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First Record of Association of Copepods with Highly Venomous Box Jellyfish *Chironex*, with Description of New Species of *Paramacrochiron* (Cyclopoida: Macrochironidae)

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***Paramacrochiron chironecicola* n. sp. (Copepoda: Cyclopoida: Macrochironidae) is described from the highly venomous box jellyfish *Chironex* sp. collected from Malampaya Sound, Palawan Island, The Philippines. This is the first record of copepods associated with cubozoan medusae, although other cnidarian groups such scyphozoans, hydrozoans, and anthozoans are common hosts for symbiotic copepods. The infection sites were on the subumbrella, pedalium, and rhopalium, but also rarely on the adradial furrow. The new species is distinguished from other congeners by a combination of the following features: (1) the fifth pedigerous somite dorsally covering the anterior part of the female genital double-somite; (2) the fine structures of the antenna (relative lengths of segments) and maxilliped (positions of terminal elements) of the female; (3) the relatively long outer spines on the exopodal segments of legs 1–4; (4) the relatively long and thick female leg 5 bearing a long protopodal seta which reaches to the distal margin of the exopod; (5) the relatively short caudal ramus in the female; and (6) the plump prosome and short urosome in the male. Since members of the genus typically parasitize scyphozoans, especially rhizostomes, the association of this parasitic copepod on cubozoans may reflect the relatively close phylogenetic relationship between cubozoans and scyphozoans.**

Key words: association, box jellyfish, copepod, Macrochironidae, Philippines, scyphozoan

INTRODUCTION

Cnidarians are important host animals for symbiotic copepods (Humes, 1985; Ho, 2001; Boxshall and Halsey, 2004). Thus far, the taxonomic groups reported as hosts have been restricted to hydrozoans, scyphozoans, and anthozoans (Humes, 1985). The symbiotic copepods from cnidarians were mainly assigned to Poecilostomatoida and Siphonostomatoida by Humes (1985), with a small number of Calanoida, Harpacticoida and Cyclopoida (Humes, 1985). No association of any order of copepods has been reported from medusae and polyps of cubozoans (cf. Boxshall and Halsey, 2004).

During our survey of the symbionts on jellyfish off Palawan Island, The Philippines, we first found copepods on the highly venomous cubozoan *Chironex* sp. (Fig. 1) on 11 May, 2014. Box jellyfish in the genus *Chironex* are mainly distributed in tropical shallow waters of the Indo-West Pacific, and have been hitherto classified into only two valid species (Lewis and Bentlage, 2009): *C. fleckeri* Southcott,

1956 and *C. yamaguchii* Lewis and Bentlage, 2009. However, Bentlage et al. (2010) placed *Chiropsella bronzie* Gershwin, 2006 in *Chironex* without any comment. They are known to be among the most venomous animals in the world, and can be fatal even to human beings (Hamner et al., 1995; Lewis and Bentlage, 2009). The present host spe-
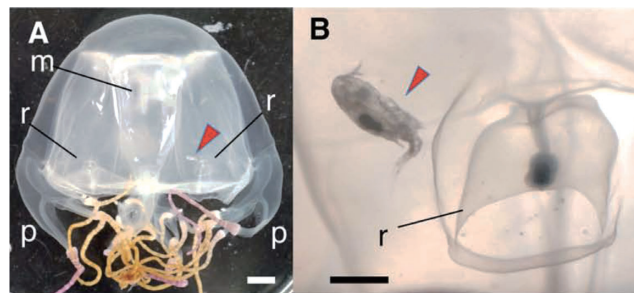
Fig. 1. *Paramacrochiron chironecicola* n. sp. associated with *Chironex* sp. collected from Palawan Island, the Philippines. **(A)** Whole specimen of *Chironex* sp., infected copepod arrowed; **(B)** magnification of infected copepod, note the urosome directed dorsally and the antenna grasping the surface of host subumbrella. Abbreviations: m, manubrium; p, pedalium; r, rhopalium. Scales = 5 mm **(A)**; 1 mm **(B)**.

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cies closely resembles *C. yamaguchii* from the type locality Okinawa, southern Japan. In fact this species has been recorded from Palawan, in The Philippines (Lewis and Bentlage, 2009), but the present specimens differ from typical *C. yamaguchii* in the number of tentacles (Sho Toshino, personal communication). The taxonomy of the present specimens of host box jellyfish is now under review, and these are tentatively identified as *Chironex* sp. The associated copepod is classified as a new species of *Paramacrochiron* Sewell, 1949 (family Macrochironidae) described herein. Copepods in this genus show close association with scyphozoans, in particular rhizostomes (Ohtsuka et al., 2012), but our finding represents the first record of the occurrence of a copepod of any species on a cubozoan host. The present report presents the taxonomy of the new copepod species with ecological notes.

Since the morphology- and molecule-based phylogenetic validity of the two copepod orders Cyclopoida and Poecilostomatoida are under debate (Kim and Kim, 2000; Boxshall and Halsey, 2004; Huys et al., 2012; Tung et al., 2014), we tentatively adopt the order Cyclopoida to accommodate the family Macrochironidae and the genus *Paramacrochiron*.

