

Micropacteridae, a new family of Remipedia (Crustacea) from the Turks and Caicos Islands

Stefan Koenemann^{a,*}, Thomas M. Iliffe^b, Joris L. van der Ham^c

^a*Institute for Animal Ecology and Cell Biology, University of Veterinary Medicine Hannover; Bünteweg 17d, 30559 Hannover, Germany*

^b*Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX 77553-1675, USA*

^c*Department of Biology, University of Louisiana at Lafayette, 300 East St. Mary Blvd., Lafayette, LA 70504, USA*

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Abstract

Recent diving explorations of anchialine caves on the Turks and Caicos Islands yielded a rather small and slender new species of Remipedia. *Micropacter yagerae* n. gen., n. sp. is distinguished from all other species of nectiopod remipedes by a number of autapomorphic characters, including an oval body terminus with fused segments, unequal pairs of terminal claws on maxilla and maxilliped, an almost complete reduction of sternal bars and pleurotergites, molar processes with relatively few, but strong spines, and frontal filaments with bifurcate processes. Based on the unique combination of derived and primitive characters, we propose to erect a new family, Micropacteridae, for this new species and genus of Remipedia. Taxonomic diagnoses for the class Remipedia, order Nectiopoda (emended due to discovery that the maxilliped is 9-segmented), and for the families Speleonectidae and Godzillidae are presented and discussed.

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Introduction

In the summer of 2003, a diving expedition investigating anchialine Caribbean caves on the Turks and Caicos Islands yielded a rather diverse collection of crustacean stygobionts. One of the specimens from Cottage Pond on North Caicos Island was recognized as belonging to the recently described remipede genus *Kaloketos* (Koenemann et al. 2004). The sample from Cottage Pond included specimens of two other species of remipedes, *Godzillius robustus* and *Lasionectes entrichoma*.

Another sample, collected from a cave on the adjacent island of Providenciales, comprised one large specimen and eight rather small, apparently juvenile individuals. While the large adult could be identified as *L. entrichoma*, taxonomic classification of the ‘juveniles’ proved difficult. Their habitus showed a certain resemblance to that of *L. entrichoma*, a fairly common species known from two of the Turks and Caicos Islands. In fact, they seemed in perfect accord with the drawing of a presumed juvenile of *L. entrichoma* (Emerson and Schram 1991, Fig. 23A and B). However, closer examination revealed features that could not be reconciled with adult morphology of *L. entrichoma* nor with that of any other remipede. The trunks of these small and strikingly slender specimens were composed

*Corresponding author.

E-mail address: stefan.koenemann@tiho-hannover.de (S. Koenemann).

of only 16 segments, and their body lengths ranged from 9 to 13 mm. To find out whether these individuals were juveniles or adults, we re-examined collection material from previous expeditions to the Turks and Caicos Islands, including the alleged juvenile of *L. entrichoma* from Schram et al. (1986). To our surprise, we found seven additional specimens labeled as “*Lasionectes* cf. *entrichoma* juveniles” that were morphologically identical with our new material. Since the older material contained two tiny individuals (3.0 and 5.4 mm, respectively) with 16 trunk segments, we were able to confidently distinguish the larger specimens as adults of a previously undescribed species.

Based on the unique combination of derived and primitive characters, the new genus and species *Micropacter yagerae* cannot be assigned to either of the two remipede families, Speleonectidae and Godzilliidae. Therefore, we propose to place *M. yagerae* in a new family Micropacteridae.

Abbreviations and definitions of morphological terms

Aesthetascs. In crustacean systematics, the term aesthetascs usually refers to chemosensory receptors that occur on the antennule (= first antenna) and occasionally also on the (second) antenna. In remipedes, however, the term aesthetascs is used to describe the dense cluster of long ‘hair-like setae’ (sensillae) on the peduncle of the antennule (Fig. 3A). Aesthetascs on the antennular flagella have not yet been reported in remipedes. However, when we discovered aesthetascs on the antennular flagella in the new family described herein (Figs. 3B and 5A, B), we re-examined material of other taxa and found identical structures in all species of Remipedia. Since these bi- to multifurcate setae are composed of single setal and aesthetasc branches, we propose the term ‘compound aesthetascs’ for these structures. They seem to accord positionally and structurally with ‘true’ aesthetascs (as they occur in most crustaceans); thus, we suggest to homologize the newly described compound aesthetascs with flagellar aesthetascs in other Crustacea. Consequently, we propose to redefine the aesthetascs on the peduncle as ‘peduncular aesthetascs’.

Brachium. This term, derived from the Latin brachium (or braccium), meaning ‘lower arm to wrist’, defines all segments distal to the elbow, including the claw (Fig. 1C).

Elbow. The main point of flexure in maxillule, maxilla and maxilliped, typically dividing a robust proximal part from a more slender distal unit (Fig. 1C).

Lacertus. Derived from the Latin lacertus for ‘upper arm’, this refers to the typically expanded segment immediately proximal to the elbow in maxillule, maxilla, and maxilliped (Fig. 1C).

SDNHM. San Diego Natural History Museum.

TS. Trunk segment(s), counted beginning at the first post-cephalic segment, thus not including maxillipeds.

ZMA. Zoological Museum Amsterdam.

Systematics

Class Remipedia Yager, 1981

Remipedia Yager, 1981, p. 328. Schram et al. (1986, p. 6); Emerson and Schram (1991, p. 5); Koenemann et al. (2003, p. 228).

Diagnosis

Hermaphroditic crustaceans with 6-segmented cephalon (including maxillipeds), head shield present. Trunk lacking tagmosis; adult trunk composed of at least 16 segments; carapace absent; female gonopores on TS 7, male gonopores on TS 14. Antennules and antennae biramous. Labrum well developed. Three pairs of post-oral cephalic appendages modified as subequal, uniramous, prehensile, raptorial mouthparts. Transverse sternal bars typically present on trunk. Trunk limbs as biramous, paddle-shaped swimming appendages. Anal somite with caudal rami.

Remarks

The new family described below is characterized by the sternal bars being reduced on most TS. Only TS 14 bears a small, flap-like remnant of a sternal bar.

Order Nectiopoda Schram, 1986

Nectiopoda Schram, 1986, p. 36. Schram et al. (1986, p. 6); Emerson and Schram (1991, p. 6); Koenemann et al. (2003, p. 228).

Diagnosis

Cephalon with paired bifurcate, preantennular ventral filaments. Antennular peduncle fused, with long, peduncular aesthetascs; both flagella equipped with bi- to multifurcate setae forking into simple setae and aesthetascs (compound aesthetascs). Antennae small, paddle-like; endopod 3-segmented, generally forming semicircular arc; exopod as 1-segmented paddle. Mandibles lacking palps. Maxillules with 6–7 segments; terminal segment developed as fang-like claw, with a single pore at the distal tip. Maxillae and maxillipeds morphologically similar; terminal segments developed as complex claws equipped with a cluster or arc of denticles typically opposed by a thumb-like pad bearing a row of filamentous, flexible setae. Maxillae 7-segmented, with three lobate endites on basal segment; main point of flexure between segments 3 and 4 (lacertus and

