

MACROMAXILLOCARIDIDAE, A NEW FAMILY OF STENOPODIDEAN SHRIMP  
FROM AN ANCHIALINE CAVE IN THE BAHAMAS, WITH THE DESCRIPTION  
OF *MACROMAXILLOCARIS BAHAMAENSIS*, N. GEN., N. SP.

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ABSTRACT

A new family of stenopodidean shrimp, Macromaxillocarididae, is described from an anchialine cave in Great Guana Cay, Exuma Cays, Bahamas. *Macromaxillocaris bahamaensis* new genus, new species, is the sole representative of the family. The new taxon clearly belongs to the infraorder Stenopodidea. However, the presence of a massive third maxilliped, pereopods that increase in length posteriorly, an epistome with two fang-like projections, and a reduced branchial formula distinguish the new family from the rest of the taxa in the infraorder. Moreover, a bifid palp of the first maxilla and an unsegmented palp of the first maxilliped, which are characters not present in the other two known families in the infraorder, support the separate status of the new family. Diagnostic characters of both, the Stenopodidae and Spongicolidae, are found in *M. bahamaensis* also, being the new taxon morphologically more similar to the Stenopodidae. Diagnoses for the infraorder and the three families, and a key to the families are presented.

INTRODUCTION

A new family, Macromaxillocarididae, and a new genus and species, *Macromaxillocaris bahamaensis*, are described from Oven Rock Cave, an anchialine cave in the Exuma Cays, Bahamas. The new family is accommodated within the infraorder Stenopodidea Claus, 1872, based on the following characters considered as diagnostic by Schram (1986) and Holthuis (1993): body shrimp-like, gills trichobranchiate, pereopods uniramous, first three pairs of pereopods chelate, pleuron of first pleomere overlaps second, petasma absent in males, females without thelycum.

Until now, the infraorder Stenopodidea was composed of two families, Stenopodidae Claus, 1872, with four genera (*Stenopus* Latreille, 1819; *Engystenopus* Alcock and Anderson, 1894; *Odontozona* Holthuis, 1946; *Richardina* A. Milne-Edwards, 1881) and about 22 species (Goy, 1992; Hendrickx, 2002) and Spongicolidae Schram, 1986, with five genera (*Spongicola* de Haan, 1844; *Microprosthem* Stimpson, 1860; *Spongicoloides* Hansen, 1908; *Spongiocaris* Bruce and Baba, 1973; *Paraspongiocaris* de Saint Laurent and Cleva, 1981) and 30 species (Saito and Takeda, 2003). The two families were separated on the basis of: 1) differences in body shape (compressed vs. depressed), 2) type of telson (oval-subtriangular vs. subquadrangular), and 3) the presence or absence of an exopod on the third maxilliped (Schram, 1986; Holthuis, 1993) (Table 1). Regarding the habitats where they occur, stenopodids are typically associated with coral rubble or dead coral heads, rocks and crevices, especially the cleaning shrimp species of the genus *Stenopus* (Goy, 1992), while other species, such as some species of *Odontozona*, can be found in deep waters on muddy substrates (Hendrickx, 2002). In spongicolids, the species of *Microprosthem* dwell in shallow water and coral rubble, whereas the species of the remaining four genera are mostly deep-water hexactinellid sponge symbionts. In gen-

eral, stenopodidean shrimps are extremely rare, with at least 15 species known from one to seven specimens (Holthuis, 1946; Bruce and Baba, 1973; Baba, 1979, 1983; Goy, 1980, 1987, 1992; de Saint Laurent and Cleva, 1981; Wicksten, 1982; Goy and Felder, 1988; Criales, 1997; Hendrickx, 2002; Okuno, 2003).

During collecting of fauna in Oven Rock Cave, in the Bahamas, we found three specimens of a stenopodid shrimp exhibiting a series of unique characters. We propose the designation of a new family, the Macromaxillocarididae, to accommodate these unusual shrimps.

MATERIALS AND METHODS

Specimens of the new species were collected from Oven Rock Cave, Great Guana Cay, Exuma Cays, Bahamas. Great Guana Cay is a 1-2 km wide by 40 km long island situated on the eastern edge of the Great Bahama Bank, abutting the Exuma Sound (Fig. 1). The cave entrance is situated in a hillside about 1 km from the southern tip of Great Guana Cay. From the 15 m wide, 2.5 m high entrance, a 40 m long dry chamber descends over an accumulation of rocks partially filling the chamber, to a tidal anchialine lake. The 1.5 m deep lake extends around the sides and rear of this chamber. An underwater room trending off from the lake is well decorated with large stalagmites at depths to 9 m. A second room, located on the far side of the first, has a small air bell in the ceiling at one end but dips to 17 m depth at the far extreme. From this point, a collapse-floored passage is followed by a low bedding plane passage reaching depths to 22 m. The explored length of the cave is more than 300 m.

Surface salinity in the entrance lake was 28.3 ppt on 7 January 2004, but increased to 33.4 ppt at 4 m and 35.1 ppt at 12 m depth. Temperature showed a similar increase from 23.5°C at the surface to 26.0°C at 4 m and 26.3 at 12 m depth. Conversely, both dissolved oxygen concentration (DO) and pH decreased with depth. DO values were 6.15 mg/l at the surface, 3.4 mg/l at 4 m and 2.9 mg/l at 12 m, while pH was 7.87 at the surface, 7.33 at 4 m and 7.27 at 12 m depth. Specimens were collected by divers using vials at 3-6 m depths. Specimens were only observed near the base of the underwater slope below the entrance lake during the later stages of dives within the cave. Since they were not seen initially, it is likely that these shrimps are living on the ceiling or within cracks in the bedrock and were subsequently dislodged by exhaust bubbles from divers.

Table 1. Comparison of diagnostic characters of the three families of the infraorder Stenopodidea.

	Stenopodidae	Spongicolidae	Macromaxillocarididae
General body shape	Compressed	Depressed	Compressed
Telson	Long, subtriangular; posterior margin with one pair of spines, sometimes with a median spine	Rounded or subquadrangular, posterior margin with three to five spines	Long, subtriangular; posterior margin with three spines
Epistome	Rounded with anterior spines oriented frontwards	Rounded with anterior spines oriented frontwards	Semicircular with two fang-like teeth
First maxilla	Distal margin of palp rounded	Distal margin of palp rounded	Distal margin of palp bifid
First maxilliped	Endopod 3-segmented	Endopod 3-segmented	Endopod unsegmented
Third maxilliped	With exopod	Typically without exopod, if present well developed or rudimentary	With exopod
	As long as or shorter than first pereopod	As long as or shorter than first pereopod	Longer than first two pereopods
	Slender, never as stout as pereopods	Slender, never as stout as pereopods	Massive, stouter than pereopods
	With simple setae	With simple setae	With articulated setae
Pereiopods	Third one the longest	Third one the longest	Fifth one the longest
	Carpus of third pereopod proportionally shorter than in first two pereopods	Carpus of third pereopod proportionally shorter than in first two pereopods	Carpus of third pereopod proportionally of about the same length in first three pereopods
Uropodal endopod	With two dorsal ridges	With single dorsal ridge	With single dorsal ridge
Branchial formula	Arthrobranchs on all three maxillipeds	Arthrobranchs on all three maxillipeds	Arthrobranchs on third maxilliped only
	Epipods on all three maxillipeds and on first four pereopods	Epipods on all three maxillipeds, they may be absent on all pereopods, or present on first three or four pairs	Epipods on third maxilliped only

The holotype was first photographed at the Caribbean Marine Research Center on Lee Stocking Island, Exuma Cays, Bahamas, in vivo on the day it was collected (Fig. 2). This same specimen was used to produce the figures; after obtaining the total lateral view (Fig. 3), it was dissected to figure all the appendages and mouthparts (Figs. 4-6). Subsequently, one of the third maxillipeds was prepared using conventional techniques to be observed through the scanning electron microscope (SEM) (Fig. 7). Two paratypes collected a year after the holotype were left untouched.

The classification proposed by Martin and Davis (2001) is followed. The material studied herein is deposited in the Colección Nacional de Crustáceos (CNCR), Instituto de Biología, Universidad Nacional Autónoma de México. The abbreviations used are: cl, carapace length; tl, total length; M, maxilliped; P, pereopod.

#### SYSTEMATICS

##### Infraorder Stenopodidea Claus, 1872

Stenopinae Claus, 1872: 500.

Stenopidea Bate, 1888, 24: 206.

Stenopodidea Holthuis, 1946, 7: 2.

Stenopodidea Martin and Davis, 2001: 72.

