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A NEW GENUS OF DEEP-SEA SOLENOCERID SHRIMP (DECAPODA: PENAEOIDEA) FROM PAPUA NEW GUINEA

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ABSTRACT

A new genus and species of deep-sea shrimp, *Maximiliaeus odoceros*, was collected from the Solomon Sea off Papua New Guinea. This penaeoid has a characteristic carapace; bearing large teeth on its entire dorsal border, and the presence of three parallel carinae that nearly run the entire length of the lateral carapace surface. Phylogenetic analysis using PEPCK and NaK sequences confirmed that this new taxon belongs to Solenoceridae.

KEY WORDS: Decapoda, deep water, *Maximiliaeus odoceros*, Papua New Guinea, Penaeoidea, Solenoceridae

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INTRODUCTION

The recent "BIOPAUPA" expedition (organized by the Muséum national d'Histoire naturelle, Paris) in 2010 surveyed the deep-sea benthic fauna off northeastern Papua New Guinea. At two stations, just off Lae and between 403-485 m in depth, several specimens of a large penaeoid shrimp (maximun body length about 15 cm excluding rostrum) were collected. They differed from all known species of Penaeoidea Rafinesque-Schmaltz, 1815 in having a strong carapace with three long and parallel lateral carinae, the dorsal carapace bearing large teeth along the entire border, and distinct teeth present on the dorsal and ventral margins of a long rostrum. This unusual penaeoid was immediately recognized to represent a genus and species new to science. After detailed comparisons and molecular analyses this new penaeoid was assigned to Solenoceridae Wood-Mason in Wood-Mason and Alcock, 1891. The discovery of this large bodied new taxon of shrimp demonstrates again that the deep-sea benthos in the "Golden Triangle" of marine biodiversity requires further exploration (see Ayhong et al., 2010).

The specimens studied are deposited in the Muséum national d'Histoire naturelle, Paris (MNHN) and National Taiwan Ocean University, Keelung (NTOU). Abbreviation used: CP before station numbers refers to gear type or beam trawl and postorbital carapace length (cl) is used as a standard measurement indicating size of the specimens. Morphological terminology generally follows Pérez Farfante and Kensley (1997), with protocols for molecular sequencing and phylogenetic analyses following Ma et al. (2009). As the antennal and antennular flagella were incomplete for all specimens examined, descriptions of their lengths are based on the longest remaining flagellum.

SYSTEMATICS

Solenoceridae Wood-Mason in Wood-Mason and Alcock, 1891

Maximiliaeus n. gen.

Type Species.—*Maximiliaeus odoceros* n. gen., n. sp.

Diagnosis.—Body robust, integument firm and covered with dense short pubescence. Rostrum relatively long and overreaching antennular peduncle, bearing distinct teeth on both upper and lower margins. Entire dorsal border of carapace carinate and bearing teeth, with epigastric tooth well separated from rostral and postrostral teeth. Carapace relatively elongated; orbital and pterygostomian spines absent; antennal, postorbital, hepatic and branchiostegal spines present, all continuous with carinae. Long and nearly straight branchiocardiac, fused hepatic and posthepatic, and branchiostegal carinae present on lateral carapace. Submarginal carina and short oblique carina anterior to hepatic depression also present. Cervical sulcus deep, accompanied with sharp carina, upper end far from dorsal carapace. Orbital-antennal and hepatic sulci present. Telson with pair of minute, subterminal, movable lateral spines.

Eyes large, cornea deeply pigmented, optic calathus with mesial tubercle low and broad. Prosartema well-developed and rigid throughout. Stylocerite also well-developed. Antennular flagella similar, subcylindrical and longer than carapace. Mandibular palp 3-segmented, distal article broad and leaf-like, penultimate article smaller and subquadrate, basal article very short and narrow. Palp of first maxilla 2-segmented, distal segment rather small. All pereiopods robust and bearing moderately long slender exopods, none flagelliform. Strong basial spine present on pereiopods I

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Table 1. *Maximiliaeus odoceros* n. gen., n. sp., branchial formula. Abbreviations: Mxp1-Mxp3, maxillipeds 1-3; P1-P5, pereiopods 1-5; s = small.

