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Description of the male of *Prosaetes rhinodontis* (Wright, 1876) (Crustacea, Copepoda, Siphonostomatoida), with a proposal to synonymize Cecropidae Dana, 1849 and Amaterasidae Izawa, 2008 with Pandaridae Milne Edwards, 1840

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Abstract

This report provides the first description of the male of *Prosaetes rhinodontis* (Wright, 1876) (Copepoda, Siphonostomatoida, Cecropidae) based on specimens collected from two whale sharks (*Rhincodon typus* Smith) held in sea pens off the west coast of Okinawa-jima Island, Japan. We argue that the morphology of *P. rhinodontis* contributes significantly to the blurring of familial limits between Cecropidae Dana, 1849 and Pandaridae Milne Edwards, 1840 and based on our detailed consideration of this matter we recommend that Cecropidae be recognized as a junior synonym of Pandaridae. Accordingly, we transfer *P. rhinodontis*, along with species of *Cecrops* Leach, 1816, *Luetkenia* Claus, 1864, *Philorthagoriscus* Horst, 1897, *Orthagoriscicola* Poche, 1902, and *Entepherus* Bere, 1936, to the Pandaridae. In addition, our critical evaluation of the morphological features of the adult female and copepodid I of *Amaterasia amanoiwatoi* Izawa, 2008 indicated that the establishment of Amaterasidae Izawa, 2008 to hold the species was unfounded because *A. amanoiwatoi* can be accommodated within Pandaridae. Thus, we transfer *A. amanoiwatoi* to Pandaridae and consider Amaterasidae to be a junior synonym of Pandaridae. Lastly, our comparisons of morphological and ecological attributes of *A. amanoiwatoi*, specimens of “*Nesippus costatus*? Wilson, 1924” (Pandaridae) reported by Lewis in 1964, and other pandarids (Pandaridae) revealed the first two taxa to be strikingly similar and suggested them to be congeners. Based on those results we propose Lewis’ specimens represent a new species, which we name *Amaterasia lewisi* n. sp. Within the Pandaridae, *Amaterasia* spp. seem to belong to the *Dinemoura*-group based primarily on their similarity to some *Nesippus* spp., while representatives of *Prosaetes*, *Cecrops*, *Luetkenia*, *Philorthagoriscus*, *Orthagoriscicola*, and *Entepherus* are more confidently considered members of the *Dinemoura*-group based on their shared possession of a narrow third pedigerous somite and dorsal plates on the fourth pedigerous somite in the adult female and a modified leg 3 terminal endopodal segment in the adult male.

Key words: whale shark, *Rhincodon typus*, systematics, parasitic copepod, parasite

Introduction

The whale shark (*Rhincodon typus* Smith) inhabits oceanic and coastal waters of all tropical and warm-temperate seas except the Mediterranean Sea. The species is distinguished for its polka-dotted coloration pattern and because it is the world’s largest fish and one of only three shark species which filter feed (Norman 2005). Despite the recent increase in the number of whale sharks captured alive

for display in public aquaria and the global expansion of the whale shark ecotourism industry (Colman 1997; Compagno 2001; Stevens 2007), the parasite fauna of *R. typus* is largely understudied. To date, seven nominal parasite species have been reported from the whale shark: the digenean *Paronatrema boholana* Eduardo, 2010 and the copepods *Acespasia pomposa* Leigh-Sharpe, 1933, *Dysgamus atlanticus* Steenstrup & Lütken, 1861, *Echthrogaleus pectinatus* Kirtisinghe 1964, *Pandarus rhincodonicus* Norman, Newbound & Knott, 2000, *Pandarus smithii* Rathbun, 1886, and *Prosaetes rhinodontis* (Wright, 1876) (Wright 1876; Leigh-Sharpe 1933; Wilson 1944; Kirtisinghe 1964; Kensley & Grindley 1973; Williams & Williams 1986; Norman *et al.* 2000; Eduardo 2010). Tang *et al.* (2010) recently determined that copepods reported as *D. atlanticus* by Wilson (1944) and Williams & Williams (1986) as well as those originally described as *E. pectinatus* by Kirtisinghe (1964) from *R. typus* are conspecific with *P. rhinodontis*. Thus, *P. rhinodontis*, represented hitherto by adult female specimens only, may only infect the whale shark and is widely distributed, occurring in the Caribbean Sea, Indian Ocean, and western North Pacific Ocean (*loc. cit.*). This report provides the first description of the male of *P. rhinodontis* based on material recently collected from two whale sharks held in captivity off the west coast of Okinawa-jima Island, Japan. In addition, the validity of the siphonostome (Siphonostomatoida) families Cecropidae Dana, 1849 and Amaterasidae Izawa, 2008 is discussed.

Materials and methods

One male (no. 27) and one female (no. 32) whale sharks were caught on 1 July 2006 and 2 April 2008, respectively, by a set net in the East China Sea, offshore from Yomitan Village, western Okinawa-jima Island, Okinawa Prefecture, Japan. After capture, each shark was transported by the Okinawa Churaumi Aquarium (OCA) staff, using methods outlined in Tang *et al.* (2010), to a multi-sea pen system moored offshore (26°40'N, 127°52'E) from Yamagawa Port, Motobu-cho, western Okinawa-jima Island, where they were cared for in captivity with other whale sharks. A copepod specimen from whale shark 27 was collected on 18 February 2009, but its attachment site was not recorded. Copepod specimens from whale shark 32 were collected by gently scraping a cotton-gloved hand over the host's oral area on 28 April 2010. Copepods were preserved in 70% ethanol, subsequently soaked in lactic acid for 1 h, and examined on a wooden slide (see Humes & Gooding 1964) using an Olympus BX51 phase contrast microscope. The copepod from whale shark 27 was measured using an ocular micrometer and illustrations were made with the aid of a drawing tube. Anatomical terminology follows Kabata (1979) and Huys & Boxshall (1991) and fish names conform to FishBase (Froese & Pauly 2011).