**Diagnosis.**—Body shrimp-like. Carapace fused to thorax. Gills trichobranchiate. Eyes stalked, compound. Antennules biramous, antennae with 5-segmented peduncle and scaphocerite. Epistome in two parts: narrow anterior portion between antennae, posterior portion usually heavily armed with spines on perimeter of circular portion to which labrum attaches. Mandibles with palp usually 3-segmented. Maxillulae with endopodal palp; maxillae biramous, with two bilobed endites. Third maxillipeds long, pediform, 7-segmented. Pereiopods uniramous; first three pairs chelate, third pair typically the largest. Pleopods without appendixes interna, first pair uniramous. Pleuron of first pleomere overlapping the second. Eggs brooded on pleopods, larvae hatched as zoeae (or later). Males without petasma, females without thelycum. Male gonopores on the coxae of the fifth pair of pereopods, females with gonopores on the coxae of

the third pair of pereopods. [Diagnosis modified from Schram (1986) and Davie (2002)]

##### Family Stenopodidae Claus, 1872

Stenopinae Claus, 1872: 500.

Stenopidae Huxley, 1879: 785.

Stenopodidae Smith and Weldon, 1909, in Harmer and Shipley 4: 162; Holthuis, 1993: 312; Martin and Davis, 2001: 72.

**Type Genus.**—*Stenopus* Latreille, 1819.

**Diagnosis.**—Body compressed. Telson elongate, lance-shaped, ending in two strong spines, sometimes with a third spine in between. Endopod of uropod with two longitudinal dorsal ridges. Propodus of second maxilliped with cristate ventral margin. Third maxilliped always with a distinct exopod, whole appendage as long as or shorter than first pereopod, never stouter than pereopods. Third pereopod the longest. One to three chelate appendages, cutting edges of chelae with series of peg-like teeth separated by chitinous lamellae distally. Branchial formula always composed of 19 branchial exites. [Diagnosis modified from Holthuis (1993) and Davie (2002)]

##### Family Spongicolidae Schram, 1986

Spongicolidae Schram, 1986: 284.

**Type Genus.**—Not designated in original description; *Spongicola* de Haan, 1844, is hereby proposed as type genus.

**Diagnosis.**—Body depressed. Telson broadly lance-shaped or subquadrangular, ending in three to five subequal spines. Uropodal endopod usually with single longitudinal dorsal ridge. Propodus of second maxilliped with rounded, unarmed ventral margin. Third maxilliped with exopod well

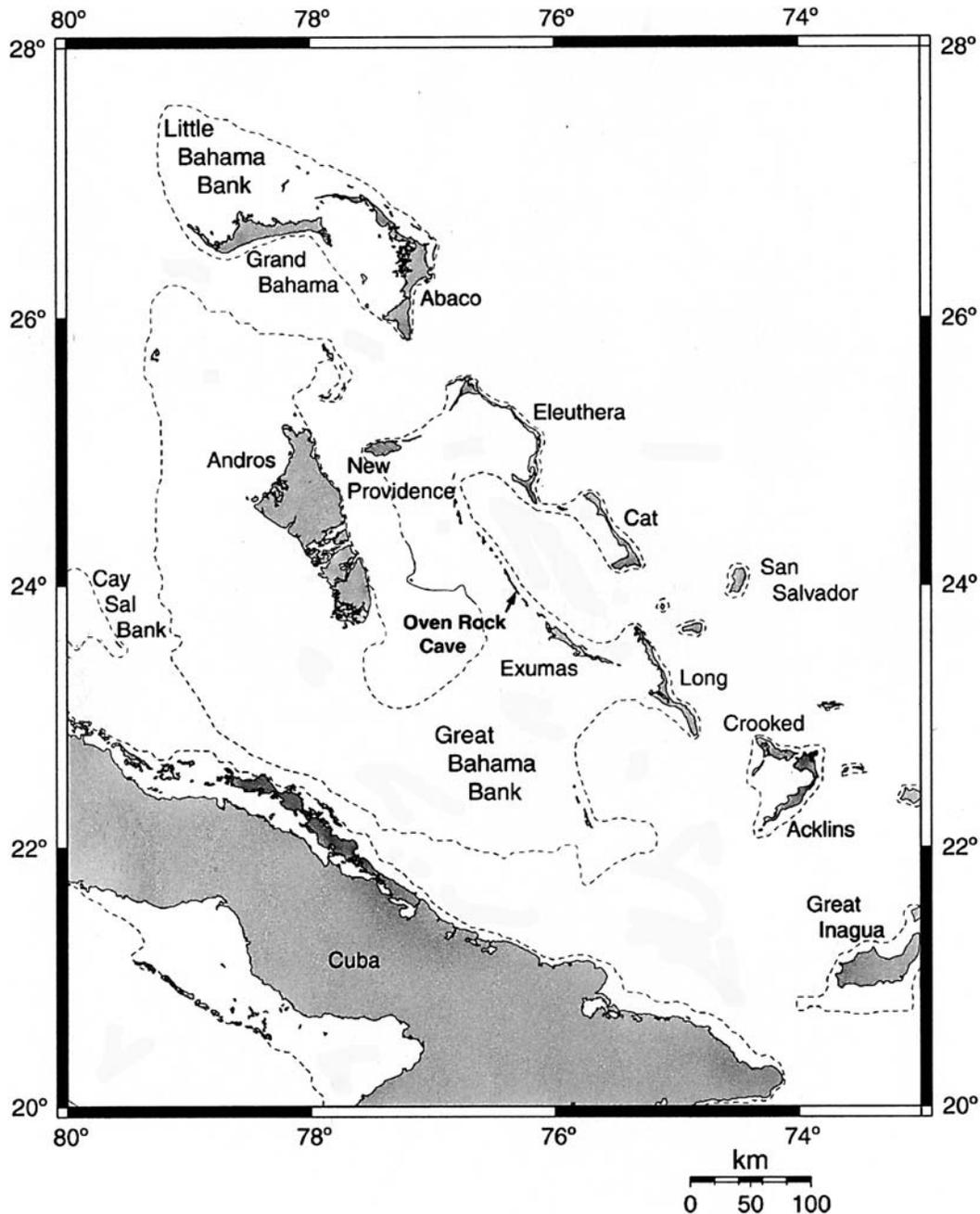


Fig. 1. Map of the Bahamas archipelago showing the location of Oven Rock Cave in relation to the major islands. The dashed line represents the approximate position of the 100 m depth contour which marks the edge of the shallow water carbonate banks.

developed, rudimentary or absent; whole appendage as long as or shorter than first pereiopod; never stouter than pereiopods. Third pereiopod the longest, except in *Paraspongicola* where the second pereiopod is longer than the third. Chelate appendages with chitinous ridges distally on cutting edges, rarely with few small sharp teeth. Branchial formula always composed of 12-19 branchial exites. [Diagnosis modified from Holthuis (1993) and Davie (2002)]

Family Macromaxillocarididae, new family

Type Genus.—*Macromaxillocaris*, new genus.

Diagnosis.—Body slightly compressed. Telson lanceolate, terminating in three spines. Uropodal endopod with single longitudinal ridge. Propodus of second maxilliped with ventral margin straight and a prominent acute tooth. Third maxilliped with well-developed exopod, whole appendage longer than first two pereiopods, stouter than all pereiopods. Pereiopods increasing in length posteriorly. Chelate appendages with chelae devoid of teeth, cutting edges smooth. Epistome with two fang-like projections. Reduced branchial formula in comparison to the rest of the species in the infraorder (Table 2). Unsegmented palp of first maxilliped. Branchial formula composed of 12 branchial exites.

