment 27 with seven elements.

Antenna (Fig. 2E) with endopod longer than exopod. Coxa bearing small seta. First endopod segment about twice length of second segment, second segment with nine setae on inner lobe and six setae on terminal lobe. Exopod indistinctly nine-segmented; last segment incompletely separated from penultimate one; both segments combined representing about one third length of exopod.

Mandible (Fig. 2F) with gnathobase bearing two strong ventral teeth, each with three to four distal projections, plus a row of eight differently shaped pointed teeth along with short spinules, and small dorsal seta. Palp with three setae on basis; reduced two-segmented endopod with one seta on first segment and four setae on second segment; exopod well developed, apparently four-segmented with one small seta and five long setae.

Maxillule (Fig. 2G) with praecoxal arthrite bearing 14 elements, nine coarse spinous setae and five ordinary setae; coxal endite and basal endites with three, four and four setae, respectively; coxal epipodite with nine setae. Endopod with six setae along inner margin and six terminal setae. Exopod with 10 setae.

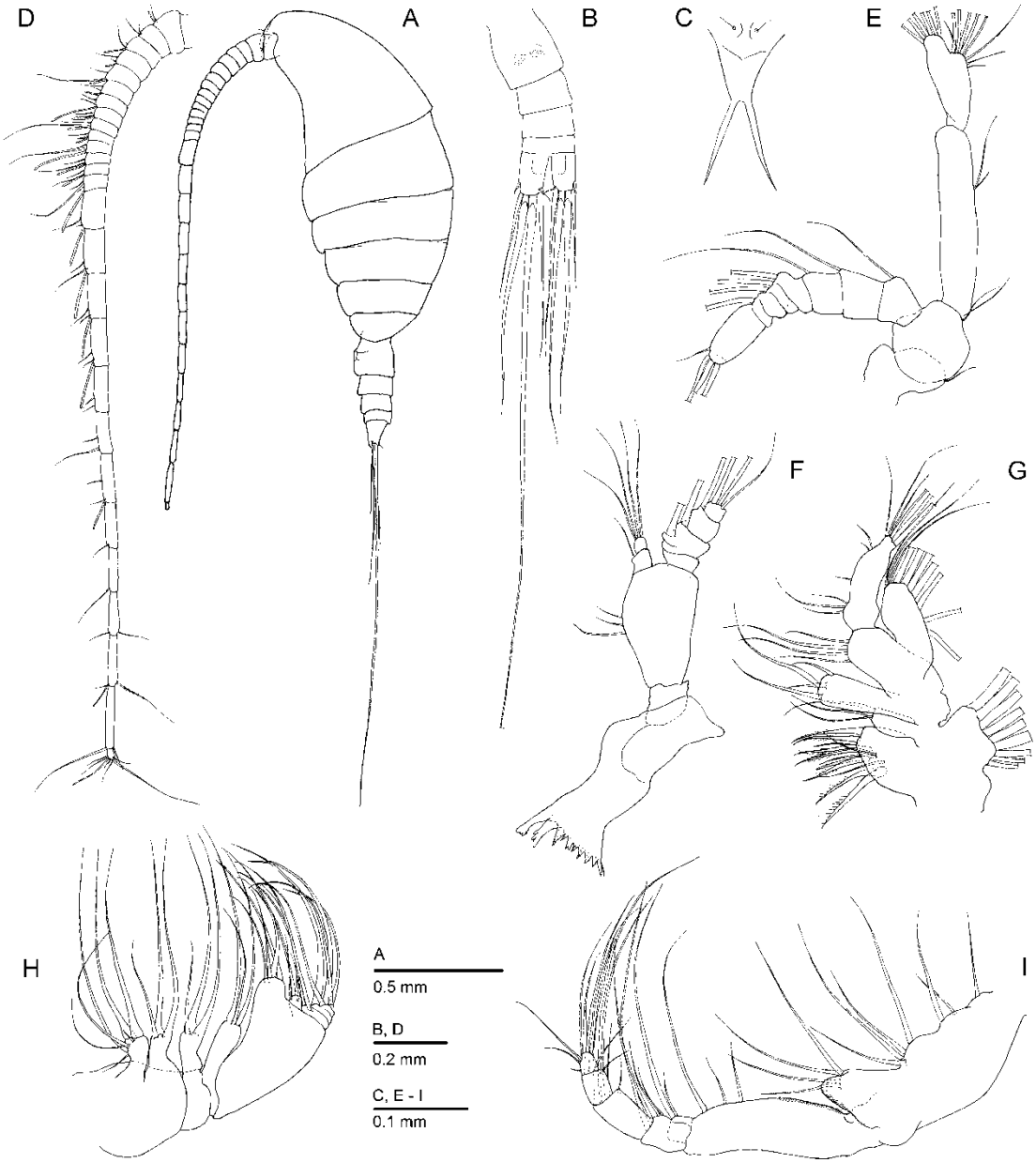

Fig. 2. *Azygonectes intermedius* gen. et sp. n; female. A. Habitus, lateral view. B. Urosome, dorsal view. C. Rostrum. D. Antennule. E. Antenna. F. Mandible. G. Maxillule. H. Maxilla. I. Maxilliped.

Maxilla (Fig. 2H) with elongate praecoxal and coxal endites bearing long and flexible setae; proximal endite with six setae and one spiniform element, longest setae on endites sparsely ornamented with setules; basis with extended distal endite; endopod condensed with 10 elements, most of them relatively weak setae with flexible tip, some spinous setae, none conspicuously modified.

Maxilliped (Fig. 2I) bearing syncoxa with rather slender and unmodified setae, distal endite extended and covered with fine setules on distal surface; basis with row of fine setules along proximal half of inner

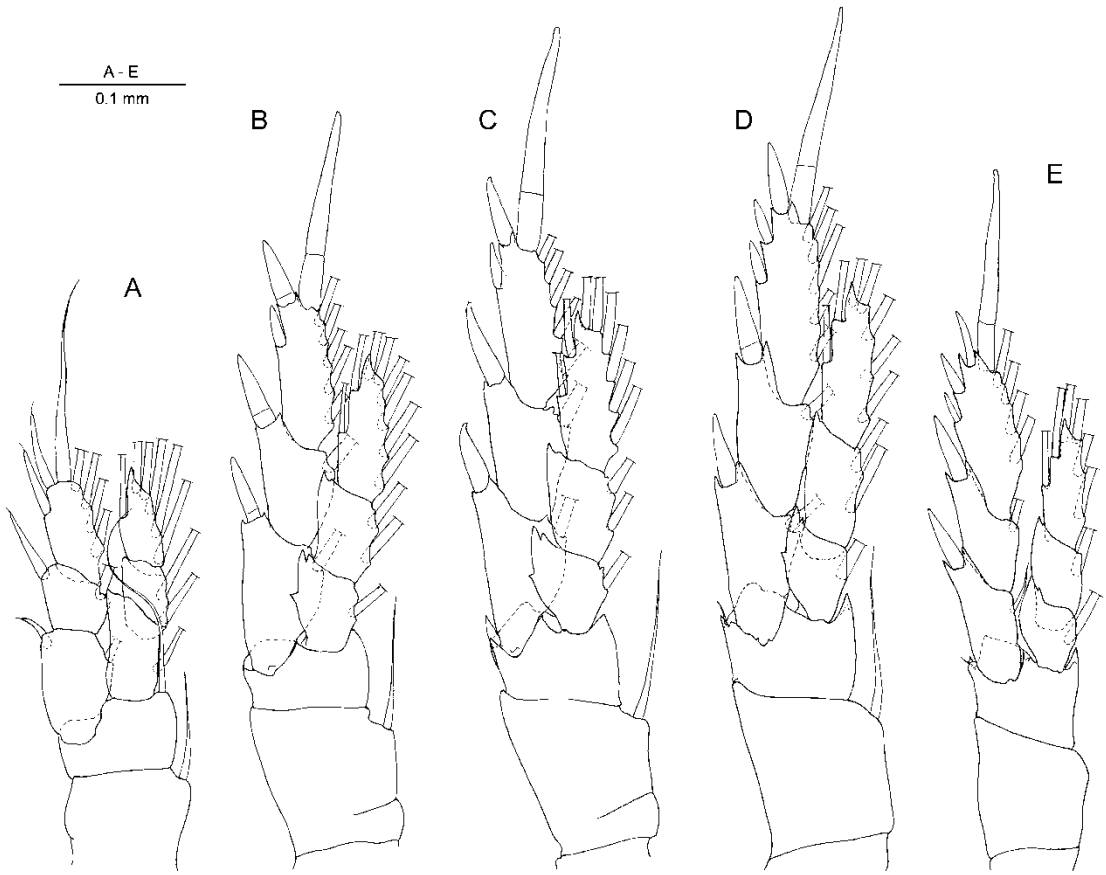

Fig. 3. *Azygonectes intermedius* gen. et sp. n.; female. A. Leg 1. B. Leg 2. C. Leg 3. D. Leg 4. E. Leg 5.

margin; three setae along distal margin, two small subequal proximal ones and one long distally. Endopod five-segmented with first two segments partially fused, third segment elongate: setae on endopod generally unmodified and ending in thread-like tip.

