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New records of bopyrid parasites (Crustacea, Isopoda, Epicaridea) of pea crabs (Crustacea, Decapoda, Pinnotheridae) with descriptions of two new species of *Rhopalione* Pérez, 1921 and a review of the genus

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Couverture / *Cover* :
Heterocepon marginatum Shiino, SMF-ZMG948b female in host *Arcotheres palaensis* (Bürger, 1895).

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New records of bopyrid parasites (Crustacea, Isopoda, Epicaridea) of pea crabs (Crustacea, Decapoda, Pinnotheridae) with descriptions of two new species of *Rhopalione* Pérez, 1921 and a review of the genus

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ABSTRACT
Pea crabs (Decapoda, Pinnotheridae De Haan, 1833) are host to multiple species of ectoparasitic (Bopyridae Rafinesque, 1815) and endoparasitic (Entoniscidae Kossmann, 1881) isopods worldwide. Among bopyrids, species of *Rhopalione* Pérez, 1921 are unusual in residing under the pleon of their pea crab hosts. Five species of *Rhopalione*, all reviewed in the present report, were previously known as parasites of pinnotherid crabs, themselves symbionts of bivalve mollusks from localities worldwide. Type material of *R. uromyzon* Pérez, 1920 and *R. incerta* (Bonnier, 1900) was examined and redescribed. Specimens of *R. atrinicolae* Page, 1985 were obtained from the stomach of a gummy shark, *Mustelus antarcticus* Günther, 1870, representing perhaps the first record of a bopyrid from the gut of any species of fish. Two new species of *Rhopalione*, *R. racemus* n. sp. and *R. rusa* n. sp., are described from pea crabs collected in South Australia and Singapore, respectively. They mostly differ in the form of the pleopods and lateral plates of females (long and slender in *R. rusa* n. sp. vs short and broad in *R. racemus* n. sp.) and midventral tubercles of males (*R. rusa* n. sp. with tubercles present on pleomeres 1-4 vs *R. racemus* n. sp. which lacks tubercles). A key for all species of *Rhopalione* and a discussion of the relationships between this genus and other pseudionine genera are provided. Additionally, three new records (*Dactylokepon* cf. *hunterae* Wells & Wells, 1966, *Heterocepon marginatum* Shiino, 1936, and *Onychocepon harpax* Pérez, 1921) and notes on two species (*H. globusus* (Markham, 1992) n. comb. and *O. giardi* Nierstrasz & Brender à Brandis, 1923) of branchial bopyrid parasites of pea crabs are included. Finally, a table of all epicaridean isopods (Bopyridae and Entoniscidae) known from pea crabs is provided with discussion of their global diversity in hopes of inspiring investigations on this understudied group.

KEY WORDS
Bivalves,
hypersymbiosis,
parasitism,
pinnotherid,
Pseudioninae,
revision,
new records,
new combination,
new species.

RÉSUMÉ
Nouvelles signalisations de parasites bopyrides (Crustacea, Isopoda, Epicaridea) de crabes petits pois (Crustacea, Decapoda, Pinnotheridae) avec la description de deux nouvelles espèces de Rhopalione *Pérez, 1921 et une révision du genre.*
Les crabes petits pois (Decapoda, Pinnotheridae De Haan, 1833) sont les hôtes de nombreuses espèces d'isopodes ectoparasites (Bopyridae Rafinesque, 1815) et endoparasites (Entoniscidae Kossmann, 1881) dans le monde entier. Parmi les bopyridés, les espèces de *Rhopalione* Pérez, 1921 ont la particularité de résider sous le pléon de leurs hôtes, les crabes petits pois. Cinq espèces de *Rhopalione*, toutes examinées dans cet article, étaient auparavant connues comme parasites de crabes pinnotherides, eux-mêmes symbiotes de mollusques bivalves dans des localités du monde entier. Le matériel type de *R. uromyzon* Pérez, 1920 et de *R. incerta* (Bonnier, 1900) a été examiné et est redécrit. Des spécimens de *R. atrinicolae* Page, 1985 ont été obtenus à partir de l'estomac d'un requin gommeux, *Mustelus antarcticus* Günther, 1870, ce qui représente peut-être le premier signalement d'un bopyride dans l'estomac d'une espèce de poisson. Deux nouvelles espèces de *Rhopalione*, *R. racemus* n. sp. et *R. rusa* n. sp., sont décrites à partir de crabes petits pois collectés en Australie du Sud et à Singapour, respectivement. Elles diffèrent principalement par la forme des pléopodes et des plaques latérales des femelles (longues et minces chez *R. rusa* n. sp. vs de courtes et larges chez *R. racemus* n. sp.) et des tubercules médio-ventraux des mâles (*R. rusa* n. sp. avec des tubercules présents sur les pléomères 1-4 contrairement à *R. racemus* n. sp. qui n'a pas de tubercules). Une clé pour toutes les espèces de *Rhopalione* et une discussion sur les relations entre ce genre et d'autres genres de pseudionines sont fournies. En outre, trois nouvelles signalisations (*Dactylokepon* cf. *hunterae* Wells & Wells, 1966, *Heterocepon marginatum* Shiino, 1936 et *Onychocepon harpax* Pérez, 1921) et des notes sur deux espèces (*H. globusus* (Markham, 1992) n. comb. et *O. giardi* Nierstrasz & Brender à Brandis, 1923) de bopyrides parasites des branchies des crabes petits pois, sont inclues. Enfin, un tableau de tous les isopodes épicarides (Bopyridae et Entoniscidae) connus des crabes petits pois est présenté avec une discussion sur leur diversité globale dans l'espoir d'inspirer des recherches sur ce groupe sous-étudié.

MOTS CLÉS
Bivalves,
hypersymbiose,
parasitisme,
Pinnotheridae,
Pseudioninae,
révision,
signalisations nouvelles,
combinaison nouvelle,
espèces nouvelles.

INTRODUCTION

Most species of pinnotherid crabs are symbionts of invertebrate hosts, with some considered to be parasitic (McDermott 2009). There are 299 described species of pinnotherids belonging to 60 genera (DecaNet 2023; Poore & Ahyong 2023) but only 22 of these species (*c.* 7%) are known to be parasitized by epicaridean isopods belonging to Bopyridae Rafinesque, 1815 and Entoniscidae Kossmann, 1881 (McDermott 2009; Boyko *et al.* 2008 onwards; Table 1). This is undoubtedly an underestimate of the number of pea crab species that are parasitized by epicarideans, particularly in the Indo-Pacific (see Williams & Boyko 2012); this underestimate is typical of parasite diversity and prevalence in many habitats (e.g., Lafferty *et al.* 2006). To date, 15 species of epicaridean hyperparasites, including two entoniscids and 13 bopyrids, have been described from pinnotherid hosts (Williams *et al.* 2023).

Species of the genus *Rhopalione* Pérez, 1921 occupy an unusual habitat for bopyrid parasites of decapods, occurring under the pleon rather than in the branchial chamber. Five species have been described in this genus; all known or presumed to be parasites of pinnotherid crabs, which themselves are symbionts (some considered to be parasitic; see Castro 2015) of a wide range of hosts, including bivalve mollusks. All species of *Rhopalione* appear to be very rare and most have not been reported since their original descriptions. Two species, including the type species, were not described or illustrated in detail and, consequently, later comparisons with other species proved difficult (Page 1985; Markham 1990). Fortunately, type material of both these poorly described species were found in the collections of the Museum national d'Histoire naturelle, Paris (MNHN). Although the holotype of one taxon, *R. incerta* (Bonnier, 1900), is in very poor condition, ample syntypic material of the type species, *R. uromyzon* Pérez, 1920, was found to permit redescription of the species and allow comparison with its congeners.

The present paper is a follow up to Williams *et al.* (2023) and provides the description of two new species of *Rhopalione* and additional new records of three species of other Pacific pinnotherid parasites, as well as a preliminary identification of one further record of a parasite from an Atlantic pinnixine pea crab. We also review the species in the enigmatic genus *Rhopalione*. A discussion is provided regarding the habitat of the parasites, the possible identity of a *nomen nudum*, and the relationships between *Rhopalione* and other pseudionine genera. A key is also given for all species of *Rhopalione*.

MATERIAL AND METHODS

Camera lucida sketches made of specimens were scanned into a Macintosh™ computer. Images were then prepared using the programs 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 (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. References are provided for taxonomic authorities of parasite taxa but not for those of hosts.

ABBREVIATIONS

Institutions

AMS	Australian Museum, Sydney;
MNHN	Muséum national d'Histoire naturelle, Paris;
NHMD	Natural History Museum of Denmark, Copenhagen;
NIWA	National Institute of Water & Atmospheric Research, Wellington, New Zealand;
NMNZ	Te Papa Tongarewa National Museum of New Zealand, Wellington;
SAM	South Australian Museum, Adelaide;
USNM	National Museum of Natural History, Smithsonian Institution, Washington D. C.

SYSTEMATICS

Order ISOPODA Latreille, 1816
Suborder EPICARIDEA Latreille, 1825
Family BOPYRIDAE Rafinesque, 1815
Subfamily KEPONINAE Boyko, Moss, Williams & Shields, 2013

Genus *Dactylokepon* Stebbing, 1910

TYPE SPECIES. — *Dactylokepon richardsonae* Stebbing, 1910, by subsequent designation.

Dactylokepon cf. ***hunterae*** Wells & Wells, 1966

"parasite in the left branchial chamber" – Rathbun 1924: 17.

"unidentified branchial parasite" – McDermott 2009: 790 [mention of Rathbun's record].

TABLE 1. — Records of parasitic isopods (Isopoda, Epicaridea) from pinnotherid hosts (Decapoda, Pinnotheridae) with localities of the parasites, host crab ranges and known bivalves ("**?**" means the bivalve host family has been suggested but not verified) and additional hosts of crabs provided. Ranges and host identities primarily derived from Schmitt *et al*. (1973) and de Gier & Becker (2020) with host names updated from McDermott (2009) and parasite identifications updated from Williams *et al.* (2023). *Ng *et al.* (2019) indicated that the records of *Nepinnotheres cardii* (Bürger, 1895) from Japan may refer to more than one species; identification of the host from this region requires verification.

Parasitic isopod	Pinnotherid crab host of parasitic isopod	Known host(s) of pinnotherid crab	Locality of parasitic isopod (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
Dactylokepon cf. *hunterae* Wells & Wells, 1966	*Glassella arenicola* (Rathbun, 1922) (Pinnixinae)	unknown (assumed Annelida: Arenicolidae)	Curaçao (western Atlantic)	Rathbun 1924
Heterocepon globosus (Markham, 1992) n. comb.	Pinnotheridae (unidentified species) (Pinnotherinae)	unidentified	Hong Kong	Markham 1992
Heterocepon marginatum Shiino, 1936	*Pinnotheres parvulus* Stimpson, 1858 (Pinnotherinae)	Bivalvia: Pectinidae, Pinnidae, Veneridae	Japan (Indo-West Pacific, Temperate Australasia)	Shiino 1936a
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	*Arcotheres palaensis* (Bürger, 1895) (Pinnotherinae)	Bivalvia: Arcidae, Mactridae, Placunidae	Philippines (Indo-West Pacific)	Janssen & Brandt 1994
Heterocepon marginatum Shiino, 1936	*Arcotheres palaensis* (Bürger, 1895) (Pinnotherinae)	Bivalvia: Arcidae, Mactridae, Placunidae	Indonesia (Indo-West Pacific)	Ahyong & Ng 2007; Ng & Ahyong 2022
Heterocepon marginatum Shiino, 1936	*Arcotheres rayi* Ahyong & Ng, 2007 (Pinnotherinae)	Bivalvia: Veneridae	Malaysia (Indo-West Pacific)	Ng & Ahyong 2022
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	Pakistan (Indo-West Pacific)	Jahangir *et al.* 2015
Onychocepon harpax Pérez, 1921	*Arcotheres palaensis* (Bürger, 1895) (Pinnotherinae)	Bivalvia: Arcidae, Mactridae, Placunidae	Indonesia (Indo-West Pacific)	Pérez 1921; Ng & Ahyong 2022
Onychocepon giardi Nierstrasz & Brender à Brendis, 1923	*Magnotheres globosus* (Hombron & Jacquinot, 1846) (Pinnotherinae)	Bivalvia: Arcidae, Mactridae, Placunidae	Indonesia (Indo-West Pacific)	Nierstrasz & Brender à Brendis 1923; Ng, pers. comm. (identification of host)

Fig. 1. — Continuation.

Parasitic isopod	Pinnotherid crab host of parasitic isopod	Known host(s) of pinnotherid crab	Locality of parasitic isopod (range of pinnotherid crab host)	References
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 Williams, Boyko & Tri, 2023	*Plenotheres coarctatus* (Bürger, 1895) (Pinnotherinae)	Bivalvia: Cyrenidae	Vietnam (Indo-West Pacific)	Williams *et al.* 2023
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
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 pelseneeri Pérez, 1920 (*nomen nudum*)	*Arcotheres palaensis* (Bürger, 1895)	Arcidae	Indonesia (Indo-West Pacific)	Pérez 1920a; 1921
Rhopalione racemus n. sp.	*Discorsotheres subglobosus* (Baker, 1907) (Pinnotherinae)	Bivalvia: Mytilidae, Pectinidae, Spondylidae	South Australia (Temperate Australasia)	Hale 1927
Rhopalione sinensis Markham 1990	unknown	Bivalvia: Pinnidae	Philippines (Indo-West Pacific)	Nierstrasz & Brender à Brandis 1931
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 tanjongrusaensis n. sp.	*Arcotheres similis* (Bürger, 1895) (Pinnotherinae)	Bivalvia: Mytilidae, Ostreidae, Placunidae	Singapore (Indo-West Pacific)	Ng & Ahyong 2022
Rhopalione uromyzon Pérez, 1920	*Discorsotheres spondyli* (Nobili, 1905) (Pinnotherinae)	Bivalvia: Spondylidae	Persian Gulf (western Indo-West Pacific)	Pérez 1920a
Rhopalione sp.	*Magnotheres globosus* (Hombron & Jacquinot, 1846) (Pinnotherinae)	Bivalvia: Pinnidae, Veneridae	Singapore (Indo-West Pacific)	Ng & Ahyong 2022
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)	Annelidae: 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
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; Longshaw *et al.* 2012

"Unidentified branchial sp." – McDermott 2009: 792, table 2 [listing of Rathbun's record].

"unidentified bopyrid" [of *Glassella arenicola* (Rathbun, 1922)] – Williams *et al.* 2023: 533 [list].

MATERIAL EXAMINED. — **Curaçao •** 1 mature ♀ (1.8 mm TL), from left branchial chamber of holotype male of *Pinnixa arenicola* Rathbun, 1922 (now *Glassella arenicola* (Rathbun, 1922)) (6 mm CL, 3 mm CW; ZMA.CRUS.D.242240); Spaansche Haven, in sand; 12°04'N, 68°52'W; 16.IV.1920; C. J. van der Horst leg.; RMNH. CRUS.I.250004.

REMARKS

The adult female is very small, damaged (missing uropods?) and appears to have been desiccated previously. However, it closely resembles the female of *D. hunterae* in general body shape, size of the frontal lamina, lack of middorsal projections on the pereomeres, shape of the coxal plates, and form and number of pleopods (Wells & Wells 1966). Owing to the damage to the female and lack of a male, we cannot confidently determine if the present specimen is conspecific with *D. hunterae*, but it is clearly a species of *Dactylokepon*. Additional differences include that the present female is much smaller than the types of *D. hunterae* (1.8 vs 6 mm), the localities, although both in the western Atlantic, are relatively distant (Curaçao vs North Carolina), and the hosts are in different subfamilies (Pinnixinae vs Pinnotherinae). This is the only bopyrid recorded from any host species in Pinnixinae.

Genus *Heterocepon* Shiino, 1936

TYPE SPECIES. — *Heterocepon marginatum* Shiino, 1936, by monotypy.