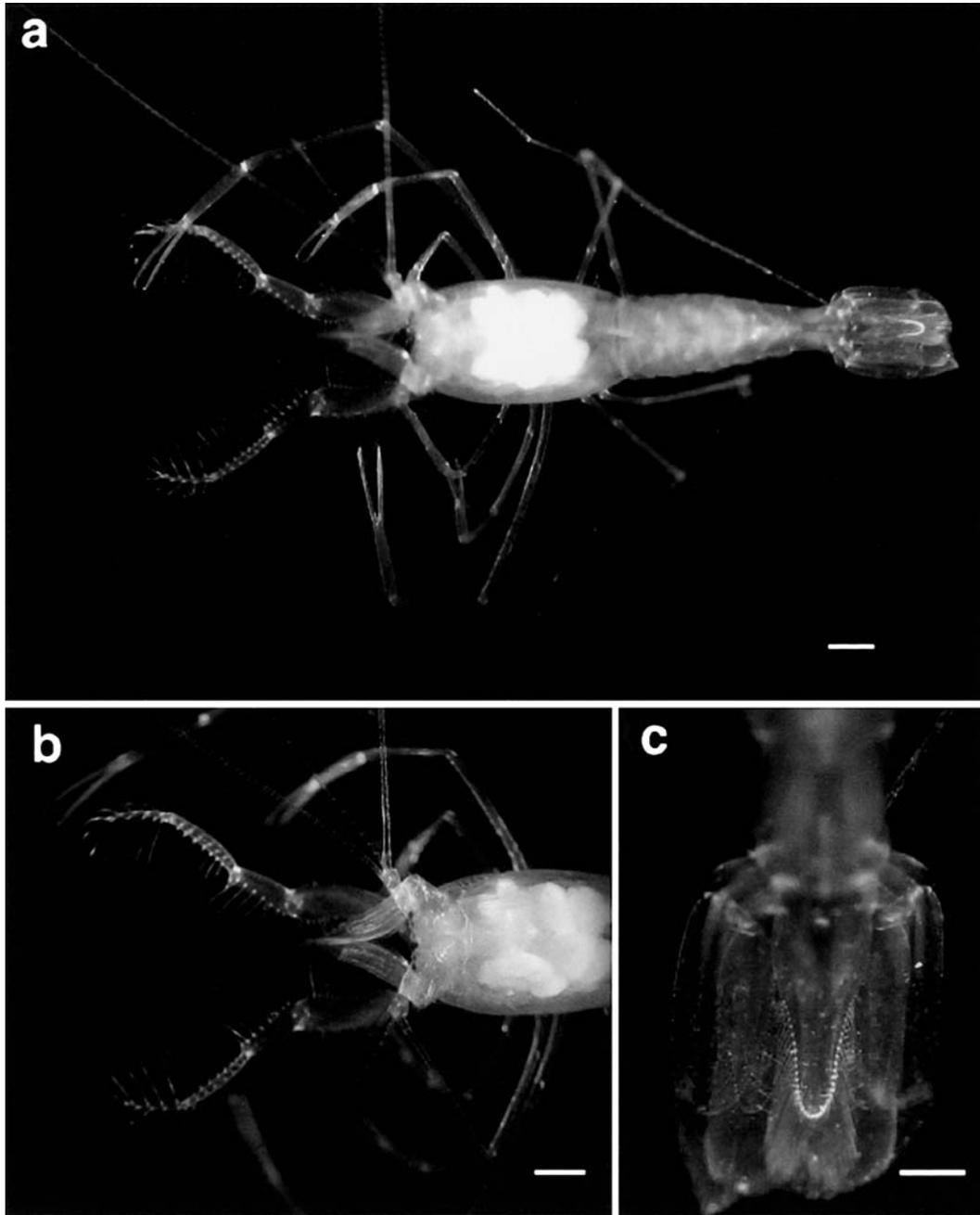


Fig. 2. *Macromaxillocaris bahamaensis*, new species, female holotype live: a, dorsal view; b, detail of cephalothorax; c, detail of telson and uropods. Scale bars represent: a-b, 1 mm; c, 0.5 mm.

**Etymology.**—The name to denote the new family is formed by “macro”, from the greek *makros*, meaning long; “maxillo”, from the latin *maxillaris*, pertaining to the jaw or the mouth area; and “carididae”, derived from *karis*, the greek word for shrimp. The resulting name describes the exceptionally long third maxilliped present in these shrimps.

***Macromaxillocaris***, new genus

**Type Species.**—*Macromaxillocaris bahamaensis*, new species.

**Diagnosis.**—Small stenopodid shrimps adapted to cave life, with body slightly compressed, unpigmented; eyes reduced, without cornea or any visual elements. Third maxillipeds bearing two rows of long articulated setae on merus, carpus, propodus and dactylus, forming sieving apparatus. Setae longitudinally grooved, groove facing mesially, borders of groove finely serrate; each seta with basal structure to avoid excessive lateral movement. Chelae of first three pereiopods similar in shape, with a constant dactylus length/propodus length ratio of 0.5. Fourth and fifth pereiopods with carpi and propodi not multiarticulated; dactyli deeply bifid. Palp of first maxilla deeply cleft.

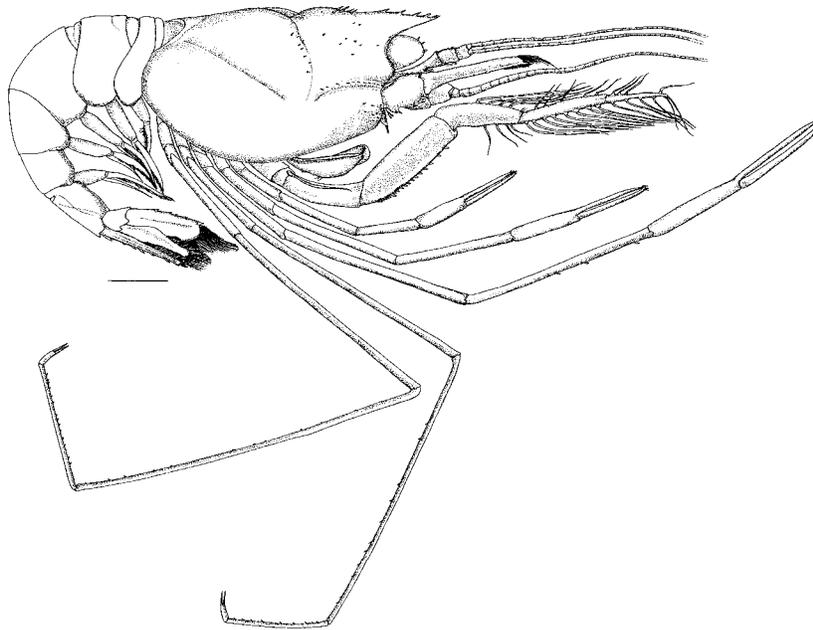


Fig. 3. *Macromaxillocaris bahamaensis*, new species, female holotype: Total lateral view. Scale bar = 1 mm.

Remarks.—The general body shape, cephalothorax and pleon, of the new genus is similar to the body plan of many stenopodideans. However, the size and shape of several appendages show unique modifications. In contrast with those seen in other genera in the infraorder, the pereiopods of *Macromaxillocaris* are all very slender and elongate, increasing in size posteriorly. In all other stenopodideans, the length proportions of the articles change substantially throughout the pereiopods; the third one being the longest, typically with a shortened carpus and with an ornamented chela that is much heavier than those of the first two pereiopods.

Although the third maxilliped in the Stenopodidae and Spongicolidae is a well developed, pediform, densely setose, 7-segmented appendage, it is always shorter and less robust than the first pereiopod. In *Macromaxillocaris*, the third maxilliped is the strongest appendage, clearly adapted to trap food particles.

*Macromaxillocaris* also represents the first form in the infraorder to be adapted to cave life. Color patterns are especially important in identifying stenopodideans, in some instances they can be used to separate species. Although common in some deep-water species, an unpigmented shallow water-form therefore represents also an important departure from the general pattern in the infraorder.

Etymology.—The name is formed as in the family name, the ending “carididae” changes to “caris”, to denote the genus. The gender is feminine.

*Macromaxillocaris bahamaensis*, new species

Figs. 2-7

Holotype.—Female, cl 4.5 mm, tl 14.4 mm; 10 January 2003; Oven Rock Cave, Great Guana Cay, Exuma Cays, Bahamas; collected by T. M. Iliffe; CNCR 23167.

Paratypes.—Female, cl 3.7 mm, tl 11.7 mm; female, cl 3.0 mm, tl 9.7 mm; 7 January 2004; Oven Rock Cave, Great Guana Cay, Exuma Cays, Bahamas; collected by T. M. Iliffe; CNCR 23168.

Description of Holotype.—Rostrum triangular in lateral and dorsal views, armed dorsally with five teeth, ventral margin straight, reaching proximal half of second antennular segment (Fig. 3). Carapace with deep and narrow cervical groove dorsally, becoming less marked laterally, disappearing before intersecting branchiostegal and cardiac grooves (Fig. 4a). Lateral portion of cervical groove with scattered spines. Branchiostegal groove shallow, slightly arched posteriorly, with line of spines running along superior margin. Cardiac groove shallow, straight in lateral view, without spines. Gastric region of carapace with series of spines forming inverted V-shape dorsally, with scattered spines laterally. Pterygostomial region with scattered spines and minute granules. Orbit rounded, smooth; antennal and pterygostomial angles simple, not produced. Posterior margin of carapace broadly rounded laterally, overlapping slightly on top of first abdominal somite (Fig. 3). Eyes reduced, not pigmented.

Sternite 5 with two projections joining mesially on ventral surface of thorax, forming inverted V-shape; sternite 6 with simple ridge, anterior margin rounded; sternite 7 with simple, straight ridge; sternite 8 with triangular projections not joining mesially; posterior portion of sternite 8 with wide V-shaped ridge (Fig. 6B).