Results

Prosaetes rhinodontis (Wright, 1876)

(Figs 1–3)

Material examined. One adult male collected from whale shark 27; 2 adult males collected from whale shark 32. All three specimens (NSMT–Cr 21704–21705) are deposited in the Crustacea collection at the National Museum of Nature and Science (NSMT), Tsukuba, Japan.

Description of adult male. Total body length (excluding caudal setae) 4.32 mm. Prosome (Fig. 1A) composed of dorsoventrally flattened cephalothorax (incorporating first pedigerous somite) and

free thoracic somite comprised of second and third pedigerous somites fused together. Paired frontal plates (Fig. 1A) well-developed, ventrally fused to anterior margin of cephalothorax but demarcated dorsally from it by suture line, without lunules. Cephalothorax with marginal membrane, slightly wider than long (2.2×2.25 mm), dorsally divided into 3 zones (2 lateral, 1 cephalic-thoracic) by pair of longitudinal sutures; each lateral zone with prominent posterior lobe extending to level of middle of free thoracic somite; anterolateral corners of ventral surface each with rudimentary postantennal process (not figured) and unornamented lobe and serrated row of scales adjacent to adhesion pad (Fig. 1B). Free thoracic somite wider than long ($650 \mu\text{m} \times 1.29$ mm), with well-developed lateral plates each with posterior marginal membrane and corrugated surface (not figured) on ventrolateral margin. Urosome (Fig. 1A) comprised of fourth pedigerous somite, genital complex, and 2 free abdominal somites. Fourth pedigerous somite wider than long ($275 \times 600 \mu\text{m}$), without posterodorsal plates. Genital complex (Fig. 1A, C) ovate, longer than wide ($900 \times 775 \mu\text{m}$), with short row of pectinate scales and 6 patches of spinules on either side of ventral midline; genital apertures situated ventrally near genital complex-abdomen junction. Abdominal somites (Fig. 1A) wider than long ($212.5 \times 325 \mu\text{m}$ and $262.5 \times 287.5 \mu\text{m}$, respectively), each with oblique lateral margins. Caudal ramus (Fig. 1D) cylindrical, more than 3 times longer than wide ($437.5 \times 137.5 \mu\text{m}$), with 6 plumose setae (seta I absent) and medial row of setules; setae II and VII subequal, each about 5 times shorter than setae III–VI.

Cephalic and natatory appendages of male similar to those of female except as follows. Antennule (Fig. 1E) with 29 weakly sclerotized setae on first segment (one minute seta indicated by arrowhead in Fig. 1E). Antenna (Fig. 2A) with corrugated surface along medial margin of second segment (basis) (indicated by arrowhead in Fig. 2A) and slim claw (endopod). Maxilliped (Fig. 2B–C) with long myxal process, two large adhesion pads along medial margin, and two corrugated areas on anterior surface of protopod (corpus). Leg 1 (Fig. 2D) with fewer spinules on protopod, naked first endopod segment, setules along lateral margin of second endopod segment, and smooth margin about insertion of middle seta of second endopod segment. Leg 2 (Fig. 2E) with fewer spinules along distolateral corner of coxa, naked lateral margin on third exopod segment, naked distolateral corner of first endopod segment, setules along lateral margin of second endopod segment, and smooth margin about insertion of second lateral-most seta of second endopod segment. Leg 3 (Fig. 3A) lacking spinules near central-most adhesion pad on coxa, fewer denticles along lateral margin of third exopod segment, naked posterior surface on each exopodal segment, naked distolateral corner of first endopod segment, setules along proximal half of lateral margin of second endopod segment, and laterally expanded distolateral corner of second endopod segment; latter with several denticulate patches, spiniform process, and accessory claw (Fig. 3B). Leg 4 (Fig. 3C) with intercoxal sclerite, fewer spinules on coxa and basis, 3-segmented exopod, and distinctly 2-segmented endopod. First exopod segment with large, naked spine inserted on protruded distolateral corner and setules and plumose seta along medial margin; second segment with small denticles along lateral margin, distolateral serrulate spine, and setules and seta along medial margin; third segment with 3 lateral serrulate spines, 4 medial plumose setae, and few setules along medial margin. First endopod segment with setules along lateral margin and medial plumose seta; second segment with 5 plumose setae, setules along lateral and medial margins, and few spinules about insertion of lateral-most seta. Leg 5 (Fig. 1C) vestigial, an unsegmented lobe situated laterally on posterior quarter of genital complex; with robust spine and 3 setae. Leg 6 (Fig. 1C) forming genital operculum at posterior end of genital complex, with stout spine, long unipinnate seta, and short naked seta.

Variability. One male from shark 32 with 4 setae on each second endopod segment of leg 4.