Legs 1–5 spine and seta formula as follows:

	Coxa	Basis	Exopod segment			Endopod segment		
			1	2	3	1	2	3
Leg 1	0-1	0-1	I-1	I-1	II, 1, 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	II, 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

Leg 1 (Fig. 3A) with slender outer exopodal spines, all with subterminal filament; spine on first exopodal segment slightly curved.

Leg 2 (Fig. 3B) with proximal outer spine on third exopodal segment reduced in size, terminal spine on exopod about three times length of adjacent outer spine; first endopodal segment with medial triangular process on outer margin and cleft distally on outer corner.

Leg 3 (Fig. 3C) with outer spine on basis and two unequal spines along outer margin of third exopodal segment; first endopodal segment with process medially on outer margin.

Leg 4 (Fig. 3D) with small outer seta on basis and three outer spines on third exopodal segment.

Leg 5 (Fig. 3E) with outer distal corner of first and second exopodal segments extended and bearing strong spine; three spines along outer margin of third exopodal segment.

Ecological notes

Sanctuary Blue Hole is located about 500 m inland from the east coast of South Andros Island near the

settlement of The Bluffs. It is part of a major north–south slump fracture zone paralleling the underwater escarpment that separates the Great Bahama Bank from the Tongue of the Ocean, a deep oceanic trench. This slump fracture extends for tens of kilometres and was formed as a result of glacio-eustatic sea level changes and gravitational stresses along the edge of the limestone banks (Palmer 1986a, b). The entrance consists of a collapse-floored fissure extending down beneath a bedrock ledge to a pool about 5 m long by 2 m wide. A rift drops vertically beneath the water surface and opens out at a depth of 25 m into a large fissure passage that extends in both directions. Water depths in the cave exceed 60 m.

A comparison of water quality values from Sanctuary and nearby Stargate Blue Hole (located about 1 km away but in the same fracture), showed striking parallels despite the fact that measurements were taken more than 2 years apart (Fosshagen & Iliffe 2003, fig. 1). This implies that the deeper waters in the two caves are remarkably stable over long periods of time. The surface layer in Sanctuary had a salinity of 3 and a temperature of 25.6°C on the date of collection. Below a sharp halocline at 21 m depth, salinity increased to 36. A temperature maximum of 27.4°C occurred at 28 m, but values dropped to 25.4°C at 58 m. Dissolved oxygen levels dropped from 2.3 mg l^{-1} at the surface to 0.04 mg l^{-1} in a hydrogen sulphide layer at 23 m, but increased to 1.76 mg l^{-1} at 31 m before falling below 0.1 mg l^{-1} at 50 m.

Copepods from 15 October 1999 were collected with a plankton net from the water column between 35 and 50 m depth. The sample contained large numbers of *Mastigodiaptomus nesus* Bowman; other calanoids recorded in small numbers were: *Bomburiella gigas* Fosshagen, Boxshall & Iliffe, *Oinella longiseta* Fosshagen, Boxshall & Iliffe (see below), one copepodid of *Bofuriella*, *Exumellina bucculenta* Fosshagen & Iliffe, *Stargatia palmeri* Fosshagen & Iliffe, and an undetermined species of *Exumella*. The species composition as well as the water quality is very similar to that of the nearby Stargate Blue Hole (see Fosshagen & Iliffe 2003). In addition to copepods, a characteristic stygobitic fauna including thermosbaenaceans, halocyprid ostracods, cirolanid isopods, remipedes and polynoid polychaetes were also sampled.

An additional female of *Azygonectes intermedius* was obtained in Basil Minn's Blue Hole, Great Exuma about 160 km from Sanctuary Blue Hole; separated by the deep Tongue of the Ocean but both situated on the shallow Great Bahama Bank. For a description of Basil Minn's Blue Hole see *Minnonectes melodactylus* (below). In addition to *Azygonectes intermedius*, the sample from 9 August 2002 contained several *Ridgewayia* sp., a few specimens of *Paramisophria* sp., *Stargatia palmeri* and an unidentified calanoid.

Remarks

A key character for females in the two epacteriscid subfamilies is the number of outer spines on the third exopodal segment of legs 3–5, with two spines in Erebonectinae and three spines in Epacteriscinae. *Azygonectes intermedius* deviates from this pattern having two outer spines on leg 3 and three spines on legs 4 and 5.

An important synapomorphy of the family is in the mandible with dominance of the exopod and reductions in the endopod and in the number of setae on the basis. The most plesiomorphic state is in the Erebonectinae. The mandible of *Azygonectes* is most similar to those of *Erebonectoides* in the Erebonectinae and *Balinella* in the Epacteriscinae, with the main differences in the ventral teeth of the gnathobase. Other characters connecting *Azygonectes* to the Erebonectinae are: rostrum with two closely set filaments at the tip, antenna with endopod longer than exopod, maxillule with nine setae on coxal epipodite and 10 setae on exopod.

Awaiting the discovery of the male, *Azygonectes* is currently placed among the most plesiomorphic genera of the family in a systematic position between *Balinella* and the Erebonectinae.

The narrow articulation between the third and second segments of exopod leg 5 and the expansion of the distal part of the second segment is reminiscent of the Ridgewayiidae in which this is a key character. Most similarities are shown to *Exumella* in the Ridgewayiidae (see Jaume & Boxshall 1995) where the rostrum has two filaments and the mandible has a dominant exopod and a similar gnathobase. These characters seem to point to a close relationship between the two families, both with species inhabiting marine caves.

Judging from its transparent appearance and the long antennule, *Azygonectes intermedius* seems to be living pelagic in the cave.

Genus *Cryptonectes* gen. nov.

Diagnosis

Female. Prosome with five well-defined pedigerous somites. Lateral border of cephalosome with distinct concave swing in middle. Urosome three-segmented. Caudal rami symmetrical with caudal seta II short and spinous. Rostrum rounded with two filaments at tip. Antennule 25-segmented, short and reaching slightly beyond first pedigerous somite. Antenna with very short

condensed endopod, about half length of exopod. Mandible with strong gnathobase bearing bifid ventral-most tooth and row of rounded teeth towards dorsal part; palp with small one-segmented endopod and four-segmented exopod. Maxillule with reduced number of setae particularly on coxa, basis and endopod with two setae on each of coxal endite and proximal basal endite. Maxilla with relatively short unmodified setae except for long spinous setae distally on endopod. Maxilliped mostly with short spinous setae except for long and modified ones on endopod which bear distal row of stiff setules and thin flexible tip. Leg 1 with small outer seta on basis, two outer spines on third exopod segment slender and pinnate. Legs 2–5 with very strong and subequal outer spines of exopods, all with two outer spines on third exopodal segment; leg 3 with outer strong curved spine on basis; leg 5 with small inner seta on first exopodal segment.

Male. Urosome four-segmented. Right antennule 21-segmented with segments II–IV fused, long pointed process on penultimate segment 20. Fifth legs with pointed process distally on inner margin of left basis, exopods modified in distal part, three-segmented on right side and ending in curved pointed process, two-segmented on left side with last segment bearing outer falcate process; endopods three-segmented, only slightly modified.

Type species

Cryptonectes brachyceratus gen. et sp. nov.

Etymology

The generic name refers to the assumed hidden life in the caves (from Greek *kryptos* meaning hidden; *nektos* meaning swimming). Gender masculine. The specific name refers to the short antennule of the animal (from Greek *brachys* meaning short; *keras* meaning horn).

Cryptonectes brachyceratus gen. et sp. nov.

Material examined

Liza Bay Cave ('Deep Pool') (22°13′N 74°12′W), Salina Point, Acklins Island, Bahamas. 14 January 1999. One female. Basil Minn's Blue Hole (23°29′N 75°46′W), Georgetown, Great Exuma Island, Exuma Cays, Bahamas. 18 March 2000. One male (mutilated). Norman's Pond Cave, Norman's Pond Cay, Exumas, Bahamas. 19 March 2000. One male. Virgo Blue Hole, Sweetings Cay, Grand Bahama Island, Bahamas. 2 December 2001. One female.

Types

Holotype. Adult female, total body length 1.16 mm, from Liza Bay Cave, Acklins Island, Bahamas, 14 January 1999, collected from water column in 5–0 m depth. Six slides BM(NH) reg. no. 2003.583.

Paratypes. Adult male, total body length 1.21 mm, from Norman's Pond Cave, Exumas, Bahamas, 19 March 2000, collected from water column in 60–10 m depth. Six slides BM(NH) reg. no. 2003.584.

Adult female, total body length 1.25 mm from Virgo Blue Hole, Grand Bahama, 2 December 2001, collected from 15–21 m depth. One vial BM(NM) reg. no. 2003.585.

