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RESEARCH

A new temporary fish parasitic gnathiid isopod, *Elaphognathia alcalai* (Crustacea: Isopoda: Gnathiidae), from Philippine coral reefs

Kim Yumul[1] · Nico J. Smit[1,2] · Kerry A. Hadfield[2] · Mary O. Shodipo[1] · Paul C. Sikkel[1,2] · Anja Erasmus[2]

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Abstract
Gnathiid isopods are the most prevalent and ecologically important temporary ectoparasites of coral reef fishes and are important for supporting the functional integrity of coral reefs. Through their role as parasites, gnathiids can influence community dynamics in their ecosystem. The family Gnathiidae constitutes 12 genera, including the genus *Elaphognathia* that can be distinguished from other genera by the deeply excavated frontal border, dramatic lengthening of the mandibles, and addition of apical cusps in adult males. There are currently 25 known species of *Elaphognathia* described over a period of 130 years, with only five species molecularly characterized. The present study contributes to the knowledge of this genus by providing a comprehensive integrative description of the 26th species of *Elaphognathia*, the first novel gnathiid species described from the Philippines. Larval gnathiids were collected in the Central Indo-Pacific (Philippines), using light traps, separated, kept alive to molt into adults, and preserved in 95% ethanol for morphological and molecular characterization. Species description was based on light and scanning electron microscopy of the adult male, prepared in the program DEscriptive Language for Taxonomy (DELTA), using a modified Gnathiidae character set. Key distinguishing features of the new species are the presence of a pseudoblade, with the anterior tip dorsally visible, a large, rounded inner lobe with semi-smooth ridges, and conical protrusions on the inferior (dorsal) and superior (ventral) margin of the mandible, as well as the excavated frontal margin with two equal superior frontolateral processes with sinuate superolateral margins. The novel species can be distinguished from other molecularly characterized *Elaphognathia* (*E. sugashimaensis* and *E. rangifer*) by ~27% variation in COI sequences. More molecular data are required in order to elucidate a more accurate phylogenetic analysis of this genus.

Keywords Integrative taxonomy · Life below water · Parasitic crustacean · Marine parasitology · Biodiversity

Introduction

Gnathiid isopods are ecologically similar to ticks and mosquitoes on land. They are the most common ectoparasites of coral reef fishes and are integral components for the functional integrity of coral reefs (Sikkel and Welicky 2019; Wolfe et al. 2020). As blood-feeders, gnathiids can impact on host behavior and trophic interactions. For example, they increase their hosts' interactions with cleaners (Grutter 2001; Sikkel et al. 2004) for which they serve as a primary food source (Grutter 1999; Grutter and Bshary 2004). They are also consumed by other fishes as well as corals (Artim and Sikkel 2013; Artim et al. 2017; Paula et al. 2021; Nicholson et al. 2024). The effects of gnathiids on hosts range from minor lesions to death, with settlement-stage fish being the most vulnerable (Grutter et al. 2008; Artim et al. 2015; Sellers et al. 2019; Allan et al. 2020). Similar to ticks and mosquitoes, gnathiids are suspected vectors of potential pathogens, such as apicomplexans and viruses (Cook et al. 2015; Hadfield and Smit 2019; Sikkel et al. 2020).

Despite their ecological importance, gnathiids are often neglected in marine ecology research, even by marine parasitologists, for three main reasons: (1) except

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✉ Anja Erasmus
23599235@mynwu.ac.za

[1] Department of Marine Biology and Ecology, Rosenstiel School of Marine, Atmospheric & Earth Science, University of Miami, Miami, FL, USA

[2] Water Research Group, Unit for Environmental Sciences and Management, North-West University, Private Bag X6001, Potchefstroom 2520, South Africa

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for species infesting elasmobranchs, larvae feed on host fish for only a brief period (minutes to hours) before returning to the benthos to rest and molt to the next developmental stage. Thus, most of their life is spent "free-living"; (2) parasitic larval stages do not resemble the non-parasitic adults, which exhibit strong sexual dimorphism; and (3) to date, the taxonomy and identification rely solely on adult males (Smit and Davies 2004; Ota et al. 2012, 2024).

The family Gnathiidae comprises 12 genera, including *Elaphognathia* Nunomura, 1992, which is morphologically distinguished by a deeply excavated frontal border, dramatic lengthening of the mandibles, and addition of apical cusps. There are currently 25 species of *Elaphognathia* described over the span of 130 years (Boyko et al. 2025), with only five having been characterized using molecular data (Ota et al. 2010; Song and Min 2016).

Although the Philippine archipelago lies at the heart of the Coral Triangle of the Central Indo-Pacific (CIP)—a region recognized as the epicenter of marine biodiversity worldwide (Carpenter and Springer 2005)—parasites in general, and gnathiid isopods in particular, remain poorly studied. To date, fewer than five studies have examined any aspect of gnathiid taxonomy and ecology in the Philippines, with just two *Gnathia* Leach, 1814 species morphologically and molecularly characterized from this marine biodiversity hotspot (Sikkel et al. 2014; Santos and Sikkel 2017; Shodipo et al. 2020, 2021).

During the present study, gnathiids were collected from fringing coral reefs off the island of Negros Oriental as part of the ongoing efforts to better understand gnathiid ecology in the CIP. The study advances knowledge of Gnathiidae taxonomy by providing a comprehensive and integrated description of the 26th known species of *Elaphognathia*—the first species of this genus from the Philippine coral reefs—based on adult male morphology, supported by molecular analysis.

Materials and methods

Juvenile gnathiids were collected on multiple occasions from fringing coral reefs off Negros Oriental Island, Philippines (Central Indo-Pacific), in 2018–2019 and 2024 using light traps made of polyvinyl chloride tubes as described in Shodipo et al. (2023) (Fig. 1a).

Once collected, the organisms were reared to adulthood in vials containing seawater. Juvenile gnathiids were allowed to feed overnight in the aquarium on captured reef fishes (see list in the host section of the description). After feeding, host fishes were released, and the engorged praniza larvae were left to molt to the next developmental stage following Shodipo et al. (2021; 2023). Adult male gnathiids (Fig. 1b) were preserved in 95% ethanol, for molecular and morphological characterization at North-West University (NWU) as approved by the NWU Anim-Care ethics committee (NWU-00784-24-A5).

