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Description of a new genus and species of bopyrid (Isopoda: Epicaridea: Bopyridae) from the pinnotherid crab, *Plenotheres coarctatus* (Bürger, 1895), associated with mangrove clams from Vietnam

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Abstract. Examination of pea crabs, *Plenotheres coarctatus* (Bürger, 1895) (Decapoda: Pinnotheridae), from mangrove clams, *Geloina coaxans* (Gmelin, 1791) (Bivalvia: Cyrenidae), collected in Vietnam led to the discovery of a new genus and species of bopyrid parasite. Herein we describe *Rhizophoracepon magnagibbus*, new genus, new species, females of which are found in the left or right branchial chamber of the pea crab hosts and are distinguished from other pinnotherid bopyrids based on rounded coxal plates with crenulate surfaces and small thin projections, lack of dorsolateral bosses, tergal projections or mid-dorsal projections on the pereomeres, and five pairs of short, subequal digitate biramous pleopods and uniramous lateral plates and uniramous uropods. Males of *R. magnagibbus* are distinguished based on their slightly tapered pleon with the pleomeres splayed out laterally, mid-ventral tubercles on pleomeres 1–4, and broad, widely separated lobes on the pleotelson. These findings expand on our knowledge of the diversity of these poorly known hyperparasites from pinnotherid crabs, which are symbionts of commercially important bivalves.

Key words. bopyrid, Cyrenidae, *Geloina coaxans*, new species, pea crab, Pinnotherinae

INTRODUCTION

Pinnotherid crabs are unusual brachyurans in that most species are symbionts of invertebrate hosts (McDermott, 2009). There are 314 described species of pinnotherids belonging to 63 genera (DecaNet, 2023) but only 23 of these species (~7%) are known to harbour epicaridean isopod parasites (Table 1). As with bopyrids and epicarideans in general (see Williams & Boyko, 2012), this is almost certainly an underestimate of the number of pinnotherid crab species that are parasitized by these isopods, particularly in the Indo-Pacific. To date, only 14 species of epicarideans have been formally described from pinnotherid hosts: two entoniscids and 12 bopyrids (McDermott, 2009; Ahyong & Boyko, 2019; McDermott et al., 2019).

Nearly all pinnotherid crabs or 'pea crabs' are themselves symbionts (some considered to be parasitic) of a wide range of hosts such as molluscs (see Castro, 2015). Among the pinnotherids, some of the symbiotic crabs live in the mantle cavities of bivalves, including commercially important species (McDermott, 2009; de Gier & Becker, 2020; Ng & Ahyong, 2022). For example, the mangrove clam *Geloina coaxans* (Gmelin, 1791) (previously *Polymesoda coaxans*) is an important commercial species in areas of Asia (Fan et al., 2013), where it can be found as a host for the pinnotherid *Plenotheres coarctatus* (Bürger, 1895). Recently, the morphology of *P. coarctatus* was thoroughly reviewed and the species moved from the genus *Pinnotheres* to the newly described genus *Plenotheres* (Ng & Ahyong, 2022). Collections of the mangrove clam *G. coaxans* from markets in Vietnam led to the discovery of several crabs with bopyrid isopods in their branchial chambers.

The purpose of the present paper is to investigate the morphology of the bopyrid parasites from these hosts. After comparison to the known species and genera of bopyrids from pinnotherid crabs, it was determined they constituted a new species and belong in a new genus.

MATERIAL AND METHODS

Camera lucida sketches made of specimens were scanned into a Macintosh™ computer. Images were then prepared using the programmes Adobe Photoshop™ and Adobe Illustrator™. In addition to conventional light micrographs, some specimens were imaged with a Macropod Pro kit (MacroscopicSolutions) and resulting pictures were aligned and stacked with the focus stacking software Zerene Stacker

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Table 1. Epicaridean parasites from pinnotherid crabs and their hosts; ranges and identities of pinnotherid crabs and their hosts primarily derived from Schmitt et al. (1973), McDermott (2009), and de Gier & Becker (2020).

Parasite	Pinnotherid crab host of parasite	Known host(s) of pinnotherid crab	Locality of parasite (range of pinnotherid crab host)	References
Bopyridae				
Dactylokepon hunterae Wells & Wells, 1966	*Tumidotheres maculatus* (Say, 1818) (Pinnotherinae)	Bivalvia: Mytilidae, Pectinidae	North Carolina, USA (western Atlantic)	Wells & Wells, 1966
Heterocepon marginatum Shiino, 1936	*Arcotheres palaensis* (Bürger, 1895) (Pinnotherinae)	Bivalvia: Arcidae, Mactridae, Placunidae	Philippines (Indo-West Pacific)	Janssen & Brandt, 1994
Heterocepon marginatum Shiino, 1936	*Nepinnotheres cardii* (Bürger, 1895)* (Pinnotherinae)	Bivalvia: Cardiidae, Mactridae, Mytilidae, Ostreidae, Pinnidae, Veneridae	Japan (Indo-West Pacific)	Morita, 1952
Heterocepon marginatum Shiino, 1936	*Pinnotheres parvulus* Stimpson, 1858 (Pinnotherinae)	Bivalvia: Pectinidae, Pinnidae, Veneridae	Japan (Indo-West Pacific, Temperate Australasia)	Shiino, 1936a
Hypocepon enoeensis Nierstrasz & Brender à Brendis, 1930	*Nepinnotheres villosulus* (Guérin, 1832) (Pinnotherinae)	Bivalvia: Arcidae, Margaritidae, Pinnidae, Tellinidae, Veneridae	Indonesia (Indo-West Pacific)	Nierstrasz & Brender à Brendis, 1930
Hypocepon enoeensis Nierstrasz & Brender à Brendis, 1930	*Nepinnotheres villosulus* (Guérin, 1832) (Pinnotherinae)	Bivalvia: Arcidae, Margaritidae, Pinnidae, Tellinidae, Veneridae	Timor, Indonesia (Indo-West Pacific)	Jahangir et al., 2015
Hypocepon globosus Markham, 1992	Pinnotheridae (unidentified species) (Pinnotherinae)	unidentified	Hong Kong	Markham, 1992
Onychocepon harpax Pérez, 1921	*Arcotheres palaensis* (Bürger, 1895) (Pinnotherinae)	Bivalvia: Arcidae, Mactridae, Placunidae	Indonesia (Indo-West Pacific)	Pérez, 1921
Onychocepon giardi Nierstrasz & Brender à Brendis, 1923	*Arcotheres palaensis* (Bürger, 1895) (Pinnotherinae)	Bivalvia: Arcidae, Mactridae, Placunidae	Indonesia (Indo-West Pacific)	Nierstrasz & Brender à Brendis, 1923
Onychocepon resupinum Shiino, 1936	*Arcotheres purpureus* (Alcock, 1900) (Pinnotherinae)	Bivalvia: Ostreidae, Veneridae	Japan (Indo-West Pacific)	Shiino, 1936b
Onychocepon resupinum Shiino, 1936	*Arcotheres boninensis* (Stimpson, 1858) (Pinnotherinae)	Bivalvia: Ostreidae	Japan (Indo-West Pacific)	Yasuoka & Yusa, 2017
Rhizophoracepon magnagibbus, new genus, new species	*Plenotheres coarctatus* (Bürger, 1895) (Pinnotherinae)	Bivalvia: Cyrenidae	Vietnam (Indo-West Pacific)	Present study
Rhopalione atrinicola Page, 1985	*Nepinnotheres atrinicola* (Page, 1983) (Pinnotherinae)	Bivalvia: Mytilidae, Pinnidae, Veneridae	New Zealand (Temperate Australasia)	Page, 1985
Rhopalione atrinicola Page, 1985	*Nepinnotheres novaezelandiae* (Filhol, 1885) (Pinnotherinae)	Bivalvia: Mesodesmatidae, Mytilidae, Ostreidae, Veneridae	New Zealand (Temperate Australasia)	Page, 1985