MATERIALS AND METHODS

The host box jellyfish *Chironex* sp. was collected from a depth of less than 50 cm in Malampaya Sound, Palawan Island, off The Philippines (10°51.95′N, 119°24.76′E) on 11 May, 2014, using a scoop net. The presence of associated copepods was noted on the host due to its transparency (Fig. 1A), so each individual jellyfish was packed in a separate plastic bag, and fixed in 5% formalin/seawater immediately after collection. The prevalence and intensity of copepods on a host could thus be calculated. Copepods that were still attached to their hosts (Fig. 1B) were carefully removed from the body surface with fine forceps, and placed in 70% ethanol. Many individuals were detached from the host during and after fixation and were collected from the plastic bags. Copepods were mounted in lactophenol on slides and observed and illustrated using a differential interference microscope (Optiphot, Nikon Co., Ltd.) with the aid of a drawing tube.

Type specimens are deposited at the Natural History and Human History Museum of Kitakyushu, Japan (KMNH IvR 500,784–500,786). Terminology follows Huys and Boxshall (1991).

RESULTS

Taxonomy

Order **Cyclopoida** Burmeister, 1834
Family **Macrochironidae** Humes and Boxshall, 1996
Genus *Paramacrochiron* Sewell, 1949
Paramacrochiron chironecicola n. sp.
(Figs. 1–5)

Material examined. 12♀♀ and 5♂♂. Holotype, ovigerous 1♀, whole specimen (KMNH IvR 500,784), body length 3.07 mm; paratypes, 2♀♀ and 1♂, dissected and mounted on glass slides with bodies in vials (KMNH IvR 500,785), 9 ♀♀ and 4♂♂, whole specimens (KMNH IvR 500,786). All types collected from body surface of host box jellyfish *Chironex* sp. from Malampaya Sound, off Palawan Island, The Philippines, May 11, 2014.

Description. *Female*. Body (Fig. 2A, B) 2.45–3.23 mm (mean ± standard deviation = 2.91 ± 0.24 mm, *n* = 12) in length, cyclopiform, somewhat depressed dorsoventrally. Cephalosome (Fig. 2A, B) almost completely fused to first pedigerous somite with suture subtly visible. Rostrum (Fig. 2C) produced ventrally and rounded at tip. Second pedigerous somite protruding posterolaterally (Fig. 2A) exhibiting maximum width; third and fourth pedigerous somites laterally expanded; fifth pediger dorsally covering anterior part of genital double-somite, up to level of gonopores. Urosome (Fig. 2B, D) gradually bent dorsally in lateral view; ratio of lengths of genital double- and three free abdominal somites 4.5: 2.0: 1.0: 3.0. Genital double-somite as long as wide; paired gonopores located dorsolaterally at one-third length. Caudal ramus (Fig. 2A, B, D) about 2.3 times longer than wide; seta III and VI plumose basally; seta V longest, with slight thickening at about one quarter length (only in one paratype); subterminal seta VII located dorsally.

Antennule (Fig. 3A) 7-segmented; armature and elements as follows: first = 4, second = 13, third = 6, fourth = 3, fifth = 4 + ae, sixth = 2 + ae, seventh = 7 + ae; terminal aesthetasc fused to contiguous seta at base. Antenna (Fig. 3B) heavily chitinized, 4-segmented; first segment with minute inner seta terminally; second segment having seta subterminally and triangular ridge at midlength; third segment small, bearing 1 terminal and 2 subterminal setae; fourth segment furnished with smoothly curved claw and 6 setae. Mandible (Fig. 3C) having serrate, long spine on convex margin; spinular rows along posterior half of concave margin; lash serrated along outer proximal margin and bipinnate terminally. Labrum (Fig. 2E) medially incised, forming two lamellar lobes. Maxillule (Fig. 2F) composed of triangular lobe with four unequal setae at tip; second innermost one serrate. Maxilla (Fig. 2G) 2-segmented; first segment trapezoid, unarmed; second segment small, having unipinnate process smoothly curved inward, naked seta and serrate spine distally. Maxilliped (Fig. 3D, E) 3-segmented; first segment longest, unarmed; second segment relatively short, with two setae subterminally, bases of which incompletely fused to segment; third segment small, triangular with two large, serrate spines fused basally to segment; naked seta between these spines, base of which fused to segment.

Legs 1 to 3 (Fig. 4A–C) biramous with 3-segmented rami; inner coxal setae of all legs plumose; basis bearing row of setules along inner margin and protruded into round process at distal corner; acute process at outer terminal corner directed outward rather than distally; outer and terminal spines of exopods relatively long. Leg 4 (Fig. 4D, E) with 3-segmented exopod and 1-segmented endopod; outer spines of exopods slender; endopod reaching midlength of third exopodal segment, with two conspicuous processes and two spinulose setae distally, between which round prominence located; row of minute spinules present at base of these setae.

Leg 5 (Fig. 2A, B, D, H, I) consisting of protopod fused to somite with long seta nearly reaching to distal margin of exopod, and free exopod curved slightly inward; exopod (Fig. 2H, I) about 3.5 times longer than wide, furnished with minute spinules along outer margin and acutely pointed triangular process and two terminal setae, outer of which unipinnate. Leg 6 (Fig. 2A, B, J) represented by small plate with two fine elements and minute prominence.