Pleon smooth, without spines or grooves, except for two shallow depressions on second and sixth somites. Pleuron of first somite narrow dorsally, becoming wider laterally, ventral margin rounded; anterolateral portion partially covered by carapace (Fig. 3). Second somite about three times the length of first, dorsally with short and shallow depression, pleuron broadly rounded laterally. Third somite longest, anterior and posterior margins slightly rounded,

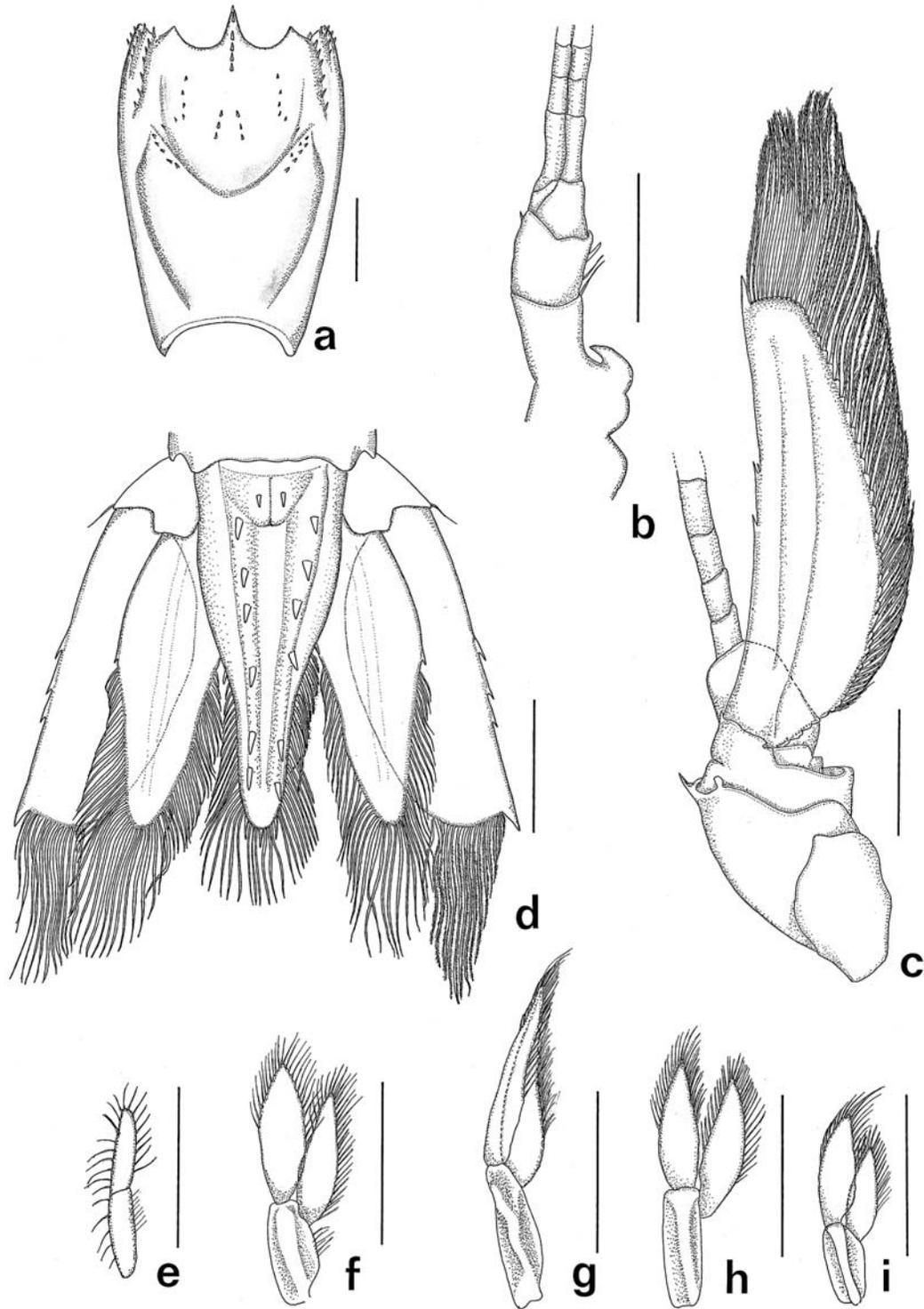


Fig. 4. *Macromaxillocaris bahamaensis*, new species, female holotype: a, dorsal view of carapace; b, antennule; c, antenna; d, telson and uropods; e-i, first through fifth pleopod. Scale bars represent: a, d-i, 1 mm; b-c, 0.5 mm.

ventrolateral margin of pleuron sinuous. Pleura of fourth and fifth somites with obtuse margins. Sixth somite twice as long as tall, posterodorsal margin overlapping telson, ventrolateral angle concave and receiving basal article of uropods. Telson of same length as internal ramus of uropods, shorter than external ramus; anterior half broad, becoming

narrower posteriorly, posterior width less than one third anterior width. Dorsal surface with median elevation close to anterior margin, divided by narrow, shallow cleft, each one of the two resulting lobes with one spine; two longitudinal ridges running almost along whole length of telson, each one with six spines; one pair of marginal spines on posterior half,

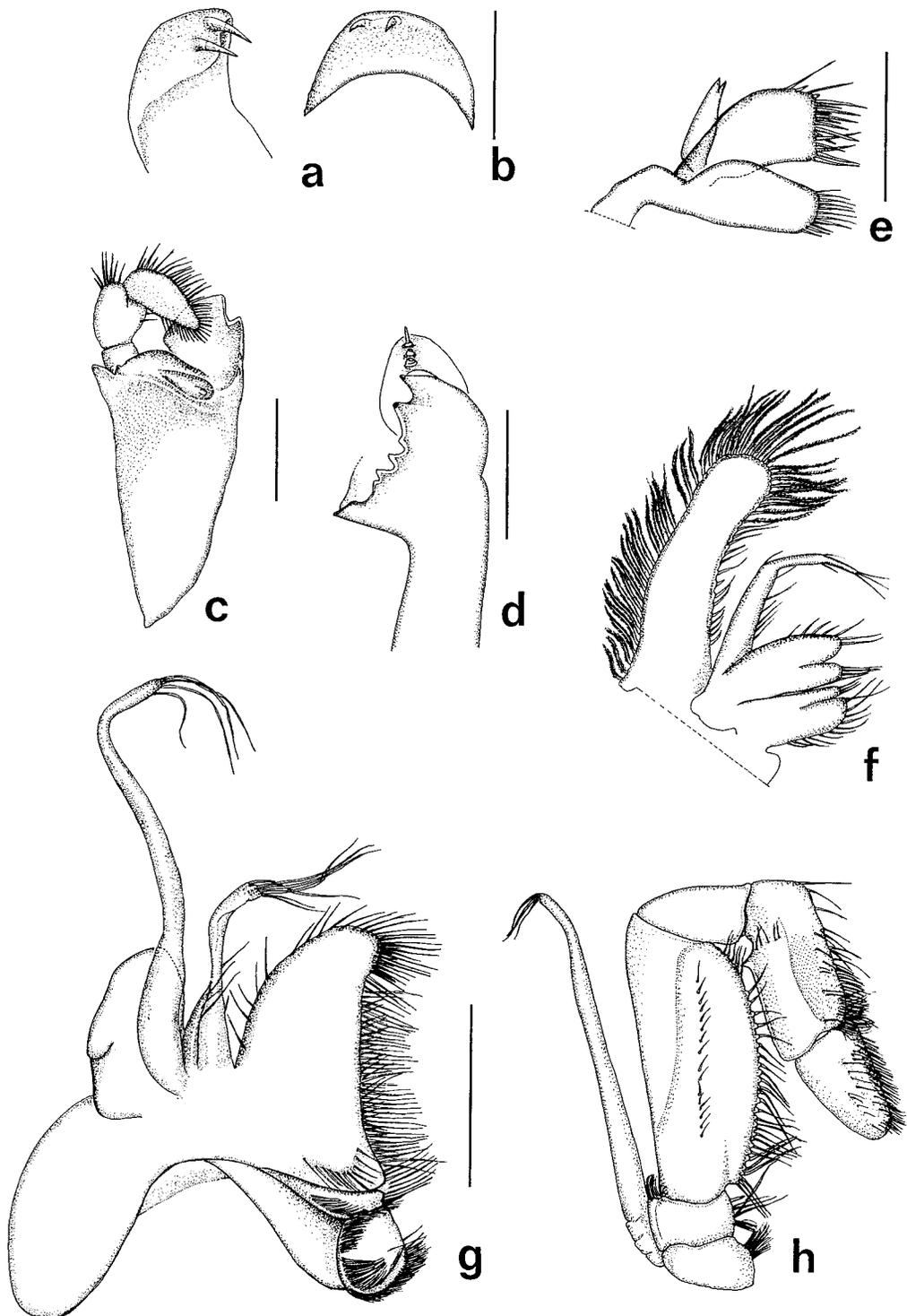


Fig. 5. *Macromaxillocaris bahamaensis*, new species, female holotype: a, epistome, lateral view; b, epistome, ventral view; c, right mandible, anterior view; d, detail of right mandible, posterior view; e, first maxilla; f, second maxilla; g, first maxilliped; h, second maxilliped. Scale bars represent: a-e, 0.5 mm; f-h, 1 mm.

close to midlength; posterior margin rounded, with three strong spines of same length; margin between marginal spines bearing long setae (Fig. 4d).

