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Three new genera of the Ridgewayiidae (Copepoda, Calanoida) from anchialine caves in the Bahamas

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SARSIA

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Stargatia palmeri gen. et sp. nov. was obtained in great numbers in plankton from very low dissolved oxygen waters of Stargate Blue Hole, South Andros at 44 m depth. The species shows similarities to *Exumellina bucculenta* Fosshagen in the modifications of the endopod of both mandible and maxillule, and by the presence of only two outer spines on the third exopod segment of legs 3 and 4. The rostrum comprises two rounded lobes without filaments. The right antennule of the male is modified in proximal part with extra geniculations. It differs from other ridgewayiids by not having the typical offset third exopod segment in the female leg 5. *Robpalmeria asymmetrica* gen. et sp. nov. was also recorded from Stargate Blue Hole. In the female the last somite of the prosome is asymmetrical. The rostrum is narrow with two filaments at the tip. The maxilliped is strongly developed, reflexed and with a condensed endopod bearing several modified setae; suggesting raptorial feeding. Leg 5 in the male has complex exopods and rudimentary endopods. *Normancavia minuta* gen. et sp. nov. was obtained from Norman's Pond Cave, Exumas. It is reminiscent of *R. asymmetrica* but differs much in leg 5 of both sexes. It is the only ridgewayiid lacking an endopod of leg 5 in the female. Leg 5 in the male bears elongated endopods with distal setal elements. All three genera, most conspicuous in *Stargatia,* have a proximal geniculation in the right antennule of the male.

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INTRODUCTION

Ridgewayiids are primitive calanoid copepods from shallow waters in tropical and subtropical areas and are often closely connected with the bottom or with caves. Five genera were hitherto known and all except *Ridgewayia* Thompson & A. Scott, 1903 were discovered in recent years. All are represented in the Caribbean area (Fosshagen & Iliffe 1998).

The most characteristic feature of the family is a modification of the exopod of leg 5 in females. The third segment has a very narrow articulation with the second and this articulation is offset medially, partly through the expansion of the distal part of the second segment. Usually ridgewayiids have primitive and only slightly modified mouthparts and 3-segmented rami of legs 1–4, with exceptions in the mouthparts of *Exumella* Fosshagen, 1970 and *Exumellina* Fosshagen, 1998, and in the legs of *Placocalanus* Ohtsuka, Fosshagen & Soh, 1996.

The most common and widely distributed genus is *Ridgewayia*, with 11 nominal species recorded in the Atlantic, Mediterranean and Indo-Pacific regions, both in and outside caves (Ferrari 1995; Barthélémy & al. 1998; Ohtsuka & al. 2000). Species are often found in swarms among corals and one species is also associated with an actiniarian (Humes & Smith 1974). *Exumella* is caught both in and outside caves (Fosshagen & Iliffe 1991), and is also found in the Mediterranean (Jaume & Boxshall 1995) and in the Indo-Pacific (Walter 1986). *Placocalanus* is caught only in benthic habitats outside caves and has also been recorded in Japan (Ohtsuka & al. 1996). *Brattstromia* Fosshagen, 1991 and *Exumellina* are monotypic and exclusively cave living. *Brattstromia* has been recorded from two caves in Belize (Fosshagen & Iliffe 1991) and *Exumellina* from one cave in the Bahamas (Fosshagen & Iliffe 1998), but now also from another cave in the area.

The three new genera to be described below were all obtained by cave diving in two anchialine caves in the Bahamas. They show various modifications of the mouthparts, thus probably reflecting some new feeding strategies within the family.

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MATERIAL AND METHODS

The copepods were obtained from Stargate Blue Hole, South Andros Island and Norman's Pond Cave, Exumas using advanced diving techniques and usually by dragging a fine-mesh hand-held net (*Ca* 100 µm) through the water.

The type material is kept in the Natural History Museum (BMNH), London. The terminology used is that of Huys & Boxshall (1991).

SYSTEMATICS

Family Ridgewayiidae M. S. Wilson, 1958 emended

The family diagnosis is based on the following eight genera: *Ridgewayia* Thompson & Scott, 1903; *Exumella* Fosshagen, 1970; *Brattstromia* Fosshagen, 1991 (in Fosshagen & Iliffe 1991); *Placocalanus* Ohtsuka, Fosshagen & Soh, 1996; *Exumellina* Fosshagen, 1998 (in Fosshagen & Iliffe 1998); *Stargatia* gen. nov.; *Palmeriella* gen. nov. and *Normancavia* gen. nov.

Diagnosis (emended)

Small copepods with total length between 0.4 and 1.6 mm. Prosome oval in dorsal view; only *Placocalanus* compressed laterally. Cephalosome and first pedigerous somite as well as fourth and fifth pedigerous somite separated or coalescent; fifth pedigerous somite sometimes asymmetrical. Rostrum with or without filaments, sometimes bifurcate, blunt or pointed at tip. Urosome 4-segmented in female and 5-segmented in male; in *Exumella*, 3-segmented in female and 4-segmented in male. Genital double-somite of female with single genital operculum located ventromedially or laterally on right side. Antennule of female 22- to 27-segmented; right antennule of male geniculate, 20- to 23-segmented. Antenna, mandible, maxillule and maxilla usually of primitive calanoid type; in *Exumellina* and *Stargatia*, endopod of mandible and maxillule enlarged and modified. Maxilliped often with some modified setae on endopod; endopod reflexed and much compressed distally in *Exumella, Palmeriella* and *Normancavia.* Leg 1 rather modified or not. Legs 1–4 usually with 3-segmented rami; third segment of exopod legs 3 and 4 with two outer spines in *Exumellina* and *Stargatia.* Leg 5 of female with 3-segmented exopod, third segment constricted basally and usually arising towards medial end of oblique distal margin of second segment; endopod lacking to 3-segmented. Leg 5 of male asymmetrical, exopods usually very complex, endopod 1- to 3-segmented, sometimes rudimentary.

Genus *Stargatia* gen. nov.

Diagnosis

Female. Body slender. Pedigerous somites 1–5 separate. Posterior corners of prosome smoothly rounded. Urosome 4-segmented with genital double-somite projecting ventrally. Caudal rami elongate, about four times longer than wide, with seta II spinous and situated posterolaterally, seta V on left side about twice length of corresponding seta on right side. Rostrum with two rounded lobes without filaments.

Antennule reaching to caudal rami; 26-segmented with segments II and III fused. Antenna with rami of subequal length; exopod 9-segmented with small slender seta on first, second and third segments. Mandible with weakly developed gnathobase; endopod strongly developed with second segment bearing strong pointed processes with filament at tip. Maxillule with two proximal setae on coxal epipodite modified into short, flattened and leaf-like structures; endopod 3-segmented with bulbous processes along inner margin. Maxilliped with weakly developed setae on syncoxal endites; some modified setae on proximal part of endopod.

Leg 1 with slender rounded process on posterior side of basis; outer spines of exopod slender and with filament. Legs 1–4 with two outer spines on third exopod segment. Leg 5 with third exopod segment not particularly constricted at base and set off near distal end of second segment; endopod 3-segmented with six setae on third segment.

Male. Urosome 5-segmented; caudal seta V on left side elongate, relatively shorter than that of female. Right antennule 22-segmented with two areas of geniculation, in complex proximal part between segments VII and XVI and with typical distal geniculation between segments XX and XXI; segments II–IV fused; segments XII–XIV diminished and with setal modifications; segments XVI and XVII separate; long pointed process distally on segment 20 (XXIV–XXV).

Mouthparts and legs 1–4 similar to those of female except for somewhat stronger and more curved outer spines on exopods, in particular in leg 2. Leg 5 with modified exopods; only slightly modified endopods; basis of right leg with strong, curved inner process.

Type species

Stargatia palmeri gen. et sp. nov.

Etymology

The generic name refers to the cave, Stargate Blue Hole, where the new copepod was obtained. The specific name is in honour of the late Robert Palmer, a cave diver and a pioneer in the exploration and scientific investigation of this cave and other Bahamian blue holes.

Habitat

Stargate Blue Hole is located about 500 m inland from the east coast of South Andros Island, Bahamas on the west side of The Bluff village. 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 to this cave is a partially roofed-over cavern with a vertical drop of 6 m to the water level. The restricted nature of the entrance limits organic input and as such, the surface water is relatively clear. Underwater, a shaft drops vertically to depths in excess of 80 m, while rift-like passages extend north and south. To the north, a 10 m wide passage with the roof at −20 m extends for 107 m to a breakdown choke. To the south, a similar passage runs for 100 m to another choke, passable on the right hand side at −37 m to reach an extremely loose boulder chamber that chokes after a further 30 m. Speleothems are present at all depths, while a thin layer of fine, brown sediment covers breakdown blocks on the floor of the cave.

Water column profiles were obtained by lowering a Hydrolab recorder water quality multiprobe logger from the surface to 80 m depth on 20 August 1997 (Fig. 1). Surface waters in the entrance pool were found to have a salinity of 3.4. A halocline between 20 and 27 m depth marked the transition to a salinity of 35. From 27 to 82 m, salinity gradually increased to 37. The general temperature trend in the water column involved a decrease from 27.4 °C at the surface to 25.0 °C at 82 m. However, secondary temperature maxima occurred above and below the halocline at 10–11 m (25.82 °C) and 30–32 m (26.12 °C). The pH decreased from 8.7 at the surface to 8.18 at 82 m. A secondary pH minimum of 8.21 occurred at the halocline at 22–24 m depth, while a secondary maximum of 8.54 was found below the halocline at 30 m. Dissolved oxygen decreased from 5.67 mg l^{-1} at the surface to 0 at 63 m and below. A secondary oxygen maximum of 2.96 mg l^{-1} occurred at 31 m depth.

Two water layers, several metres thick, characterized by reduced water clarity and an abundance of copepods, are present in the cave at 16–20 m and at 43 m depth. Below the shallower layer, water clarity increases considerably. Wall rock changes in colour from light brown outside to grey within the layer.

