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First record and molecular characterisation of two *Gnathia* species (Crustacea, Isopoda, Gnathiidae) from Philippine coral reefs, including a summary of all Central-Indo Pacific *Gnathia* species

Mary O. Shodipo [a], Paul C. Sikkel [b,c,*], Nico J. Smit [c], Kerry A. Hadfield [c]

[a] *Institute of Environmental and Marine Sciences, Silliman University, Dumaguete City, 6200, Negros Oriental, Philippines*
[b] *Department of Biological Sciences and Environmental Sciences Program, Arkansas State University, PO Box 599, State University, Jonesboro, AR, 72467, USA*
[c] *Water Research Group, Unit for Environmental Sciences and Management, North-West University, Private Bag X6001, Potchefstroom, 2520, South Africa*

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ABSTRACT

Due to their unusual life cycle that includes parasitic larval and free living adult stages, gnathiid isopods are typically overlooked in biodiversity surveys, even those that focus on parasites. While the Philippines sits within the region of highest marine biodiversity in the world, the coral triangle, no gnathiid species have been identified or described from that region. Here we present the first records of two gnathiid species collected from the Visayas, central Philippines: *Gnathia malaysiensis* Müller, 1993, previously described from Malaysia, and *G. camuripenis* Tanaka, 2004, previously described from southern Japan. This paper provides detailed morphological redescriptions, drawings and scanning electron microscope images as well as the first molecular characterisation of both species, Furthermore, a summary of the Central-Indo Pacific *Gnathia* species is provided.

1. Introduction

Gnathiid isopods are marine crustacean ectoparasites that do not permanently live on their fish hosts. They are only parasitic in their three larval stages and do not feed as adults (Smit and Davis, 2004; Tanaka, 2007; Smit et al., 2019). They can be found in all the world's oceans, in many different habitats and varying depths; however, they are best known in tropical and temperate regions (Smit and Davis, 2004). Within the Gnathiidae, the genus *Gnathia* Leach, 1814 is by far the most specious of the 12 currently accepted genera with 133 valid species (Boyko et al., 2008 onwards). As gnathiids have been reported as one of the more common marine ectoparasites in coral reef habitats (Grutter, 1994, 1996; Grutter and Poulin, 1998), it is no surprise that the majority of *Gnathia* species are known from coral reef environments (Svavarsson and Bruce, 2012, 2019; Hadfield et al., 2019). This is specifically true for the Central Indo-Pacific (CIP) marine ecosystem realm that, according to Spalding et al.'s (2007) marine ecoregions of the world, includes coral reefs systems such as the Great Barrier Reef and the Coral Triangle. To date, more than a third (46/133) of the *Gnathia* species have either been originally described or reported from the CIP (Table 1).

The Philippines is within the CIP's Coral Triangle and is at the centre of the centre of marine biodiversity (Carpenter and Springer, 2005). Yet, to date, only four unidentified species of gnathiid isopods have been mentioned in literature (Santos and Sikkel, 2017) and no Philippine gnathiids have been described or named. Thus, especially given the high biodiversity of the region, research on coral reef gnathiids in the Philippines lags far behind other regions, with only five gnathiid studies to our knowledge being conducted to date: one study in the Luzon region the North of the Philippines (Cruz-Lacierda and Nagasawa, 2017) and the other four in the Visayas region in the central Philippines (Sikkel et al., 2014; Santos and Sikkel, 2017; Shodipo et al., 2019, 2020).

In 2018, as part of an ongoing ecological study on gnathiid isopods in the central Philippines (Sikkel et al., 2014; Santos and Sikkel, 2017; Shodipo at el., 2019, 2020), gnathiids were collected from fringing coral reefs off the islands of Siquijor and Negros Oriental. Therefore, the aims of this paper were to provide detailed morphological descriptions and molecular characterisation of the adult males collected using both light and electron microscopy and to provide a summary of all known *Gnathia* species from the CIP.

* Corresponding author. Department of Biological Sciences and Environmental Sciences Program, Arkansas State University, PO Box 599, State University, Jonesboro, AR, 72467, USA.
E-mail address: psikkel@astate.edu (P.C. Sikkel).

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Table 1
Summary of all currently known species of *Gnathia* Leach, 1814 from the Central Indo-Pacific marine ecosystem realm as defined by Spalding et al. (2007). Where applicable, the substratum indicates where free living adults have been collected and hosts are listed for parasitic larval stages. Bold indicates information from the present study.

Species	Location	Size (mm)	Depth (m)	Substratum/Host	References
Gnathia acrorudus Svavarsson and Bruce, 2019	Australia (Heron Island)	1.7–2.8	0–11	coral rock on boulder zone; dead coral	Svavarsson and Bruce (2019)
Gnathia albipalpebrata Ota, 2014	Japan (Okinawa Island)	9.1–10.3		*Triaenodon obesus* (Rüppell, 1837)	Ota (2014)
Gnathia alces Monod, 1926	Andaman Sea; Gulf of Thailand; Malacca Strait	2.2–2.8	9–77	coarse sand	Monod (1926); Svavarrson (2002)
Gnathia asperifrons Holdich and Harrison, 1980	Australia (Lizard Island)	1.8	intertidal	littoral rock	
Gnathia aureamaculosa Ferreira and Smit, 2009 in Ferreira et al. (2009)	Australia (Lizard Island)	1.7–2.9	6–8	*Hemigymnus melapterus* (Bloch, 1791); dead coral	Ferreira et al. (2009); Svavarsson and Bruce (2012)
Gnathia biorbis Holdich and Harrison, 1980	Australia (Northern Queensland)	3.6–5.2	intertidal	barnacle tests; dead coral	Holdich and Harrison (1980); Svavarsson and Bruce (2019)
**Gnathia calmani* Monod, 1926	Australia (Heron Island)	2.6	intertidal	dead coral	Holdich and Harrison (1980)
Gnathia camuripenis Tanaka, 2004	Japan (Ishigaki and Kumejima islands); **Philippines (Siquijor and Negros Oriental)**	**2.0**–3.2	0.5–17.1	coral rubble; **coral reef**; sand and mud sediment	Tanaka (2004); Ota (2012); **present study**
Gnathia capricornica Svavarsson and Bruce, 2019	Australia (Lizard Island)	1.8–1.9	4.5–11	coral rubble; dead coral	Svavarsson and Bruce (2019)
Gnathia carinodenta Svavarsson and Bruce, 2019	Australia (Heron Island)	2.7–3.3	0–30	coral rubble; dead coral	Svavarsson and Bruce (2019)
Gnathia coralmaris Svavarsson and Bruce, 2012	Coral Sea (Mellish Reef)	1.9–2.3	6		Svavarsson and Bruce (2012)
Gnathia cornuta Holdich and Harrison, 1980	Australia (Northern Queensland)	3.0–3.4	0–22	dead coral; sediment; waterlogged tree branch	Holdich and Harrison (1980); Svavarsson and Bruce (2019)
Gnathia dejimagi Ota, 2014	Japan (Ishigaki and Okinawa islands)	11.9–14.4		*Nebrius ferrugineus* (Lesson, 1831); *Triaenodon obesus* (Rüppell, 1837)	Ota (2014)
Gnathia excavata Ota, 2012	Japan (Kumejima Island)	2.5	125–147		Ota (2012)
Gnathia falcipenis Holdich and Harrison, 1980	Australia (Northern Queensland)	3.5–4.0	1–10	coral reef rocks; coral rubble; dead coral; wood	Holdich and Harrison (1980); Svavarsson and Bruce (2019)
Gnathia formosa Svavarsson and Bruce, 2019	Australia (Heron Island)	4.4–4.8	7–20	dead coral; sponge	Svavarsson and Bruce (2019)
Gnathia glaucostega Svavarsson and Bruce, 2019	Australia (Heron Island)	3.7–5.3	20	*Glaucostegus typus* (Anonymous [Bennett], 1830); dead coral	Svavarsson and Bruce (2019)
Gnathia grandilaris Coetzee, Smit, Grutter and Davies, 2008	Australia (Lizard Island); Japan (Okinawa Island)	5.7–8.8		*Carcharhinus amblyrhynchos* (Bleeker, 1856); *Himantura* sp.; *Neotrygon kuhlii* (Müller and Henle, 1841); *Pateobatis fai* (Jordan and Seale, 1906); *Triaenodon obesus* (Rüppell, 1837)	Coetzee et al. (2008); Ota and Hirose (2009b)
Gnathia grutterae Ferreira, Smit and Davies 2010	Australia (Heron and Lizard Islands)	2.2–3.9	16–26	*Arothron hispidus* (Linnaeus, 1758); *Epibulus insidiator* (Pallas, 1770); *Hemigymnus melapterus* (Bloch, 1791); *Oxycheilinus digramma* (Lacepède, 1801); *Rhinecanthus aculeatus* (Linnaeus, 1758); *Sufflamen chrysopterum* (Bloch and Schneider, 1801); *Thalassoma lunare* (Linnaeus, 1758); coral rubble; dead coral	Ferreira et al. (2010); Svavarsson and Bruce (2019)
Gnathia halei Cals, 1973	Australia (Northern Queensland)		136	fine gravel	Cals (1973)
Gnathia hamletgast Svavarsson and Bruce, 2012	Coral Sea (Chesterfield Reefs)	2.6		coral rock	Svavarsson and Bruce (2012)
Gnathia kumejimensis Ota, 2012	Japan (Kumejima Island)	4.5–5.5	68–101	dead coral; rock rubble	Ota (2012)
Gnathia latidens (Beddard, 1886)	Coral Sea (Flinders Passage)	2.5	12.8		Beddard (1886)
Gnathia lignophila Müller, 1993	Malaysia (Pulau Babi Besar Island);	1.9–2.9	intertidal	sand mud flat; wood	Müller (1993)
Gnathia limicola Ota and Tanaka, 2007 in Ota et al. (2007)	Japan (Okinawa Island)	2.2–2.6	shallow	muddy tidal flat	Ota et al. (2007)
Gnathia maculosa Ota and Hirose, 2009	Japan (Okinawa Island)	3.9–5.8		*Taeniurops meyeni* (Müller and Henle, 1841)	Ota and Hirose (2009a)
Gnathia malaysiensis Müller, 1993	Malaysia (Pulau Babi Besar Island); **Philippines (Siquijor and Negros Oriental)**	**1.4–3.0**	1–**10**	dead coral; **coral reef**	Müller (1993); **present study**
Gnathia marionis Svavarsson and Bruce, 2012	Coral Sea (Marion Reef)	2.5–3.0	10	lagoon pinnacle	Svavarsson and Bruce (2012)
Gnathia masca Farquharson and Smit (2012) in Farquharson et al. (2012)	Australia (Lizard Island)	2.6–3.1	10–29	*Arothron stellatus* (Anonymous, 1798); *Arothron hispidus* (Linnaeus, 1758); *Epinephelus malabaricus* (Bloch and Schneider, 1801); *Lethrinus lentjan* (Lacepède, 1802); *Lethrinus ornatus* Valenciennes, 1830; coral rubble	Farquharson et al. (2012); Svavarsson and Bruce (2012)
		2.7–3.1		dead coral; in barnacles, semipermanent logs and wood	