Description

Female. Total body length 1.16 and 1.25 mm. Body (Fig. 4A, B) with ratio of prosome length to urosome length *Ca* 2.7:1. Cephalosome with middle of lateral margin deeply concave. Urosome (Fig. 4B) three-segmented; last two urosomites of equal length, last one with distal undulate frill. Caudal rami symmetrical; seta II short and spinous.

Rostrum (Fig. 4C) elongate lobe with two filaments at tip.

Antennule (Fig. 4D) 25-segmented; short, reaching slightly beyond first pedigerous somite; segments I–III fused, segments VIII–XIII much condensed, seta on segment IX greatly elongate, aestetascs on segments XIV–XVIII relatively well developed, elements on terminal segment relatively short.

Antenna (Fig. 4E) with exopod about double length of endopod. First segment of endopod with two equal setae near distal inner margin, distal segment well developed with nine setae on inner lobe and seven setae on elongate terminal lobe.

Mandible (Fig. 4F) with very strong gnathobase bearing strong bifid ventral-most tooth, rounded at tip; row of four rounded major teeth with minor additional teeth, and unipinnate dorsal seta. Palp with reduced one-segmented endopod bearing three setae; exopod four-segmented and normally developed.

Maxillule (Fig. 5A) with reduced number of setae; praecoxal arthrite with 12 elements, most spinous setae relatively long; coxal endite and basal endites with two, two and one setae, respectively; coxal epipodite with five long setae. Endopod two-segmented with two small setae along inner margin and five terminal long setae. Exopod with eight setae concentrated distally.

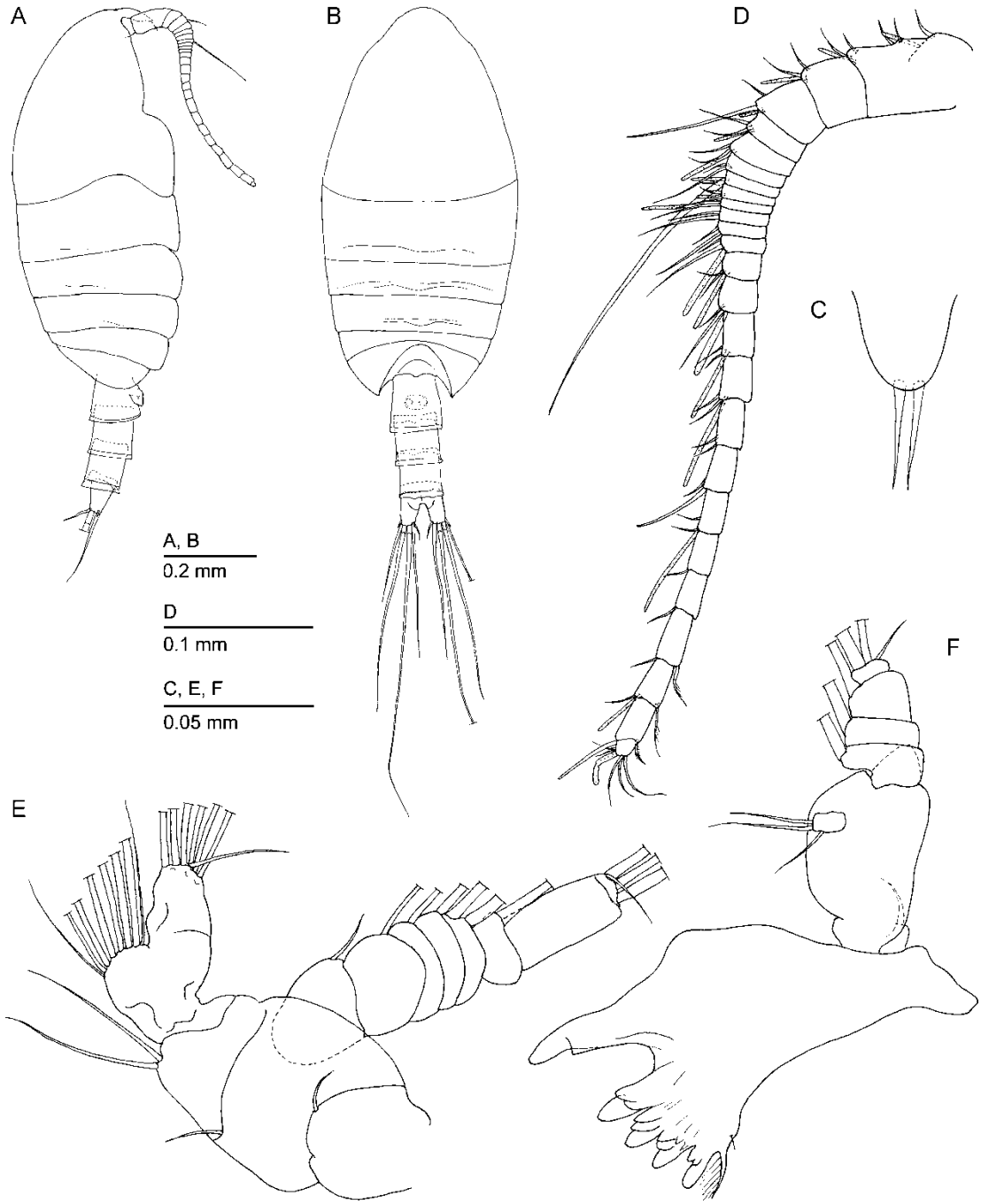

Fig. 4. *Cryptonectes brachyceratus* gen. et sp. n.; female. A. Habitus, lateral view. B. Habitus, dorsal view. C. Rostrum. D. Antennule. E. Antenna. F. Mandible.

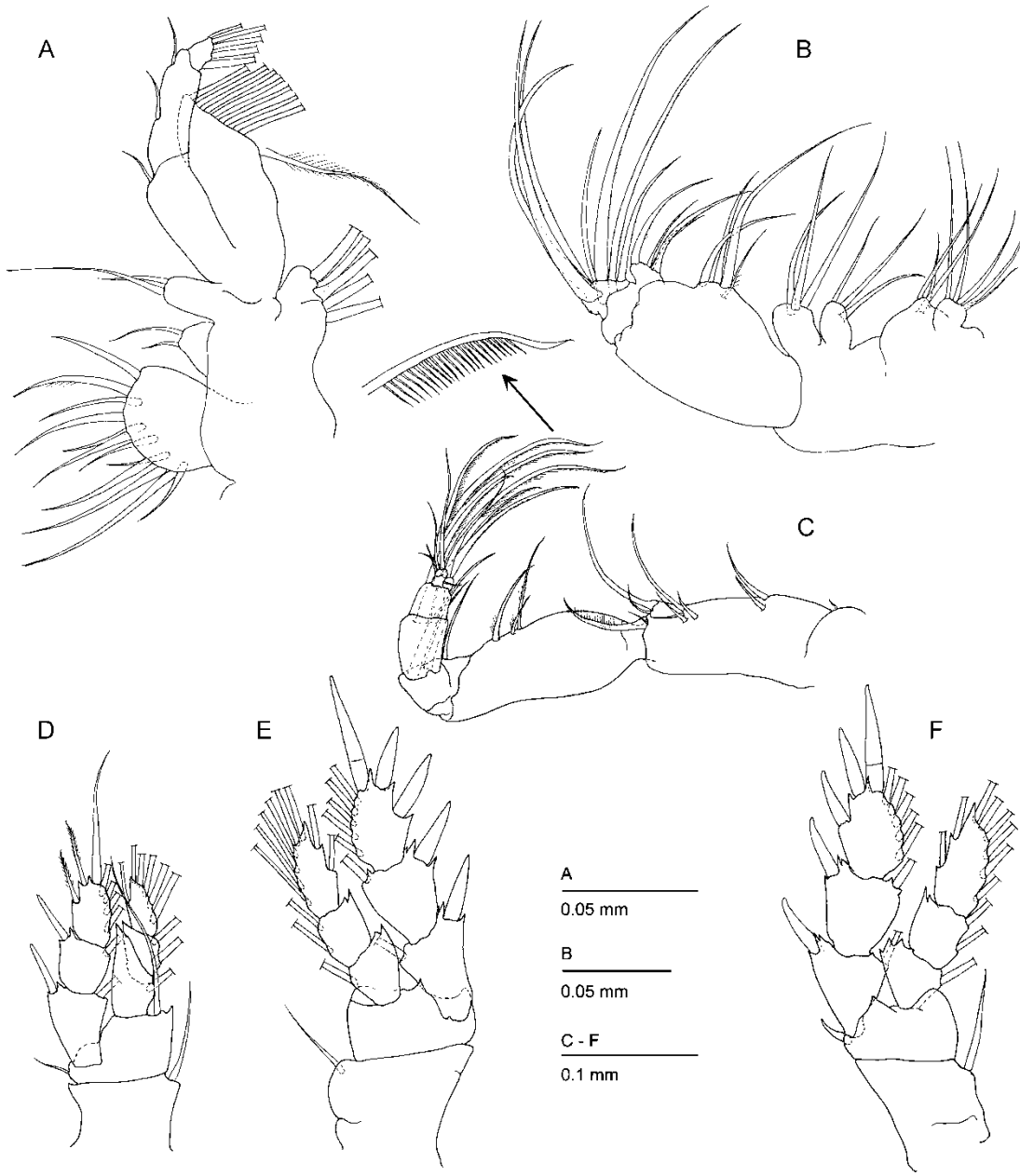

Fig. 5. *Cryptonectes brachyceratus* gen. et sp. n.; female. A. Maxillule. B. Maxilla. C. Maxilliped with detail of seta. D. Leg 1. E. Leg 2. F. Leg 3.