Heterocepon marginatum Shiino, 1936
(Figs 1; 2)

Heterocepon marginatum Shiino, 1936a: 161, 165-168, fig. 2 [ex *Pinnotheres parvulus* Stimpson, 1858, Japan]; 1936c: 185 [ex *P. parvulus*, Japan]; 1972: 9 [list]. — Morita 1940: 76-77 [ex *Pinnotheres* sp., Japan]; 1949: 13-14, figs A-E [ex *Nepinnotheres cardii* (Bürger, 1895), Japan; description of cryptoniscus larva]; 1951: 48 [ex *N. cardii*, Japan]; 1952: 54-59, figs 1-3; 1953a: 10, 13 [ex *N. cardii*, Japan; 1953b: 14-20, figs 1-4 [ex *N. cardii*, Japan; description of epicaridium larva, bopyridium, juvenile male and female]; 1955: 53-59 [ex *N. cardii*, Japan; fig. 1-5]. — Danforth 1963: 8 [list]. — Wells & Wells 1966: 57 [mention]. — Janssen & Brandt 1994: 12-17, 24, table 1, figs 3-9 [ex *Arcotheres palaensis* (Bürger, 1895), Philippines]. — Saito *et al.* 2000: 42 [list]. — Boyko & Williams 2001: 656 [mention]. — Miura *et al.* 2014: 31, 35, 36 [mention]. — Ozeki *et al.* 2014: 49 [mention]. — Williams *et al.* 2023: 532 [list], 539 [mention].

"bopyrid isopod" – Janssen 1986: 15, 23, fig. 5 [ex *A. palaensis*, Philippines].

"hyperparasite" – Janssen 1986: 18 [ex *A. palaensis*, Philippines].

"bopyrid"– Ahyong & Ng 2007: 200 [ex *A. palaensis*, paralectotype female (SMF-ZMG948b), Palau; photographs examined herein]. — Ng & Ahyong 2022: 145 [ex ZRC 1987.537-539; specimen examined herein], 148 [ex ZRC 1993.120-122; host examined herein], 195 [ex ZRC 2013.1416; specimens examined herein].

"unidentified bopyrids" [of *Arcotheres palaensis* (in part) and *Arcotheres rayi*] – Williams *et al.* 2023: 533 [list].

MATERIAL EXAMINED. — **Peninsular Malaysia or Singapore •** 1 ovigerous ♀ (4.5 mm TL), 1 mature ♂ (3.0 mm TL), from left branchial chamber of female *Arcotheres palaensis* (Bürger, 1895) (5.7 mm CL, 9.6 mm CW; ZRC 1987.537-539), ex *Tegillarca granosa* (Linnaeus, 1758) (Arcidae); from markets; 20.XI.1986; P. K. L. Ng, leg.; ZRC 2023.0257.
Malaysia • 1 mature ♀ (3.5 mm), 1 mature ♂ (1.8 mm), from right branchial chamber of female *Arcotheres rayi* Ahyong & Ng, 2007 (5.0 mm CL, 7.0 mm CW; ZRC 2013.1416), ex *Paphia* sp. (Veneridae); Pahang, Bentong Market; 10.V.2010; M. Low leg.; ZRC 2023.0262 • 1 mature ♀ (3.2 mm), mature ♂ (2.8 mm), from left branchial chamber of female *A. rayi* (4.9 mm CL, 8.0 mm CW; ZRC 2013.1416), ex *Paphia* sp. (Veneridae); Pahang, Bentong Market; 10.V.2010; M. Low leg.; ZRC 2023.0263 • 1 ovigerous ♀ (3.4 mm), 1 mature ♂ (2.6 mm), from right branchial chamber of female *A. rayi* (5.0 mm CL, 7.5 mm CW; ZRC 2013.1416), ex *Paphia* sp. (Veneridae); Pahang, Bentong Market; 10.V.2010; M. Low leg.; ZRC 2023.0264 • 1 ovigerous ♀ (3.6 mm), 1 mature ♂ (3.2 mm), from right branchial chamber of female *A. rayi* (4.9 mm CL, 8.0 mm CW; ZRC 2013.1416), ex *Paphia* sp. (Veneridae); Pahang, Bentong Market; 10.V.2010; M. Low leg.; ZRC 2023.0265 • 1 immature ♀ (2.5 mm), from left branchial chamber of female *A. rayi* (3.8 mm CL, 5.7 mm CW; ZRC 2013.1416), ex *Paphia* sp. (Veneridae); Pahang, Bentong Market; 10.V.2010; M. Low leg.; ZRC 2023.0266 • 1 ovigerous ♀ (4.0 mm), 1 mature ♂ (2.9 mm), from right branchial chamber of female *A. rayi* (5.0 mm CL, 8.5 mm CW; ZRC 2013.1416), ex *Paphia* sp. (Veneridae Rafinesque, 1815); Pahang, Bentong Market; 10.V.2010; M. Low leg.; ZRC 2023.0267 • 1 ovigerous ♀ (4.2 mm), 1 mature ♂ (3.5 mm), from left branchial chamber of female *A. rayi* (6.0 mm CL, 10.0 mm CW; ZRC 2013.1416), ex *Paphia* sp. (Veneridae); Pahang, Bentong Market; 10.V.2010; M. Low leg.; ZRC 2023.0269 • 1 ovigerous ♀ (3.6 mm), 1 mature ♂ (2.8 mm), from left branchial chamber of female *A. rayi* (4.7 mm CL, 8.0 mm CW; ZRC 2013.1416), ex *Paphia* sp. (Veneridae); Pahang, Bentong Market; 10.V.2010; M. Low leg.; ZRC 2023.0270 • 1 ovigerous ♀ (3.6 mm), 1 mature ♂ (2.8 mm), from left branchial chamber of female *A. rayi* (4.6 mm CL, 8.0 mm CW; ZRC 2013.1416), ex *Paphia* sp. (Veneridae); Pahang, Bentong Market; 10.V.2010; M. Low leg.; ZRC 2023.0271 • 1 ovigerous ♀ (3.0 mm), 1 mature ♂ (2.8 mm), 1 immature ♂ (1.0 mm), from right branchial chamber of female *A. rayi* (4.7 mm CL, 7.3 mm CW; ZRC 2013.1416), ex *Paphia* sp. (Veneridae); Pahang, Bentong Market; 10.V.2010; M. Low leg.; ZRC 2023.0272.
"**Singapore?**" • 1 ovigerous ♀ *A. palaensis* (7.1 mm CL, 9.0 mm CW; with swollen empty right branchial chamber), ex *T. granosa*; market; 8.XII.1987; P. K. L. Ng leg.; ZRC 1993.120-122.

REMARKS

This is the first record of the species from Malaysia and likely Singapore based on the host branchial chamber swelling; however, because some specimens were obtained from markets where field sites were not noted, the country of origin remains unclear for some of the museum lots. The female (Figs 1A, D; 2) and male (Fig. 1B) specimens match the original description. An additional parasitized oviger-

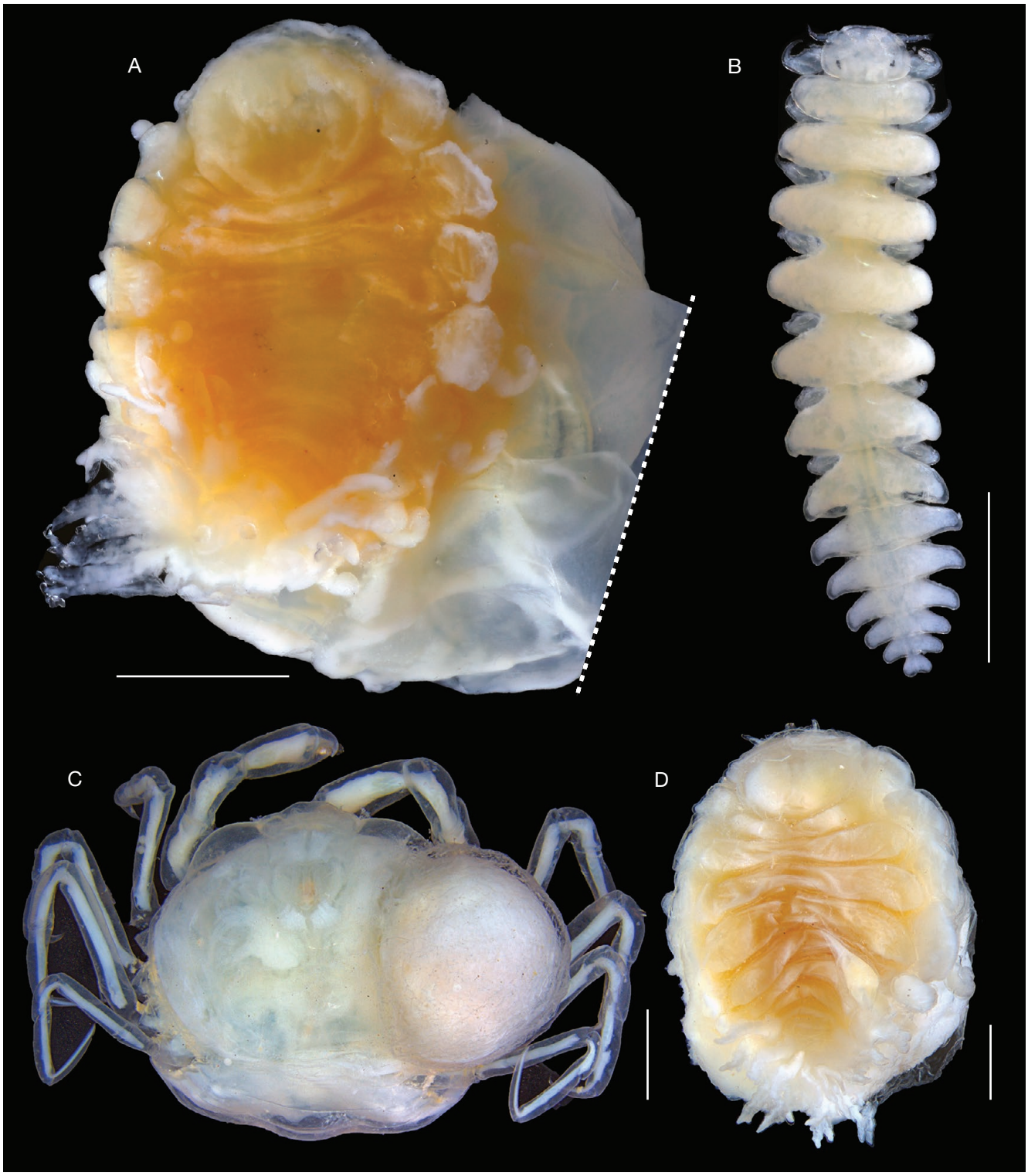

Fig. 1. — *Heterocepon marginatum* Shiino, 1936, ZRC 2023.0264 (**A**), ZRC 2023.0269 (**B**), SMF-ZMG948b (**C**, **D**): **A**, female, dorsal view (dashed line shows where oostegites are cut-off in the picture); **B**, male, dorsal view; **C**, female in host *Arcotheres palaensis* (Bürger, 1895); **D**, female, dorsal view. Scale bars: A, B, D, 1 mm; C, 2.5 mm.

ous female *Arcotheres palaensis* (ZRC 1993.120-122) was examined but the swollen branchial chamber was empty. In light of the identity of the host, the bopyrid was probably *H. marginatum*.

In situ photographs of a female specimen in a host *Arcotheres palaensis* (SMF-ZMG948b) (Fig. 1C) and the extracted female (Fig. 1D) were examined. The female bopyrid identity was confirmed, but no male was present.

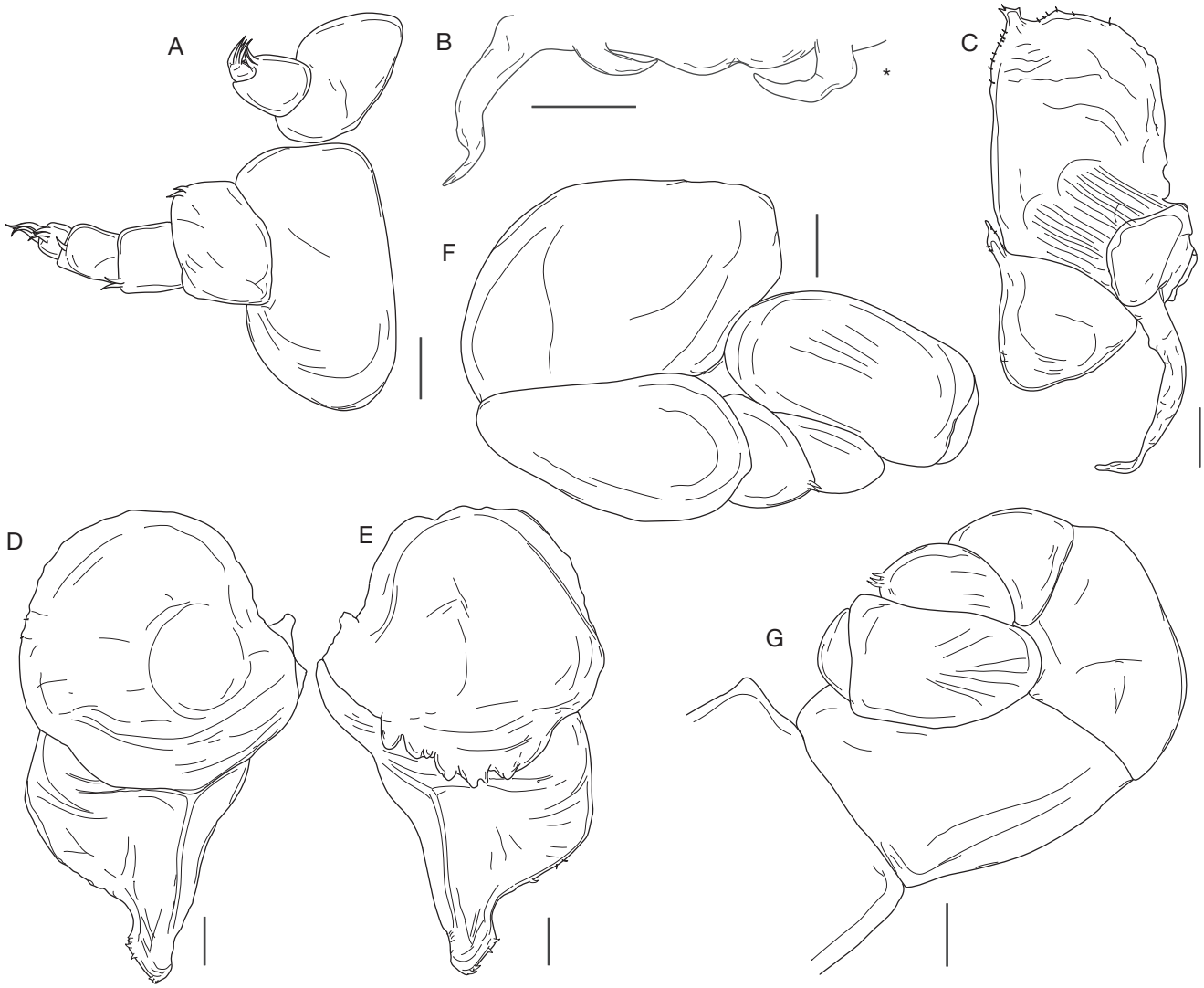

FIG. 2. — *Heterocepon marginatum* Shiino, 1936, ZRC 2023.0271 (**A**-**I**): **A**, right antenna and antennule of female; **B**, barbula of female (asterisk shows missing outer lobe); **C**, left maxilliped of female, outer view with outer barbular lobe attached; **D**, left oostegite 1 of female, outer view; **E**, left oostegite 1 of female, inner view; **F**, left pereopod 1 of female; **G**, left pereopod 7 of female. Scale bars: A, F, G, 50 µm; B, 250 µm; C-E, 200 µm.

Heterocepon globusus (Markham, 1992) n. comb.