Stargatia palmeri gen. et sp. nov. (Figs 2–5)

Material examined

The new species was obtained twice in Stargate Blue Hole, South Andros Island, Bahamas. It was caught using a diver-held plankton net in the water column on 24 August 1997 at 33–36 m depths in North Passage, and at 44 m depth in the hypoxic "cloud layer" of the

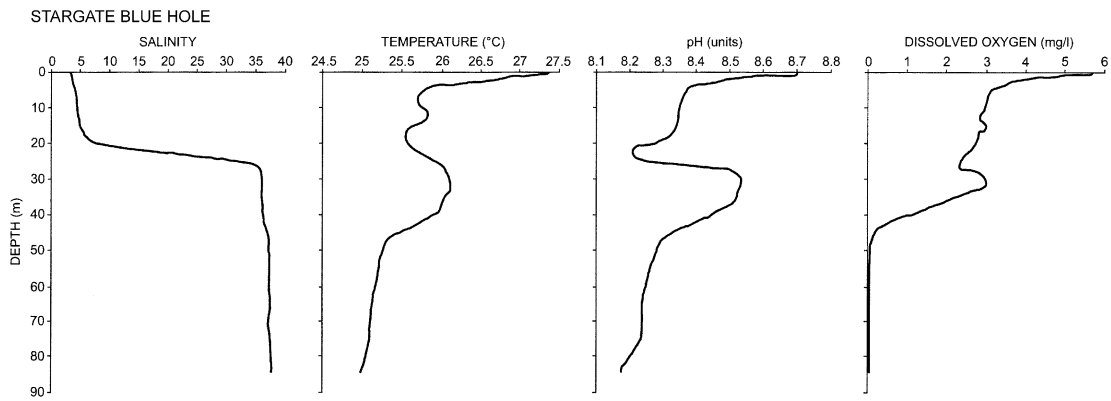

Fig. 1. Vertical profiles of salinity, temperature, pH, and dissolved oxygen in Stargate Blue Hole, South Andros Island, Bahamas. A Hydrolab Datasonde III profiler was used to obtain the measurements on 20 August 1997.

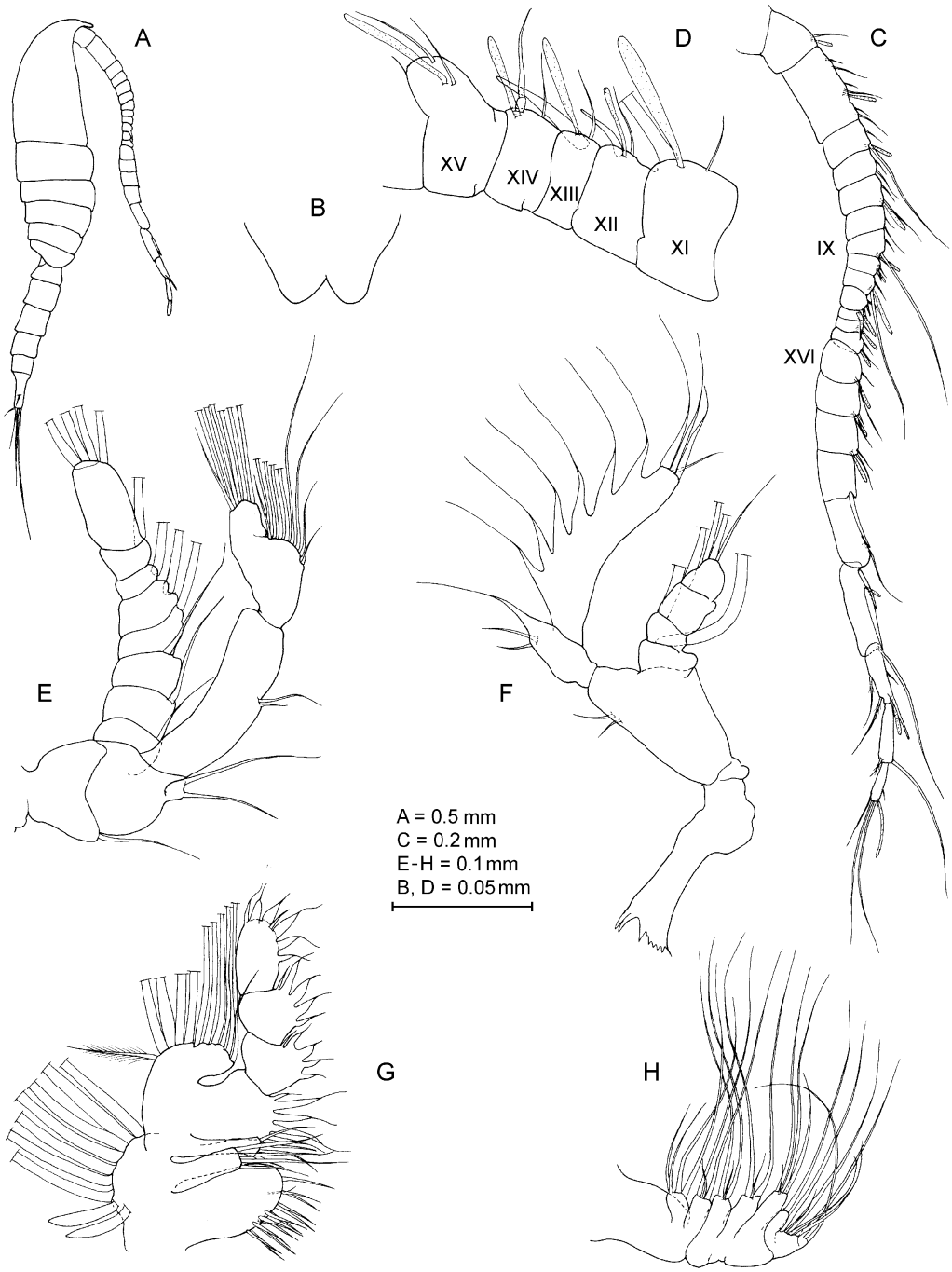

Fig. 2. *Stargatia palmeri* gen. et sp. nov., male. A. Habitus lateral view. B. Rostrum. C. Right antennule. D. Right antennule, segments XI–XV. E. Antenna. F. Mandible. G. Maxillule. H. Maxilla.

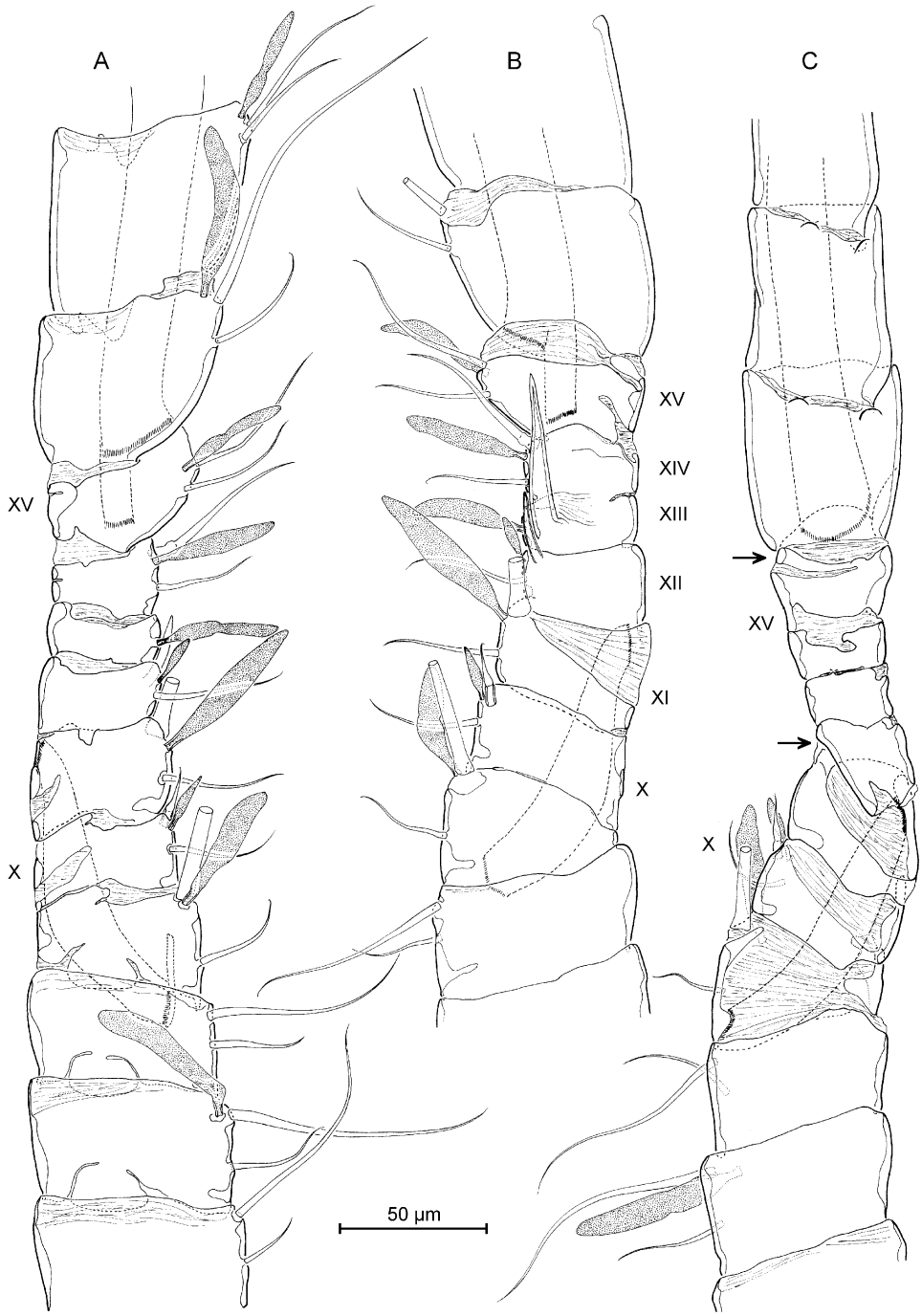

Fig. 3. *Stargatia palmeri* gen. et sp. nov., male right antennule with segments VII–XVII and the proximal flexure zone. A. Dorsal view. B. Ventral view. C. Posterior view; arrows point to flexure joints between segments XI and XII, and between XV and XVI. Only muscles that are associated with the joints are drawn. (Figure drawn by Rony Huys)