(*continued on next page*)

2. Materials and methods

Sample collection was conducted between August 2018 and August 2019 in the Visayas region, Philippines. A total of 12 sites were sampled, all shallow coral reefs (<10 m) (Fig. 1A, Table 2).

Gnathiids were collected using light traps, adapted from0 Artim et al. (2015) and Artim and Sikkel (2016). The traps were set at dusk and retrieved the following morning by skin diving/snorkelling and then transported by boat to the laboratory where they were emptied into individual 10 L plastic buckets with aerators. The contents of each trap were filtered with a funnel and 55 μm plankton mesh. Gnathiids were then sorted by size using dissecting microscopes and placed in fresh, filtered, aerated seawater. Third stage praniza larvae were separated and left to moult into adults. When possible, the largest zuphea were fed using host fish (Labridae and Pomacentridae), which were placed in the aquarium overnight. Once fed, host fish were removed and the gnathiids were left to moult into adults (Fig. 1 B–C). Adult males were preserved in 95% ethanol.

Selected adult males were cleaned and prepared for scanning electron microscopy (SEM; PhenomWorld) and illustrations using an Olympus BX41 compound microscope and an Olympus SZX7 dissecting microscope with a camera lucida following the protocol of Hadfield et al. (2019). Species descriptions were based on the adult male gnathiids, prepared in DELTA (DEscriptive Language for TAxonomy) using a general Gnathiidae character set, following the terminology used in Svavarsson and Bruce (2012, 2019) and Hadfield et al. (2019). Material is deposited in the Los Angeles County Museum of Natural History.

Total genomic DNA was isolated from male gnathiid specimens following the manufacturer's protocol for animal tissue extraction of the NucleoSpin® Tissue Genomic DNA Tissue Kit (Macherey-Nagel, Düren, Germany). DNA amplifications for the partial mitochondrial cytochrome c oxidase subunit I (COI) gene (approximately 680 bp) was performed with the aid of a ProFlex™ PCR thermal cycler (Applied Biosystems by Life Technologies). and universal invertebrate primers LCO1490 (5′-GGTCAACAAATCATAAAGATATTGG-3′) and HC02198 (5′ TAAACTTCAGGGTGACCAAAAAATCA-3′) (Folmer et al., 1994). PCR reactions were performed with volumes of 25 μl, using 12.5 μl Thermo Scientific DreamTaq PCR master mix, 1.25 μl of each primer, 8.5 μl of PCR-grade nuclease-free water and 1.5 μl of DNA. The PCR conditions were as follows: initial denaturation at 94 °C for 5 min; followed by 35 cycles of a 94 °C denaturation for 30 s, annealing at 47 °C for 50 s with an end extension at 72 °C for 2 min; and ending with a final extension of 72 °C for 10 min. PCR products were purified and sequenced in both directions by a commercial sequencing company, Inqaba Biotechnical Industries (Pty) Ltd, Pretoria, South Africa. Novel COI sequences were trimmed, assembled and edited using the bioinformatics software platform, Geneious R7.1.3 (Biomatters, Auckland, New Zealand; Kearse et al., 2012).

3. Results

Suborder: Cymothoida Wägele, 1989
Superfamily: Cymothooidea Leach, 1814.
Family: Gnathiidae Leach, 1814.
Genus *Gnathia* Leach, 1814.
Diagnosis. A detailed diagnosis of *Gnathia* was recently provided by Hadfield et al. (2019).

Table 1 (*continued*)

Species	Location	Size (mm)	Depth (m)	Substratum/Host	References
Gnathia meticola Holdich and Harrison, 1980	Australia (Northern Queensland)		Lower/ midshore		Holdich and Harrison (1980)
Gnathia mortenseni Monod, 1926	Gulf of Thailand	2.7–3.0	18–55	coarse sand; muddy sand	Monod (1926); Svavarsson (2002)
**Gnathia nasuta* Nunomura, 1992	Japan (Amami, Kerama and Okinawa islands)	1.9–4.4	8.5–412	sandy and muddy sediment	Nunomura (1992); Ota (2013)
Gnathia nicembola Müller, 1989	Fiji Islands	2.6	76–84		Müller, 1989
Gnathia nubila Ota and Hirose, 2009	Japan (Okinawa Island)	9.0–10.0		*Aetobatus narinari* (Euphrasen, 1790)	Ota and Hirose (2009b)
Gnathia parvirostrata Ota, 2014	Japan (Ishigaki Island)	10.6–11.1		*Galeocerdo cuvier* (Péron and Lesueur, 1822)	Ota (2014)
Gnathia perimulica Monod, 1926	Gulf of Thailand; Malaysia (Pulau Babi Besar Island)	1.6–2.2	1–27	dead coral	Monod (1926); Müller (1993)
Gnathia philogona Monod, 1926	Malaysia (Pulau Babi Besar Island); Malacca Strait	1.9	1–3	dead coral	Monod (1926); Müller (1993)
Gnathia rhytidoponera Cohen and Poore, 1994	Western Coral Sea	3.8	287–303	epibenthic sledge	Cohen and Poore (1994)
Gnathia rufescens Ota, 2015	Japan (Okinawa Island)	6.2–10.6		*Himantura* sp.	Ota (2015)
Gnathia scabra Ota, 2012	Japan (Kumejima Island)	2.4	67.5–76.0	dead coral; rock rubble	Ota (2012)
Gnathia serrula Kensley, Schotte and Poore, 2009	Thailand (Phuket Island)	3.0	5.0–5.4	coral rubble; dead coral	Kensley et al. (2009)
Gnathia teruyukiae Ota, 2011	Japan (Ishigaki Island)	6.8–8.7		*Taeniurops meyeni* (Müller and Henle, 1841)	Ota (2011)
Gnathia trimaculata Coetzee, Smit, Grutter and Davies, 2009	Australia (Lizard Island); Japan (Okinawa Island)	4.0–7.6		*Carcharhinus amblyrhynchos* (Bleeker, 1856); *Carcharhinus falciformis* (Müller and Henle, 1839); *Carcharhinus melanopterus* (Quoy and Gaimard, 1824); *Himantura*sp.; *Rhinoptera javanica* Müller and Henle, 1841; *Taeniurops meyeni* (Müller and Henle, 1841)	Coetzee et al. (2009); Ota and Hirose (2009a)
Gnathia varanus Svavarsson and Bruce, 2012	Australia (Lizard Island)	3.8–4.0	15	dead coral	Svavarsson and Bruce (2012)
Gnathia variobranchia Holdich and Harrison, 1980	Australia (Heron and Lizard Islands); Coral Sea (Chesterfield Reefs)	1.6–2.0	1–30	coral rock; dead coral; silt; small rubble	Holdich and Harrison (1980); Svavarsson and Bruce (2012; 2019)
Gnathia wisteri Svavarsson and Bruce, 2012	Australia (Heron and Lizard Islands)	2.4–3.7	8–30	coarse sand; coral heads and rubble; dead coral; sediment	Svavarsson and Bruce (2012; 2019)

* Type locality not in the Central Indo-Pacific.

