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Branchial parasitic isopods (Crustacea: Isopoda: Bopyridae: Pseudioninae) of hermit crabs (Crustacea: Decapoda: Diogenidae) from the western Pacific, with descriptions of a new genus and three new species

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Abstract. Members of the bopyrid subfamily Pseudioninae are obligate parasites of crustaceans, with the majority of species infesting the branchial chambers of their hosts. These parasites infest a broad range of decapod crustaceans, including members of the Anomura (hermit crabs and their relatives). The purpose of the current research was to expand knowledge of these parasites from the Indo-West Pacific and especially from the Philippines, a region that is an epicenter of marine biodiversity. In total, 2,175 hermit crabs from the Philippines were examined; 112 (5.1%) were infested with pseudionines belonging to four genera, including three species that are new to science. In addition, three species are reported from the Philippines for the first time and include new host records. *Asymmetrione* Codreanu, Codreanu & Pike, 1965, is represented by two species: *A. asymmetrica* (Shiino, 1933), found infesting the hermit crabs *Calcinus gaimardii*, *C. minutus*, and *Dardanus lagopodes*, and *A. harmoniae*, new species found infesting the hermit crab *D. lagopodes* from the Philippines and Indonesia. We redescribe *Bopyrissa magellanica* Nierstrasz & Brender à Brandis, 1931, the type species of *Bopyrissa* Nierstrasz & Brender à Brandis, 1931, and designate a lectotype. *Bopyrissa xiphidiostega*, new species was found infesting *C. gaimardii*, *C. minutus*, and *D. lagopodes*; females possess a unique lateral extension of the first oostegite that overlaps the basis of pereopod 1. *Bopyrissa marami*, new species is described based on specimens infesting *C. gaimardii*, *C. latens* and *C. minutus* whereas *Pseudione novaeguineensis* Danforth, 1971, and *P. kensleyi* Williams & Schuerlein, 2005, are both transferred to *Bopyrissa*, with *B. kensleyi* recorded for the second time from Singapore. We erect *Eremitione*, new genus to accommodate nine species previously placed in *Pseudione* Kossmann, 1881, that infest hosts in Lithodidae and Paguroidea. *Eremitione clibanaricola* (Shiino, 1933), new combination was found infesting *C. gaimardii* and *C. minutus*. The holotype of *Pseudione calcinii* Shiino, 1933 (now *Eremitione calcinii* (Shiino, 1933), new combination) was examined and illustrated. Finally, *Pagurion tuberculata* Shiino, 1933, was found infesting *D. lagopodes* in the Philippines and Indonesia; study of these specimens supports the synonymy of *Pagurion arrosor* An, Li & Markham, 2013 with *P. tuberculata*. These findings show that the diversity of bopyrid fauna in the Indo-West Pacific has been underestimated. A key to all genera of pseudionines that infest hermit crabs is provided, as well as keys to all species of *Asymmetrione*, *Bopyrissa*, and *Eremitione*, new genus.

Key words. Epicaridea, host-parasite relationships, Indo-West Pacific, parasite, Philippines

INTRODUCTION

Members of the isopod family Bopyridae (currently composed of nine subfamilies containing approximately 605 species) are obligate parasites of crustaceans and this taxon contains over 75% of the described species of epicaridean isopods (Williams & Boyko, 2012). Among bopyrids, the largest subfamily is Pseudioninae (~38%; >235 species) whose species are mostly branchial parasites of a wide range of hosts (Anomura, Astacidea, Axiidea, Brachyura, Caridea, and Gebiidea) but this subfamily may not be monophyletic and requires revision (Williams & Boyko, 2012; Boyko et al., 2013; An et al., 2015; Boyko et al., 2017). The majority of branchial bopyrids occur in either the left or right gill chamber of the host at about equal frequency; however, certain species occur predominantly or exclusively on only one side (Markham, 1986). It is possible, but relatively rare, for double infestation of a single host by two different species of bopyrids to occur (e.g., Shiino, 1933; An et al., 2007).

Hermit crabs are common hosts for a wide range of symbionts (Williams & McDermott, 2004), including strict parasites, of which bopyrid isopods make up a substantial proportion (Markham, 2003; McDermott et al., 2010). As predicted by Markham (1989), the biodiversity of the bopyrid fauna in the Philippines is underestimated and our investigations in this region have led to the discovery of new species parasitising

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other anomurans, including porcelain and hermit crabs (Williams & Madad, 2010; Williams & Boyko, 2016). The present study reports on species belonging to four genera of pseudionine isopods (*Asymmetrione* Codreanu, Codreanu & Pike, 1965, *Bopyrissa* Nierstrasz & Brender à Brandis, 1931, *Eremitione*, new genus and *Pagurion* Shiino, 1933) found on hermit crab hosts from the Philippines, Indonesia, and Singapore, including the description of three new species.

MATERIAL AND METHODS

Hermit crabs were collected by hand (J. D. Williams, collector; abbreviated in Material examined sections herein as JDW) from intertidal and shallow subtidal areas of the Oriental Mindoro province of the Philippines between July 1997 and July 2000 [see Williams (2001) for map of the region and collecting sites; see Table 1 in Williams & Boyko (2016) for longitude/latitude data on the collecting sites indicated in the Material examined section below]. Specimens were either fixed directly in 70% ethyl alcohol or in 4% seawater/formalin. After identification of associated gastropod species and measurement of aperture length with calipers, shells containing hermit crabs were cracked and the hermit crabs were removed. In addition to the collections indicated above, a small number of parasitised hermit crabs from the Philippines collected by Paul Cassidy were sent to the first author and additional parasitised hermit crabs from Indonesia were obtained from the Zoological Reference Collection of the Lee Kong Chian Natural History Museum (formerly the Raffles Museum of Biodiversity Research) (ZRC); these records were not included in the calculations of prevalence.

In total, 2,175 hermit crabs from the Philippines were examined under a dissecting microscope for parasites after lifting of the carapace to expose the interior of the branchial chambers; if present, bopyrid specimens were extracted and isolated for subsequent analysis via light or scanning electron microscopy (SEM). Host size is given as shield length (SL) for hermit crabs. Isopod size is given as maximal length of females (from anterior border or head or arched pereomeres to terminus of uropods) and males; all measurements (of hosts and parasites) were made with a micro-scale tool (Electron Microscopy Sciences) or ocular micrometer. Parasite prevalence was calculated based on collections that had the presence of parasites; collections without any parasites were excluded from calculations of prevalence. All means (lengths, prevalence) are reported with standard deviation.

For SEM preparation, specimens were dehydrated in an ascending ethanol (EtOH) series, starting with 70% EtOH and ending with 100% EtOH (10 min per dilution through 95% and 15 min × 3 for 100% EtOH). Drying was accomplished with a Samdri 795 Critical Point Dryer. Once dried, the individual specimens were mounted on aluminum stubs, coated with gold using an EMS-550 sputter coater, and viewed with a Hitachi S-2460N or FEI Quanta 250 SEM. Figures were produced using Adobe Photoshop and measurements of structures were made using ImageJ software. Adobe Illustrator was utilised to develop final images based on drawing tube sketches of specimens.

Museum specimens of *Asymmetrione asymmetrica* (Shiino, 1933) (National Science Museum, Tokyo, NSMT-Cr 14402), *Propseudione rhombicosoma* Shiino, 1933 (Seto Marine Biological Laboratory, Kyoto University, SMBL Type No.50), *Pseudione calcinii* Shiino, 1958 (National Science Museum, Tokyo, NSMT-Cr 14473), *Pseudione clibanaricola* Shiino, 1933 (Seto Marine Biological Laboratory, Kyoto University, SMBL Type No.42), *Pseudione novaeguineensis* Danforth, 1971 (Natural History Museum of Los Angeles County, LACM CR 1969–122.2, LACM CR 1969–122.3, LACM CR 1969–122.4), and *Bopyrissa magellanica* Nierstrasz & Brender à Brandis, 1931 (Natural History Museum of Denmark, NHMD 85028, NHMD 300413) were borrowed in order to confirm species diagnoses of Philippine material and for comparative analysis. Type and voucher specimens from the present study are deposited in the National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (USNM) and the ZRC; some samples were retained by the first author (see Material examined section for each species for details).

This paper is based in large part on the master's thesis work of Madad (2008) with modifications to conform to current taxonomy. Additional material, such as the redescription of *Bopyrissa magellanica* Nierstrasz & Brender à Brandis, 1931 and erection of *Eremitione*, new genus, are solely the work of the first two authors and the authorship of *Eremitione*, new genus should be credited to Williams & Boyko *in* Williams, Boyko & Madad (ICZN, 1999: Recommendation 50A; see also Ng, 1994). References are provided for authors and dates of all parasitic taxa but not for those of hosts.

RESULTS

In total, 2,175 Philippine hermit crabs were examined, of which 112 (5.1%) were parasitised by bopyrids. Eleven species of hermit crabs were identified among the Philippine samples (see Table 1) as well as one species identified only to genus. Four species of hermit crabs (*Calcinus gaimardii*, *C. latens*, *C. minutus*, and *Dardanus lagopodes*) made up 84% of the collections and were the most commonly parasitised (Table 1). In addition to those hosts listed in Table 1, *Calcinus pulcher* Forest, 1958, *C. laevimanus* (Randall, 1840), *Ciliopagurus strigatus* (Herbst, 1804), *Dardanus pedunculatus* (Herbst, 1804), *Diogenes* sp. and *Paguristes runyanae* Haig & Ball, 1988, were collected in small quantities (<75 specimens) but no specimens were parasitised by branchial bopyrids. Three specimens of *Clibanarius* cf. *virescens* (Krauss, 1843) were parasitised by *Asymmetrione asymmetrica* but prevalence data was not recorded for this host.

Six species of parasitic isopods were found: *Asymmetrione asymmetrica* (4 host individuals parasitised), *Asymmetrione harmoniae*, new species (3 host individuals parasitised),

Table 1. List of hermit crab host species parasitised and their branchial parasitic isopods based on collections in the Philippines from 1996–2000. Number of hosts examined, total number of hosts parasitised and number of individual parasite species found on the hosts. See Williams & Boyko (2016) for additional data on these hosts and parasitism by abdominal parasites.

Host species	Number of hosts examined	Total Parasitised (%)	Parasite species - number (%)
Calcinus gaimardii (H. Milne Edwards, 1848)*	992	86 (8.7)	*Bopyrissa marami* new species – 72 (7.3) *Bopyrissa xiphidiostega* new species – 8 (0.8) *Eremitione clibanaricola* new combination – 5 (0.5) Unidentified branchial bopyrid – 1 (0.1)
Calcinus latens (Randall, 1840)	505	1 (0.2)	*Bopyrissa marami* new species – 1 (0.2)
Calcinus minutus Buitendijk, 1937	208	10 (4.8)	*Asymmetrione asymmetrica* – 1 (0.5) *Bopyrissa marami* new species – 5 (2.5) *Bopyrissa xiphidiostega* new species – 3 (1.4) *Eremitione clibanaricola* new combination – 1 (0.5)
Dardanus lagopodes (Forskål, 1775)	123	11 (8.9)	*Asymmetrione asymmetrica* – 1 (0.8) *Asymmetrione harmoniae* new species – 2 (1.6) *Bopyrissa xiphidiostega* new species – 7 (5.7) *Pagurion tuberculata* – 1 (0.8)

**C. gaimardii* is very similar to *C. morgani* Rahayu & Forest, 1999 (see Malay et al., 2018) and the species are sympatric. Our specimens appear to most closely match *C. gaimardii* based on morphology and color pattern.