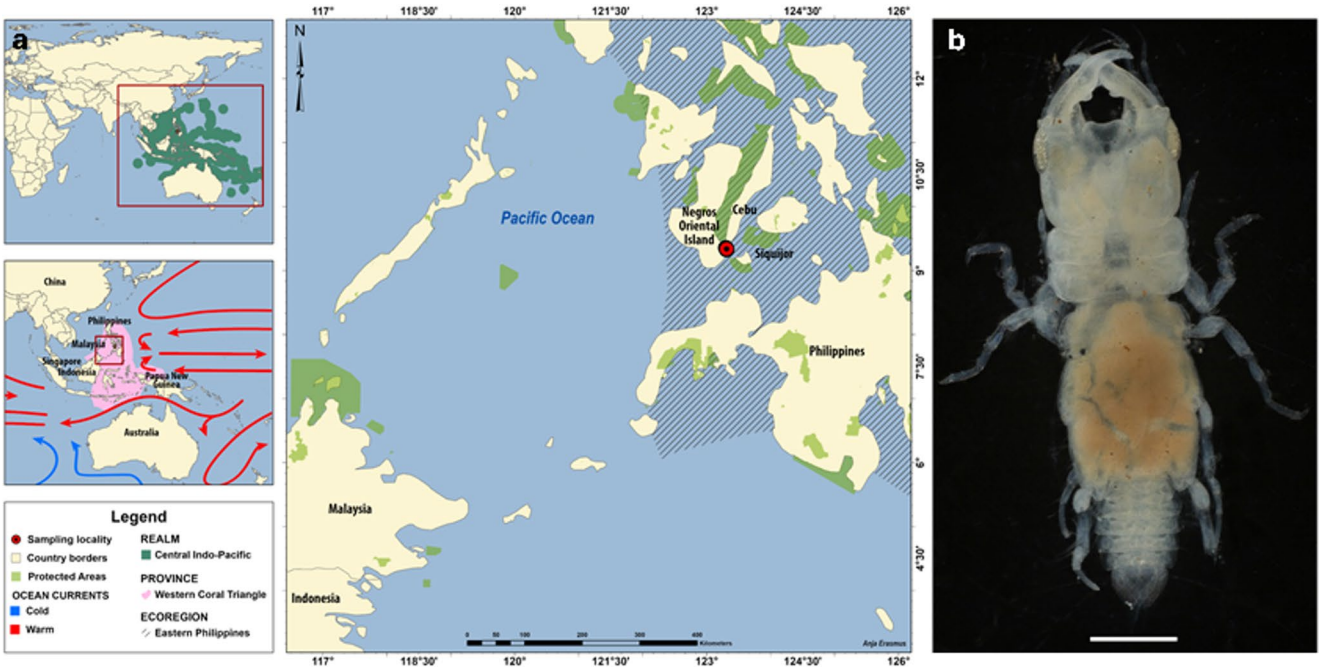

Fig. 1 (**a**) Study area map indicating Marine Ecoregions of the World (MEOW) realm, province, and ecoregion (based on Spalding et al. 2007); (**b**) Light microscope photo of adult male holotype of *Elaphognathia alcalai* sp. nov. (NMCR 99225). Scale bar: 500 µm

Molecular characterization

DNA for molecular analyses (n=3 males) was extracted using the PCRBio Rapid Extract PCR kit (PCRBiosystems, Analytical Solutions, Randburg, South Africa), according to the manufacturer's protocol. Partial fragments of the mitochondrial cytochrome c oxidase subunit I (COI) amplified with LCO1490 and HCO2198 primers, and internal transcribed spacer 2 of ribosomal DNA (ITS2) amplified with 3 S and ITS2.2 primers. Primer sequences are provided in Table 1. The PCR was carried out as described in Erasmus et al. (2023). PCR products were purified using the ExoSAP Protocol, followed by Sanger sequencing in both forward and reverse directions through Inqaba Biotechnical Industries (Pty) Ltd, Pretoria, South Africa. Resulting sequences were trimmed, assembled, and edited using Geneious v. 11.1.4 (RRID: SCR_010519) (Biomatters, Auckland, New Zealand; Kearse et al. 2012). The invertebrate mitochondrial generic code was applied for translation into amino acids to confirm that there were no stop codons.

Sequences used in the phylogenetic analyses were obtained from GenBank and BOLD. Outgroups were selected based on results from Wetzer (2001) and Ota et al. (2022). The final alignments were done using MUSCLE (Edgar 2004), through Geneious (Table 2). The resulting COI alignment included 405 bp, and 638 bp for the ITS alignment. The best substitution model was predicted using jModelTest 2.1 (Posada 2008), based on the Akaike information criterion (AIC). The Hasegawa-Kishino-Yano (HKY) substitution model was applied to construct both phylogenetic trees. Bayesian inference (BI) was performed using MrBayes on ACCESS, and maximum likelihood (ML) estimates were performed with PhyML v. 3.0 (available at http://www.atgcmontpellier.fr/phyml/). The resulting phylogenetic trees were visualized using FigTree v. 1.4.4 (Rambaut 2012) and Adobe Illustrator v. 26.4.1.

Morphological characterization

Individuals (whole, stained, and dissected) were sorted for morphological characterization using various microscopy techniques, including dissection (NIKON AZ100M), light (NIKON Eclipse 80*i* compound microscope), and scanning electron microscopy (Phenom Pro Desktop SEM), as in Erasmus et al. (2023). Image stacks were merged and processed using Adobe Photoshop. Scaled pencil sketches were made from a phase-contrast light microscope with a camera lucida, and digital illustrations from these combined with photomicrographs, were completed using Adobe Illustrator and an Apple iPad with a 2nd generation Apple Pencil. Figure plates were compiled in Adobe Illustrator.

Subsequently, the light and scanning electron micrographs and illustrations of the adult male were used for species description, which was prepared in the DEscriptive Language for Taxonomy program (DELTA) using a modified Gnathiidae character set (Erasmus et al. 2025). Terminology was followed for the male descriptions as in Monod (1926), Cohen and Poore (1994), and Smit and Hadfield (2022), while the setal classification was based on Watling (1989) and Svavarsson and Bruce (2019). Total length (TL) was measured from the frontal margin (including the processes, excluding the mandibles) to the posterior end of the pleotelson. Type material is deposited in the National Museum of Natural History, an institution of the National Museum of the Philippines.

Table 1 Selected PCR primers for gene regions used for the amplification of DNA

Primer	Nucleotide sequence	Reference
COI		
LCO1490	5′-GGTCAACAAATCATAAAGATATTGG-3′	Folmer et al. 1994
HCO2198	5′-TAAACTTCAGGGTGACCAAAAAATCA-3′	
ITS2		
3 S-forward	5′-GGTACCGGTGGATCACGTGGCTAGTG-3′	Grutter et al. 2000
ITS2.2-reverse	5′-CCTGGTTAGTTTCTTTTCCTCCGC-3′	

Systematics

Suborder Cymothoida Wägele, 1989.

Superfamily Cymothooidea Leach, 1814.

Family Gnathiidae Leach, 1814.

Elaphognathia Monod, 1926.

Type species. *Anceus ferox* Haswell, 1884 accepted as *Elaphognathia ferox* (Haswell, 1885); subsequent designation by Cohen and Poore (1994).

***Elaphognathia alcalai* sp. nov.**

Zoobank number: urn: lsid: zoobank.org: pub: A946F3C4-B35E-4E17-A7B4-29CB3B6F87B6.