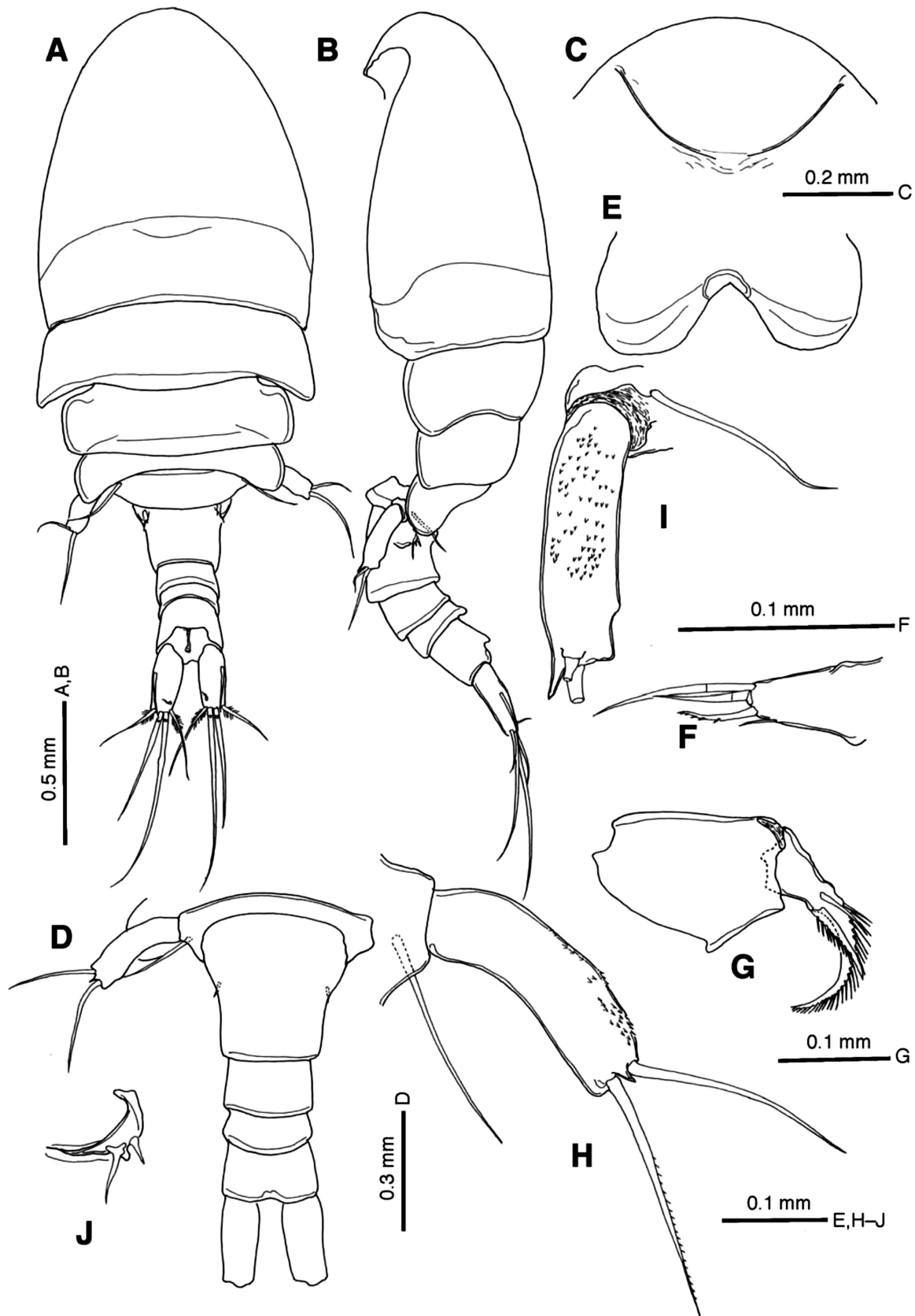*Male*. Body (Fig. 5A) 2.09–2.38 mm (mean ± standard