Bopyrissa marami, new species (78 host individuals parasitised), *Bopyrissa xiphidiostega*, new species (18 host individuals parasitised), *Eremitione clibanaricola* (Shiino, 1933), new combination (6 host individuals parasitised), *Pagurion tuberculata* (2 host individuals parasitised), and one unidentified pseudionine (specimen lost). Similar to the results of a previous study on athelgine bopyrids (Williams & Boyko, 2016), none of the 128 hermit crabs from the province of Palawan in the Philippines were parasitised by pseudionines in their branchial chambers. Among the parasitised hosts, three hermits were simultaneously infested with two bopyrids each (2.7%, 3 of 112 parasitised hermit crabs): one *D. lagopodes* with *A. harmoniae*, new species and *B. xiphidiostega*, new species, one *C. minutus* with *B. xiphidiostega*, new species and *Parathelges aniculi* (Whitelegge, 1897) (see p. 57 in Williams & Boyko, 2016), and one *C. gaimardii* with *E. clibanaricola* (Shiino, 1933), new combination and *B. marami*, new species. Three hermit crabs were also simultaneously infested with bopyrids and rhizocephalan barnacles (2.7%, 3 of parasitised 112 hermit crabs; a conservative estimate of prevalence because hosts were only examined for the externae of the rhizocephalans): one *C. minutus* with *A. asymmetrica* and *Dipterosaccus* sp., and two *C. gaimardii* with *B. marami*, new species and unidentified rhizocephalans. Two hermits (one *C. gaimardii* and *C. minutus*) were doubly infested with *B. marami*, new species and an unidentified entoniscid isopod (prevalence not calculated because hosts were not systematically dissected to detect entoniscids). Finally, 2.6% (2 of 78) of *B. marami*, new species were hyperparasitised by cabiropid parasitic isopods (Cryptoniscoidea: Cabiropidae).

Key to genera of Pseudioninae Codreanu, 1967, with species infesting hermit crabs

1. Females with rudimentary oostegites on pereomeres VI and VII.....*Pagurocryptella* Boyko & Williams, 2010
– Females lacking rudimentary oostegites on pereomeres VI and VII.....2
2. Females usually greatly distorted, typically 90° or more (if not distorted then with propodal sockets on pereopods).....3
– Females less distorted (generally <70°) or nearly symmetrical, lacking propodal sockets on pereopods.....5
3. Females with some biramous pleopods.....4
– Females with no biramous pleopods ....*Bopyrophryxus* Codreanu, 1965
4. Females with propodal sockets on pereopods, first two pereopods much larger than the others ....*Asymmetrione* Codreanu, Codreanu & Pike, 1965
– Females without propodal sockets on pereopods, pereopods subequal in size ....*Parasymmetrione* An, Markham & Yu, 2010
5. Females with biramous uropods.....6
– Females with uniramous uropods or lacking uropods 7
6. Females with 6 pairs of pleonal lateral plates..... .....*Pagurion* Shiino, 1933
– Females with 5 pairs of pleonal lateral plates..... .....*Parapagurion* Shiino, 1933
7. Females with pleomere 6 ventrally displaced, not visible in dorsal view 8
– Females with pleomere 6 not ventrally displaced, visible in dorsal view 9
8. Males with uniramous pleopods ....*Bopyrissa* Nierstrasz & Brender à Brandis, 1931
– Males with biramous pleopods.....*Propseudione* Shiino, 1933
9. Females with pleopod 5 uniramous.....10
– Females with pleopod 5 biramous..... *Eremitione*, new genus
10. Females with pleopods 1 and 2 biramous, 3 and 4 uniramous .....*Pseudionella* Shiino, 1949
– Females with pleopods 1–4 biramous .... *Parapseudione* Nierstrasz & Brender à Brandis, 1931

TAXONOMY

Bopyridae Rafinesque, 1815

Pseudioninae Codreanu, 1967

Asymmetrione Codreanu, Codreanu & Pike, 1965

Key to species of *Asymmetrione* based on females [*A. imarani* Kazmi & Khatoon, 2016, not included in the key]

1. Greater than 50° body asymmetry 2
– Less than 50° body asymmetry 9
2. Pleomere 5 with ovate and dorsally displaced lateral plates as well as pair of swellings on dorsal surface of pleotelson 3
– Pleomere 5 without ovate and dorsally displaced lateral plates or pair of swellings on dorsal surface of pleotelson 5
3. Lateral plates of fifth pleomere ovate 4
– Lateral plates of fifth pleomere spherical ..... *A. dardani* Bourdon, 1968
4. Body asymmetry 65–70°; barbula central region with numerous digitations laterally ..... *A. harmoniae* new species
– Body asymmetry ca. 100°; barbula central region with three digitations laterally ... *A. globifera* An, Markham & Yu, 2010
5. Outer lobes of barbula digitate on margins 8
– Outer lobes of barbula smooth on margins 6
6. Pleopods tuberculate ..... *A. nossibensis* Bourdon, 1976
– Pleopods smooth 7
7. Lateral plates on pleomeres 1–3 ..... *A. clibanarii* Markham, 1975
– Lateral plates on pleomeres 1–5 ..... *A. sallyae* Williams & Schuerlein, 2005
8. Second oostegites dissimilar ... *A. asymmetrica* (Shiino, 1933)
– Second oostegites similar ..... *A. shiinoi* Codreanu, Codreanu & Pike, 1965
9. Uropods uniramous 10
– Uropods biramous 11
10. Lateral plates lacking on pleomeres 1–5 ..... *A. aequalis* Pardo, Boyko & Mantelatto, 2009
– Lateral plates present on pleomeres 1–5 ..... *A. foresti* (Bourdon, 1968)
11. Oostegite 1 posterior lobe larger than anterior ..... *A. ambodistorta* Markham, 1985a
– Oostegite 1 lobes subequal in size ..... *A. desultor* Markham, 1975

Key to species of *Asymmetrione* based on males [*A. imarani* Kazmi & Khatoon, 2016, not included in the key]

1. Antennae of seven articles each 2
– Antennae of five or six articles each 4
2. Posterolateral lobes of pleotelson short, not extending beyond anal cone ..... *A. foresti* (Bourdon, 1968)
– Posterolateral lobes of pleotelson long, extending beyond anal cone 3
3. Body widest across pereomeres 3 and 4 ..... *A. aequalis* Pardo, Boyko & Mantelatto, 2009
– Body widest across pereomere 2 ..... *A. desultor* Markham, 1975
4. Antennae of five articles each; maxilliped apparently absent* 5
– Antennae of six articles each; maxilliped present 8
5. All pereomeres subequal in width ..... *A. clibanarii* Markham, 1975
– Pereomeres three and four wider than others 6
6. Head separated from pereomere 1; pleotelson with elongate and tapered posterolateral lobes ..... *A. globifera* An, Markham & Yu, 2010
– Head fused with pereomere 1; pleotelson with short to moderate and rounded posterolateral lobes 7
7. Antennae extending well beyond margin of head; extensive pigmentation on pereon and pleon ..... *A. sallyae* Williams & Schuerlein, 2005
– Antennae extending short distance beyond margin of head; small pigmentation spots on pereon and pleon ..... *A. ambodistorta* Markham, 1985a
8. Posterolateral lobes of pleotelson short; eyes absent ..... *A. dardani* Bourdon, 1968
– Posterolateral lobes of pleotelson long; eyes present 9
9. Posterolateral lobes of pleotelson with inner margins contiguous ..... *A. shiinoi* Codreanu, Codreanu & Pike, 1965
– Posterolateral lobes of pleotelson broadly separated 10
10. Head trapezoidal, indistinctly separated from pereomere 1 .... *A. harmoniae* new species
– Head ovate, distinctly separated from pereomere 1 11
11. Antennae extending beyond lateral margins of all pereomeres ..... *A. asymmetrica* (Shiino, 1933)
– Antennae not extending beyond lateral margins of any pereomeres ..... *A. nossibensis* Bourdon, 1976

*Maxillipeds have only been described for males of five species of *Asymmetrione* (*A. asymmetrica*, *A. dardani*, *A. harmoniae* new species, *A. nossibensis*, and *A. shiinoi*); it is unknown if other species exhibit this feature and it can easily be overlooked.

Asymmetrione asymmetrica (Shiino, 1933)
(Fig. 1A, B, E)

Pseudione asymmetrica Shiino, 1933: 249, 273–277, figs. 9, 10 [Tanabe Bay, Japan; infesting *Clibanarius bimaculatus* (De Haan, 1849) Shiino, 1952: 38, 41 [mention]; Shiino, 1958: 30 [Shirahama, Japan; infesting *C. bimaculatus*]; Danforth, 1963: 11 [list]; Codreanu et al., 1965: 225, 227, 234, 242, 243 [designated as type of *Asymmetrione*; implied as nominotypical subspecies]; Shiino, 1972: 7 [list]; Markham, 1978: 103 [mention]; Markham, 1985a: 107 [mention]; Harada, 1991: 201 [type specimen data]; An et al., 2010: 2068 [mention].

Asymmetrione asymmetrica — Codreanu, 1967: 209 [mention]; Markham, 1975: 264, 265 [list]; Bourdon, 1976: 366 [mention]; Markham, 1985b: 3–5, fig. 1 [Thailand, infesting *Clibanarius merguiensis* de Man, 1888]; Haig & Ball, 1988: 163 [Indonesia; infesting *Clibanarius englaucus* Ball & Haig, 1972]; Trilles & Hipeau-Jacquotte, 1996: 119 [mention]; Kazmi & Markham, 1999: 879 [mention]; Trilles, 1999: 326 [mention]; Saito et al., 2000: 36 [list]; Kensley, 2001: 222 [list]; Markham, 2003: 72 [list]; Saito & Kinoshita, 2004: 4, 6 [list]; Williams & Schuerlein, 2005: 101 [mention]; Madad, 2008: 2, 6, 15, 16, 19, 25, 26, 46, 47, 49, 51 [Philippines, infesting "*Calcinus gaimardii* (H. Milne Edwards, 1848)" (misidentification of *Clibanarius* cf. *virescens* [Krauss, 1843], see below), *Calcinus minutus* Buitendijk, 1937; Japan, infesting *C. bimaculatus*]; An et al., 2010: 2069 [list]; McDermott et al., 2010: 8 [list]; Trilles & Hipeau-Jacquotte, 2012: 258, 301 [mention, list]; Tudge et al., 2012: 289, fig. 70.31 [Japan; infesting *C. virescens*].