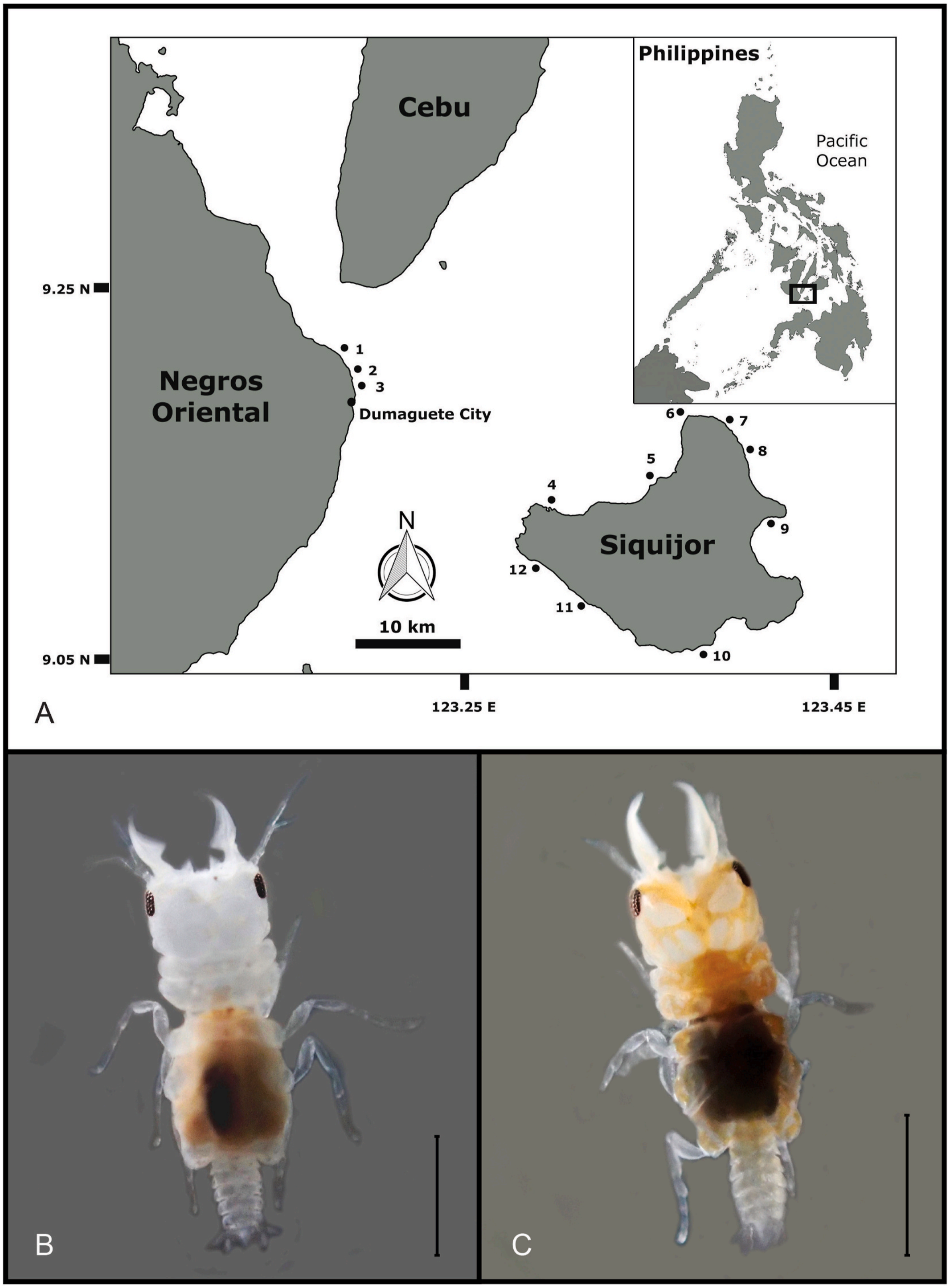

Fig. 1. Map of study sites in the central Visayas, Philippines and live specimen photos of the collected gnathiids. A, The first three sampling sites (denoted by black dots and numbered) are in Negros Oriental and the last eight are in Siquijor Island: Cangmating (1), Agan-an (2) and Bantayan (3), Caticugan, (4), Cangbasa (5), Sandugan (6), Tulapos (7), Bino-ongan (8), Olang (9), Talayong (10), Tubod (11) and Paliton (12); B, *Gnathia malaysiensis* Müller, 1993 live specimen; C, *Gnathia camuripenis* Tanaka, 2004 live specimen.

3.1. Gnathia malaysiensis Müller, 1993

Figs. 2–4.

Gnathia malaysiensis Müller, 1993: 3–17. —Chew, Rahim and Ross, 2014: e2014017.

Holotype. 1 ♂ (2.3 mm TL), fringing reef of Besar Island, Johor, Malaysia (Museum für Naturkunde Berlin: ZMB 26944). Not examined.

Material examined. 13 ♂♂ (1.4–3.0 mm TL; mean 2.0 mm TL) (two dissected); (9°08′39.0"N 123°30′29.3"E); 5 m depth; August 2018; coral reef; coll: M. Shodipo and P. Sikkel.

Representative DNA sequences: Newly generated mitochondrial cytochrome c oxidase subunit I (COI) partial sequences of *Gnathia malaysiensis* have been submitted to NCBI GenBank database (http://www.ncbi.nlm.nih.gov/genbank/) with the following accession numbers: MW837265, MW837266.

Table 2
Table of all 12 sites in the Philippines where specimens of *Gnathia camuripenis* Tanaka, 2004 and *Gnathia malaysiensis* Müller, 1993 were sampled between August 2018–2019.

Location (Province, Municipality)	Sampling site	Species	GPS
Negros Oriental, Dumaguete City	Bantayan	*Gnathia camuripenis* and *Gnathia malaysiensis*	9°19′43.4″N 123°18′42.56″E
Negros Oriental, Sibulan	Cangmatting	*Gnathia camuripenis* and *Gnathia malaysiensis*	9°21′18.4″N 123°17′58.9″E
Negros Oriental, Sibulan	Agan-an	*Gnathia camuripenis* and *Gnathia malaysiensis*	9°20′17.0″N 123°18′40.5″E
Siquijor, San Juan	Tubod	*Gnathia camuripenis* and *Gnathia malaysiensis*	9°08′31.0″N 123°30′29.1″E
Siquijor, San Juan	Paliton	*Gnathia camuripenis* and *Gnathia malaysiensis*	9°10′25.7″N 123°27′34.7″E
Siquijor, Siquijor	Caticugan	*Gnathia camuripenis*	9°13′17.4″N 123°29′04.9″E
Siquijor, Larena	Cangbasa	*Gnathia camuripenis* and *Gnathia malaysiensis*	9°14′53.6″N 123°34′53.9″E
Siquijor, Larena	Sandugan	*Gnathia camuripenis* and *Gnathia malaysiensis*	9°17′04.6″N 123°35′41.9″E
Siquijor, Enrique Villanueva	Bino-ongan	*Gnathia camuripenis*	9°16′23.1″N 123°39′04.8″E
Siquijor, Enrique Villanueva	Tulapus	*Gnathia camuripenis* and *Gnathia malaysiensis*	9°28′71.2″N 123°64′30.9″E
Siquijor, Maria	Olang	*Gnathia camuripenis*	9°12′45.3″N 123°40′22.9″E
Siquijor, Lazi	Talayong	*Gnathia camuripenis* and *Gnathia malaysiensis*	9°05′50.2″N 123°36′16.3″E

3.1.1. Male

Body 2.3 times as long as greatest width, widest at pereonite 3; dorsal surfaces with tubercles or granules, sparsely setose. *Cephalosome* quadrate, 0.7 as long as wide, lateral margins convex; dorsal surface with numerous tubercles or granules; dorsal sulcus wide, deep, extended; paraocular ornamentation weakly developed, posteromedian tubercle present. *Frontolateral processes* present. *Frontal margin* straight, median point excavate. *External scissura* present, wide, deep. *Mediofrontal process* present, weak, acute, without notch, with fine setae. *Superior frontolateral process* present, single, strong, acute, with 2 pairs of long simple setae. *Inferior frontolateral process* absent. *Supraocular lobe* pronounced, wide; accessory supraocular lobe not pronounced. *Eyes* present, elongate, 0.4 as long as cephalosome length, contiguous with head surface, ommatidia arranged in rows, eye colour black.