Hypocepon globosus Markham 1992: 287-289, figs 10-11. — Huang 2001: 326 [list]. — Morton 2003: 46 [list]. — Li 2003: 140 [list]. — An *et al.* 2009: 351 [list]. — Williams *et al.* 2023: 532 [list].

TYPE MATERIAL EXAMINED. — **Hong Kong •** ovigerous holotype ♀ (4.0 mm TL), mature allotype ♂ (3.5 mm TL), from unknown branchial chamber of unspecified "Pinnotheridae sp."; no other locality data; examined by S. T. Ahyong; AMS P37275.

REMARKS

An examination of the description and illustrations of *Hypocepon globosus* from Hong Kong (South China Sea) shows that although this species was placed in *Hypocepon* Nierstrasz & Brender à Brandis, 1930, it actually belongs to *Heterocepon* Shiino, 1936, a genus that Markham (1992) apparently did not consider. The female and male of *Hypocepon globosus* differ markedly from those of the type and only other species of *Hypocepon*, *H. enoeensis* Nierstrasz & Brender à Brandis, 1930 from Indonesia. All the generic characters for females of *Heterocepon marginatum* Shiino, 1936, the type species of the genus, agree with those of *Hypocepon globosus*, including the overall body shape of the female, barbell-shaped pleomeres, expanded, ovate coxal plates, large frontal lamina, and structure of the pleopods. The characters of the males of *Hypocepon globosus* and *Heterocepon marginatum*, including shape of the body, splayed pleomeres, presence of ovate raised pleopods and shape of the pleotelson, are also similar. In fact, the females and males are so similar that it is possible that *Hypocepon globosus* and *Heterocepon marginatum* are synonymous, but without examination of the types of both species, such a synonymy would be premature. One possible specific difference is in the uropods of the female, which are uniramous in *Heterocepon marginatum* but biramous in *Hypocepon globosus*. For the present, we transfer *Hypocepon globosus* to *Heterocepon* as *Heterocepon globosus*, n. comb.

Genus *Onychocepon* Pérez, 1921

TYPE SPECIES. — *Onychocepon harpax* Pérez, 1921, by monotypy.

Onychocepon harpax Pérez, 1921
(Fig. 3)

Onychocepon harpax Pérez, 1921: 59-61, figs 1, 2 [ex *Pinnotheres palaensis* Bürger, 1895 (now *Arcotheres palaensis* (Bürger, 1895)), Ambon, Indonesia]. — Perkins 1925: 182 [mention]. — Shiino 1936b: 164 [comparison with other species in the genus]. — Wells & Wells 1966: 56 [mention]. — Danforth 1972: 170, 172 [comparison with other species in the genus]. — McDermott 2009: 792, table 2 [list]. — Williams *et al.* 2023: 532 [list].

"bopyrid" – Ng & Ahyong 2022: 148, 167, fig. 12F [ex ZRC 2018.762; specimens examined herein].

"unidentified bopyrids" [of *Arcotheres palaensis* (in part)] – Williams *et al.* 2023: 533 [list].

MATERIAL EXAMINED. — **Indonesia** • 1 ovigerous ♀ (5.1 mm TL), 1 mature ♂ (3.6 mm TL), from right side of pleon of female *Arcotheres palaensis* (Bürger, 1895) (7.2 mm CL, 11.3 mm CW; ZRC 2018.0762), ex *Anadara antiquata* (Linnaeus, 1758) (Arcidae Lamarck, 1809); Lombok, Teluk Kodek; 12.XI.2013; S. Dwiono leg.; ZRC 2023.0258.

REMARKS
This is only the second record of *O. harpax*, also from Indonesia. It agrees with the description of Pérez (1921) for all male and female characters (Figure 3 with illustration of female parts); the female bears uniramous uropods, a character not specified by Pérez (1921).

Onychocepon giardi
Nierstrasz & Brender à Brandis, 1923

Onychocepon giardi Nierstraz & Brender à Brandis, 1923: 81-83, pl. 5, fig. 13a-f [ex "*Pinnotheres* Latr. Spec., wahrscheinlich *P. acrophilus* [sic] Bürger" but see type material examined]. — Shiino 1936b: 164 [comparison with congeners]. — Danforth 1963: 8 [list]; 1972: 170, 172 [comparison with congeners]. — Wells & Wells 1966: 56 [mention]. — Suharsono 2014: 153 [list]. — Williams *et al.* 2023: 532 [list].

TYPE MATERIAL EXAMINED. — **Indonesia** • 1 ovigerous syntype ♀ (3.5 mm TL), 1 mature syntype ♂ (3.3 mm TL), from right side of pleon of male *Magnotheres globosus* (Hombron & Jacquinot, 1846) (7.9 mm CL, 8.2 mm CW; ZMA.CRUS.D.103553), ex unknown bivalve; Maluku, between Gisser and Seram-Laut, Gisser anchorage, Stn. 17; 03°53'9.2"S, 130°51'56.2"E; 26.VIII.1899; *Siboga* leg.; ZMA.CRUS.I.100553.

REMARK
The correct identity of the host of *O. giardi* was brought to our attention by Peter Ng (ZRC) during his research visit to RMNH. We have seen a photograph of the syntype male and female.

Genus *Rhopalione* Pérez, 1920

TYPE SPECIES. — *Rhopalione uromyzon* Pérez, 1920, by original designation.

REMARKS
The occurrence of female bopyrid isopods under the pleons of brachyuran crabs is apparently restricted to members of the genera *Rhopalione* and *Spathione* Boyko & van der Meij, 2018. All other bopyrids that occur abdominally are in subfamilies other than Pseudioninae and occur on anomurans and caridean shrimps but never on brachyurans. This unique site of parasitization might correlate with the morphology of the host carapace. All species of *Rhopalione* parasitize genera of pinnotherid crabs (Pinnotherinae) in which, for females at least, the carapace is very soft and weakly calcified. This is in marked contrast to the carapace of other brachyurans infested by bopyrids, which is well calcified in both sexes and offers more protection to the parasite; this is true even in the gall crabs (Cryptochiridae Paulson, 1875), which are parasitized by species of *Spathione*. The adaptation to an abdominal mode of infestation by species of *Rhopalione* might have allowed for maximal protection by the host, which is better obtained in an abdominal position; alternatively, *Rhopalione* is a relatively large bopyrid and the space afforded under the pleon is much larger than the branchial chamber (see further remarks below). In gall crabs, the parasitization of the pleon by species of *Spathione* may be a response to the host living in corals and making branchial parasitization more difficult. However, the soft carapace of pinnotherids and coral habitat of gall crabs do not preclude parasitization within the branchial chamber as four genera of keponine bopyrids (*Heterocepon* Shiino, 1936, *Hypocepon* Nierstrasz & Brender à Brandis, 1930, *Onychocepon* Pérez, 1921, and *Rhizophoracepon* Williams, Boyko & Tri, 2023) are composed of entirely branchial bopyrids of pinnotherids, while a fourth genus (*Dactylokepon* Stebbing, 1910) contains one additional species known from pinnotherid branchial chambers. Likewise, the sole species of *Carcinione* Bourdon, 1983 is a branchial parasite of gall crabs. Clearly, the mode of infestation exhibited by species of *Rhopalione* and *Spathione* is unusual among bopyrids found on pinnotherids and gall crabs but further discussion here is restricted to species of *Rhopalione* (see Boyko & van der Meij 2018 for a fuller discussion on *Spathione*).

In other brachyuran hosts, the female parasites obtain food by piercing the gill lamellae and rarely leave evidence of their feeding. In contrast, females of species of *Rhopalione* are oriented with the dorsal surface appressed to the sternites of the host (Page 1985) and pierce the weakly calcified ventral surface of the pleon, leaving noticeable holes in the exoskeleton (see Remarks under *Rhopalione rusa* n. sp.). Females of species of *Rhopalione* are far more dependent on the secondary sexual modification of the host than other pseudionine species. Ordinarily, a female bopyrid occurring in a brachyuran branchial chamber is relatively unaffected by the sex of the host, as the host branchial chamber is not sexually dimorphic. However, in species of *Rhopalione* the parasite is found either on female

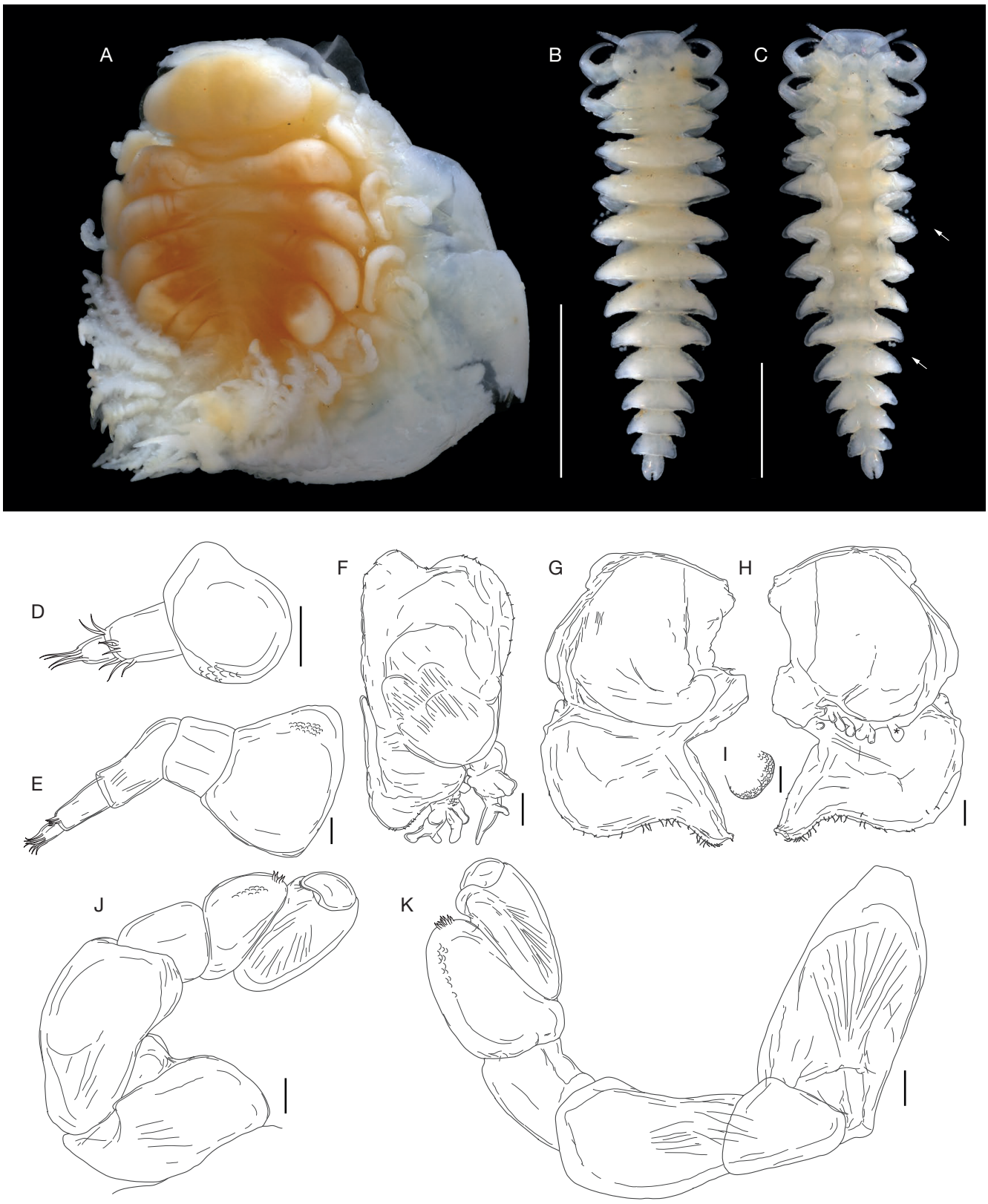

FIG. 3. — *Onychocepon harpax* Pérez, 1921, ZRC 2023.0258 (**A**-**K**): **A**, female, dorsal view; **B**, male, dorsal view; **C**, male, ventral view (arrows indicate attached ciliates); **D**, left antennule of female; **E**, left antenna of female; **F**, left maxilliped and barbular lobes of female; **G**, left oostegite 1 of female, outer view; **H**, left oostegite 1 of female, inner view, asterisk shows lobe drawn in close-up; **I**, close-up of lobe from inner ridge of oostegite 1 of female; **J**, left pereopod 1 of female; **K**, left pereopod 7 of female. Scale bars: A, 2 mm; B, C, 1 mm; D, E, I-K, 50 µm; F-H, 200 µm.

crab hosts, which have a much broader pleon, or on male crab hosts that are usually feminized by the parasite, becoming modified with broader pleons (see Page 1985). How the parasite accomplishes this feminization of the male host, which also has female-type pleopods accompanied by male gonopods (Page 1985), is unknown but is likely hormonal in origin. Changes in sexual characters of male crab hosts has been documented in some bopyrids (e.g. Hiraiwa & Sato 1939; Reverberi 1942; Reinhard 1956; Bourdon 1968; Romero-Rodríguez & Román-Contreras 2011) but is usually limited to primary reproductive structures (gonopores, gonopods, pleopods) and with a much less pronounced effect on external morphology and secondary sexual characters. It is also highly variable, as all hosts are not equally affected by their parasites in terms of modification of sexual characters. A side-effect of the abdominal mode of life is that no specimens of any species of *Rhopalione* exhibit marked torsion of the body (dextral or sinistral), as commonly seen in many other bopyrid taxa.

The relationships of *Rhopalione* and *Spathione* to other pseudionine bopyrids are difficult to discern. *Rhopalione* was once considered a part of Ioninae H. Milne Edwards, 1840 *sensu lato* (now Keponinae Boyko, Moss, Williams & Shields, 2013) but was moved to Pseudioninae Codreanu, 1967 by Boyko & van der Meij (2018), as the pleonal lateral plates of the female are very well developed and proximally constricted, the dorsomedial regions of the pereomeres are raised into low bosses, and the maxilliped and oostegites are comparable to other genera in the subfamily. Within Pseudioninae, however, these two genera are difficult to place, as they bear no general resemblance to any other taxon. The males of *Rhopalione*, with their distinctive pleonal morphology and strong dorsoventral curvature, are also unlike other pseudionine species, and indeed other bopyrid taxa excepting *Spathione*. Bourdon (1983) cited *Rhopalione*, *Gigantione* Kossmann, 1881, and *Carcinione* Bourdon, 1983, as the only three genera infesting brachyurans that did not appear to belong to Ioninae, but he did not formally assign any of them to a subfamily. However, Bourdon's (1983) consideration of the status of *Rhopalione* was based solely on information in Pérez (1920a). Subsequent work by Page (1985) and Markham (1990) suggested that *Rhopalione* was a member of Ioninae (of uncertain placement) but this was refuted by Boyko & van der Meij (2018) who demonstrated that the genus belongs to Pseudioninae. *Gigantione* may be paraphyletic (Boyko, unpublished) but its position, as defined by the type species *G. moebii* Kossmann, 1881 (see also Bourdon 1969), suggests placement within Pseudioninae as well. *Carcinione* was also placed in Pseudioninae by Boyko & van der Meij (2018).

Rhopalione incerta (Bonnier, 1900)

Orbione incerta Bonnier, 1900: 61, 379 [list]. — Danforth 1970: 14 [mention].

Orbione (?) *incerta* Bonnier, 1900: 222 [list], 282-284, text fig. 50 [host unknown, Madagascar]. — Nierstrasz & Brender à Brandis 1923: 66 [list]. — Page 1985: 199 [mention].

Rhopalione incerta – Pérez 1920a: 1617 [mention]. — Nierstrasz & Brender à Brandis 1923: 68, 69 [mention]. — Bourdon 1976: 353 [mention]. — Page 1985: 201 [mention]. — Markham 1990: 562 [mention]. — Kensley 2001: 226 [list]. — An *et al.* 2014: 2, table 2 [list], 4 [key to species]. — Ahyong & Boyko 2019: 283, 286 [mention], 287 [key to species]. — Williams *et al.* 2023: 533 [list].