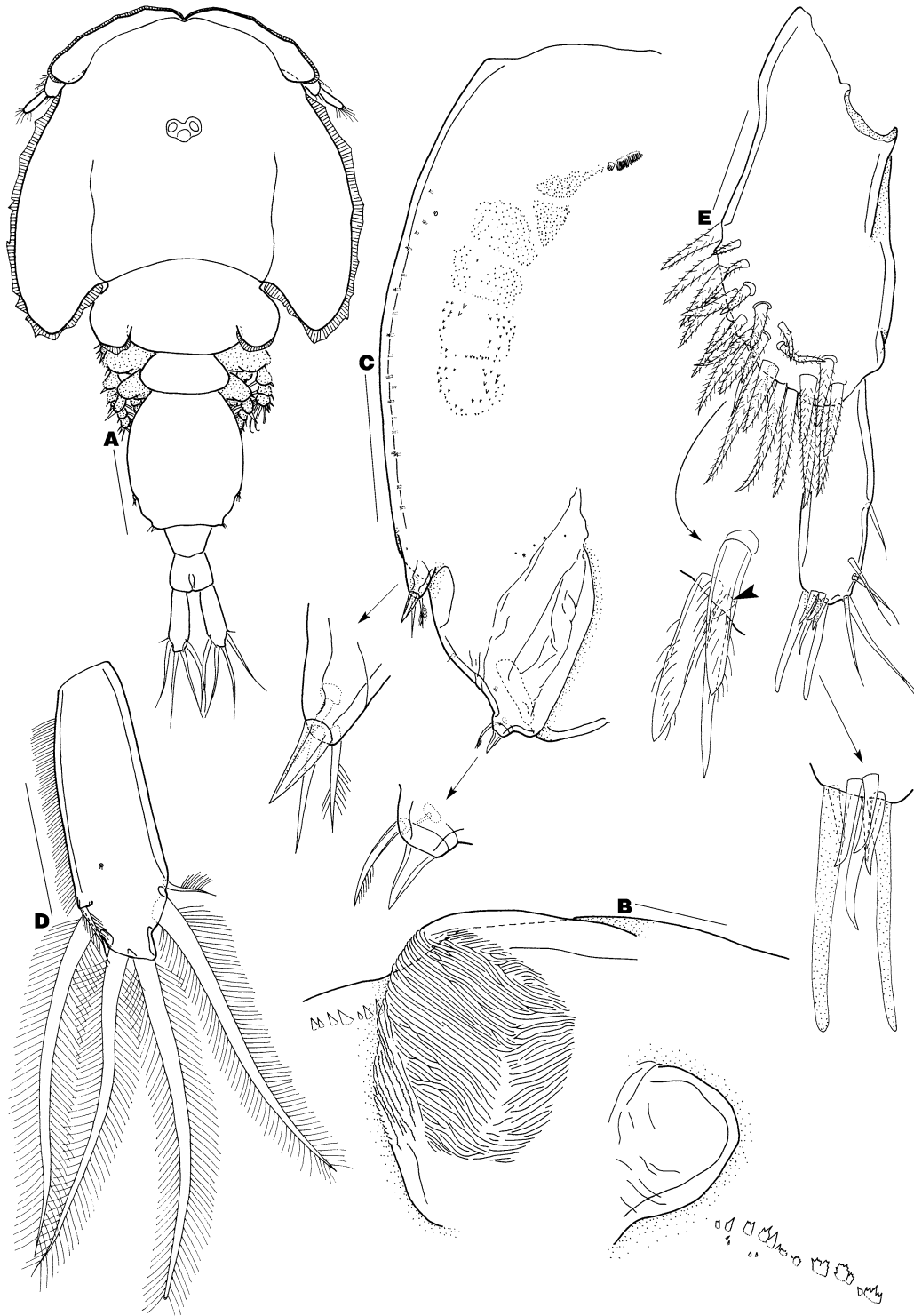


FIGURE 1. *Prosaetes rhinodontis* (Wright, 1876), adult male. A, habitus, dorsal; B, adhesion pad, lobate structure, and ornamentation on right anterolateral margin of cephalothorax, ventral; C, right side of genital complex, with detail of legs 5 and 6, ventral; D, right caudal ramus, dorsal; E, right antennule, with detail of elements near anterodistal margin of first segment and at tip of second segment, ventral. Scale bars: A = 1.00 mm; B = 50 μ m; C–D = 200 μ m; E = 100 μ m.