Parasite	Pinnotherid crab host of parasite	Known host(s) of pinnotherid crab	Locality of parasite (range of pinnotherid crab host)	References
Rhopalione incerta (Bonnier, 1900)	unknown	unknown	Madagascar	Bonnier, 1900
Rhopalione kali Ahyong & Boyko 2019	*Serenotheres besutensis* (Serène, 1967) (Pinnotherinae)	Bivalvia: Mytilidae	Malaysia (Indo-West Pacific)	Ahyong & Boyko, 2019
Rhopalione sinensis Markham, 1990	*Arcotheres atrinae* (Sakai, 1939) (Pinnotherinae)	Bivalvia: Pinnidae	Hong Kong (Indo-West Pacific)	Markham, 1990
Rhopalione sinensis Markham, 1990	*Arcotheres sinensis* (Shen, 1932) (Pinnotherinae)	Bivalvia: Mytilidae, Ostreidae, Pectinidae (?), Veneridae	China (Indo-West Pacific)	An et al., 2014
Rhopalione sinensis Markham, 1990	*Arcotheres sinensis* (Shen, 1932) (Pinnotherinae)	Bivalvia: Mytilidae, Ostreidae, Pectinidae (?), Veneridae	Taiwan (Indo-West Pacific)	Kuo et al., 2018
Rhopalione uromyzon Pérez, 1920	*Discorsotheres spondyli* (Nobili, 1905) (Pinnotherinae)	Bivalvia: Spondylidae	Persian Gulf (western Indo-West Pacific)	Pérez, 1920
Rhopalione sp.**	*Discorsotheres subglobosus* (Baker, 1907) (Pinnotherinae)	Bivalvia: Mytilidae, Pectinidae, Spondylidae	South Australia (Temperate Australasia)	Hale, 1927
Rhopalione sp.	*Magnotheres globosus* (Hombron & Jacquinot, 1846) (Pinnotherinae)	Bivalvia: Pinnidae, Veneridae	Singapore (Indo-West Pacific)	Ng & Ahyong, 2022
unidentified bopyrids***	*Arcotheres palaensis* (Bürger, 1895) (Pinnotherinae)	Bivalvia: Arcidae, Mactridae, Placunidae	Indonesia (Indo-West Pacific)	Ng & Ahyong, 2022
unidentified bopyrids***	*Arcotheres rayi* Ahyong & Ng, 2007 (Pinnotherinae)	Bivalvia: Veneridae	Malaysia (Indo-West Pacific)	Ng & Ahyong, 2022
unidentified bopyrid****	*Arcotheres similis* (Bürger, 1895) (Pinnotherinae)	Bivalvia: Mytilidae, Ostreidae, Placunidae	Singapore (Indo-West Pacific)	Ng & Ahyong, 2022
unidentified bopyrid*****	*Glassella arenicola* (Rathbun, 1922) (Pinnixinae)	unknown (assumed Annelida: Arenicolidae)	Curaçao (western Atlantic)	Rathbun, 1924
Entoniscidae				
Pinnixion sexdecennia McDermott, Williams & Boyko, 2019	*Austinixa gorei* (Manning & Felder, 1989) (Pinnixinae)	Axiidea: Callianassidae	Florida, USA (western Atlantic)	McDermott et al., 2019
Pinnixion sexdecennia McDermott, Williams & Boyko, 2019	*Tubicolixa chaetopterana* (Stimpson, 1860) (Pinnixinae)	Annelida: Chaetopteridae, Terebellidae Axiidea: Callianassidae	New Jersey, North Carolina, Florida, USA (western Atlantic)	McDermott et al., 2019
Pinnixion sexdecennia McDermott, Williams & Boyko, 2019	*Zaops ostreum* (Say, 1817) (Pinnotherinae)	Bivalvia: Anomiidae, Mytilidae, Ostreidae, Pectinidae	North Carolina, USA (western Atlantic)	McDermott et al., 2019

Parasite	Pinnotherid crab host of parasite	Known host(s) of pinnotherid crab	Locality of parasite (range of pinnotherid crab host)	References
Pinnotherion vermiforme Giard & Bonnier, 1889	*Pinnotheres pisum* (Linnaeus, 1767) (Pinnotherinae)	Bivalvia: Anomiidae, Cardiidae, Donacidae, Glycymerididae, Mactridae, Myidae, Mytilidae, Nuculidae, Ostreidae, Pharidae, Pinnidae, Psammobiidae, Trigoniidae, Veneridae Chordata: Ascidiacea	France, United Kingdom (northeastern Atlantic, Mediterranean)	Atkins, 1933

*Ng et al. (2019) indicated that the records of *Nepinnotheres cardii* from Japan may refer to more than one species; identification of the host from this region requires verification.
**noted as "large parasitic Isopod (Epicarid) beneath the abdomen".
***multiple hosts infested, may represent more than one parasitic isopod species.
****noted as "females with bopyrids under pleon".
*****noted as "parasite in the left branchial chamber".

(10–65 images from bottom to top of specimens). Carapace length (CL) and width (CW) are provided as an indicator of size for the host crabs; measurements include the bulge caused by the parasite. Isopod size is given as total body length (TL; anterior margin of head to posterior margin of pleotelson). Measurements were made to 0.01 mm using an ocular micrometer. Specimens are deposited in Zoological Reference Collection, Lee Kong Chian Natural History Museum (formerly the Raffles Museum) (ZRC). References are provided for taxonomic authorities of parasite taxa but not for those of hosts; hosts identified by P.K.L. Ng (ZRC).

SYSTEMATICS

Order Isopoda Latreille, 1816

Suborder Epicaridea Latreille, 1825

Family Bopyridae Rafinesque, 1815

Subfamily Keponinae Boyko, Moss, Williams & Shields, 2013

Genus *Rhizophoracepon*, new genus

Type species. *Rhizophoracepon magnagibbus*, new species, by present designation.