O. incerta – Richardson 1904a: 857 [discussion of generic placement]; 1904b: 52 [discussion of generic placement]. — Chopra 1923: 419, 446, 447 540 [discussion of generic placement]. — Cattley 1938: 240 [discussion of generic placement].

[*Orbione*] *incerta* – Shiino 1949: 53 [mention].

"Orbione? *penei*" [*sic*] – Markham 1990: 563 (error for *Orbione* (?) *incerta*).

TYPE MATERIAL EXAMINED. — **Madagascar • holotype** ♀ (4.35 mm, damaged), ex "*Pilumnus*" [*sic*] (= Pinnotheridae sp. indet.); Nossi-Lava; 1896; Bastard leg.; MNHN-IU-2024-3186 (= Ep125).

REDESCRIPTION

Female (based on extant parts of holotype and description and figure in Bonnier (1900); measurements extrapolated from extant body segments).

Body length 7.68 mm, maximal width 9.19 mm, head length 1.53 mm, head width 2.85 mm. Pereon essentially straight, right side coxal plates more produced laterally. All body regions and pereomeres distinctly segmented. Head broader than long, strongly produced with frontal lamina equal to approximately one-twelfth length of head, pereomere 1 median not obscured by head; barbula with two thin projections. Eyes absent. Antennule of three articles, antenna of five articles. Maxilliped with palp. First oostegite proximal lobe ovate, distal lobe subtriangular with median acute projection, internal ridge with number of small projections. Pereon of seven pereomeres, broadest across pereomere 5, gradually tapering anteriorly and posteriorly; pereomeres 1-3 with slightly convex posterior margins, 4-7 with concave posterior margins. Coxal plates as large, bilobed lobes on pereomeres 1-5, clearly separated from pereomeres and with tapered distal margin on right side of body. Dorsolateral bosses on pereopods 1-5 large, oblong, and clearly demarcated with right ones slightly larger than left. Pereomeres 1-6 lacking clearly demarcated median region and tergal projections. Oostegites enclosing marsupium. Pereopods all subequal, posterior pairs slightly longer. Pleon with five distinct pleomeres plus pleotelson; posterior margins of all pleomeres concave and sinuous. Pleomeres 1-5 with biramous pleopods and uniramous lateral plates; endopodites and exopodites of all pleopods elongate and tapered, subequal in size; lateral plates strongly produced and distally tapered to subacute tips; edges and surfaces of all lateral plates smooth; uropods uniramous, subequal in shape and size to pleopods and lateral plates.

Male

Unknown.

KEY TO SPECIES OF *RHOPALIONE* PÉREZ, 1920
(BASED ON CHARACTERS OF MALES AND FEMALES)

1 Females with short, rounded pleopods and lateral plates ..... *Rhopalione racemus* n. sp.
— Females with elongate pleopods and lateral plates 2

2 Females with pleopods and lateral plates acute distally ..... *Rhopalione incerta* (Bonnier, 1900), male unknown
— Females with pleopods and lateral plates rounded distally 3

3 Females with coxal plates acute distally ..... *Rhopalione atrinicola* Page, 1985
— Females with coxal plates rounded distally 4

4 Males with large, reniform pleopods and midventral tubercles ..... *Rhopalione rusa* n. sp.
— Males with rounded pleopods, midventral tubercles absent 5

5 Males with pleopods displaced laterally ..... *Rhopalione sinensis* Markham, 1990
— Males with pleopods close to median of pleon 6

6 Male with pleotelson deeply bifurcated ..... *Rhopalione kali* Ahyong & Boyko, 2019
— Male with pleotelson small, rounded, not bifurcated ..... *Rhopalione uromyzon* Pérez, 1920

REMARKS

The holotype specimen jar contains the same kind of label as found in many of the vials of the *R. uromyzon* syntypes and was in the house of Dr Pérez at the time of his death. Although its rediscovery is fortuitous, the holotype is in very poor condition. The head, oostegites, pereopods, lateral plates and pleopods of the left side, and both uropods are absent, presumably as the result of loss after dissection. However, the salient features of the pereomeres and pleomeres that remain allow for verification of Bonnier's (1900) illustrated features. Although Bonnier (1900) wrote a fairly lengthy text description, he was somewhat imprecise in his descriptions of most of the appendages and provided an illustration of only the dorsal aspect of the whole specimen. It is clear, however, that *R. incerta* is indeed a *Rhopalione*, despite statements to the contrary by some other authors (e.g. Nierstrasz & Brender à Brandis 1923), and that it is most closely related to *R. atrinicolae* from New Zealand. Characters that the two species share include the maxilliped with distinct palp, oostegite 1 not produced over cephalon, and outer lobe of bilobed coxal plates on pereomeres 1-4 distally acute or subacute. The two species differ in the shape of the head (distinctly wider in *R. incerta*), the degree of acute prolongation of outer lobe of bilobed coxal plates on pereomeres 1-4 (acute in *R. atrinicolae* vs. subacute in *R. incerta*), internal ridge of oostegite 1 (smooth in *R. atrinicolae* vs. with several small digitations in *R. incerta*), shape of the lateral plates and pleopods (distally rounded in *R. atrinicolae* vs. acute in *R. incerta*), and the uropods (biramous in *R. atrinicolae* vs. uniramous in *R. incerta*). This last character may not be a valid one to separate the species, given its variability in *R. uromyzon*.

Although Bonnier (1900) indicated that the host of *R. incerta* was a species of "*Pilumnus*", the host pleon is still present in the vial with the holotype and is clearly that of a female pinnotherid.

Rhopalione uromyzon Pérez, 1920
(Figs 4; 5)

Rhopalione uromyzon Pérez, 1920a: 1615-1617, figs 1-3 [ex *Ostracoteres spondyli* Nobili, 1905 (now *Discorsotheres spondyli* (Nobili, 1905)), Persian Gulf]. — Pérez 1920b: 102-103, fig. 45 [information from Pérez 1920a]. — Nierstrasz & Brender à Brandis 1923: 69 [mention]. — Shiino 1952: 34 [mention]. — Bourdon *et al.* 1981: 500-501 [mention]. — Page 1985: 199-201 [mention]. — Markham 1990: 562 [mention]. — Kensley 2001: 226 [list]. — An *et al.* 2014: 1, 2, table 1 [mention; list], 4 [key to species]. — Ahyong 2018: 561 [mention]. — Ahyong & Boyko 2019: 283-284, 286 [mention], 287 [key to species]. — Williams *et al.* 2023: 533 [list].

not *Rhopalione uromyzon* – Nierstrasz & Brender à Brandis 1931: 175-176 [host unknown, Zamboanga, Philippines; specimen examined herein] (identified as *Rhopalione sinensis* Markham, 1990).

TYPE MATERIAL EXAMINED. — **United Arab Emirates** • 1 syntype ♀ (8.1 mm TL), ex female *Discorsotheres spondyli* Nobili, 1905 (6.8 mm CW), St. LIII, "banc au N.E. de l'île Arzana et pêche côtière dans les polypiers" [Îsle Arzana or Arzanah Island, 24°48'N, 52°34'E]; 1901; Mission Bonnier-Pérez Côtes d'Arabie leg.; MNHN-IU-2024-3187 (= Ep910) • 1 syntype ♀ (6.30 mm TL), 1 syntype ♂ (3.00 mm TL), ex female *D. spondyli* (damaged, unmeasurable), St. LIII, "banc au N.E. de l'île Arzana et pêche côtière dans les polypiers"; 1901; Mission Bonnier-Pérez Côtes d'Arabie leg.; MNHN-IU-2024-3188 (= Ep911) • 2 syntype ♀ (4.35, 5.55 mm TL), 2 syntype ♂ (3.45, 3.68 mm TL), ex ♀ *D. spondyli* (5.6 mm CW), St. LIV, "dragages à 5 brasses, 8 milles au N. N. O. d'Arzana"; 1901; Mission Bonnier-Pérez Côtes d'Arabie leg.; MNHN-IU-2024-3189 (= Ep912) • 1 syntype ♀ (3.15 mm TL), 1 syntype ♂ (1.50 mm TL), ex female *D. spondyli* (4.5 mm CW), St. LIV, "dragages à 5 brasses, 8 milles au N. N. O. d'Arzana"; 1901; Mission Bonnier-Pérez Côtes d'Arabie leg.; MNHN-IU-2024-3190 (= Ep913). **No data [United Arab Emirates]** • 1 syntype ♀ (3.15 mm TL), 1 syntype ♂ (3.08 mm TL), host not present; MNHN-IU-2024-3191 (= Ep914) • 1 syntype ♀ (6.15 mm TL), 2 syntypes ♂ (2.1, 4.8 mm TL), host not present; MNHN-IU-2024-3192 (= Ep915)• 1 syntype ♀ (4.35 mm TL), ex female *D. spondyli* (damaged, unmeasurable); MNHN-IU-2024-3195 (= Ep919) • 1 syntype ♀ (3.90 mm TL), 1 syntype ♂ (2.85 mm TL), host not present; MNHN-IU-2024-3193 (= Ep917) • 1 syntype ♀ (4.65 mm TL), 2 syntypes ♂ (1.01, 3.08 mm TL), ex 1 of 2 females *D. spondyli* (damaged, unmeasurable);

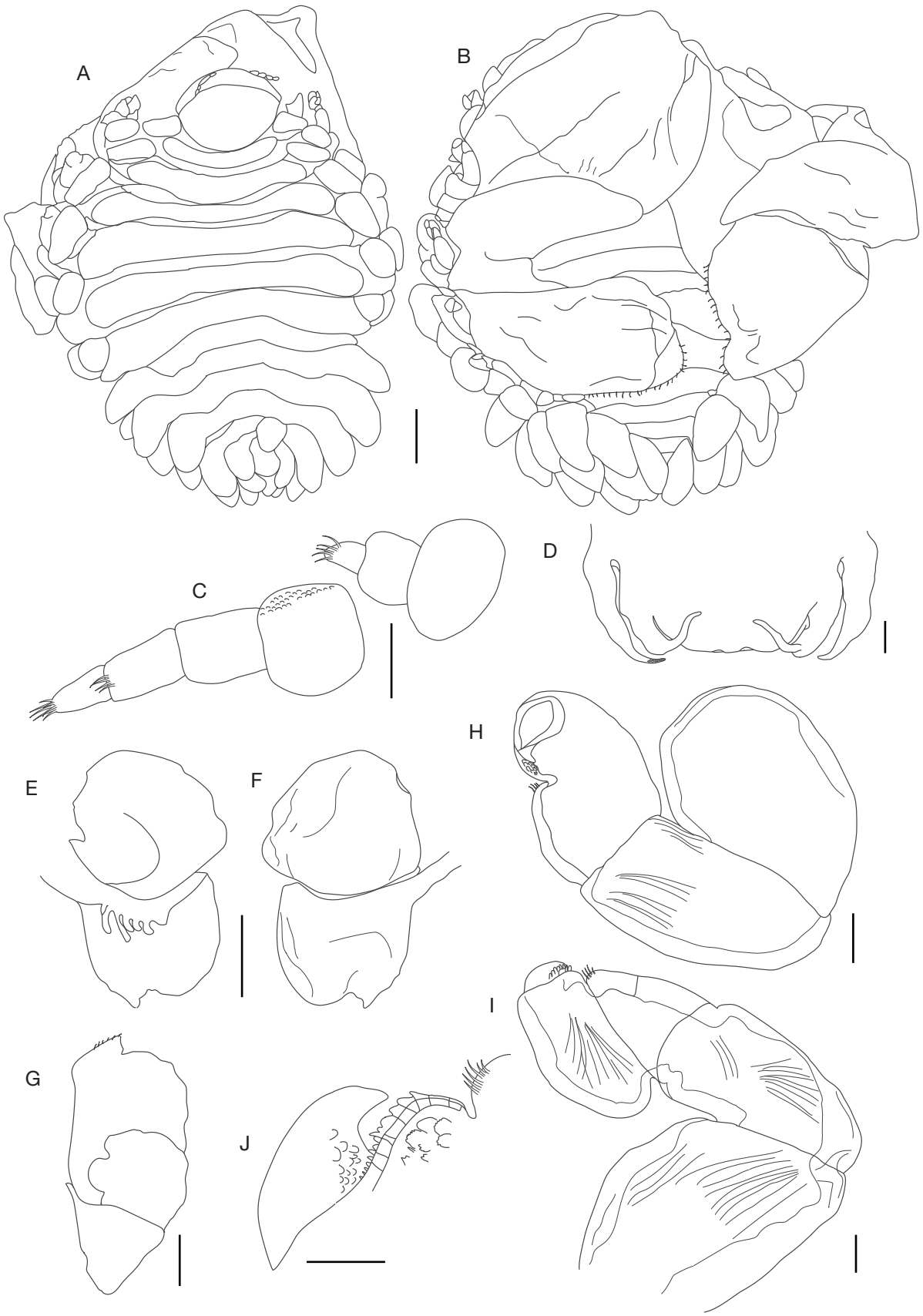

Fig. 4. — *Rhopalione uromyzon* Pérez, 1920, syntype female (MNHN-IU-2024-3187) (8.1 mm): **A**, dorsal view; **B**, ventral view; **C**, right antennule and antenna; **D**, barbula; **E**, left oostegite 1, inner view; **F**, left oostegite 1, outer view; **G**, left maxilliped, outer view; **H**, left pereopod 1; **I**, left pereopod 7; **J**, close-up view of dactylus, propodus and carpus ending of pereopod 7. Scale bars: A, B, 1 mm; C, G, I, 100 µm; D, 200 µm; E, F, 500 µm; H, 250 µm; J, 50 µm.

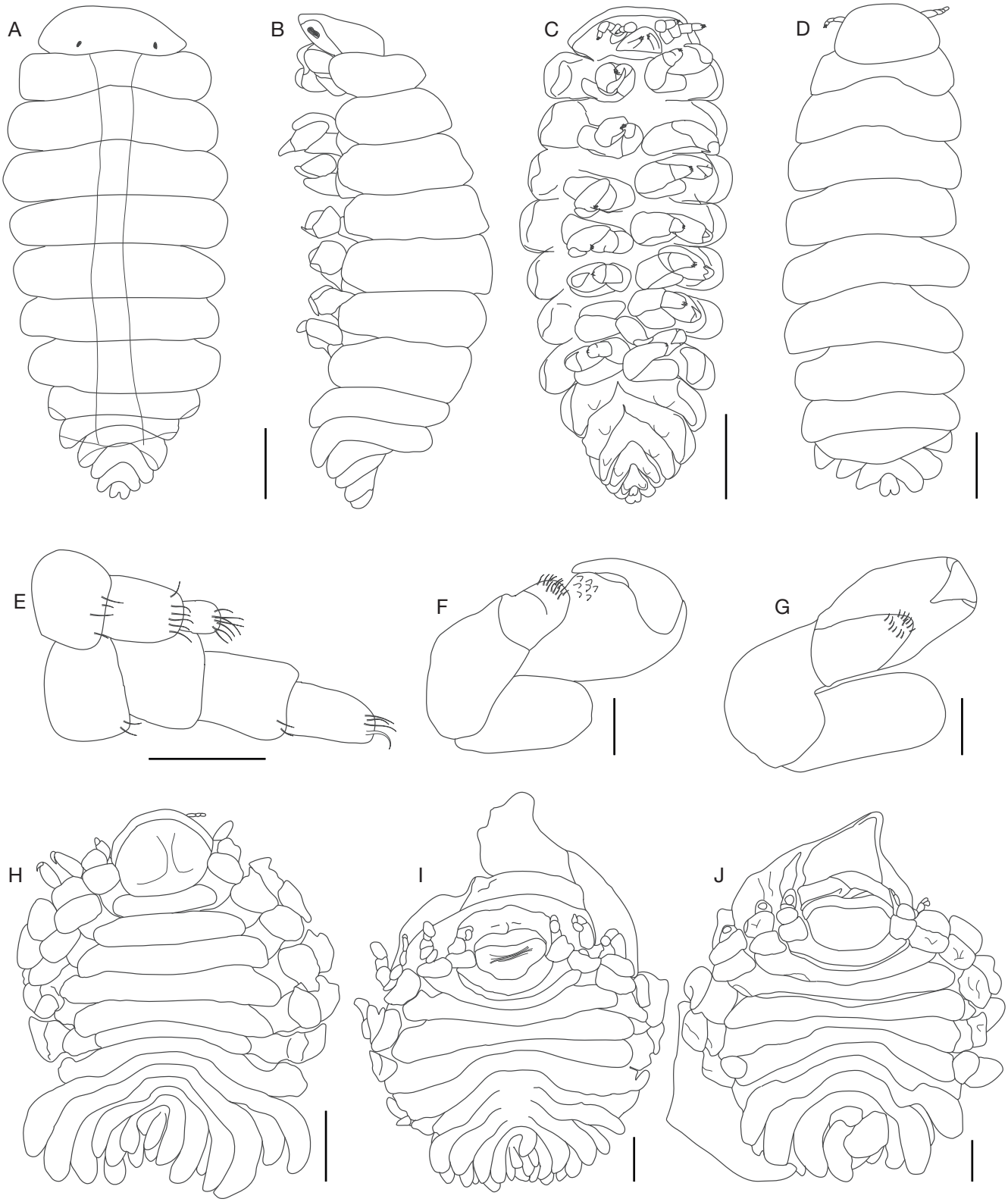

FIG. 5. — *Rhopalione uromyzon* Pérez, 1920: two syntype males (MNHN-IU-2024-3189) (**A**-**C**, **E**-**G**: 3.45 mm, D: 3.68 mm), one syntype female (MNHN-IU-2024-3196) (**H**, 3.90 mm), 2 syntype females (**I**, 4.35 mm, **J**, 5.55 mm): **A**, dorsal view; **B**, lateral view; **C**, ventral view; **D**, dorsal view, **E**, left antennule and antenna; **F**, left pereopod 1; **G**, left pereopod 7; **H**-**J**, dorsal views. Scale bars: A-D, H, 500 µm; E-G, 100 µm; I, J, 1 mm.