GenBank accession numbers: COI *Elaphognathia alcalai* sp. nov. (PX625788) of 672 bp; ITS2 *Elaphognathia alcalai* sp. nov. (PX608478; PX608479; PX608480) of 635–696 bp.

(Figs.2, 3, and 4)

Type material

Holotype: 1 ♂ (TL: 2.9 mm; NMCR 99225; Figure 1b), collected and reared from larvae collected on the fringing coral reefs off Negros Oriental Island, Philippines (Central Indo-Pacific), in 2018–2019 and 2024 using light traps (9°05'38.5"N; 123°11'39.9"E), 2–7 m depth. *Paratype*: 1 ♂ (TL 2.7 mm), same information as holotype.

Table 2 Selected sequences used for phylogenetic analysis

Species	Host	Locality	GenBank accession numbers		Reference
			COI	ITS	
Elaphognathia alcalai sp. nov.	Domino damselfish (*Dascyllus trimaculatus* [Rüppell, 1829])	Philippines: Off Negros Oriental Island	PX625788	PX608478	Present study
Elaphognathia cornigera (Nunomura, 1992)	Not reported	Japan: Kumamoto, Amakusa	-	AB519156	Ota et al. 2010
Elaphognathia discolor (Nunomura, 1988)	Not reported	Japan: Miyagi, Shizugawa	-	AB519159	Ota et al. 2010
Elaphognathia nunomurai Ota et al. 2010	Not reported	Japan: Okinawa, Haneji	-	AB519157	Ota et al. 2010
Elaphognathia rangifer (Monod 1926)	Not reported	Japan: Okinawa, Nakagusuku	AB713955	-	Ota et al. 2012
			-	AB519158	Ota et al. 2010
Elaphognathia sugashimaensis (Nunomura, 1981)	Not reported	South Korea: Ganggu harbour	KX078775	-	Song and Min 2016
Gnathia camuripenis Tanaka, 2004	Not reported	Philippines: Off Negros Oriental Island	MW804341	-	Shodipo et al. 2021
Gnathia jimmybuffetti Erasmus et al. 2023	Various species of grunt, *Haemulon* spp.	USA: Florida Keys	OR064533	-	Erasmus et al. 2023
Gnathia limicola Ota & Tanaka, 2007	Not reported	Japan: Okinawa, Haneji	AB713956	-	Ota et al. 2012
Gnathia maculosa Ota & Hirose, 2009	Blue-spotted stingray (*Neotrygon kuhlii* [Müller & Henle, 1841])	Japan: Okinawa, Kumejima Island	AB713961	-	Ota et al. 2012
Gnathia malaysiensis Müller, 1993	Not reported	Philippines: Off Negros Oriental Island	MW837266	-	Shodipo et al. 2021
Gnathia marleyi Farquharson, Smit & Sikkel, 2012	Not reported	US Virgin Islands: Puerto Rico	MT186595	-	Pagán et al. 2020
Gnathia maxillaris (Montagu, 1804)	Not reported	Portugal: Porto Frades	PMACA067-17	-	BOLD 2025
Gnathia tridens Menzies & Barnard, 1959	Giant kelpfish (*Heterostichus rostratus* Girard, 1854)	USA: California, San Diego	PV213449	-	Erasmus et al. 2025
Gnathia trimaculata Coetzee, Smit, Grutter & Davies, 2009	Giant guitarfish (*Rhynchobatus djiddensis* [Forsskål, 1775])	Japan: Okinawa, Nakagusuku	AB713957	-	Ota et al. 2012
OUTGROUPS					
Cirolana rugicauda Heller, 1861	Not reported	Namibia: South of Luderitz	AF260840	-	Wetzer 2001
Thaumastognathia bicorniger Ota et al. 2022	Japanese swellshark (*Cephaloscyllium umbratile* Jordan & Fowler, 1903)	Japan: Off Yui, Shimizu, Shizuoka Pref., Suruga Bay	-	LC642773	Ota et al. 2022

Other material

2 ♂ stained and dissected with lignin pink, 2 ♂ used for SEM imaging, and 3 ♂ used for DNA extraction, same information as the holotype.

Distribution

Philippines, Central Indo-Pacific.

Hosts

Domino damselfish (*Dascyllus trimaculatus* [Rüppell, 1829]) and representatives from five additional families as experimental hosts: butterflyfish (Chaetodontidae [Rafinesque, 1815]), rabbitfish (Siganidae [Richardson, 1837]), grouper (Serranidae [Bonaparte, 1831]), emperor bream (Lethrinidae [Bonaparte, 1831]), and goatfish (Mullidae [Rafinesque, 1815]).

Etymology

This species of *Elaphognathia* is named in honor of Angel Chua Alcala (1929–2023): a pioneer of community-led marine resource management in the Philippines.

Description of male

Body (Fig. 2a) 2.5 times as long as greatest width, widest at pereonite 3; dorsal surfaces smooth or punctate, sparsely setose. *Cephalosome* (Figs. 2a and d and 4a) rectangular, 0.8 as long as wide, lateral margins parallel, posterior margin concave; dorsal surface punctate; dorsal sulcus pyriform, deep, short; paraocular ornamentation absent, posteromedian tubercle present, weak; and lateral tubercles sparsely setose. *Frontolateral processes* present, equal. *Frontal margin* produced, truncate, median point excavate. *External scissura* absent. *Mediofrontal process* absent. *Superior frontolateral processes* present, single, strong, acute, superolateral margins sinuate, reaching proximal margin of mandible internal lobe, with 3 pairs of long simple setae. *Inferior frontolateral process* absent. *Mesioventral margin* concave; smooth; anterior tip not dorsally visible. *Supraocular lobe* not pronounced, rounded, accessory supraocular lobe not pronounced. *Eyes* (Figs. 2a and b and 4a) present, elongate, 0.4 as long as cephalosome length, contiguous with head surface, ommatidia arranged in rows, eye color dark brown.

Pereon (Fig. 2a) lateral margins subparallel or widening posteriorly, with few setae; anteriorly punctate. *Pereonite 1* partially fused dorsally with cephalosome; dorsolateral margins fully obscured by cephalosome. *Pereonite 2* wider than pereonite 1. *Pereonite 4* with anterior constriction, median groove absent. *Areae laterales* present on pereonite 5; dorsal sulcus as thin groove. *Pereonite 6* with weak lobi laterales; lobuii weak, globular. *Pereonite 7* short. *Pleon* (Fig. 2a) epimera not dorsally visible on all pleonites. *Pleonite* lateral margins with 1 pair of simple setae, with 2 pairs of simple setae medially. *Pleotelson* 1.0 times as long as anterior width, not covered in pectinate scales; lateral margins smooth, anterolateral margins concave, with 1 pair of submarginal setae; posterolateral margin convex, distally weakly concave, with 1 pair of submarginal setae; middorsal surface with 1 pair of submedian setae, apex with 2 long setae.