Etymology. The genus name is a combination of *Rhizophora*, to denote the mangrove habitat of the host clams and pea crabs, and -*cepon*, a commonly used suffix for bopyrid genera, especially in Keponinae. The gender is masculine.

Diagnosis. Female head subovate, frontal lamina thin and extending to lateral margins of head. Eyes absent. Antennules and antennae with two and five articles each, respectively. Barbula with two slender subequal falcate pointed lateral projections on each side, middle region smooth. Maxilliped with large palp present. Coxal plates on pereomeres 1–7 rounded with crenulate surface and small thin projections; dorsolateral bosses and tergal projections absent. Mid-dorsal projections on pereomeres absent. Oostegites enclosing brood pouch; oostegite 1 with subcircular anterior article, subequal in size to posterior article, internal ridge digitate, posterior article rounded with distolateral triangular projection. Pereopods subequal in structure, posterior pairs slightly longer than anterior. Pleon with six segments, first five pleomeres each bearing a pair of biramous digitate pleopods and uniramous digitate lateral plates, surfaces crenulate. Endopodites, exopodites, and lateral plates subequal in size. Terminal pleomere ending in uniramous uropods, surface smooth, margins slightly crenulate. Male head ovate, distinctly separated from first pereomere. Minute eyes near posterolateral corners. Antennules of three articles each; antennae of six articles each. No pereomeres with mid-ventral tubercles. Pereopods subequal in size and structure except anterior three pairs with longer dactyli. Pleon with six pleomeres. First five pleomeres with low, rounded pleopods bearing nipple-like extension, mid-ventral tubercles present on pleomeres 1–4. Pleomere 6 without uropods, posterolaterally extended into two flat, broad, smooth rami separated by large triangular median indentation.

Remarks. *Rhizophoracepon*, new genus, belongs to Keponinae as the females and males possess all the diagnostic characters of that subfamily (Boyko et al., 2013), particularly the five pairs of lateral plates of the female with weakly tuberculate to filamentous marginal projections. The new genus differs from all others in Keponinae in having females with rounded coxal plates with crenulate surfaces and small thin projections (apomorphy), no dorsolateral bosses, tergal projections or mid-dorsal projections on the pereomeres, and five pairs of short, subequal digitate biramous pleopods and uniramous lateral plates and uniramous uropods. No species in any other keponine genera have this combination of characters. The male has a slightly tapered pleon with the pleomeres splayed out laterally, mid-ventral tubercles on pleomeres 1–4, and broad, widely separated lobes on the pleotelson, a combination of characters that distinguishes it from the males of other keponine genera. Interestingly, the shape of the male pleon is similar to the males of species of *Rhopalione* Pérez, 1920; however, the females of the new genus and species do not show any similarity to those of species of *Rhopalione*.

***Rhizophoracepon magnagibbus*, new species**
(Figs. 1–4)

Type material examined. Holotype: mature female (5.9 mm TL; ZRC 2023.0051), from left branchial chamber of female *Plenotheres coarctatus* (Bürger, 1895) (7.7 mm CL, 10.4 mm CW; ZRC 2022.0054), from mangrove clam, *Geloina* (=*Polymesoda*) *coaxans* (Gmelin, 1791) (Cyrenidae), Dong Rui Mangrove forest, Tien Yen district, Quang Ninh Province, northeastern Vietnam, from Ba Che Market, Ba Che Town, coll. V. T. Ngo, 9–13 March 2022. Allotype: mature male (3.4 mm TL; ZRC 2023.0052), same locality data and host as holotype. Paratypes: mature female (5.7 mm TL), mature male (2.5 mm TL) (ZRC 2023.0053), from left branchial chamber of female *P. coarctatus* (7.8 mm CL, 9.7 mm CW; ZRC 2022.0054), same locality data as holotype; mature female (7.1 mm TL), mature male (3.8 mm TL) (ZRC 2023.0054), from right branchial chamber of female *P. coarctatus* (7.1 mm CL, 11.3 mm CW; ZRC 2022.0054), same locality data as holotype.

Additional material examined. Female *P. coarctatus* (8.9 mm CL, 11.5 mm CW) (ZRC 2022.0055) with right branchial chamber swollen but empty, same locality data as holotype.

Etymology. The species name is a combination of *magna-* (large) and *-gibbus* (hump), in reference to the extremely large bulge that the bopyrid makes in the carapace of the host. Used as an adjective.

Description. Female holotype (ZRC 2023.0051) length 6.2 mm; maximum width (across pereomere 5; not including extended oostegites) 4.0 mm; head length 0.9 mm; head width 1.8 mm; pleon length 1.8 mm. All segments of body distinct (Fig. 2H).

Head subovate, frontal lamina thin and extending to lateral margins of head. Eyes absent. Antennules and antennae with two and five articles each, respectively, terminally setose (Fig. 3A). Barbula with two slender, subequal, falcate pointed lateral projections on each side, middle region smooth (Fig. 3B). Maxilliped with prominent anterior segment, large thick palp present, plectron triangular, short and acute (Fig. 3G).

Pereon broadest across pereomeres 3 and 4. Coxal plates on pereomeres 1–7 rounded with crenulate surface and small thin projections (Figs. 2D, H, 3H), dorsolateral bosses and tergal projections absent. Mid-dorsal projections on pereomeres absent (Fig. 2I). Oostegites enclosing brood pouch (Fig. 2E), oostegite 1 (Fig. 3E, F) with subcircular anterior article, subequal in size to posterior article, internal ridge digitate, posterior article rounded with distolateral triangular projection. Pereopods subequal in structure, posterior pairs slightly longer than anterior (Fig. 3C, D). All pereopods with elongate meri and ischia, and blunt dactyli.

Pleon with six segments, first five pleomeres each bearing a pair of biramous digitate pleopods and uniramous digitate lateral plates, surfaces crenulate (Fig. 3I–L). Endopodites, exopodites, and lateral plates subequal in size. Terminal pleomere ending in uniramous uropods, similar to but broader than fifth pleopods, surface smooth, margins slightly crenulate (Fig. 3K, L).

Male allotype (ZRC 2023.0052) length 3.4 mm; maximum width (across pereomere 3) 1.2 mm; head length 0.3 mm; head width 0.6 mm. All body regions and segments distinct (Figs. 2F, 4A).

Head ovate, distinctly separated from first pereomere (Figs. 2F, 4A). Minute eyes near posterolateral corners (Fig. 4A). Antennules of three articles each; antennae visible beyond margins of head in dorsal view, of six articles each; both bearing setae on two distalmost articles (Fig. 4C).

Pereomeres 2 and 3 subequal in width, patches of pigmentation on pereomeres 2–7 (Fig. 4A). No pereomeres with mid-ventral tubercles. Pereopods subequal in size and structure except anterior three pairs with longer dactyli (Fig. 4B, D, E).