	Somite							
	VII (Mxp1)	VIII (Mxp2)	IX (Mxp3)	X (P1)	XI (P2)	XII (P3)	XIII (P4)	XIV (P5)
Pleurobranchiae	–	–	1	1	1	1	1	1
Arthrobranchiae	s	2	2	2	2	2	2	–
Podobranchiae	–	1	–	–	–	–	–	–
Epipods	1	1	1	1	1	1	1	–
Exopods	1	1	1	1	1	1	1	1

and II. Exopod of uropods armed with subterminal distolateral spine. Gill formula as shown in Table 1.

Thelycum open, sculpture rather simple. Structure of petasma unknown.

Phylogenetic Relationship.—This new genus has several unusual characters such as distinct teeth on the ventral margin of the rostrum. Among penaeoids, these ventral teeth are present in species of *Penaeus* Fabricius, 1798 sensu lato, *Heteropenaeus* De Man, 1896, *Pelagopenaeus* Pérez Farfante and Kensley, 1997 (Penaeidae Rafinesque-Schmaltz, 1815), *Haliporoides* Stebbing, 1914, and *Hymenopenaeus* Smith, 1882 (Solenoceridae). Only species assigned to Sicyoniidae Ortmann, 1898 have the entire dorsal carapace armed with teeth. However, these species lack ventral rostral teeth. Furthermore, no known penaeoidean have three long and straight carinae running almost along the entire lateral surface on the carapace, although the lateral carapaces of *Pelagopenaeus* (Penaeidae) and *Gordonella* Tirmizi, 1960 (Solenoceridae) have many long carinae, but these are not straight and parallel. Following the definitions and keys of Pérez Farfante and Kensley (1997), the present new genus has a postorbital spine (though this spine is almost at the level of the antennal spine) and therefore can be attributed to Solenoceridae. Within Solenoceridae, this New Guinean form keys out to *Haliporus* Bate, 1881 by processing a movable lateral telsonic spines (though minute and rudimentary) and lacking a postcervical spine. However, the new genus differs from *Haliporus* (see Crosnier, 1988; Pérez Farfante and Kensley, 1997) by all the characters as mentioned above, as well as having much large eyes (vs. eyes small to moderately small), prosartema well developed and foliaceaous (vs. small to rudimentary), telson without fixed lateral spines (vs. with 1 pair fixed and 3 pairs of movable lateral spines), mandibular palp with distal segment much larger than intermediate segment (vs. intermediate segment much larger than distal segment), palp of first maxilla 2-segmented (vs. 1-segmented), and the lateral pleon weakly carinated (vs. entire lateral surface more or less covered with complex ridges).

The inclusion of two protein gene sequences, phosphoenol-pyruvate carboxy-kinase (PEPCK) and sodium-potassium ATPase-α subunit (NaK), from this new genus (holotype, GenBank no. JN977136, JN977135, respectively) into the currently most comprehensive and robust molecular phylogenetic tree of Penaeoidae by Ma et al. (2009), demonstrates that the present new genus can be attributed to Solenoceidae and is close to *Haliporus* (Fig. 1). The molecular gene tree of Ma et al. (2009), however, is unresolved for most of the genera within each family and tribe and the topology is different from the phylogenetic grouping of solenocerid genera as proposed by Kubo (1949) and Pérez Farfante (1977). The exact phylogenetic position of *Maximiliaeus* within Solenoceridea requires further investigations. For example, all other solenocerids have a first maxilla with a 1-segmented palp (vs. 2-segmented in the new genus). Interestingly, the posterior part of the dorsal carapace in *Haliporus curvirostris* Bate, 1881, is more or less denticulate. This may imply that the presence of posterodorsal teeth on the carapace is a synapomorphy in Solenoceridae. Furthermore, of the three long lateral keels on the carapace, only the lower one (branchiostegal carina) is entire. The upper keel seems to be divided into three (antennal, gastro-orbital, and branchiocardiac carinae) by the orbito-antennal and cervical sulci. The intermediate keel seems to be divided into two (the short oblique carina in front of the hepatic depression, fused hepatic and posthepatic carinae by the hepatic sulcus). However, the phylogenetic significance and character status (polarity) of the various carapace carinae, sulci, and spines, as well as the shape of the petasma are currently not fully understood. Consequently, these characters at present do not provide enough evolutionary information into the relationship of *Maximiliaeus* with other solenocerids.