Asymmetrione asymmetrica asymmetrica — Bourdon, 1968: 313 [table of characters], 314.

Material examined. Japan: 1 dextral ovigerous ♀ (3.2 mm), 1 mature ♂ (1.2 mm) (NSMT-Cr 14402) from right

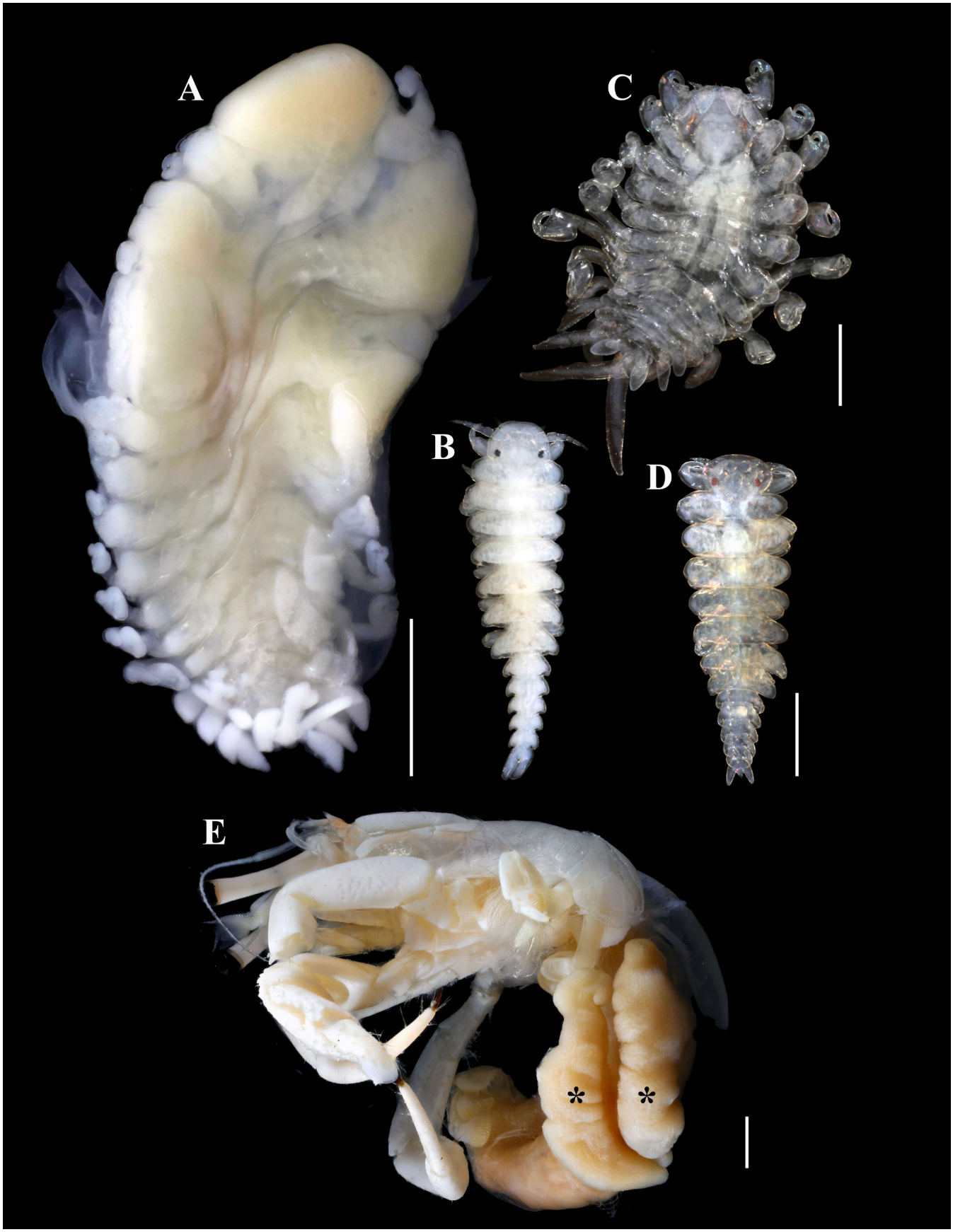

Fig. 1. *Asymmetrione asymmetrica* (Shiino, 1933), USNM 1493912 (A, B), JDW pers. coll. (E), and *Asymmetrione harmoniae* new species, USNM 1493917 (C, D). A, mature female, dorsal view; B, male paired with female shown in A, dorsal view; C, immature female, dorsal view; D, male paired with female shown in C, dorsal view; E, lateral view of *Calcinus minutus* doubly infested with *Asymmetrione asymmetrica* and *Dipterosaccus* sp. (two externae indicated by *). Scale bars = 1 mm (A, B, E); 500 µm (C, D).

branchial chamber of *Clibanarius bimaculatus* (De Haan, 1849) (host not in jar), Seto, Shirihama, Japan; Philippines: 1 dextral ovigerous ♀ (4.6 mm), 1 ♂ (2.2 mm) (USNM 1493912) from right branchial chamber of ♀ *Clibanarius* cf. *virescens* (2.7 mm SL), Batangas, Sombrero Island, coll. JDW, 30 January 1999; 1 dextral ovigerous ♀ (4.5 mm), 1 ♂ (1.8 mm) (pers. coll.) from right branchial chamber of ♂ *Calcinus minutus* (3.4 mm SL), also with two externae of *Dipterosaccus* sp. (Rhizocephala), Batangas, Anilao, coll. JDW, 13 February 1999; 1 dextral ovigerous ♀ (5.2 mm), 1 ♂ (3.4 mm) (USNM 1493913) from right branchial chamber of ♀ *C*. cf. *virescens* (2.8 mm SL), Puerto Galera, Small Lalaguna Beach, coll. JDW, 17 June 2000; 1 dextral ♀ (5.5 mm), 1 ♂ (2.2 mm) (USNM 1493914) from right branchial chamber of ♀ *C*. cf. *virescens* (3.2 mm SL), Puerto Galera, Small Lalaguna Beach, coll. JDW, 17 June 2000.

Type locality. Tanabe Bay, Seto, Japan (Shiino, 1933).

Distribution. Tanabe Bay, Seto, Shirihama, Japan (Shiino, 1933); Thailand (Markham, 1985b); Irian Jaya, Indonesia (Haig & Ball, 1988); Batangas, Puerto Galera, Philippines (Madad, 2008, herein).

Hosts. Diogenidae: *Calcinus minutus* Buitendijk, 1937, *Clibanarius bimaculatus* (De Haan, 1849), *C. englaucus* Ball & Haig, 1972, *C. merguiensis* de Man, 1888, *C. virescens* (Krauss, 1843), *C*. cf. *virescens* and *Dardanus lagopodes* (Forskål, 1775).

Size range (length). Females to 5.5 mm, males to 3.4 mm. Mean length of adult female specimens was 4.6 ± 0.9 mm (n=5) and mean length of male specimens was 2.2 ± 0.8 (n=5).

Remarks. The Japanese specimens examined here are the ones reported by Shiino (1958).

The Philippine females (e.g., Fig. 1A) most closely match Markham's (1985b) specimens of *A. asymmetrica* from Thailand. One specimen (USNM 1493914) exhibited more pronounced tergal projections than others, but is generally consistent with Shiino's (1933) description of *A. asymmetrica* as well. The males (e.g., Fig. 1B) are as described and illustrated by Shiino (1933); however, their pleons are more elongate than that of the one illustrated by Markham (1985b).

Prior to the present study, there were 11 well-described recognised species of *Asymmetrione*, five of which are found within in the Indo-West Pacific: *A. asymmetrica*, *A. foresti* (Bourdon, 1968), *A. globifera* An, Markham & Yu, 2010, *A. nossibensis* Bourdon, 1976, and *A. sallyae* Williams & Schuerlein, 2005. A sixth species of Indo-West Pacific *Asymmetrione* is described below. Kazmi & Khatoon (2016) described an additional species, *Asymmetrione imarani* Kazmi & Khatoon, 2016 infesting *Diogenes violaceus* Henderson, 1893 collected from an unspecified locality in Pakistan. Although identifiable as a member of *Asymmetrione*, the description is incomplete and lacking in male and female diagnostic characters to distinguish it from other species in the genus; thus, we consider this taxon a *species inquirenda*. A second species mentioned in their text (*Asymmetrione* sp. 1) remains to be described.

Clibanarius virescens was not previously known as a host of *A. asymmetrica* prior to the record of Tudge et al. (2012). Some of the specimens examined by Madad (2008) were originally identified as *Calcinus gaimardii* but have been reidentified herein as *C*. cf. *virescens*. *Dardanus lagopodes* (Forskål, 1775) was not previously reported as a host of *A. asymmetrica*.

Ecology. Mean prevalence of *A. asymmetrica* was 0.72 ± 0.32% over the two collections in which the parasite was found (n=309 total hermits examined). A total of four female and male pairs of *A. asymmetrica* was extracted from *C. minutus* and *C*. cf. *virescens* in the Philippines. One of the *C. minutus* hosts was also parasitised by a rhizocephalan, identified as *Dipterosaccus* sp. (*fide* R. Yoshida, pers. commun) (Fig. 1E). *Calcinus minutus* Buitendijk, 1937, is also known to be parasitised by *Peltogaster latus* Van Baal, 1937, in Indonesia (Van Baal, 1937; Fransen et al., 1997), although the host was identified in Van Baal (1937) only as "*Calcinus* spec" (repeated as "*Calcinus* sp." in McDermott et al., 2010). *Peltogaster latus* occurs on its hosts as a single externa, while species of *Dipterosaccus*, while sometimes occurring singly may also occur with two or three externae per host (Van Baal, 1937; Yoshida et al., 2013).

Asymmetrione harmoniae, new species
(Figs. 1C, D, 2, 3)

Asymmetrione nossibensis — Madad, 2008: 2, 5, 6, 16, 27, 28, 46, 47, 49, 51, 82, fig. 7F [Philippines, infesting *Dardanus lagopodes* (Forskål, 1775)] (not *A. nossibensis* Bourdon, 1976).

Material examined. Philippines: 1 dextral mature ♀ holotype (14.8 mm), 1 mature ♂ allotype (4.6 mm) (ZRC 2018.0827), from right branchial chamber of ♂ *Dardanus megistos* (Herbst, 1804) (12.4 mm SL), Panglao, Momo Beach, Sta. M7, reef platform with seagrass, 9°36.1′N, 123°45.2′E, 0–3 m, coll. Panglao Expedition 2004, 1 June 2004; 1 dextral ovigerous ♀ paratype (5.2 mm), 1 ♂ paratype (2.3 mm) (USNM 1493915) from right branchial chamber of ♂ *Dardanus lagopodes* (Forskål, 1775) (3.8 mm SL), host also infested with *Bopyrissa xiphidiostega*, new species (USNM 1493992), Mactan Island, Cebu, coll. P. Cassidy, 6 December 1996; 1 dextral ovigerous ♀ paratype (9.6 mm), 1 ♂ paratype (2.9 mm) (USNM 1493916) from right branchial chamber of ♂ *D. lagopodes* (6.4 mm SL), Batangas, Sombrero Island, coll. JDW, 30 January 1999; 1 early juvenile non-type ♀ (2.3 mm), 1 non-type mature ♂ (2.0 mm) (USNM 1493917) from right branchial chamber of ♀ *D. lagopodes* (2.3 mm SL), Batangas, Sombrero Island, coll. JDW, 30 January 1999; Indonesia: 1 dextral mature ♀ paratype (11.2 mm) (ZRC 2018.0828), 1 mature ♂ paratype (3.0 mm), from right branchial chamber of ♂ *D. lagopodes* (6.9 mm SL), North Sulawesi, Tanjung Merah, coll. 31 March 2003.