Pleon with six pleomeres, 1 and 2 subequal in width, others each narrower than preceding one (Figs. 2G, 4B). First five pleomeres with low, rounded pleopods bearing nipple-like extension, mid-ventral tubercles present on pleomeres 1–4 (Fig. 4B). Pleomere 6 without uropods, posterolaterally extended into two flat, broad, smooth rami separated by large triangular median indentation (Figs. 2F, G, 4A, B).

Remarks. A total of nine specimens (smallest 9.0 mm CL, 9.4 mm CW; largest 11.8 mm CL, 13.2 mm CW) of *Plenotheres coarctatus* (Bürger, 1895) were collected at the type locality between 9–13 March 2022, four of which bore a male and

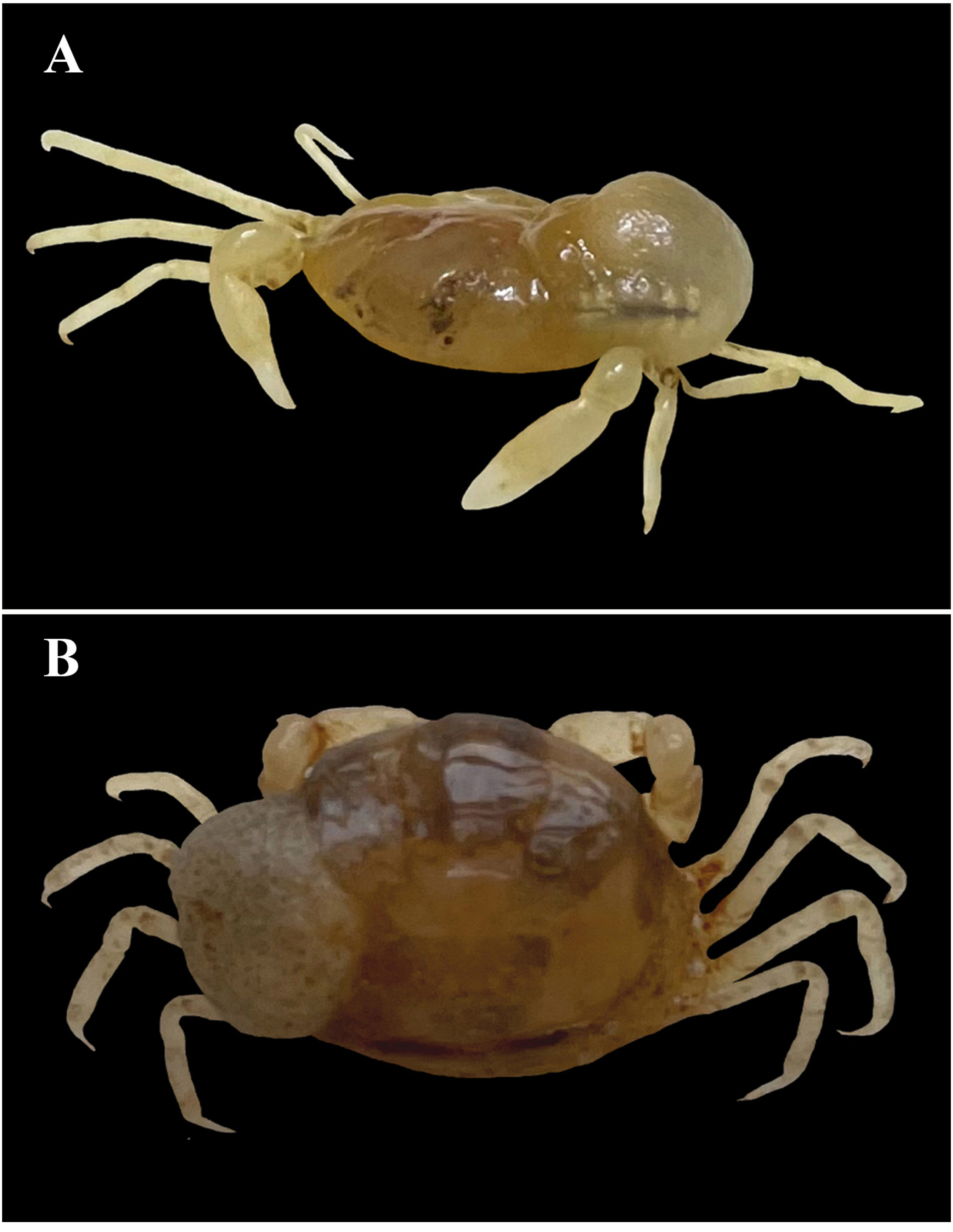

Fig. 1. Live images of the host crab *Plenotheres coarctatus* (Bürger, 1895) and the parasitic isopod *Rhizophoracepon magnagibbus*, new genus, new species. A, *Plenotheres coarctatus*, oblique lateral view showing swelling of left branchial chamber caused by *R. magnagibbus* (male parasite can be seen through swelling by the paired, opaque white dots to side of dark mid-line); B, *Plenotheres coarctatus*, dorsal view showing swelling of left branchial chamber caused by *R. magnagibbus*.