Fig. 2. *Paramacrochiron chironecicola* n. sp., female (paratypes, KMNH IvR 500,785). **(A)** Habitus, dorsal view; **(B)** habitus, lateral view; **(C)** rostrum; **(D)** urosome, ventral view; **(E)** labrum; **(F)** maxillule; **(G)** maxilla; **(H)** left leg 5, ventral view; **(I)** left leg 5, dorsal view; **(J)** left leg 6.
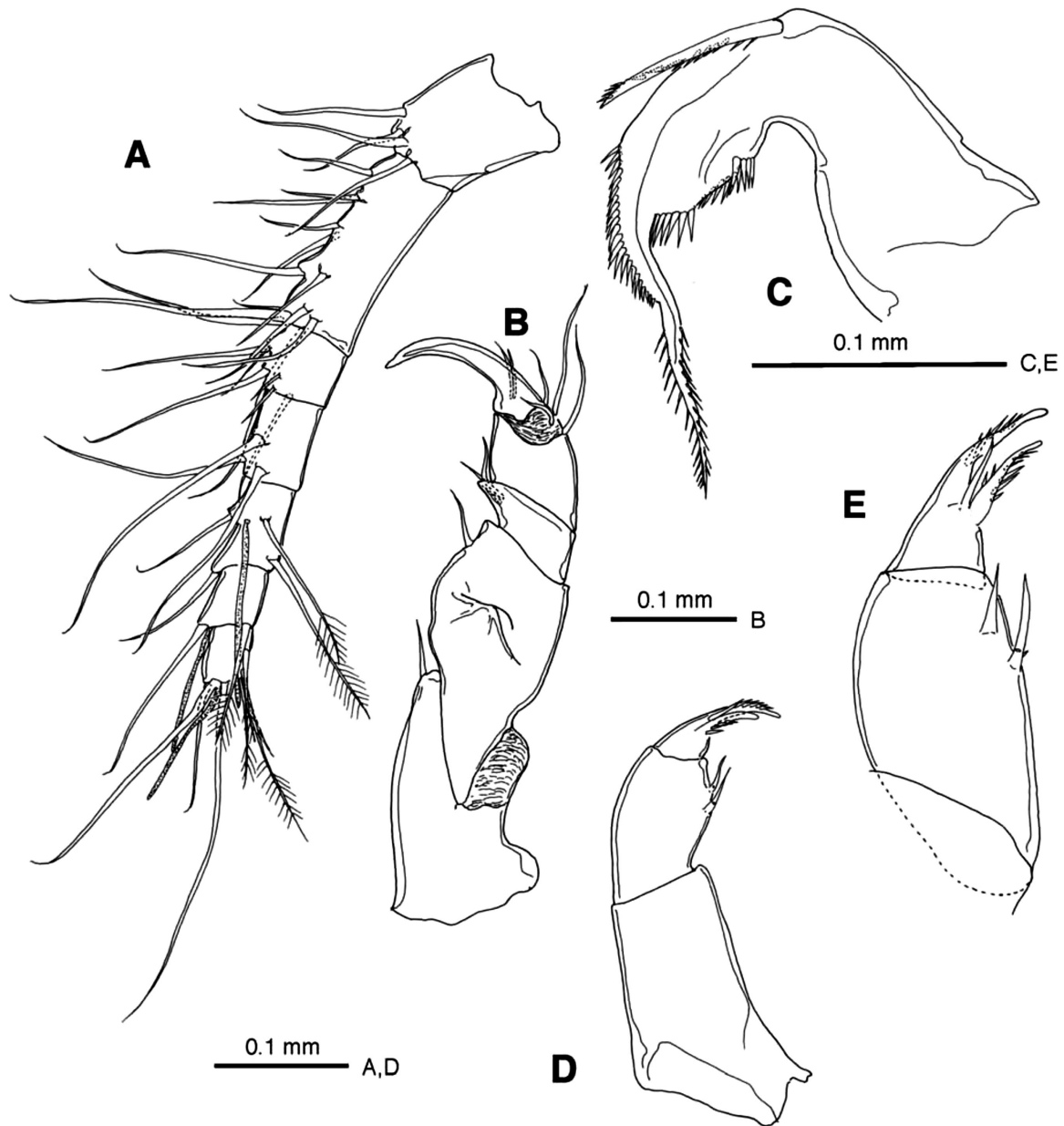
Fig. 3. *Paramacrochiron chironecicola* n. sp., female (paratypes, KMNH IvR 500,785). **(A)** Antennule; **(B)** antenna; **(C)** mandible; **(D)** maxilliped; **(E)** terminal segments of maxilliped.

deviation = 2.24 ± 0.13 mm, $n = 5$) in length, similar to that of female, but more compact than that of female; urosome not bent dorsally. Fifth pedigerous somite not covering genital somite dorsally; genital somite (Fig. 5B) expanded laterally, as long as four post-genital somites combined; caudal ramus (Fig. 5C) ca. 2.7 times longer than wide; caudal seta IV dorsally covered with triangular lamellar process at base.

Antennule 7-segmented; armature elements similar to those of female except for presence of one medial and one subterminal aesthetascs on second segment and one aesthetasc on fourth segment. Antenna (Fig. 5D) to maxilla similar to those of female. Maxilliped (Fig. 5E, F) well developed, 4-segmented; first segment short, unarmed; second segment furnished with two spinular rows along posterior margin and two setae midway; third segment small, unarmed;

fourth segment with elongate claw curved smoothly; claw with one stout proximal and one minute subproximal setae; claw-tip furrowed.

Legs 1–3 similar to those of female. Leg 4 (Fig. 5G) also similar to that of female. Leg 5 (Fig. 5H) composed of incorporated protopod with one dorsal seta and unisegmented exopod with two setae of nearly equal length and triangular process terminally; exopod 2.9 times longer than wide, with minute prominences dorsally. Leg 6 (Fig. 5B) represented by genital operculum with two terminal setae of nearly equal length, inner of which furnished with minute triangular prominences at base.