Etymology.—The present new genus is remarkable in Penaeoidea by having a rigid carapace bearing many long lateral carinae and with the entire dorsal border including the rostrum fully armed. The fully armed and ridged carapace resembles the fluted or Maximilian style armour of medieval knights. The arbitrary combination of "Maximilian" and "*Penaeus*" thus refers to a penaeoid with a Maximilian style armature on the carapace. Gender: masculine.

Maximiliaeus odoceros n. sp.

Figs. 2-4

Material Examined.—Holotype: Papua New Guinea, BIOPAPUA, stn CP3646, 6°46.190′S, 147°50.244′E, 460-485 m, 24 August 2010, female 48.4 mm cl, MNHN-IU-2011-5393.

Paratypes: Papua New Guinea, BIOPAPUA, stn CP3645, 6°46.394′S, 147°50.605′E, 418-403 m, 24 August 2010, 2 females 14.3 and 27.0 mm cl, MNHN-IU-2011-5394, 1 female 29.4 mm cl, NTOU M01162.

Description.—Body robust, integument firm and covered with dense short pubescence. Rostrum sigmoidal shaped and with distinct lateral (or adrostral) carina, nearly horizontal, slightly overreaching scaphocerite and about 0.8 times as long as carapace length; upper border armed evenly with 13 teeth, including 2 teeth on carapace, all teeth distinct and progressively smaller anteriorly; lower border bearing 4 teeth at anterior half, teeth also progressively smaller anteriorly. Epigastric tooth distinctly separated from rostral teeth. Postrostral carina well developed along entire dorsal carapace, armed with 2 teeth behind dorsal extremity of cervical sulcus. Carapace relatively elongated. Orbital margin straight, but obliquely inclined forward ventrally. Orbital and pterygostomian spines absent. Antennal, postorbital, hepatic, and branchiostegal spines present, all continuous with carinae. Antennal spine large, continuous with