Antennula (Figs. 2b and c and 4d) shorter than antenna; peduncle article 1 without tubercles; article 2 1.0 times as long as article 1; article 3 1.7 times as long as article 2, 2.7 times as long as wide; flagellum 1.3 times as long as article 3, with 5 articles; article 3 with 1 aesthetasc seta, and 1 simple seta; article 5 terminating with 2 aesthetasc seta, and 2 simple setae. *Antenna* (Figs. 2b and c and 4d) peduncle with 4 articles; antenna peduncle article 3 2.0 times as long as wide, 2.0 times as long as article 2, with 2 penicillate setae, and 8 simple setae; article 4 1.5 times as long as article 3, 2.6 times as long as wide, with 3 penicillate setae, and with 16 simple setae; flagellum 1.4 times as long as article 4, 2.0 times as long as article 3, with 7 articles, terminating with 2 simple setae.

Mandible (Figs. 2a, d and e and 4c and d) 1.1 as long as width, and 1.3 as long as length of cephalosome, crescent, weakly curved inwards, distally; apex 35% of total length; mandibular seta present; two pronounced conical protrusions at the base, inferior (dorsally visible) and superior margins (ventrally visible). *Carina* present, smooth, along proximal half. *Incisor* absent. *Blade* present, dentate, arc-shaped, midventrally convex, dentate along 40% of margin, 5–6 denticulations. *Pseudoblade* present, anterior tip dorsally visible, one-third along blade. *Internal lobe* present, large, rounded semi-smooth ridges, one-fourth along blade, obscuring pseudoblade. *Basal neck* short. *Erisma* absent. *Lamina dentata* absent.

Maxilliped (Figs. 2f and 4b) 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 7 plumose setae, and 4 simple setae; endite extending to mid-margin of article 3; with 1 coupling setae.

Pylopod (Fig. 2g) article 1 1.3 as long as wide, with three distinct areolae, without distolateral lobe; posterior and lateral margins forming rounded curve; lateral margin with 28–30 large plumose setae; mesial margin with scale-setae on distal part only; surface with 1 simple setae; distal margin with 2 simple setae; article 2 1.2 as long as wide; with 2 simple setae; article 3 absent.

Pereopods 2–6 (Fig. 3a–e) with long simple setae, covered in pectinate scales, with some penicillate setae; propodus distal RS slightly longer than proximal RS; inferior margins with prominent tubercles. *Pereopod 2* with tubercles on merus and carpus; basis 1.8 times as long as greatest width, superior margin with 3 setae, inferior margin with 9 setae; ischium 0.65 times as long as basis, 1.6 as long as wide, superior margin with 8 setae, inferior margin with 7 setae; merus 0.6 as long as ischium, 1.2 as long as wide, superior margin with 3 setae, superior margin with bulbous protrusion, inferior margin with 7 setae; carpus 1.25 as long as ischium, 2 as long as wide, superior margin with 2 setae, inferior margin with 5 setae; propodus 1.3 times as long as ischium, 3.7 times as long as wide, superior margin with 5 simple setae, inferior margin with 4 simple setae, and 2 robust setae; dactylus 0.3 as long as propodus. *Pereopods 3 and 4* similar to pereopod 2. *Pereopod 5* not similar to pereopod 6.

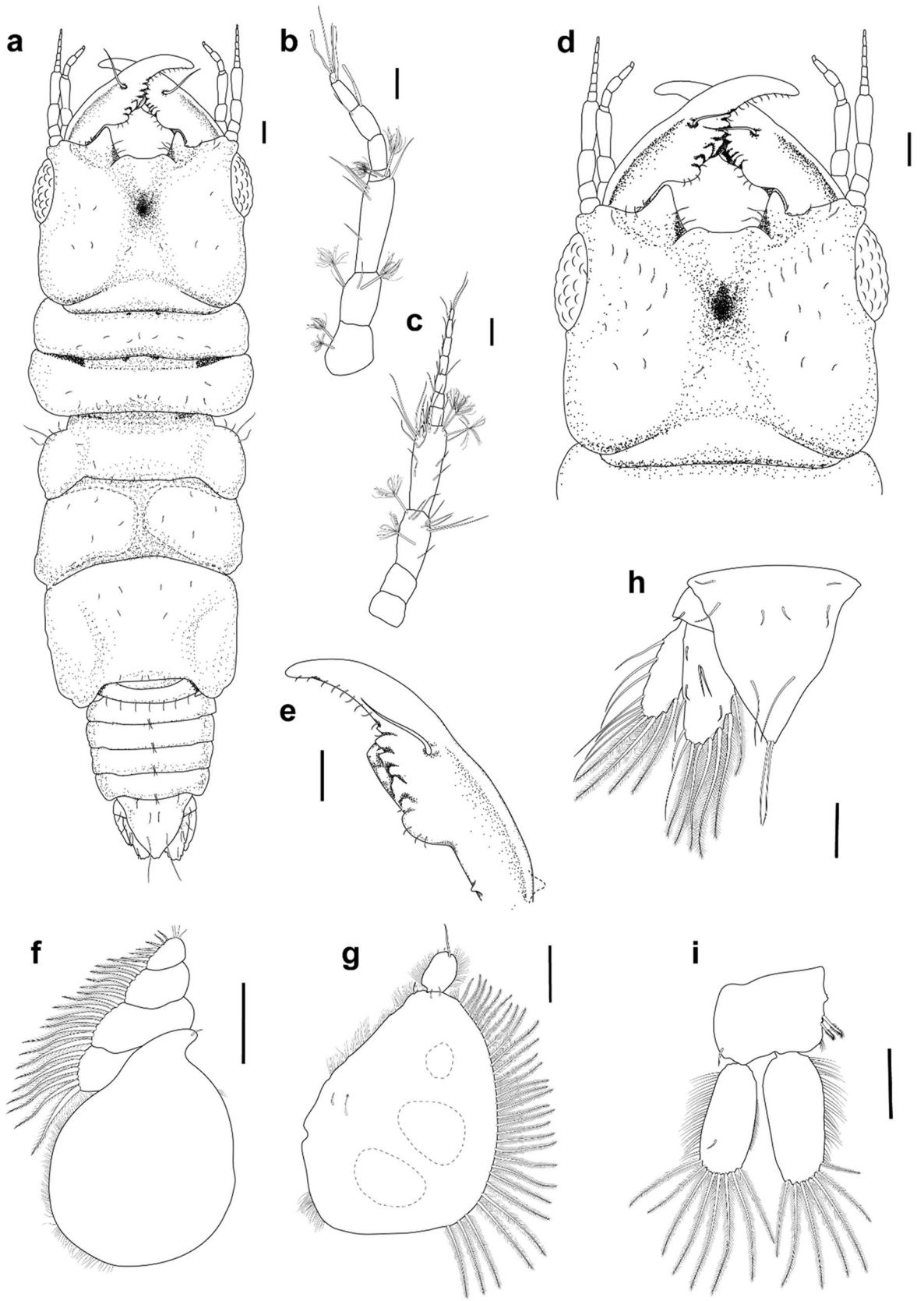

Fig. 2 *Elaphognathia alcalai* sp. nov. Male holotype (2.9 mm) (NMCR 99225). **a** habitus dorsal view; **b** antennula; **c** antenna; **d** dorsal view of cephalosome; **e** mandible; **f** maxilliped; **g** pylopod; **h** pleotelson and uropods dorsal view; **i** pleopod 2. Scale bars: 100 µm