Antennular peduncle half as long as antennal scale. Stylocerite hook-like, situated on proximal portion of

article. Second antennular article 1.3 times as long as wide, distal margin irregular, with strong lateral spine 0.5 times as long as article (Fig. 4b). Third antennular article divided, giving origin to antennular flagella. Antenna with scaphocerite 3.8 times as long as broad, including distolateral

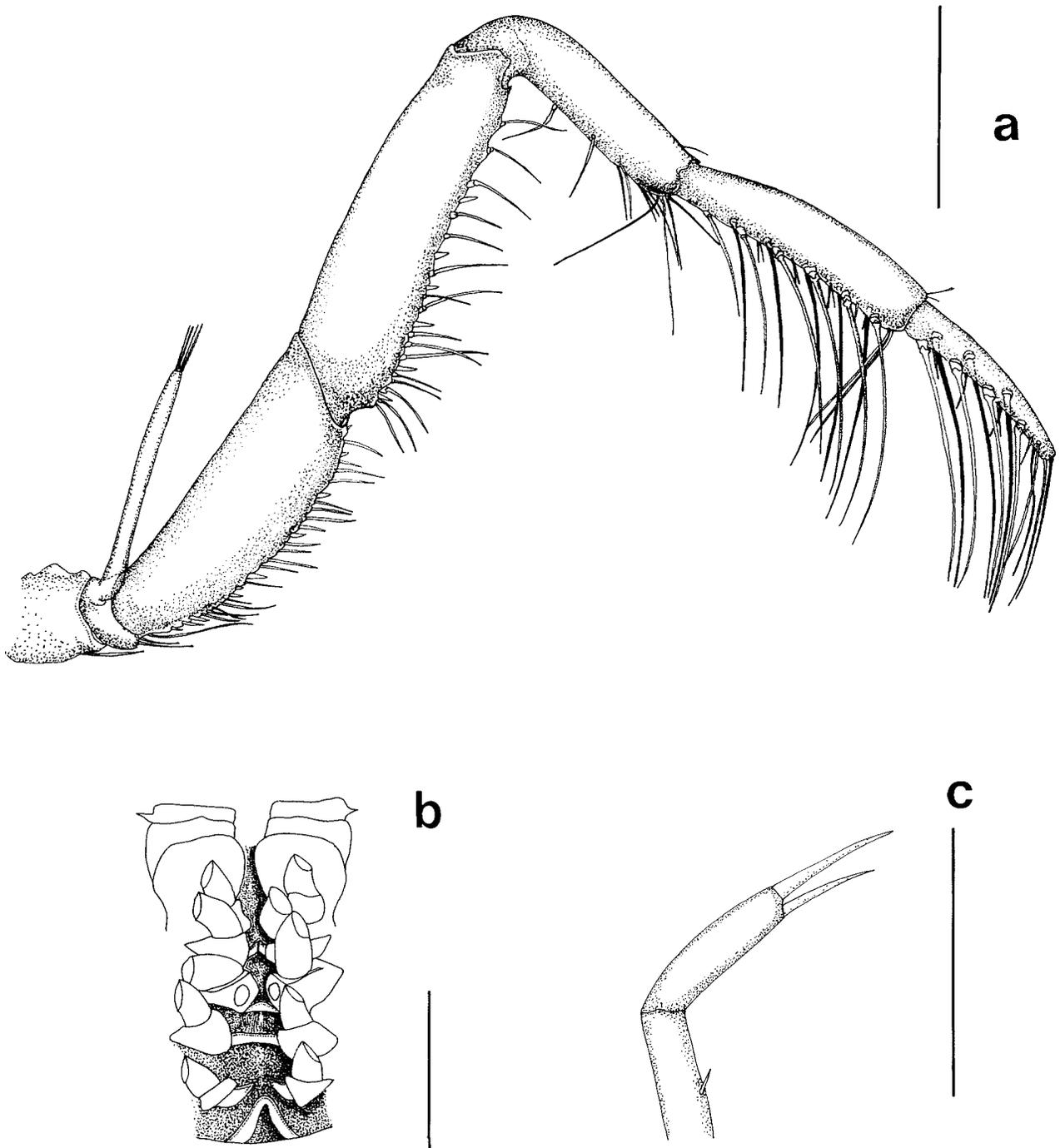


Fig. 6. *Macromaxillocaris bahamaensis*, new species, female holotype: a, third maxilliped; b, ventral view of thorax; c, dactylus of fourth pereiopod. Scale bars represent: a-b, 1 mm; c, 0.5 mm.

tooth; lateral margin slightly arched, with two large and one small teeth at midlength, mesial margin simple; distolateral tooth completely projected beyond distal margin of scaphocerite; basicerite with row of sharp spines on ventrolateral surface; antennal flagellum simple (Fig. 4c).

Epistome protruding pterygostomian angle in lateral view of carapace, formed by semicircular projection bearing two fang-like teeth (Figs. 3, 5a-b). Mandibles asymmetrical, palp with three articles, bent into space between molar and incisor processes; molar process with one distinct strong short

spine and two blunt knobs, incisor process of right mandible with irregular cutting edge formed by seven denticles of different sizes (Figs. 5c-d).

First maxilla with distal lacinia elongated, superior margin rounded, inferior and mesial margins straight; mesial margin bearing simple, strong, short setae interspersed with short spines. Proximal lacinia not as robust as distal one, mesial margin rounded, with simple, short setae. Palp tapering distally, distal margin bifid, devoid of setae (Fig. 5e).

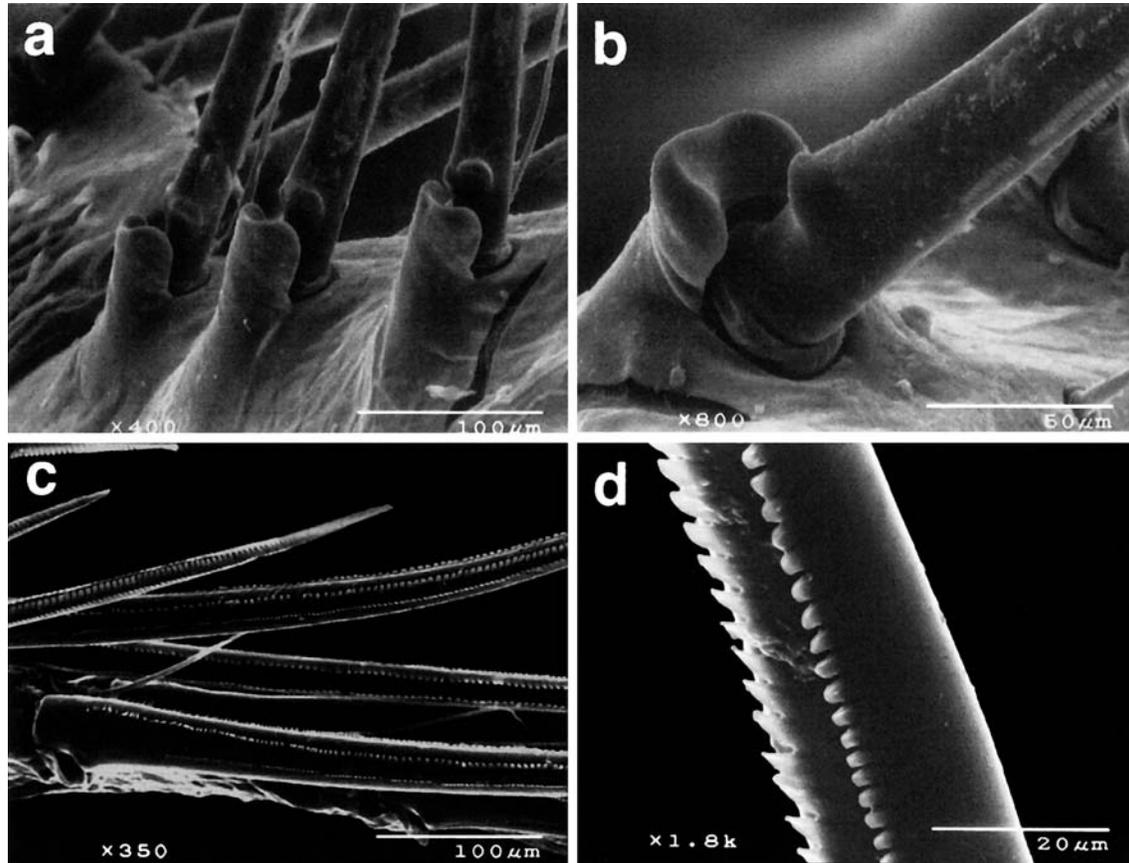


Fig. 7. *Macromaxillocaris bahamaensis*, new species, female holotype, all SEM micrographs of articulated setae of third maxilliped: a-b, details of basal portion; c-d, details of grooves and serrate edges.