Description. Holotype female outline ovoid, body margins slightly distorted dextrally (~65°; paratypes up to 70°) (Fig.

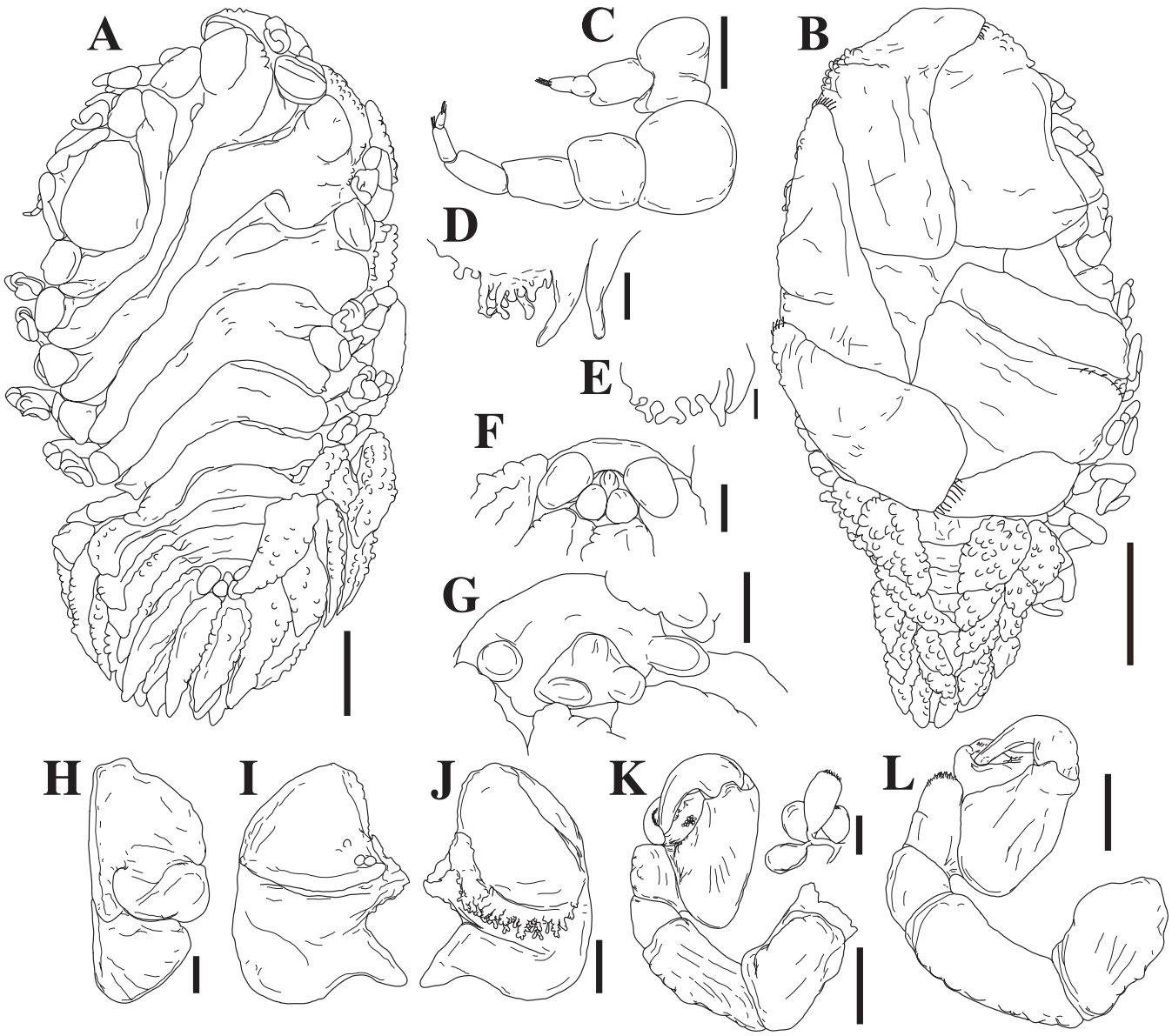

Fig. 2. *Asymmetrione harmoniae* new species, female holotype, ZRC 2018.0827 (A, C, D, G–L) and paratypes ZRC 2018.0828 (B, F), USNM 1493916 (E). A, dorsal view; B, ventral view; C, right antennule (top) and antenna (bottom); D, left barbula; E, left barbula; F, pleon, dorsal view; G, pleon, dorsal view; H, left maxilliped, outer view; I, left oostegite, outer view; J, left oostegite 1, inner view; K, left pereopod 1, inset shows ciliates attached to propodus; L, left pereopod 6. Scale bars = 2 mm (A, B); 250 μm (C, G); 1 mm (D, I, J); 250 μm (E); 500 μm (H, K, L); 25 μm (K inset).

2A); total length 14.8 mm, maximal width at third pereomere. Antennae and pereopods visible in dorsal view; head distinct from first pereomere, broader than long, surface smooth, front with broad recurved, medially notched lamina; anterolateral corners of head rounded; eyes and pigmentation absent. Maxilliped distally tapering, palp lacking, spur short and thin (Fig. 2H). Antennules of three articles each (Fig. 2C); basal article subquadrate with rounded lateral projection, lacking setae; second article subcylindrical, lacking setae; third article elongate with lateral indentations possibly indicating fusion of articles, tuft of apical setae. Antennae of six articles each (Fig. 2C); basal article ovate, lacking setae; article 2 ovate, lacking setae; articles 3–5 subcylindrical, distal articles progressively narrower, distalmost with ring of distal setae, terminal article minute, tuft of small setae at tip. Barbula with two pairs of acute, distally recurved, tapered, laterally smooth lobes, subequal in length; central region with narrow lateral area of irregular digitate projections (Fig. 2D, E). Pereomeres dorsally, ventrally and laterally distinct; narrow coxal plates on pereomeres 1–5 with large dorsolateral bosses; coxal plates and bosses absent on pereomeres 5–7 (Fig. 2A). Oostegites fully enclosing brood pouch (Fig. 2B); first oostegite (Fig. 2I, J) external surface smooth; anterior segment subtriangular, internal surface with posterior ridge entirely lined with numerous large digitate projections; posterior segment inner margin rounded, outer margin with posterolateral tapered projection; oostegites 2–5 large and ovate, increasing in size posteriorly, all with area of setae on anterior margins; fifth oostegite with posterior marginal fringe of setae (Fig. 2B). Pereopods subequal in shape but with proportionally longer ischia posteriorly (Fig. 2K, L), basis wide and subqudrate, ischium cylindrical with ventral edge bearing area of low tubercles, meri subquadrate, carpi conical, larger posteriorly, propodi swollen distoventrally

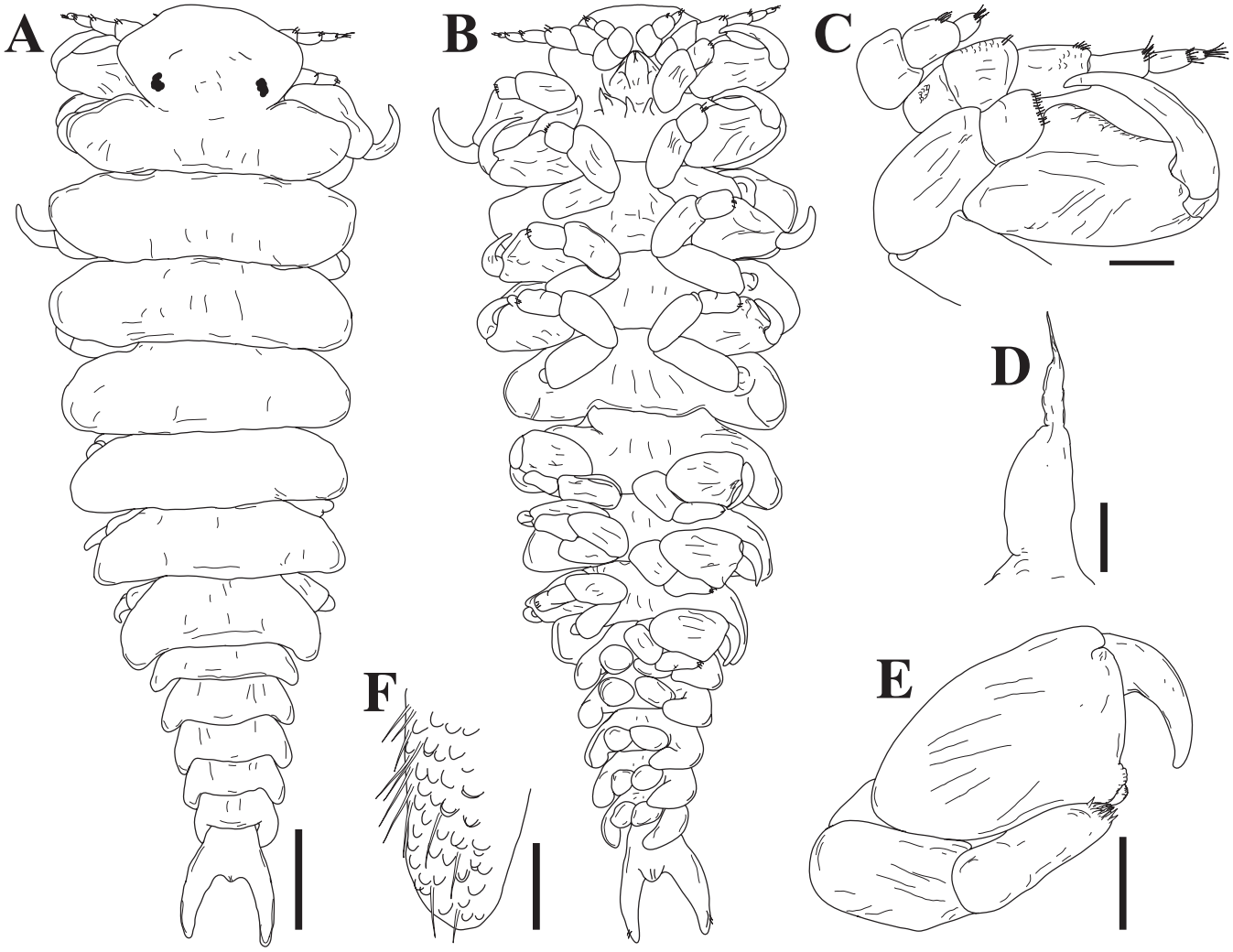

Fig. 3. *Asymmetrione harmoniae*, new species, male allotype, ZRC 2018.0827 (A–F). A, dorsal view; B, ventral view; C, left antennule, antenna and pereopod 1; D, left maxilliped; E, left pereopod 7; F, distal end of left lateral lobe on terminal pleomere, dorsal view. Scale bars = 500 μm (A, B); 250 μm (C, D, F); 1.0 mm (E).

with deep socket for insertion of dactyli; dactyli strongly recurved. Pleon approximately 35% as long as head plus pereon (Fig. 2A); five pleomeres plus pleotelson, all dorsally and laterally separated; pleomeres laterally rounded, 1–4 with large foliose lateral plates bearing tubercles on surfaces, pleomere 5 with pair of ovate, dorsally displaced lateral plates (Fig. 2F, G), surfaces smooth; five pairs of well developed biramous foliose pleopods, endopod and exopod (Fig. 2B) margins and surfaces covered in tubercles (Fig. 2B); uropods biramous, similar to pleopods, with tubercles on surfaces (Fig. 2A); pleotelson with medially placed anal cone flanked by pair of rounded, dorsally projecting, structures similar to lateral plates of fifth pleomere but smaller and more rounded (Fig. 2F, G).