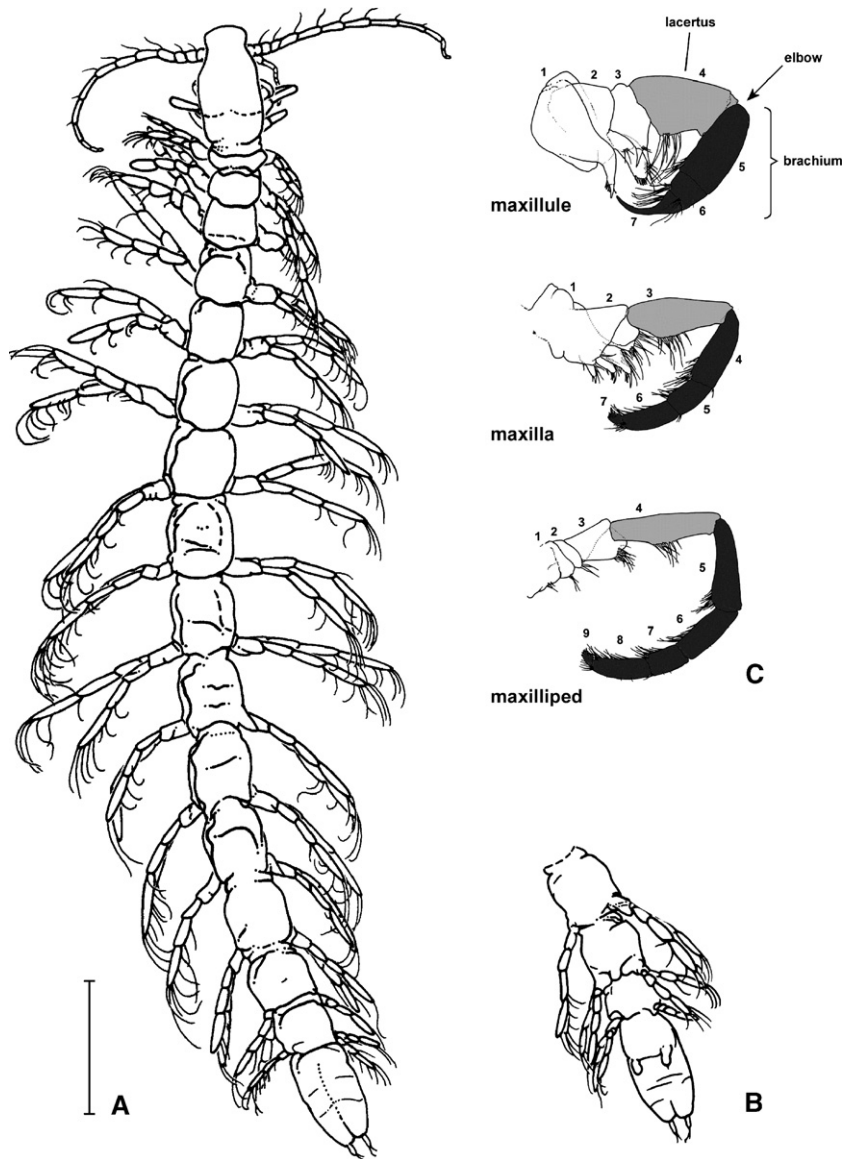


Fig. 1. (A, B) Drawings from Emerson and Schram (1991, Fig. 23) of alleged juveniles of *Lasionectes entrichoma*, now recognized as *Micropacter yagerae* n. fam., n. gen., n. sp.; scale bar = 1 mm. (C) The three prehensile limbs of *Speleonectes parabenjamini*; light shading = lacertus, dark shading = brachium; numbers indicate individual limb segments.

brachium). Maxillipeds 9-segmented, main point of flexure between segments 4 and 5 (lacertus and brachium); endites of basal segments reduced, pad-like. Trunk limbs with 3-segmented exopod; endopod 4-segmented, basal segment reduced; anterior and posterior trunk limbs more slender than those of mid-trunk, armature more reduced. Anal segment with simple caudal rami.

Remarks

One important new character is added in the diagnosis presented herein: The maxillipeds of some remipedes are described as being composed of 8

segments. However, re-examination of collection and type material by SK has not confirmed this. Maxillipeds appeared to be 9-segmented on all specimens examined. The first three proximal segments have complex, interconnected joints that make it difficult to detect each individual segment. Moreover, some taxa in both families, Speleonectidae and Godzilliidae, show a tendency toward reduced size and degree of articulation of the basal segments. This reduction, however, very likely is an advanced condition resulting from the progressive specialization of these limbs as prehensile, fang-like appendages (Koenemann et al. 2003).

Family Speleonectidae Yager, 1981

Speleonectidae Yager, 1981, p. 328. Schram et al. (1986, p. 6); Koenemann et al. (2003, p. 228).

Morlockiidae Garcia-Valdecasas, 1984, p. 329.

Genera

Type genus: *Speleonectes* Yager, 1981. Additional genera: *Lasionectes* Yager and Schram, 1986; *Cryptocorynetes* Yager, 1987; *Kaloketos* Koenemann et al., 2004.

Diagnosis

Head shield subquadrangular to subrectangular, often slightly tapered anteriorly. Transverse sternal bars of trunk isomorphic or heteromorphic. Ventral ramus of antennules well developed, typically with 7–15 segments, longer than 35% of length of dorsal ramus. Mandibles asymmetrical. Maxillules 7-segmented; endite of segment 3 well developed, but shorter than endites of segments 1 and 2; segment 4 long, medial margin expanded. Maxillary lacertus typically shorter than that of maxilliped. Maxillary and maxillipedal brachia typically distinctly longer than lacerti.

Remarks

The family Speleonectidae presently includes four genera: *Speleonectes* (9 species), *Lasionectes* (2 species), *Cryptocorynetes* (2 species), and *Kaloketos* (1 species). The genus *Cryptocorynetes* is characterized by distinct autapomorphies that are not included in the diagnosis. The maxillae and maxillipeds of *Cryptocorynetes haptodiscus* have ‘swollen’, dilated segments equipped with numerous round, disc-like (‘discoid’) organs. This anatomy is unparalleled within the Nectiopoda. Presumably, *Cryptocorynetes* has specialized to feed on particular prey organisms that can be handled more effectively with these modified prehensile limbs.

The diagnosis of the family was initially based on the description of *Speleonectes lucayensis* Yager, 1981. Schram et al. (1986) provided an emended diagnosis based on redescriptions of *S. lucayensis* and *S. ondinae* (originally described as *Morlockia ondinae* Garcia-Valdecasas, 1984) and on the inclusion of *Lasionectes*. However, the addition of newly described species and two genera since 1986 has further weakened the already unstable diagnosis. Compared to the other nectiopod family, the Godzilliidae (see below), the Speleonectidae are diagnosed by the absence of synapomorphies. Possible advanced characters are either autapomorphies (e.g. the discoid organs in *Cryptocorynetes*) or not shared by all taxa (e.g. heteromorphic sternal bars). The presence of (sym)plesiomorphies in the Speleonectidae, however, should not be used to define a monophyletic group.

Family Godzilliidae Schram et al., 1986

Godzilliidae Schram et al., 1986, p. 6.

Genera

Type genus: *Godzillius* Schram et al., 1986. Additional genera: *Pleomothra* Yager, 1989; *Godzilliognomus* Yager, 1989.

Diagnosis

Shape of cephalic shield not subrectangular, with concave or convex lateral margins, or with pointed posterolateral corners. Ventral flagella of antennules short, less than 25% of length of dorsal flagella, number of segments sometimes greatly reduced (*Godzillius* and *Godzilliognomus*). Maxillules with 6 (*Pleomothra*) or 7 segments, variable in size and shape; segment 3 greatly reduced, without endites (*Godzillius* and *Godzilliognomus*), or modified as elongate, secondary elbow segment (*Pleomothra*); segment 4 (proximal to main elbow) long and robust, with endite as large, flexible process (*Godzillius*), greatly reduced (*Godzilliognomus*) or modified (*Pleomothra*). Specialization of maxillae and maxillipeds as prehensile limbs well developed, with large, robust lacertus and slender, partly fused brachium, bearing dense arrays of setae or spines along entire margins. Pleurotergites well developed, with pointed posterolateral corners on entire trunk. Sternal bars sublinear, isomorphic.

Remarks

Unlike the Speleonectidae, the Godzilliidae feature a number of derived characters. These include, in particular, several modifications in the three prehensile cephalic limbs. However, some of the features used by Schram et al. (1986), who erected and defined this family when but a single genus and species was known, became diagnostically insufficient when two additional taxa were designated as godzilliid genera. In fact, the assignment of *Godzilliognomus frondosus* Yager, 1989 and *Pleomothra apletocheles* Yager, 1989 to the Godzilliidae required a much reduced redefinition of the family. For example, several distinct characters of *Godzillius* and *Godzilliognomus* are not shared with *Pleomothra*. These include very short ventral rami of the antennules composed of only 2 or 3 segments (7 in *Pleomothra*), nearly symmetrical mandibles (asymmetrical in *Pleomothra* and Speleonectidae), maxillules with 7 segments, and terminal claws of maxillae and maxillipeds composed of sharply pointed, well-separated, long denticles (claw type of *Pleomothra* shared with some speleonectids).