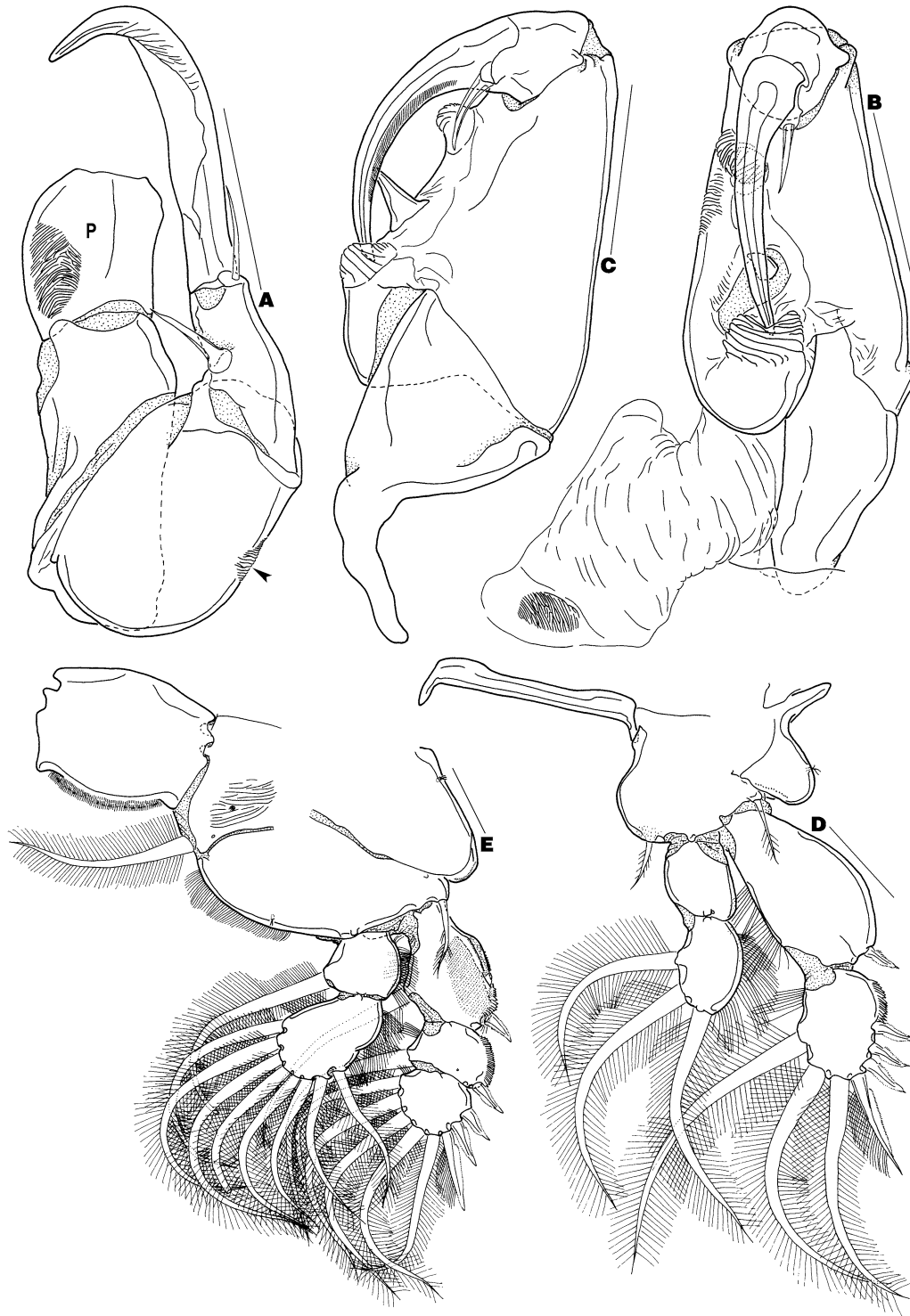


FIGURE 2. *Prosaetes rhinodontis* (Wright, 1876), adult male. A, right antenna, ventral; B, left maxilliped, medial; C, same, posterior; D, left leg 1, anterior; E, left leg 2, anterior. Scale bars: A–C = 200 μ m; D–E = 100 μ m.