Pereon lateral margins subparallel, with few setae; anteriorly with numerous fine granules. *Pereonite 1* not fused dorsally with cephalosome; dorsolateral margins not obscured by cephalosome. *Pereonite 2* as wide as pereonite 1. *Areae laterales* present on pereonite 5. *Pereonite 6* without lobi laterales; lobuii absent. *Pleon* covered in pectinate scales, epimera not dorsally visible on all pleonites. *Pleonite* lateral margins with 1 pair of simple setae, with 2 pairs of simple setae medially. *Pleotelson* 1.1 times as long as anterior width, covered in pectinate scales; lateral margins finely serrate; anterolateral margins convex, with 4 submarginal setae; posterolateral margin weakly concave, with 2 submarginal setae; mid-dorsal surface with 2 sub-median setae; apex with 2 setae.

Antennula peduncle article 2 0.8 times as long as article 1, with 3 penicillate setae; article 3 2.3 times as long as article 2, 4.6 times as long as wide, with 2 penicillate setae. Antennula flagellum as long as article 3, with 5 articles; article 3 with 1 aesthetasc seta and 2 simple setae; article 4 with 1 aesthetasc seta and 1 simple seta; article 5 terminating with 1 aesthetasc seta and 4 simple setae. *Antenna* peduncle article 3 3.8 times as long as wide, 2.3 times as long as article 2, with 1 penicillate seta and 9 simple setae; article 4 1.2 times as long as article 3, four times as long as wide, with 3 penicillate setae and 15 simple setae; flagellum as long as article 5, with 6 articles.

Mandible 0.5 as long as width of cephalosome, triangular, weakly curved distally; apex 20% of total length; mandibular seta present. *Carina* present, smooth. *Incisor* dentate. *Blade* present, dentate, proximally convex, dentate along 80% of margin. *Pseudoblade* absent; internal lobe, dorsal lobe and erisma absent; basal neck short.

Maxilliped 5-articled; article 1 lateral margin with continuous marginal scale-setae; article 2 lateral margin with 5 plumose setae; article 3 lateral margin with 6 plumose setae; article 4 lateral margin with 5 plumose setae; article 5 with 8 plumose setae; endite extending to mid-margin of article 3.

Pylopod article 1 1.8 as long as wide, without distolateral lobe; posterior and lateral margins forming rounded curve; lateral margin with 28 large plumose setae; mesial margin with continuous scale-setae; distal margin with 3 simple setae; article 2 1.4 as long as wide, with 9 simple setae; article 3 minute.

Pereopods 2–6 with long simple setae; inferior margins with pectinate scales and weak tubercles. *Pereopod 2* with tubercles on merus and carpus; basis 2.8 times as long as greatest width, superior margin with 8 setae, inferior margin with 3 setae; ischium 0.7 times as long as basis, 2.6 as long as wide, superior margin with 4 setae, inferior margin with 6 setae (one penicillate); merus 0.6 as long as ischium, 1.7 as long as wide, superior margin with 3 setae, inferior margin with 7 setae; carpus 0.4 as long as ischium, 1.7 as long as wide, superior margin with 2 setae, inferior margin with 2 setae (one biserrate); propodus 0.8 times as long as ischium, 3.8 times as long as wide, superior margin with 2 setae, inferior margin with 2 robust setae; dactylus 0.6 as long as propodus. *Pereopods 3 and 4* similar to pereopod 2 except pereopod 3 with tubercles along inferior margin. *Pereopod 5* similar to pereopod 6. *Pereopod 6* basis 3.3 times as long as greatest width, superior margin with 4 setae and 1 penicillate setae, inferior margin with 6 setae (one penicillate); ischium 0.9 as long as basis, 3.3 as long as greatest width, superior margin with 6 setae, inferior margin with 8 setae; merus 0.5 as long as ischium, twice as long as wide, superior margin with 5 setae, inferior margin with 5 setae, with dense patch of scale-setae; carpus 0.8 as long as ischium, 2.4 times as long as wide, superior margin with 2 setae, inferior margin with 5 setae; propodus 0.6 as long as ischium, 4 times as long as wide, superior margin with 4 setae, inferior margin with 2 setae (one penicillate), and 2 robust setae; dactylus 0.6 as long as propodus.

Penes low tubercles, medially united; penial process 0.4 times as long as basal width.

Pleopod 2 exopod 1.5 as long as wide, distally broadly rounded, with 9 plumose setae; endopod 1.8 as long as wide, distally narrowly rounded, with 8 plumose setae; appendix masculina absent; peduncle 0.8 times as wide as long, mesial margin with 2 coupling setae, lateral margin with 1 simple seta.

Uropod rami extending beyond pleotelson, apices narrowly rounded. *Peduncle* with 1 dorsal seta. *Uropod endopod* 2.7 as long as greatest width, dorsally with 2 setae; lateral margin sinuate, lateral margin with 2 simple setae; proximomesial margin sinuate, with 6 long plumose setae. *Uropod exopod* not extending to end of endopod, 3.9 times as long as greatest width; lateral margin weakly sinuate, with 4 simple setae; proximomesial margin convex, with 7 long plumose setae.

Distribution. Besar Island, Johor, Malaysia (Müller, 1993); Republic of the Philippines (current study).

Hosts. Not known.

Remarks. *Gnathia malaysiensis* may be identified by a large superior frontolateral processes with concave outer margins and a pair of long simple setae on each process; small acute mediofrontal process with or without a notch; dorsal surface of cephalosome with numerous tubercles

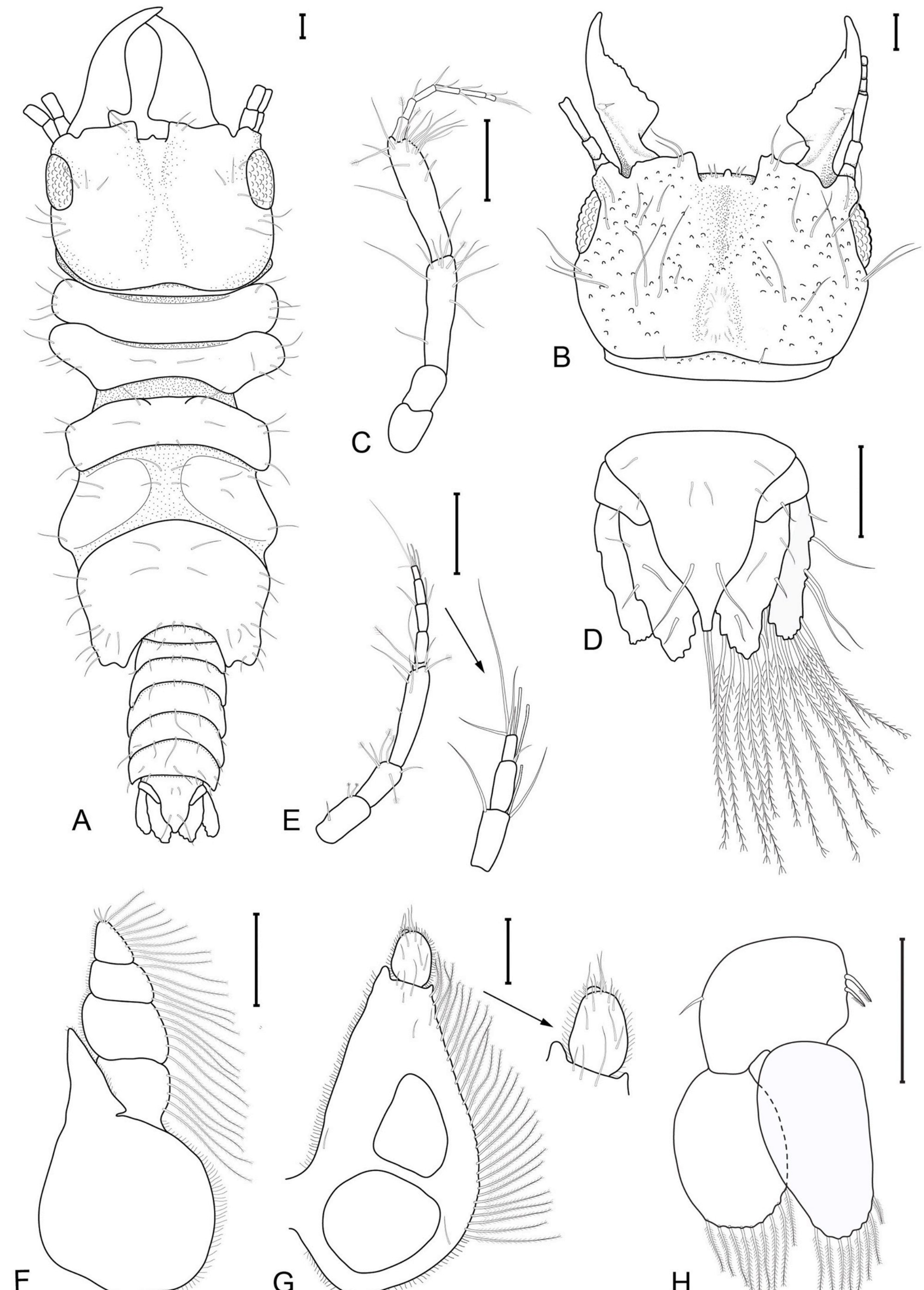

Fig. 2. *Gnathia malaysiensis* Müller, 1993 male (3.0 mm TL). A, habitus dorsal view; B, dorsal view of cephalosome; C, antenna; D, dorsal view of pleotelson and uropods; E, antennula; F, maxilliped; H, pylopod; I, pleopod 2. Scale bars: 100 μm.

or granules and long simple setae.