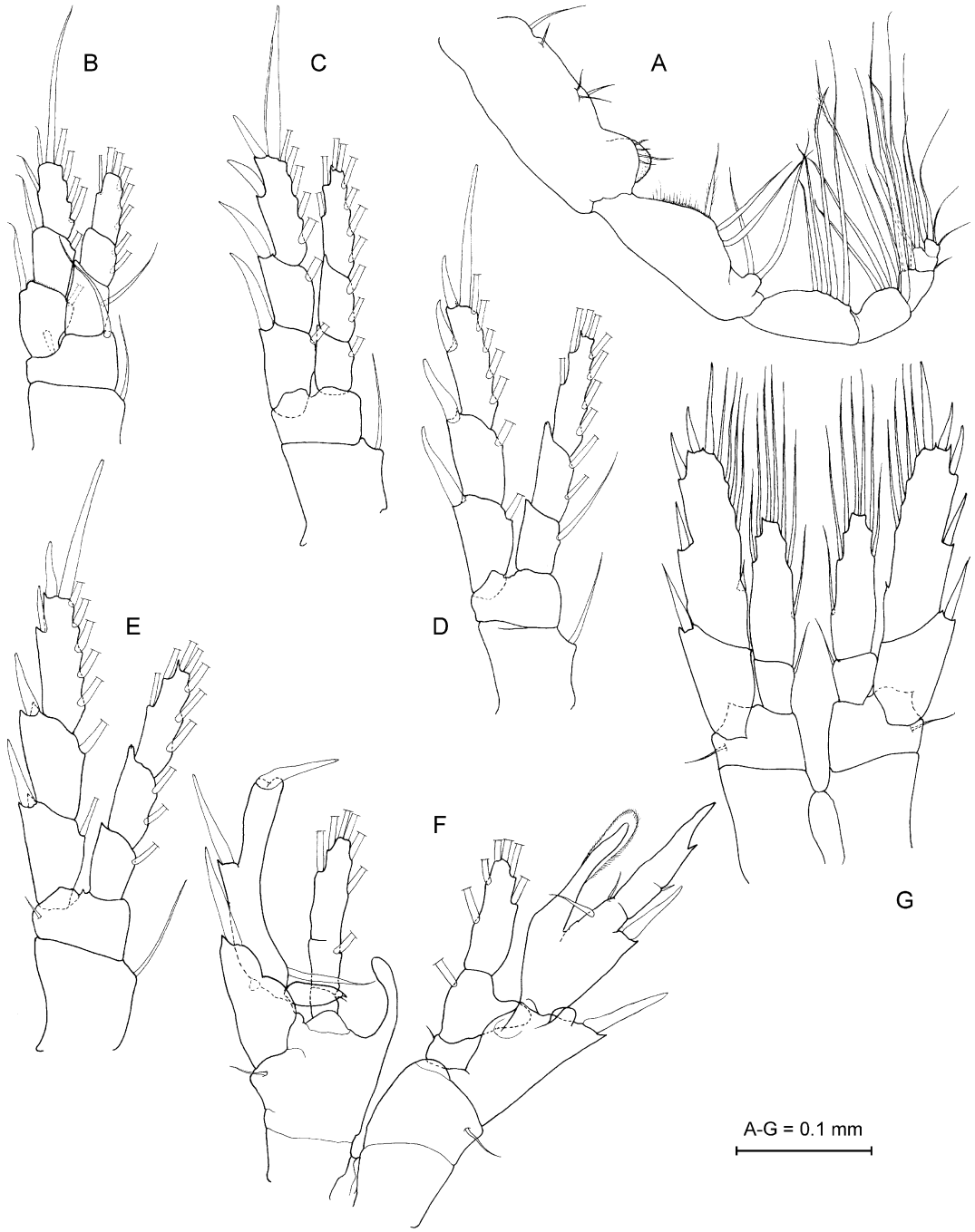

Fig. 4. *Stargatia palmeri* gen. et sp. nov., male. A. Maxilliped. B. Leg 1. C. Leg 2. D. Leg 3. E. Leg 4. F. Fifth legs, posterior view. G. Fifth legs, copepodid stage V, anterior view.

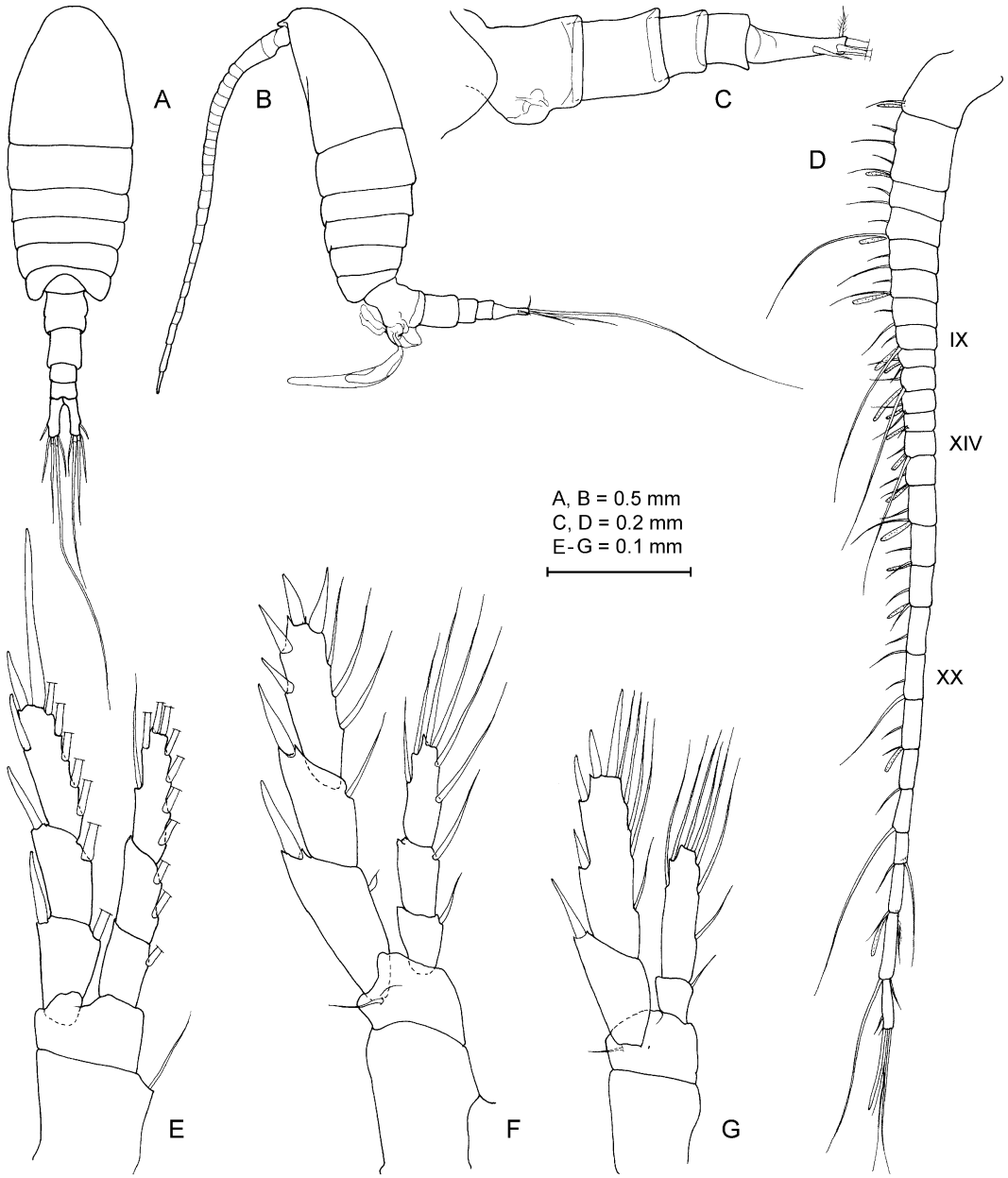

Fig. 5. *Stargatia palmeri* gen. et sp. nov., female. A. Habitus, dorsal view. B. Habitus, lateral view. C. Urosome, lateral view. D. Antennule. E. Leg 2. F. Leg 5. G. Leg 5, copepodid stage V.

entrance shaft; the first sample contained few specimens while the deepest sample had hundreds of specimens in all stages.

Types

Holotype. Adult male, total length 1.57 mm from Stargate Blue Hole, 24 August 1997 caught at 44 m depth. One vial deposited in BMNH registration number 2001.6997.

Paratypes. Twenty males and 20 females in one vial, and two males and two females dissected on eight slides

from the same sample as the holotype. Deposited in BMNH registration numbers 2001.6998–7041.

Description

Adult male (Figs 2, 3, 4A–F). Total length of 12 individuals, 24 August 1997 at 44 m depth ranged between 1.49 and 1.58 mm, mean 1.57 mm. In dorsal view, prosome oval, about 1.6 times length of urosome. Rostrum (Fig. 2B) directed ventrally as two small rounded lobes without filaments. First pedigerous somite separate from cephalosome. Fifth pedigerous somite with evenly rounded lobes laterally on posterior margin (Fig. 2A).