Micropacteridae n. fam.

“Juvenile *Lasionectes entrichoma*” Emerson and Schram (1991, Fig. 23A and B).

Type genus*Micropacter* n. gen.**Diagnosis**

Head shield subrectangular. Trunk composed of 16 segments. Sternal bars heteromorphic, but almost completely reduced. Anal somite fused with TS 16 and 15 (the latter at least partly fused), forming an oval body terminus. Ventral flagella of antennules very short. Mandibles asymmetrical; left incisor process with 4 denticles, right incisor with 3 denticles; molar processes small, apical surface with 9–16 long curved spines. Segment 3 of maxillule with reduced endite. Maxillae and maxillipeds about equally long; brachia fused to 2 equally long segments (plus terminal claws); claws of maxillae different from those on maxillipeds.

Micropacter* n. gen.*Etymology**

Micropacter means ‘Tiny Hunter’ and is combined from the Greek words mikros (small, tiny) and epakter, genitive epakteros (hunter, fisher). The gender is masculine.

Type species*M. yagerae* n. sp.**Diagnosis**

As for family; see above.

***Micropacter yagerae* n. sp.**

Figs. 1–6.

Etymology

The epithet *yagerae* is chosen in honor of Prof. Jill Yager, who discovered the first remipede crustacean in 1979 and has made significant contributions to the biology of Remipedia.

Type material

Holotype (Zoological Museum Amsterdam; ZMA Crust. Rem. 204751), 10.4 mm, Turks and Caicos Islands, Providenciales Island, Airport Cave (21°46.66'N, 72°16.28'W), from water column at 5–6 m depth, 10 June 2003, collected by T. Iliffe.

Paratypes (PT). (A) as holotype, except as specified: 5 PT (in coll. SK), 9.2–13.1 mm; 2 PT (prepared for SEM investigation, in coll. JvdH), 9.0–9.3 mm; 1 PT (SDNHM 2199), 7.4 mm, 5 April 1983, collected by D. Williams. (B) Providenciales Island, Old Blue Hill Cave, collected by D. Williams: 2 PT (SDNHM 2193), 8.9 and 3.0 mm, from clear water pool, 6 April 1983; 3 PT (SDNHM 2200), 5.4–8.8 mm, from clear water pool, 7

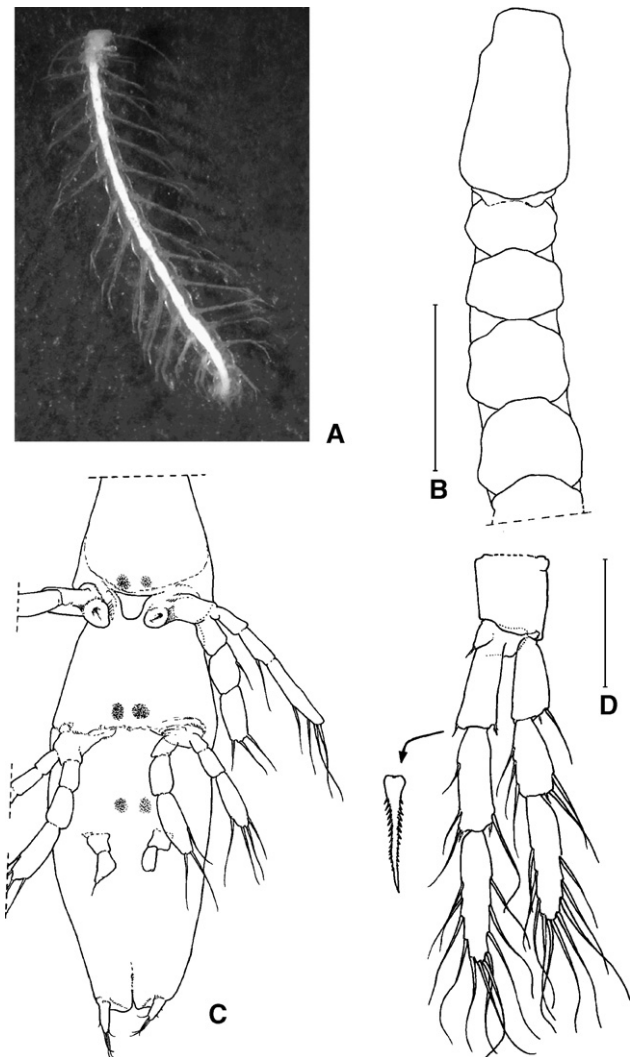


Fig. 2. *Micropacter yagerae* n. fam., n. gen., n. sp. (A) Photograph of a live paratype specimen. (B) Dorsal view of head shield and anterior trunk segments, 12.9 mm paratype; scale bar = 1 mm. (C) Posterior trunk in ventral view showing fusion of anal somite with trunk segments 16 (with incipient, uniramous limbs) and 15, 10.5 mm paratype. (D) Thoracopod with enlarged spine of segment 2 of endopod, 13.1 mm paratype; scale bar = 0.5 mm.

April 1983; 1 PT (SDNHM 2201), 9.8 mm, from tannic pool, 22 November 1983.

Diagnosis

A small and slender species; adult body length usually 9–11 mm, exceptionally up to 13.1 mm. Trunk composed of 16 segments in all specimens examined. Head shield subrectangular, rather long and narrow, tapered anteriorly, with concave anterolateral margins (Figs. 1A and 2B). Frontal filaments with bifurcate subapical processes. First TS reduced, shorter than TS 2. Sternal bars almost completely reduced on all TS, except on TS 14 which bears a small, flap-like sternal bar (Figs. 1B and 2C).