The original description of *G. malaysiensis* was based on a single adult male, thus the descriptive information provided here based on 13 specimens collected from the Philippines provides a better understanding of intraspecific variation within this species. The main similarities between the Malaysian and Philippine specimens includes the distinctive superior frontolateral process, the mandibles, the tubercles and setae on the cephalosome, shape and setae of the pleotelson, and absence of an appendix masculina on pleopod 2. Variations observed included the shape of the small mediofrontal process, the number of plumose setae on the distal four articles of the maxilliped (Malaysia = 4:6:4:8; Philippines = 5:6:5:8) and the number of plumose setae on the enlarged proximal article of the pylopod (Malaysia = 27; Philippines = 28). There are also small variations in the number of plumose setae on the endo- and exopods of the pleopods, for example, Müller (1993) reported 8 plumose setae on both the endo- and exopods of pleopod 2 with the Philippine specimens having 9 plumose setae on the exopod and 8 on the endopod. These minor variations between the Malaysian and Philippine *G. malaysiensis* can be considered as intraspecific differences.

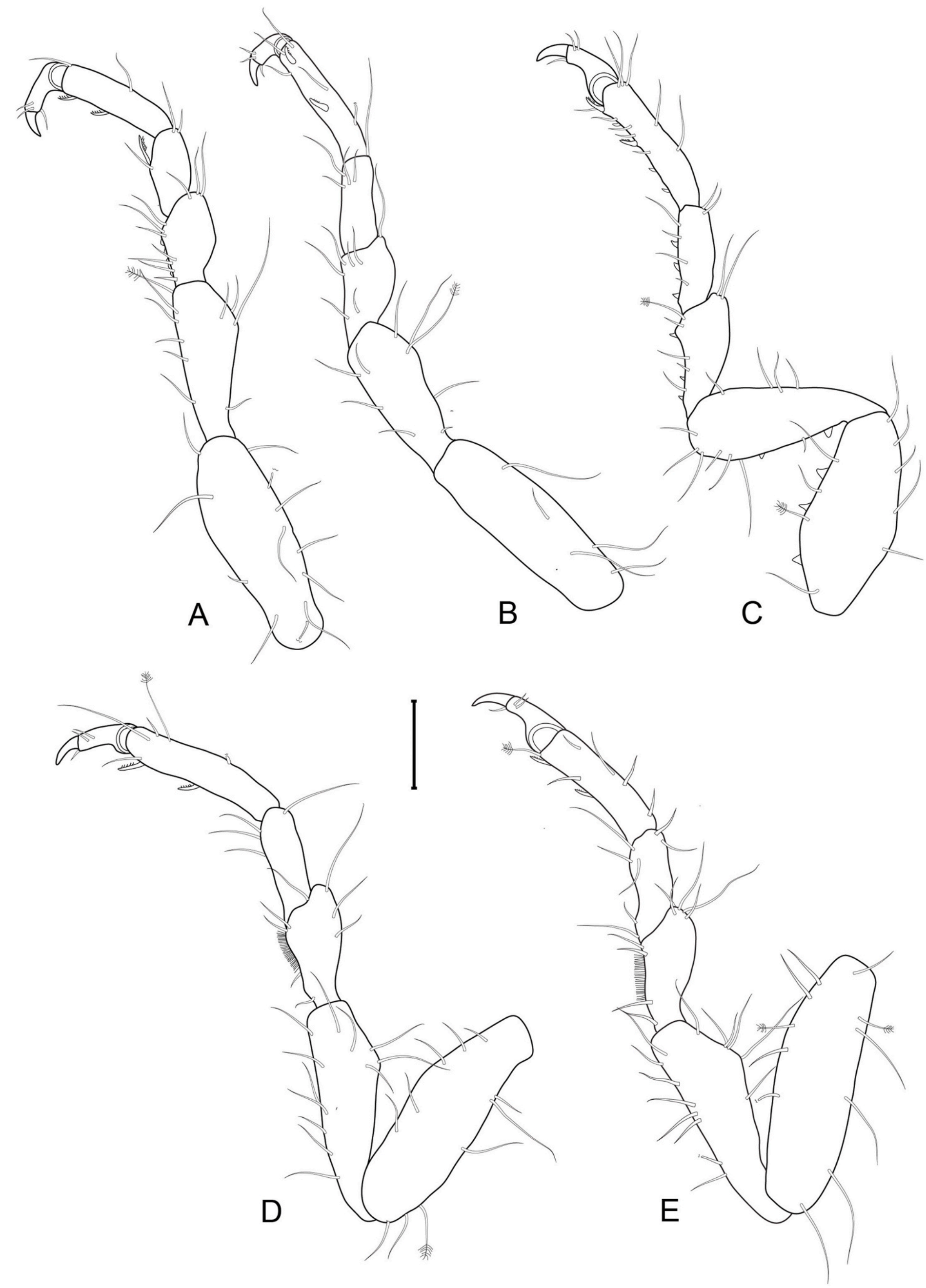

Fig. 3. *Gnathia malaysiensis* Müller, 1993 male (3.0 mm TL). A–E pereopods 2–6, respectively. Scale bar: 100 μm.

3.2. *Gnathia camuripenis* Tanaka, 2004

Figs. 5–7.

Gnathia camuripenis Tanaka, 2004: 51–60.—Ota et al., 2007: 1266–1277.

Type material. Holotype: ♂ (2.5 mm TL); 7 May 1998; 0.5–1 m depth in coral rubble; Urasoko Bay, Ishigaki Island, Japan (124 °13′ E, 24° 27′ N); coll. Y. Takada (National Museum of Nature and Science, Tokyo: NSMT Cr 15701). Paratypes: 4 ♂♂ (2.1–2.8 mm), 4 ♀♀ (2.3–3.1 mm), 5 praniza (1.9–3.0 mm TL) (NSMT Cr 15702–15707; Natural History Museum and Institute, Chiba: CBM-ZC 7888–7894), 21 Oct. 1997, 13 Jan. 1998, 7 May 1998 and 5 Nov 2003. Not examined.

Material examined. 7 ♂♂ (2.0–2.3 mm TL; mean 2.1 mm TL) (one dissected); (9°08′39.0"N 123°30′29.3"E); 5 m depth; August 2018; coral reef; coll: M. Shodipo and P. Sikkel .

Representative DNA sequences: Newly generated mitochondrial cytochrome c oxidase subunit I (COI) partial sequences of *Gnathia camuripenis* have been submitted to NCBI GenBank database (http://www.ncbi.nlm.nih.gov/genbank/) with the following accession numbers: MW804308, MW804340, MW804341.

3.2.1. *Male*

Body 3.1 times as long as greatest width, widest at pereonite 5; dorsal surfaces punctate, sparsely setose. *Cephalosome* quadrate, as long as wide, lateral margins sub-parallel; dorsal surface smooth; dorsal sulcus narrow, deep, extended; paraocular ornamentation forming a ridge extending from middle of the eye posteriorly, posteromedian tubercle present. *Frontolateral processes* present. *Frontal margin* straight, median point with process. *External scissura* present, wide, shallow. *Mediofrontal process* present, strong, rounded, without ventral notch and setae.