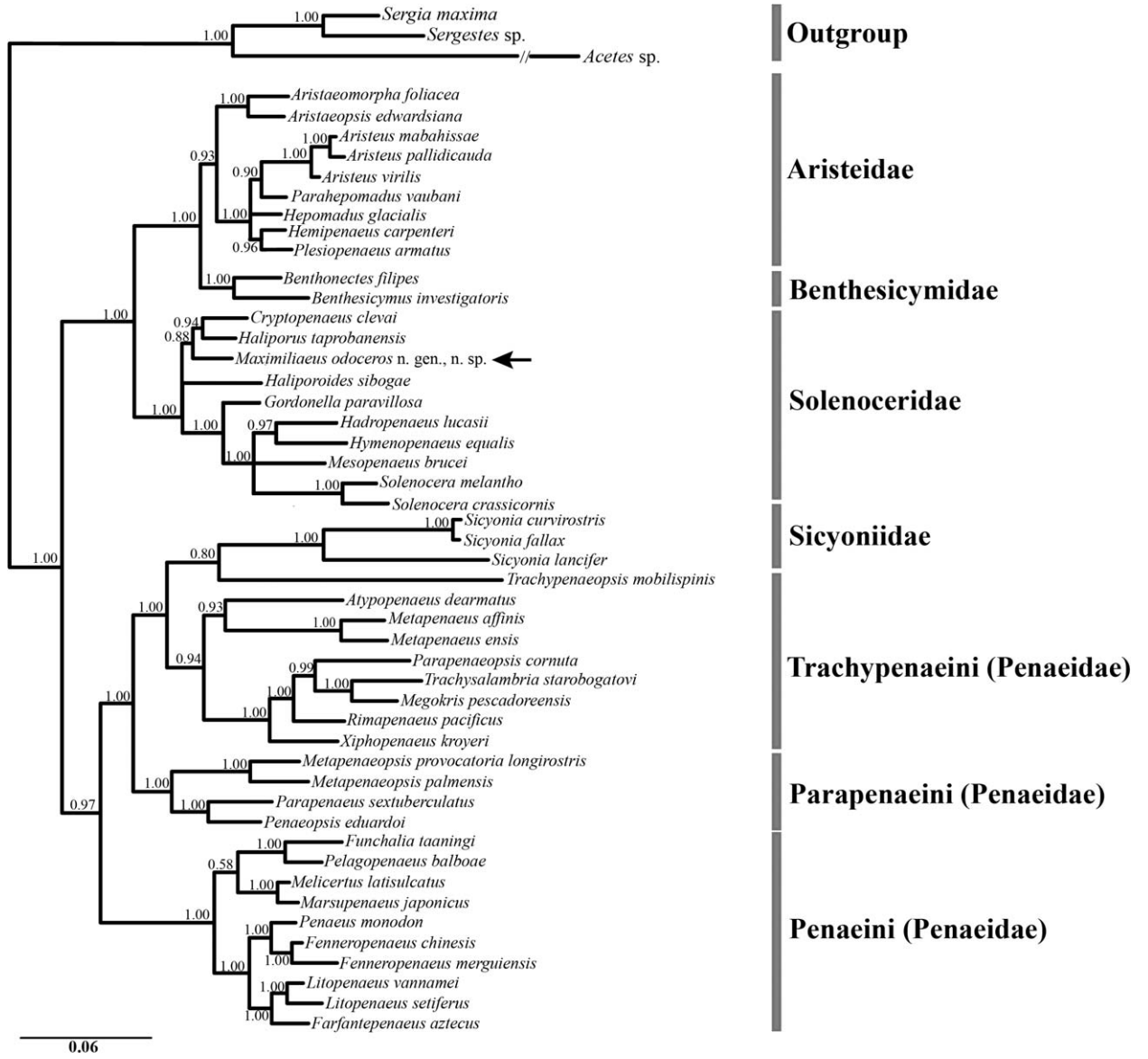

Fig. 1. Bayesian inference tree from combined PEPCK and NaK analysis with the adding of *Maximiliaeus odoceros* n. gen., n. sp. (indicated by an arrow) into the molecular phylogenetic work of Penaeoidea by Ma et al. (2009). Numbers above branches indicate posterior probabilities.

short antennal carina. Postorbital spine also large, almost immediately behind antennal spine and only situated at slightly higher level, continuous with short gastro-orbital carina to nearly cervical sulcus. Hepatic spine smaller but distinct, continuous with nearly straight and well-marked branchiocardiac carina almost to posterior margin of carapace. Branchiostegal spine similar in size as hepatic spine, situated at anterior border of carapace and continuous with straight and well-marked branchiostegal carina which extending along entire lateral carapace to posterior margin. Slightly above branchiostegal carina another well-marked straight carina, i.e., fused hepatic and post-hepatic carinae, running parallel with branchiostegal carina from slightly behind anterior margin to almost posterior margin of lateral carapace. Thus, lateral carapace altogether with 3 long and parallel sharp keels. Cervical sulcus deep and with sharp carina, strongly curving posteriorly at upper end, upper extremity far from dorsal carapace and more or less at level of upper end of orbital margin; ventrally below hepatic spine short and merged with hepatic sulcus. Orbital-antennal sulcus distinct but without carina (or somewhat faintly ridged in small individuals), ventrally merged with cervical and hepatic sulci. Hepatic sulcus very short, not extending behind hepatic spine. Merged area of orbital-antennal, cervical, and hepatic sulci as wide depression (hepatic depression) at anterolateral carapace below postorbital spine. Short oblique carina present between hepatic depression and anterior border of carapace; carina not continuous with anterior margin of carapace, sloping downwards posteriorly, situated at level slightly higher than hepatic carina. Submarginal carina present but not strong.