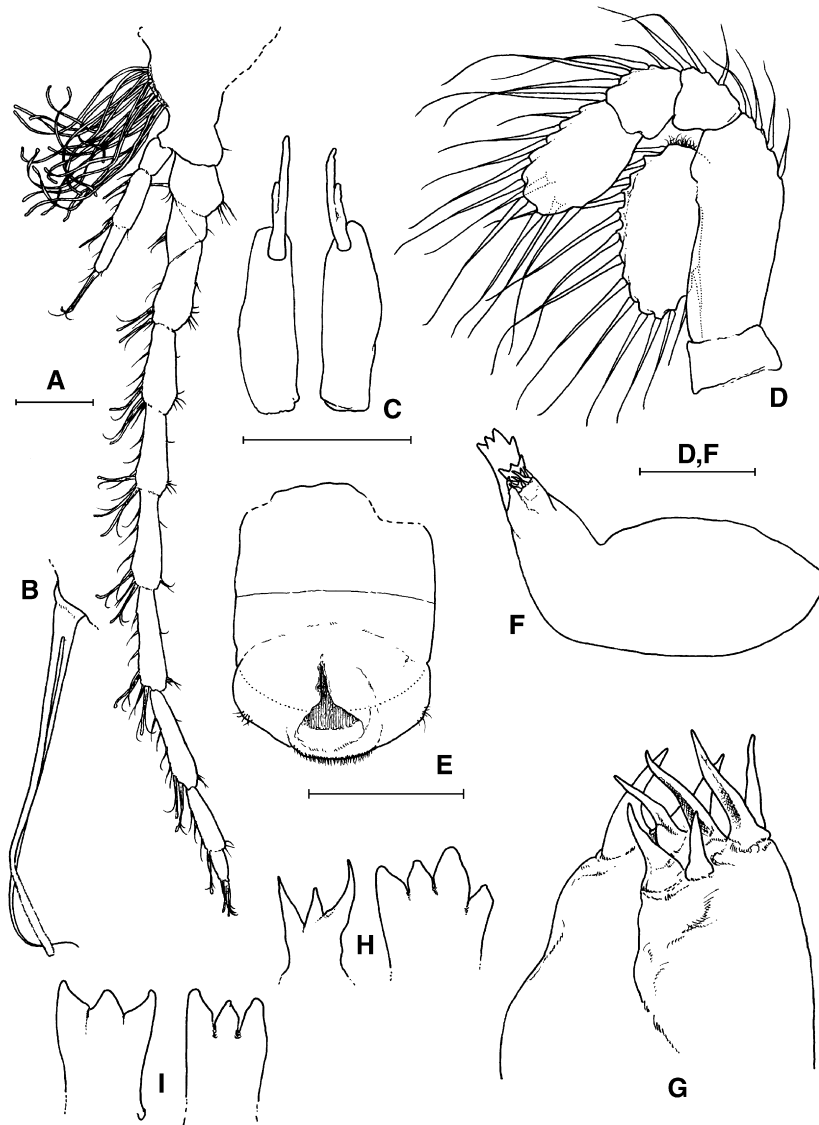


Fig. 3. *Micropacter yagerae* n. fam., n. gen., n. sp. A, D–H = 13.1 mm paratype; C = 10.2 mm paratype. (A) Antennule; scale bar = 0.1 mm. (B) Enlarged compound aesthetasc of antennule. (C) Frontal filaments; scale bar = 0.1 mm. (D) Antenna; scale bar D, F = 0.1 mm. (E) Labrum; scale bar = 0.1 mm. (F) Left mandible; scale bar = 0.1 mm. (G) Molar process of left mandible. (H) Enlarged lacinia mobilis and incisor process of left mandible. (I) Enlarged lacinia mobilis and incisor process of right mandible.

Pleurotergites nearly completely reduced. Anal somite and TS 16 and 15 fused, forming an oval body terminus (Figs. 1B and 2C). Ventral flagella of antennules very short, with 3 segments (Fig. 3A). Mandibles asymmetrical; left lacinia mobilis with 3 long, pointed denticles; right lacinia with 3 blunt denticles (Fig. 3F–I). Prehensile cephalic limbs about equally long, but maxillules more robust than maxillae and maxillipeds (Fig. 4). Lacerti of maxillules enlarged, with 2 prominent corner spines and several smaller marginal spines. Brachia of both maxillae and maxillipeds fused to 2 equally long segments (plus terminal claw), respectively; claws of maxillae with 1 long denticle and 4 shorter denticles (Figs. 5C and 6D); claws of maxillipeds with a

horseshoe-like arc composed of 9–10 fused denticles (Figs. 5D and 6C).

Description

The character states described below were observed on all specimens examined, unless stated otherwise.

Body very slender and short, length range 3.0–13.1 mm (most specimens reaching 9–11 mm); body composed of 16 TS (Figs. 1A and 2A). Pleurotergites completely reduced; sometimes weakly developed, with broadly rounded distolateral corners (Figs. 1A and 2B). Transverse sternal bars reduced to thin rims on all sternites, except on TS 14 which bears a convex flap (Figs. 1B and 2C). Female gonopores (on limbs of TS 7)

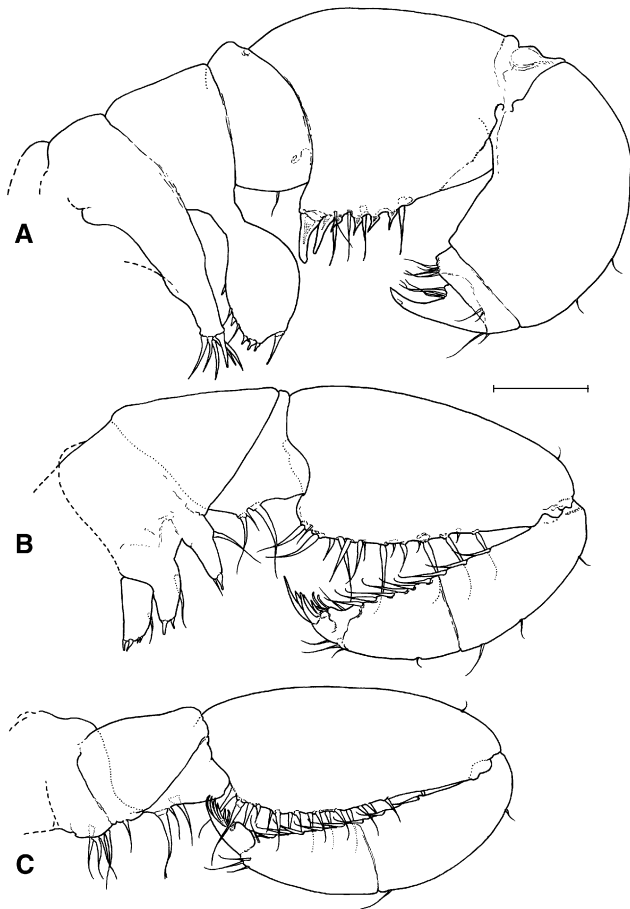


Fig. 4. *Micropacter yagerae* n. fam., n. gen., n. sp.; 13.1 mm paratype. (A) Maxillule. (B) Maxilla. (C) Maxilliped. Scale bar = 0.1 mm.

as small round buds (Fig. 5F); male gonopores as large, proximomedial, basal dilations on limbs of TS 14 (Fig. 2C). Anal somite, TS 16 and 15 fused, forming an oval body terminus with vestigial caudal rami; sutures between somites sometimes partly detectable; limbs on TS 16 not fully developed, as 1- or 2-segmented limb buds (Fig. 2C).

Head shield tapering anteriorly, about 1.8 times longer than wide, with concave anterolateral margins; anterior margin of TS 1 only slightly covered by head shield (Figs. 1A and 2B). Frontal filaments with long, bifurcate, subapical processes (Fig. 3C).

Antennules (Fig. 3A and B): Peduncular pad small, bearing rows of comparatively few, very fine aesthetascs. Dorsal flagellum short, about 15–20% of body length, composed of 10 segments; each segment equipped with several short, simple setae, and 1 or 2 bi- or multifurcate compound aesthetascs that fork into simple setae and aesthetascs (Figs. 3B and 5A, B). Ventral flagellum very short, (shorter than head shield), 3-segmented, exhibiting some degree of fusion. Terminal segments of both dorsal and ventral flagella with 1 apical compound

aesthetasc each, composed of 2 simple setae and 2 aesthetascs.

Antennae (Fig. 3D): Protopod 2-segmented; proximal segment naked, distal segment with 4 setae. Exopod as wide as adjacent distal segment of protopod, equipped with ca. 16 long setae on outer margin and a row of pubescent setules on apex. Endopod bent in a semi-circular way; first segment with about 3 setae; second segment with single row of 5 setae; distal segment with a row of ca. 9 setae on outer margin and 2 setae on distomedial margin. All setae plumose (feather-like with long, faint setules).

Labrum with 3 disjunct clusters of pubescent setules on apical margin (Fig. 3E).

Mandibles asymmetrical (Fig. 3F–I). Left incisor process with 4 large denticles; left lacinia mobilis fork-like, with 3 long, pointed denticles (Fig. 3H). Right incisor process and lacinia mobilis equipped with 3 large denticles each (Fig. 3I). Molar processes of both mandibles small; apical surface ovate, with 9–16 strong, curved spines (Fig. 3G).

Maxillules more robust than maxillae and maxillipeds (Fig. 4A). Segment 1 with long, slender endite, equipped with 6 naked, pointed apical spines. Segment 2 with ovate endite; medial and apical margins bearing a few setae and short spines; subapical lateral margin with 1 long slender spine. Endite of segment 3 greatly reduced. Segment 4 (= lacertus) very robust; medial margin distinctly expanded, oblique, bearing a few setae, a row of 4 short, pointed spines parallel to a row of 4–5 long spines (all finely serrate), and 2 strong, naked spines on proximal corner (Fig. 5E). Segment 5 very robust, broadly rounded, slightly longer than fourth segment. Segment 6 very short, with a single cluster of setae on distal margin. Claw well developed.