Urosome elongate, 5-segmented, with first four somites subequal, anal somite of slightly shorter length. Caudal rami elongate, about four times as long as wide; seta II spinous and situated posterolaterally, seta V on left side longer than corresponding seta on right side. Right antennule (Figs 2C, D, 3) 22-segmented with two areas of geniculation, typical one between segments 18 and 19 (XX–XXI), and complex proximal one with several modifications from segments 7 to 13 (IX–XV) (Fig. 3); segment 2 (II–IV) compound; segments 8–13 (X–XV) condensed, appearing to have flexure joint between XI and XII, and between XV and XVI; each segment with three elements – seta, spine and aesthetasc on XII and XIII, two setae (one modified) and aesthetasc on XIV; segment XIX with long smooth spine distally; double-segment XXIV–XXV with long stylet-like process distally, extending more than half length of next segment. Left antennule as in female.

Antenna (Fig. 2E) with rami of subequal length. Exopod 9-segmented with 11 setae; three proximal ones small, each originating from distinctly separated segments. Distal compound segment of endopod with distinct inner lobe bearing nine setae and elongate terminal lobe with seven setae.

Mandible (Fig. 2F): coxa reduced in size; gnathobase with pointed teeth, two ventral ones longest, isolated and deeply incised. Basis of palp with two inner setae. Endopod enlarged and highly modified; first segment with three elements, two setae and a distal long pointed process with filament; second segment with coarsely serrated inner margin, with 10 elements, nine of which are pointed processes gradually tapering into long thin filament, and one ordinary seta at tip of endopod. Exopod generally unmodified, indistinctly 4-segmented with six setae, proximal seta strong and curved.

Maxillule (Fig. 2G): praecoxal arthrite with 15 elements. Coxal epipodite with nine setae, two proximal ones modified into short, smooth and flattened setae, pointed at tip. Coxal endite and first basal endite each with four setae, second basal endite with five modified setae. Endopod elongated, distinctly 3-segmented with five, five, and seven elements, respectively, most of which with bulbous base and ending in filament. Exopod with 11 setae.

Maxilla (Fig. 2H) with well-developed lobes. First praecoxal endite with four setae, two long and two short. Basal endite with four setae. Endopod indistinctly 3-segmented, with eight setae. Long setae on maxilla bearing widely spaced setules.

Maxilliped (Fig. 4A): syncoxa with weak setae, distal lobe with dense patch of short setules. Proximal part of basis with comb of fine and long setules. Five distal segments of endopod free with four, four, three, three, and four setae, respectively, one seta on each of first and second segments serrated at tip, some other setae on endopod abruptly tapering into thin thread.

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,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	0-0	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 1 (Fig. 4B) with slender process, rounded at apex, on posterior side of basis. Exopod with slender outer spines, gradually decreasing in length towards distal part; all with filament at tip.

Leg 2 (Fig. 4C): exopod with very strong and curved outer spines; spines on first and second segments strongest; first outer spine on third segment of exopod reaching beyond base of second spine.

Leg 3 (Fig. 4D) with two outer spines on third segment of exopod and very similar to leg 2. Some variation in length and shape of outer spines of exopod, generally shorter and straighter than in leg 2. In some specimens, minute setules present on basis.

Leg 4 (Fig. 4E) with small seta on basis, outer spines on exopod straight.

Fifth legs (Fig. 4F) with strongly modified exopods, endopods only slightly transformed.

Right leg with strong, curved and rounded process on inner margin of basis; exopod 2-segmented, first segment with long outer spine reaching beyond origin of first spine of next segment, inner margin with bulbous appendage-like process with curved pointed apex; second segment slender with two long spines, terminal one pointing inwards, one seta present proximally on inner margin. Endopod indistinctly 3-segmented, first segment with minute inner seta, second and third segments partially fused.

Left leg with 2-segmented exopod, proximal segment with two rounded lobes distally and strong outer spine,

distal compound segment with long outer spine in middle, segment divided into two branches, inner spatulate one with thin distal part covered with setules, and outer pointed part proximally with two inner setae and two notches on outer margin. Endopod 3-segmented, first segment with minute inner seta, second segment greatly extended along outer margin.

Adult female (Fig. 5A–F). Total length of 11 individuals, 24 August 1997 at 44 m depth, ranged between 1.53 and 1.61 mm, mean 1.58 mm. Body somewhat less slender than in male with prosome about 1.9 times longer than urosome. Urosome 4-segmented (Fig. 5C). Genital double-somite produced and rounded midventrally and about length of following somite. Caudal rami as in male but with seta V on left side longer, about double length of corresponding seta on right side.

Antennule (Fig. 5D) 26-segmented and extending backwards just beyond last urosomal somite. Segments II and III fused, segments II, IV, VI, VIII, XIX, and XX with two setae on anterior margin, segments V, IX, XI, XIV, XX, XXIII, and XXVI with elongate setae. Aesthetascs relatively short.

Legs 2 (Fig. 5E) and 3 with outer spines of exopod weaker, more slender and straighter than in male.

Leg 5 (Fig. 5F): exopod with strong subequal outer spines on first and second segments, first segment with short bulbous inner seta; third segment inserted closer to distal end of second segment than usually found within family, with four spines, first one slightly shorter than three subequal distal ones, inner margin of segment with three setae; endopod with one, one, and six setae on first, second, and third segments, respectively.

Copepodid stage V. Leg 5 female (Fig. 5G): basis with outer lateral seta; exopod 2-segmented, first segment with long outer spine, second segment with nine elements (two outer and two distal spines and five inner setae), proximal seta thin and slender; endopod 2-segmented, first segment with inner seta, second segment with seven setae.

Leg 5 male (Fig. 4G): differs from those of female in slight asymmetry of inner proximal element of second segment of exopod, bearing stout spine on left leg and notch on corresponding site on right leg.

Ecological notes

The greatest numbers of *Stargatia* were obtained from very low dissolved oxygen levels (0.3 mg l^{-1}) in the vertical shaft of the cave at 44 m depth. Clouds of bacteria or aggregations of particles near the pycnocline were observed by divers not far from where *Stargatia* was caught. Other calanoids recorded at Stargate Blue Hole in August 1997 at depths below 30 m were two specimens, one female on 22 August and one copepodid on 25 August, of *Bomburiella gigas* Fosshagen, Boxshall & Iliffe, 2001 (Fosshagen & al. 2001), and several specimens of *Exumellina bucculenta* (Fosshagen & Iliffe 1998). The last species co-occurred with both *Stargatia palmeri* and *Bomburiella gigas*. This is the first record of *Exumellina bucculenta* from outside its type locality at Norman's Pond Cave, Exuma Cays. In North Passage below the halocline, another new ridgewayiid to be described below (*Robpalmeria asymmetrica*) was obtained, and ostracods, thermosbaenaceans and polychaetes were also collected below the halocline.

Above the halocline, on 25 August at 12–15 m depth, with a salinity of 4.5, thousands of specimens of *Mastigodiaptomus nesus* Bowman, 1986 in all stages were sampled and no other copepods were caught.

Remarks

At first glance, *Stargatia palmeri* does not seem to fit into the Ridgewayiidae. Unlike other members of the family, *Stargatia palmeri* does not have the distinct character of the third exopodal segment of female leg 5 set off from the middle of the inner margin of the second segment. However, with similarities to *Exumellina bucculenta*, such as the presence of the two outer spines on the third exopodal segment of legs 3–4, the modifications of the endopods of the mandible and maxillule, and leg 5 of the male, the species shows clear affinities to the family. Two modified proximal setae on the coxal epipodite of the maxillule are also present in both species. This character was overlooked in *Exumellina bucculenta* during the first examination (Fosshagen & Iliffe 1998). The geniculate right antennule in the male shows some unusual features, in particular in the modified proximal segments X–XVI, where there seems to be two geniculations, one between XI and XII and one between XV and XVI. A proximal geniculation between segments XV and XVI has been reported in calanoids from a *Heterorhabdus* sp. (Boxshall & Huys 1998), but as far as is known, no geniculation between segments XI and XII has been observed previously. A proximal geniculation, however, seems to be present among members of more derived calanoid families like the Diaptomidae, Parapontellidae, Pontellidae and Pseudodiaptomidae. A closer and detailed examination of the male antennule of these and other families might reveal that proximal genculations are widespread among calanoids. Boxshall & Huys (1998) suggest that

the proximal geniculation is evolutionary labile as it occur occasionally in misophrioids and cyclopoids.

A distinctly 3-segmented endopod on the maxillule as in *Stargatia palmeri* is rare among calanoids and a second segment with five setae is a condition with one seta more than predicted for the ancestral copepod by Huys & Boxshall (1991).

There is a slight sexual dimorphism in the swimming legs, in particular in the exopods of legs 2 and 3 where the outer spines are stronger and more curved distally in the male than in the female.

Some females were observed with four inner setae on the third exopodal segment of leg 5.

It is somewhat unexpected to find a very similar leg 5 in both sexes in copepodid stage V, especially as the legs of the male are only slightly modified at this stage, when there are such profound changes during the last moult. In adult males of *Ridgewayia*, with highly modified leg 5, the same limb in stage V is rather transformed (Wilson 1958; Fosshagen 1970; Ferrari 1995).

This species, with its total length of about 1.6 mm, is the largest ridgewayiid hitherto recorded.

Genus *Robpalmeria* gen. nov.

Diagnosis

Female. Pedigerous somites 1–5 separate. Posterior corners of prosome asymmetrical with right side extended backwards. Urosome 4-segmented with elongate genital double-somite. Caudal rami about three times longer than wide, asymmetrical with setae V and VI longer on left than on right side. Rostrum narrow, with two filaments at tip. Antennule 25-segmented, reaching middle of genital double-somite, segments II–IV fused. Antenna with endopod longer than exopod, compound distal endopod segment elongate with seven setae along inner margin; exopod 7-segmented with segments II–IV fused. Mandible bearing three equally long pointed teeth ventrally on gnathobasis; palp with exopod and endopod of equal length. Maxillule and maxilla generally unmodified. Maxilliped strongly developed, reflexed endopod condensed distally and bearing several differently modified setae, one particularly long and strong seta on second free segment. Leg 1 with long slender process on posterior side of basis; outer spines of exopod slender and without filaments at tip. Legs 3 and 4 with three outer spines on third exopod segment. Leg 5 with third segment of exopod set off near middle of second segment; endopod 3-segmented with five setae on third segment.