MNHN-IU-2024-3194 (= Ep918) • 1 syntype ♂ (3.41 mm TL), ex 1 of 2 females *D. spondyli* (damaged, unmeasurable); MNHN-IU-2024-3199 (= Ep916) • 1 syntype ♀ (3.90 mm TL), ex female *D. spondyli* (damaged, unmeasurable); MNHN-IU-2024-3196 (= Ep920) • 1 syntype ♀ (3.08 mm TL), ex female *D. spondyli* (5.20 mm); MNHN-IU-2024-3197 (= Ep921).

NON-TYPE MATERIAL EXAMINED. — **No data** [**United Arab Emirates**] • 1 cryptoniscid larva (0.45 mm TL), host not present; MNHN-IU-2024-3198 (= Ep922).

REDESCRIPTION

Female (Fig. 4), based on MNHN-IU-2024-3187

Body length 8.10 mm, maximal width 6.74 mm, head length 1.60 mm, head width 1.98 mm. Pereon essentially straight, left and right side subequal (Fig. 4A, B). All body regions and pereomeres distinctly segmented. Head broader than long, strongly produced with frontal lamina equal to approximately one-fifth length of head (Fig. 4A), small portion of pereomere 1 median obscured by cephalon; barbula (Fig. 4D) with two thin, distally tapering projections, entirely covered in minute papillae. Eyes absent. Antennule (Fig. 4C) of three articles, antenna (Fig. 4C) of four articles. Maxilliped (Fig. 4G) with thin distally acute spur; palp absent, distolateral margin subquadrate, produced and with short setae on edge. First oostegite proximal lobe ovate, distal lobe subtriangular with median acute projection (Fig. 4E, F), internal ridge with several thin, distally rounded projections (Fig. 4E). Pereon composed of seven pereomeres, broadest across pereomere 5, gradually tapering anteriorly and posteriorly; pereomeres 1 and 2 with convex posterior margins, 4 nearly straight, 5-7 with concave posterior margins (Fig. 4A). Coxal plates as large, irregular lobes on pereomeres 1-5, clearly separated from pereomeres. Dorsolateral bosses on pereopods 1-6 large, oblong, and clearly demarcated with left and right sides subequal. Pereomeres 1-6 with clearly demarcated elongate median region having raised and rounded aspect; no tergal projections. Oostegites enclosing marsupium (Fig. 4B). Pereopods all subequal (Fig. 4H-J) with indistinct separation of propodus, carpus and merus in anterior pairs; edge of propodus meeting tip of dactylus with area of low serrate scales, and distally acute, proximally subquadrate teeth (Fig. 4J); distoventral tip of carpus with tuft of thick setae; ventral margin of carpus and distal portion of merus with thin, short setae. First pair of pereopods surrounding head region, others evenly spaced. Pleon with five distinct pleomeres plus pleotelson; posterior margins of pleomeres 1 and 2 sinuous, those of 3-5 becoming progressively concave (Fig. 4A). Pleomeres 1-5 with biramous pleopods and uniramous lateral plates (Fig. 4B); endopodites and exopodites of all pleopods rounded and subequal in size; lateral plates strongly produced and distally rounded; edges and surfaces of all lateral plates smooth; uropods typically uniramous (see under Variation below), subequal in shape and size to pleopods and lateral plates.

Male (Fig. 5A-G), based on MNHN-IU-2024-3189

Length 3.45 mm, maximal width 1.56 mm, head length 0.28 mm, head width 1.04 mm, pleon length 0.72 mm. Head subovate, widest posteriorly, distinct from first segment of pereon (Fig. 5A, D). Eyes usually present, small (Fig. 5A). Antennule (Fig. 5E) of three articles, distally setose, antenna (Fig. 5E) of four articles, distally setose, not extending beyond margin of cephalon. Pereomere 3 broadest, others tapering anteriorly and posteriorly. All pereomeres directed laterally, distolateral margins of rounded, dorsal margin produced into a gently rounded arch (Fig. 5B). No detectable pigmentation. Pereopods (Fig. 5F, G) subequal, all articles distinctly separated, palm of propodus with row of low blunt teeth, distoventral tip of carpus with distal tuft of setae. Pleon with five segments plus pleotelson. Pleomere 1 directed laterally, 2-5 directed progressively posterolaterally, distolateral margins of all pleomeres rounded; pleomeres 1 and 2 strongly produced medially into rounded arch as for pereomeres, 3-5 dorsoventrally flattened; pleotelson subtriangular with short posterolateral lobes separated by shallow medial indentation; anal cone not observed, distal tips of posterolateral lobes without setae; midventral tubercles absent; pleopods present as very low rounded swellings; uropods absent.

Variation

Head shape of female is variable from nearly rounded (Fig. 5H) to oblong (Fig. 5I, J), but always broader than long; occasionally the barbula has a reduced medial projection. The antenna usually has four but may have five articles, the distalmost article very small and slender. The anteroposterior compression of the pereomeres is variable, with pereomeres broadly separated in some specimens while in others they have thin median portions. The pleomeres are occasionally indistinctly separated. Lateral plate development ranges from oblong to distinctly elongate. Uropods are uniramous or biramous, but always resemble the pleopods. One specimen lacks both pleomere 5 and the uropods, and one has a lateral plate of pleomere 6 and biramous uropods only on the left side, but this is a developmental defect. Eyes of males can be present (Fig. 5A) or absent (Fig. 5D). The pleotelson of the male may lack the median indentation.

REMARKS

Pérez (1920a) gave only "du golfe Persique" as the locality data for *R. uromyzon*, but several lots contain original data labels, and complete station data for the Mission Bonnier-Pérez was listed by Nobili (1906). Pérez (1920a) listed "plus de 130 exemplaires" of the host *Ostracotheres spondyli* [now *Discorsotheres spondyli* (Nobili, 1905)] that were collected by Mission Bonnier-Pérez, but Nobili (1906) only cited 124 specimens from stations LIII and LIV. This suggests that the parasitized crabs (at least 14 specimens based on the material examined) were not given to Nobili for study, and therefore should not be included in the type series of *O. spondyli*. Most of the jars of *R. uromyzon* contain a small handwritten label "vient de chez Mr. Le Prof. Pérez Novembre 1945," suggesting that all were in the possession of Pérez when he died. Many of the vials now lack original data labels but are clearly part of the type series. All the hosts are female, as were apparently all the pinnotherid hosts collected by the Mission Bonnier-Pérez (Pérez 1920a). One lot (MNHN-IU-2024-3194) contains the name

"*Hypurione*" handwritten on a small label; this is evidently a manuscript name for the genus Pérez eventually named *Rhopalione*. The cryptoniscid larva (MNHN-IU-2024-3198) is only questionably referred to this species as the details of its collection are unknown and Pérez himself questioned its identity on the specimen label; it is not considered part of the type series. An additional female *D. spondyli* (7.30 mm) was found in the same jar with the type vials of *R. uromyzon*, but given that it was ovigerous, it probably never possessed any parasites and may have been used as comparative material.

Rhopalione pelseneeri Pérez, 1920 *nomen nudum*

Rhopalione pelsenseeri Pérez, 1920a: 1617 [ex unidentified pinnotherid crab, Lombok, Indonesia]. — de Man 1921: 260 [mention]. — Nierstrasz & Brender à Brandis 1923: 68 [list]. — Perkins 1925: 182 [mention]; 1931: 176 [mention]. — Danforth, 1963: 11. — Page 1985: 199, 200 [mention]. — McDermott 2009: 790, 792, table 2 [mention, list]. — An *et al.* 2014: 2, table 1 [list]. — Ahyong & Boyko 2019: 286 [discussion of identity].

"*Rhopalione* infesting a pinnotherid in Lombok" – Markham 1990: 562.

Remarks

This name has been cited numerous times in the literature, but Pérez (1920a) is the only report on this species and he neglected to provide any description or illustration that might have served to make the name available. This name likely cannot be placed into synonymy with *R. uromyzon* or *R. incerta*, given that Pérez saw material of all three "taxa." Ahyong & Boyko (2019) noted that Pérez (1920a) did not identify the pinnotherid host for this species, but Pérez (1921) thanked J. G. de Man for identifying the host as *Pinnotheres arcophilus*, a junior subjective synonym of *Arcotheres palaensis* (Bürger, 1895). There are no other records of specimens of *Rhopalione* from this host and the species may be distinct, albeit undescribed.

Rhopalione atrinicolae Page, 1985
(Fig. 6)

Rhopalione atrinicolae Page, 1985: 199-201, figs 10, 11 (ex *Pinnotheres atrinicola* Page, 1983 (now *Nepinnotheres atrinicola* (Page, 1983)), New Zealand). — McLay 1988: 329 [mentioned erroneously as a gill parasite]. —Markham 1990: 562 [mention]. — Taylor & Morrison 2008: 194, table 1 [ex *N. atrinicola*, New Zealand]. — McDermott 2009: 788, 790, 792, tables 1, 2 [mention, list]. — An *et al.* 2014: 2, table 1 [list], 4 [key to species]. — Ahyong & Boyko 2019: 283 [mention], 286, 287 [mention, key to species]. — Williams *et al.* 2023: 532 [list].

Type material examined. — **New Zealand** • ovigerous (with epicaridium larvae) holotype ♀ (10.0 mm TL), from pleon of non-ovigerous female *Nepinnotheres atrinicola* Page, 1983 (14.6 mm CL, 15.8 mm CW), ex *Atrina zelandica* (Gray, 1835) (Pinnidae); Whangarei Harbour between High Island and mainland; 0-1 m; 13.V.1982; B. Dobson, G. Miles, C. Turbott & C. Worthington leg.; NMNZ Cr.3022 • Mature allotype ♂ (5.5 mm TL), collected with holotype; Whangarei Harbour between High Island and mainland; 0-1 m; 13.V.1982; B. Dobson, G. Miles, C. Turbott & C. Worthington leg.; NMNZ Cr.3022 • 1 ovigerous (with epicaridium larvae) paratype ♀ (9.1 mm TL), mature paratype ♂ (5.0 mm TL), non-ovigerous paratype ♀ (9.0 mm TL), mature paratype ♂ (4.3 mm TL), from pleon of non-ovigerous female *N. atrinicola* Page, 1983 (two hosts: 15.2 mm CL, 12.2 mm CW & unmeasurable CL (damaged), 17.8 mm CW (parasites separated from hosts so not possible to match them), ex *A. zelandica* (Gray, 1835) (Pinnidae); Hauraki Gulf, channel between Takatu and Kawau Islands, 23.IX.1971; M.V. *Ikatere* on R/V *Grace*, leg.; NMNZ Cr.3090.

Other material examined. — **New Zealand** • 4 mature ♀ (10.6-12.1 mm TL), from stomach of *Mustelus antarcticus* Günther, 1870 (Chondrichthyes, Triakidae); Hauraki Gulf; *c.* 36.73°S, 175.05°E, 24.VII.1949; J. Morton leg.; NIWA 160626.

Description (modified from Page 1985)

Female

Body nearly straight, ovate in outline, longer than wide; all segments distinct. Head subquadrate, separated from pereon, wider than long, medially indented, anterior and posterior margins convex, lateral margins rounded; thin frontal lamina. Eyes present or absent. Antennules of three articles each, antennae of five articles each, both setose, neither visible dorsally. Maxilliped longer than wide; broad non-articulated palp, with distal recurved lobe, apex rounded; plectron short, slender, straight. Barbula with pair of smooth, slender falcate projections laterally, deeply concave medially. Pereon nearly straight. Pereomeres dorsally distinct, produced laterally into tapered, rounded lobes; widest at pereomere 5; margins straight or weakly curved, mid-dorsal bosses and projections absent; irregularly-shaped dorsolateral bosses and distally acute coxal plates on all seven pereomeres. Oostegites completely enclosing brood pouch, strongly vaulted ventrally, protruding beyond anterior margins of body, visible dorsally. Oostegite 1 longer than wide; anterior lobe rounded, with shallow emargination, subequal to distal lobe; internal ridge smooth; posterior lobe with acute, nearly straight distal projection on margin. Oostegite 5 posterior margin fringed with setae. Pereopods isomorphic, subchelate. Pleon short, five pleomeres, all dorsally distinct, each with lateral plates produced into slender, distally rounded lobes, similar in size and shape to corresponding five pairs of biramous pleopods. Uniramous uropods similar in size and shape to pleopods and adjacent lateral plates of pleomere 5.

Male

Body elongate, fusiform, straight, length 3.0 × width; all segments distinct. Head transversely ovate in dorsal view, shorter than pereomere 1; anterior margin broadly curved, almost straight medially; posterior margin broadly curved; eyes present. Antennules of three articles each, antennae of five articles each, both with terminal setae. Pereomeres 1-7 subequal in length, lateral margins rounded, 1-4 with posterior margins concave; all pereomeres subequal in width; midventral projections absent. Pereopods isomorphic in size and shape, subchelate. Pleon with subquadrate outline; pleomeres distinct, distal margins rounded, posteriorly recurved, apices blunt; pleopods 1-5 bulbous, uniramous. Pleotelson rounded posteriorly.

FIG. 6. — *Rhopalione atrinicolae* Page, 1985 paratype specimens (**A**, **B**: NMNZ Cr. 3090) and non-type specimens (**C**, **D**: NIWA 160626): **A**, female, dorsal view; **B**, male, dorsal view. **C**, female, dorsal view; **D**, female, dorsal view, arrow shows lateral plate with slightly crenulate edge. Scale bars: A, C, D, 2 mm; B, 1 mm.