Maxilla (Fig. 5B) with well-developed endites on syncoxa bearing relatively short and stout setae, proximal endite with five setae; basal endite situated near middle of inner margin; endopod much condensed with strong claw-like spinous setae.

Maxilliped (Fig. 5C) with minute seta on praecoxal endite, most setae on coxa rather spinous and curved, basis with three setae along distal margin, proximal and distal seta of subequal length, middle seta short. Endopod five-segmented with first two segments

partially fused, first segment with one short and one long modified seta (not shown in figure), most long setae on endopod modified distally with long setules and ending in thin flexible tip.

Legs 1–5 spine and seta formula as follows:

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

Leg 1 (Fig. 5D) with small outer seta and pointed distal inner margin on basis; outer exopodal spines of subequal length, spine on first and second exopodal segments smooth, two spines on third segment slender and pinnate. Outer distal corner of first endopodal segment elongate and pointed, reaching outer corner of second segment.

Leg 2 (Fig. 5E) with subequal stout outer spines on exopod, terminal spine on exopod slightly less than twice length of adjacent outer spine, inner process near insertion of outer spine on first and second exopodal segments bidentate; outer distal corner of first and second endopodal segments with distinct cleft.

Legs 3 and 4 (Figs 5F, 6A) with two outer spines along third exopodal segment and three outer pointed processes on first endopodal segment. Leg 3 bears curved spine and leg 4 small seta on outer margin of basis.

Leg 5 (Fig. 6B) with inner distal corner of basis extended into long pointed process, minute inner seta on first exopodal segment.

Description

Male. Total body length 1.21 mm. Body with ratio of prosome length to urosome length *Ca* 2.6:1. Urosome (Fig. 6C) four-segmented; distinct striate frill on posterior margin of urosomites 2 and 3. Caudal rami apparently as in female (some setae broken off).

Rostrum as in female. Right antennule (Fig. 6D) 21-segmented with segments II–IV fused; anteroventral margin of segment 20 with pointed process, aestetasc and seta.

Leg 5 (Fig. 6E, F) asymmetrical, greatest modifications distally on exopods. Left basis with inner margin produced into long pointed process. Second endopodal segment longer and broader on right than on left side, with distal outer margin on right side produced into curved and rounded process. Left exopod two-segmented, first segment with strong smooth outer spine, second segment with two unequal setae along outer margin, proximal seta shortest; outer corner of segment transformed into falcate process, seta with bulbous base situated medially on inner margin of segment. Right exopod three-segmented, first and second segments with strong and smooth outer spine, one on second segment slightly curved and longest; third segment bearing falcate process with long thin outer seta and thick inner seta near base.

Ecological notes

Liza Bay Cave lies beneath a low hill about 1 km inland from the east coast of Acklins Island. Multiple sinkhole entrances in the hillside provide access to a series of large, interconnected chambers that contain shallow brackish pools. A large colony of bats inhabits the cave and roost directly over the pools. The pools are floored with gravel, guano and fine silt. Typical pools are 20 m long by 5–10 m wide, but with only 20–30 cm water depth. Most pools are within 10–20 m of cave entrances and so are in twilight conditions during the day. The salinity in the pools was measured at 34 with a refractometer, while the water temperature was 25.5°C. Copepods were collected with a plankton net from the water column in a deeper hole between 0 and 5 m water depth. Other invertebrates collected from the cave pools included amphipods, archiannelid polychaetes, atyid shrimp and a new laomediid shrimp *Naushonia manningi* (Alvarez & al. 2000).

One specimen was obtained in each of the caves Basil Minn's Blue Hole, Norman's Pond Cave and Virgo Blue Hole. For cave descriptions of Basil Minn's Blue Hole see *Minnonectes melodactylus* gen. et sp. nov. below and for Norman's Pond Cave see Fosshagen & Iliffe (1998).

Virgo Blue Hole on Sweetings Cay at the east end of Grand Bahama Island is part of the Zodiac Caverns, an underwater cave system discovered by Rob Palmer in 1983 (Palmer 1985). The entrance to Virgo Blue Hole is in a submerged depression along the shore of a shallow inland lake near the centre of Sweetings Cay. The cave is reached by way of the narrow, mangrove-bordered Zodiac Creek which extends off the south side of Haulover Creek, a wide tidal channel separating Sweetings Cay from Grand Bahama. From the end of the Zodiac Creek, dive gear was carried overland for several hundred metres to the edge of Lake 3, a small pond containing the submerged entrance to Gemini Blue Hole. Gemini is a traverse cave that connects through a passage at 15 m depth to the larger Lake 2 to the south. Virgo Blue Hole is located on the opposite end of Lake 2, about 200 m away. The low, silty

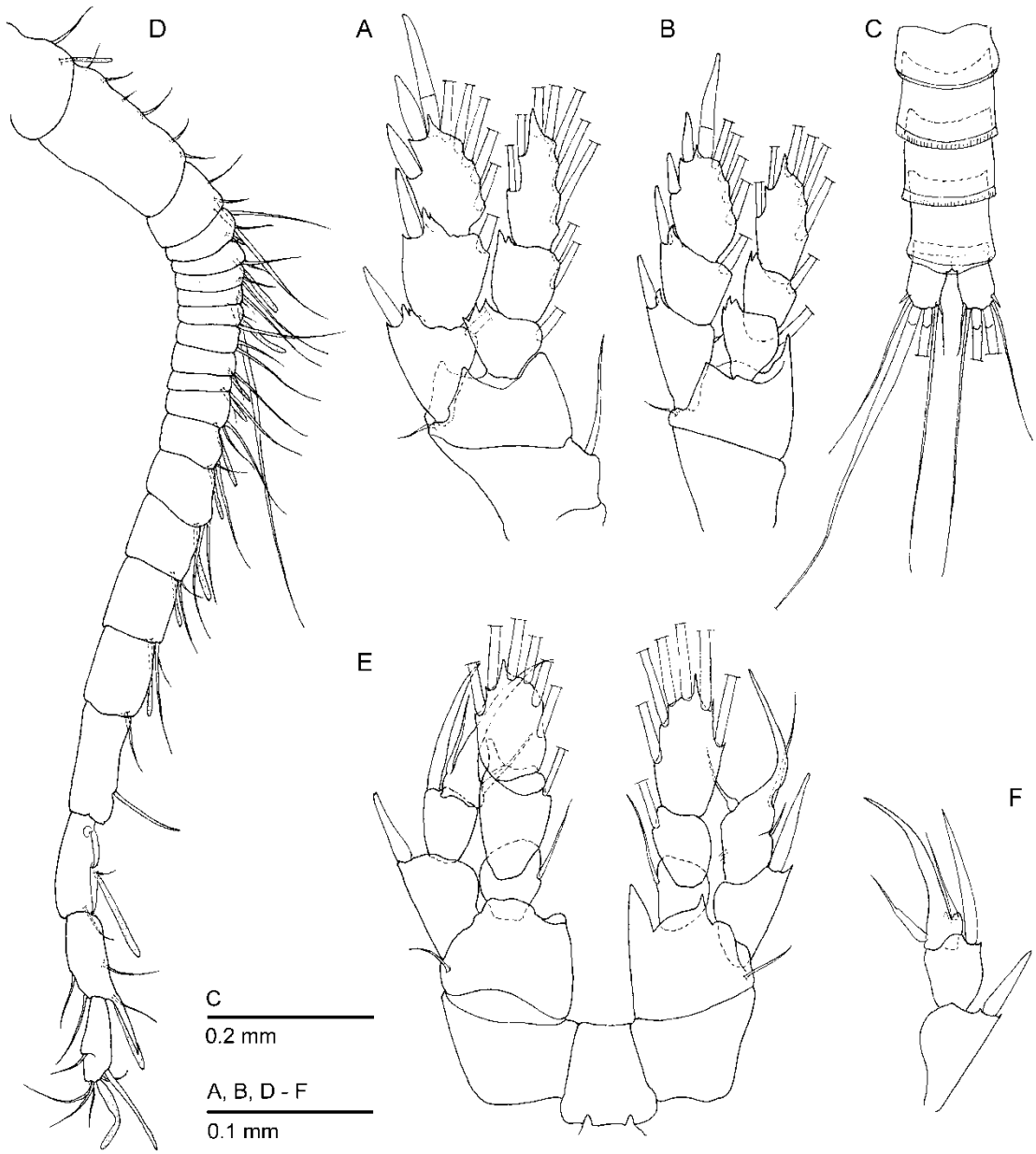

Fig. 6. *Cryptonectes brachyceratus* gen. et sp. n.; female (A, B), male (C–F). A. Leg 4. B. Leg 5. C. Urosome, dorsal view. D. Right antennule. E. Leg 5, posterior view. F. Right exopod leg 5, anterior view.

entrance passage of Virgo opens onto a series of large chambers, well decorated with stalactites and stalagmites, at 15–22 m depth.