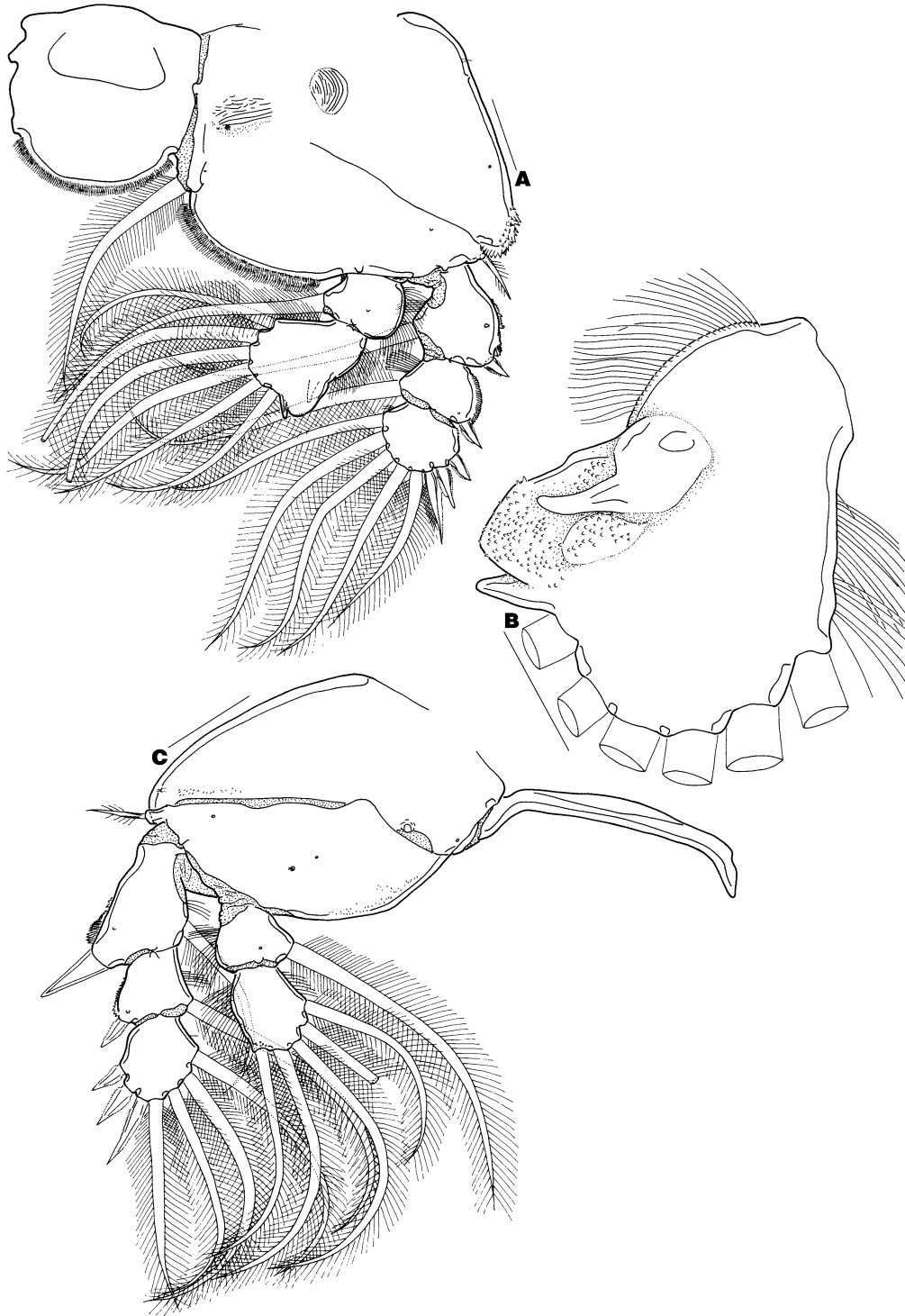


FIGURE 3. *Prosaetes rhinodontis* (Wright, 1876), adult male. A, left leg 3, anterior; B, second endopod segment of left leg 3, posterior; C, right leg 4, anterior. Scale bars: A, C = 100 μm ; B = 50 μm .

Remarks. The specimens described above were identified as *Prosaetes rhinodontis* (Wright, 1876) based on the presence of a conical myxal process issuing from a slim corpus maxillipedis and similarities in body tagmosis, caudal rami shape, antennule armature, and structure of the mandible, maxillule, maxilla, and legs 1–3 with those of the female of *P. rhinodontis* (see Tang *et al.* 2010). These male specimens were collected from the same host species and locality as the female *P.*

rhinodontis specimens reported in Tang *et al.* (2010). Examination of our male specimens and the female specimens reported on by Tang *et al.* (*op. cit.*) revealed misinterpretations of the female by those authors: the armature on the anterodistal corner of the second segment of the antennule reported as being 7 setae + aesthetasc is actually 6 setae + 2 aesthetascs (as in the male, see enlarged drawing in Fig. 1E) and failure to note the female possession of a naupliar eye, a lobe immediately adjacent to the adhesion pad on the anterolateral corner of the cephalothorax (lobe on female is about one-fourth size of male lobe depicted in Fig. 1B), a short spiniform seta on the first segment of antennule (as in the male, see arrowhead indication in Fig. 1E), an adhesion pad on the pedestal of the antenna (as in the male, see Fig. 2A), an adhesion pad at the base of the hyaline membrane attached to the medial base of the maxilliped (as in the male, see Fig. 2B), and an adhesion pad on the sternite between legs 1 and 2 (not figured for either sex herein).

To the best of our knowledge, *P. rhinodontis* has been reported previously from the whale shark on just five occasions (Wright 1876; Wilson 1944; Kirtisinghe 1964; Williams & Williams 1986; Tang *et al.* 2010). Among the nearly 300 individuals amassed in those collections, none was male, and thus, this study represents the first collection of the male of this species. The apparent rarity of male *P. rhinodontis* may reflect a highly female-biased sex ratio in this species, which is not unusual among caligoids (Caligoidea Dana, 1853; a siphonostome superfamily *sensu* Yamaguti (1963) comprised of Caligidae Burmeister, 1835, Euryphoridae C. B. Wilson, 1905, Pandaridae Milne Edwards, 1840, Cecropidae Dana, 1849, Trebiidae C. B. Wilson, 1905, and Dissonidae Yamaguti, 1963) according to Benz (1981), or which may in some cases simply be an artifact stemming from limited (volume or seasonality) sampling scope.

Tang *et al.* (2010) noted that females of *P. rhinodontis* use their antennae and maxillipeds to attach to the filtering pads (*sensu* Motta *et al.* 2010) located within the oral cavity of a whale shark. The two males of *P. rhinodontis* from whale shark 32 were collected from the mouth. Unfortunately, the attachment site of the male *P. rhinodontis* specimen from whale shark 27 was not recorded; however, we note here that this male was sent to us in a vial also containing 3 female and 7 male *Pandaridus* sp. which were likely collected at the same attachment site as the male *P. rhinodontis*. Hence, additional collections are needed to fully appreciate the attachment site of male *P. rhinodontis*.

Discussion

Validity of Cecropidae

Robust evidence supporting the validity of Cecropidae has always been thin and cecropids (Cecropidae) and pandarids (Pandaridae) share many morphological characteristics (Kabata 1979). In reviewing this topic, Kabata (*op. cit.*) proposed the possibility that the only characteristic distinguishing cecropids from pandarids is the structure of the female maxilliped. In advancing that opinion, Kabata (*op. cit.*) considered that amongst pandarids the corpus maxillipedis is squat and exhibits a well-developed myxal region that is displaced distally and the subchela (endopod + claw) is oriented perpendicular to the long axis of the corpus when closed. In contrast, Kabata (*op. cit.*) considered that the corpus maxillipedis of cecropids is slender, with the myxal region sometimes possessing processes. Nevertheless, Kabata (*op. cit.*) noted that distinguishing cecropids and pandarids is a task vexed by difficulty and since then, no real progress has been made regarding this matter. Recently, Tang *et al.* (2010) pointed out that a squat corpus maxillipedis is not a universal feature among pandarids, as the female of *Dinemoura discrepans* Cressey, 1967 has a slim corpus maxillipedis (see Fig. 205 in Cressey 1967; Fig. 1G in Ho & Lin 2011) more typical of cecropids.

However, Tang *et al.* (*op. cit.*) accepted Cecropidae and transferred *Prosaetes rhinodontis* (Wright, 1876) from Pandaridae to Cecropidae based primarily on the female's slim corpus maxillipedis. Based on the present study as well as a reconsideration of Tang *et al.* (*op. cit.*) we feel that the morphology of *P. rhinodontis* adds significantly to the blurring of familial limits between Pandaridae and Cecropidae and once again calls into serious question the validity of Cecropidae. Five primary lines of evidence support our position regarding this matter, as follows.