Second maxilla with scaphognathite elongated anteriorly, bordered with long plumose setae, posterior lobe missing; coxal and basal endites deeply bilobed, sparsely bordered with simple setae; endopodite unsegmented, simple with scattered setae (Fig. 5f).

First maxilliped with coxa rolled distally, with marginal setae; basis approximately trapezoidal, gnathal border with long setae, line of submarginal setae close to proximomesial angle; endopodite unsegmented, with long setae apically; exopodite twice as long as endopod, with four apical long setae, basal portion wide; epipodite oval-shaped, devoid of setae (Fig. 5g).

Second maxilliped subpediform, endopod 5-segmented, dactylus oval-shaped, gnathal border densely lined with short setae; propodus 1.5 times as long as dactylus, approximately rectangular, distal portion of gnathal border

with short setae, conspicuous denticle on proximomesial margin; carpus short, subtriangular; merus broad, mesial margin rounded with regularly placed setae, external surface with line of short setae running medially; ischium half as long as wide, with patch of setae on distolateral angle, scattered setae on mesial margin; basis with small dense patch of seta on mesial margin. Exopod long, slender, devoid of setae except for three apical ones (Fig. 5h).

Third maxilliped pediform, basis visible in lateral view, exopod shorter than ischium. Ischium slightly arched, directed anteriorly in same direction as longitudinal body axis, 3.7 times longer than wide, becoming wider distally; inferior margin with line of small spines irregularly spaced (Fig. 6a). Merus longest article, 3.3 times longer than wide, articulation with ischium at approximately 45° angle; straight in lateral view, directed upwards (Figs. 3, 6a), slightly arched in dorsal view, directed somewhat laterally (Fig. 2b); inferior margin with line of small spines, becoming more separated distally. Carpus 0.7 times as long as merus, proximal width almost twice distal width (Fig. 3); straight in lateral view, oriented parallel to longitudinal body axis (Fig. 3), straight in dorsal view, directed laterally at 45° angle with respect to longitudinal body axis (Figs. 2a-b). Propodus somewhat longer than carpus, constant thickness throughout; in dorsal view oriented laterally, at a slightly higher angle than carpus relative to longitudinal body axis (Figs. 2a-b). Dactylus shortest article, simple, tapering distally (Figs. 3, 6a). Merus,

Table 2. Branchial formula of *Macromaxillocaris bahamaensis* new species.

	Maxillipeds			Pereiopods				
	I	II	III	I	II	III	IV	V
Pleurobranchs			1	1	1	1	1	1
Arthrobranchs			1	1	1	1	1	
Podobranchs		1						
Epipods			1					
Exopods	1	1	1					

carpus, propodus and dactylus bearing two rows of long articulated setae, respectively, one on ventral and one on dorsal margins, forming sieving apparatus (Figs. 2a-b, 3). Articulated setae grooved longitudinally, groove facing mesially, borders of groove finely serrate (Figs. 7c-d); basal portion of seta with knob that fits into cylindrical structure and prevents excessive lateral movement (Figs. 7a-b).

First pair of pereopods shortest, all articles simple, without spines; ischium shortest article, merus 1.8 times as long as ischium, carpus 1.3 times as long as ischium, propodus the longest article, chela slender, 2.2 times as long as ischium; dactylus length/chela length ratio 0.53, cutting edges of fingers devoid of teeth (Fig. 3). Second pair of pereopods similar to first pair but longer; ischium shortest article, merus twice the length of ischium, carpus 1.7 times as long as ischium, propodus longest article, chela slender, 2.1 times as long as ischium; dactylus length/chela length ratio 0.51, cutting edges of fingers devoid of teeth (Fig. 3). Third pair of pereopods similar to but longer than first two pairs; ischium shortest article, merus and carpus 1.8 times as long as ischium, propodus longest article, chela slender, 1.9 times as long as ischium; dactylus length/chela length ratio 0.51, cutting edges of fingers devoid of teeth (Fig. 3). In female holotype coxa expanded mesially with circular genital pore (Fig. 6b). Fourth pair of pereopods longer than anterior three pairs, not chelate; carpus longest article, undivided, with scattered minute spines along ventral margin; propodus undivided, with scattered minute spines along ventral margin; dactylus deeply biunguiculate (Figs. 3, 6c). Fifth pair of pereopods longest; 3, 1.9, 1.2 and 1.1 times as long as first through fourth pairs, respectively; carpus longest article, undivided, with scattered minute spines along ventral margin; propodus undivided, with row of regularly spaced spines along ventral margin; dactylus deeply biunguiculate (Fig. 3).

First pair of pleopods uniramous, second through fifth pairs biramous; third pair largest, fourth and fifth pairs progressively decreasing in size. All pleopods without appendix interna (Figs. 4e-i).

Uropods with protopod approximately triangular, with single lateral seta (Fig. 4d). Endopod lanceolate, borders of posterior half lined with long setae, single tooth on middle lateral margin, single medial longitudinal ridge; of about same length as telson (Fig. 2c). Exopod with mesial margin broadly rounded; lateral margin straight, devoid of setae, with three teeth in middle region; posterolateral tooth reaching beyond posterior margin of blade (Fig. 4d).

**Etymology.**—The specific epithet “*bahamaensis*” is derived from “Bahamas”, making reference to the place of origin of the new species.

**Remarks.**—A small amount of variation was observed among the three specimens examined. They all were females. The holotype shows well-developed genital pores on the mesial surface of the coxae of the third pereopods. All three specimens had rounded abdominal pleura. The specimens ranged in total length from 9.7 to 14.4 mm, preserving the same body proportions. The most noticeable variation was seen in the setation pattern of the third maxilliped. The articulated setae occur from the merus to the dactylus,

however the number and length of the setae on each article varied among the specimens.

#### Key to the Families of Stenopodidea, Modified from Holthuis (1993)

1. Body compressed. Telson elongate lance-shaped. Propodus of second maxilliped with cristate ventral margin armed with teeth or hooked proximal spines. Third maxilliped always with distinct exopod . . . . . 2
- Body depressed. Telson broadly ovoid or subquadrangular. Propodus of second maxilliped with rounded, unarmed ventral margin. Exopod of third maxilliped sometimes absent or rudimentary . . . . . Spongiicolidae
2. Third maxilliped shorter than or as long as first pereopod. Telson ending in two strong spines, sometimes with much smaller spine in between. Uropodal endopod with two longitudinal dorsal ridges. Branchial formula always composed of 19 branchial exites . . . . . Stenopodidae
- Third maxilliped massive, longer than first two pereopods. Telson ending in three strong spines. Uropodal endopod with single longitudinal dorsal ridge. Branchial formula composed of 12 branchial exites . . . . . Macromaxillocarididae

#### DISCUSSION

The Macromaxillocarididae clearly represents a new group within the Stenopodidea. However, its position relative to the other two known families is not clear due to the combination of characters found in the new taxon (Table 1). Superficially it resembles the Stenopodidae. The Macromaxillocarididae shares with Stenopodidae the compressed body, an elongated telson and an exopod on the third maxilliped; it shares an uropodal endopod with a single dorsal ridge and a reduced branchial formula with some species in the Spongiicolidae.

Most species in the infraorder have one pleurobranch on the third maxilliped (M3) and on all pereopods (P1-P5); one arthrobranch on M1-M2, and two arthrobranches from M3 to P5; one podobranch on M2; one epipod from M1 to P5; and one exopod on all three maxillipeds (de Saint Laurent and Cleva, 1981; Saito and Takeda, 2003). Important departures from this general pattern are also present, particularly in the genera *Spongiocaris* and *Spongiocoloides*, in which the pereopods may lack epipods and the exopods on the maxillipeds may be rudimentary or absent (Saito and Takeda, 2003). The branchial formula of *Macromaxillocaris bahamaensis* is reduced when compared to the general stenopodidean pattern (Table 2). However, as in the new species, at least three species of *Spongiocoloides* (*S. galapagensis* Goy, 1980; *S. inermis* [Bouvier, 1905]; and *S. profundus* Hansen, 1908) have one arthrobranch from M3 to P5 and lack epipods on the pereopods (Saito and Takeda, 2003). Additional reductions in the branchial formula of *M. bahamaensis* include the absence of arthrobranches and epipods on M1-M2 (Table 2). Saito and Takeda (2003) showed for the Spongiicolidae that the plesiomorphic state of the branchial formula corresponds to the general stenopodidean pattern described above, and that the reduced formulae are derived states. *Spongiocoloides galapagensis*, *S. inermis*, and *S. profundus*, with the most reduced branchial formulae, are the most derived species from a phylogenetic point of view. In this context, the branchial

formula of *M. bahamaensis* would indicate that this is a much derived state rather than a primitive one within the infraorder.