Cryptonectes brachyceratus was obtained in the cave from 15 to 21 m depth. Also collected from this cave were the calanoids *Balinella ornata* Fosshagen, Boxshall & Iliffe, *Brattstromia longicaudata* Fosshagen, undescribed species of the Ridgewayiidae and Fosshageniidae, thermosbaenaceans, halocyprid ostracods, cirolanid isopods, amphipods and remipedes.

The records of *Cryptonectes brachyceratus* show a distribution of the copepod in caves on three separate platforms (banks) with deep channels in between. Two of the caves, Norman's Pond and Basil Minn's, are on

Great Bahama Bank, Virgo on Little Bahama Bank and Liza Bay on Acklins Island. Records of this species and of *Brattstromia longicaudata* previously only found in Belize (Fosshagen & Iliffe 1991), and of *Oinella ornata* from the Exumas (Fosshagen & al. 2001) show that species of cave-living calanoids may have a wide distribution, although populations are isolated from each other by great oceanic depths.

Remarks

Cryptonectes brachyceratus exhibits several reductions and apomorphic characters both in mouthparts and swimming legs. Having two outer spines on the third exopodal segment of legs 1–5 in the female, this character connects the species to the two genera in the Erebonectinae in which this is a key character and one of the few apomorphic ones; for this reason the new genus is included in the subfamily. The mouthparts in the Erebonectinae are generally unmodified and showing some of the most plesiomorphic characters of the Calanoida. The new genus has several characters in common with the many genera of the Epacteriscinae, such as a short endopod of the antenna, reductions in the number of setae on the mandible and maxillule. The most extreme apomorphic state of these characters, however, is developed in *Epacteriscus*. A rare plesiomorphic character in *Cryptonectes* is the presence of an outer basal seta on leg 1, a character also found in *Erebonectes* and *Bomburiella*. Thus, the new genus shows a mosaic of characters from both subfamilies.

Judging from the compact and stout appearance, the short antennule and strong spines on the outer margin of swimming legs, the animal seems to live a benthic life. Strong and specialized setae on the maxilla and maxilliped suggest raptorial feeding.

Genus *Minnonectes* gen. nov.

Diagnosis

Male. Cephalosome and first pedigerous somite fused dorsally. Urosome five-segmented with very short anal segment. Caudal seta II long and slender. Rostrum broad, bilobed and with long filament near rounded tip. Right antennule geniculate and indistinctly 24-segmented, with partial fusion of segments II, III and IV. Antenna with endopod shorter than exopod, proximal segment of endopod longer than distal. Mandibular palp with small one-segmented endopod carrying two setae; ventral-most tooth of gnathobase enlarged, bifid and rounded distally. Maxillule relatively slender and with reduced number of setae. Maxilla with condensed endopod bearing four to five very long and strong elements having black club-shaped tips. Maxilliped with endopod bearing long strong setae with black, lamellate and rounded tips. Leg 1 with two outer spines on third exopod segment stout and of reduced length. Legs 3 and 4 with three outer spines on third exopod segment; leg 3 with outer spine on basis. Leg 5 with three-segmented rami, only slightly modified, mainly in third segment of exopods; right third segment with strong falcate process and bearing inner and outer setae proximally; left third segment reduced with three slender seta-like elements.

Type species

Minnonectes melodactylus gen. et sp. nov.

Etymology

The generic name refers to part of the cave's name (Basil Minn's Blue Hole) and the animal swimming in it (from Greek *nektos* meaning swimming). Gender masculine. The specific name refers to the black distal part of the strong setae of the maxilla and maxilliped (from Greek *melas* meaning black; *daktylos* meaning finger).

Minnonectes melodactylus gen. et sp. nov.

Material examined

Only one male specimen obtained in Basil Minn's Blue Hole, Great Exuma Island, Bahamas, 18 March 2000.

Type

Holotype. Adult male, total body length 1.57 mm, from Basil Minn's Blue Hole, Great Exuma Island, Bahamas (23°29′N 75°46′W), 18 March 2000, collected from water column in 50–10 m depth in the dome room. Six slides BM(NH) reg. no. 2003.586.

Description

Male. Total body length 1.57 mm. Body (Fig. 7A) with ratio of prosome length to urosome length *Ca* 2.0:1. Cephalosome and first pedigerous somite fused dorsally. Urosome (Fig. 7A, B) five-segmented, with only trace of anal somite ventrally. Dorsal posterior margin of fourth urosomite with undulate frill. Caudal rami apparently symmetrical and with plumose setae (some setae broken); seta II long and slender, seta V longer than length of urosome.

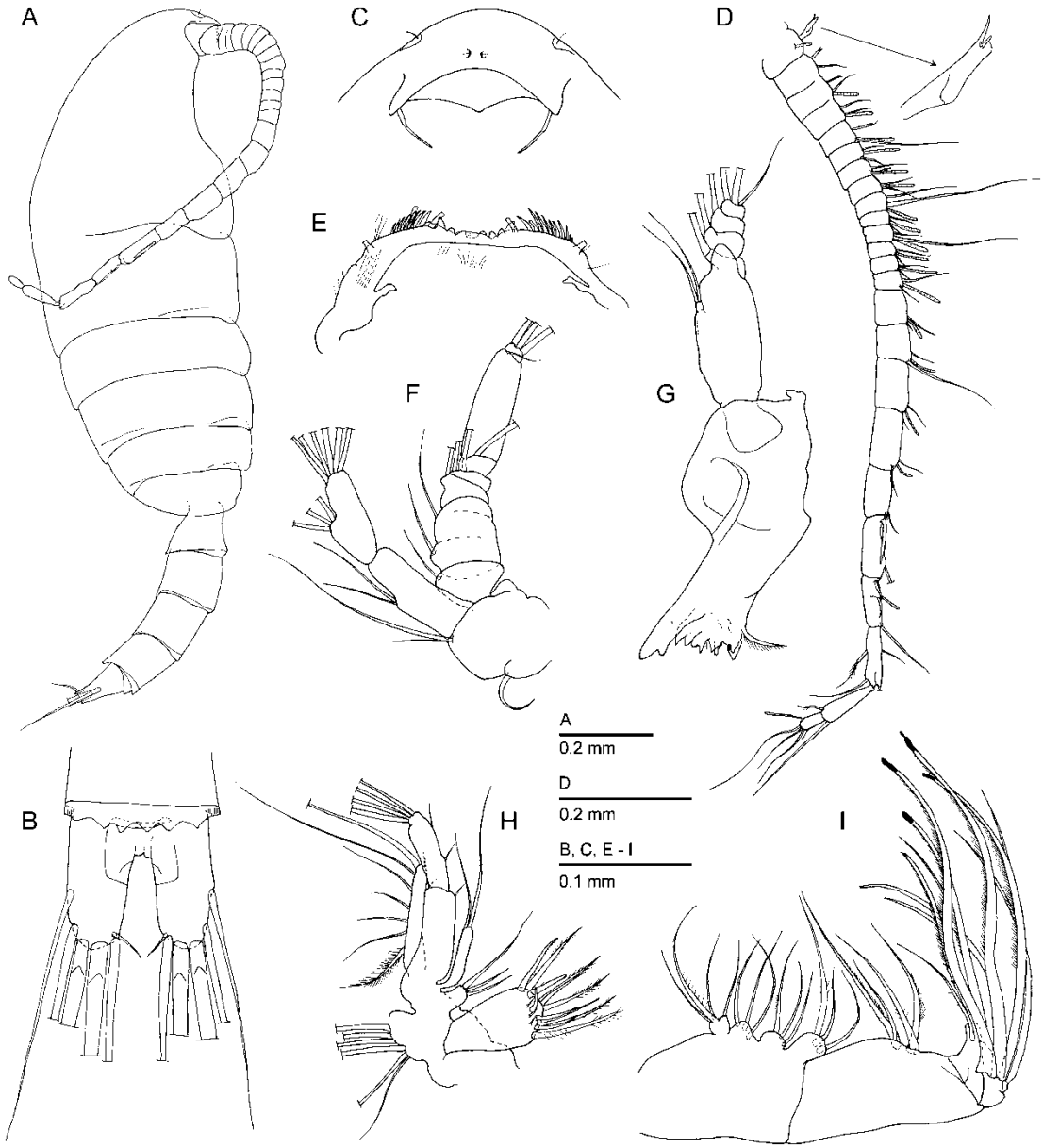

Fig. 7. *Minnonectes melodactylus* gen. et sp. n.; male. A. Habitus, lateral view. B. Caudal rami, dorsal view. C. Rostrum. D. Right antennule. E. Labrum. F. Antenna. G. Mandible. H. Maxillule. I. Maxilla.