Remarks. Including the present new species, the genus *Paramacrochiron* now accommodates nine species from the tropical waters of the Indo-West Pacific (Ohtsuka et al.,
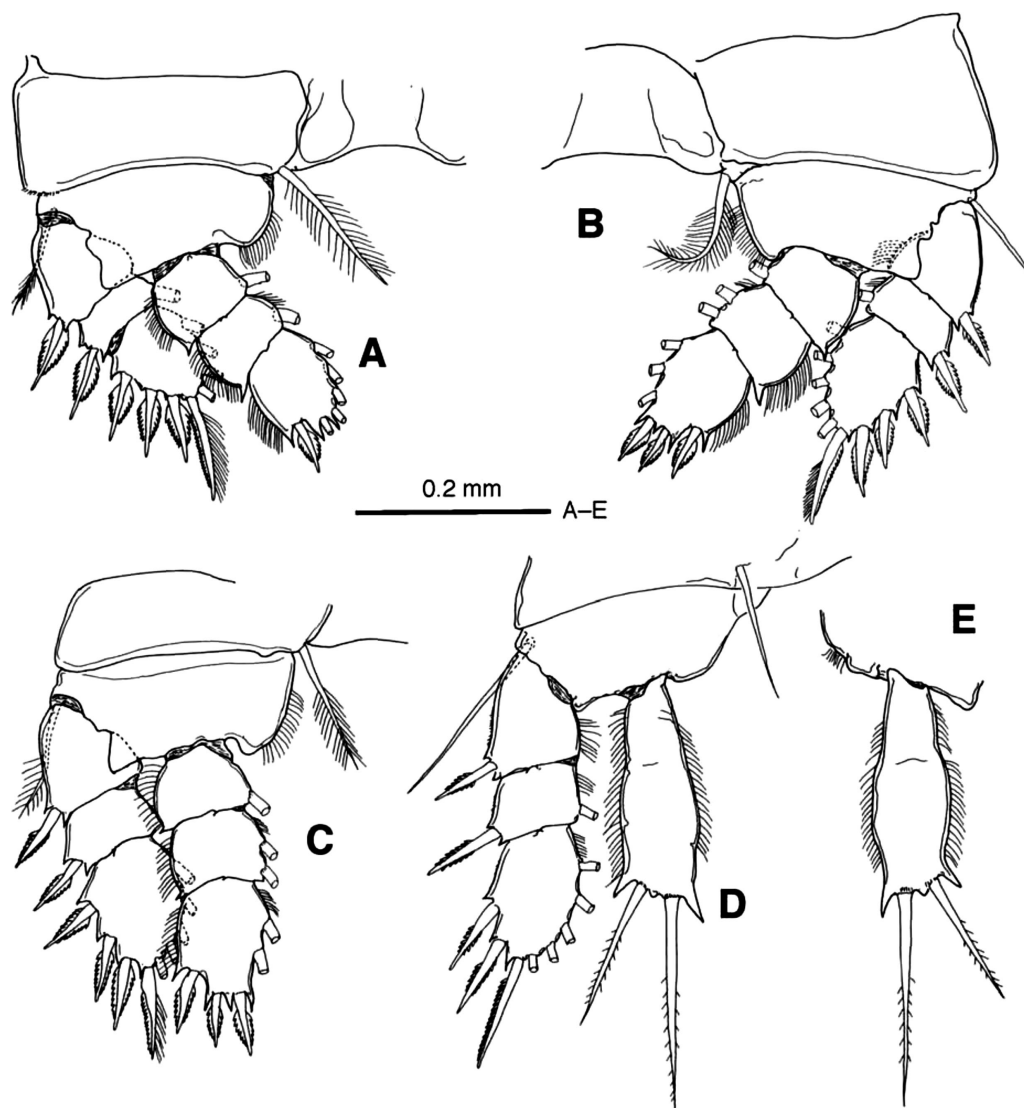
Fig. 4. *Paramacrochiron chironecicola* n. sp., female (paratypes, KMNH IvR 500,785). **(A)** Leg 1, anterior view; **(B)** leg 2, anterior view; **(C)** leg 3, anterior view; **(D)** right leg 4, anterior view; **(E)** endopod of left leg 4, anterior view.

2012; present study). The female of the new species most closely resembles those of *P. amboinense* Mulyadi, 2005 from Indonesia (Mulyadi, 2005) and *P. thailandicum* Ohtsuka, Boxshall and Srinui, 2012 from Thailand (Ohtsuka et al., 2012) in the following features: (1) the size ranges of both sexes (female, 2.4–3.2 mm; male, 1.9–2.4 mm); (2) the anterolateral expansion of the female genital double-somite; (3) the endopod of female leg 4 reaching to the midlength of the third exopodal segment. However, the female of the new species is distinguishable from those of these congeners by: (1) the genital double-somite nearly as long as wide (1.4 to 1.5 times as long as wide in the latter two species); (2) shorter chitinized element on the third maxillipedal segment of the female positioned at the inner margin (outer in both other species); (3) the length of the longest outer marginal spines on legs 1–4 exceeds the maximum width of exopodal segment (not so long in both other species); (4) the basal seta of leg 5 is as long as the exopodal segment (shorter than the segment in both other species); (5) the exopod of

leg 5 relatively thick (slender in both other species); and (6) the presence of minute spinules along the outer margin of the exopod of leg 5 (absent in *P. amboinense*).