Maxillae (Fig. 4B): Endites of segment 1 with groups of apical spines and setae, and 1 long seta on medial surface, respectively. Segment 2 with broadly rounded, flat endite, bearing a few spines and setae. Segment 3 (= lacertus) long and robust, medial margin expanded, with 2 rows of setulose setae (these brush-like with short setules; Fig. 6B) that vary in length, and with a few small setae on medial margin. Segments 4–6 expanded, fused to 2 segments, medial margins bearing a row of setulose setae. Claw composed of 5 long, thin, and pointed denticles; one denticle dominant, almost twice as long as adjacent denticles, with pore-like opening on mid-proximal stem (Figs. 5C and 6D).

Maxillipeds about as long as maxillae (Figs. 4C and 6A). Proximal segments 1–3 with oblique, complex (interconnected) articulation, bearing a few medial setulose setae. Fourth segment (= lacertus) long and robust, slightly expanded, with 2 rows of setulose setae of varying length, and with a few small setae on medial margin. Segments 5–8 fused to 2 segments, slightly expanded, medial margins with a row of setulose setae.

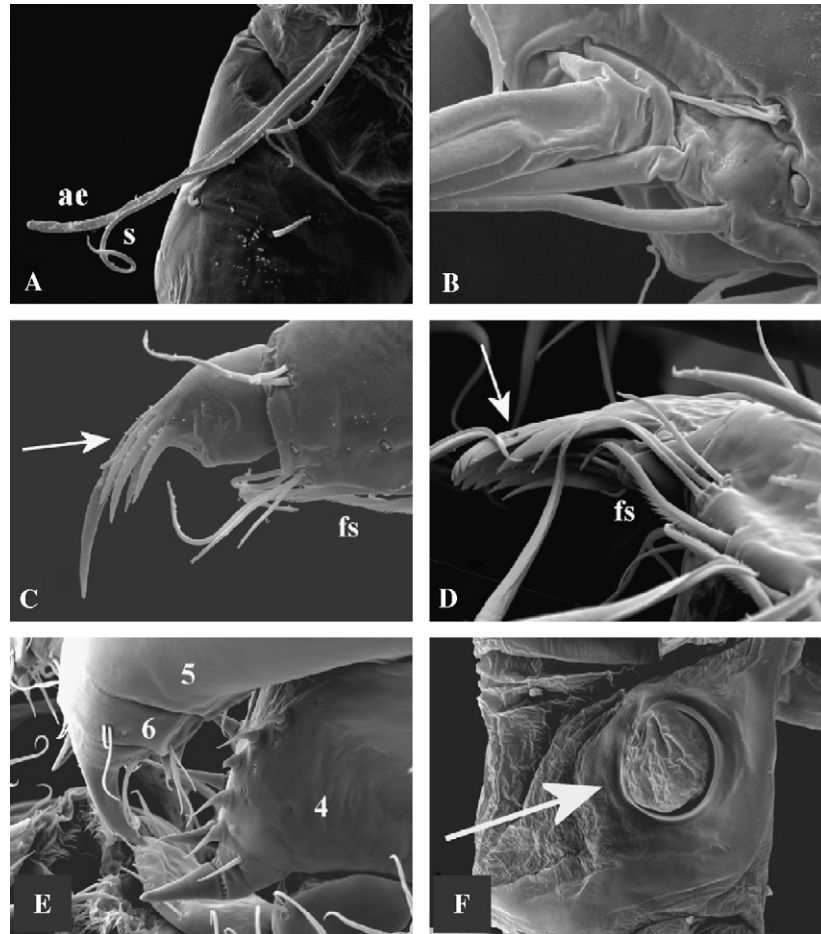


Fig. 5. *Micropacter yagerae* n. fam., n. gen., n. sp., 9.3 mm paratype. (A) Compound aesthetasc of antennule. (B) Enlarged basal part of a trifurcate compound aesthetasc (accompanied by 2 single, regular setae). (C) Claw of maxilla; arrow points to pore (D) Claw of maxilliped; arrow points to pore. (E) Detail of maxillule (medial view); numbers indicate individual segments. (F) Female gonopore, indicated by arrow. Abbreviations: ae = aesthetasc, fs = feathered seta, s = setal branch.

Claws different from those of maxillae, forming a horseshoe-like arc with 9–10 fused denticles; pore-like opening present on distal (fused) part of arc (Figs. 5D and 6C).

Appendages of TS 1–15 (Fig. 2C and D): Endo- and exopods long and slender, bearing relatively few long, plumose setae, and single serrate spines on distal corners; appendages of TS 16 incipient, as 1- or 2-segmented limb buds.

Anal segment fused to TS 16 and 15, forming a ‘swollen’, oval body terminus; caudal rami reduced, very small (Figs. 1A, B and 2C).

Ecological profile of type locality

The Caicos Islands are a geographical and geological extension of the Bahamas archipelago. These limestone islands are situated along the margins of a shallow water platform, the Caicos Bank, and are surrounded on all sides by deep ocean. Airport Cave is located 50 m from the car park at the Providenciales International Airport

and about 2 km inland from the coast near the midpoint of the island of Providenciales at the northwestern corner of the Caicos Bank (Fig. 7). The cave consists of a crescent-shaped fissure extending along the base of a larger sinkhole. A narrow ravine-like passage extends down for 20 m to a tidal, anchialine pool in total darkness with a maximum depth of 14 m. A colony of bats roost over the pool and their guano makes up much of the sediment. We used a Hydrolab Datasonde III electronic water quality analyzer to profile water quality in the pool as a function of depth. Salinity in the pool was 2 ppt at the surface, increased steeply to 17 ppt at 3 m, then more gradually to a maximum of 25 ppt at 14 m (Fig. 8). Water temperature showed a similar trend, increasing sharply from 24.2 °C at the surface to 25.6 °C at 6 m, before decreasing to 25.5 °C at 14 m. Dissolved oxygen levels were low throughout the water column, dropping from a little less than 1 mg/l at the surface to 0.1 mg/l at 4 m and 0.04 mg/l at 14 m. Values for pH dropped from 7.25 at the surface to a minimum

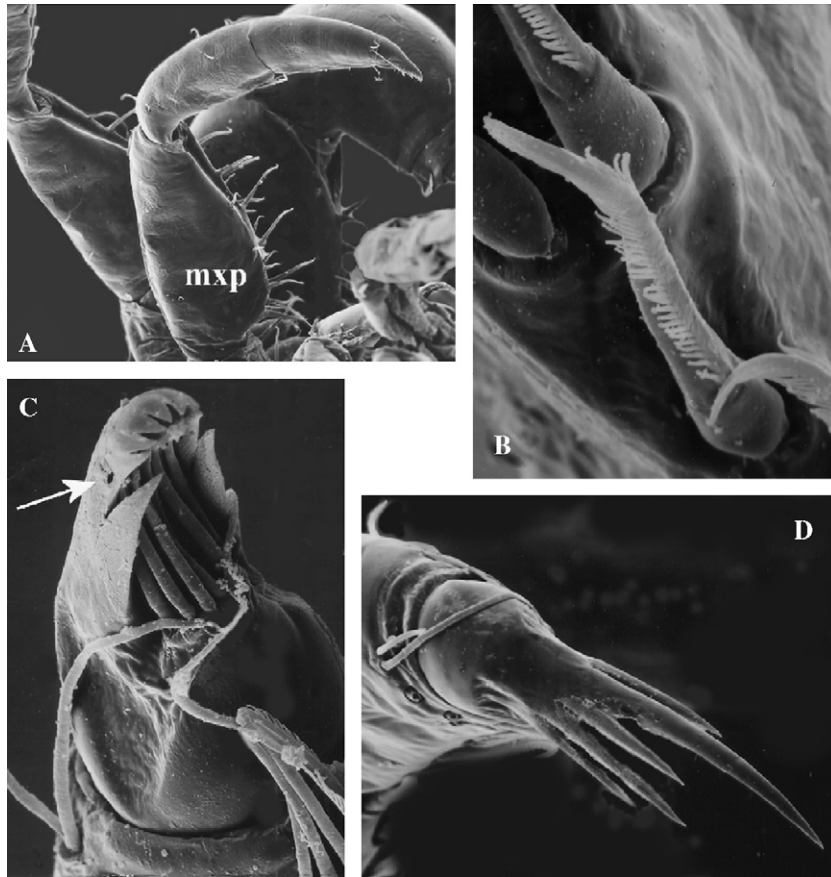


Fig. 6. *Micropacter yagerae* n. fam., n. gen., n. sp. Unpublished SEM photos from study by Emerson and Schram (1991). (A) Prehensile cephalic limbs; mxp = maxilliped. (B) Setulose seta on maxilliped. (C) Claw of maxilliped; arrow points to pore. (D) Claw of maxilla.