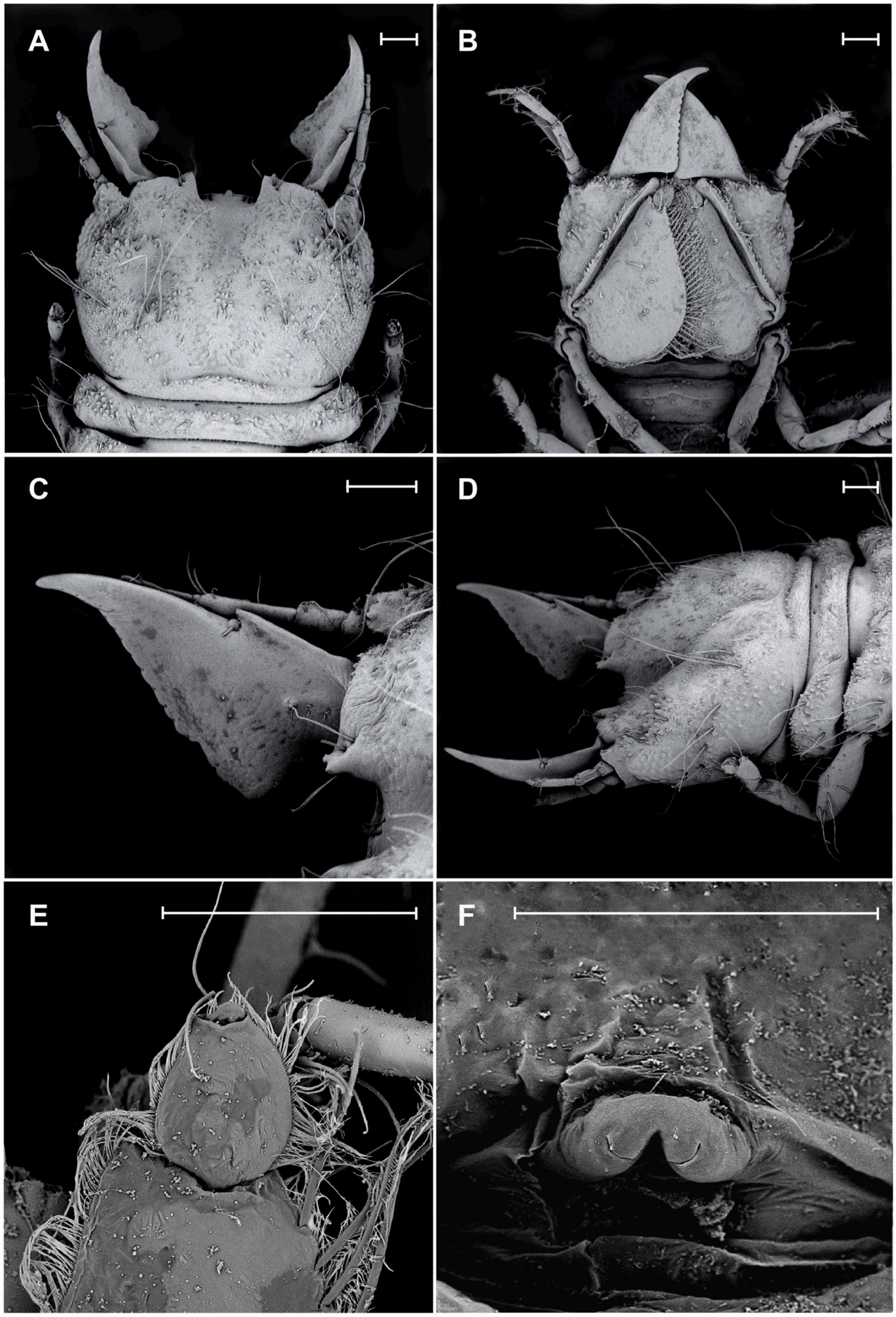

Fig. 4. *Gnathia malaysiensis* Müller, 1993 male scanning electron microscope (SEM) images. A, dorsal view of cephalosome; B, ventral view of cephalosome; C, mandible; D, lateral view of cephalosome; E, pylopod article 2 and 3; F, penes. Scale bars: 100 μm.

Superior frontolateral process present, paired, strong, equally apically bifid, extending to form a weak ridge, with 2 pairs of long simple setae. *Inferior frontolateral process* absent. *Supraocular lobe* pronounced, pointed; accessory supraocular lobe not pronounced. *Eyes* present, elongate, 0.3 as long as cephalosome length, contiguous with head surface, ommatidia arranged in rows, eye colour dark brown.

Pereon lateral margins subparallel, with few setae; anteriorly smooth. *Pereonite 1* partially fused dorsally with cephalosome; dorsolateral margins not obscured by cephalosome. *Pereonite 2* wider than pereonite 1. *Areae laterales* present on pereonite 5. *Pereonite 6* with weak lobi laterales; lobuii absent. *Pleon* covered in pectinate scales, epimera not dorsally visible on all pleonites. *Pleonite* lateral margins with 3 pairs of simple setae, with 2 pairs of simple setae medially. *Pleotelson* 1.1 times as long as anterior width, partially covered in pectinate scales; lateral margins sparsely crenulated; anterolateral margins convex, with 4 submarginal setae; posterolateral margin weakly concave, with 2 submarginal setae; mid-dorsal surface with 2 sub-median setae, apex with 2 setae.

Antennula peduncle article 2 as long as article 1, with 2 penicillate setae; article 3 1.9 times as long as article 2, 3.4 times as long as wide,

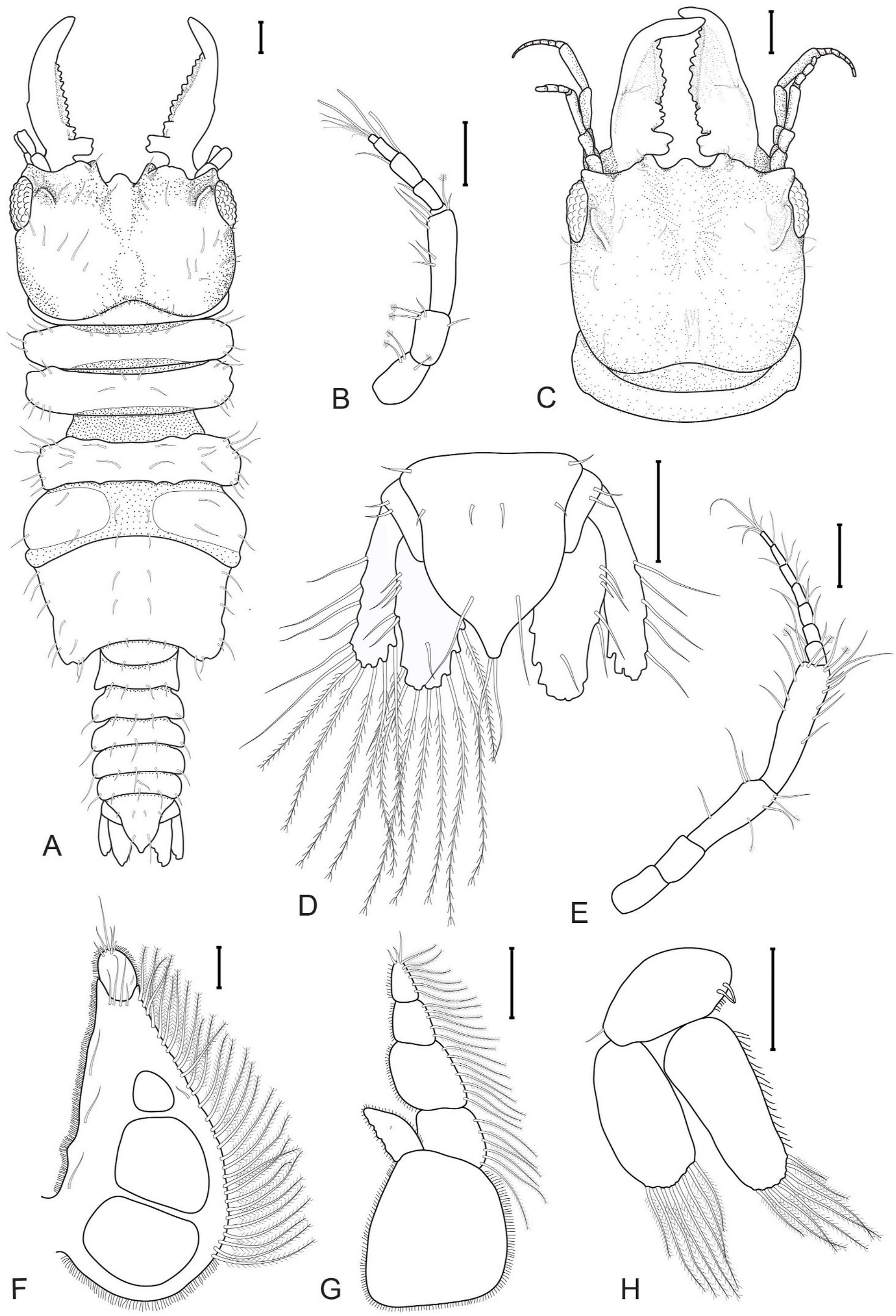

Fig. 5. *Gnathia camuripenis* Tanaka, 2004 male (2.2 mm TL). A, habitus dorsal view (slightly curled); B, antennula; C, dorsal view of cephalosome (perpendicular view); D, dorsal view of pleotelson and uropods; E, antenna; F, maxilliped; H, pylopod; I, pleopod 2. Scale bars: 100 μm.

with 1 penicillate seta. Antennula flagellum as long as article 3, with 5 articles; article 3 with 1 aesthetasc seta and 1 simple seta; article 4 with 1 aesthetasc seta and 1 simple seta; article 5 terminating with 1 aesthetasc seta, and 4 simple setae. *Antenna* peduncle article 3 2.7 times as long as wide, 2.2 times as long as article 2, with 2 penicillate setae and 5 simple setae; article 4 1.4 times as long as article 3, 3.8 times as long as wide, with 3 penicillate setae and 14 simple setae; flagellum 1.1 times as long as article 5, with 7 articles.

*Mandibl*e 0.8 as long as width of cephalosome, cylindrical, strongly curved distally; apex 30% total length; mandibular seta present. *Carina* present, smooth. *Incisor* knob-like. *Blade* present, dentate, with distinct angle, dentate along 100% of margin. *Pseudoblade* present, dentate. *Internal lobe* present, large, bifid, irregular; dorsal lobe absent; basal neck short; erisma present.