Males of *Paramacrochiron* are known for eight congeners. The male of *P. amboinense* is unknown. The male of the present new species is having a relatively long urosome (ratio of prosome to urosome = 1.18), while those of *P. pacificum* (Wilson, 1950) and *P. thailandicum* have ratios of 1.38 and 1.04, respectively. The males of other species fall within this range. The basal spine of the fourth maxillipedal segment is relatively long, reaching beyond the second seta on the second segment in *P. chironecicola*, but not so long in *P. ennorense* Reddiah, 1968, *P. japonicum*, *P. sewelli* Reddiah, 1968, and *P. thailandicum*. In *P. maximum* (Thompson and Scott, 1903) it seems to be nearly the same length as the second segment based on Thompson and Scott (1903, fig. 10). In *P. pacificum* and *P. rhizostomae* Reddiah, 1968 the element was not described. In the present study the male of *P. pacificum* is re-examined (see
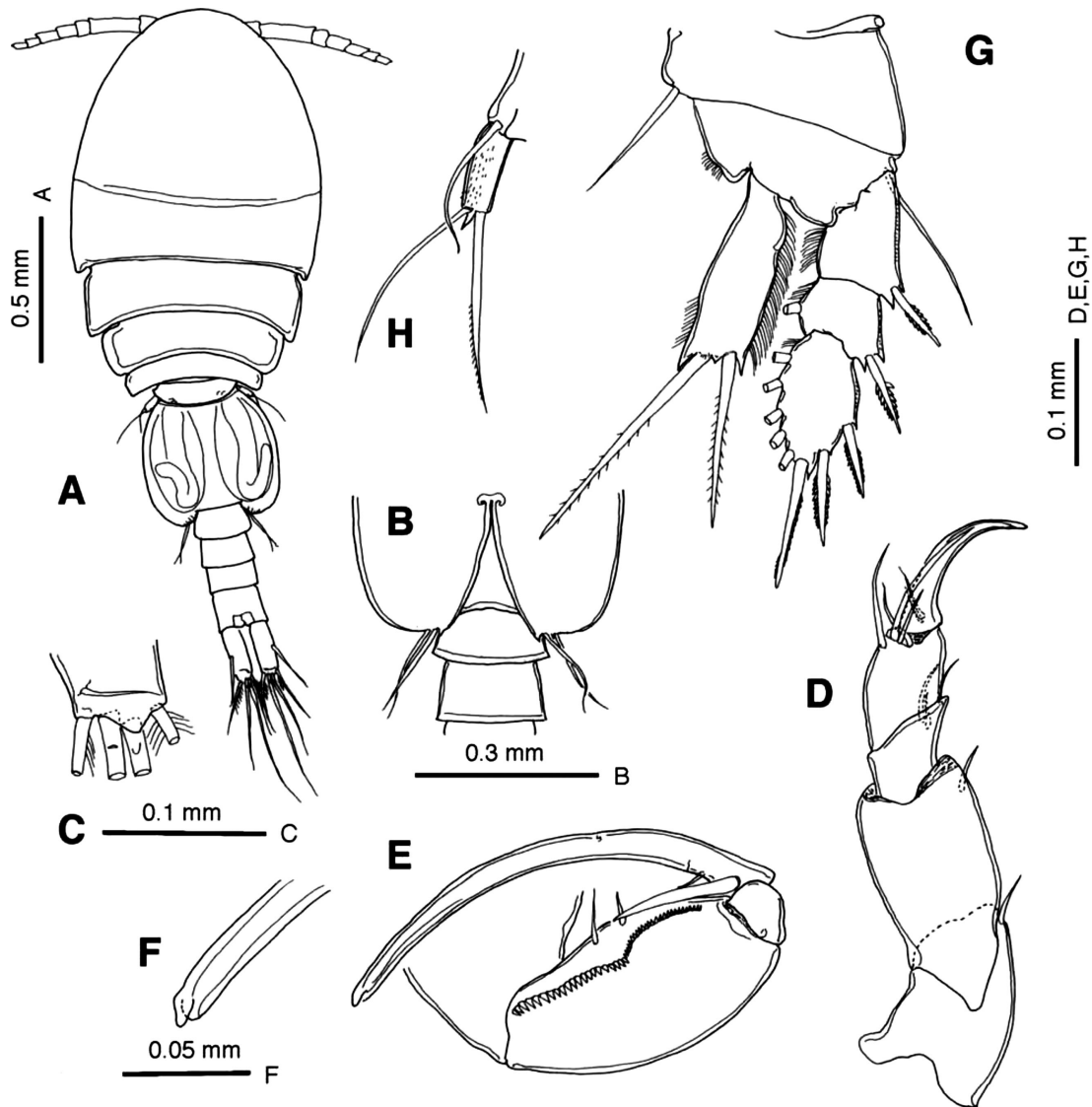
Fig. 5. *Paramacrochiron chironecicola* n. sp., male (paratype, KMNH IvR 500,785). **(A)** Habitus, dorsal view; **(B)** genital somite, ventral view; **(C)** terminal portion of right caudal ramus, dorsal view; **(D)** antenna; **(E)** maxilliped; **(F)** terminal tip of maxillipedal claw; **(G)** leg 4, anterior view; **(H)** left leg 5, dorsal view.

below), and this element was observed to reach as far as the proximal seta on the second segment (see Fig. 6M).