Remarks

The description of Page (1985) is comprehensive, and his illustrations are sufficient to recognize the species; the female (Fig. 6A) and male (Fig. 6B) paratype specimens (NMNZ Cr. 3090) were examined and photographed. All female specimens of *R. atrinicolae* have distally acute coxal plates which distinguishes this species from all others in the genus. The specimens obtained from the stomach of a gummy shark, *Mustelus antarcticus,* are in surprisingly good condition (Fig. 6C, D) and match well the original description by Page (1985). Two specimens have bifid tips on some pleopods and one specimen has lateral plates with slightly crenulate edges (Fig. 6D). The gummy shark *M. antarcticus* feeds predominately on benthic crustaceans but can opportunistically feed on a wide range of species, including occasionally bivalves (e.g., Coleman & Mobley 1984; Yick *et al.* 2007). There do not appear to be any published records of the shark feeding on horse mussels, but to have four specimens of *R. atrinicolae* in its gut, it is most likely that the shark fed on one or more of these bivalves within which pea crabs parasitized by the bopyrids resided. It is unknown whether there were also specimens of the host pinnotherid in the shark's gut; the bopyrid specimens were originally in the Dominion Museum (Wellington) but now in the NMNZ and there are no records of their host pea crabs or mussels (Mills, pers. comm.). There are previous records of pea crabs from the gut contents of bony fish (Miller, 1967) but, to our knowledge, no records of bopyrids in any bony fish or sharks. This is surprising given that some bopyrid hosts are abundant food resources for their predators; this likely reflects an artifact of bopyrids being placed into the category of "other" during gut content analyses. These parasites may play a more important role in trophic interactions than previously thought (see Lafferty *et al.* 2008 for discussion of this across other parasite taxa and Sikkel & Welicky 2019 for discussion on crustacean parasites specifically).

Rhopalione sinensis Markham, 1990
(Fig. 7)

Rhopalione uromyzon – Nierstrasz & Brender à Brandis 1931: 175-176 [host unknown, Zamboanga, Philippines; specimen examined herein] (not *Rhopalione uromyzon* Pérez, 1920).

Rhopalione sinensis Markham, 1990: 555, 560-562, fig. 3 (ex *Pinnotheres sinensis atrinae* Sakai, 1939 (now *Arcotheres atrinae* (Sakai, 1939)), Hong Kong); 1992: 299, table 1 [list]. — Huang 1994: 530 [list]; 2001: 327 [list]. — Li 2003: 140, 153, 158, table 1 [list]. — Morton 2003: 43, table 4 [list]. — An *et al.* 2009: 351 [list]; 2014: 1-2, fig. 1 (ex *Arcotheres sinensis* (Shen, 1932), Fujian Province, China), 4 [key to species]. — McDermott 2009: 790, 792, table 2 [list]. — Kuo *et al.* 2018: 1434-1448, fig. 1 (ex *A. sinensis*, Taiwan). — Ahyong & Boyko 2019: 286 [comparison with *R. kali*], 287 [key to species]. — Williams *et al.* 2023: 533 [list], 539 [mention].

Type material examined. — **China** • non-ovigerous holotype ♀ (3.9 mm TL), ex ♀ *Pinnotheres sinensis atrinae* Sakai, 1939 (now *Arcotheres atrinae* (Sakai, 1939) (6.5 mm CW); Hong Kong, Deep Bay, 16.IV.1954; B. Morton leg.; USNM 233554.

Other material examined. — **Philippines** • 1 non-ovigerous ♀ (7.13 mm TL), ex unknown host (pinnotherid); Zamboanga, St. Cruz Island; 24.II.1914; Dr Th. Mortensen's Pacific Expedition 1914-16, leg.; NHMD-1184775.

Description (modified from Markham 1990; An *et al.* 2014)

Female

Body nearly straight, ovate in outline, longer than wide; all segments distinct. Head ovate, separated from pereon, wider than long, anterior and posterior margins convex, lateral margins rounded; thin frontal lamina. Eyes absent. Antennules of three articles each, antennae of five articles each, both setose, neither visible dorsally. Maxilliped longer than wide; broad non-articulated palp, apex rounded; plectron short, slender, straight. Barbula with one or two pairs of smooth, slender falcate projections laterally, weakly concave medially. Pereon nearly straight. Pereomeres dorsally distinct, produced laterally into tapered, rounded lobes; widest at pereomere 4; margins straight or weakly curved, mid-dorsal bosses and projections absent; irregularly-shaped dorsolateral bosses and rounded coxal plates on all seven pereomeres. Oostegites completely enclosing brood pouch, strongly vaulted ventrally, protruding beyond anterior margins of body, visible dorsally. Oostegite 1 longer than wide; anterior lobe rounded, larger than distal lobe; internal ridge digitate; posterior lobe with acute, nearly straight distal projection on margin. Oostegite 5 posterior margin fringed with setae. Pereopods isomorphic, subchelate. Pleon short, five pleomeres, all dorsally distinct, each with lateral plates produced into slender, distally rounded lobes, similar in size and shape to corresponding five pairs of biramous pleopods. Uniramous uropods similar in size and shape to pleopods and adjacent lateral plates of pleomere 5.

Male

Body elongate, fusiform, straight, length 3.0 × width; all segments distinct. Head transversely ovate in dorsal view, longer than pereomere 1; anterior margin broadly curved, medially concave; posterior margin broadly curved; eyes present. Antennules of three articles each, antennae of six articles each, both with terminal setae. Pereomeres 1-7 subequal in length, lateral margins rounded, pereomere 1 with posterior margin concave; all pereomeres subequal in width; midventral projections absent. Pereopods isomorphic in size and shape, subchelate. Pleon with tapered outline; pleomeres distinct, distal margins rounded, posteriorly recurved, apices blunt; pleopods 1-5 bulbous, uniramous. Pleotelson indented posteriorly.

Remarks

Markham (1990) described *R. sinensis* based on the holotype female from Hong Kong. He noted that it closely resembled the female of *R. uromyzon*, but that *R. sinensis* had a head broader than long, well separated coxal plates, and indistinct dorsal separation of pleomeres whereas *R. uromyzon* had a nearly oval head, "somewhat separated coxal plates", and

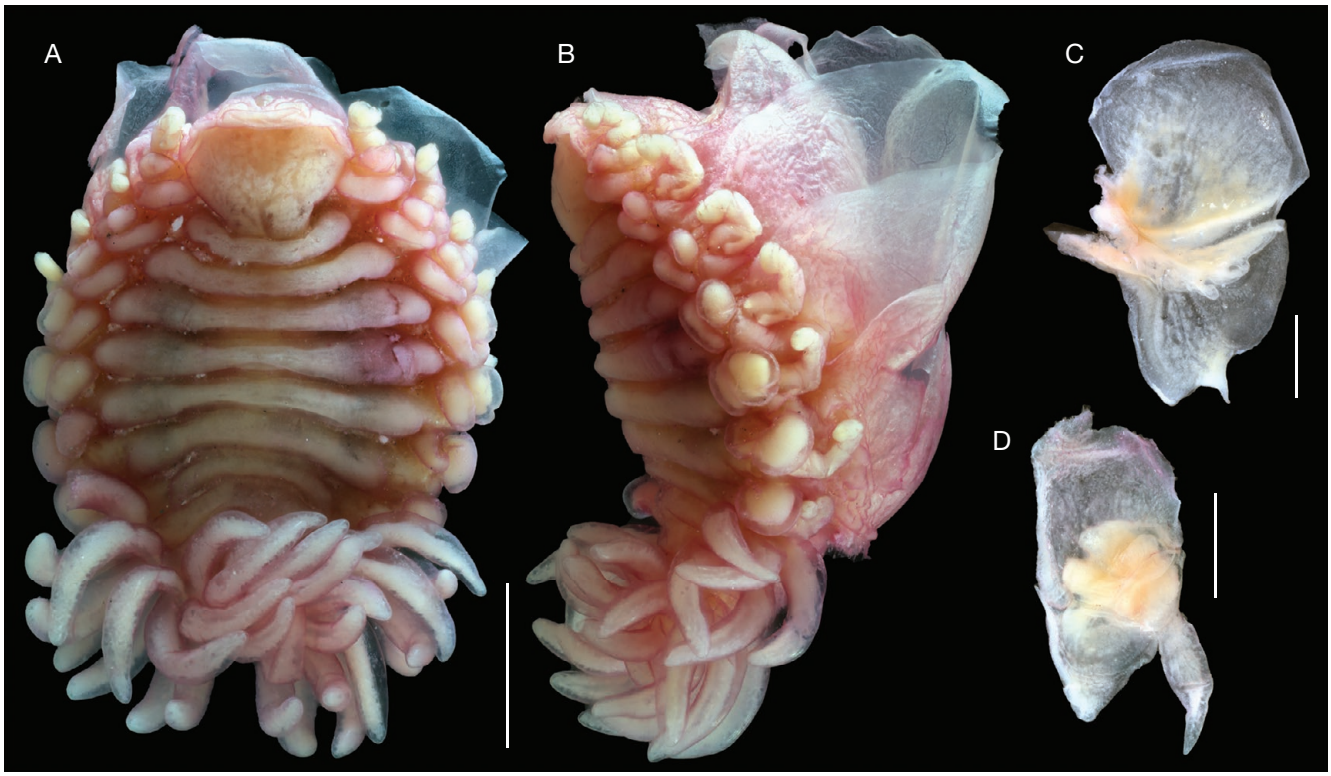

Fig. 7. — *Rhopalione sinensis* Markham, 1990 (NHMD-1184775): **A**, female, dorsal view; **B**, female, lateral view; **C**, left oostegite 1, inner view; **D**, left maxilliped, outer view. Scale bars: A, B, 2 mm; C, D, 100 µm.

distinct dorsal separation of all pleomeres. The holotype of *R. sinensis* was examined and found to agree with the description of Markham (1990) in all features except that the five projections on the inner ridge of the oostegite 1 are more clearly demarcated and spaced than indicated by Markham (1990: fig. 3I) and more like those seen in specimens of *R. uromyzon* from the Persian Gulf, and that the inner projection of the barbula is present, but only about half the length of the outer projection. Additionally, examination of the maxilliped and oostegite 1 of *R. uromyzon* shows them to be indistinguishable from those of *R. sinensis*. Based on female morphology, it is very difficult to distinguish *R. sinensis* from *R. uromyzon* except for the shape of the pleopods, which are much slenderer and more elongate in *R. sinensis*; however, the males do show differences in that those of *R. sinensis* have the pleopods displaced laterally while those of *R. uromyzon* have the pleopods located closer to the pleon median.

The single female specimen (Fig. 7) from the Philippines cited by Nierstrasz & Brender à Brandis (1931) was examined and is identifiable as *R. sinensis* rather than *R. uromyzon*; it matches in body form (Fig. 7A, B), maxilliped (Fig. 7D), and oostegite 1 (Fig. 7E) morphology. The host for this specimen was given by Nierstrasz & Brender à Brandis (1931) as a *Pinna* bivalve but, as pointed out by Page (1985), the host must have been a *Pinna*-infesting pinnotherid.

Rhopalione kali Ahyong & Boyko, 2019

isopod parasite – Serène 1967: 819 [mention].

Rhopalione sp. – Ahyong & Ng 2005: 124 [mention]. — An *et al.* 2014: 2, table 1 [list].

Rhopalione kali Ahyong & Boyko, 2019: 284-286, fig. 1 [ex *Serenotheres besutensis* (Serène, 1967), Perhentian Besar, South China Sea, east coast of peninsular Malaysia, 05°55'N, 102°45'E), 4 m depth]. — Williams *et al.* 2023: 533 [list].

Description (modified from Ahyong & Boyko 2019)

Female

Body nearly straight, subcircular in outline, wider than long when including coxal plates; all segments distinct. Head subquadrate, separated from pereon, wider than long, anterior and posterior margins convex, lateral margins almost straight; wide frontal lamina. Eyes absent. Antennules of three articles each, antennae of five articles each, both visible dorsally, neither with setae. Maxilliped longer than wide; broad non-articulated palp with short, recurved, digitate apex; plectron short, slender, straight. Barbula with smooth, slender falcate projection and round blunt lobe laterally, shallowly concave medially. Pereon nearly straight. Peremeres dorsally distinct, produced laterally into blunt, rounded lobes; widest at pereomere 4; margins straight or weakly curved, mid-dorsal bosses or projections absent; irregularly-shaped dorsolateral bosses and coxal plates on all seven pereomeres, fusion of dorsolateral bosses and coxal plates

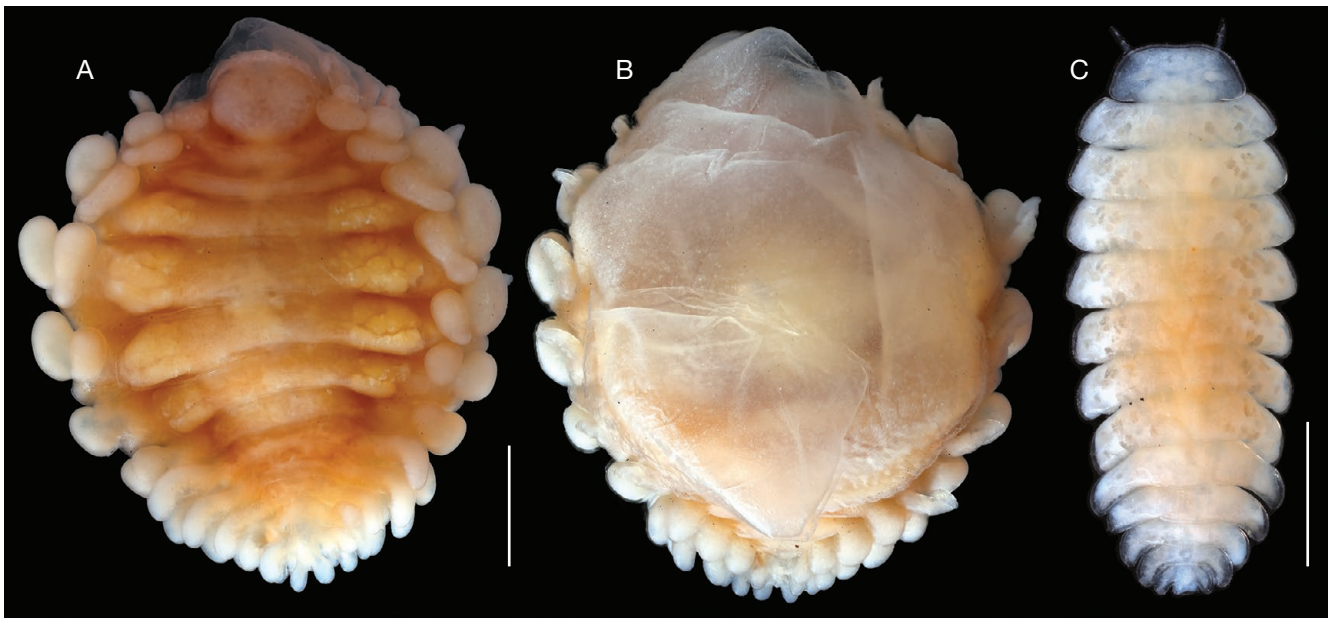

Fig. 8. — *Rhopalione racemus* n. sp. holotype and allotype specimens (SAM C16386): **A**, holotype female, dorsal view; **B**, holotype female, ventral view; **C**, allotype male, dorsal view. Scale bars: A, B, 2 mm; C, 1 mm.

in posterior two pereomeres. Oostegites completely enclosing brood pouch, strongly vaulted ventrally, not protruding beyond anterior margins of body, not visible dorsally. Oostegite 1 longer than wide; anterior lobe rounded, with shallow emargination, longer than distal lobe; internal ridge with few irregular slender digitations and rounded lobes; posterior lobe with acute, slightly recurved distal projection on margin. Oostegite 5 posterior margin fringed with setae. Pereopods isomorphic, subchelate. Pleon short, five pleomeres, all dorsally distinct, each with lateral plates produced into slender, distally rounded lobes, similar in size and shape to corresponding five pairs of biramous pleopods. Uniramous uropods similar in size and shape to pleopods and adjacent lateral plates of pleomere 5.