Maxilliped 5-articled; article 1 lateral margin with continuous marginal scale-setae; article 2 lateral margin with 6 plumose setae; article 3 lateral margin with 7 plumose setae; article 4 lateral margin with 5 plumose setae; article 5 with 6 plumose setae; endite extending to mid-margin of article 3.

Pylopod article 1 1.8 as long as wide, without distolateral lobe; posterior and lateral margins forming rounded curve; lateral margin with 30 large plumose setae; mesial margin with continuous scale-setae; distal margin with 4 simple setae; article 2 1.4 as long as wide, with 6 simple setae; article 3 absent.

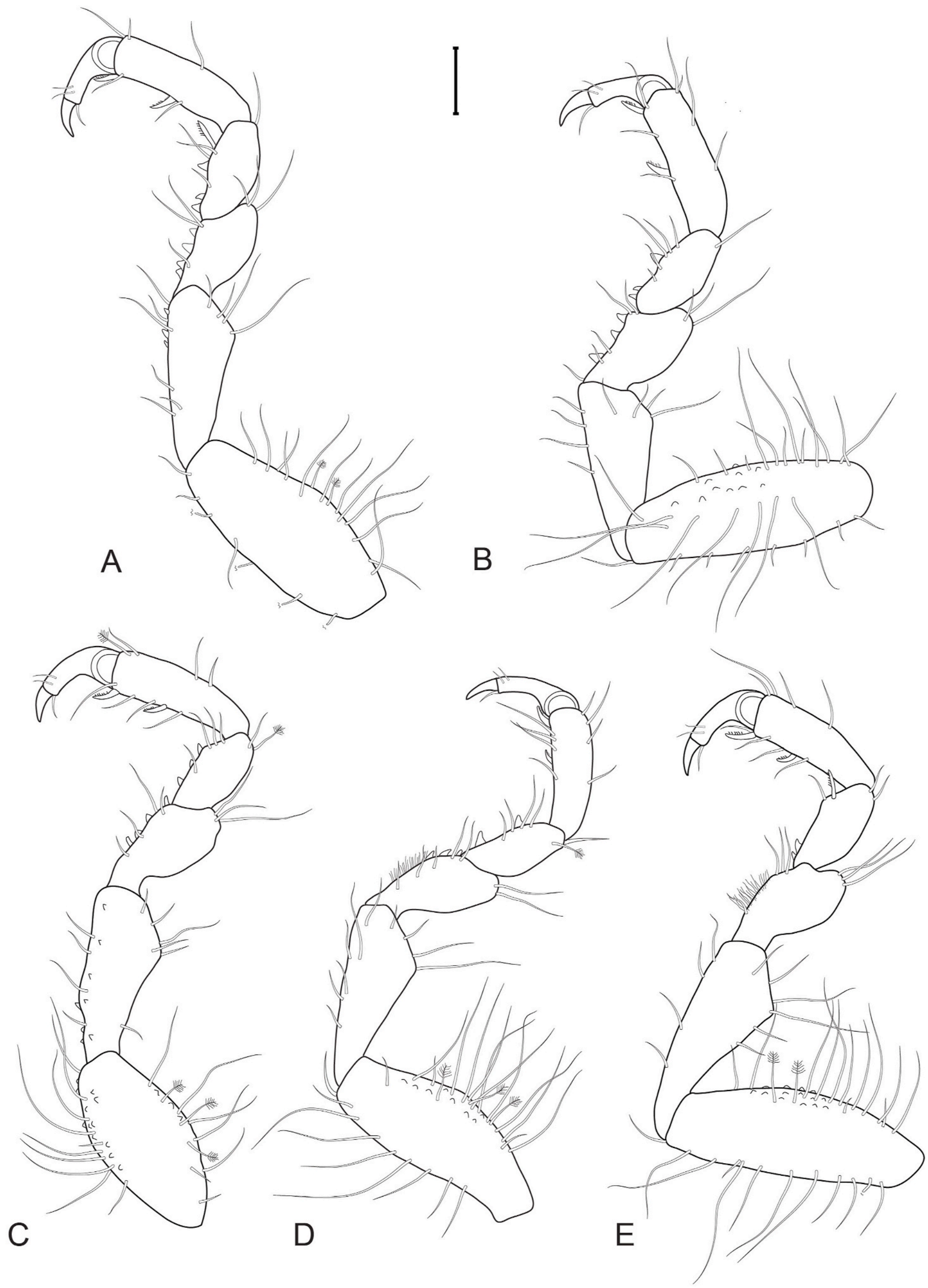

Fig. 6. *Gnathia camuripenis* Tanaka, 2004 male (2.2 mm TL). A–E pereopods 2–6, respectively. Scale bar: 100 μm.

Pereopods 2–6 with long simple setae and randomly covered in pectinate scales; inferior margins with weak tubercles. *Pereopod 2* with tubercles on ischium to carpus; basis 2.3 times as long as greatest width, superior margin with 14 setae (two penicillate), inferior margin with 7 setae; ischium 0.7 times as long as basis, 2.5 as long as wide, superior margin with 4 setae, inferior margin with 6 setae; merus 0.6 as long as ischium, 1.7 as long as wide, superior margin with 3 setae, inferior margin with 3 setae; carpus 0.6 as long as ischium, 1.9 as long as wide, superior margin with 1 setae, inferior margin with 4 setae (one biserrate); propodus 0.8 times as long as ischium, 3.1 times as long as wide, superior margin with 3 setae, 2 simple setae, and 2 robust setae; dactylus 0.7 as long as propodus. *Pereopods 3 and 4* similar to pereopod 2. *Pereopod 5* similar to pereopod 6. *Pereopod 6* without tubercles; basis 2.9 times as long as greatest width, superior margin with 14 setae, and 2 penicillate setae, inferior margin with 12 setae; ischium 0.8 as long as basis, 2.7 as long as greatest width, superior margin with 6 setae, inferior margin with 4 setae; merus 0.5 as long as ischium, 1.4 times as long as wide, superior margin with 3 setae, inferior margin with 4 setae, with dense patch of scale-setae; carpus 0.5 as long as ischium, 2 times as long as wide, superior margin with 2 setae, inferior margin with 2 setae; propodus 0.6 as long as ischium, 2.8 times as long as wide, superior margin with 4 setae, inferior margin with 3 setae, and 2 robust setae; dactylus 0.8 as long as propodus.

Penes produced, penial process 3.9 times as long as basal width.

Pleopod 2 exopod 2 as long as wide, distally broadly rounded, with 8 plumose setae; endopod 2.4 as long as wide, distally narrowly rounded, with 8 plumose setae; appendix masculina absent; peduncle 0.5 times as wide as long, mesial margin with 2 coupling setae, lateral margin with 1 simple seta.

Uropod rami extending beyond pleotelson, apices broadly rounded. *Peduncle* with 2 dorsal setae. *Uropod endopod* 2.5 as long as greatest width, dorsally with 1 seta; lateral margin straight and sinuate, lateral