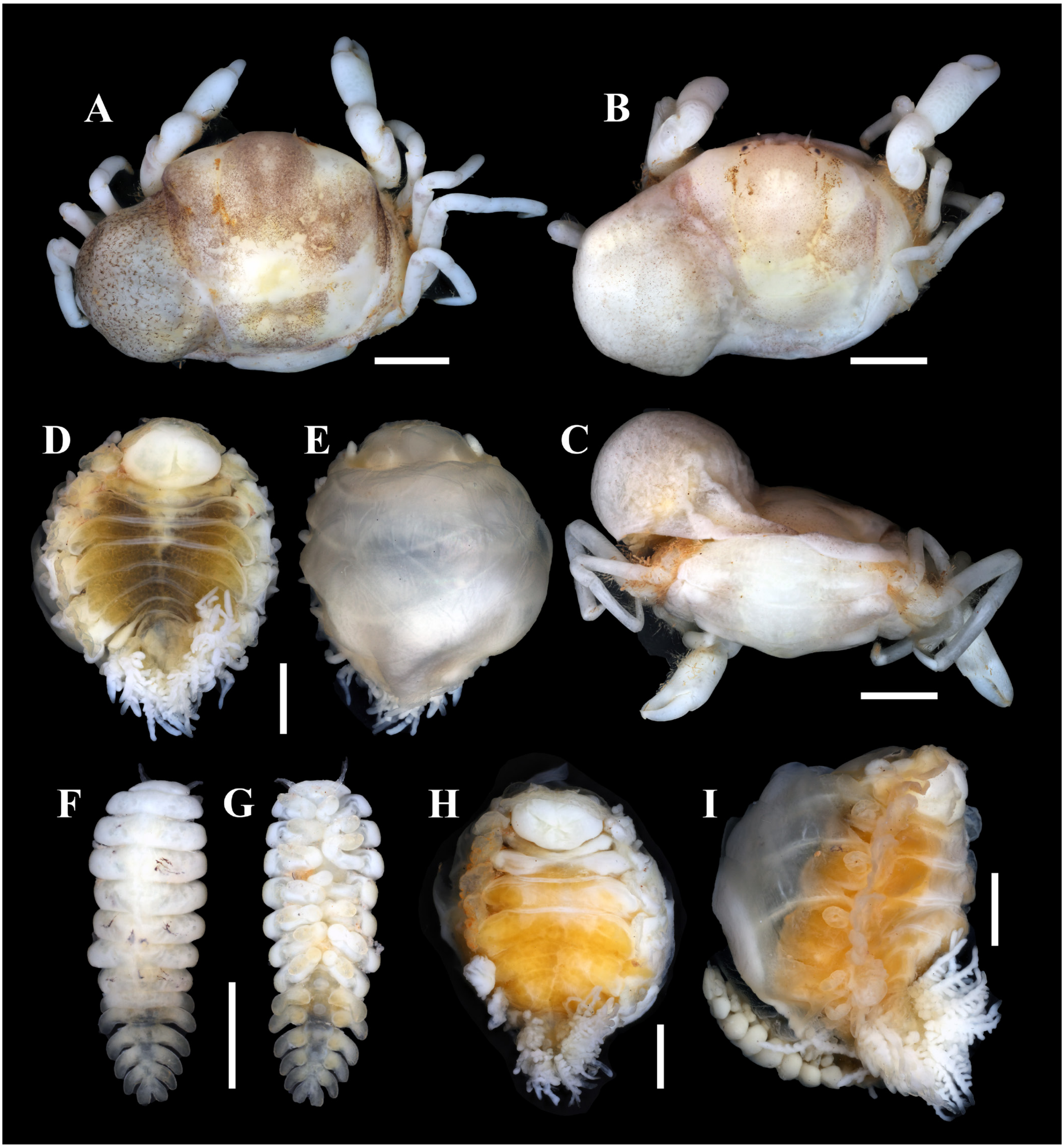

Fig. 2. Light microscope images of the host crab *Plenotheres coarctatus* (Bürger, 1895) (ZRC 2022.0054) and the parasitic isopod *Rhizophoracepon magnagibbus*, new genus, new species. A, *P. coarctatus*, dorsal view showing swelling of left branchial chamber caused by *R. magnagibbus* (ZRC 2023.0053); B, *P. coarctatus* (Bürger, 1895), dorsal view showing swelling of left branchial caused by *R. magnagibbus* (ZRC 2023.0054); C, *P. coarctatus*, posterior view showing vaulted left branchial caused by *R. magnagibbus* (ZRC 2023.0054); D, paratype female, dorsal view (ZRC 2023.0053) from host shown in A; E, paratype female, ventral view from host shown in A; F, allotype male, dorsal view (ZRC 2023.0052); G, allotype male, ventral view (ZRC 2023.0052); H, holotype female, dorsal view (ZRC 2023.0051); I, paratype female and male pair, lateral view (ZRC 2023.0054), from host shown in B, C. Scale bars = 2.5 mm (A–C), 1.25 mm (D, E, H, I), 1 mm (F, G).