(1) The male of *P. rhinodontis* has a slim body, a feature more characteristic of male caligoids other than cecropids according to Benz (1993), and lacks posterodorsal plates on the fourth pedigerous somite, a condition exhibited by most (but not all) male pandarids, e.g., see Cressey (1967).

(2) The male of *P. rhinodontis* shares the apomorphic, modified terminal endopodal segment of leg 3 with male cecropids and male pandarids of the *Dinemoura*-group (*sensu* Kabata 1979) (cf. Fig. 3B herein, Fig. 983 in Kabata (1979), and Fig. 265 in Cressey (1967)). Among the known males of the *Dinemoura*-group, this feature may have become reduced (e.g., see Fig. 343 in Cressey 1967) or lost amongst representatives of *Nesippus* Heller, 1868.

(3) The second and third pedigerous somites are fused in the female of *P. rhinodontis* as in the female of some pandarids of the *Dinemoura*-group and most cecropids (cf. Fig. 2A in Tang *et al.* (2010), Fig. 1A in Benz & Deets (1987), and Fig. 986 in Kabata (1979)).

(4) The female of *P. rhinodontis* has a narrow third pedigerous somite without dorsal plates as do females of the *Dinemoura*-group and nearly all cecropids (cf. Fig. 2A in Tang *et al.* (2010), Fig. 190 in Cressey (1967), and Fig. 936 in Kabata (1979)). The female of *Cecrops latreillii* Leach, 1816 possesses a small dorsal plate on the third pedigerous somite; however, that character state was regarded as being derived within Cecropidae by Benz & Deets (1988).

(5) The female of *P. rhinodontis* has a slender corpus maxillipedis similar to that of the pandarid *D. discrepans* and all female cecropids (cf. Fig. 3C in Tang *et al.* (2010), Fig. 205 in Cressey (1967), and Fig. 2F in Benz & Deets (1988)).

In addition to the above, our reassessment of Cecropidae revealed no possible revision of the family capable of establishing its familial integrity. Thus, with no justification to accept the validity of Cecropidae other than maintaining systematic stability, we consider the family a junior synonym of Pandaridae and we no longer support using the form of the corpus maxillipedis as discussed above to incontrovertibly diagnose Pandaridae. Based on that decision, we transfer *Cecrops* Leach, 1816, *Luetkenia* Claus, 1864, *Philorthagoriscus* Horst, 1897, *Orthagoriscicola* Poche, 1902, *Prosaetes* C. B. Wilson, 1907, and *Entepherus* Bere, 1936 to Pandaridae. We realize that our action may "raise the hackles" of some copepodologists and that some may criticize us for having proceeded with this action without undertaking a combined phylogenetic analysis of Cecropidae and Pandaridae. However, we maintain that our failed search to find a single unequivocal synapomorphy for Cecropidae and the ability to accommodate all cecropids within Pandaridae cancels the necessity for such an analysis. That said, our transfer of all cecropids to Pandaridae comes with no judgement regarding the monophyly of the former cecropid taxa within Pandaridae, as that consideration will necessitate a thorough phylogenetic analysis of the newly swollen pandarid membership.

Validity of Amaterasidae

Izawa (2008) established Amaterasidae (Siphonostomatoidea) to hold *Amaterasia amanoiwatoi* Izawa, 2008 based on 5, 16, 41, and 13 individuals (all presumed to be females) of copepodids I, III, IV, and V, respectively, found encysted in galls in fins of a single striped triggerfish (*Xanthichthys lineopunctatus* (Hollard)) captured in the eastern Pacific, off Clarion Island, Mexico, and one

developing adult female found inside an encysted copepodid V. Unfortunately, Izawa (*op. cit.*) did not recognize that Lewis (1964) had described a similarly bizarre species which he tentatively reported as “*Nesippus costatus?* Wilson, 1924” based on what he referred to as younger and older early encysted stages, a late encysted stage, and a recently excysted stage, all presumed to be males, taken from cysts in fins of fishes representing Acanthuridae, Diodontidae, Scaridae, Labridae, Pomacentridae, and Zanclidae captured off Hawaii. The morphological and ecological attributes of Izawa’s and Lewis’ specimens are strikingly similar and suggest them to be congeners. Furthermore, comparisons of the illustrations provided by those authors (*loc. cit.*) reveal that Lewis’ “younger early encysted stage” represents copepodid IV, the “older early encysted stage” represents copepodid V, and the “late encysted stage” and “recently excysted stage” represent the immature adult male.

Izawa (2008) stated that *A. amanoiwatoi* resembled pandarids and dissonids (Dissonidae) but was distinct from those groups by possessing [three] free pedigerous somites without dorsal plates, genital apertures situated distally on the genital complex, adhesion pads on the first free pedigerous somite, an indistinctly 4-segmented antennule, a medial coxal seta on legs 1–3, bimerous rami on legs 1–3, and unimerous rami on leg 4 in the adult. He also noted that the encysted copepodid I of *A. amanoiwatoi* differed from the copepodid I of the pandarid *Nesippus orientalis* Heller, 1868 (as *N. alatus* C. B. Wilson, 1905) by possessing a 3-segmented antennule, an accessory process on the medial margin of the antennal claw, one seta and two modified elements (one lash-like) on the maxillule, a maxilla and maxilliped that originate side by side, two proximal processes on the corpus maxillipedis, and a 2-segmented maxilliped shaft. Nevertheless, our critical evaluation of these features, coupled with recent morphological information on the copepodid I of the pandarid *Gangliopus pyriformis* Gerstaecker, 1853 (see Izawa 2010a), indicates that the establishment of Amaterasidae was unfounded for the following reasons.