Rostrum (Fig. 7C) two large processes far apart, each slightly rounded at tip and bearing long filament subdistally.

Right antennule (Fig. 7D) 24-segmented with segments II–IV partially separated; modified setae on proximal part up to and including segment VII; distal process, aestetasc or seta probably broken off on segment 22. Distal part of left antennule from segment XVI onwards missing, but remaining limb similar to that of right side except that one of setae on segments XII and XIV has become more elongate.

Antenna (Fig. 7F) with exopod slightly longer than endopod. Proximal endopod segment slightly longer than distal; distal one with three setae on inner lobe and

six setae on terminal lobe. Exopod indistinctly eight-segmented with segments 2 and 3 partially separated; penultimate segment elongate and last two segments combined about half length of exopod.

Labrum (Fig. 7E) ornamented along margin from middle towards outer part with three to four coarse teeth, outermost teeth largest and with adjacent cylindrical projection, then cluster of spinules, scattered setules and one short cylindrical projection.

Mandible (Fig. 7G) with gnathobase bearing strong bifid ventral-most tooth; row of four major teeth and additional minor teeth connected, and dorsal unipinnate seta. Palp with much reduced one-segmented endopod with two setae; exopod normally developed.

Maxillule (Fig. 7H) relatively slender and with reduced number of setae; praecoxal arthrite with 13 setal elements plus three short stout processes; coxal endite and basal endites with three, two and one setae, respectively, proximal basal endite elongate; coxal epipodite with six setae. Endopod with two small setae along inner margin and four terminal setae. Exopod slender with eight unequal setae distributed evenly along outer margin, subterminal seta very small.

Maxilla (Fig. 7I) with rounded endites on syncoxa and bearing relatively short and flexible setae, proximal endite with four setae and one short process; basis with four setae of unequal length and with different ornamentation; endopod with 11 elements, of which four to five setae very long and strong, highly modified with black club-shaped rounded tips, fine setules along most of their length and with some proximal spinules.

Maxilliped (Fig. 8A) with minute seta on praecoxal endite, long setae on coxa smooth, one small seta on distal endite with bulbous base; basis with three setae, proximal and distal ones of subequal length, middle seta short. Endopod apparently four-segmented with fusion of first two segments; long seta on ancestral first segment with black, smooth and rounded distal part; seven long and strong setae along endopod modified in distal part, black, broadened, lamellate and with rounded tip.

Legs 1–4 spine and seta formula as follows:

	Coxa	Basis	Exopod segment			Endopod segment		
			1	2	3	1	2	3
Leg 1	0-1	0-1	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 1 (Fig. 8B) with pointed process distally on inner margin and medially on distal margin of basis; all exopodal spines with subterminal ornamentation on inner side, two outer spines on third exopodal segment of reduced length, terminal spine of exopod with hyaline frill along outer margin.

Leg 2 (Fig. 8C) with outer spines on exopod on first, second, and proximal one on third segment of subequal length, outer distal spine on third segment slightly longer than other outer spines and about half length of terminal spine; inner process at insertion of outer spine on first and second exopodal segments elongate and with multidentate inner base. Outer distal corner of second endopodal segment with distinct cleft.

Legs 3 and 4 (Fig. 8D, E) with three spines of unequal length along outer margin of third exopodal segment. Leg 3 with outer spine on basis and leg 4 with small seta in same position.

Leg 5 (Fig. 8F) with both rami three-segmented, slightly asymmetrical with greatest modifications in third segment of exopod. Second endopodal segment on right side with outer distal margin produced into pointed process. First and second exopodal segments on both sides armed with strong outer spine, that on first segment flanged along inner margin, that on second segment flanged on both sides. Third exopodal segment on right side with falcate process, near base of which with one outer and one inner subequal seta; third exopodal segment on left side small, with three dissimilar slender elements, two distal ones and one seta-like medially on outer margin.

Ecological notes

Basil Minn's Blue Hole is a wholly submerged cave that crosses beneath Great Exuma Island from northeast to southwest. The cave is entered through a karst window consisting of a large lake with two openings into the cave. A 10–12 m wide passage extends for several hundred metres at 50 m depth, before opening into a 50 m wide room, well decorated with underwater stalactites and stalagmites. This circular room contains a breakdown mound in the centre with an air dome above, but no apparent opening to the surface. The cave is tidally influenced, acting as a water source for the lake. Water in the cave is fully marine with hydrogen sulphide present at 30 m depth and sporadically in other locations.

In addition to the new species, the sample from 18 March 2000 contained the calanoids *Cryptonectes brachyceratus* (see above), *Ridgewayia* spp. and *Paramisophria* sp.; cyclopoids, harpacticoids, amphipods, thermosbaenaceans, halocyprid ostracods, cirolanid isopods and polychaetes were also obtained.

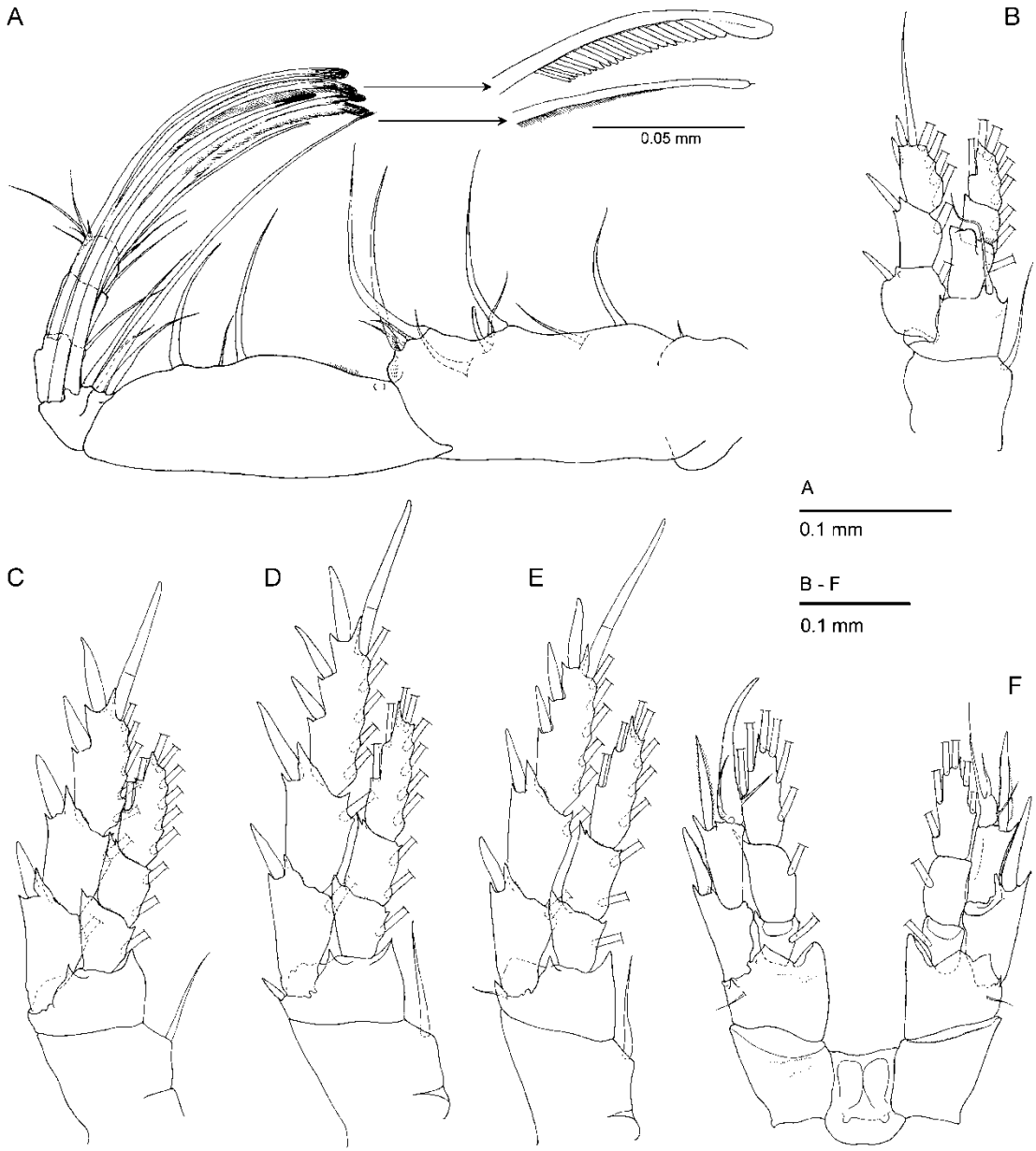

Fig. 8. *Minnonectes melodactylus* gen. et sp. n.; male. A. Maxilliped. B. Leg 1. C. Leg 2. D. Leg 3. E. Leg 4. F. Leg 5, posterior view.