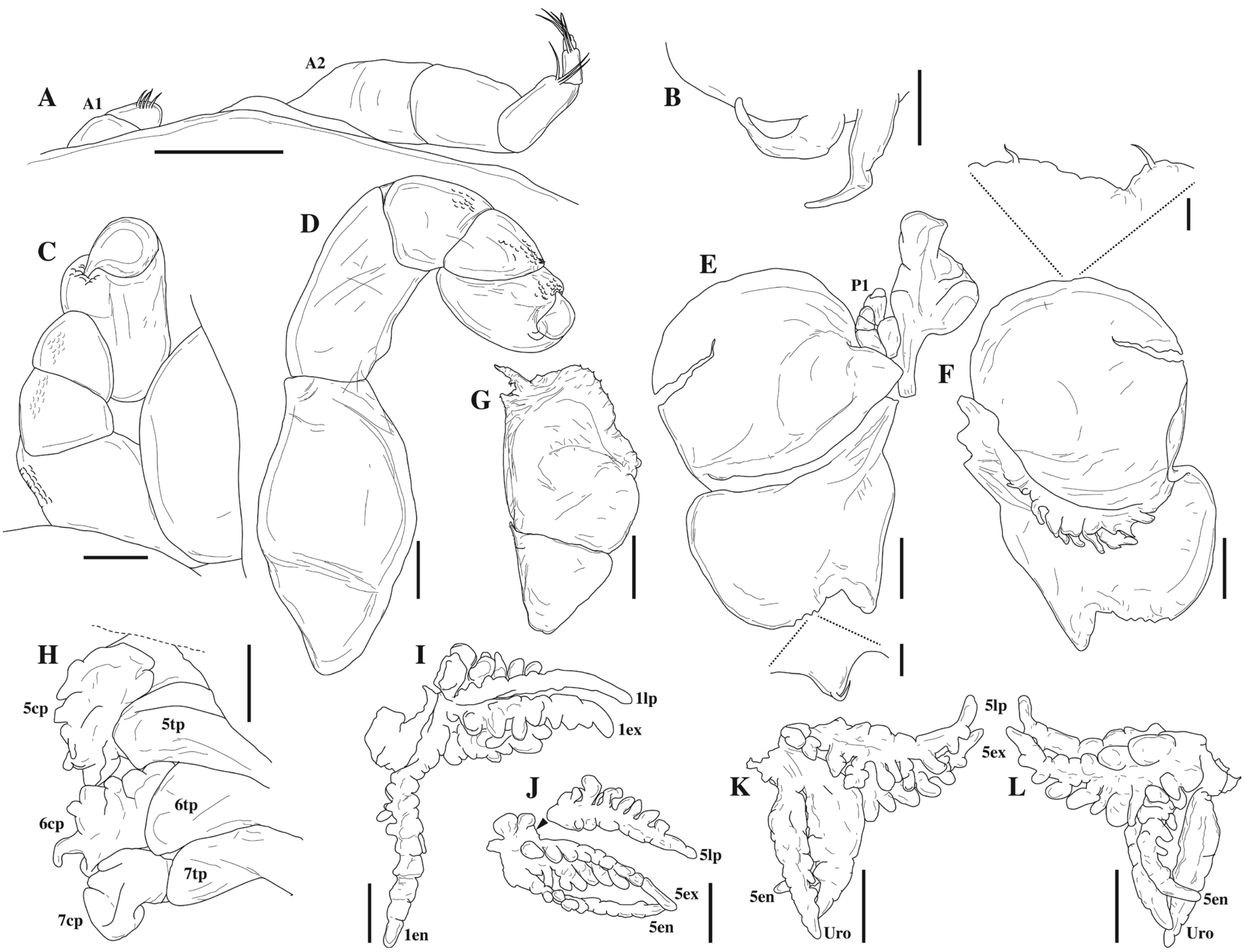

Fig. 3. *Rhizophoracepon magnagibbus*, new genus, new species, paratype females (ZRC 2023.0054). A, left antennule (A1) and antenna (A2); B, left barbula; C, left pereopod 1; D, left pereopod 7; E, left oostegite 1, outer view (dashed lines show close up of setae on posterior lobe); F, left oostegite 1, inner view (dashed lines show close up of setae on anterior lobe); G, left maxilliped, outer view; H, coxal plates and tergal projections on pereomeres 5–7; I, pleopod and lateral plate of pleomere 1, left side, dorsal view; J, pleopod and lateral plate of pleomere 5, left side, dorsal view (arrow shows where lateral plate was attached); K, uropods plus pleopod and lateral plate of pleomere 5 from left side, dorsal view; L, uropods plus pleopod and lateral plate of pleomere 5 from left side, ventral view. (cp = coxal plates, en = endopod, ex = exopod, lp = lateral plate, tp = tergal projections, Uro = uropods). Scale bars = 100 mm (A, C, D), 500 µm (B, E–L), 25 µm (insets of E, F).

female pair of bopyrid isopods in the branchial chamber or showed evidence of prior infestation. The parasitized side of the carapace is greatly deformed (Figs. 1, 2A–C). For example, in one host specimen (ZRC 2022.0054) the width of the carapace is ~7% wider (7.1 mm versus about 7.6 mm) when the extension caused by the parasitic isopod is added and thickness is ~58% greater (5.7 mm versus 9.0 mm).

Ecology. The Dong Rui Mangrove forest is a brackish water environment (ca. 24.5–29.1‰; Nguyen et al., 2020). From a collection in this region (March 2013, Tien Yen District, Quang Ninh province, Vietnam), the pea crab *P. coarctatus* was found in approximately 3% of larger mangrove clams (20 pea crabs found in 25 kg of dissected clams of sizes 22–25 individuals/kg) and smaller clams (five pea crabs found in 5 kg of dissected clams of sizes 30–35 individuals/kg). Overall prevalence of hyperparasitic isopods was 20% (5 of the total 25 pea crabs infested) in this sample. However, none of the pea crabs from the larger clams were infested with hyperparasitic isopods, whereas all five pea crabs from the smaller clams were infested with hyperparasitic isopods (significantly different from a predicted equal distribution: $p < 0.001$ Fisher Exact Probability Test). The larger and smaller clams were from the same clutch (i.e., same age). We cannot definitely state the pea crabs from the 2013 collection were infested with *Rhizophoracepon magnagibbus*, new genus, new species, as other yet undiscovered bopyrids may infest this host, but based on the locality and host, this is the most likely hyperparasitic isopod present.

DISCUSSION

Although *Rhizophoracepon magnagibbus*, new genus, new species, is presently only known from Vietnam, the geographic range of its host crab *Plenotheres coarctatus* spans the Philippines, Indonesia, Peninsular Malaysia, Singapore, and Thailand. In this region the pea crabs are

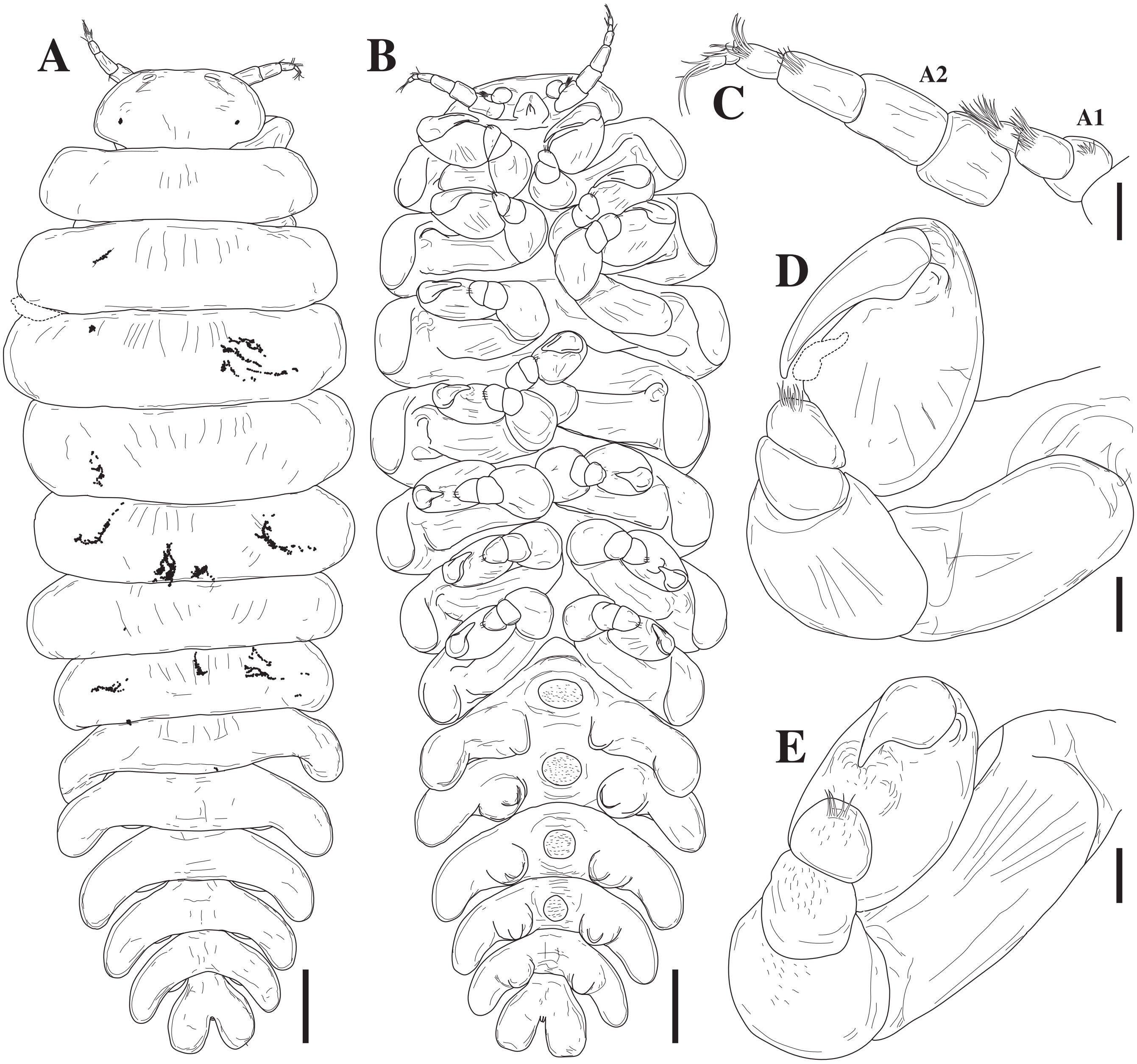

Fig. 4. *Rhizophoracepon magnagibbus*, new genus, new species, allotype male (ZRC 2023.0052). A, dorsal view; B, ventral view; C, right antennule (A1) and antenna (A2); D, left pereopod 1; E, left pereopod 7. Dashed lines in A, D indicate debris adhering to specimen. Scale bars = 250 µm (A, B), 50 µm (C–E).