Male. Urosome 5-segmented. Caudal rami with seta V on right side slightly longer than corresponding seta on left side. Right antennule 21-segmented, with segments II–IV and XVI–XVII fused; pointed process distally on segment 19 (XXIV–XXV). Leg 5 large with highly modified exopods; right side with long inwardly directed curved process; endopods rudimentary.

Type species

Robpalmeria asymmetrica gen. et sp. nov.

Etymology

The generic name is in honour of Robert Palmer, a pioneer in the investigation of the caves of Andros. The specific name refers to the asymmetry of the distal part of the prosome and caudal setae.

Robpalmeria asymmetrica gen. et sp. nov. (Figs 6, 7)

Material examined

Stargate Blue Hole, South Andros Island, Bahamas. 24 August 1997: two females, one male. 26 August 1997: one male.

Types

Holotype. Adult female, total body length 0.89 mm, caught at 33–36 m depth of North Passage, 24 August 1997. One vial BMNH registration number 2001.7042.

Paratypes. One female and one male dissected and mounted on five slides, all at the same locality and with the same date of collection as the holotype. One male partially dissected and mounted on one slide, the rest of the animal kept in a vial, from Stargate Blue Hole South Passage, 26 August 1997 at 33–39 m depth. BMNH registration numbers 2001.7043–7045.

Description

Female (Fig. 6A, B). Body length 0.89 mm. Ratio of prosome to urosome length *Ca* 2.2:1. Fifth pedigerous somite asymmetrical, extended on right side to middle of genital double-somite. Urosome 4-segmented. Genital double-somite about length of following two somites combined. Caudal rami about three times longer than wide, with spinous seta II, setae V and VI on left ramus longer than corresponding setae on right, seta VI on right side with small unilateral tuft near its base. Rostrum (Fig. 6C) small with two filaments at tip.

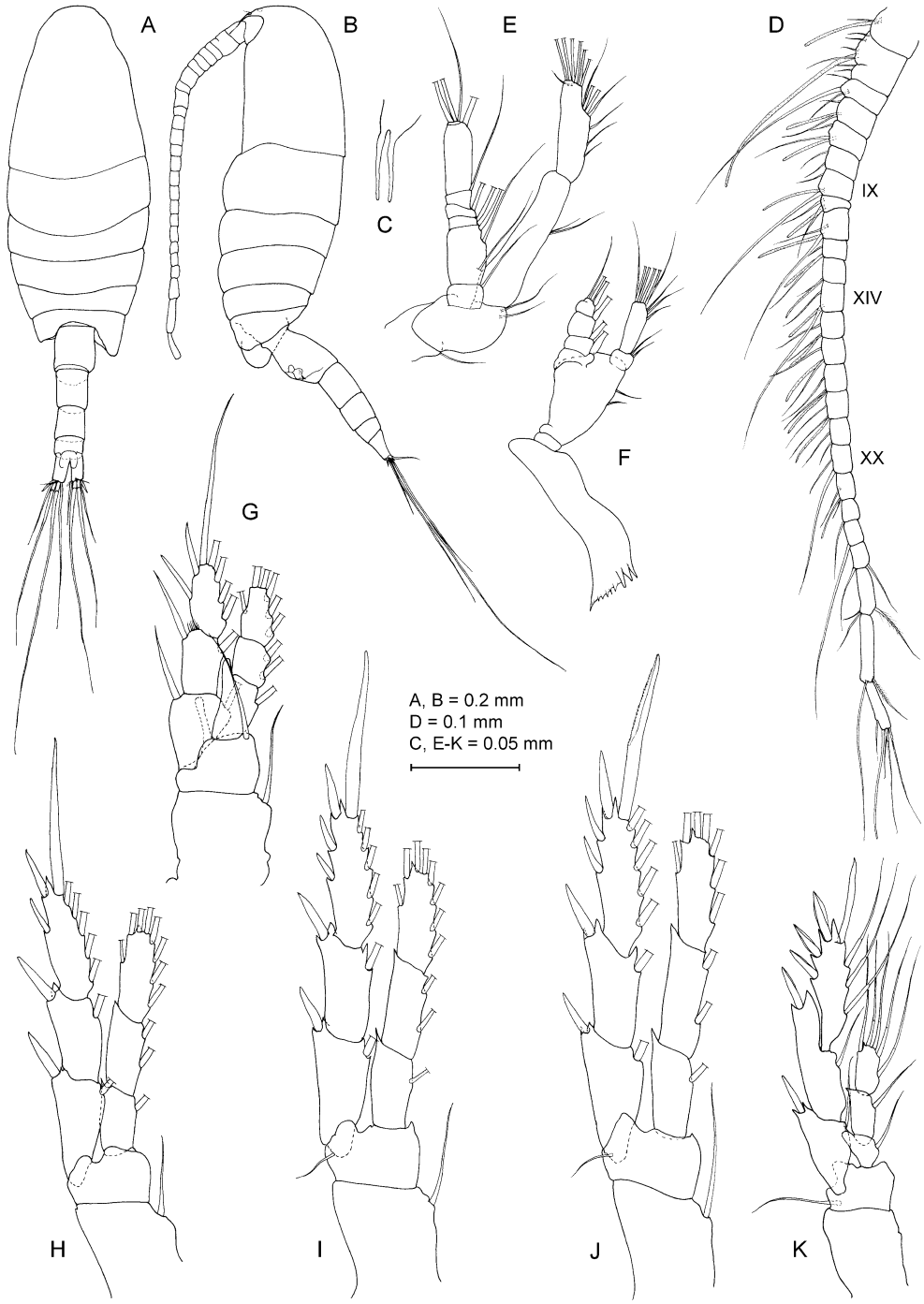

Fig. 6. *Robpalmeria asymmetrica* gen. et sp. nov., female. A. Habitus, dorsal view. B. Habitus, lateral view. C. Rostrum. D. Antennule. E. Antenna. F. Mandible. G. Leg 1. H. Leg 2. I. Leg 3. J. Leg 4. K. Leg 5.

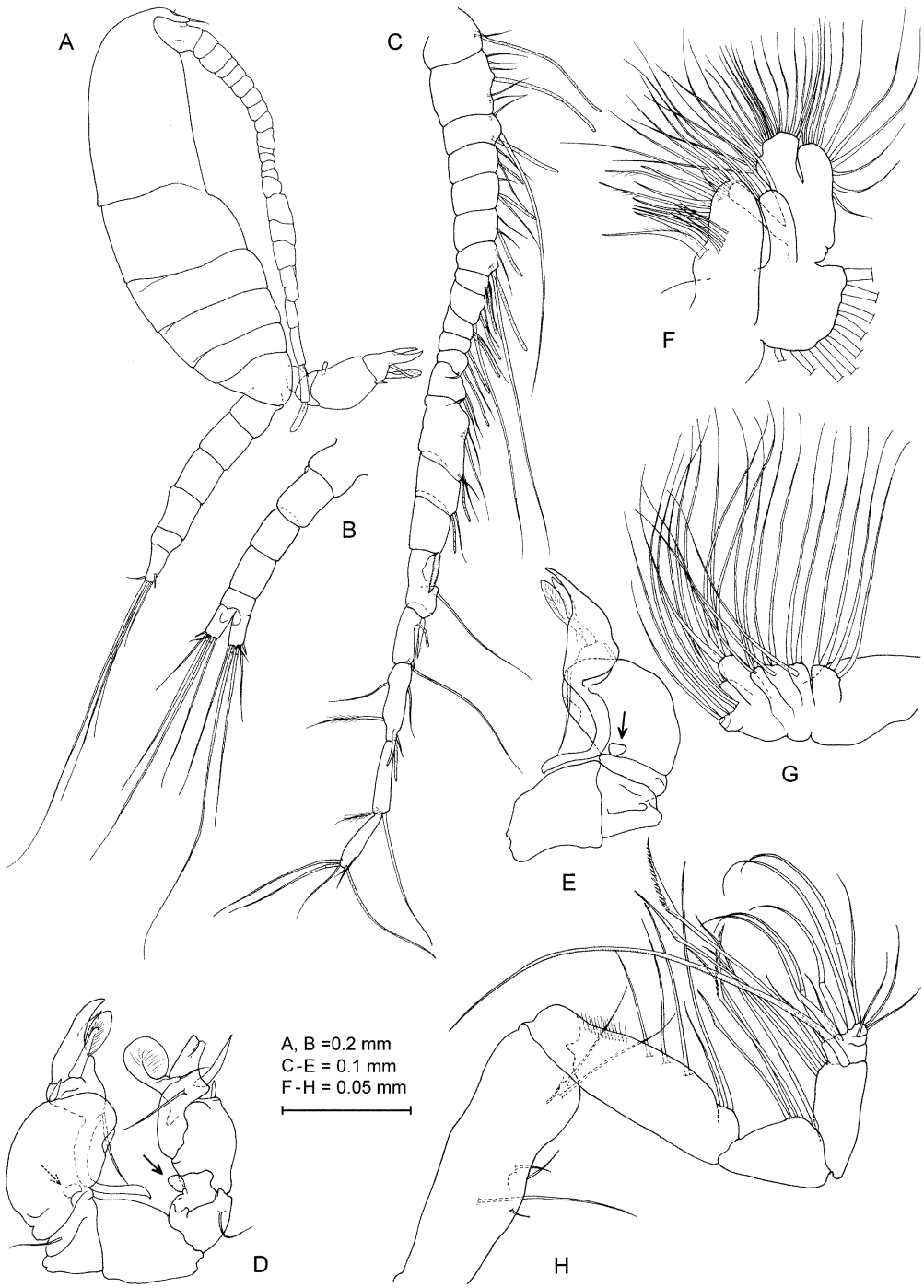

Fig. 7. *Robpalmeria asymmetrica* gen. et sp. nov., male (A–E), female (F–H). A. Habitus, lateral view. B. Urosome, dorsal view. C. Right antennule. D. Fifth legs, posterior view (endopods indicated by arrows). E. Right leg 5, anterior view (endopod indicated by an arrow). F. Maxillule. G. Maxilla. H. Maxilliped.