Remarks

According to the spine and seta formula for legs 1–4, *Minnonectes* clearly falls into the subfamily Epacteriscinae. Although only the male is known, the new species shows many similarities to *Enantronia canariensis* where only the female is known. Both species have a broad, pointed and bilobed rostrum, very similar antenna and labrum, the gnathobase of the mandible with a bifid ventral-most tooth, although with an extra seta on the mandibular endopod in *Enantronia*, the maxillule in the new species differs only in a more elongate proximal basal endite bearing two instead of three setae in *Enantronia*, and *Minnonectes* has one

spine instead of one seta on the basis of leg 3 in *Enantronia*.

Leg 5 in *Minnonectes* is reminiscent of the same leg in *Enantronoides*, *Bunderia*, *Oinella* (see below), and *Gloinella*, all having in common rather weak transformations in the third exopodal segment on both sides.

At present only one sex is known in *Enantronia*, *Enantronoides* and *Minnonectes* and the discovery of the missing sex might clarify the taxonomic position and affinities of these genera.

The unique modifications of endopodal setae of the maxilla and maxilliped in *Minnonectes*, however, seem to justify the erection of a new genus for this taxon.

Genus *Oinella* Fosshagen, Boxshall & Iliffe, 2001

Diagnosis

Male. Urosome five-segmented with anal somite minute and concealed. Caudal rami symmetrical with seta II long and setose. Right antennule geniculate, 21-segmented, with acute process distally on segment 20, segments IX and XI with particularly long seta. Leg 5 with three-segmented rami; slightly asymmetrical with third segment of right exopod bearing long straight process distally and third segment of left exopod with two subequal short elements distally.

Oinella longiseta Fosshagen, Boxshall & Iliffe, 2001

Sanctuary Blue Hole, South Andros, Bahamas, 15 October 1999. One adult male collected with plankton net from water column in 50–35 m depth. Total body length 0.93 mm. Dissected and mounted on seven slides. BM(NH) reg. no. 2003.587.

Previously one incomplete female and one male copepodid stage V have been described from Oven Rock Cave, Great Guana Cay, Exuma Cays (Fosshagen & al. 2001). The new record of an adult male permits a more complete description of the species.

Description

Male. In dorsal view, prosome oval with five distinctly separated pedigerous somites, fifth pedigerous somite short with rounded posterolateral margins (Fig. 9A). Ratio of prosome length to urosome length *Ca* 2.8: 1. Rostrum (Fig. 9C) broad with lateral corners each with minute filament near tip.

Urosome (Fig. 9B) apparently four-segmented with subequal somites, but minute anal somite might be telescoped within preceding somite. Caudal rami symmetrical with seta II long and setose.

Right antennule (Fig. 9E) 21-segmented, reaching just beyond second pedigerous somite; segments II–IV fused, segments IX and XI bearing extra long seta, segment 20 (XXIV–XXV) with long acute process distally, distal segment 21 consists of fused segments XXVI–XXVIII. Left antennule as in female with extra long seta on segments IX and XIV but segments XXVI–XXVIII partially fused.

Antenna with one inner seta on coxa, four long setae along inner margin of exopod and one small seta in addition to three long setae distally on exopod.

Labrum (Fig. 9D) with multidentate margin, outer tooth on both sides broad and molar-like.

Mandible as in female, with extremely long seta on penultimate segment of exopod reaching end of prosome. Other mouthparts generally as in female; maxilliped with one minute seta on praecoxa and four setae on second coxal endite.

Leg 1 as in female. Legs 2–4 (Figs 9F, 10A, B) (partly missing in damaged female specimen) typical for Epacteriscinae; bases without any outer element and distal spine on third exopodal segment long and smooth.

Fifth legs (Fig. 10C) with three-segmented rami; endopods slightly asymmetrical with third segment bearing seven setae on right side (which may indicate an abnormality in the single specimen) and six setae on left side. Exopods slightly transformed with greatest modifications in third segment; right side bears three unequal elements: outer short process, distal long straight process and inner medial slender spine; left side bears three subequally long elements: outer medial spine, distal process in socket and distal inner spine.

Ecological notes

The species co-occurred with *Azygonectes intermedius* in Sanctuary Blue Hole; and for other species and cave description see above.

Remarks

The male from Sanctuary Blue Hole and the female from Oven Rock Cave are considered conspecific. They are recorded from localities about 120 km apart and separated by the deep Tongue of the Ocean but they are from the same shallow Great Bahama Bank. They show general similarity, agreement in size and particularly in the modified seta on the mandibular palp. No other species of the family bear such an extremely long seta on this limb. The shape of the rostrum and the elements of the caudal rami agree with those of the male copepodid V recorded previously.

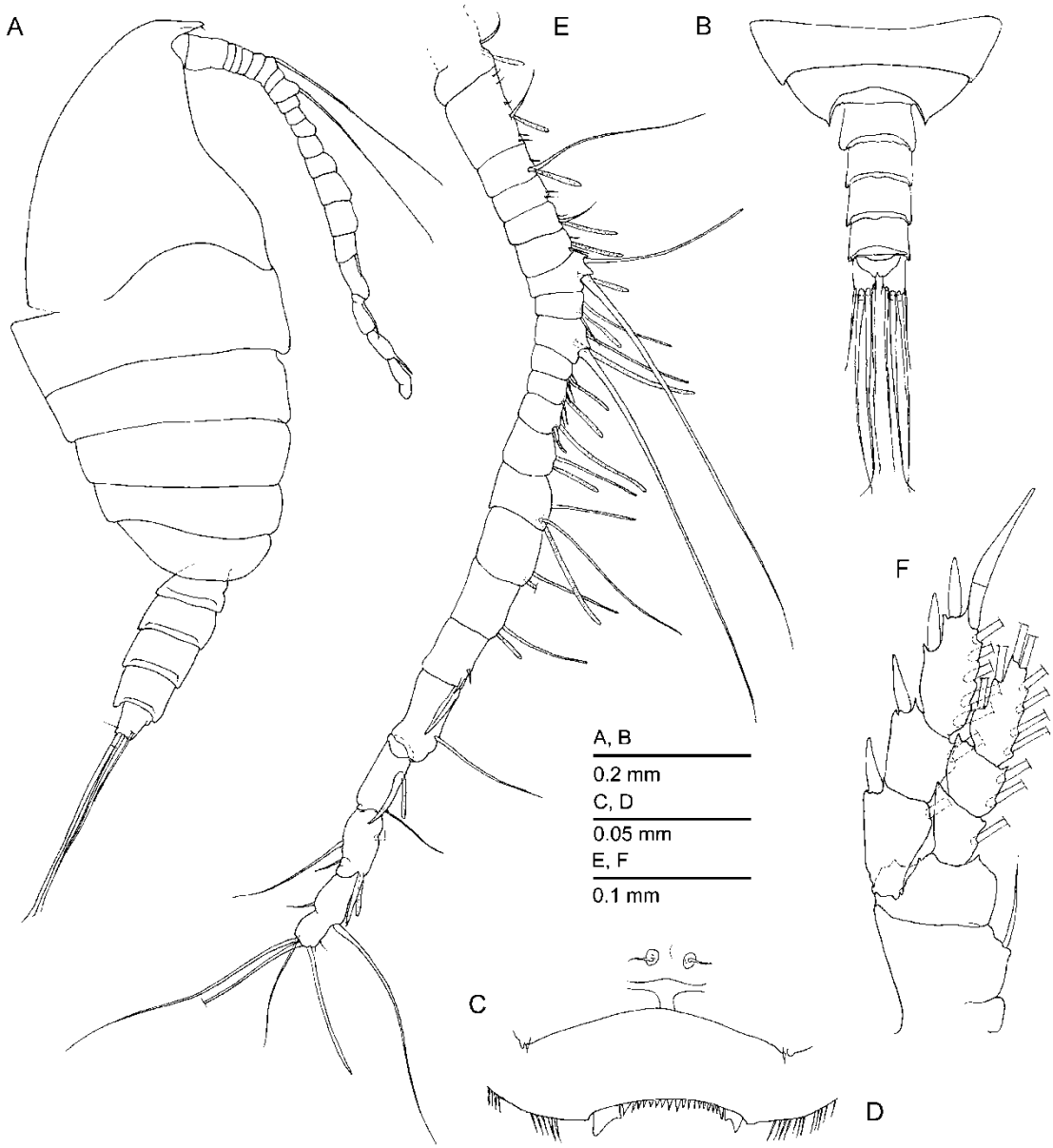

Fig. 9. *Oinella longiseta* Fosshagen, Boxshall & Iliffe; male. A. Habitus, lateral view. B. Urosome, dorsal view. C. Rostrum. D. Labrum. E. Right antennule. F. Leg 2.