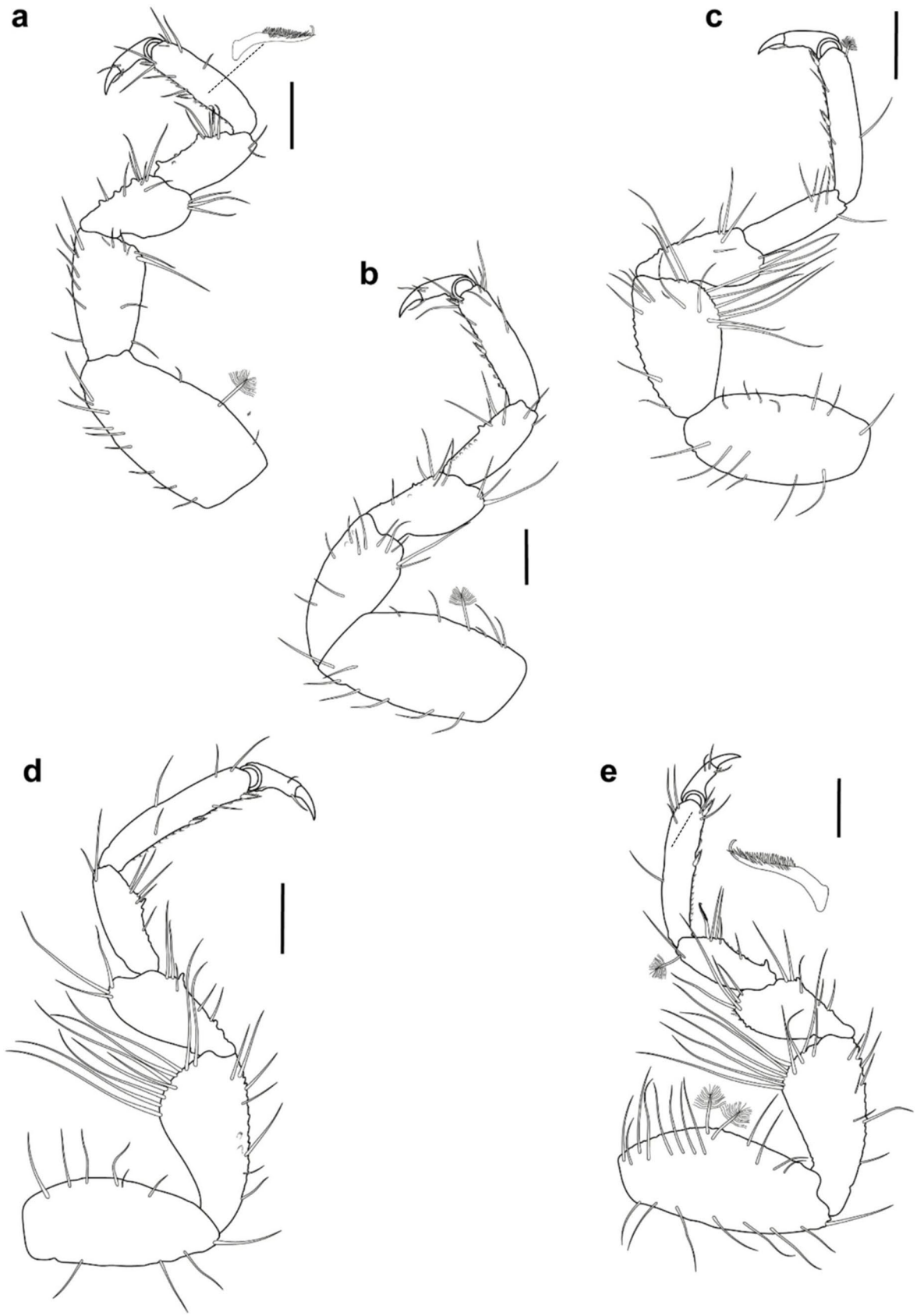

Fig. 3 *Elaphognathia alcalai* sp. nov. Male dissected specimen (2.2 mm). (**a-e**) pereopods 2–6, respectively. Scale bars: 100 μm