Male

Body elongate, fusiform, slightly curved, length 2.2 × width; all segments distinct. Head transversely ovate in dorsal view, longer than pereomere 1; anterior margin broadly curved, almost straight medially; posterior margin broadly curved; eyes present but weakly pigmented. Antennules of three articles each, antennae of five articles each, both with terminal setae. Pereomeres 1-7 subequal in length, lateral margins rounded, posterior margins straight or at most weakly sinuous; pereomere 1 narrower than pereomere 2; pereomeres 2-4, 6, 7 subequal in width, narrower than pereomere 5; midventral projections absent. Pereopods isomorphic in size and shape, subchelate. Pleon broadly tapering to rounded outline; pleomeres distinct, distal margins produced as slender tapering lobes, posteriorly recurved, apices blunt; pleopods 1-5 bulbous, uniramous. Pleotelson deeply bifurcate posteriorly.

Remark

Only the type material of *R. kali* is known.

Rhopalione racemus n. sp.
(Figs 8; 9)

urn:lsid:zoobank.org:act:91BC048C-A4A0-4959-A322-504403BE1E36

"large parasitic Isopod (Epicarid)" – Hale 1927: 174 [ex *Pinnotheres subglobosus* Baker, 1907 (now *Discorsotheres subglobosus* (Baker, 1907), Gulf St. Vincent, South Australia; specimen examined herein]. — Silas & Alagarsiwami 1967: 1191 [reference to Hale's findings].

"the isopod mentioned by Hale" – Page 1985: 201 [mention].

? "an undescribed species of *Rhopalione*" – Poore *et al.* 2002: 124 [see Remarks below].

Rhopalione sp. – McDermott 2009: 792, table 2 [list]. — An *et al.* 2014: 2, table 1 [list]. — Ahyong 2018: 557 [ex *Discorsotheres subglobosus* (Baker, 1907), Gulf St. Vincent, South Australia]. — Williams *et al.* 2023: 533 [list].

Type material. — **Holotype**. **Australia** • ovigerous ♀ (8.9 mm TL), from under pleon of ♀ *Discorsotheres subglobosus* (Baker, 1907) (10.5 mm CL, 11.7 mm CW), ex *Equichlamys bifrons* (Lamarck, 1819) (Pectinidae Rafinesque, 1815); South Australia, Port Willunga; 25.II.1990; N. Holmes leg.; SAM C16386.
Allotype. **Australia** • mature ♂ (3.8 mm TL), collected with holotype; South Australia, Port Willunga; 25.II.1990; N. Holmes leg.; SAM C16386.
Paratype. **Australia** • 1 mature ♀ (6.4 mm TL; male not present), from under pleon of female *D. subglobosus* (7.6 mm CL, 8.6 mm CW), ex *E. bifrons*; South Australia, Gulf St. Vincent; no date; A. Zietz leg.; SAM C1397.

Etymology. — The specific name, *racemus*, is a Latin noun meaning a bunch of grapes, which the shapes of the pleopods and lateral plates resemble; it is used in apposition.

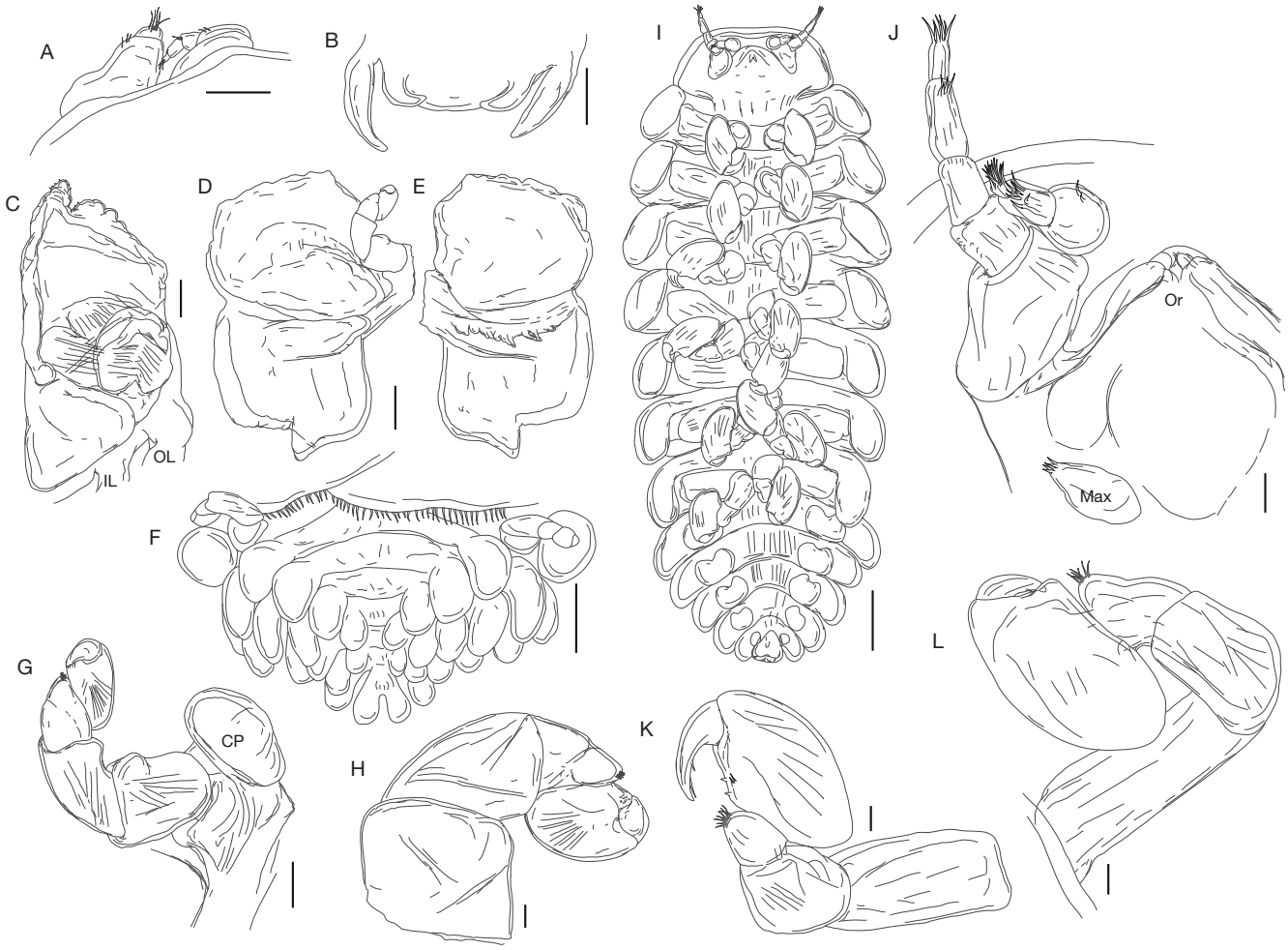

Fig. 9. — *Rhopalione racemus* n. sp. holotype (**A**-**H**) and allotype (**I**-**L**) specimens (SAM C16386): **A**, left antennae; **B**, barbula; **C**, left maxilliped, with base of barbular lobes shown; **D**, left oostegite 1, outer view; **E**, left oostegite 1, inner view; **F**, pereomere 7 and pleon, ventral view; **G**, left pereopod 1 and coxal plate; **H**, left pereopod 7; **I**, ventral view; **J**, right antennae, oral cone and maxilliped; **K**, right pereopod 1; **L**, left pereopod 7. Abbreviations: **CP**, coxal plate; **IL**, inner barbular lobe; **Max**, maxilliped; **OL**, outer barbular lobe; **Or**, oral cone. Scale bars: A, G, H, 100 µm; B, D, E, I, 500 µm; C, 250 µm; F, 1 mm; J-L, 50 µm.

Description

Female

Holotype (Figs 8A, B, 9A-H). Length 8.9 mm; maximal width at posterior margin of pereomere 46.9 mm (not including coxal plates); head length 1.5 mm; head width 1.8 mm. Body nearly straight (Fig. 8A, B), subcircular in outline but slightly longer than wide when including coxal plates, not distorted; all segments distinct. Head ovate, separated from pereon, slightly wider than long, anterior and posterior margins convex, lateral margins rounded; wide frontal lamina. Eyes absent. Antennules (Fig. 9A) of two articles each, antennae (Fig. 9A) of five articles each, both visible dorsally, few setae distally. Maxilliped (Fig. 9C) longer than wide; narrow non-articulated palp with blunt apex; spur elongate, slender, distally actute. Barbula (Fig. 9B) laterally with outer elongate, smooth, slender falcate projection and inner short acute curved projection; shallowly convex medially. Pereon nearly straight (Fig. 8A). Pereomeres dorsally distinct, produced laterally into blunt, rounded lobes; widest at pereomere 4; margins weakly curved, mid-dorsal bosses or projections absent; irregularly shaped dorsolateral bosses and coxal plates on all seven pereomeres, dorsolateral bosses and coxal plates in posterior pereomeres not fused. Oostegites completely enclosing brood pouch (Fig. 8B), strongly vaulted ventrally, protruding beyond anterior margins of body, visible dorsally. Oostegite 1 (Fig. 9D, E) longer than wide; anterior lobe rounded, subequal in length to distal lobe; internal ridge with numerous irregular slender digitations (Fig. 9E); posterior lobe with acute, triangular distal projection on margin. Oostegite 5 (Fig. 9F) posterior margin fringed with setae. Pereopods isomorphic, subchelate (Fig. 9G, H); small curved dactylus, propodus ovate, carpus and merus fused, ischium and basis tubular, relatively short (Fig. 9G). Pleon short (Fig. 8A; 9F), five pleomeres, all dorsally distinct, each with lateral plates produced into short, distally rounded lobes, similar in size and shape to corresponding five pairs of biramous pleopods (Fig. 9F). Uniramous uropods (Fig. 9F) similar in size and shape to pleopods and adjacent lateral plates of pleomere 5.

Male

Allotype (Figs 8C; 9I-L). Length 3.8 mm; maximal width at posterior margin of pereomere 4 1.6 mm; head length 0.4 mm; head width 0.9 mm. Body elongate, fusiform, straight, length 2.4 × width; all segments dorsally and ventrally distinct (Figs 8C; 9I). Head transversely ovate in dorsal view, about two-thirds as long as pereomere 1 (along midline) (Fig. 8C); anterior and posterior margins nearly straight; eyes absent. Antennules (Fig. 9J) of three articles each, antennae (Fig. 9J) of five articles each, both with terminal setae. Pereomeres 1-7 (Figs 8C; 9I) subequal in length, lateral margins subquadrate, posterior margins straight or at most slightly concave; pereomeres 1 and 7 subequal in width, 0.85 × width of pereomere 2; pereomeres 2-6 subequal in width; midventral projections absent (Fig. 9I). Pereopods isomorphic in size and shape, subchelate; dactyli of anterior pair longer than others, setose; propodus ovate, with setae along edge corresponding to region meeting distal end of dactylus; carpus and merus fused, end of carpus with small setae; ischium and basis tubular, bases longer on posterior pereopods (Fig. 9K, L). Pleon (Figs 8C; 9I) broadly tapering to rounded general outline; pleomeres dorsally and ventrally distinct, distal margins produced, posteriorly slightly recurved, lateral margins rounded, medioventral tubercles absent; pleopods 1-4 (Fig. 9I) reniform, pleopods 5 rounded, uniramous. Pleotelson (Fig. 8C, I) slightly indented posteriorly.

Remarks

Females of *Rhopalione racemus* n. sp. can be distinguished from all other species in the genus by the shape of the pleopods and lateral plates which are short and rounded; females of all other species have markedly elongate pleopods and lateral plates**.** The specimens reported by Hale (1927) are the paratypes examined and designated as such herein. We consider the specimens cited by Ahyong (2018; SAM C12813) that were collected from same host species in a known locality (Gulf St. Vincent) for *R. racemus* n. sp. to be this species, although they were not examined for this study.

Poore *et al.* (2002) noted that "an undescribed species of *Rhopalione* has been identified from Australia by J. Markham" but this has not been described; it may be conspecific with *R. racemus* n. sp. but given the lack of information on the locality and host, this is far from certain.

Rhopalione rusa n. sp.
(Figs 10; 11)

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"bopyrids under pleon" – Ng & Ahyong 2022: 173 [ex ZRC 2019.0534; specimens examined herein].

"unidentified bopyrid" [of *Arcotheres similis*] – Williams *et al.* 2023: 533 [list].

Type material. — **Holotype**. **Singapore** • ovigerous ♀ (6.8 mm TL), from left side of pleon of female *Arcotheres similis* (Bürger, 1895) (ZRC 2019.0534; 6.0 mm CL, 7.6 mm CW), ex *Modiolus philippinarum* Hanley, 1843 (Mytilidae Rafinesque, 1815); off Changi Beach, intertidal area next to Carpark 7, near ferry terminal; 22.IV.2019; S. K. Tan *et al.* leg.; ZRC 2023.0259.
Allotype. **Singapore** • Mature ♂ (4.1 mm TL), collected with holotype; off Changi Beach, intertidal area next to Carpark 7, near ferry terminal; 22.IV.2019; S. K. Tan *et al.* leg.; ZRC 2023.0260
Paratype. **Singapore** • 1 ovigerous ♀ (5.5 mm TL; male not present), from right side of pleon of female *A. similis* (ZRC 2019.0534; 5.6 mm CL, 7.5 mm CW), ex *Modiolus philippinarum* Hanley, 1843 (Mytilidae); off Changi Beach, intertidal area next to Carpark 7, near ferry terminal; 22.IV.2019; S. K. Tan *et al.* leg.; ZRC 2023.0261.

Etymology. — The species is named after the type locality of Changi Beach which, in 1604, was originally called "Tanjong Rusa" (tanjong meaning cape and rusa being Malay for deer which could refer to the extinct Indian muntjac (*Muntiacus muntjak* (Zimmerman, 1780)) or the once thought extinct Sambar deer (*Rusa unicolor* Kerr, 1792). The change of name from Tanjong Rusa to Tanjong Changi occurred between 1604 and 1828 (Gibson-Hill 1954; Borschberg 2017; https://eresources.nlb.gov.sg/infopedia/articles/SIP_245_2004-12-15.html). The name is a noun in apposition.