of 6.54 at 4 m before slightly recovering to 6.66 at 14 m. Remipedes were observed actively swimming in the cave water column, primarily at 5–6 m depth. At this location, salinity was 17.5 ppt, temperature 25.6 °C, dissolved oxygen 0.1–0.3 mg/l, and pH 6.6. Specimens were collected by scuba divers in individual vials containing ambient water. Other stygobitic species inhabiting Airport Cave include the nebaliacean *Speonebalia cannoni* Bowman, Yager and Iliffe, 1995, and the caridean shrimp *Agostocaris williamsi* Hart and Manning, 1986.

Specimens of *M. yagerae* n. sp. had been collected in 1983 from Old Blue Hill Cave, located 300 m to the northeast of Airport Cave on Providenciales. However, no remipedes were observed during dives in Old Blue Hill Cave in June 2003. This cave consists of a large sinkhole with two pools separated by breakdown boulders and located on opposite sides of the collapse depression. One pool beneath a 7 m high limestone cliff is open to sunlight and has tannic water in the surface layer (several meters). The second pool is sheltered from direct sunlight in a shallow cave and contains clear water. In June 2003, a Hydrolab Datasonde III electronic water quality analyzer carried by a diver

was used to investigate water quality profiles in the tannic pool. Salinity was found to gradually increase from 13 ppt at the surface to 33 ppt at 23 m (Fig. 9). Temperature and dissolved oxygen both displayed similar depth profiles, sharply dropping from 29 °C and 5.9 mg/l at the surface to 25.5 °C and 0.28 mg/l at 5 m, then declining more gradually to 25.2 °C and 0.12 mg/l at 23 m depth. Values for pH dropped steeply from 8.1 at the surface to a minimum of 7.1 at 8–14 m depth, then increased slowly to 7.24 at 23 m. Other stygobitic species inhabiting Old Blue Hill Cave include the shrimp *Typhlatya garciai* Chace, 1942, reported by Buden and Felder (1977), and a new genus of epacteriscid copepods being described by Fosshagen and Iliffe (in press).

Discussion

The discovery of *M. yagerae* n. sp. presents some interesting challenges to the current taxonomic structure below the order level within the class Remipedia. The new species is distinguished from all other nectiopod remipedes by a number of unique features and

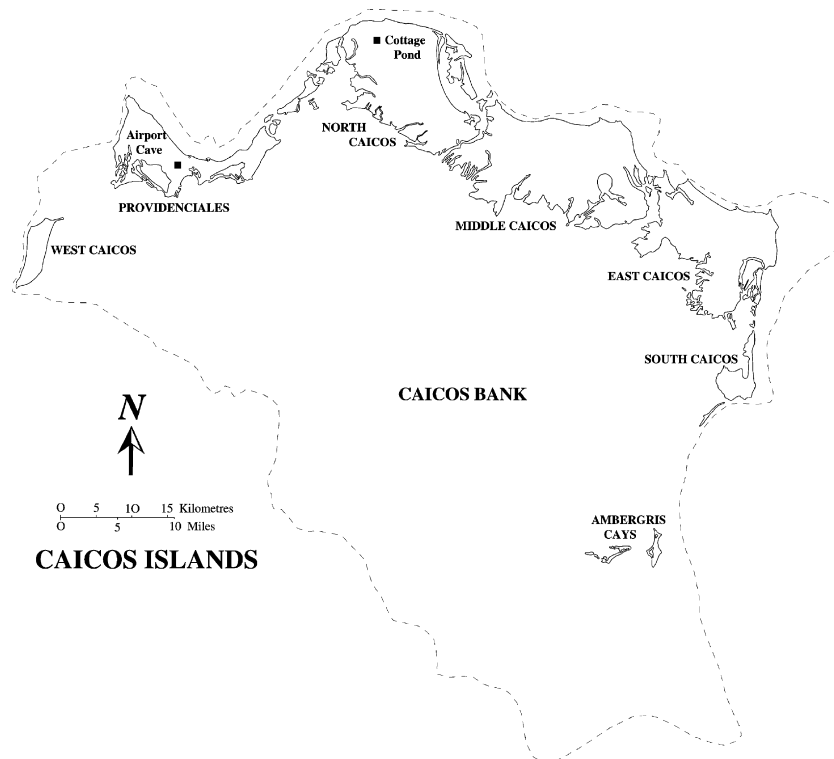


Fig. 7. Map of the Caicos Islands, showing locations of anchialine caves known to contain remipedes. Cottage Pond on North Caicos Island is inhabited by *Kaloketos pilosus*, *Godzillius robustus*, and *Lasionectes entrichoma*; Airport Cave and Old Blue Hill Cave on Providenciales both contain *Micropacter yagerae* and *Lasionectes entrichoma*. The latter two caves are located close together, indicated by a single dot on the map. Dashed line shows 100 m depth contour marking outer edge of shallow-water Caicos Bank.

morphological peculiarities. These autapomorphic features include an oval body terminus with fused segments, unequal pairs of terminal claws on maxilla and maxilliped, an almost complete reduction of sternal bars and pleurotergites, molar processes with relatively few but strong spines, and frontal filaments with bifurcate subapical processes (Table 1).

With a mean body length of 8.6 mm and a maximum length of 13.1 mm ($n = 16$), *M. yagerae* is the second-smallest species after *G. frondosus* (mean body length 5.1 mm, maximum length 9.3 mm, $n = 9$; Koenemann et al. 2006). Like *G. frondosus*, *M. yagerae* has a trunk composed of merely 16 segments. This is the lowest number of adult TS recorded in Remipedia; it may represent a developmental lower limit in the adult stage, since the male gonopores of the hermaphroditic remipedes are located on TS 14.

At first glance, the habitus of *M. yagerae* resembles that of a speleonectid remipede. In fact, adult specimens of *M. yagerae* were previously presumed to be juveniles of *L. entrichoma* (Emerson and Schram 1991). The ‘speleonectid appearance’ of *M. yagerae* includes, in particular, its slender body with almost completely reduced pleural tergites combined with a subrectangular head shield. Moreover, the three pairs of prehensile

cephalic limbs do not show any of the conspicuous modifications typical of the godzilliids, e.g. a modified maxillary lacertus or the distinct subdivision of expanded lacertus and thin brachium on maxillae and maxillipeds (Table 1).