Antennular peduncle about half as long as carapace length. Prosartema well developed and rigid throughout; somewhat oval, narrowing anteriorly and with convex tip,

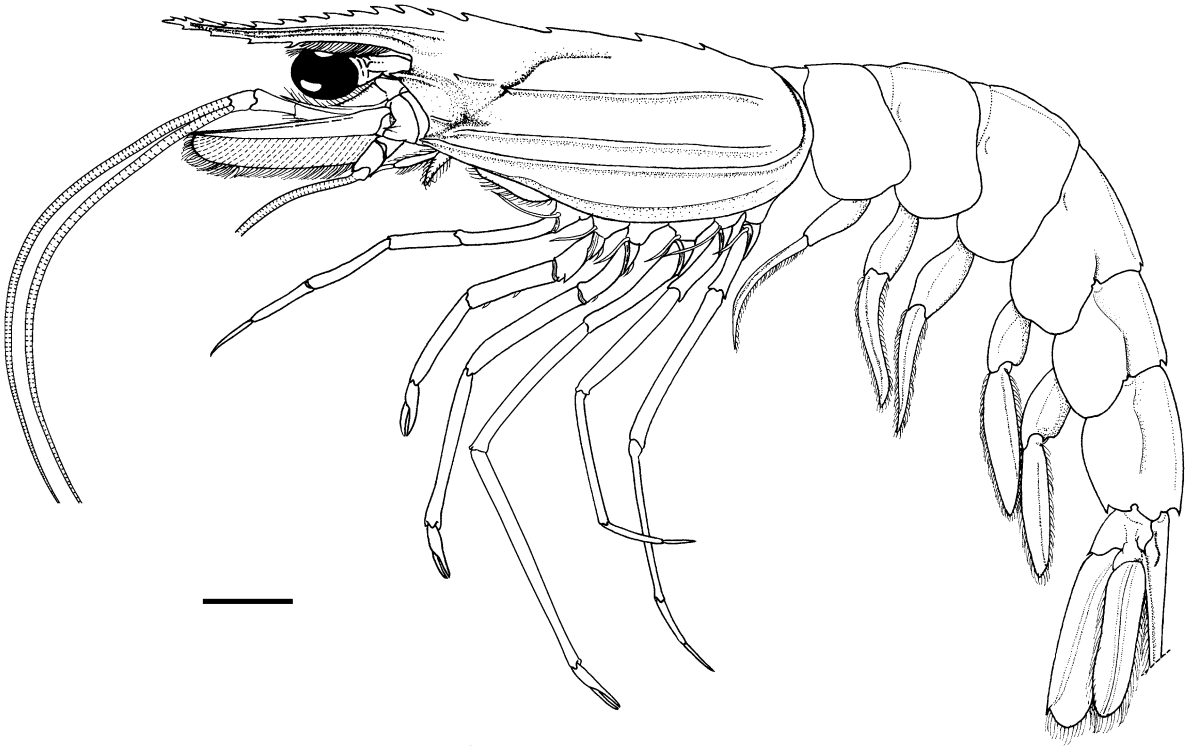

Fig. 2. *Maximiliaeus odoceros* n. gen., n. sp., female holotype 48.4 mm cl (MNHN-IU-2011-5393), lateral view (setae partially omitted). Scale bar: 10 mm.

extending to about 3/4 of first antennular segment; bearing dense long setae at tip, setae slightly exceeding first antennular segment to reaching middle of second antennular segment. Stylocerite sharply pointed and about half as long as first antennular segment. Distolateral spine strong and sharp, extending to about middle of second antennular segment. Antennular flagella (with tip missing) subequal in size and length, both subcylindrical and with lower flagellum slightly thicker, about 1.2 times longer than carapace. Scaphocerite distinctly overreaching antennular peduncle, lateral rib ending in sharp spine that falls short of distal margin of lamella. Antennal flagella incomplete but at least longer than body length.