Antennule (Fig. 6D) 25-segmented, extending backwards to middle of genital double-somite; segments II–IV fused bearing one extra long aesthetasc; elongate seta on segments V, IX, XI, XIV, XX, XXIII and XXVI; posterior margin of segment X narrow.

Antenna (Fig. 6E) with endopod slightly longer than exopod; exopod 7-segmented with segments II–IV fused; distal segment of endopod elongate bearing seven setae along inner margin and seven terminal setae.

Mandible (Fig. 6F): gnathobase with three ventral pointed teeth of equal size; basis with two inner setae; exopod and endopod of subequal length; first segment of endopod short with two setae, second segment elongate with three inner and six terminal setae.

Maxillule (Fig. 7F): praecoxal arthrite with 14 elements; coxal epipodite with nine unmodified setae; coxal endite and proximal basal endite each with four setae; distal basal endite with five setae. Endopod condensed, unsegmented and with 13 setae. Exopod with 11 setae.

Maxilla (Fig. 7G) generally unmodified with long and slender subequal setae except for two shorter ones distally on endopod. Proximal praecoxal endite with four setae. Basal endite and proximal endopod segment well developed. Endopod indistinctly 3-segmented.

Maxilliped (Fig. 7H) powerfully developed and reflexed with distal part of endopod much condensed. First and second segments of free endopod long and of about equal length, each with four unequal setae; first segment with one unmodified seta and three setae with serrated tip; second segment with one unmodified seta, two setae with coarsely serrated tip and one very long seta finely striated along most of its length. Distal part of endopod with three partly fused segments carrying 11 relatively short and stout setae, most of which are curved distally.

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	1-0	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. 6G) with slender process, rounded distally, in middle of posterior side of basis; exopod with long slender outer spines, outer distal margin of second segment with tuft of long setules; first segment of endopod with rounded extension distally on outer margin.

Leg 2 (Fig. 6H): first outer spine on third segment of exopod slender and reaching base of second spine.

Leg 3 (Fig. 6I): basis with outer seta; outer spines on first and second segments of exopod subequal, third segment of exopod with three outer spines gradually increasing in length distally.

Leg 4 (Fig. 6J) differing from leg 3 in possession of seven setae on third segment of endopod instead of eight.

Leg 5 (Fig. 6K): third segment of exopod with first and second outer spine of equal length, distal spine nearly twice length of third outer spine, three setae along inner margin; endopod 3-segmented bearing five setae on third segment.

Adult male (Fig. 7A). Total length of two specimens 0.91 and 0.94 mm. Differing from female in 5-segmented urosome and different asymmetry of caudal setae, geniculate right antennule, and in fifth legs. Asymmetry of fifth pedigerous somite of female not confirmed in male. Prosome about 1.8 times longer than urosome.

Urosome (Fig. 7B) 5-segmented; caudal seta V longer on right ramus than on left.

Right antennule (Fig. 7C) 21-segmented; segments II–IV fused; segments XIV and XV with three elements, one seta, one aesthetasc and distally one curved spinous seta; segments XVI and XVII fused; segment XIX with strong serrated spine distally; double-segment XXIV–XXV with distal process not reaching beyond half length of next segment. Distal and penultimate segments (20 and 21) of about equal length.

Fifth legs (Fig. 7D) with strongly developed and complex exopods; endopod on both rami reduced to minute rounded bulb. Right exopod (Fig. 7J) with large bulbous first segment bearing small outer spine and small depression in middle of inner margin; compound distal segment with strong outer flanged fan-shaped seta and long inner inwardly directed curved extension, with seta at base, reaching intercoxal connection; distal part of exopod curved, tapering to pointed process and carrying two elements.

Left exopod (Fig. 7I) with first segment bearing small outer spine, complex distal part with outer long pointed spine, two unequal setae on posterior side, distal flattened and cleft process and inner large fan-shaped process.

Ecological notes

Only two records and four specimens of *Robpalmeria asymmetrica* were found in Stargate Blue Hole (see *Stargatia palmeri* for cave description); two females and one male on 24 August 1997 in North Passage between 33 and 36 m depth and one male on 26 August in South Passage between 33 and 39 m depth, both

localities well below the halocline. Other calanoids present in North Passage were some *Stargatia palmeri* and *Exumellina bucculenta*, and in South Passage some *Exumellina bucculenta* and two specimens of an undetermined phaennid. This is to our knowledge the first record of this family from an anchialine cave.

Remarks

On account of the characteristic offset third segment of the exopod in female leg 5, as well as the primitive 3-segmented rami of all legs in the female, the species readily fits into the Ridgewayiidae.

A slight transformation, not as pronounced as that of *Stargatia palmeri* of segments XIV and XV in the male right antennule also indicates a proximal geniculation in *Robpalmeria asymmetrica.* Judging from the structure of the powerful and reflexed maxilliped with highly modified setae, it is suggested that *Robpalmeria asymmetrica* has a specialized mode of feeding, probably a raptorial habit. A similar modified maxilliped is found in *Normancavia minuta* (see below), and modified setae like those of *Robpalmeria asymmetrica* are present on the first and second free endopod segments of the monotypic genera *Brattstromia, Stargatia* and *Exumellina.* However, in the last three genera the distal part of the endopod is well defined and not as condensed as that of *Robpalmeria asymmetrica.* The three genera with a reflexed and condensed endopod: *Robpalmeria, Normancavia* and *Exumella,* have a rostrum with two filaments in common. Except for a reduced endopod of the mandible and a gnathobase with deeply incised teeth in *Exumella*, characters in common with the Epacteriscidae (Fosshagen & al. 2001), the other mouthparts of these three genera do not differ conspicuously from each other.

Genus *Normancavia* gen. nov.

Diagnosis

Female. Cephalosome incompletely separated from first pedigerous somite. Genital double-somite produced mid-ventrally and shorter than following two somites combined. Anal somite with two pointed posterior extensions dorsally. Tapering rostrum rounded with two filaments at tip. Antennule 25-segmented, extending backwards to end of prosome. Antenna with exopod and endopod subequal in length; distal segment of endopod without distinct inner lobe and with five setae along inner margin. Other mouthparts and legs 1–4 generally as in *Robpalmeria* but with slight reduction in number of setae on mouthparts and no process on basis of leg 1. Leg 5 with 3-segmented exopod bearing two inner setae on third segment; endopod lacking.

Male. Urosome 5-segmented. Right antennule 21-segmented, pointed process distally on segment 19 (XXIV–XXV). Leg 5 with highly modified exopods; right endopod 2-segmented with four setae distally, two of which very long; left endopod 1-segmented with two slender elements at tip.

Type species

Normancavia minuta gen. et sp. nov.

Etymology

The generic name refers to Norman's Pond Cave where several new copepods have been caught recently. The specific name points to the small size of the species.

Habitat

Norman's Pond Cave is one of the notable blue holes in the Exumas, located near the north end of Norman's Pond Cay. The cave has been described in Fosshagen & Iliffe (1998) and Kornicker & Iliffe (1998, 2000). Its entrance is a 2 m wide by 8 m long sinkhole located just above the high-tide line and extending horizontally 210 m to a depth of 86 m.

Water column profiles were obtained by a diver carrying a Hydrolab recorder water quality multiprobe logger from the surface to 83 m depth on 10 September 1996 (Fig. 8). Surface waters in the entrance pool were found to have a salinity of 35.3. Salinity gradually increased to 37.1 at 54 m depth and below. The general temperature trend in the water column involved a decrease from 28.9 °C at the surface to 25.7 °C at 83 m. However, a secondary temperature minimum occurred at 22–24 m (25.99 °C). The pH decreased from 7.77 at the surface to 7.01 at 83 m. A secondary pH minimum of 7.16 occurred at 18 m depth, while a secondary maximum of 7.22 was found at 28–30 m. Dissolved oxygen decreased from 5.90 mg l^{-1} at the surface to 0.11 mg l^{-1} at 83 m. A secondary oxygen maximum of 2.70 mg l^{-1} occurred at 10 m depth.

Normancavia minuta gen. et sp. nov. (Figs 9, 10)

Material examined

Norman's Pond Cave, Norman's Pond Cay, Exumas, Bahamas. 4 May 1993: one male. 9 September 1996: two females, three males. 19 March 2000: seven females, eight males.

Types

Holotype. Adult female, total body length 0.51 mm, 9 September 1996, caught with a plankton net at 20–15 m depth or with a suction bottle at 50 m depth. One vial BMNH registration number 2001.7046.

Paratypes. All paratypes are from the same locality as the holotype but collected at different dates. 4 May 1993: one male dissected and mounted on two slides. 9 September 1996: one female and one male on seven slides. 19 March 2000: one female on two slides and four females and four males in one vial. BMNH registration numbers 2001.7047–7058.

Description

Female (Fig. 9A). Total length of five females ranged between 0.50 and 0.57 mm, mean 0.54 mm. Ratio of prosome to urosome length *Ca* 2.3:1.

Urosome (Fig. 9B) 4-segmented. Genital double-somite produced ventrally in middle, shorter than following two somites combined. Spermatophore small, about half length of genital double-somite. Anal somite with two long pointed posterior extensions dorsally. Caudal rami about twice as long as wide, caudal seta V thickened, tapering abruptly distally into thinner part.