The reduction of the branchial formula in spongicolids is correlated with the emergence of a sponge symbiosis, the shrimps live inside a sponge and movement is reduced to a minimum (Saito and Takeda, 2003). In *M. bahamaensis*, the proposed crevicular existence with reduced mobility and hence the low metabolism is consistent with the reduced branchial formula. As pointed out by Saito and Takeda (2003), several authors have considered the composition of the branchial formula as diagnostic for major groups among decapods (Burkenroad, 1981; Hong, 1988; Pohle and Marques, 1998), a notion that strengthens the creation of Macromaxillocarididae.

The presence of the massive third maxillipeds is the most distinguishing character of the new taxon. Their size, position, and form suggest that they are preferentially used to trap food particles rather than for grooming. Hence the structure formed by these two appendages is called a "sieving apparatus". In contrast, in all other stenopodids the third maxilliped and often the first pereopod have an active role in the grooming of appendages. Third maxillipeds used for grooming are very setose, and may have dense patches of setae called setiferous organs. The third maxilliped possesses simple and articulated grooved setae. The latter are present in all three families, as we found by examination of three genera (*Stenopus*, Stenopodidae; *Microprosthema*, Spongicolidae; *Macromaxillocaris*, Macromaxillocarididae). However, in the new taxon they appear to be larger, with a more developed basal support structure and the corresponding knob on each seta (Figs. 7a-b). The serrate edges along the grooves of these setae could be used for scraping in the Stenopodidae and Spongicolidae. Their presence in the Macromaxillocarididae could represent a plesiomorphic condition.

Unique to the new taxon, relative to the rest of the infraorder, is the increase in size posteriorly of the pereopods, and the similar proportions of the articles in the first three pereopods without the third one being considerably heavier than the others. In all other stenopodids, the third pereopod is the largest and stoutest of all, except for *Paraspongicola* where the second pereopod is the largest. Often the carpus is proportionally shorter and the chela different from those of the first two pereopods. The relative size of the pereopods is an important character throughout the Decapoda in defining higher taxonomic categories. Since the pattern throughout the Stenopodidae and Spongicolidae is highly conserved, we consider this departure in the Macromaxillocarididae an important diagnostic feature.

Mouth appendages are rarely used for species identification and usually lack diagnostic value. In *M. bahamaensis*, the first maxilla and the first maxilliped show noteworthy variations from those of the rest of the stenopodids. The first maxilla in the new taxon has a palp whose distal end is not simple and rounded as in the rest of stenopodids; instead, it is deeply cleft giving it a bifid appearance (Fig. 5e). The first maxilliped of all other stenopodids, to the best of our knowledge, has a palp (endopod) that is either 2- or 3-segmented; whereas in the new species it is unsegmented (Fig. 5g).

Although of negligible or no functional significance, the two described morphological variations are unique to *M. bahamaensis*, adding to the rest of unique characters present.

In the shallow habitats occupied by stenopodids, coral rubble or rocky substrates, species can be brightly colored with eyes normally developed. In habitats at depths ranging from 100 to 2400 m, on muddy substrates and as sponge symbionts, adaptations to life in darkness have evolved. For example, several deep-water species of *Odontozona* (*O. spongicola* [Alcock & Anderson, 1899], *O. edwardsi* [Bouvier, 1908], and *O. foresti* [Hendrickx, 2002]) and *Spongicoloides* (*S. galapagensis* [Goy, 1980], *S. hawaiiensis* [Baba, 1983], and *S. novaezelandiae* [Baba, 1979]) have unpigmented eyes (Baba, 1979, 1983; Goy, 1980; Wicksten, 1982; Hendrickx, 2002). In this regard, *M. bahamaensis*, being a shallow-water species, represents the first true stygobitic form within the infraorder, living in a cave and showing the typical adaptations to cave life (reduced eyes, without cornea or any visual elements, only ocular peduncle remains; unpigmented body; and elongated, slender appendages).

Like *M. bahamaensis*, the rare thalassinid shrimp *Naushonia manningi* Alvarez, Villalobos and Iliffe, 2000, belongs to a marine group but is the only species of that group to inhabit a cave on an island. *Macromaxillocaris bahamaensis* is the only stenopodid that inhabits an anchialine cave on an island.

With the inclusion of *M. bahamaensis* described here, Oven Rock Cave now contains 20 stygobitic species. According to criteria set by Culver and Sket (2000) where 20 obligate aquatic or terrestrial cave species is used as an arbitrary cutoff point, Oven Rock Cave ranks among only 20 other caves and wells worldwide regarded as "hotspots for subterranean biodiversity". It is the only site in the Caribbean region and only the second anchialine cave so designated, together with the Walsingham Cave System in Bermuda. Other stygobitic fauna inhabiting Oven Rock Cave includes five species of halocyprid ostracodes (*Spelaeoecia capax* Kornicker, 1990 [in Kornicker et al., 1990], *S. styx* Kornicker, 1990 [in Kornicker et al., 1990], *Deeveya exleyi* Kornicker and Iliffe, 1998, *Danielopolina exuma* Kornicker and Iliffe, 1998; and *D. kakuki* Kornicker and Iliffe, 2000); four species of epacteriscid calanoid copepods (*Bofuriella vorata* Fosshagen, Boxshall and Iliffe, 2001; *Oinella longiseta* Fosshagen, Boxshall and Iliffe, 2001; *Enantronoides bahamensis* Fosshagen, Boxshall and Iliffe, 2001; and *Bomburiella gigas* Fosshagen, Boxshall and Iliffe, 2001); three undescribed species of remipedes (*Pleomothra* sp., *Cryptocorynetes* sp., and *Godzilliognomus* sp.); two species of hippolytid shrimp (*Barbouria cubensis* (Von Martens, 1872) and *Parhippolyte sterreri* (Hart and Manning, 1981)); two species of cirrolanid isopods (*Cirrolana* (*C.*) *troglexuma* Botosaneanu and Iliffe, 1997 and *Bahalana exumina* Botosaneanu and Iliffe, 2002); the amphipod *Spelaeonicippe provo* Stock and Vermeulen, 1982; the polynoid polychaete *Pelagomacellicephala iliffei* Pettibone, 1985; and the undescribed thermosbaenacean *Tulumella* sp.; bairdiid podocopid ostracodes, misophrioid

and harpacticoid copepods, nerillid polychaetes and nemerteans.