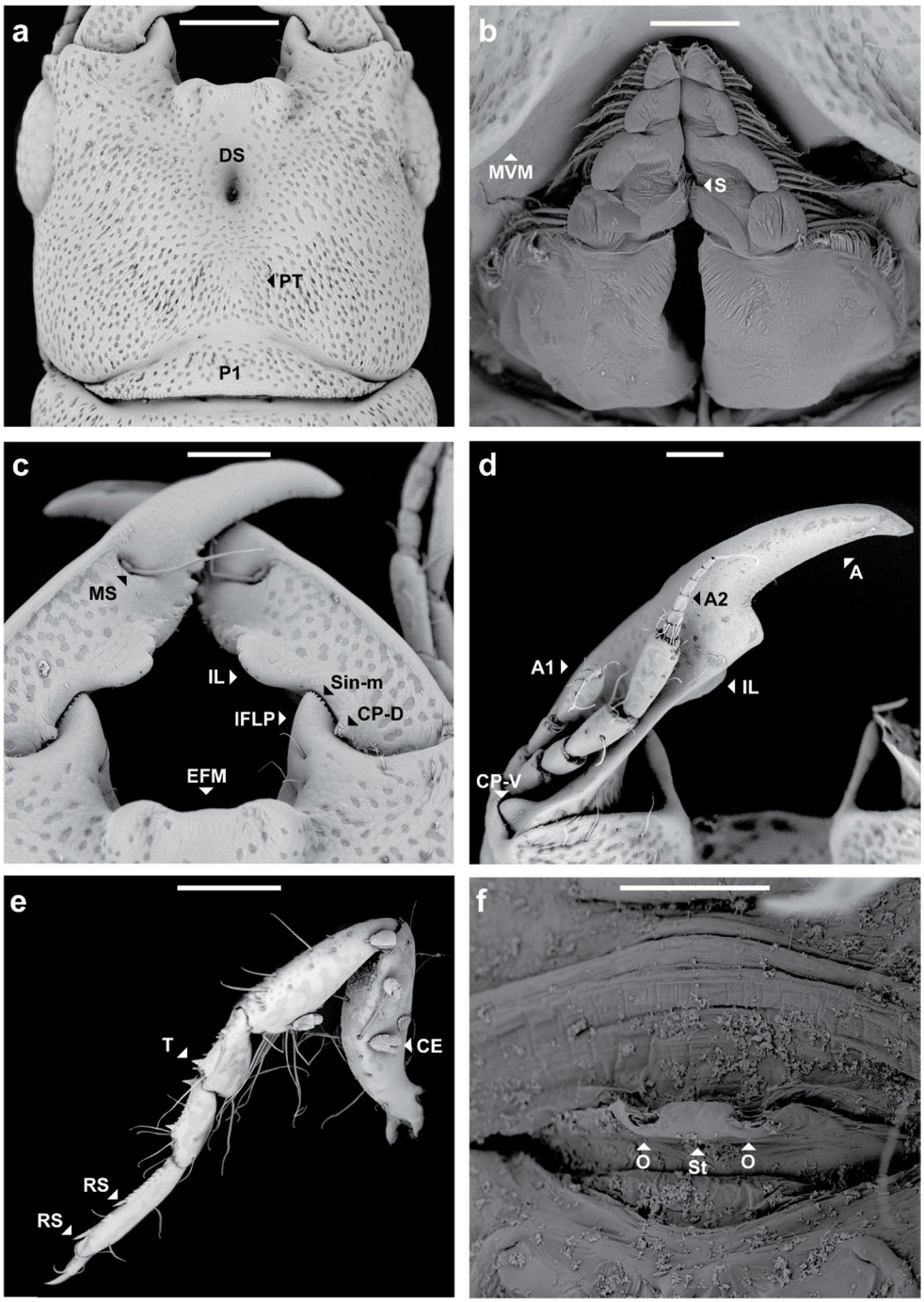

Fig. 4 Scanning electron micrographs of *Elaphognathia alcalai* sp. nov. **a** dorsal cephalon **b** ventral maxillipeds **c** dorsal mandibles **d** ventral mandible with antennae **e** fourth leg with attached ciliate epibionts **f** penial process. Abbreviations: *A* apex; *A1* antennula; *A2* antenna; *CE* ciliate epibionts; *CP-D* conical protrusion, dorsally visible; *CP-V* conical protrusion, ventrally visible; *DS* dorsal sulcus; *EFM* excavated frontal margin; *IFLP* inferior frontolateral process; *IL* internal lobe; *MS* mandibular seta; *MVM* mesioventral margin; *O* opening; *P1* pereonite 1; *PT* posterior tubercle; *RS* robust seta; *S* seta; *Sin-m* sinuate margin; *St* sternal; *T* tubercles. Scale bars: **a**, **e**) 200 µm; **b**, **c**, **d**) 100 µm; **f**) 80 µm

Pereopod 6 with tubercles on merus and carpus; basis 2 times as long as greatest width, superior margin with 12 simple setae, and 2 penicillate setae, inferior margin with 8 setae; ischium 0.85 as long as basis, 2 as long as greatest width, superior margin with 10 setae, inferior margin with 8 setae; merus 0.5 as long as ischium, 1.3 times as long as wide, superior margin with 4 setae, inferior margin with 5 setae, with dense patch of scale-setae; carpus 1 as long as ischium, 2 times as long as wide, superior margin with 2 setae, inferior margin with 5 setae; and 1 robust setae; propodus 1.5 as long as ischium, 4 times as long as wide, superior margin with 4 setae, inferior margin with 2 simple setae, and 2 robust setae; dactylus 0.3 as long as propodus.

Penes (Fig. 4f) contiguous, non-prominent papillae, penial openings almost flush with surface, separated by 50% of sternal width, penial process 0.3 times as long as basal width.

Table 3 Genetic matrix of COI alignment with the percentage similarity below the diagonal division, and the nucleotide p-distances above the diagonal division. Column headings represent the corresponding numbers in the rows

	COI sequences	1	2	3	4	5	6	7	8	9	10	11	12	13
1	***PX625788 Elaphognathia alcalai* sp. nov**	---	0.313	0.334	0.351	0.376	0.388	0.415	0.410	0.418	0.431	0.457	0.467	0.486
2	KX078775 *Elaphognathia sugashimaensis*	74.8	---	0.343	0.393	0.392	0.382	0.400	0.513	0.431	0.401	0.382	0.421	0.482
3	AB713955 *Elaphognathia rangifer*	73.3	72.3	---	0.401	0.499	0.426	0.396	0.508	0.491	0.428	0.338	0.496	0.430
4	AB713957 *Gnathia trimaculata*	71.6	69.1	68.6	---	0.434	0.447	0.456	0.463	0.486	0.364	0.418	0.493	0.469
5	PMACA067-17 *Gnathia maxillaris*	70.6	69.6	64.4	67.2	---	0.436	0.412	0.443	0.424	0.482	0.417	0.564	0.567
6	MW837266 *Gnathia malaysiensis*	69.9	70.1	67.7	65.9	67.4	---	0.381	0.445	0.400	0.441	0.392	0.437	0.494
7	PV213449 *Gnathia tridens*	68.9	69.1	69.4	65.7	68.6	70.6	---	0.375	0.297	0.506	0.422	0.451	0.471
8	MT186595 *Gnathia marleyi*	68.9	63.2	63.5	65.2	67.2	66.9	71.1	---	0.342	0.543	0.478	0.482	0.537
9	OR064533 *Gnathia jimmybuffetti*	67.9	67.4	64.7	64	67.9	69.1	75.6	72.6	---	0.567	0.431	0.454	0.543
10	AB713961 *Gnathia maculosa*	67.2	68.6	67.4	71.6	64.4	66.4	63.5	61.2	60.5	---	0.456	0.495	0.474
11	MW804341 *Gnathia camuripenis*	65.9	70.1	72.8	67.7	68.4	69.4	67.9	65.4	67.9	65.7	---	0.458	0.465
12	AB713956 *Gnathia limicola*	65.2	67.9	64.2	63.7	60.7	66.9	66.2	64.7	66.4	63.7	66.4	---	0.541
13	AF260840 *Cirolana rugicauda*	64.2	64.4	67.4	64.7	60.7	63.7	64.9	61.7	61.7	64.7	65.4	62	---

Pleopod 2 exopod (Fig. 2i) 2.3 as long as wide, distally broadly rounded, with 8 plumose setae; *endopod* twice as long as wide, distally broadly rounded, with 7 plumose setae; appendix masculina absent; peduncle 1.35 times as wide as long, mesial margin with 2 coupling setae, lateral margin with 1 simple seta.

Uropod (Fig. 2h) rami extending beyond pleotelson, apices narrowly rounded. Peduncle with 1 dorsal setae. *Uropod endopod* 2.6 as long as greatest width, dorsally with 4 setae; lateral margin straight or weakly sinuate, lateral margin with 3 simple setae; proximomesial margin weakly convex or sinuate, with 6 long plumose setae. *Uropod exopod* not extending to end of endopod, 3 times as long as greatest width; lateral margin straight or weakly sinuate, with 7 simple setae; proximomesial margin sinuate or weakly convex, with 4 long plumose setae.