Rostrum (Fig. 9C) tapering to rounded apex with two filaments at tip.

Antennule (Fig. 9D) 25-segmented, extending backwards to end of prosome; segments II–IV fused with partial division between segments III and IV; aesthetascs on segments I, II, V, VI, and VII long and of equal length; distal segment (XXVII–XXVIII) distinctly shorter than penultimate segment (XXVI).

Antenna (Fig. 10D) with exopod and endopod subequal in length. Setation of exopod as in *Robpalmeria*, last segment of endopod with five setae along inner margin and seven setae distally.

Mandible (Fig. 10E): gnathobase as in *Robpalmeria*; basis with one inner seta. Endopod 2-segmented, first segment with one seta, second segment with two inner and four terminal setae. Exopod 5-segmented, setal formula one, one, one, one, two.

Maxillule (Fig. 10F) very similar to that of *Robpalmeria*, but with reduced number of setae on coxal endite (two), distal part of endopod (seven) and exopod (10).

Maxilliped (Fig. 10G) and maxilla generally similar to those of *Robpalmeria*, but with weaker setae and somewhat less transformed modified setae than in maxilliped of *Normancavia*.

Leg 1 (Fig. 9E): no process observed on posterior side of basis, otherwise similar to *Robpalmeria.*

Legs 2–4 (Fig. 9F–H) similar to those of *Robpalmeria* in setation except for outer seta on basis of leg 3 lacking in *Normancavia*; leg 2 with proximal outer spine on third segment of exopod stout and not reaching base of second spine; legs 3 and 4 with relatively shorter and weaker first and second outer spines of third segment on exopod than those of *Robpalmeria.*

Leg 5 (Fig. 9I) with reduced setation, endopod lacking; third segment of exopod with first outer spine about two thirds length of second spine, distal spine about same length as distal inner spine, latter directed inwards and curved distally, two setae along inner margin.

Adult male (Fig. 10A). Total length of six specimens measured between 0.49 and 0.51 mm, mean 0.50 mm. Differing from female in its 5-segmented urosome,

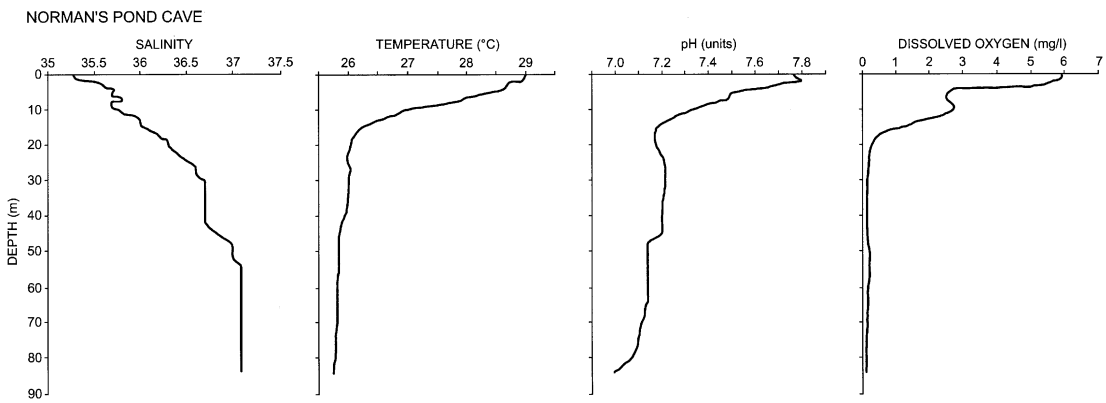

Fig. 8. Vertical profiles of salinity, temperature, pH, and dissolved oxygen, in Norman's Pond Cave, Exuma Cays, Bahamas. A Hydrolab Datasonde III profiler was used to obtain these measurements on 10 September 1996.

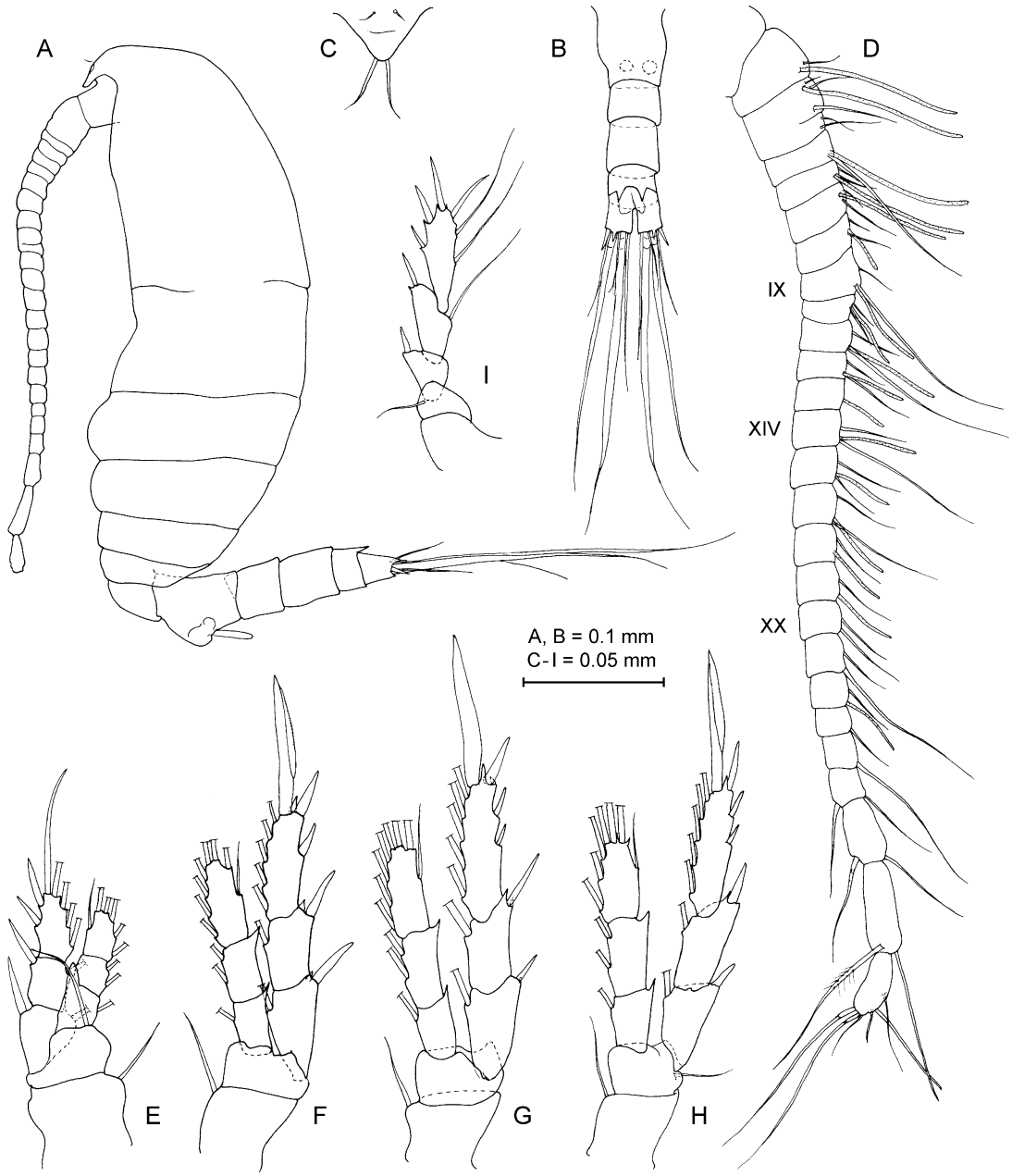

Fig. 9. *Normancavia minuta* gen. et sp. nov., female. A. Habitus, lateral view. B. Urosome. C. Rostrum. D. Antennule. E. Leg 1. F. Leg 2. G. Leg 3. H. Leg 4. I. Leg 5.

slightly different caudal setae, geniculate right antennule, and leg 5. Prosome about 2.4 times longer than urosome.

Urosome (Fig. 10B) with caudal seta V not as abruptly tapering distally as in female; setae VI and VII slightly asymmetrical.

Right antennule (Fig. 10C) 21-segmented, very similar to that of *Robpalmeria,* but with distal segment distinctly shorter than penultimate and both segments more condensed than those of *Robpalmeria.*

Fifth legs (Fig. 10H, I) with complex exopods and simple elongate endopods. Right leg (Fig. 10H) with