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#### REFERENCES

- Alcock, A., and A. R. S. Anderson. 1894. Natural history notes from H. M. Indian marine survey steamer "Investigator", commander C. F. Oldham, R. N., commanding. Ser. II, No. 14. An account of a recent collection of deep-sea Crustacea from Bay of Bengal and Laccadive Sea. *Journal of Asiatic Society of Bengal* 63(2): 141-185.
- , and ———. 1899. An account of deep-sea Crustacea dredged during the surveying-season of 1897-98. Natural history notes from H. M. Indian marine survey ship "Investigator", commander T. H. Heming, R. N., commanding. Ser. III, No. 2. *Annals and Magazine of Natural History*, series 7, 3: 1-27, 278-292.
- Alvarez, F., J. L. Villalobos, and T. M. Iliffe. 2000. *Naushonia manningi*, new species (Decapoda: Thalassinidea: Laomedidae), from Acklins Island, Bahamas. *Journal of Crustacean Biology* 20, Special Number 2: 192-198.
- Baba, K. 1979. A new stenopodidean shrimp (Decapoda, Natantia) from the Chatham Rise, New Zealand. *Pacific Science* 33: 311-314.
- . 1983. *Spongicoloides hawaiiensis*, a new species of shrimp (Decapoda: Stenopodidea) from the Hawaiian Islands. *Journal of Crustacean Biology* 3: 477-481.
- Bate, C. S. 1888. Report on the Crustacea Macrura collected by H. M. S. "Challenger" during the years 1873-76. Reports on the Scientific Results of the Voyage of H. M. S. Challenger during the years 1873-76, *Zoology* 24: I-XC1-942.
- Botosaneanu, L., and T. M. Iliffe. 1997. Four new stygobitic cirrolanids (Crustacea: Isopoda) from the Caribbean - with remarks on intergeneric limits in some cirrolanids. *Bulletin de L'Institut Royal des Sciences Naturelles de Belgique, Biologie* 67: 77-94.
- , and ———. 2002. Stygobitic isopod crustaceans, already described or new, from Bermuda, the Bahamas, and Mexico. *Bulletin de L'Institut Royal des Sciences Naturelles de Belgique, Biologie* 72: 101-112.
- Bouvier, E. L. 1905. Sur les Pénéides et les Sténopides recueillis par les expéditions françaises et monégasques dans l'Atlantique. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris*, 140: 980-983.
- . 1908. Sur les relations zoologiques des crevettes de la tribu des Sténopidés. *Comptes rendus hebdomadaires des Séances de l'Académie des Sciences, Paris*, 146: 887-891.
- Bruce, A. J., and K. Baba. 1973. *Spongiocaris*, a new genus of stenopodidean shrimp from New Zealand and South African waters, with a description of two new species (Decapoda, Natantia, Stenopodidea). *Crustaceana* 25: 153-170.
- Burkenroad, M. D. 1981. The higher taxonomy and evolution of Decapoda (Crustacea). *Transactions of the San Diego Society of Natural History* 19: 251-268.
- Claus, C. F. W. 1872. Grundzüge der Zoologie zum Gebrauche an Universitäten und höhern Lehranstalten sowie zum Selbststudium. Zweite vermehrte Auflage. Marburg und Leipzig. N. G. Elwert'sche Universitäts-Bihandlung, 1170 pp.
- Criales, M. M. 1997. *Microprosthema granatense*, new species, from the southern Caribbean, with a key to shrimps of the genus *Microprosthema* from the western Atlantic and a new record of *Odontozona libertae* (Decapoda: Stenopodidea). *Journal of Crustacean Biology* 17: 538-545.
- Culver, D. C., and B. Sket. 2000. Hotspots of subterranean biodiversity in caves and wells. *Journal of Cave and Karst Studies* 62: 11-17.
- Davie, P. J. F. 2002. Crustacea: Malacostraca: Phyllocarida, Hoplocarida, Eucarida (Part I). pp. 172-177. In: A. Wells and W. W. K. Houston, (eds.) *Zoological Catalogue of Australia*, Vol. 19.3A, CSIRO Publishing, Melbourne, Australia.
- de Haan, W. 1844. Crustacea. pp. 165-196. In: P. F. de Siebold, *Fauna Japonica sive descriptio animalium, quae in itinere per Japoniam, jussu et auspicio superiorum, qui summum in India batava imperium tenent, suscepto, annis 1823-1830 collegit, notis, observationibus et adumbrationibus illustravit*.
- de Saint Laurent, M., and R. Cleve. 1981. Crustacés Décapodes: Stenopodidea. pp. 151-188. In: *Résultats des Campagnes MUSORSTOM, Collection Mémoires ORSTOM no. 91*. Paris.
- Fosshagen, A., G. A. Boxshall, and T. M. Iliffe. 2001. The Epacteriscidae, a cave-living family of calanoid copepods. *Sarsia* 86: 245-318.
- Goy, J. W. 1980. *Spongicoloides galapagensis*, a new shrimp representing the first record of the genus from the Pacific Ocean (Crustacea: Decapoda: Stenopodidea). *Proceedings of the Biological Society of Washington* 93: 760-770.
- . 1987. *Microprosthema emmiltum*, new species, and other records of stenopodidean shrimps from the eastern Pacific (Crustacea: Decapoda). *Proceedings of the Biological Society of Washington* 100: 717-725.
- . 1992. A new species of *Stenopus* from Australia, with a redescription of *Stenopus cyanoscelis* (Crustacea: Decapoda: Stenopodidae). *Journal of Natural History* 26: 79-102.
- , and D. L. Felder. 1988. Two new species of *Microprosthema* from the western Atlantic (Crustacea: Decapoda: Stenopodidea). *Journal of Natural History* 22: 1277-1292.
- Hansen, H. J. 1908. Crustacea Malacostraca. I. The Danish Ingolf-Expedition 3(2): 1-120.
- Harmer, S. F., and A. E. Shipley. 1909. The Cambridge Natural History, Volume IV. Crustacea, Trilobites and Eurypterida, Introduction to Arachnida, King-Crabs, Tardigrada (water-bears) and Pentastomida, Scorpions, Spiders, Mites, Ticks, etc., Pycnogonida. Macmillan and Co., London, 566 pp.
- Hart, C. W. Jr., and R. B. Manning. 1981. The cavernicolous caridean shrimp of Bermuda (Alpheidae, Hippolytidae, and Atyidae). *Journal of Crustacean Biology* 1: 441-456.
- Hendrickx, M. E. 2002. A new deep water species of *Odontozona* Holthuis (Decapoda, Stenopodidae) from the southern Gulf of California, Mexico. *Crustaceana* 75: 405-412.
- Holthuis, L. B. 1946. Biological results of the Snellius Expedition XIV. The Stenopodidae, Nephropsidae, Scyllaridae, and Palinuridae. *Temminckia* 7: 1-178.
- . 1993. The recent genera of the caridean and stenopodidean shrimps (Crustacea, Decapoda) with an appendix on the Order Amphionidacea. Leiden, Nationaal Natuurhistorisch Museum, 328 pp.
- Hong, S. Y. 1988. Development of epipods and gills in some pagurids and brachyurans. *Journal of Natural History* 22: 1005-1040.
- Huxley, T. H. 1879. On the classification and the distribution of the crayfishes. *Proceedings of the Zoological Society of London* 1878: 751-788.
- Kornicker, L. S., and T. M. Iliffe. 1998. Myodocopid Ostracoda (Halocypridina, Cladocopina) from anchialine caves in the Bahamas, Canary Islands, and Mexico. *Smithsonian Contributions to Zoology* 599: 1-93.
- , and ———. 2000. Myodocopid Ostracoda from Exuma Sound, Bahamas, and from marine caves and Blue Holes in the Bahamas, Bermuda and Mexico. *Smithsonian Contributions to Zoology* 606: 1-98.
- , J. Yager, and D. Williams. 1990. Ostracoda (Halocyprididae) from anchialine caves in the Bahamas. *Smithsonian Contributions to Zoology* 495: 1-51.
- Latreille, P. A. 1819. *Salicoques, Carides*. Nouveau dictionnaire d'histoire naturelle appliquée aux arts, à l'agriculture, à l'économie rural et domestique, à la médecine, etc., édition 2, 30: 68-73.
- Martin, J. W., and G. E. Davis. 2001. An Updated Classification of the Recent Crustacea. *Natural History Museum of Los Angeles County, Science Series* 39, 124 pp.

- Milne-Edwards, A. 1881. Compte-rendu sommaire d'une exploration zoologique faite dans l'Atlantique, a bord du navire "Le Talisman" C. R. Academie Scientifique Paris, 93: 931-936.
- Okuno, J. 2003. A new species of the genus *Odontozona* Holthuis, 1946 (Crustacea: Decapoda: Stenopodidae) from submarine caves in southern Japan. *Natural History Research* 7: 167-180.
- Pettibone, M. 1985. Worms from a cave in the Bahamas and from experimental wood panels in deep water off the North Atlantic (Polynoidea: Macelliecephalinae, Harmothoinae). *Proceedings of the Biological Society of Washington* 98(1): 127-149.
- Pohle, G., and F. Marques. 1998. Phylogeny of the Pinnotheridae: larval and adult evidence, with emphasis on the evolution of gills. *Invertebrate Reproduction and Development* 33: 229-239.
- Saito, T., and M. Takeda. 2003. Phylogeny of the family Spongicolidae (Crustacea: Stenopodidea): evolutionary trend from shallow-water free-living to deep-water sponge-associated habitat. *Journal of the Marine Biological Association of the United Kingdom* 83: 119-131.
- Schram, F. R. 1986. *Crustacea*. New York, Oxford University Press, 606 pp.
- Stimpson, W. 1860. *Prodromus descriptionis animalium evertibratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata Missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit, Part VIII*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1860: 22-48.
- Stock, J. H., and J. J. Vermeulen. 1982. Amsterdam expeditions to the West Indian Islands, report 16: A representative of the mainly abyssal Family Pardaliscidae (Crustacea, Amphipoda) in cave waters of the Caicos Islands. *Bijdragen tot de Dierkunde* 52: 3-12.
- von Martens, E. 1872. Ueber Cubanische Crustaceen nach den Sammlungen Dr J. Gundlach's. *Archiv für Naturgeschichte* 38: 77-147, 256-258.
- Wicksten, M. K. 1982. Two species of *Odontozona* (Decapoda: Stenopodidea) from the eastern Pacific. *Journal of Crustacean Biology* 2: 130-135.

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