often rare in collections of the bivalves, although prevalence can be quite variable based on location of collection (Ng & Ahyong, 2022) and the prevalence of *R. magnagibbus* among these crabs is known only from a single collection where 20% of pea crabs had the hyperparasite (see Ecology section for detailed notes). For the few pinnotherid bopyrids investigated, the prevalence of hyperparasites is reported as low to moderate levels (~2–22%); for example, the bopyrid *Heterocepon marginatum* Shiino, 1936a was in 2.4% of the pea crab *Arcotheres palaensis* (Bürger, 1895) from *Anadara maculosa* (Reeve, 1844) (Janssen & Brandt, 1994), the bopyrid *Onychocepon resupinum* Shiino, 1936b was found in 11.8% of the pea crab *Arcotheres boninensis* (Stimpson, 1858) from the oyster *Saccostrea kegaki* Torigoe & Inaba, 1981 (Yasuoka & Yusa, 2017), and the bopyrid isopod *Rhopalione sinensis* Markham, 1990 was found in 7.7–22.1% of *Arcotheres sinensis* (Shen, 1932) from the oyster *Magallana angulata* (Lamarck, 1819) (Kuo et al., 2018).

The pea crab *P. coarctatus* occurs in two mangrove bivalves (*Geloina coaxans* and *Glauconome* spp.) representing two different families of Cyrenoidea (Ng & Ahyong, 2022). Nothing is known of any potential differences in bopyrid isopod infestation rates of the pea crab hosts in these morphologically distinct bivalves, and future studies could examine host crab and clam specificity. The mangrove clam *G. coaxans* is known to be an important member of the mangrove ecosystem, feeding on mangrove detritus and serving to transfer energy to higher trophic levels (Bachok et al., 2003; Nguyen et al., 2012). However, the impacts of pinnotherids on these hosts has not been quantitatively studied. As in other ecosystems, the impacts of parasites are often overlooked and largely underestimated (see Lafferty et al., 2006; Carlson et al., 2020 and references therein); this is particularly true of "Swiftian symbioses" (Boyko & van der Meij, 2018) where the interactions of primary symbionts (pinnotherids) and their hyperparasites (bopyrids) is poorly known. Yasuoka & Yusa (2017) found that male pea crabs were significantly more often infested by bopyrids and suggested these larger crabs may consequently become trapped in the oyster hosts; thus, the hyperparasites could have negative short-term impacts on the oysters (including lowering their wet weight). In the present study, preliminary data shows that infested crabs were more often found in smaller clam hosts, which may be further evidence that the hyperparasites negatively impact growth of the clams or that, after infestation, crabs are more readily trapped in smaller host clams. However, research is needed to determine cause and effect in this system (i.e., the hyperparasites may not be the cause of the reduced host clam size or trapping of crabs, rather it is possible that smaller clams more often come to harbor the hyperparasites due to some factor which enhances larval isopod settlement in these clams). It should be noted, as Yasuoka & Yusa (2017) indicated, that bopyrids reduce the reproduction of the pea crabs and therefore could have positive long-term impacts on the oysters by reducing the prevalence of the pea crabs, although this remains to be demonstrated at the population level. Future studies should expand on such research and experimentally investigate how bopyrid parasites might mediate the impacts of pea crabs on clam hosts.

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LITERATURE CITED

Ahyong, ST & Boyko CB (2019) *Rhopalione kali* sp. nov., first known epicaridean parasite on the Malaysian pinnotherid crab, *Serenotheres besutensis* (Serène, 1967). Zootaxa, 4950(2): 283–288.

An J, Niu X, Markham JC & Jiang X (2014) First record and description of male *Rhopalione sinensis* Markham, 1990, from China, with remarks on genus *Rhopalione* Pérez, 1920 (Crustacea: Isopoda: Bopyridae). Chinese Journal of Oceanology and Limnology, 32(3): 1–4.

Atkins D (1933) *Pinnotherion vermiforme* Giard and Bonnier, an entoniscid infecting *Pinnotheres pisum*. Proceedings of the General Meetings for Scientific Business of the Zoological Society of London, 1933(2): 319–63, pls. 1–4.

Bachok Z, Mfilinge PL & Tsuchiya M (2003) The diet of the mud clam *Geloina coaxans* (Mollusca, Bivalvia) as indicated by fatty acid markers in a subtropical mangrove forest of Okinawa, Japan. Journal of Experimental Marine Biology and Ecology, 292: 187–197.

Bonnier J (1900) Contribution a l'étude des épicarides. Les Bopyridae. Travaux de La Station Zoologique de Wimereux, 8: 1–476, pls. 1–41.

Boyko CB, Moss J, Williams JD & Shields JD (2013) A molecular phylogeny of Bopyroidea and Cryptoniscoidea (Crustacea: Isopoda). Systematics and Biodiversity, 11: 495–506. https://doi.org/10.1080/14772000.2013.865679

Boyko CB & van der Meij SET (2018) A trifecta of Swiftian symbioses: stony corals, gall crabs and their parasites (Scleractinia; Brachyura: Cryptochiridae; Isopoda: Epicaridea and Cirripedia: Rhizocephala). Zoological Journal of the Linnean Society, 184(2): 304–329.

Carlson CJ, Hopkins S, Bell KC, Doña J, Godfrey SS, Kwak ML, Lafferty KD, Moir ML, Speer KA, Strona G, Torchin M & Wood CL (2020) A global parasite conservation plan. Biological Conservation, 250: 108596. https://doi.org/10.1016/j.biocon.2020.108596

Castro P (2015) Symbiotic Brachyura. In: Castro P, Davie PJF, Guinot D, Schram FP & Von Vaupel Klein JC (eds.) Treatise on Zoology—Anatomy, Taxonomy, Biology, The Crustacea, vol. 9C. Brill, Leiden, pp. 543–581.

DecaNet (eds.) (2023) DecaNet. Pinnotheridae De Haan, 1833. https://www.marinespecies.org/aphia.php?p=taxdetails&id=106775 (Accessed through World Register of Marine Species, 10 July 2023).

Fan H, He B & Pernetta JC (2013) Mangrove ecofarming in Guangxi Province China: an innovative approach to sustainable mangrove use. Ocean & Coastal Management, 85: 201–208. https://doi.org/10.1016/j.ocecoaman.2013.04.009

de Gier W & Becker C (2020) A review of the ecomorphology of pinnotherine pea crabs (Brachyura: Pinnotheridae), with an updated list of symbiont-host associations. Diversity, 12(11): 431. https://doi.org/10.3390/d12110431

Hale HM (1927) The Crustaceans of South Australia Part I. Government Printer, Adelaide, 201 pp.