However, closer examination does reveal several derived characters that appear morphologically similar to features in the Godzilliidae. These apomorphies comprise a very short ventral antennular ramus, a completely reduced endite of the third maxillary segment, and the fusion of brachial segments in maxillae and maxillipeds. The salient question is whether these apomorphies are indeed shared characters, or whether they have evolved independently in godzilliids and micropacterids. Comparing the maxillary and maxillipedal brachia in *M. yagerae*, to those of the godzilliids we notice several evident differences. The brachia in *M. yagerae* are round and expanded; their inner margins covered with sparse rows of long setae. This anatomy is typical of speleonectids. In all three species of godzilliids, the brachia of maxillae and maxillipeds are very thin and narrow, bearing a dense cover of short spines or setae along the inner margins. More importantly, however, the fused brachial segments in godzilliids show two or three faint sutures, and the fused sections are of

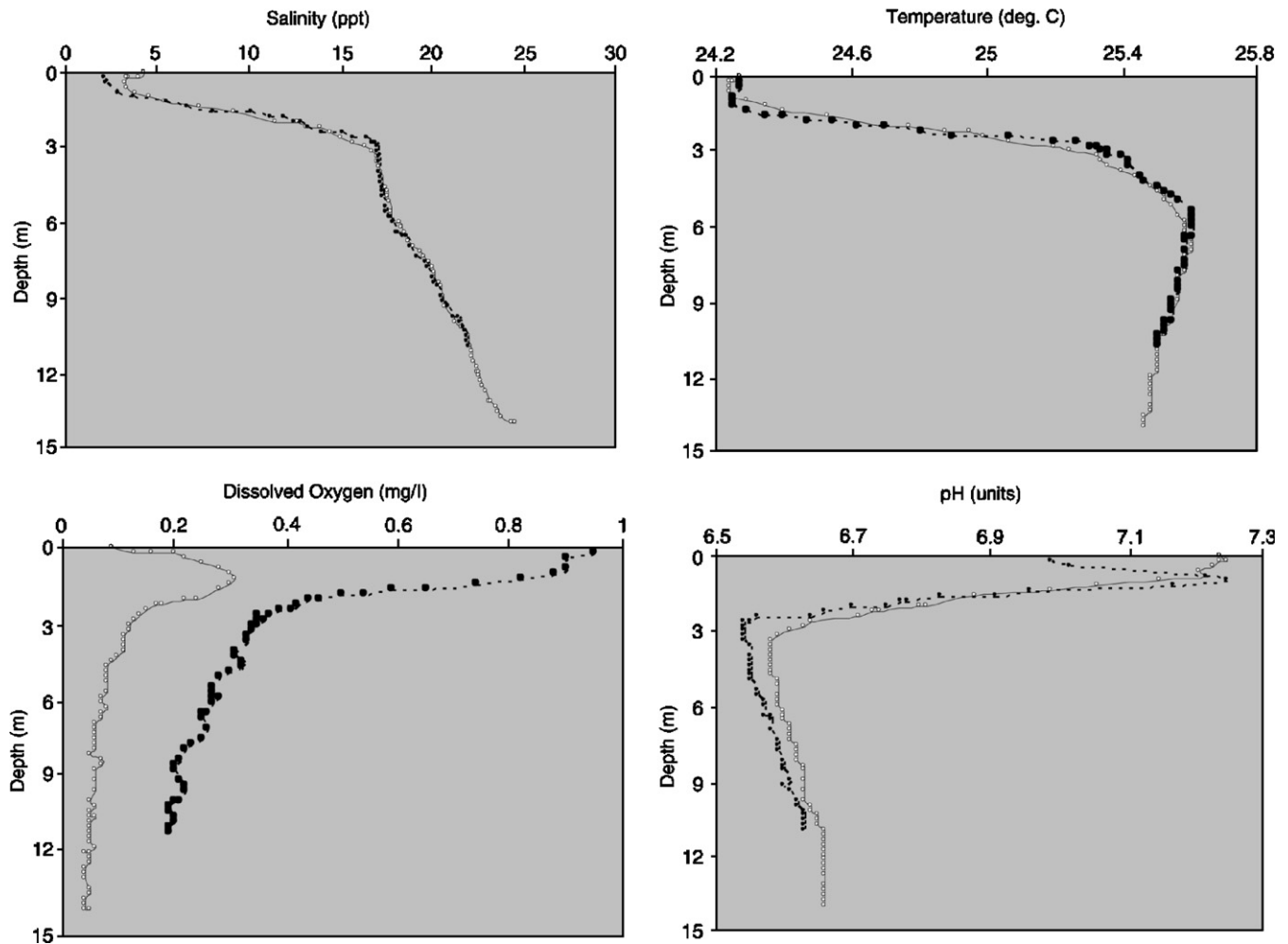


Fig. 8. Water quality profiles from Airport Cave, Providenciales, obtained on 10 June 2003 with a Hydrolab Datasonde 3 electronic water quality analyzer carried by a scuba diver and programmed to take data at 2-second intervals. Two profiles each of salinity, temperature, dissolved oxygen, and pH as a function of depth were obtained in the cave: initial profile in undisturbed water at front of pool at beginning of diving operations is indicated by solid black squares and a dashed trend line; second profile obtained at rear of pool after some disturbance and mixing of water column by divers is indicated by small white circles and a thin, solid trend line.

unequal length (i.e. more distal sections are much shorter than the proximal section). In *M. yagerae*, there is a distinct, straight suture that divides the brachium in two equal halves (not considering the terminal claw). Therefore, we have reason to assume that the fusion of brachia evolved independently in godzilliids and micropacterids, and that the fused sections are not homologous.

Other important diagnostic characters of *M. yagerae* are the claws of maxillae and maxillipeds. While the maxillary and maxillipedal claws of nectiopods are distinct autapomorphies within the Crustacea, we have no convincing evidence to define one of the different types of claws found in extant Remipedia as apomorphic. In speleonectids, the predominant type of claw is a horseshoe-like arc composed of up to 30 fused denticles. The two species of *Lasionectes*, however, have a 'longfinger'-type claw, with one prominent, long spike

accompanied by several small, partly fused denticles. This claw type is also found in the godzilliid *P. apretocheles*. The claws of the other two species of Godzilliidae, *G. robustus* and *G. frondosus*, have a grappling-hook appearance, with 5–10 well-separated denticles of approximately equal length. *M. yagerae* is the first remipede that shows different types of claws on maxillae and maxillipeds. While the maxillipeds terminate in horseshoe-like arcs with 9–10 fused denticles, the maxillae have claws with five separate denticles, one of which is twice as long as the remaining four. This unique type of claw appears to represent an intermediate form between the longfinger and the grappling-hook claw types.

From a taxonomic point of view, *M. yagerae* leaves us with a dilemma. It shares several plesiomorphic characters with the Speleonectidae, but also exhibits some derived features that might be shared with the