Eyes large, cornea deeply pigmented, bean shaped and with maximum diameter 1/3-1/5 carapace length (cornea relatively larger in smaller specimens); mesial tubercle on optic calathus represented by blunt but broad low projection. Mandibular palp 3-segmented, distal article broad and leaf-like, much larger than penultimate article; penultimate article subquadrate and about 1/3 as long as distal article, narrowing posteriorly and with proximal margin about half as long as distal margin; basal article very short and narrow. Palp of first maxilla 2-segmented, gently narrowing to rounded apex and with distal segment small; basal segment with mesial margin densely setose; distal segment bearing 2 tufts of long setae distally. Maxilliped III more or less extending to tip of scaphocerite, distal segment 3/4-4/5 as long as penultimate segment. (See Table 1 for gill formula.)

Robust pereiopods, bearing moderately long slender exopods. Pereiopod I extending to about mid-length of scaphocerite; coxa not particularly protruded medially, bearing long sharp subdisto-ventral spine on basis and similar but smaller spine on ischium, ventral margin of merus with 2 small spines at middle and subdistal regions. Pereiopod II extending to about 4/5 of scaphocerite; coxa not particularly protruded medially, basis with long sharp subdisto-ventral spine, ischium with 0-1 small subdisto-ventral spine, merus unarmed. Pereiopods III extending to tip of scaphocerite, coxa produced medially into large ear-like flaps consisting of two layers and with outer layer larger. Pereiopod IV extending to 2/5-3/5 of scaphocerite, coxa produced medially into large round plate. Pereiopod V extend to 3/5-4/5 of scaphocerite, with narrow coxal plate more or less rounded and bearing a small distomesial spine (this spine reduced to a minute sharp protuberance on holotype). Basis to merus all unarmed in pereiopods III to V.

Pleon with sharp dorsal carina on somites II to VI, those of III to V with posterior incisions while those of IV to VI also ending in sharp posterior spine (minute in that of IV); lateral surfaces only with fainted longitudinal ridges from posterior part of somite IV to somite VI and running through hinges of somites; somite VI bearing distinct subdistoventral spine. Telson tapering to terminal point, with blunt dorsolateral ridges becoming sharp near tip, bearing weak median sulcus developed into short median carina near tip, armed with 1 pair of minute (sometimes very rudimentary and nearly absent) lateral movable spines at about distal 1/10. Uropods slightly longer than telson, only exopod bearing sharp distolateral spine that conspicuously falls short of distal margin of lamella.

Thelycum open. Median protuberance (between pereiopods IV) as simple strongly elevated longitudinal ridge. Thoracic sternite XII (between pereiopods III) medially elevated into low blunt longitudinal ridge. Posterior protuberance