Male (Figs. 1D, 3) body unpigmented, elongated, all segments clearly separated dorsally, ventrally and laterally; head trapezoidal, indistinct from first pereomere, approximately 1.6 times as wide as long, anterolateral corners rounded and laterally produced; head approximately 85% as wide as first pereomere; eyes present posterolaterally; antennules of three articles each, antennae of six articles each, both distally setose (Fig. 3C). Maxilliped with elongate palp (Fig. 3D). Pereomeres not widely separated, maximal width at second and third pereomeres, gradually tapering anteriorly and posteriorly; midventral tubercles absent; generally isomorphic pereopods but with progressively smaller dactyli and propodi and larger ischia in posterior pairs (Fig. 3C, E). Pleon with five segments plus pleotelson. Pleomeres progressively narrower posteriorly, distinctly separated, posterolateral margins rounded and ventrally curved; globose uniramous medial pleopods on pleomeres 1–5 (Fig. 3B). Pleotelson with two elongate tapered posterolateral lobes (Fig. 3A, B); prominent medial anal cone present, small tuft of setae and region of scales on distolateral tips of projections (Fig. 3F); uropods absent.

Type locality. Panglao, Momo Beach, Sta. M7, reef platform with seagrass, 9°36.1′N, 123°45.2′E, 0–3 m, Philippines.

Etymology. In Greek mythology, Harmonia was the daughter of Zeus and Electra and sister to Dardanus. The specific name is given because *A. harmoniae*, new species appears to be the sister species to *A. dardani* Bourdon, 1968.

Distribution. Batangas, Cebu and Panglao, Philippines; Sulawesi, Indonesia.

Hosts. Diogenidae: *Dardanus lagopodes* (Forskål, 1775), *D. megistos* (Herbst, 1804).

Size range (length). Mean length of mature female specimens was 10.2 ± 4.0 mm (n=4). Mean length of male specimens was 3.2 ± 1.0 mm (n=4).

Remarks. *Asymmetrione harmoniae*, new species was originally identified as *A. nossibensis* by Madad (2008). However, *Asymmetrione harmoniae*, new species is distinct from all previously described species in the genus and most similar to *A. dardani* Bourdon, 1968 (see Figs. 180–182 in Bourdon, 1968) and *A. globifera* An, Markham & Yu, 2010 (see Fig. 1 in An et al., 2010). All three of these species have the fifth pleomere with ovate and dorsally displaced lateral plates as well as a pair of more spherical swellings on the dorsal surface of the pleotelson. The new species differs from both of those previously described in the following characters (those of *A. dardani* and *A. globifera* in parentheses): 1) female body right side second and third pereomere lateral margins moderately projected laterally (those of *A. dardani* and *A. globifera* much more strongly projected with *A. globifera* also having oostegites on those segments extending outward beyond the outline of the body); 2) barbula lateral projections smooth (also smooth in *A. globifera* but highly digitate in *A. dardani*); 3) barbula central region with small area of numerous digitate projections laterally but smooth medially (similar condition in *A. dardani* but *A. globifera* with only three discrete projections laterally); 4) inner ridge of first oostegite with fringe of digitate projections along entire length (similar condition in *A. dardani* but *A. globifera* with only four stout digitate projections medially; 5) tubercles on margins of pereopods weakly developed (strongly developed in *A. dardani*; not shown or described in *A. globifera* so unclear if they are lacking or merely overlooked); 6) dorsal lobes on pleotelson spherical in shape, lateral plates of fifth pleomere ovate (similar condition in *A. globifera* but both sets of structures in *A. dardani* are spherical); Male: 1) head trapezoidal (similar in *A. globifera* but ovate in *A. dardani*); 2) eyes present (also present in *A. globifera* but lacking in *A. dardani*); 3) antenna of six articles (also in *A. dardani* but with five articles in *A. globifera*; 4) maxilliped palp elongate and distally tapered (stout in *A. dardani*; condition unknown for *A. globifera*); 5) lateral margins of pleomeres strongly curved ventrally (similar condition in *A. globifera*; weakly directed ventrally in *A. dardani*); 6) pleotelson with elongate distolateral lobes (similar shape in *A. globifera*; short lobes in *A. dardani*).

The peculiar ovate to spherical fifth pleomere lateral plates found on *A. dardani*, *A. globifera* and *A. harmoniae*, new species, are very similar to those seen in species of *Pseudostegias* Shiino, 1933 (Bopyridae: Athelginae). However, although some species of *Pseudostegias* have dorsal structures on the pleotelson (see Williams & Boyko, 2016), none have paired spherical lobes similar to those found on these three species of *Asymmetrione*.

Yu & An (2008: 691) listed *Asymmetrione dardani* from the Chinese fauna but without mentioning the identity of the host; this record is questionable because *A. dardani* is otherwise known only from Morocco (Bourdon, 1968). Although not included in a synonymy list for *A. globifera* in An et al. (2010), the specimens from the Yu & An (2008) record are most likely conspecific with *A. globifera* based on their locality (the material may even be the same as that upon which *A. globifera* was described). An et al. (2010) compared *A. globifera* to *A. nossibensis* Bourdon, 1976 but, as noted above, *A. globifera* is much more similar to *A. dardani*. *Asymmetrione nossibensis* lacks the globose fifth pleomere lateral plates and dorsal spheres on the pleotelson. An et al. (2010) reported *A. globifera* from both *Dardanus hessii* (Miers, 1884) and a *Spiropagurus* sp. but did not describe or illustrate the sole female found on the latter host; that specimen should probably be reexamined as its host identity shows doubt about its conspecificity with those found on *D. hessii*.

A juvenile female (Fig. 1C) already shows the development of the lateral plates on the fifth pleomere but does not yet show the dorsal swellings on the pleotelson. This specimen also shows how the birfucated frontal lamina develops by a weak subdivision in the medial region that becomes progressively larger as the individual matures.

Ecology. Prevalence was 0.99% (2 of 203 hermit crabs examined) in the one collection for which host data was available. In total, three mature specimens and one immature specimen of *A. harmoniae*, new species were extracted from the hermit crabs *Dardanus lagopodes* and *D. megistos* in the Philippines. This is the first record of *Dardanus megistos* as a host for this species; the other Philippine material from *D. lagopodes* was previously cited by Madad (2008) but misidentified as *A. nossibensis*. In addition, *A. harmoniae*, new species was found in *D. lagopodes* collected in Indonesia. One of the Philippine *Dardanus lagopodes* was doubly infested with *A. harmoniae*, new species in the right brachial chamber and *Bopyrissa xiphidiostega*, new species in the left brachial chamber.

Bopyrissa Nierstrasz & Brender à Brandis, 1931

Bopyrissa Nierstrasz & Brender à Brandis, 1931: 176–177 [type species: *Bopyrissa magellanica* Nierstrasz & Brender à Brandis, 1931, by monotypy].

Urocryptella Codreanu & Codreanu, 1963: 284 [unavailable name; type species not designated in original publication as required by ICZN, 1999: Article 13.3].

Diagnosis. Female body elongate, curved dextrally or sinistrally into s-shape; all segments distinct. Frontal lamina weakly developed, smooth. Barbula with either two lateral projections (outer usually more than three times as long as inner) or single lateral projection; medial region smooth or with few low lobes. Maxilliped with or without palp. First oostegites with tapered to sharply recurved posterolateral point; internal ridge smooth or with few low projections. Coxal plates weakly developed on pereomeres 1–4 on at least one side; tergal projections not present; pereomeres 2

and 3 subequal in breadth, broader than four; lateral margins of pereomeres 1–6 subquadrate; transition in shape from pereomeres 1–6 gradual, 1–4 not abruptly different than 5–6. Pereopods with short carpi, scales on outer surface of meri, and dorsal surfaces of bases not expanded. Six pleomeres, first five dorsally visible and produced into weakly developed lateral plates, directed posterolaterally; sixth pleomere ventrally displaced, not visible in dorsal view; overall pleon much narrower than pereon but not markedly narrower than posterior pereomere; four or five pairs of biramous, lanceolate pleopods, edges and surfaces smooth or tuberculate; uropods present, lanceolate, uniramous, edges and surfaces smooth.

Male body gradually tapered anteriorly and posteriorly from widest pereomere; all body regions distinct. Anterior pereopods not markedly larger than others. Pleon of six distinct pleomeres; pleopods uniramous, tuberculiform; posterolateral margins of pleotelson slightly to strongly produced into posterolateral lobes; no uropods. Worldwide distribution in temperate and tropical waters, infesting hosts in Paguroidea.

Remarks. Prior to the present study, there were seven species included in *Bopyrissa* (Boyko et al., 2008 onwards). Herein, we describe two new species and transfer *Pseudione novaeguineensis* Danforth, 1971 and *P. kensleyi* Williams & Schuerlein, 2005, to *Bopyrissa*. Although *P. novaeguineensis* was incompletely described, Danforth (1971, p. 100) clearly stated that the sixth pleomere, which he called the telson, was "fused to the mid-ventral surface of pleomerere V" and examination of the female holotype confirms this. This character places the species in *Bopyrissa* rather than *Pseudione* Kossmann, 1881. Danforth's (1971) Figure 1F also shows a ventrally displaced sixth pleomere, therefore what appears to be the sixth pleomere in his Figure 1B (dorsal view) are actually the uropods but apparently incorrectly drawn without a medial division between them. *Bopyrissa kensleyi* was described from a female with an abnormally developed posterior pleon and examination of a female with normal development shows that the species properly belongs in *Bopyrissa*. *Bopyrissa dawydoffi* (Codreanu & Codreanu, 1963) was so incompletely described and lacking any illustrations that, while we follow Markham (1978) in placing it in *Bopyrissa*, the species may belong to another genus; topotypic material from Vietnam needs to be collected and studied.