Knowing the structure of the swimming legs of *Oinella* it is now clear that the genus falls into the subfamily Epacteriscinae. The weakly modified leg 5 of the male with three-segmented rami is in common with the genera *Bunderia*, *Edaxiella*, *Enantronoides* and *Gloinella*. It is most reminiscent of *Enantronoides* with a similar rostrum; the antennule with an extra long seta on segments IX and XIV in the female, and a pointed process distally on segment XXV of the right antennule in the male; the lack of an endopod on the mandibular palp; a reduction in the number of setae on the maxillule and strong spinous setae on the

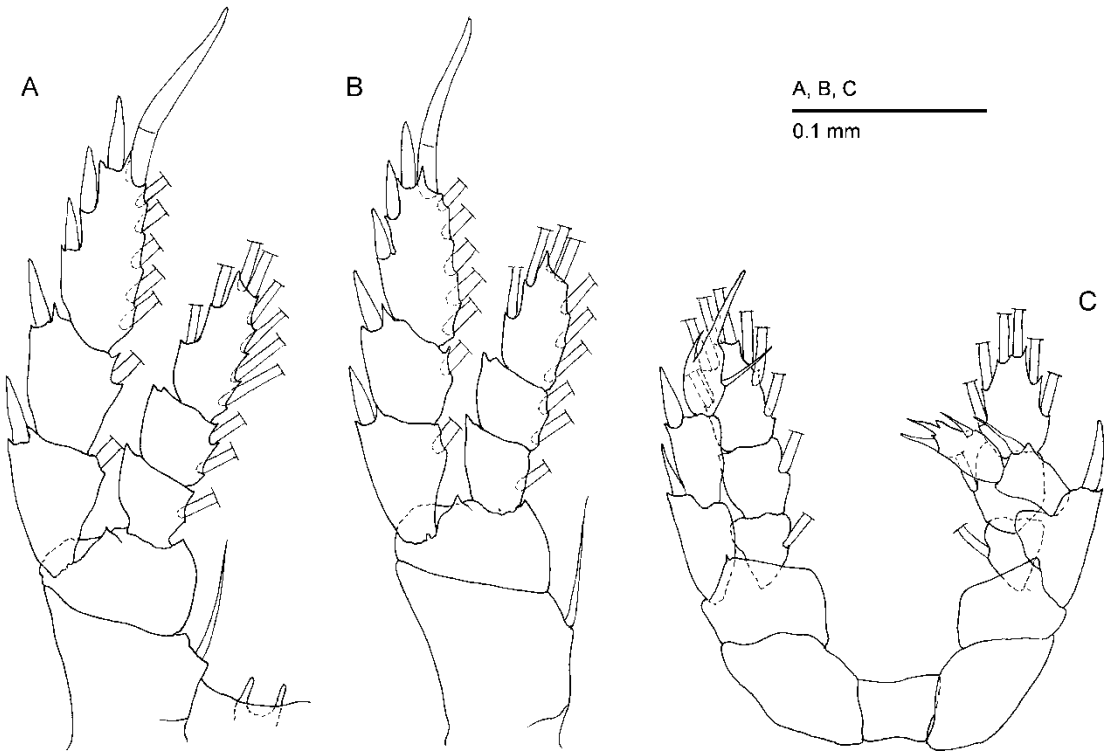

Fig. 10. *Oinella longiseta* Fosshagen, Boxshall & Iliffe; male. A. Leg 3. B. Leg 4. C. Leg 5, posterior view.

maxilla and maxilliped. Characters distinguishing the two genera, apart from the long distal seta on the mandibular exopod, are: the larger size of *Enantronoides*, a distinctly five-segmented urosome and asymmetrical caudal rami of the male *Enantronoides*; a short proximal endopodal segment of the antenna devoid of elements in *Oinella* against a normally developed segment in *Enantronoides*.

Balinella ornata Fosshagen, Boxshall & Iliffe, 2001

Hitherto only one male and one female specimen have been recorded from Norman's Pond Cave, Exumas in 1993 and 1994 (Fosshagen & al. 2001). New records were made in 2001 from three different caves on Sweetings Cay, Grand Bahama at depths between 15 and 25 m: Virgo Blue Hole 2 December (five males, eight copepodids), Sagittarius Blue Hole 3 December (one female), and Lucy's Cave 4 December (two females). The new records are on Little Bahama Bank, divided by deep water from Norman's Pond Cave on Great Bahama Bank.

Both males and females had an elongate seta V on the left caudal ramus, and not on the right side of the female as stated in Fosshagen & al. (2001). One very small specimen of a male *Balinella* was observed from Lucy's Cave, possibly representing another species of the genus.

Enantronoides bahamensis Fosshagen, Boxshall & Iliffe, 2001

Until now only one male specimen has been recorded in 1995 from Oven Rock Cave, Great Guana Cay, Exumas (Fosshagen & al. 2001). Two more male specimens were obtained from the same locality on 21 March 2001 in a suction bottle from 10–20 m depth.

Bomburiella gigas Fosshagen, Boxshall & Iliffe, 2001

This is the largest species among the epacteriscids with females up to 3.3 mm in total length and has been recorded previously from two localities, from Oven Rock Cave, Great Guana Cay, Exumas in 1995, 1996,

and 1998 and from Stargate Blue Hole, South Andros in 1997 (Fosshagen & al. 2001). Now new records are made of one female on 21 July 2001 at 15 m depth and two females and one copepodid on 14 August 2002 at 5–20 m depth from Oven Rock Cave and one female and two copepodids from Sanctuary Blue Hole, South Andros (situated about 1 km away from Stargate Blue Hole) on 15 October 1999 at 35–50 m depth.

Bofuriella vorata Fosshagen, Boxshall & Iliffe, 2001

Previously this species has only been obtained at Oven Rock Cave, Great Guana Cay, Exumas (Fosshagen & al. 2001). Now a new record of one copepodid stage V has been made at Sanctuary Blue Hole, South Andros on 15 October 1999 at 35–50 m depth.

CONCLUDING REMARKS

In the 17 genera of the family, most are monotypic, and specimens are rare, and in five genera (*Enantronia*, *Enantronoides*, *Azygonectes*, *Minnonectes*, and *Iboyella*) only one sex is known. Only *Epacteriscus* and *Enantiosis* have more than one species, with three and seven species, respectively (Fosshagen & al. 2001).

Since the phylogenetic analysis (Fosshagen & al. 2001), five new genera have been added (*Bunderia* Jaume & Humphreys, 2001; *Iboyella* Boxshall & Jaume, 2003; and the present three new genera) plus the males of *Balinella ornata* Fosshagen, Boxshall & Iliffe, 2001 and *Oinella longiseta* Fosshagen, Boxshall & Iliffe, 2001. No attempt has been made to expand the analysis, as new taxa most certainly await discovery.

The family is very diverse and shows an array of different structures of mouthparts from the most plesiomorphic *Erebonectes* to the most apomorphic *Epacteriscus*. All species have a strong mandibular gnathobase, a mandibular palp with a normal exopod but the inner part is reduced, sometimes with the loss of the endopod; setal reductions in the mouthparts, and strong spinous setae on the maxilla and maxilliped are apparent. This speaks for predatory habits and might infer that the different genera are specialized for different diets. A long antennule may indicate a pelagic life in caves, and a short antennule combined with strong outer spines on swimming legs indicate a benthic existence.

In contrast to epacteriscids, ridgewayiids, which have a well-developed mandibular endopod and high numbers of unmodified setae on mouthparts, were often abundant in plankton in several caves. Some of these ridgewayiids may be considered suspension feeders and may in turn constitute a possible prey for epacteriscids. Most common were species of *Ridgewayia* (pers. obs.), *Brattstromia* (Fosshagen & Iliffe 1991), *Exumellina* (Fosshagen & Iliffe 1998), and *Stargatia* (Fosshagen & Iliffe 2003). The ridgewayiids *Exumella* and *Brattstromia* which have been obtained in both plankton and baited traps (Fosshagen & Iliffe 1991; Jaume & Boxshall 1995; pers. obs.) have modified and strong spines on the maxilliped; in *Exumella*, however, the inner part of the mandibular palp is reduced and reminiscent of species of epacteriscids. Thus, a mandibular palp with reductions on its inner part seems to be indicative of predatory habits as well as pointing to a systematic relationship between the families. Further connections are found in *Azygonectes*, where the third exopodal segment of leg 5 in the female is set off in the characteristic way of ridgewayiids, and in *Stargatia*, where the same limb is reminiscent of epacteriscids. In addition, *Stargatia* bear asymmetrical setae on caudal rami, a common character among epacteriscids.

With the discovery of several new species in the two families, it appears that they must be considered quite closely related.

ACKNOWLEDGEMENTS

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