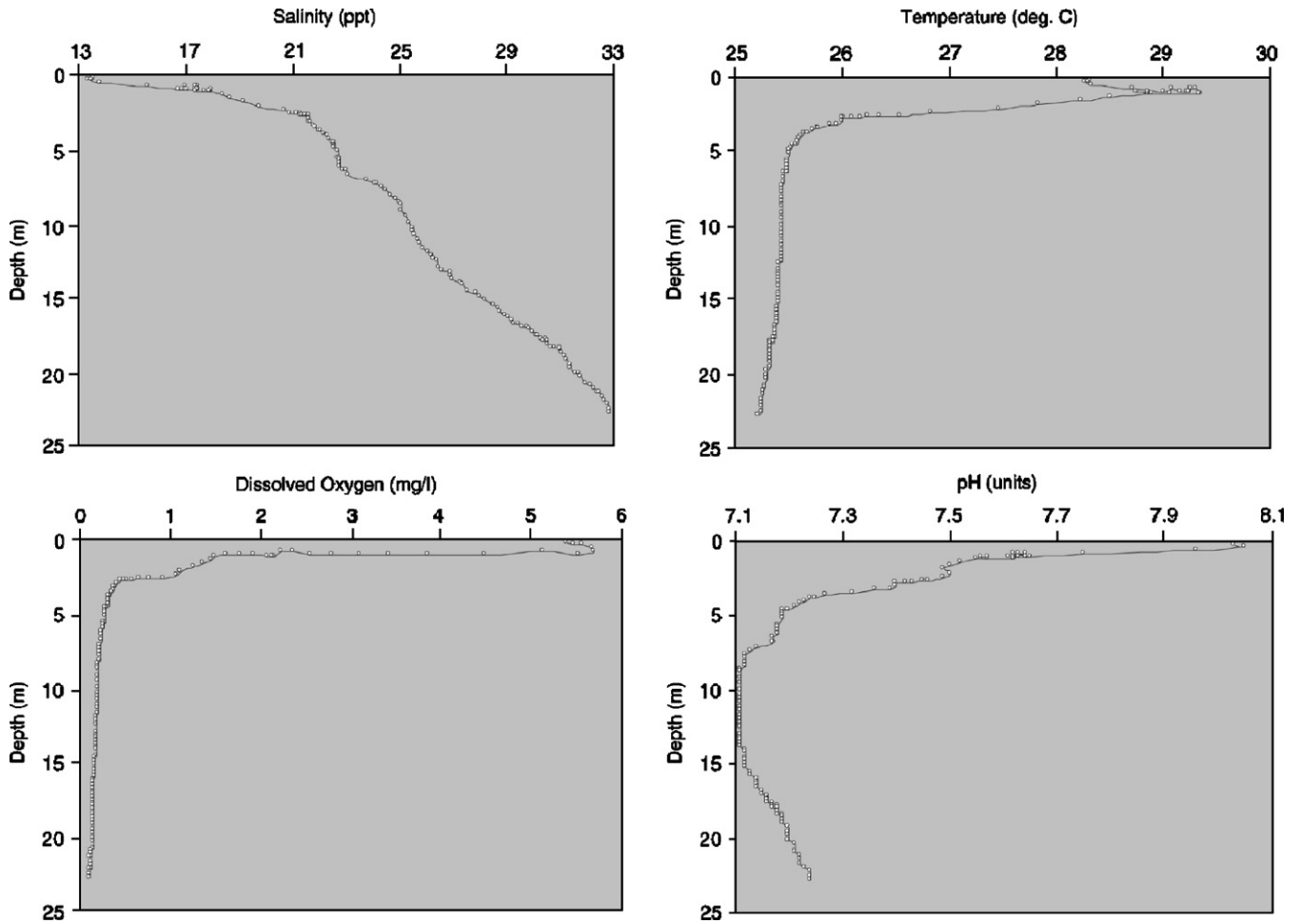


Fig. 9. Water quality profiles of salinity, temperature, dissolved oxygen, and pH as a function of depth from Old Blue Hill Cave, Providenciales, obtained on 12 June 2003.

Godzilliidae. However, an assignment to the Speleonec-
tidae based on a few symplesiomorphies certainly
cannot be justified. *M. yagerae* exhibits too many
distinct apomorphies that would be incompatible with
the diagnosis of that family, e.g. a very short ventral
antennular ramus, fused brachia on maxillae and
maxillipeds, and a reduced third maxillulary endite.
Initially, the type genus *Speleonectes* of the family
Speleonec-
tidae was described as a taxon of primitive
nectiopods, characterized by the lack of advanced
features. The assignment of additional genera, however,
inevitably undermined the concept of a primitive
Speleonec-
tidae, e.g. by including the discoid organs in
Cryptocorynetes and the morphology of the prehensile
limbs in *Lasionectes* as diagnostic characters (Table 1).

An assignment of *M. yagerae* to the Godzilliidae, on
the other hand, also seems highly problematical. The
addition of *Pleomothra* has weakened the diagnosis of
this family already; the inclusion of *Micropacter* would
have an even more destabilizing impact. In this case, the
diagnosis would have to be reduced to merely two

characters: fused brachia on maxillae and maxillipeds,
and a reduced third maxillulary endite (a 'very short'
ventral antennular ramus is not present in *Pleomothra*).
However, we think that the fusion of maxillary and
maxillipedal brachia cannot be homologized between
godzilliids and *Micropacter*. At this point, it remains
undecided whether the reduced third maxillulary endite
is also a homoplasious, independently evolved charac-
ter, or an apomorphy shared with (some of) the
godzilliids.

Conclusions

Based on the unique combination of derived and
primitive characters, we cannot assign *M. yagerae* n. sp.
to either one of the existing families, Speleonec-
tidae and Godzilliidae. Therefore, we suggest a separate family for
this new genus and species.

The special position of *M. yagerae* reveals a rather
unstable taxonomic architecture within the Nectiopoda.

Table 1. Comparison of main diagnostic characters among families of Nectiopoda

	Micropacteridae	Speleonectidae		Godzilliidae		
	<i>Micropacter</i>	<i>Cryptocorynetes</i>	Speleonectids	<i>Godzillius</i>	<i>Godzilliognomus</i>	<i>Pleomothra</i>
Head shield	Subrectangular (much longer than wide)	Subquadrangular (slightly longer than wide)	Subquadrangular to subrectangular	Pear-shaped (longer than wide)	Broadly rounded (slightly longer than wide), with convex lateral margins	Subrectangular (longer than wide), with posterolateral spines
Frontal filaments	Bifurcate, with bifurcate processes	Bifurcate, with simple processes	Bifurcate, with simple processes	Bifurcate, with simple processes	Bifurcate, with simple processes	Bifurcate, with simple processes
A 1, ventral flagellum	Very short (3 segments)	Well developed (10–12 segments)	Generally well-developed (7–15 segments)	Very short (2 segments)	Very short (2 segments)	Short (7 segments)
Mandibles, molar process	With 9–16 strong, curved spines	With dense rows of thin, flexible spines	With dense rows of thin, flexible spines	With dense rows of thin, flexible spines	With dense rows of thin, flexible spines	With dense rows of thin, flexible spines
Max 1	7-segmented	7-segmented	7-segmented	7-segmented, S6 very narrow	7-segmented	6-segmented
Max 1, segment 3	Endite reduced	Endite developed, with spines	Endite developed, with spines	Endite reduced	Endite reduced	Reduced and modified
Max 1, lacertus	Expanded	Expanded	Expanded	Expanded, modified	Only slightly expanded	Massive, modified
Max 2+mxp, brachium	Expanded; fusion (2 equally long segments)	Expanded; no fusion	Expanded (slightly expanded in <i>Lasionectes</i>); no fusion	Very thin; fusion (3 unequally long segments)	Very thin; fusion (2 unequally long segments)	Very thin; fusion (2 unequally long segments)
Max 2, claw	5 separate denticles (1 denticle twice as long as others)	Horseshoe-like arc with 8–9 fused denticles	Horseshoe-like arc or longfinger-type claw	10 separate denticles of unequal length	5 separate denticles of unequal length	Longfinger-type claw with 5 denticles
Mxp, claw	Horseshoe-like arc with 9–10 fused denticles	Horseshoe-like arc with 8–9 fused denticles	Horseshoe-like arc or longfinger-type claw	10 separate denticles of unequal length	5 separate denticles of unequal length	Longfinger-type claw with 5 denticles
Sternal bars	Heteromorphic (flap on TS 14)	Heteromorphic	Heteromorphic or isomorphic	Isomorphic	Isomorphic	Isomorphic
Trunk segments	16 (fused, oval body terminus)	32 (anal somite free)	21/41 (anal somite free)	29 (anal somite free)	16 (anal somite free)	26 (anal somite free)
Pleurotergites	Almost completely reduced	Well-developed, with rounded corners	Reduced to well-developed	Well-developed, with pointed corners	Well-developed, with pointed corners	Well-developed, with pointed corners

“Speleonectids” include the genera *Speleonectes*, *Lasionectes*, and *Kaloketos*; in this group, the maximum number of adult trunk segments varies from 21 in *Speleonectes epilimnius* to 41 in *S. tanumekes*. Abbreviations: A 1 = antennule (first antenna); Max 1 = maxillule (first maxilla); Max 2 = maxilla (second maxilla); Mxp = maxilliped; S = segment; TS = trunk segment. See Discussion text for further explanations, e.g. of claw types.

Two quite different changes to the classification could resolve the present dilemma:

- (1) Eliminating the family Godzilliidae and assigning all nectiopod genera to one family, the Speleonectidae.
- (2) Elevating problematic genera with advanced features to separate families, for example *Cryptocorynetes* and *Pleomothra*.

The advantage of the first option would be an uncomplicated, conflict-free assignment of new taxa. However, there is no guarantee that this would remain the most solid solution in the long run. The future discovery of new taxa might expose a more complex pattern of relationships. Obviously, an ideal taxonomy would reflect such a phylogenetic pattern within the Nectiopoda. At present, we are preparing to conduct comprehensive analyses of molecular and morphological datasets to analyze the phylogenetic relationships of Remipedia and provide a more stable taxonomy for this group.

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