(1) Three free pedigerous somites without dorsal plates are features of dissonids (see Fig. 1A in Boxshall *et al.* 2008) and some *Nesippus* spp. (see Figs 305 & 346 in Cressey 1967).

(2) The genital apertures in all caligoids are situated ventrally near the posterior margin of the genital complex (Boxshall & Halsey 2004).

(3) Adhesion pads on the anterolateral corners of the first free pedigerous somite are possessed by some pandarids (see Fig. 7c in Lewis 1966; Fig. 1 in Benz 1992).

(4) The presence of an indistinctly 4-segmented antennule in *A. amanoiwatoi* requires verification, as a 2-segmented antennule in the adult of both sexes is standard for all other caligoids (Boxshall & Halsey 2004), including the immature adult male of Lewis’ “*N. costatus?*” (see Fig. 20g in Lewis 1964). Comparisons of illustrations of the adult of *A. amanoiwatoi* and Lewis’ “*N. costatus?*” clearly reveal most of the appendages of the former species not to be fully developed.

(5) A medial coxal seta on legs 2–3 is possessed by dissonids (see Fig. 2D–E in Boxshall *et al.* 2008) and some pandarids (see Figs 302–303 in Cressey 1967). The presence of a medial coxal seta, as well as a medial seta on the first segment of each ramus, on leg 1 of *A. amanoiwatoi* requires verification, as the armature formula of 0-0, I-0, and 0-0 on the leg 1 coxa, first exopod segment, and first endopod segment, respectively, is standard for caligoids (see Boxshall & Halsey 2004), including the excysted adult of Lewis’ “*N. costatus?*” (see Fig. 21g in Lewis 1964).

(6) Bimerous rami on legs 1–3 and unimerous rami on leg 4 are characteristic of species in some pandarid genera such as *Gangliopus* Gerstaecker, 1854, *Phyllothyreus* Norman, 1903, *Achtheinus* C. B. Wilson, 1908, *Pseudopandarus* Kirtisinghe, 1950, *Pannosus* Cressey, 1967, *Dinemoleus* Cressey & Boyle, 1978, and *Nesippus* (Cressey 1967; Cressey & Boyle 1978; Izawa 2010b).

(7) Most of the copepodid I features of *A. amanoiwatoi*, including the lash-like element on the maxillule, are also possessed by the copepodid I of *G. pyriformis* (see Izawa 2010a). The latter species differs from the former by having a 4-segmented antennule and a maxilliped shaft

completely fused with the claw. Izawa (*op. cit.*) did not mention the relative positions of the maxilla and maxilliped in the copepodid I of *G. pyriformis*.

As we can find no robust, family-level synapomorphy for Amaterasidae and as *A. amanoiwatoi* and “*N. costatus?*” both can be accommodated within Pandaridae, we relegate Amaterasidae to a junior synonym of Pandaridae. That decision is bolstered by the fact that the maxillipeds of *A. amanoiwatoi* and Lewis’ “*N. costatus?*” are virtually identical to those of some pandarids. Within Pandaridae, Izawa’s (2008) immature adult female of *A. amanoiwatoi* superficially resembles some *Nesippus* spp. in that it lacks dorsal plates on the third free thoracic somite, genital complex, and abdomen and has 1 abdominal somite, unmodified bimerous rami on legs 1–3, and unmodified unimerous rami on leg 4. However, given that Izawa’s female specimen was not fully developed and dramatic changes occur in the relative proportions of body somites and plates as adult female pandarids fully mature (see Shiino 1954; Kabata 1979; Dippenaar & Jordan 2006), it is risky to remark on the possible affiliations of *A. amanoiwatoi* within *Nesippus*. Thus, unless the discovery and full description of adult females of *A. amanoiwatoi* challenges our position, we consider *Amaterasia* Izawa, 2008 a valid taxon.

Despite their similarities, we do not consider Lewis’ (1964) “*N. costatus?*” conspecific with *N. crypturus* Heller, 1868 (senior synonym of *N. costatus* C. B. Wilson, 1924; see Cressey 1967). Lewis’ (1964) immature adult male differs from the mature adult male of *N. crypturus* (see Cressey 1967) regarding the shape of the first free thoracic somite and genital complex, relative lengths of the lateral spines on legs 1–4, and the exopod chaetotaxy of legs 3 and 4. Lewis’ specimens can be accommodated in *Amaterasia*, given that their general morphology and ecology are so similar to those of *A. amanoiwatoi*. Nonetheless, the reported chaetotaxy of legs 1–3 of Lewis’ and Izawa’s specimens prevent us from considering them conspecific. Based on the aforementioned facts, we propose that Lewis’ (1964) specimens of “*N. costatus?*” represent a new species, which we name *Amaterasia lewisi* **n. sp.** Finally here, we note that collections and descriptions of sexually mature adults of both sexes of *A. lewisi* **n. sp.** are needed to fully appreciate its taxonomic affinities.