Remarks

Although various Gnathiidae species have been described from the Indian Ocean, seven *Elaphognathia* species have been reported from the Central Indo-Pacific: *Elaphognathia amboinenesis* (Cals, 1978) from Indonesia; *E. australis* Svavarsson & Bruce 2012, from Chesterfield reefs, Coral Sea; *E. forceps* (Holdich & Harrison, 1980) from Townsville, Australia; *E. korachaensis* Svavarsson & Gisladottir 2002, from Thailand; *E. queenslandica* Svavarsson & Bruce 2019; from southern Great Barrier Reef, Australia; *E. rangifer* (Monod 1926) from Indonesia; and *E. rimifrons* (Holdich & Harrison, 1980) from Townsville, Australia. None of these species resemble the new species described in the present study.

Compared to species from the rest of the world, the frontal margin and mandibles of the new species is similar to *E. discolor* (Nunomura, 1988), *E. gladia* Kensley, Schotte & Poore, 2009, *E. lucanoides* (Monod 1926), *E. monodi* (Gurjanova, 1936), *E. strombosa* Nunomura, 2012 and *E. sugashimaensis* (Nunomura, 1981) in having excavated frontal margins, equal superior frontolateral processes, and mandibles with inner lobes. Although the superior frontolateral processes in all of the above-mentioned species are equally acute processes, the new species exhibits distinct sinuate superolateral margins, with the distal end reaching the proximal margin of the mandible internal lobe. *Elaphognathia alcalai* sp. nov. also differs in having a large, rounded internal lobe with semi-smooth ridges vs. absent in *E. discolor*, *E. lucanoides*, *E. monodi*, and *E. sugashimaensis*, two lobes in *E. gladia*, and low and weakly sinuate lobe in *E. strombosa*.

Table 4 Genetic matrix of ITS2 alignment with the percentage similarity below the diagonal division, and the nucleotide p-distances above the diagonal division. Column headings represent the corresponding numbers in the rows

	ITS2 sequences	1	2	3	4	5	6
1	PX608478 ***Elaphognathia alcalai* sp. nov.**	---	0.272	0.292	0.318	0.314	0.384
2	AB519159 *Elaphognathia discolor*	60.1	---	0.282	0.304	0.289	0.329
3	AB519156 *Elaphognathia cornigera*	57.2	65.2	---	0.045	0.227	0.353
4	AB519157 *Elaphognathia nunomurai*	56.9	63.8	91.2	---	0.197	0.369
5	AB519158 *Elaphognathia rangifer*	56.7	65.1	69.7	72.4	---	0.444
6	LC642773 *Thaumastognathia bicorniger*	47.7	54.4	54.4	53	48.4	---

Phylogenetic results

Six consensus sequences were generated for the new species for each gene region, with 100% similarity. Sequence length varied from 606 to 690 bp and 635–696 bp for COI and ITS2, respectively. Excluding the outgroups, the resulting alignments included eleven verified (species where the sequence was accompanied by either a description of the gnathiid or clear photos/illustrations to confirm the identity of the species sequenced) Gnathiidae species for COI (Table 3) and four for ITS2 (Table 4). *Cirolana rugicauda* (Cirolanidae) was used as the outgroup in the COI phylogenetic analysis (Fig. 5) (Wetzer 2001). The gnathiid *Thaumastognathia bicorniger* was used to root the ITS analysis (Fig. 6) (Ota et al. 2022). The topology supports species variation, with some clades well supported. At present, there are still very few published gnathiid sequences available, and hence phylogenetic inference for this family is preliminary and incomplete. Based on the COI dataset, the closest congener within *Elaphognathia* is 25.2%, and 39.9% for ITS2, indicating interspecific differentiation.

Discussion

The Philippine archipelago is recognized for its exceptionally high marine biodiversity. Although extensive research in the Visayas region over the past decade has led to the first records of *Gnathia malaysiensis* Müller, 1993, and *G. camuripenis* Tanaka, 2004 in the Philippines, the species described in this study represents the first novel *Elaphognathia* species discovered from this marine biodiversity hotspot (Shodipo et al. 2020, 2021). The majority of species

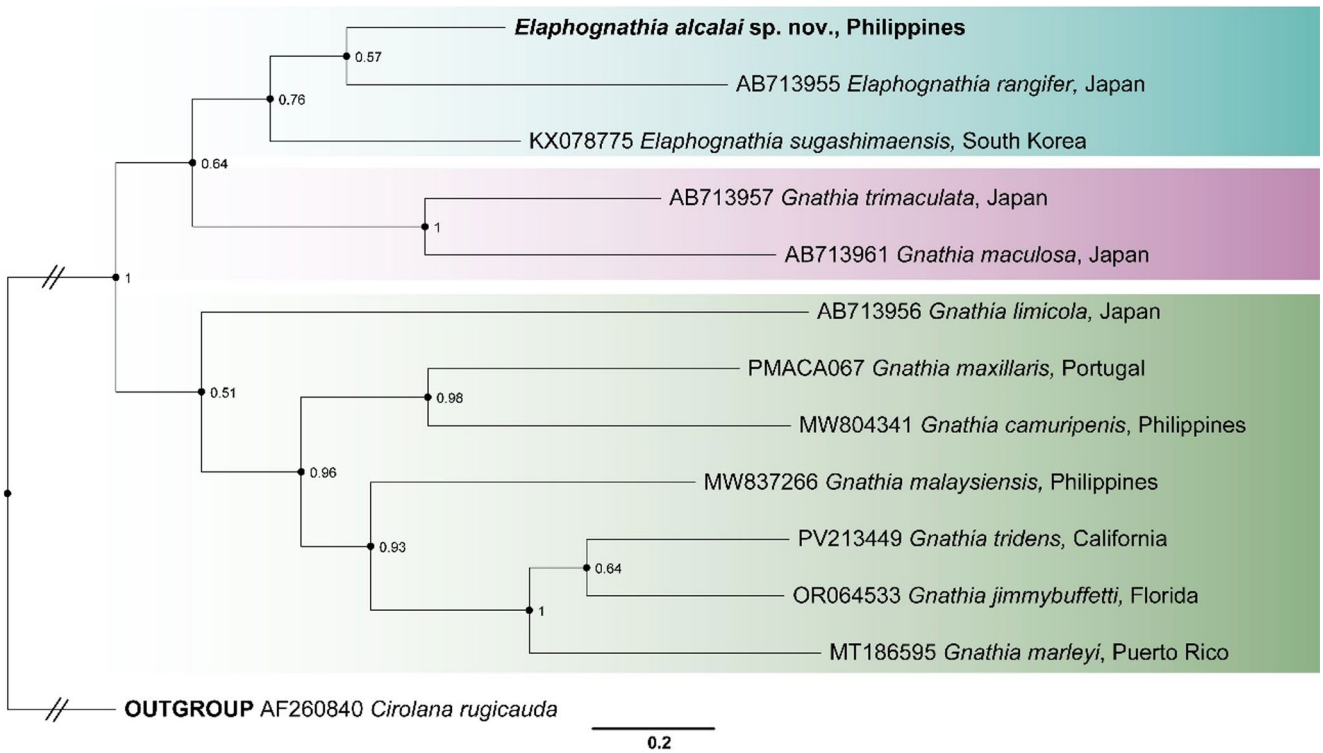

Fig. 5 Bayesian inference (BI) consensus tree for representative sequences of Gnathiidae based on the COI dataset. The novel sequence for *Elaphognathia alcalai* (PX625788) is highlighted in bold. Colored boxes represent *Elaphognathia* (blue), gnathiids infesting elasmobranch hosts (purple) and teleost hosts (green). Nodal support is indicated at the nodes; the scale bar indicates the expected number of substitutions per site