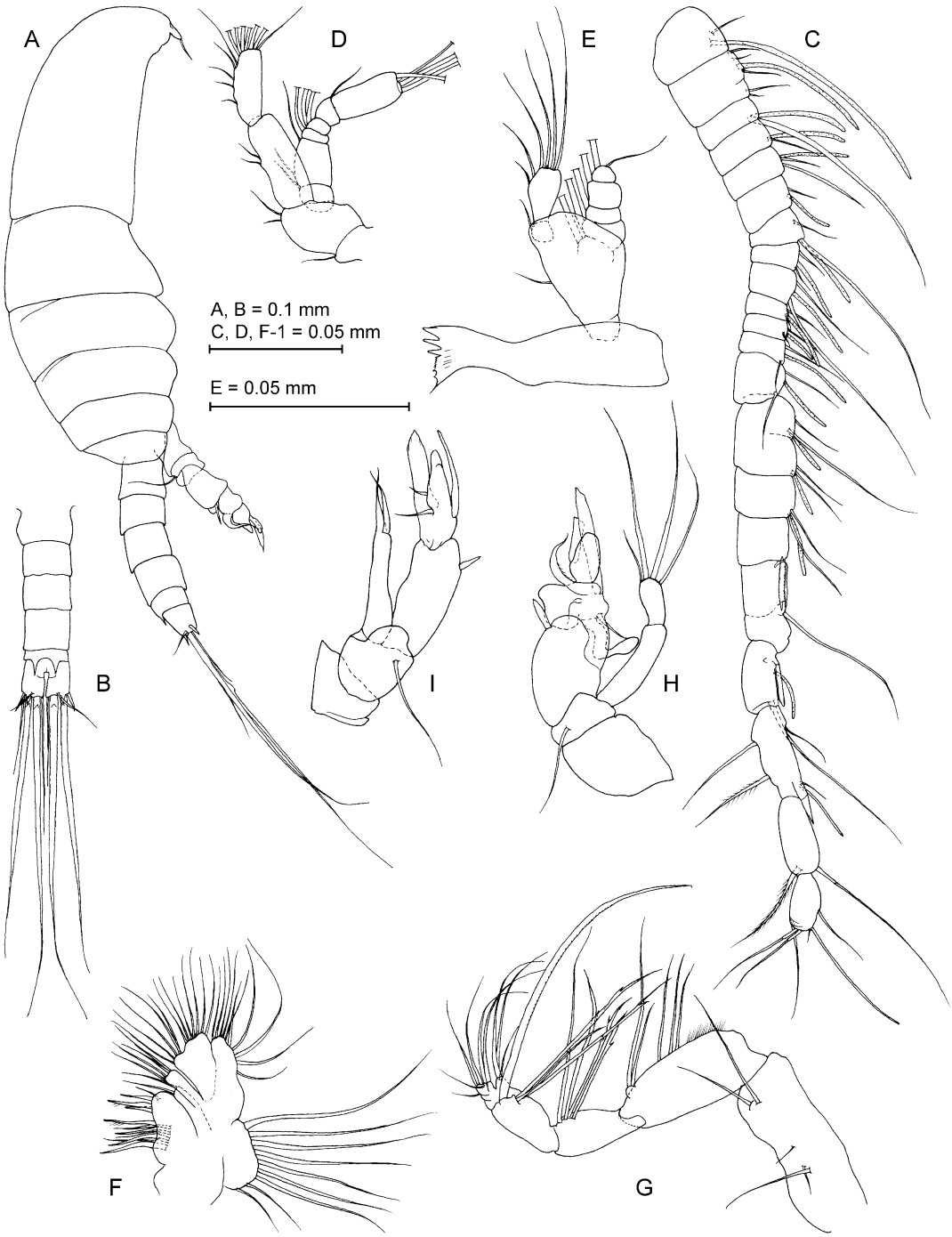

Fig. 10. *Normancavia minuta* gen. et sp. nov., female (D–G), male (A–C, H, I). A. Habitus, lateral view. B. Urosome, dorsal view. C. Right antennule. D. Antenna. E. Mandible. F. Maxillule. G. Maxilliped. H. Right leg 5, posterior view. I. Left leg 5, posterior view.

3-segmented exopod; first segment with outer spine and excavated inner margin in distal half on posterior side; second segment with inner extension, curved inwards at right angle and with broad, rounded tip; slender seta inserted close to extension; distal lateral seta-like curved process, flexible at tip; inner long flattened element with angular apex; third segment rounded with outer flattened process, angular at tip. Endopod 2-segmented and elongate; second segment short with four setae distally, two of which relatively long.

Left leg (Fig. 10I) with 2-segmented exopod; first segment elongate with short, stout outer spine; distal segment with three main elements: long outer curved smooth spine, medial process rounded at apex with two setae proximally on inner margin, and inner process pointed and thin at apex. Endopod 1-segmented, slender, tapering into flexible point and with one seta subdistally on lateral margin.

Ecological notes

Normancavia minuta has been recorded from Norman's Pond Cave only and three times in the years 1993, 1996 and 2000 with 21 specimens in total. This notable anchialine cave is situated close to the coast and the waters are fully marine [for a further description of the cave see Fosshagen & Iliffe (1998) and Kornicker & Iliffe (1998)].

In addition to *Normancavia minuta*, two other monotypic genera of calanoids have their type locality in this cave; the ridgewayiid *Exumellina bucculenta* (Fosshagen & Iliffe 1998) and the epacteriscid *Balinella ornata* Fosshagen, Boxshall & Iliffe, 2001 (Fosshagen & al. 2001). Other calanoids present were undetermined species of *Ridgewayia, Exumella, Miostephos* Bowman, 1976*, Pseudocyclops* Brady, 1872, and arietellids. Two new monotypic genera of misophrioid copepods with the species *Huysia bahamensis* and *Protospeleophria lucayae* have been described from this cave (Jaume & al. 1998). Remipedes, the new peracarid order Bochusacea (Gutu & Iliffe 1998), thermosbaenaceans, amphipods and three halocyprid ostracods (Kornicker & Iliffe 1998, 2000) are among other noteworthy cave-adapted animals from this locality. A major part of the animals from this cave seem to be novelties.

Remarks

Normancavia minuta is most closely related to *Robpalmeria asymmetrica* from Stargate Cave, Andros Island on account of the similar mouthparts, in particular the modified and reflexed maxilliped, and the swimming legs. The number of setae is slightly reduced in the endopods of the antenna, mandible and maxillule, in *Normancavia minuta.* Apart from the different body size, the two species are best distinguished by leg 5 of both sexes. In the female of *Normancavia minuta,* the endopod is completely lacking, a character not known in any other member of the family, whereas the endopod in *Robpalmeria asymmetrica* is well developed and 3-segmented. In the male of *Normancavia minuta,* the endopods are elongated and carry long setae on the right side, whereas in *Robpalmeria asymmetrica* the endopods are minute bulbous rudiments on both sides. *Normancavia minuta* is one of the smallest ridgewayiids known, only surpassed by smaller benthic *Placocalanus* species (Ohtsuka & al. 1996).

CONCLUDING REMARKS

At present, the Ridgewayiidae includes eight genera with more than 20 species. They show a great diversity in habitat and morphology, often with some extreme plesiomorphic states in combination with unusual apomorphies. Most of them seem to be epibenthic and there is a tendency within the family to find habitats in shallow water in hidden places like soft sediments, crevices in rocks, among corals and in caves.

Placocalanus is the only genus caught exclusively from outside caves, in soft sediments.

Ridgewayia and *Exumella* are from both outside and inside caves, mostly obtained using plankton nets and dredges, while *Brattstromia, Exumellina, Stargatia, Robpalmeria,* and *Normancavia* are exclusively from caves, mostly caught with diver-held plankton nets. *Exumella* and *Brattstromia* have in addition also been caught in baited traps in caves (Fosshagen & Iliffe 1991; Jaume & Boxshall 1995).

Several genera, like *Ridgewayia, Brattstromia, Exumellina,* and *Stargatia*, have been obtained in large numbers in plankton in caves and they seem to occur in swarms. Their mouthparts indicate particle feeding, although with great differences in the morphology of the mandible and maxillule. It is suggested that the enlarged endopods and very thin structures of these two appendages in *Exumellina* and *Stargatia* are well suited for catching and leading tiny or flimsy particles to the mouth, as well as a planktonic adaptation helping the animals to stay in a certain layer.

Other genera, like *Exumella, Palmeriella* and *Normancavia* with reflexed and strongly developed maxillipeds armed with modified setae, and with a condensed distal part of the endopod, suggest a raptorial mode of feeding. In most genera, except for *Ridgewayia*

and *Placocalanus*, the endopod of the maxilliped has some specialized setae, usually with a uniserrate tip.

The most plesiomorphic, unspecialized species seem to be among the widely distributed and epibenthic *Ridgewayia*.

A radiation of the family into different habitats both outside and inside caves seems to have taken place. Several plesiomorphic characters have been retained, but many apomorphic mouthpart characters are developed in the cave-living and assumed planktonic genera like *Stargatia* and *Exumellina*. In contrast, the most apomorphic legs 1–4 are present in *Placocalanus* which is benthic outside caves.

In the family, the genera *Stargatia* and *Exumellina,* both caught pelagic in caves, are readily grouped together, sharing the following derived characters: the endopods of the mandible and maxillule are greatly enlarged and modified, the second segment of the endopod in the mandible is transformed into an elongated and flattened structure with thin elements; the coxal epipodite of the maxillule bears proximally two short modified setae; legs 3 and 4 bear only two spines on the outer margin of the third exopodal segment. This last character of the legs is in common with the two cave-living genera, *Erebonectes* and *Erebonectoides,* in the subfamily Erebonectinae in the Epacteriscidae (Fosshagen & al.2001).

The six other genera of the Ridgewayiidae are very diverse, certainly reflecting different habitats and feeding strategies. They are all characterized by the modified exopod of leg 5 in the female, other obvious synapomorphic characters are difficult to find.

Ridgewayia is the most generalized and widely distributed genus within the family, rich in species and considered one of the most primitive of calanoids. Most closely related to *Ridgewayia* is *Brattstromia* with some slightly modified setae on the maxilliped. Further change continues through *Exumella, Robpalmeria* and *Normancavia*, where the maxilliped becomes reflexed and the endopod is condensed with modified setae, some of which are long and strong, all indicating a transition to raptorial feeding.

In the six genera, the other mouthparts do not differ much except for the mandible in *Exumella* which has a reduced endopod and enlarged ventral teeth on the gnathobase.

In the same genera, except for *Placocalanus*, the swimming legs 1–4 are basically primitive with 3-segmented rami. In the benthic *Placocalanus*, there are profound modifications and reductions of legs 1–4 as well as in the antennule.

It has been pointed out by Othsuka & al. (1997) that within the calanoid families such as the Centropagidae, Heterorhabdidae, Phaennidae, and Pontellidae, there are both particle-feeding and carnivorous genera or species. This is also certainly true among the Ridgewayiidae, where such a great variety of morphology and life styles has been revealed.

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NOTE ADDED IN PROOF

Recently one male of *Stargatia palmeri* has been obtained from Basil Minn's Blue Hole, Great Exuma Island, Bahamas.