Jahangir S, Siddiqui G, Ayub Z & Boyko CB (2015) New record of the pea crab *Nepinnotheres villosulus* (Guérin-Meneville, 1831) (Brachyura: Pinnotheridae) from clams and cockles of Pakistan (northern Arabian Sea). Marine Biodiversity Records, 8: e135.

Janssen HH & Brandt A (1994) *Heterocepon marginatum* Shiino, 1936, (Crustacea: Isopoda: Epicaridea: Bopyridae) a new hyperparasite from the Philippines, and a short review of the biology of the Bopyridae. The Philippine Scientist, 31: 5–31.

Kuo A-L, Lin F-J, Hsu J-T, Chan Y-S & Ueng T-T (2018) The population structure and parasitic relationships of oyster (*Crassostrea angulata*), *Arcotheres sinensis* (Pinnotheridae), and *Rhopalione sinensis* (Bopyridae) at the oyster reefs of western Taiwan. Crustaceana, 91(12): 1433–1451.

Lafferty KD, Dobson AP & Kuris AM (2006) Parasites dominate food web links. Proceedings of the National Academy of Sciences, 103(30): 11211–11216.

Latreille PA (1816) Le Règne Animal Distribuè d'Après son Organisation, pour Servir de Base a l'Histoire Naturelle des Animaux et d'Introduction a l'Anatomie Comparée. Volume 3. Les Crustacés, les Arachnides et les Insectes. Deterville, Paris, xxix + 653 pp.

Latreille PA (1825) Familles naturelles du règne animal, exposé succinctement et dans un ordre analytique avec l'indication de leurs genres. J. B. Baillière, Paris, 570 pp.

Markham JC (1990) Further notes on the Isopoda Bopyridae of Hong Kong. In: Morton B (ed.) Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 1986. Volume 2. Hong Kong University Press, Hong Kong, pp. 555–568.

Markham JC (1992) Second list of additions to the Isopoda Bopyridae of Hong Kong. In: Morton B (ed.) The Marine Flora and Fauna of Hong Kong and Southern China III. Proceedings of the Fourth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 11–29 April 1989. Volume 1. Hong Kong University Press, Hong Kong, pp. 277–302.

McDermott JJ (2009) Hypersymbioses in the pinnotherid crabs (Decapoda: Brachyura: Pinnotheridae): a review. Journal of Natural History, 43: 785–805.

McDermott JJ, Williams JD & Boyko CB (2019) A new genus and species of parasitic isopod (Bopyroidea: Entoniscidae) infesting pinnotherid crabs (Brachyura: Pinnotheridae) on the Atlantic coast of the USA, with notes on the life cycle of entoniscids. Journal of Crustacean Biology, 40(1): 97–114.

Morita S-I (1952) The effects of epicaridization on the external characters of a pinnotherid crab (*Pinnotheres cardii* Buerger). Dobutsugaku Zasshi, 61(2): 22–26.

Ng PKL & Ahyong ST (2022) The pea crab genus *Arcotheres* Manning, 1993 (Crustacea: Brachyura: Pinnotheridae) from Singapore and Peninsular Malaysia, with a reappraisal of diagnostic characters and descriptions of two new genera. Raffles Bulletin of Zoology, 70: 134–248.

Ng PKL, Ahyong ST & Clark PF (2019) The identity of *Pinnotheres socius* Lanchester, 1902 (Decapoda, Brachyura, Pinnotheridae). Crustaceana, 92(6): 685–692.

Nguyen TT, Hamaoka H, Sogabe A, Tran ĐQ, Mai TN & Omori K (2012) Food sources of macro-invertebrates in an important mangrove ecosystem of Vietnam determined by dual stable isotope signatures. Journal of Sea Research, 72: 14–21.

Nguyen TT, Nguyen ĐT & Mai TN (2020) Carbon storage potential of mangrove forests from Northeastern Vietnam. Regional Studies in Marine Science, 40: 101516. https://doi.org/10.1016/j.rsma.2020.101516

Nierstrasz HF & Brender à Brandis GA (1923) Die Isopoden der Siboga-Expedition. II. Isopoda Genuina. I. Epicaridea. Siboga-Expeditie, 32b: 57–121, pls. 4–9.

Nierstrasz HF & Brender à Brandis GA (1930) Résultats scientifiques du voyage aux Indes Orientales Néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. Isopoda Epicaridea. Mémoires du Musée Royal d'Histoire Naturelle de Belgique (Hors Série), 3(1)(II): 12–17.

Page RDM (1985) Review of the New Zealand Bopyridae (Crustacea: Isopoda: Epicaridea). New Zealand Journal of Zoology, 12: 185–212.

Pérez C (1920) Sur un type nouveau d'Epicarides, *Rhopalione uromyzon* n. g. n. sp. parasite sous-abdominal d'un Pinnothère Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, 170: 1615–1617.

Pérez C (1921) Sur un céponien nouveau, *Onychocepon harpax* (n. g., n. sp.), parasite branchial d'un pinnothère. Comptes Rendus Hebdomadaires de l'Academie des Sciences de Paris, 176(2): 59–61.

Rafinesque CS (1815) Analyse de la Nature ou Tableau de l'Univers et des Corps Organisés. Palerme, pp. 1–124.

Rathbun MJ (1924) Resultaten eener reis van Dr. C.J. van Der Horst in 1920. Brachyuran crabs collected at Curaçao. Bijdragen tot de Kennis der Fauna van Curaçao, 23: 13–21.

Schmitt WL, McCain JC & Davidson ES (1973) Pars 3. Decapoda I Brachyura I: Fam. Pinnotheridae. In: Gruner H-E & Holthius LB (eds.) Crustaceorum Catalogus. W. Junk, Den Haag [= The Hague], 160 pp.

Shiino SM (1936a) Bopyrids from Shimoda and other districts. Records of Oceanographic Works in Japan, 8(1): 161–176.

Shiino SM (1936b) Bopyrids from Tanabe Bay III. Memoirs of the College of Science, Kyoto Imperial University, Series B, 11(3): 157–174.

Wells MJ & Wells HW (1966) *Dactylokepon hunterae* and *Bopyrina pontoniae*, two new species of bopyrid isopods from North Carolina. Crustaceana, 11(1): 53–60.

Williams JD & Boyko CB (2012) The global diversity of parasitic isopods associated with crustacean hosts (Isopoda: Bopyroidea and Cryptoniscoidea). PLoS ONE, 7(4): e35350. https://doi.org/10.1371/journal.pone.0035350

Yasuoka N & Yusa Y (2017) Effects of a crustacean parasite and hyperparasite on the Japanese spiny oyster *Saccostrea kegaki*. Marine Biology, 164: 217. https://doi.org/10.1007/s00227-017-3250-6