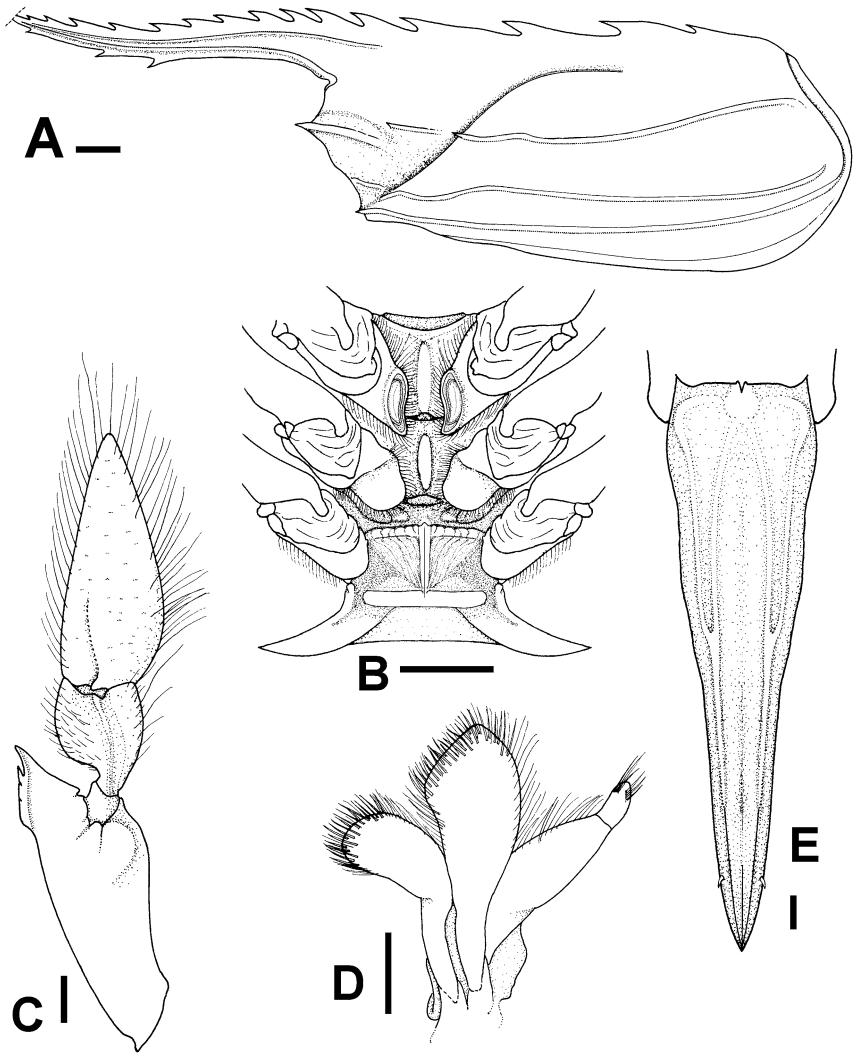

Fig. 3. *Maximiliaeus odoceros* n. gen., n. sp. A, E, Female paratype 29.4 mm cl (NTOU M01162); B, Female holotype 48.4 mm cl (MNHN-IU-2011-5393); C, D, Female paratype 27.0 mm cl (MNHN-IU-2011-5394). A, Carapace and cephalic appendages, lateral view (setae partially omitted); B, Thelycum; C, Left mandible, ventral view; D, Left first maxilla, ventral view; E, Telson, dorsal view. Scale bars: A, 2.5 mm; B, 5 mm, C-E, 1 mm.

(between pereiopods V) somewhat as an inverted subtriangular protuberance and with anterior margin slightly convex to nearly straight, bearing well-marked sharp median longitudinal ridge, surface of protuberance sometimes with nearly straight sutures converging at posterior apex of protuberance. Median and posterior protuberances separated by wide deep groove which bearing pair of low rounded flaps laterally. Thoracic ridge entire, blunt but high.

Colour.—Body generally reddish-pink (Fig. 4A). Teeth on rostrum and dorsal carapace with white tips. Eyes blackish-brown. Antennular flagella orangish-red proximally and distally, intermediate part somewhat whitish. Antennal flagella orangish-red. Anterolateral and posterolateral carapace, antennal peduncle paler in color. Pleon with somites I to V mostly pale whitish-pink; dorsal carinae and posterodorsal borders of somites, as well as anterodorsal border of somite I, bearing thick reddish-pink bands; somte VI and tail fan mostly reddish-pink. Maxilliped III reddish distally, but whitish proximally. Pereiopods mostly whitish-pink and with some reddish-pink markings. Pleopods mostly reddish-pink and with some whitish-pink markings.

The smallest specimen is mostly yellowish (Fig. 4B). Lateral carapace translucent, with thick lateral transverse red band having white anterior margin. Anterior half of rostrum also banded with white, red and white. Epigastric tooth whitish. Antennular flagella proximally yellowish and distally whitish. Maxilliped III and pereiopods similar in color to adults. Pleopods mostly yellowish, with red and white spots on peduncles.

Distribution.—Presently known only from the type locality; the western part of the Solomon Sea, off Papua New Guinea, at depths of 403-485 m.