The congener *Paramacrochiron pacificum* (= *Pseudanthessius pacificus* Wilson, 1950) was described from surface plankton collected from off Luzon Island, The Philippines (Wilson, 1950). In the original description the general appearances of both sexes and the structure of female leg 5 differ markedly from those of the new species, although the morphology of the antenna and female leg 4 are similar. Two syntypes (1 ♀, dissected; 1 ♂, whole specimen: USNM No. 74145) and five non-type specimens (1 ♀, 4 ♂♂: USNM No. 74097) of *P. pacificum* are deposited at the National Museum of Natural History, Smithsonian Institution, USA (T Chad Walter, personal communication). We were allowed to dissect one female and one male among the non-type specimens. The body and some appendages of these specimens are briefly illustrated and compared to those of *P. chironecicola* n. sp. (Fig. 6A–O). Due to the following differences

between the new species and *P. pacificum*, we concluded that these are distinctly different species: (1) the end of the fifth pedigerous somite of the female reaches to the level of the genital apertures in lateral view (in *P. pacificum* not so: Fig. 6A, B); (2) the genital somite of the male is slightly shorter than wide (clearly shorter than wide: Fig. 6J, K); (3) the absence of an inner nipple-like projection on the third antennal segments of both sexes (present: arrowhead in Fig. 6D, L); (4) the proximal spine of the third maxillipedal segment of the female is located on the inner margin (outer margin: Fig. 6E, F); (5) the spinular row on the basis of male maxilliped almost entirely along the length of the margin (shorter: Fig. 6M); and (6) the inner terminal seta on the endopod of the male leg 4 just reaches to the terminal spine of the third exopodal segment (far beyond it: Fig. 6N). The exopod of leg 5 of each sex of *P. pacificum* is furnished with minute prominences visible in dorsal view (Fig. 6H, O) as observed in the new species. The knob at the inner corner
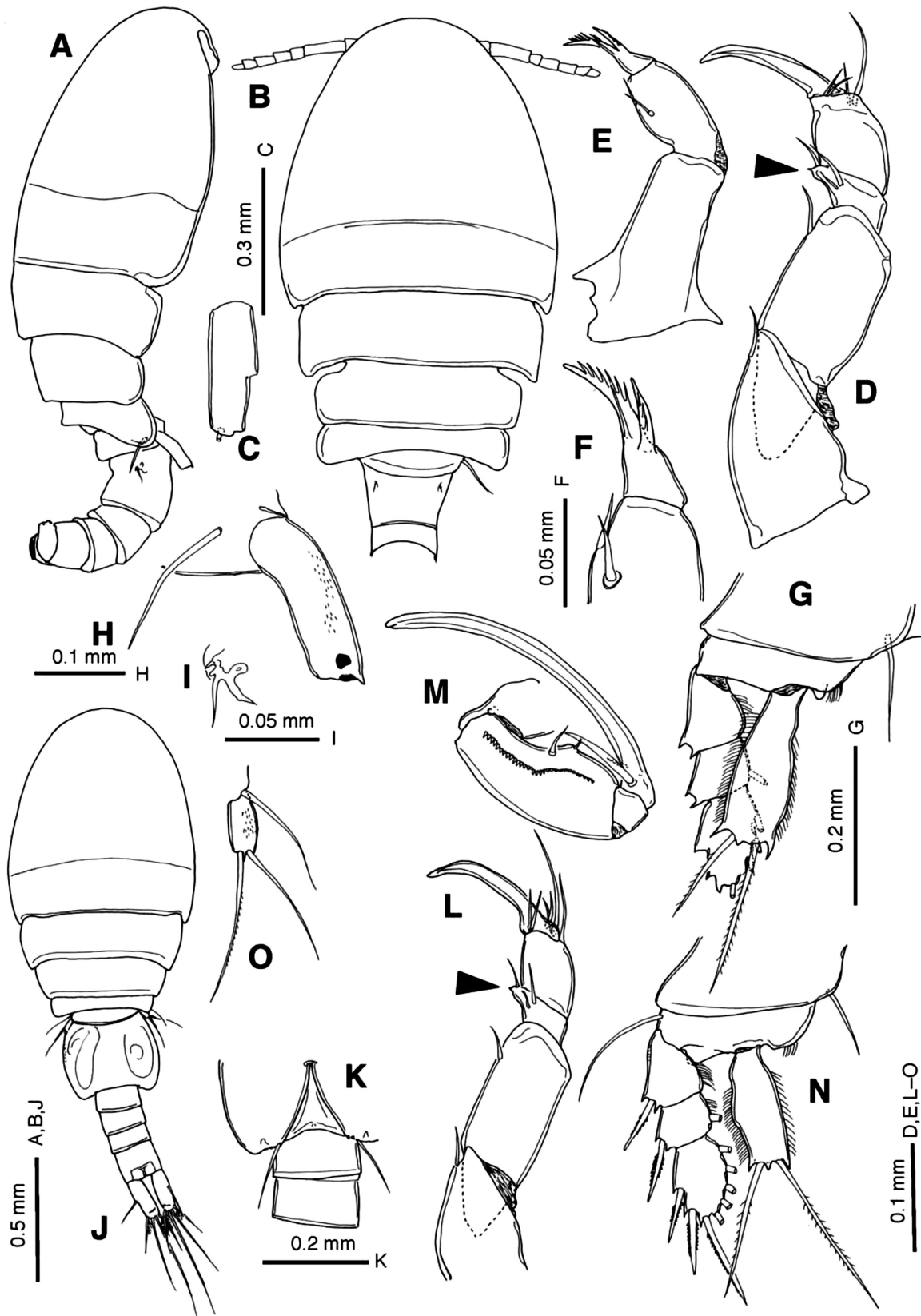
Fig. 6. *Paramacrochiron pacificum* (Wilson, 1950). Female (USNM No. 74097), (A–I); male (USNM No. 74097), (J–O). **(A)** Habitus. lateral view, caudal rami broken; **(B)** prosome and genital double-somite, dorsal view; **(C)** left caudal ramus, setae missing, ventral view; **(D)** antenna, nipple-like structure arrowed; **(E)** maxilliped; **(F)** terminal segments of maxilliped; **(G)** left leg 4, posterior view; **(H)** right leg 5, dorsal view; **(I)** right leg 6; **(J)** habitus, dorsal view; **(K)** genital somite and 2 abdominal somites, ventral view; **(L)** antenna, nipple-like structure arrowed; **(M)** maxilliped; **(N)** left leg 4, posterior view; **(O)** right leg 5, dorsal view.