Urocryptella was erected by Codreanu & Codreanu (1963) for three species: *Pseudione diogeni* Popov, 1929, *P. fraissei* Carayon, 1943 and *Urocryptella dawydoffi* Codreanu & Codreanu, 1963; however, no type species was indicated and the name is unavailable (as per ICZN, 1999: Article 13.3). Markham (1978) and Bourdon (1979) regarded *Urocryptella* as a synonym of *Bopyrissa*.

Of the 14 currently recognised species of *Bopyrissa*, including two species described herein, seven are found within the Indo-West Pacific region (Boyko et al., 2008 onwards): *B. dawydoffi* (Codreanu & Codreanu, 1963), *B. kensleyi* Williams & Schuerlein, 2005, *B. liberorum* Markham, 1985b, *B. marami*, new species, *B. novaeguineensis* (Danforth, 1971), new combination, *B. pyriforma* (Shiino, 1958), and *B. xiphidiostega*, new species. All *Bopyrissa* species have been reported from diogenid hermit crabs (Markham, 1985b; herein).

Key to species of *Bopyrissa* based on females

1. Lateral plates large, exceeding width of pleon ..... *B. dawydoffi* (Codreanu & Codreanu, 1963)
– Lateral plates not exceeding width of pleon 2
2. Oostegite 1 posterior lobe elongate, tapering, acute 3
– Oostegite 1 posterior lobe short, rounded 8
3. Single lateral, elongate, tapered lobe on barbula 4
– Small medial lobe present in addition to lateral lobe 6
4. Oostegite 1 inner ridge nearly smooth; maxilliped anterior anterior margin smooth ..... *B. diogeni* (Popov, 1929)
– Oostegite 1 inner ridge with several rounded lobes; maxilliped anterior margin with notch 5
5. Lateral margin of first pereomere projecting anteriorly beyond lateral margin of head ..... *B. distorta* An, Gong & Paulay, 2018
– Lateral margin of first pereomere not projecting anteriorly beyond lateral margin of head .... *B. pyriforma* (Shiino, 1958)
6. Maxilliped without palp ..... *B. xiphidiostega*, new species
– Maxilliped with non-articulating palp 7
7. Outer lobe of barbula nearly smooth ..... *B. magellanica* Nierstrasz & Brender à Brandis, 1931
– Outer lobe of barbula digitate ..... *B. guamensis* An, Gong & Paulay, 2018
8. Pleomere 5 with distinct medial separation between lobes ... 9
– Pleomere 5 without distinct medial separation between lobes 12
9. Head extending anteriorly well beyond pereomere 1 ..... *B. novaeguineensis* (Danforth, 1971), new combination
– Head almost entirely subsumed into pereomere 1 10
10. Barbula with single outer lobe, maxilliped with articulated palp ..... *B. liberorum* Markham, 1985b
– Barbula with small additional medial lobe, maxilliped without palp 11
11. Lateral lobe of barbula and medial region tuberculate ..... *B. fraissei* (Carayon, 1943)
– Lateral lobe of barbula and medial region smooth ..... *B. oceania* An, Gong & Paulay, 2018
12. Posterior lobe of oostegite 1 with recurved projection, barbula without small additional medial lobe ..... *B. wolffi* Markham, 1978
– Posterior lobe of oostegite 1 with triangular projection, barbula with small additional medial lobe 13
13. Maxilliped without palp, barbula outer lobe smooth, antenna with fusion of segments ..... *B. kensleyi* (Williams & Schuerlein, 2005), new combination
– Maxilliped with palp, barbula outer lobe digitate, antenna without fusion of segments ..... *B. marami*, new species

Key to species of *Bopyrissa* based on males [*B. dawydoffi* (Codreanu & Codreanu, 1963), not included in the key]

1. Pleotelson with greatly extended lateral lobes, longer than width of pleotelson 2
– Pleotelson with weakly projecting (or absent) lateral lobes, at most extending as far as width of pleotelson 3
2. Pleomere 5 lateral lobes extending over anterior half of pleotelson; body nearly elliptical in outline ..... *B. liberorum* Markham, 1985b

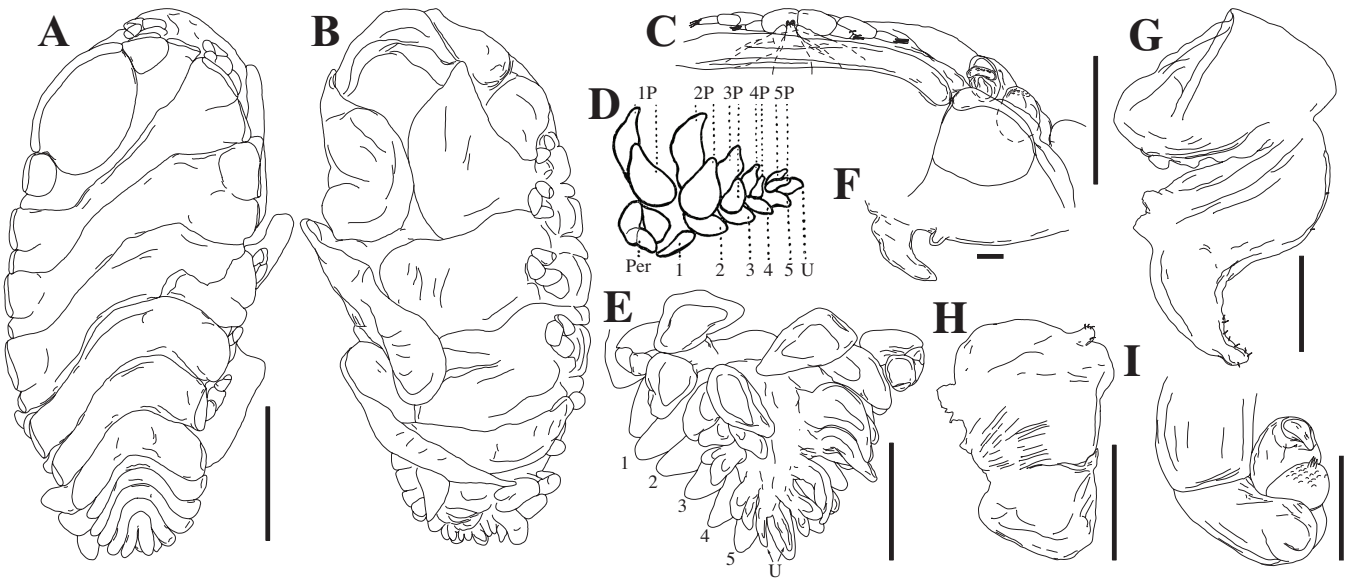

Fig. 4. *Bopyrissa magellanica* Nierstrasz & Brender à Brandis, 1931, female specimens, NHMD 85028 ("holotype?" = lectotype) (A, B), NHMD 300413, specimen #3 (C, F, G), NHMD 300413, specimen #5 (E), and NHMD 300413, specimen #4 (G, H). A, dorsal view. B, ventral view. C, antennules, antennae, mouthparts and right side of pereomere with pereopod 1. D, pleon, lateral view (numbers at top indicate pleopods (1P–5P), numbers at bottom indicate pleomeres; Per = pereopod; U = uropods). E, pleon, ventral view (numbers to left indicate pleomeres; U = uropods). F, right barbula. G, right oostegite 1, inner view (minute scales on inner ridge not shown). H, right maxilliped, inner view. I, left pereopod 6. Scale bars = 500 μm (A, B), 250 μm (C, E–G), 100 μm (F, I); D not to scale, modified from Nierstrasz & Brender à Brandis (1931).

– Pleomere 5 lateral lobes scarcely extending over pleotelson; body nearly linear in outline..... .....*B. novaeguineensis* (Danforth, 1971), new combination
3. No midventral tubercles on pleomeres 1–5.....4
– Midventral tubercles on some pleomeres.....10
4. Pleotelson rounded, low ridges with setae..... .....*B. xiphidiostega*, new species
– Pleotelson with posterolateral lobes of various lengths.....5
5. Pereomeres 5 and 6 broader than anterior pereomeres.....6
– Pereomeres 2–5 subequal in width.....7
6. Anal cone not projecting..... *B. pyriforma* (Shiino, 1958)
– Anal cone projecting..... *B. kensleyi* (Williams & Schuerlein, 2005), new combination
7. Pleopods large, oblong, laterally positioned inflated lobes ....*B. wolffi* Markham, 1978
– Pleopods small, rounded, inflated lobes not extending to lateral margins of pleomeres.....8
8. Pleopods not present on pleomere 5, medially positioned 9
– Pleopods present on pleomeres 1-5, not medially positioned . .....*B. diogeni* (Popov, 1929)
9. Pleopods present on pleomeres 1–4, pleopods nearly spherical.....*B. marami*, new species
– Pleopods present on pleomeres 1–3, pleopods conical..... .....*B. guamensis* An, Gong & Paulay, 2018
10. Midventral tubercle on pleomere 1 only.....11
– Midventral tubercles on pleomeres 1–5 12
11. Pleopods on pleomeres 1–3 .... *B. distorta* An, Gong & Paulay, 2018
– Pleopods on pleomeres 1–5 .... *B. oceania* An, Gong & Paulay, 2018
12. Pleopods and midventral tubercles nearly spherical..... ..... *B. fraissei* (Carayon, 1943)
– Pleopods oblong; midventral tubercles conical..... .....*B. magellanica* Nierstrasz & Brender à Brandis, 1931

***Bopyrissa magellanica* Nierstrasz & Brender à Brandis, 1931**

(Figs. 4, 5)

Bopyrissa magellanica Nierstrasz & Brender à Brandis, 1931: 175–179, figs. 26, 27 [Costa Rica; infesting *Clibanarius albidigitus* Nobili, 1901]; Codreanu, 1961: 138; Danforth, 1963: 7 [list]; Danforth, 1970: 44 [list]; Bourdon, 1972: 835 [mention]; Markham, 1978: 103, 107; Markham, 1982: 333; Markham, 1992: 3 [table]; Markham, 2003: 72 [list]; Espinosa-Pérez & Hendrickx, 2006: 222 [table]; Ortiz & Lalana, 2006: 17 [list]; Brusca & Wehrtmann, 2009: 209 [list]; McDermott et al., 2010: 8 [table].

Bopyrella [*sic*] *magellanica* — Markham, 2003: 72 [list].

Material examined. Costa Rica: dextral ♀ lectotype (herein designated) (2.0 mm) (NHMD 85028; jar in vial has typed note "holotype?"), 6 dextral ♀ paralectotypes (1.5–2.9 mm), 1 ♂ paralectotype (1.1 mm), 2 cryptoniscus larvae paralectotypes (NHMD 300413), all from *Clibanarius albidigitus* Nobili, 1901 (sexes and sizes unknown), Punta Arenas, 23 August 1890.