Remarks.—The holotype has the tip of the telson missing while the tip of the rostrum is missing in all three paratypes. The remaining rostral teeth in the paratypes are 12-13 dorsal and 3 ventral teeth. The two larger paratypes (27.0 and 29.4 mm cl) are similar to the holotype. However, the young female (14.3 mm cl) differs con-

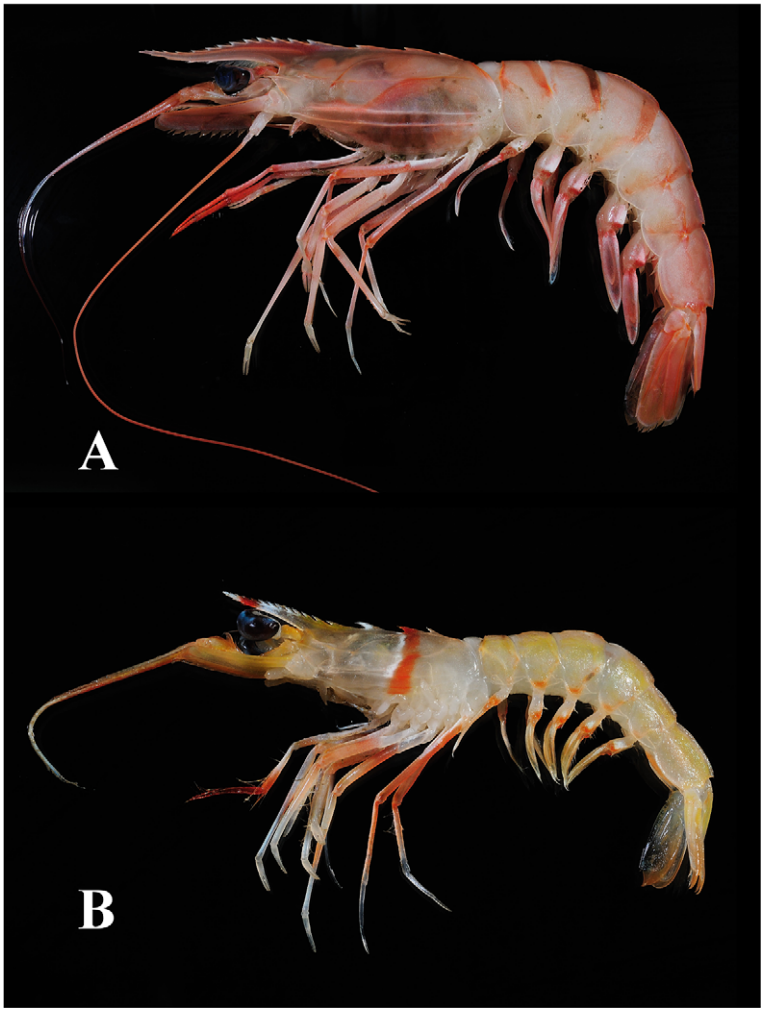

Fig. 4. *Maximiliaeus odoceros* n. gen., n. sp., lateral view; A, Female holotype 48.4 mm cl (MNHN-IU-2011-5393); B, Female paratype 14.3 mm cl (MNHN-IU-2011-5394).

siderably from the others in both coloration (see Fig. 4) and general appearance. This specimen has the rostrum shorter (0.55 carapace length) and markedly directed upwards, pereiopods relatively longer (with pereiopods II and V extending to tip of scaphocerite while pereiopod III exceeding scaphocerite by chela), posterior spines at the dorsal carinae of pleon minute, telson slightly longer than uropods, distolateral spine on exopod of uropods only slightly falling short of distal margin of lamella, and coxal plates of pereiopods III and IV not medially produced at all.

Although the new genus and species is large in size and occurs in relatively shallow waters, only four specimens were collected despite the BIOPAUPA expedition having sampled 150 stations covering a vast area of the Bismark and Solomon Seas. Moreover, only females were collected.

Etymology.—The arbitrary combination of the Greek "*odous*" (tooth) and "*keros*" (horn) refers to the entire dorsal carapace bearing teeth in this species. The name is treated as a noun in apposition.

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