Table 1. Infection of copepodids of *Paramacrochiron chironecicola* n. sp. on immature individuals of *Chironex* sp. collected from Palawan Island, The Philippines.

Host number	Bell height (mm)	No. of copepods			Infection sites
		Attached	Detached	Total	
1	28.5	2	11	13	Aradial furrow, manubrium
2	31.1	2	12	14	Subumbrella, rhopalium
3	50.6	0	0	0	–
4	48.2	0	6	6	–
5	41.8	0	10	10	–
6	39.1	1	8	9	Pedalium
7	55.5	17	1	18	Pedalium

of the basis of female leg 4 is more pointed than in *P. chironecicola* (Fig. 6G). Leg 6 of the female is similar in both species (Fig. 6I).

Etymology. The new specific name "*chironecicola*" is a noun in apposition with the genus name, derived from a combination of the generic name of the host box jellyfish *Chironex* and the Latin "*cola*" meaning "dweller".

Ecological notes. Surface water temperature and salinity of the collection site were 36.65°C and 33.75, respectively.

Six individuals of the host box jellyfish *Chironex* sp. were parasitized by copepodids of *Paramacrochiron chironecicola* n. sp. (prevalence = 85.7%) (Table 1). The bell height of the infected host ranged from 28.5 to 55.5 mm and the intensity of infection varied from 6 to 18 (mean intensity 11.7) individuals per a host. With the exception of the largest host (No. 7) most of individual parasitic copepods were detached from the hosts after fixation. The attachment sites of the copepods were the surface on the subumbrella, pedalium, and rhopalium, but also rarely on the adradial furrow. We consider this distribution over the host to be natural, as we confirmed *in situ* the presence of some living copepods on the surface of the subumbrella of living hosts.

No dissected specimens had nematocysts in the gut, suggesting that the copepods feed on mucus of the host or on prey captured by the host.

DISCUSSION

Cnidarians have been colonized by over 400 species of symbiotic copepods, but cubozoans had never previously been recorded as host species (Humes, 1985; Ho, 2001; Boxshall and Halsey, 2004). This is the first record of occurrence of copepod parasitization of a cubozoan. Their rare occurrence on cubozoans may reflect the high toxicity of the host's nematocysts. Since we found a number of ovigerous females plus copulatory pairs of the present new species on the *Chironex* sp. collected from The Philippines, we infer that it is a true symbiotic interaction rather than an accidental attachment. The genus *Paramacrochiron* had thus far comprised eight species, five of which were described from rhizostome or unknown medusae and two from plankton samples (Ohtsuka et al., 2012). The host-specificity of *Paramacrochiron* seems to be relatively high on scyphozoans, in particular rhizostomes (cf. Boxshall and Halsey, 2004; Ohtsuka et al., 2012).

Recently the development and molecular phylogeny of

cubozoans have been studied intensively in order to clarify their phylogenetic position within the Cnidaria (Collins, 2002; Bentlage et al., 2010; Toshino et al., 2013). These developmental and phylogenetic data strongly support the close relationship of cubozoans to scyphozoans. The association of *P. chironecicola* on *Chironex* sp. may indirectly reflect the close phylogenetic relationship between scyphozoans and cubozoans. Since the species diversity of cubozoans is rich in tropical and subtropical waters of the Indo-West Pacific (Bentlage et al., 2010) where species of *Paramacrochiron* are exclusively distributed (e.g., Thompson and Scott, 1903; Wilson, 1950; Reddiah, 1968; Mulyadi, 2005; Ohtsuka et al., 2012), other undescribed copepod species likely await discovery.

The symbiotic interaction of *P. maximum* with its host medusa *Catostylus mosaicus* (Quoy and Gaimard, 1824) has been suggested to represent commensalism, as the copepod feeds on the mucus of the host (Browne and Kingford, 2005). The host jellyfish harbor other symbionts other than copepods, including fish, spider and portunid crabs, shrimps, phyllosoma larvae, and amphipods (Browne and Kingford, 2005). Some of these symbionts are carnivores (Browne and Kingford, 2005), and may prey upon the parasitic copepods. In the case of *P. chironecicola* n. sp., however, it seems to be well protected from such potential predators by the toxicity of the host and the absence of other symbionts. Since examined copepods never had nematocysts or identifiable items in the gut, the new species may also feed on the mucus of the host.

ACKNOWLEDGMENTS

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