Description

Female

Holotype (Figs 10A-C; 11A-G). Length 6.8 mm; maximal width at posterior margin of pereomere 4 5.0 mm (not including extended coxal plates); head length 0.9 mm; head width 1.4 mm. Body nearly straight (Fig. 10A, B), subcircular in outline but approximately as wide as long when including coxal plates, not distorted; all somites distinct. Head ovate, separated from pereon, 1.6 × wider than long, anterior and posterior margins convex, lateral margins rounded; wide frontal lamina. Eyes absent. Antennules (Fig. 11A) of three articles each, antennae (Fig. 11A) of five articles each, both visible dorsally, few setae distally. Maxilliped (Fig. 11D) longer than wide; broad non-articulated palp with blunt apex; spur elongate, recurved, distally triangular (Fig. 11D inset), covered by large round accessory lobe. Barbula (Fig. 11B) laterally with pair of elongate, smooth, broad falcate projections, distally tapering; shallowly convex medially. Pereon nearly straight (Fig. 10B). Pereomeres dorsally distinct, produced laterally into blunt, rounded lobes; widest at pereomere 4; margins weakly curved, mid-dorsal bosses or projections absent; ovoid dorsolateral bosses on pereomeres 1-6, round on pereomere 7, all dorsolateral bosses distinctly separated from lateral portion of pereomeres; ovoid coxal plates on all seven pereomeres, shorter than dorsolateral bosses on pereomeres 1-4, longer than dorsolateral bosses on pereomeres 5-7, dorsolateral bosses and coxal plates in posterior pereomeres not fused. Oostegites completely enclosing brood pouch (Fig. 10C), strongly vaulted ventrally, not protruding beyond anterior margins of body, not visible dorsally. Oostegite 1 (Fig. 11E, F) longer than wide; anterior lobe rounded, larger than distal lobe; internal ridge with few irregular low digitations (Fig. 11F); posterior lobe with acute, triangular distal projection on margin. Oostegite 5 (Fig. 11C) posterior margin fringed with setae. Pereopods isomorphic, subchelate (Fig. 11E, G), small curved dactylus, propodus ovate with scales around region that meets tip of dactylus, carpus and merus triangular, ischium and basis tubular, carpus with distal setae and scales. Pleon short

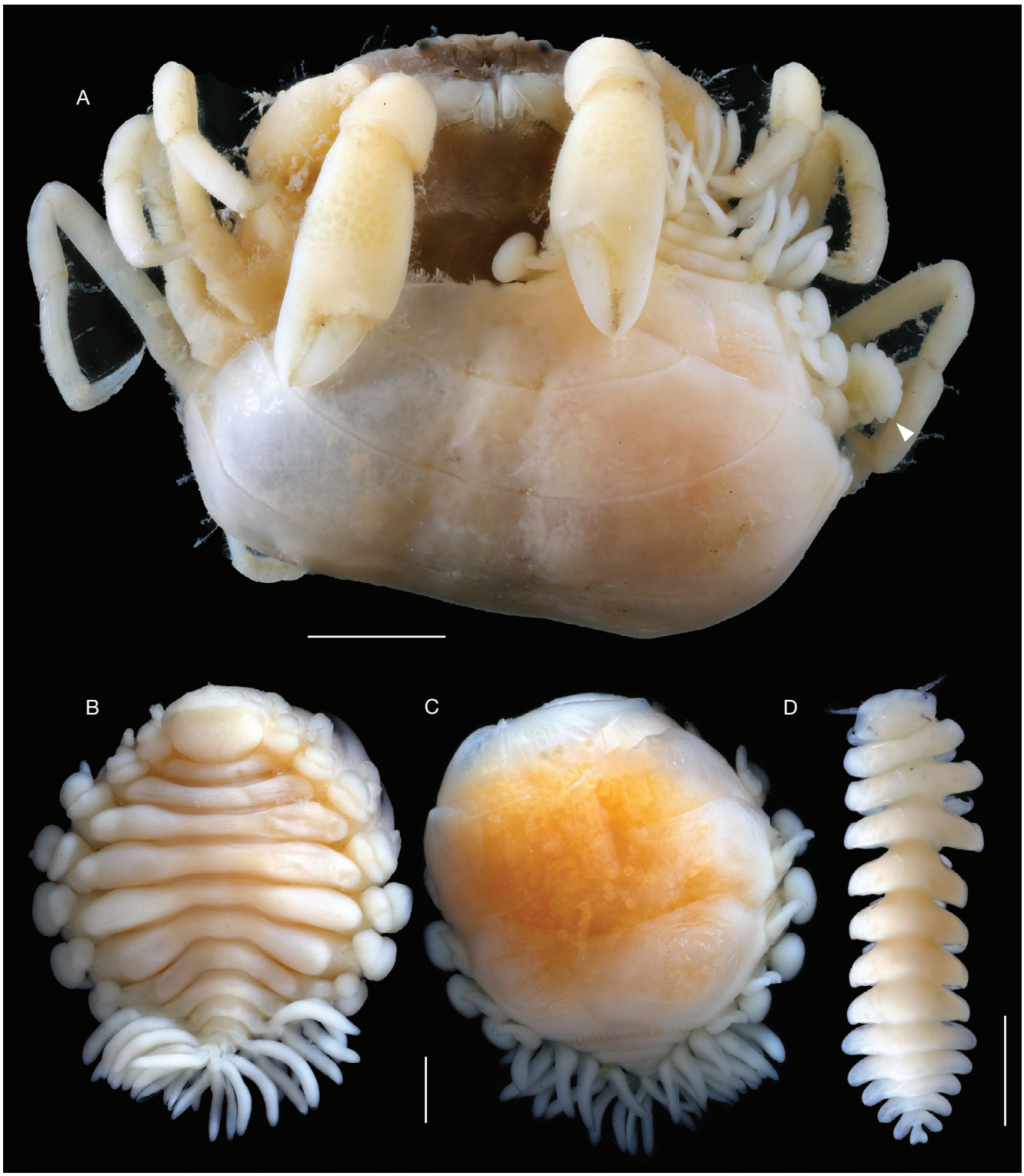

Fig. 10. — *Rhopalione rusa* n. sp. holotype (ZRC 2023.0259) and allotype (ZRC 2023.0260) specimens: **A**, ventral view of host pinnotherid *Arcotheres similis* (Bürger, 1895) with *Rhopalione* sp. *in situ* on left side of pleon (posterior end of male shown by arrow); **B**, holotype female, dorsal view; **C**, holotype female, ventral view; **D**, allotype male, dorsal view. Scale bars: A, 2 mm; B-D, 1 mm.

(Fig. 10B), five pleomeres, all dorsally distinct, each with lateral plates produced into long, slender, distally rounded lobes, similar in size and shape to corresponding five pairs of biramous pleopods (Figs 10B; 11C); endopodites with small basal swelling (observable in lateral view), decreasing in size on posterior pleomeres. Uniramous uropods (Fig. 10B; 11C) similar in size and shape to pleopods and adjacent lateral plates of pleomere 5.

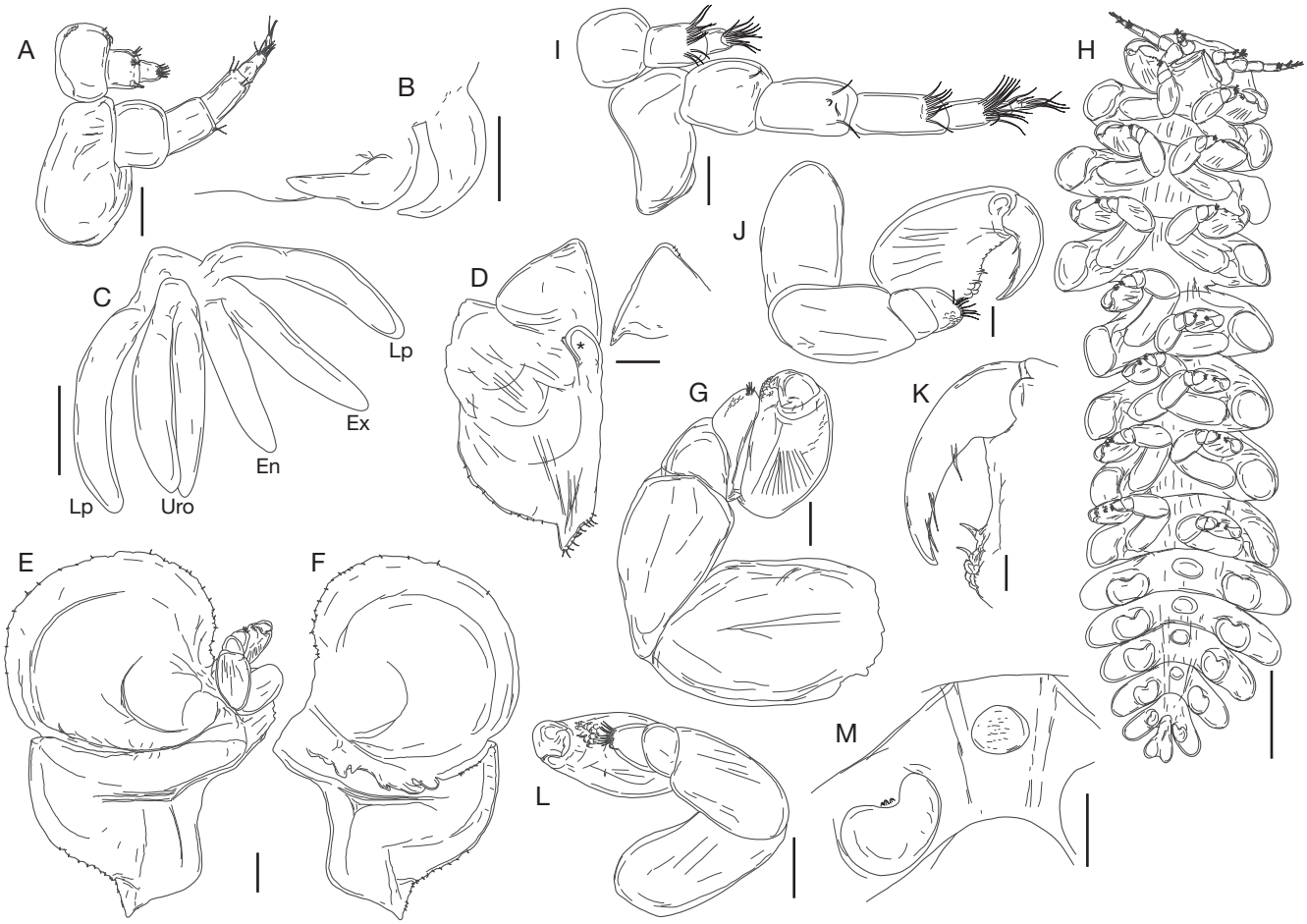

Fig. 11. — *Rhopalione rusa* n. sp. holotype (ZRC 2023.0259, **A**-**G**) and allotype (ZRC 2023.0260, **H**-**M**) specimens (ZRC 2019.0534): **A**, left antennae; **B**, barbula, left side; **C**, dorsal view of terminus of pleon showing fifth pleomere with lateral plates on both sides and biramous pleopod shown only on right side and uropods; **D**, left maxilliped, outer view; inset shows inner view of anterior lobe and spur obscured by lobe of maxilliped (*); **E**, left oostegite 1 and pereopod 1, outer view; F, left oostegite 1, inner view; **G**, left pereopod 7; **H**, ventral view; **I**, left antennae; **J**, right pereopod 1; **K**, right pereopod 1, close-up of dactyl and propodus; **L**, right pereopod 7; **M**, pleomere showing pleopod 4 on right side and mid-ventral tubercule. Abbreviations: **En**, endopod; **Ex**, exopod; **Lp**, lateral plate; **Uro**, uropods. Scale bars: A, G, L, M, 100 µm; B, D-F, 250 µm; C, H, 500 µm; J-K, 50 µm.

Male

Allotype (Figs 10D; 11H-M). Length 4.1 mm; maximal width at pereomeres 2-5 1.3 mm; head length 0.4 mm; head width 0.8 mm. Body elongate, fusiform, straight, length 3.2 × width; all somites dorsally and ventrally distinct (Figs 10D; 11H). Head transversely ovate in dorsal view, about half as long as pereomere 1 (along midline) (Fig. 10D); anterior and posterior margins weakly convex; irregularly shaped eyes. Antennules (Fig. 11I) of three articles each, antennae (Fig. 11I) of five articles each, both with terminal setae. Pereomeres 1-7 (Figs 10D; 11H) subequal in length, lateral margins rounded, posterior margins straight or at most slightly concave; pereomeres 2-5 subequal in width; pereomeres 1, 6, 7 narrower, subequal in width; midventral projections absent (Fig. 11H). Pereopods isomorphic in size and shape, subchelate, dactyli of anterior two pairs longer than others, all dactyli with setae, propodus ovate, with setae along edge corresponding to region that meets distal end of dactylus, carpus and merus triangular, end of carpus with small setae and scales, ischium and basis tubular (Fig. 11H, J, K). Pleon (Figs 8C; 9I) broadly tapering with triangular general outline; pleomeres dorsally and ventrally distinct, distal margins splayed, posteriorly slightly recurved, lateral margins rounded; pleomeres 1-4 with medioventral tubercles (Fig. 11H); pleopods 1-5 (Fig. 11H, M) reniform, uniramous, with minute setae in concave region (Fig. 11M). Pleotelson (Figs 10D; 11H) narrow anteriorly, widening posteriorly, indented posteromedially.

Remarks

Females of *Rhopalione rusa* n. sp. are most similar to *R. racemus* n. sp. in the shape of the pereomeres, which are greatly inflated laterally, forming a kind of barbell shape; however, the females differ in the form of the pleopods and lateral plates which are long and slender in *R. rusa* n. sp. but short and broad in *R. racemus* n. sp. Additionally, the barbula of females of *R. rusa* n. sp. bears two subequal lobes whereas that of females of *R. racemus* n. sp. have the outer lobe much longer than the inner. Males of the two species are also similar with both having five pairs of reniform pleopods but *R. rusa* n. sp. has midventral tubercles on pleomeres 1-4 whereas

R. racemus n. sp. lack midventral tubercles. *Rhopalione racemus* n. sp. is known only from *Discorsotheres subglobosus* collected in South Australia (Temperate Australasia) vs *Rhopalione rusa* n. sp., which is only known from *Arcotheres similis* collected in Singapore (Central Indo-Pacific) (see Spalding *et al.* 2007 for discussion of marine ecoregions).

The material of *Rhopalione* cited by Ng & Ahyong (2022) comprises the type series as designated herein. The holotype female left approximately four puncture holes from the mouthparts in ventral pleomeres 1 and 2 (toward midline) of the host; the paratype female left puncture holes in ventral pleomeres 1 and 2 (toward midline) of the host.

Rhopalione sp.

Rhopalione sp. – Ng & Ahyong 2022: 230, fig. 75E, F [ex *Magnotheres globosus* (Hombron & Jacquinot, 1846), Singapore]. — Williams *et al.* 2023: 533 [list].

Material examined. — **Singapore** • 1 ♀ *Magnotheres globosus* (Hombron & Jacquinot, 1846) (10.7 mm CL, 14.6 mm CW), ex *Pinna atropurpurea* G. B. Sowerby I, 1825 (Pinnidae); Changi East, east of Tanah Merah Ferry Terminal beach, near Changi Point, intertidal area; 14-16.XII.2016; S. K. Tan *et al.* leg.; ZRC 2017.1020.

Remarks

A female parasite was figured in color by Ng & Ahyong (2022) and appears to be a new species; unfortunately, the specimen could not be located in the ZRC during this study. There is evidence of parasitism on the host, as there are at least three small puncture marks on the left side of pleomeres 1 and 2, indicating feeding by the female bopyrid.

The host (ZRC 2017.1020) as seen in Ng & Ahyong (2022: fig. 75A) appears to have any asymmetrical carapace with the right side swollen, suggesting branchial parasitism by another species of bopyrid; however, we have seen the specimen and it is not parasitized branchially.

DISCUSSION

Based on current data, epicaridean infestation in pea crabs is not equally distributed across host taxa. Currently, 10% of the 206 species in Pinnotherinae are known to host epicarideans (18 bopyrids and two entoniscids) whereas only 3% of the 87 species in Pinnixinae do the same (one bopyrid and two entonicids); no species of the four in Pinnixulalinae or the two in the enigmatic *Alarconia* Glassell, 1938 have been reported with parasites (host numbers from DecaNet 2023). Additionally, records of epicarideans from any pea crabs are rather rare, with only *Heterocepon marginatum* and *Rhopalione sinensis* being reported more than twice based on new material in the literature prior to the present work (Table 1).

As would be predicted by the high levels of biodiversity for bopyrids in the Central Indo-Pacific and Temperate Northern Pacific (Williams & Boyko 2012), the bopyrids of pea crabs likewise show the highest diversity in these ecoregions (10 of the 15 described species; ecoregions as defined by Spalding *et al.* 2007) with the remainder scattered across the globe in Temperate Australasia (2), Western Indo-Pacific (2), and Temperate Northern Atlantic (1). A few species have been reported from more than one ecoregion but only one, *Hypocepon enoeensis*, has been recorded from two regions other than Central Indo-Pacific and Temperate Northern Pacific (see Table 1). Interestingly, the global diversity of entoniscids found in pinnotherids (Table 1) shows a much different pattern, with no species found outside of the Atlantic Ocean but this is almost certainly an artifact of sampling (entoniscids are commonly overlooked as endoparasites, vs ectoparasitic bopyrids that cause branchial swelling or are easily observed under the host pleon as in *Rhopalione*). Additional specimens and likely a greater diversity of many epicaridean species from pea crabs can be obtained from examination of bivalve hosts in markets, as demonstrated by some of the material reported on in the present study. Although "seafood market" is an undesirable type locality for any new species, the presence of parasites in market specimens is an indicator of where to look for the species in the wild by identifying which bivalves to look for and which pinnotherids are known to host the epicarideans.

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