Amaterasia lewisi **n. sp.** and *A. amanoiwatoi* are extraordinary examples of the ecological diversity displayed by parasitic copepods, as they are the only pandarids known to fully encyst in fishes; each species encysting in fins of coral reef fishes during the post-naupliar phase of development. No frontal filament has been observed in any copepodid stage of *A. lewisi* **n. sp.** or *A. amanoiwatoi* (see Lewis 1964 and Izawa 2008, respectively). This lifestyle contrasts sharply with that of other pandarids, whose copepodids II–V (= chalimus I–IV) anchor to the host’s external surface by a frontal filament secreted by an anteriorly located gland on the cephalothorax (Wilson 1907; Grabda 1973; Izawa 2010b). Furthermore, the infective stages, including adults, of most pandarids are found on elasmobranchs and records of pandarids from teleosts are few (Cressey 1967; Kabata 1979; Benz & Deets 1988), with some possibly resulting from identification errors. It remains to be determined whether the life cycles of *A. lewisi* **n. sp.** and *A. amanoiwatoi* involve one host, as is typical for caligoids (see Benz 1993), or two hosts, as is typical for siphonostomes of Pennellidae Burmeister, 1835 (see Kabata 1979). Lastly, it is exciting to contemplate that the extraordinary lifestyle of *Amaterasia* spp. may be an adaptation to living in a coral reef environment where the activity of “cleaner” organisms is high. By passing through the post-naupliar development phase encysted, *Amaterasia* spp. may be better protected from cleaners that feed on ectoparasites.

Similarities within Pandaridae

Cressey (1967) considered Pandaridae to be comprised of two groups, each defined by the general habitus, including the presence or absence of dorsal plates on the three free pedigerous somites. Group I (*sensu* Cressey 1967; = *Pandaridus*-group *sensu* Kabata 1979) members are characterized by

a solid, one-piece body appearance and the presence of dorsal plates on each free pedigerous somite and comprises the memberships of *Pandarus* Leach, 1816, *Gangliopus*, *Perissopus* Steenstrup & Lütken, 1861, *Phyllothyreus*, *Achtheinus* [this genus recently resurrected by Izawa (2010b)], *Pseudopandarus*, and *Pannosus*. Group II (*sensu* Cressey 1967; = *Dinemoura*-group *sensu* Kabata 1979) members are characterized by a narrow third pedigerous somite (this somite is typically free but is secondarily fused to the second pedigerous somite in some species), which forms a short neck dividing the body into anterior and posterior parts, and dorsal plates on the fourth pedigerous somite only (some *Nesippus* spp. lack dorsal plates on this somite) and prior to this report comprised the memberships of *Dinemoura* Latreille, 1829, *Echthrogaleus* Steenstrup & Lütken, 1861, *Demoleus* Heller, 1865, *Nesippus*, *Paranesippus*, *Pagina* Cressey, 1963, and *Dinemoleus*. The presence of a clavus versus crista on the maxilla and unmodified versus lamelliform legs 1–4 were used also by Cressey (1967) and Dojiri (1983), respectively, to separate Group I and Group II, respectively, but Benz (1993) rightfully argued that these features overlapped between the two groups. While the informal consideration of these groups seems to have been helpful regarding considerations of the membership of Pandaridae and each group may comprise a clade (monophyletic group), neither group has been formally demonstrated to comprise a natural taxon through a thorough phylogenetic analysis.

Within Pandaridae, *Amaterasia* spp. seem to belong to the *Dinemoura*-group based primarily on their similarity to some *Nesippus* spp. However, this interpretation is tentative pending the discovery and full descriptions of the ovigerous females of *A. amanoiwatoi* and *A. lewisi* **n. sp.** Regarding the species of *Prosaetes*, *Cecrops*, *Luetkenia*, *Philorthogoriscus*, *Orthogoriscicola*, and *Entepherus* (all former representatives of Cecropidae), we more confidently consider these taxa to be members of the *Dinemoura*-group based on the presence of a narrow third pedigerous somite and dorsal plates on the fourth pedigerous somite in the adult female and a modified leg 3 terminal endopodal segment in the adult male. The last feature typically consists of an accessory claw, a spiniform process, and a denticulated area near the lateral margin, and one can argue that the feature seems secondarily reduced in *Nesippus* spp. Although *Achtheinus* spp. (members of the *Pandarus*-group) also exhibit sexual dimorphism in the leg 3 endopod (see Izawa 2010b), the structure of that limb in males of this genus does not appear to be homologous with that in males of the aforementioned taxa as the modification comprises an apical lamellar process on the terminal endopodal segment. *Prosaetes rhinodontis* seems closely related to *Echthrogaleus* spp. based on the following shared features: maxilla of both sexes with a spinulated lobe and clavus in addition to canna and calamus; female with fused pedigerous somites 2 and 3 (as in *Echthrogaleus denticulatus* Smith, 1874, *E. pellucidus* Shiino, 1963, *E. disciarai* Benz & Deets, 1987, and *E. mitsukurinae* Izawa, 2012), spinulated patches on the ventral surface of the genital complex (as in *E. denticulatus* (Tang pers. observation) and *E. disciarai*), 1 abdominal somite lacking dorsal plates, 3-segmented exopod and 2-segmented endopod on legs 2 and 3 (although variability in the segmentation of the exopod of legs 2 and 3 has been noted for *E. coleoptratus* (Guérin-Méneville, 1837) (see Kabata 1979) and *E. mitsukurinae* was reported to have 3-segmented rami on legs 2 and 3 (see Izawa 2012), and armature elements on leg 4 rami reduced to small spines; and male with 2 abdominal somites, 3-segmented exopod and 2-segmented endopod on legs 2–4, and distolateral protrusion and large lateral spine on first exopod segment of leg 4 (except for *E. coleoptratus*). *Prosaetes rhinodontis* can be distinguished from *Echthrogaleus* spp. by having a longer corpus maxillipedis in both sexes, as well as reduced dorsal plates on the fourth pedigerous somite, a comparatively shorter genital complex (about two-thirds the length of the cephalothorax), smaller leg 3 protopodal segments, and non-lamelliform rami on leg 4 in the female.

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