Description. Female (Fig. 4) body length 1.5–2.9 mm, head dextrally deflexed with ~45–60° distortion angle. Body slightly S-shaped, all body regions and segments distinct (Fig. 4A, B). Head suboval, deeply set into pereon; thin frontal lamina covered with scales (Fig. 4A; scales not drawn); eyes absent. Antennules and antennae of 3 articles each; terminal articles with setae at distal tips, scales covering surface (Fig. 4C). Maxilliped with acute spur; short, rounded non-articulated palp with few small setae present (Fig. 4H). Barbula with two projections on each side, one very small medial lobe and one larger digitiform lateral lobe (Fig. 4F). Oostegites completely enclosing brood chamber (Fig. 4B),

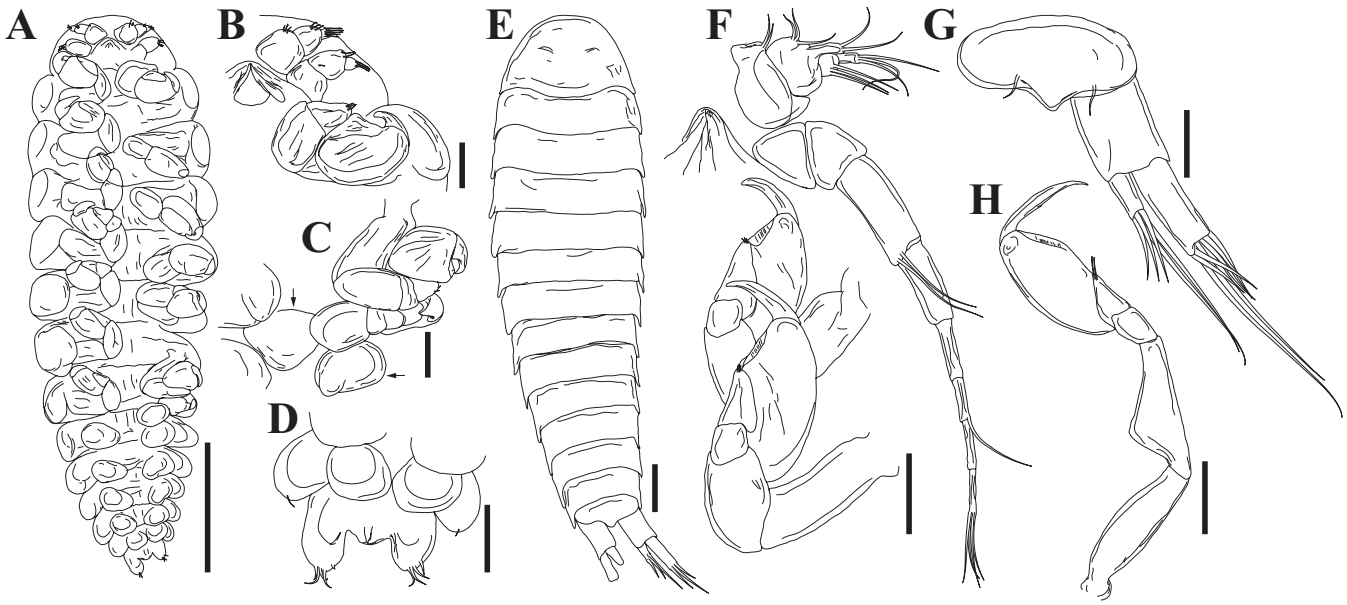

Fig. 5. *Bopyrissa magellanica* Nierstrasz & Brender à Brandis, 1931, male paralectotype, NHMD 300413, specimen #5 (A–D) and cryptoniscus larva, NHMD 300413 (E–H). A, ventral view; B, left antennule, antenna, mouthparts and pereopod 1; C, left pereopods 6 and 7 (vertical arrow indicates midventral tubercle of seventh pereomere, horizontal arrow indicates first left pleopod); D, terminal segments of pleon, ventral view; E, cryptoniscus larva, dorsal view; F, left antennule, antenna, mouthparts and pereopods 1 and 2; G, pygidium and right uropod, dorsal view; H, left pereopod 7. Scale bars = 250 µm (A); 25 µm (B–D, F–H); 50 µm (E).

setae on posterior margin of fifth oostegites; anterior lobe of oostegite 1 ovate, posterior lobe triangular, strongly recurved with few setae on distal tip; inner ridge of oostegite 1 with few low, rounded lobes covered with scales (Fig. 4G). Pereon of 7 distinct pereomeres, broadest across pereomeres 3 and 4, tapering towards pleon posteriorly. Dorsolateral bosses and coxal plates on segments 1–4, tergal projections approximately half length of dorsolateral bosses on segments 1–4; segments 5–7 with dorsolateral bosses continuing entire length of each segment, tergal projections absent (Fig. 4A). Pereopods 1–7 subequal in size, setae on anterior tip of carpus, scales on all pereopodal articles (Figs. 4C, I). Pleon of 5 distinct dorsally visible pleomeres, all pleonal segments with lateral plates, sixth pleomere present but not visible in dorsal view (Fig. 4A). Five pairs of biramous pleopods, first pair largest; first and second pairs flattened, ovate; third to fifth pairs elongate, digitiform; fifth pair smallest; pair of small, digitiform, uniramous uropods present on pleomere 5 (Fig. 4D, E).

Male (Fig. 5A–D) body length 1.1 mm, maximal width at pereomeres 3 and 4. Head suboval, distinct from pereomere 1, all segments distinct (Fig. 5A); eyes absent. Antennules and antennae of 3 articles each; terminal articles with setae at distal tips, scales covering surfaces (Fig. 5B). Anterior pereopods largest, size slightly decreasing posteriorly with pereopods 6 and 7 smallest, carpi with setae, scales on all pereopodal articles (Fig. 5B, C). Mid-ventral tubercle as low, rounded lobe between seventh pereopods (Fig. 5C). Pleon of 5 distinct pleomeres, tapering posteriorly (Fig. 5A); low, triangular mid-ventral tubercles present on all pleomeres (not visible at low power), minute on pleomeres 4 and 5. Pleopods semi-circular with rounded medial extension, extension prominent on pleopods 1–3, reduced on 4 and 5 (Fig. 5C, D). Pleotelson with anal fissure, produced distolaterally, distolateral ends with setae, uropods absent (Fig. 5D).

Cryptoniscus larva (Fig. 5E–H) length 0.6–1.2 mm, maximum width at pereomere 3; body tear-drop shaped (Fig. 5E). Head anterior margin concave, posterior margin sinusoidal, widest at posterolateral junction with pereomere 1 (Fig. 5E); eyes lacking. Antennules of three articles each (Fig. 5F), basal article approximately three times wider than long, distomedial region with tuft of setae, article 2 with rounded base and produced into digitiform extension that overlaps article 1, tufts of setae on base and extension, article 3 with small rounded base and digitiform extension, distal setae present (Fig. 5F). Antennae of eight articles each (four peduncular and four flagellar) (Fig. 5F), articles 1 and 2 triangular, articles 3 and 4 cylindrical, article 3 with long distal setae; flagellar articles subequal in length, much narrower than peduncular articles, second flagellar article with terminal setae (additional articles may have setae but are too closely applied to cuticle to be observable), distalmost article with tuft of terminal setae (Fig. 5F). Oral cone triangular, anteriorly directed (Figs. 5F). Pereomere 3 broadest, tapering posteriorly. Body pigmentation lacking. Pereomeres 1–7 with entire (not toothed) coxal plates. Pereopods 1–7 isomorphic, dactyli long and slightly curved, small notch or seta approximately half distance from base of dactylus, most prominent on posterior pereopods (Fig. 5F, H); each propodus with cuticular ridge corresponding to dactylus, lined with very short setae; each carpus with distal tuft of setae (Fig. 5F, H). Pleon with 5 pleopods. Pleotelson approximately three times wider than long, rounded laterally, with small rounded medial extension, long setae on either side of extension (Fig. 5G). Uropods biramous, composed of wide basal segment, short endopod, exopod approximately twice as long and wide as endopod, long distal setae on endopods and exopods (Fig. 5G).

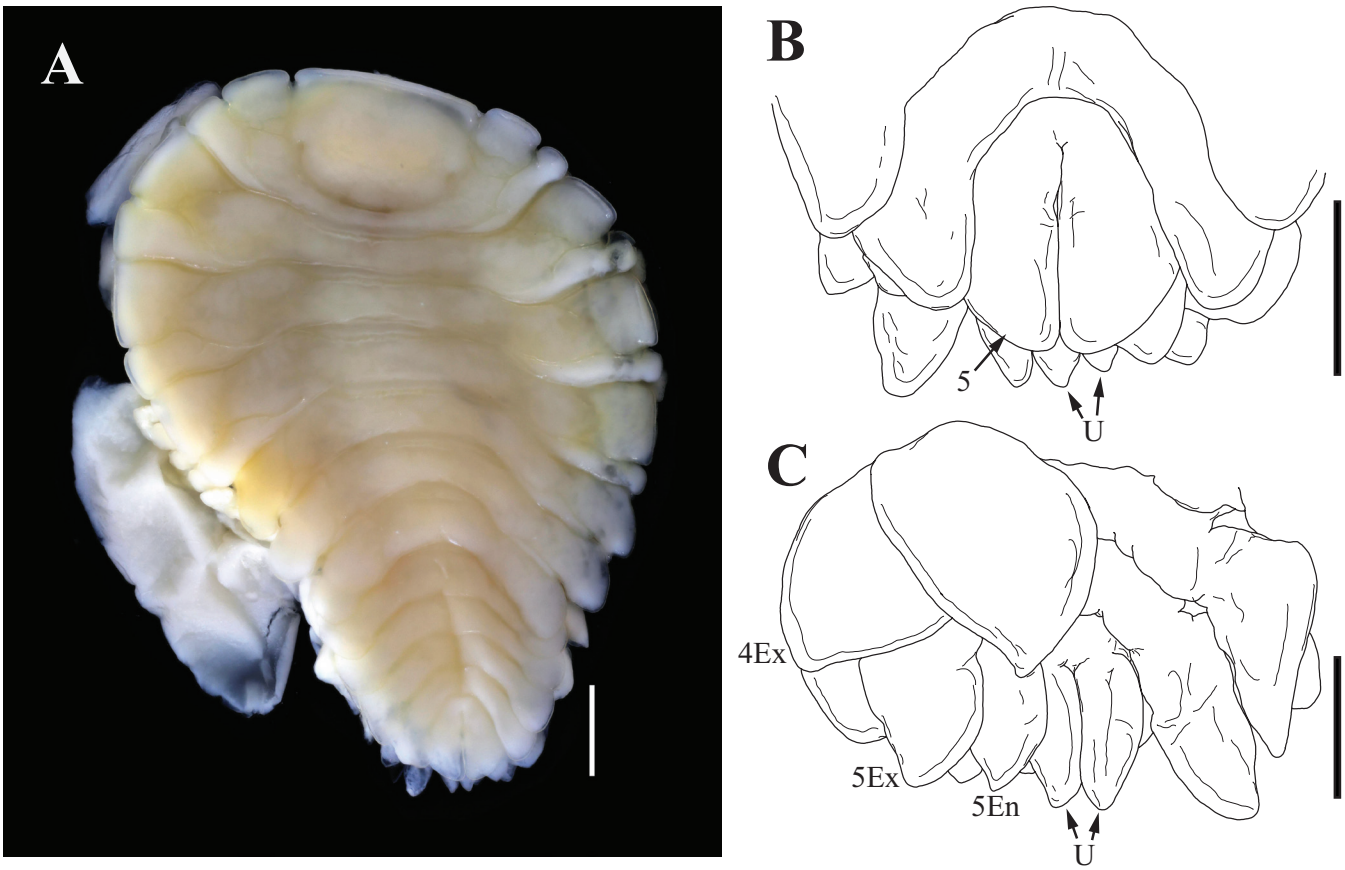

Fig. 6. *Bopyrissa kensleyi* (Williams & Schuerlein, 2005), new combination, ZRC 2018.0830. A, female, dorsal view; B, pleon, dorsal view (fifth pleomere indicated, U = uropods); C, pleon, ventral view (numbers indicate pleopods, Ex = exopod, En = endopod, U = uropods). Scale bars = 1.0 mm (A); 500 μm (B, C).