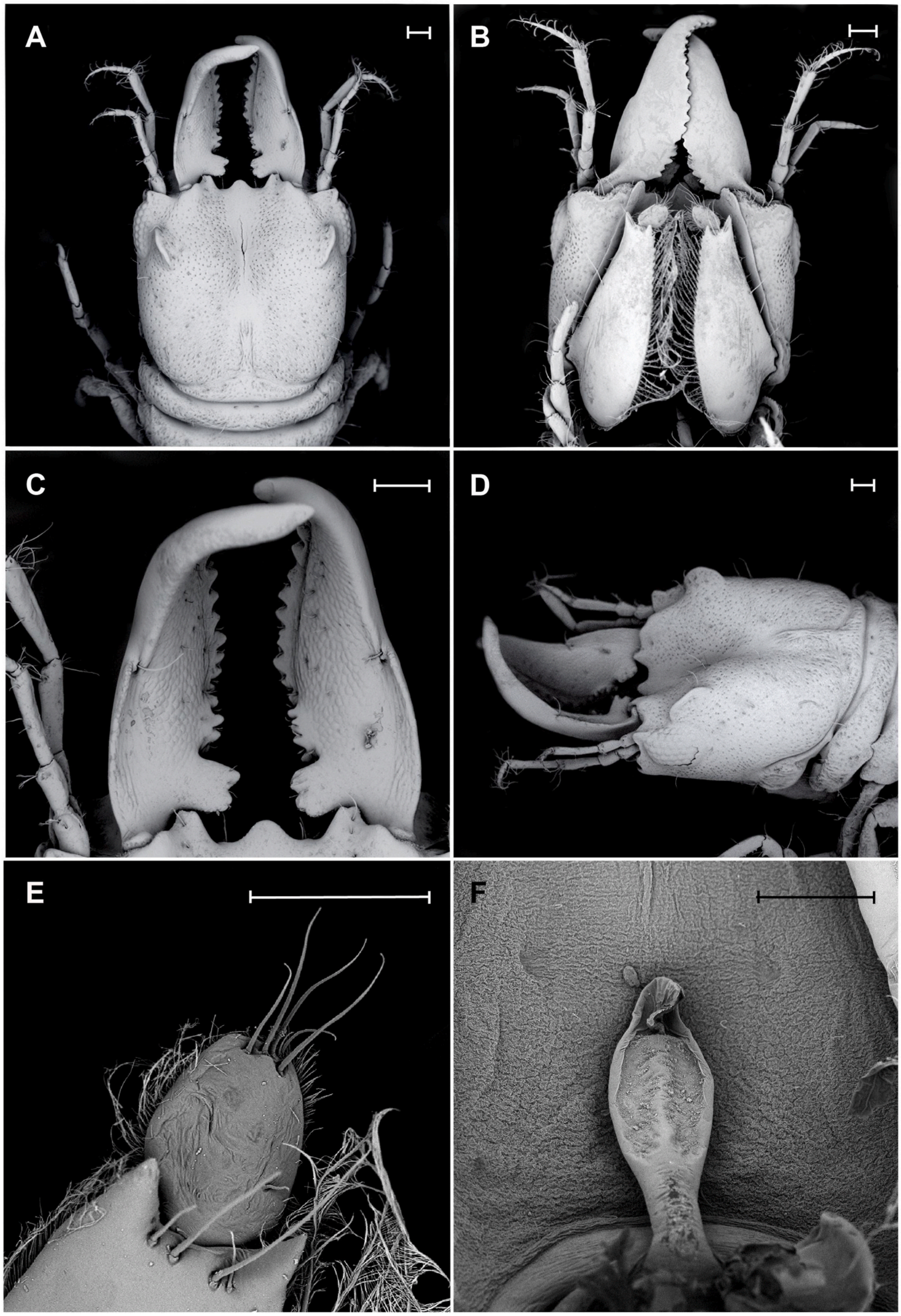

Fig. 7. *Gnathia camuripenis* Tanaka, 2004 male scanning electron microscope (SEM) images. A, dorsal view of cephalosome; B, ventral view of cephalosome; C, mandible; D, lateral view of cephalosome; E, pylopod article 2; F, penes. Scale bars: 100 μm.

margin with 5 simple setae; proximomesial margin sinuate, with 7 long plumose setae. *Uropod exopod* not extending to end of endopod, 3.5 times as long as greatest width; lateral margin straight, with 6 simple setae; proximomesial margin convex, with 5 long plumose setae.

Distribution. Ishigaki Island, Japan (Tanaka, 2004); Republic of the Philippines (present study).

Hosts. Not known.

Remarks. *Gnathia camuripenis* may be identified by its distinct and long fused penes; mandibles with dentate blade and two internal lobes; strong, rounded mediofrontal process without a ventral notch; and prominent paraocular ornamentation.

Tanaka (2004) based his description of *G. camuripenis* on five males and therefore already captured some morphological differences within this species. The main differences between the specimens from Japan and the Philippines can be found in the number of setae, especially plumose setae, on the different articles of the maxillipeds, pereopods and pleopods. The seven males from the Philippines are thus very similar in most morphological features to those from Ishigaki Island, Japan, indicating very little regional differences within this species.

3.3. Molecular analysis

The partial mitochondrial cytochrome c oxidase subunit I (COI) sequences obtained in this study are the first sequences for *Gnathia malaysiensis* (2 sequences; 99.7% similarity and 2 base pair differences) and *Gnathia camuripenis* (3 sequences; 100% similarity and no base pair differences). The sequences were verified as belonging to Gnathiidae using BLASTn (Basic Local Alignment Search Tool; http://www.ncbi.nlm.nih.gov/blast). The trimmed COI sequences (approximately 450 and 660 bp for the two species respectively; no stop codons on Invertebrate mitochondrial code frame 1) were compared to other *Gnathia* COI sequences from GenBank but due to the limited availability of published sequences, no alignment was performed.

4. Discussion

Due to its exceptionally high marine biodiversity, the Philippines has been the subject of numerous marine biodiversity studies. However, as with most coral reef regions, sampling has been biased towards vertebrates and macroinvertebrates. Cryptofauna in general (Plaisance et al., 2011), and parasites in particular have been mostly ignored, and there has been no systematic sampling of gnathiid biodiversity in this region. Given the ecological importance of parasites in coral reef systems in general (e.g., Tuttle et al., 2017), and gnathiids in particular (Sikkel and Welicky, 2019), this constitutes a major gap in biodiversity studies. Indeed, gnathiids have been identified as among the priority species necessary to support the functional integrity of coral reefs (Wolfe et al., 2020).

While the work in the Visayas region over the past decade has resulted in extensive sampling of gnathiids (Sikkel et al., 2014; Santos and Sikkel, 2017; Shodipo et al. 2019, 2020), until now, none of the species captured have been identified. Our descriptions here thus represent the first gnathiid species identified from the Philippines. One species, *Gnathia malaysiensis*, corresponds to "Gnathiid morph 3" reported by Santos and Sikkel (2017 – Fig. 3c). The other species redescribed here, *Gnathia camuripenis*, was not found in that study and is thus newly discovered in this region.

Light traps, rather than fish hosts, were used to collect the specimens for this study. Therefore, hosts for either species were not apparent. In general, there is a paucity of information on gnathiid hosts as, in most cases, the free-living males are collected and described without linking them to their parasitic larvae. Of the 46 *Gnathia* spp. known from the CIP, host information is only available for 13 species (Table 1). Interesting to note is that those species parasitise a very wide range of host taxa including both teleost and elasmobranchs, indicating no level of host specificity amongst *Gnathia* from the CIP. While DNA from blood meals can be sequenced to identify hosts (Hendrick et al., 2019), without sufficient sequences from gnathiids, the host and gnathiid cannot be matched.

Based on previous studies (Sikkel et al., 2014; Cruz-Lacierda and Nagasawa, 2017; Santos and Sikkel, 2017), 34 of 37 investigated fish species from 14 families in the central Philippines have been shown to be infested by gnathiid isopods. Five fish species were infested by more than one gnathiid morph (Santos and Sikkel, 2017) and *G. malaysiensis* was found on the greatest number of hosts (8) by Santos and Sikkel (2017). Hosts included four species of wrasse (Labridae): *Cheilinus trilobatus* (Lacepède, 1801), *Halichoeres podostigma* (Bleeker, 1854), *Labrichthys unilineatus* (Guichenot, 1847); two species of parrotfish (Labridae): *Leptoscarus vaigiensis* (Quoy and Gaimard, 1824), *Scarus* sp.; one species of mullet (Mugilidae): *Parupeneus barberinoides* (Bleeker, 1854); and two species of Pomacentridae: *Abudefduf vaigiensis* (Quoy and Gaimard, 1824), and *Dascyllus trimaculatus* (Rüppell, 1829).

Population-genetic structuring, speciation, and thus genetic and species diversity within a clade and/or region are a function of factors that promote dispersal versus isolation of populations within species. Unlike most marine species, gnathiids do not have a pelagic dispersal phase and rarely occur more than 1 m above the bottom (Nicholson et al., 2020). Thus, they are unlikely to be dispersed via typical ocean currents, which would limit their expected geographic range and create high potential for population-genetic structuring and speciation. The two most likely mechanisms that would allow long-distance dispersal and thus act to reduce genetic structuring and speciation are "hitch-hiking" on hosts, and tropical cyclones (Pagán et al., 2020). For species that inhabit coral reefs, dispersal via the former mechanism requires a broad host range and/or infestation of species that can swim long distances in a short period of time. Indeed, the most widely distributed gnathiid documented to date is the CIP species *Gnathia trimaculata* Coetzee, Smit, Gutter and Davies, 2009 that feeds on sharks from Lizard Island on the Great Barrier Reef, Australia and Okinawa Island, Japan, thus potentially occurring right across the CIP (Table 1). Dispersal via the latter mechanism requires frequent tropical cyclones. *Gnathia malaysiensis* appears to feed on a wide range of hosts. Combined with the proximity of Malaysia and the Philippines, which are also connected via island chains, and the frequent occurrence of tropical cyclones in the region, the finding of *G. malaysiensis* in both the Philippines and Malaysia is not surprising. However, the Visayas to southern Japan is a much longer distance, over deep channels separating the Philippines and Taiwan, and Taiwan and Japan, making dispersal of *G. camuripenis* via shallow reef-associated hosts more difficult. Thus, it is likely that this species relies heavily on large, highly mobile, hosts and cyclones for dispersal.

Although a disproportionate number of described tropical gnathiid species of the genus *Gnathia* have been collected from the CIP (46/133), this is a vast region, and a disproportionate number of these species have been described from two small islands off north-eastern Australia, alone (see Table 1). With the exception of the species *G. trimaculata*, that feed on sharks, none of the species from these northern Great Barrier Reef sites have been reported from other parts of the CIP. Thus, the number of species described clearly represents a very small fraction of the gnathiid biodiversity in this region. Moreover, the geographic ranges and host associations of potential pathogens transmitted by the vast majority of these species are completely unknown. Resolving these knowledge gaps will require a concerted effort.

Declaration of competing interest

The authors declare no conflicts of interest.

Acknowledgments

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