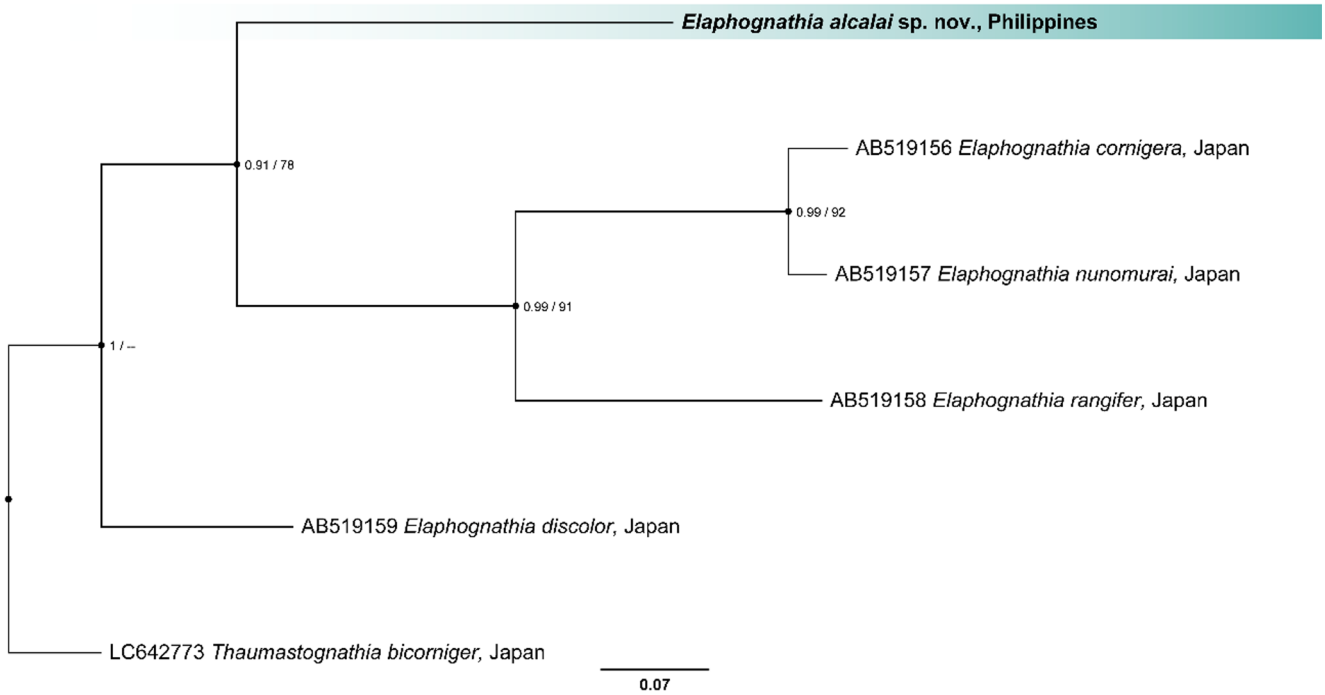

Fig. 6 Bayesian inference (BI) consensus tree for representatives of the genus *Elaphognathia* (PX608478*) based on ITS2 sequences. The novel sequence for *Elaphognathia alcalai* is highlighted in bold. Nodal support for BI and ML is indicated (BL/ML); the scale bar indicates the expected number of substitutions per site

within this genus were reported from the Indian and Pacific Oceans, including Australia (seven species), Indonesia (two species), and Japan (eight species). Thus, the known distribution of *Elaphognathia* ranges mostly along the tropical zone, with some species reaching into the temperate zones; however, this can also be attributed to the investigative focus of these regions and limited knowledge on the morphology of the juveniles in this genus.

This study revealed ciliate epibionts on the leg surface of laboratory-reared male *Elaphognathia alcalai* sp. nov. (Fig. 4e). Previously, similar protozoan and fungal-like structures were reported by Monod (1926) from *Paragnathia formica* (Hesse, 1864), epizoic foraminifers by Svavarsson and Davidsdottir (1994) on *Gnathia stygia* (G. O. Sars, 1877), as well as on wild-caught praniza collected from the evileye blaasop *Amblyrhynchote honckenii* (Bloch, 1785), the pleon of *Gnathia pantherina* Smit & Basson, 2002 male from De Hoop Nature Reserve in South Africa, and the pereon of museum *Gnathia africana* Barnard, 1914 male (Smit and Davies 2004). More dedicated research on the relationship between these epibionts and gnathiid basibionts is needed, as previous reports are limited to observations, and quantitative data are rare.

With *Elaphognathia alcalai* sp. nov., a total of 26 species of *Elaphognathia* have now been described worldwide, with only six—including this species—molecularly characterized over the span of approximately 140 years. This highlights a significant gap in molecular data necessary to enable a more accurate phylogenetic analysis of the genus *Elaphognathia* and the family Gnathiidae as a whole. In addition to the gap in molecular research, larval and adult female morphology is also lacking for most species. This gap is closing as COI and ITS sequences are now available for linking juveniles and females with adult male *Elaphognathia alcalai* sp. nov.

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Author contributions KY—Field collection, rearing and development of specimens, formal analysis, investigation, data curation, microscopy, illustrations, writing—original draft, writing—editing, visualization; NJS—Conceptualization, supervision, resources, investigation, writing—editing; KAH—Conceptualization, supervision, resources, investigation, writing—editing; MOS—field collection, rearing and development of specimens, permits, writing—editing; PCS—Field

collection, rearing and development of specimens, supervision, funding, writing—editing; AE—Investigation, data curation, microscopy, illustrations, writing—editing, visualization, supervision.

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Data availability Data will be made available on request.

Declarations

Permits and ethics Collection of samples was permitted by the Department of Agriculture-Bureau of Fisheries and Aquatic Resources (0154-18 DA-BFAR) in accordance with Philippine laws and regulations (RA 9147; FAO 233), and all methods and protocols were performed as approved by the University of Miami animal ethics committee (23-004 LF). Preserved specimens were shipped to North-West University (NWU) as a donation for further identification, where all methods and protocols were performed as approved by the NWU AnimCare ethics committee (NWU-00784-24-A5).

Competing interests The authors declare no competing interests.

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