Type locality and distribution. Punta Arenas, Costa Rica.

Host. Diogenidae: *Clibanarius albidigitus* Nobili, 1901 (Nierstrasz & Brender à Brandis, 1931). This host identification was also reported in McDermott et al. (2010) but the source of the host identification was not stated therein. Nierstrasz & Brender à Brandis (1931) gave the host identification only as "*Clibanarius* sp."; however, the types of *Stegias angusta* Nierstrasz & Brender à Brandis (1931) were also collected in Punta Arenas at the same time as the types of *B. magellanica* and, in fact, there is a pair of *B. magellanica* in the jar with the types of *S. angusta* as well as a hermit crab, which is identifiable as *C. albidigitus*.

Size range (length). Females to 2.9 mm, males to 1.1 mm.

Remarks. Although Markham (1978) examined the type series and provided some notes, this is the first time the species has been fully redescribed. The original description by Nierstrasz & Brender à Brandis (1931) provided only dorsal views of a male and female and a lateral view of a female pleon, without designation of a holotype. The lateral view of the female pleon (Fig. 4D herein) was incorrectly labeled, presumably by Brender à Brandis, with pleomere 1 inexplicably labeled "VIII" (no isopod has either a pereomere or pleomere "8") and pereopod 7 labeled as "PerVIII"; the drawing is reproduced herein (Fig. 4D) with corrected labeling. The original text stated that females had five pairs of biramous pleopods and no uropods. Examination of the type series shows that the species has five pairs of biramous pleopods as well as uniramous uropods. In some specimens, the fifth pair of pleopods are so small they are difficult to distinguish and most of the specimens have some damage to the pleopods, making counts difficult; this could have been the source of Nierstrasz & Brender à Brandis's (1931) error. The female specimen with a typed note "holotype?" in the vial is designated herein as the lectotype.

Markham (1978) stated that he examined all eight female specimens in the type series of *B. magellanica* (one female is currently missing from the vial) and compared their characters with those of *B. wolffi* Markham, 1978; he did not, however, provide a redescription of *B. magellanica*. He stated that the characters of *Bopyrissa* included: females with an S-shaped body, frontal laminae present but reduced, five pleomeres with four pairs of biramous pleopods and one pair of uniramous uropods. This is not correct because all species in *Bopyrissa* have six pleomeres, although the sixth pleomere is ventrally displaced and not visible in dorsal view. Specimens of *B. diogeni* (Popov, 1929) have been described with four pairs of biramous pleopods and uniramous fifth pleopods (Bourdon, 1968). However, we have seen specimens of *B. wolffi* from Belize that have five pairs of biramous pleopods plus uniramous uropods, so it is possible that there is intraspecific variation in pleopod counts.

To our knowledge, this is the first description of a cryptoniscus larva for any species in the genus *Bopyrissa*. The larval morphology for *B. magellanica* is similar to that documented for other pseudionines (e.g., Bourdon, 1968; Anderson & Dale, 1981); however, whereas many of the previously described species have distinct teeth on the posterior margin of the pleotelson [= pygidium *sensu* Bourdon (1968)], *B. magellanica* lacks these teeth. Cryptoniscus larvae may provide many taxonomically informative features (see Boyko & Williams, 2015) but presently we lack descriptions of this stage in many epicaridean genera.

Bopyrissa kensleyi (Williams & Schuerlein, 2005), new combination

(Fig. 6)

Pseudione kensleyi Williams & Schuerlein, 2005: 96, 103–106, figs. 7–9 [Singapore; infesting *Clibanarius infraspinatus* (Hilgendorf, 1869)]; Madad, 2008: 548 [mention]; Markham, 2009: 232 [list]; McDermott et al., 2010: 9 [list]; Bruce & Wong, 2015: 162 [list].

Material examined. Singapore: 1 sinistral mature ♀ (8.0 mm) (ZRC 2018.0830) from left branchial chamber of ♂ *Clibanarius infraspinatus* (6.3 mm SL), Changi, Sta. CP1, coll. Toh Chay Hoon, 26 July 2013.

Type locality. Noordin Beach, Pulau Ubin, Singapore, Johore Strait, South China Sea (Williams & Schuerlein, 2005).

Distribution. Singapore (Williams & Schuerlein, 2005; herein).

Hosts. *Clibanarius infraspinatus* (Hilgendorf, 1869) (Williams & Schuerlein, 2005; herein).

Size range (length). Females to 8.0 mm, males to 1.5 mm.

Remarks. This is the second record of this species, from the same host and general vicinity (Singapore) as the type specimens. The female morphology corresponds to the original description (Fig. 6A–C). The uropods of the holotype are asymmetrical (one being bifurcated) and were recognised as being abnormal when the species was described; the present female has normally-developed uropods (Fig. 6B, C). The species was originally placed in *Pseudione* because the lateral plates of the fifth pleomere did not overlap the sixth pleomere but discovery of this specimen with a normally developed posterior end shows that the species belongs in *Bopyrissa* with the sixth pleomere (pleotelson) being ventrally displaced and not visible in dorsal view. Within *Bopyrissa*, the species is most similar to *B. pyriforma* but differs in symmetry of the female (sinistral in *B. kensleyi*, new combination vs. dextral in *B. pyriforma*), development of the dorsolateral bosses (large on pereomeres 1–4 on both sides of the body in *B. kensleyi*, new combination vs. large on pereomeres 1–4 only on one side of the body in *B. pyriforma*), form of the barbula (elongate lateral lobe with medial multi-lobed projection in *B. kensleyi*, new combination vs. single elongate lateral lobe in *B. pyriforma*), shape of the distal lobe of oostegite 1 (more elongate and recurved in *B. kensleyi*, new combination vs. *B. pyriforma*), and the degree of protrusion of the anal cone of the male (strong in *B. kensleyi*, new combination vs. not protruded in *B. pyriforma*).

Bopyrissa marami, new species

(Figs. 7–12)

Pseudione sp. A Madad, 2008: 2, 4–6, 37–45, 48, 49, 64, 88–99, figs. 10–15, table 3 [Philippines; infesting *Calcinus gaimardii* (H. Milne Edwards, 1848), *C. latens* (Randall, 1840), and *C. minutus* Buitendijk, 1937].

Material examined. Philippines: Dextral ♀ holotype (4.2 mm) (USNM 1493918), mature ♂ allotype (1.5 mm) (USNM 1493919), from right branchial chamber of ♂ *Calcinus gaimardii* (2.9 mm SL), Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; Paratypes: 1 dextral ovigerous ♀ (4.0 mm), 1 ♂ (1.6 mm) (USNM 1493920, on SEM stubs) from right branchial chamber of ♀ *C. gaimardii* (3.2 mm SL), Cebu, Olango Island, coll. JDW, 9 July 1997; 1 dextral ♀ (4.9 mm) hyperparasitised by *Cabirops* sp., 1 ♂ (1.6 mm) (JDW pers. coll.) from right branchial chamber of ♂ *C. gaimardii* (3.9 mm SL), Batangas, Sombrero Island, coll. JDW, 13 July 1997; 1 dextral ovigerous ♀ (3.8 mm) (USNM 1493921) from right branchial chamber of ♀ *Calcinus latens* (Randall) (3.0 mm SL), Batangas, Sombrero Island, coll. JDW, 13 July 1997; 1 dextral ovigerous ♀ (4.4 mm), 1 ♂ (1.50 mm) (USNM 1493922) from right branchial chamber of ♂ *C. gaimardii* (2.9 mm SL), Batangas, Sombrero Island, coll. JDW, 13 July 1997; 1 dextral ovigerous ♀ (5.0 mm), 1 ♂ (1.7 mm) (USNM 1493923) from right branchial chamber of ♂ *C. gaimardii* (3.6 mm SL), Puerto Galera, Lalaguna Beach, coll. JDW, 10 July 1997; 1 dextral ovigerous ♀ (4.7 mm), 1 ♂ (1.8 mm) (USNM 1493924) from right branchial chamber of ♀ *C. gaimardii* (3.6 mm SL), Puerto Galera, Lalaguna Beach, coll. JDW, 10 July 1997; 1 dextral ovigerous ♀ (4.2 mm), 1 ♂ (1.7 mm) (USNM 1493925) from right branchial chamber of ♂ *C. gaimardii* (3.9 mm SL), Puerto Galera, Big Lalaguna Beach, coll. JDW, 31 July 1997; 1 dextral ovigerous ♀ (4.2 mm), 1 ♂ (1.5 mm) (USNM 1493926) from right branchial chamber of ♀ *C. gaimardii* (3.3 mm SL), Puerto Galera, Big Lalaguna Beach, coll. JDW, 31 July 1997; 1 dextral ovigerous ♀ (4.3 mm), 1 ♂ (1.3 mm) (USNM 1493927) from right branchial chamber of ♀ *C. gaimardii* (3.2 mm SL), Puerto Galera, Big Lalaguna Beach, coll. JDW, 31 July 1997; 1 dextral ovigerous ♀ (3.9 mm), 1 ♂ (1.50 mm) (USNM 1493928) from right branchial chamber of ovigerous ♀ *C. gaimardii* (3.5 mm SL), Puerto Galera, Big Lalaguna Beach, coll. JDW, 31 July 1997; 1 dextral ovigerous ♀ (3.16 mm), 1 ♂ (1.06 mm) (USNM 1493929), from right branchial chamber of ♀ *C. gaimardii* (2.3 mm SL), Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; 1 dextral ovigerous ♀ (3.5 mm), 1 ♂ (1.4 mm) (USNM 1493930), from right branchial chamber of ♀ *C. gaimardii* (2.2 mm SL), Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; 1 dextral ♀ (2.9 mm), 1 ♂ (1.1 mm) (USNM 1493931), from right branchial chamber of ♂ *C. gaimardii* (2.4 mm SL), Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; 1 dextral ♀ (5.0 mm), 1 ♂ (1.9 mm) (USNM 1493932), from right branchial chamber of ♂

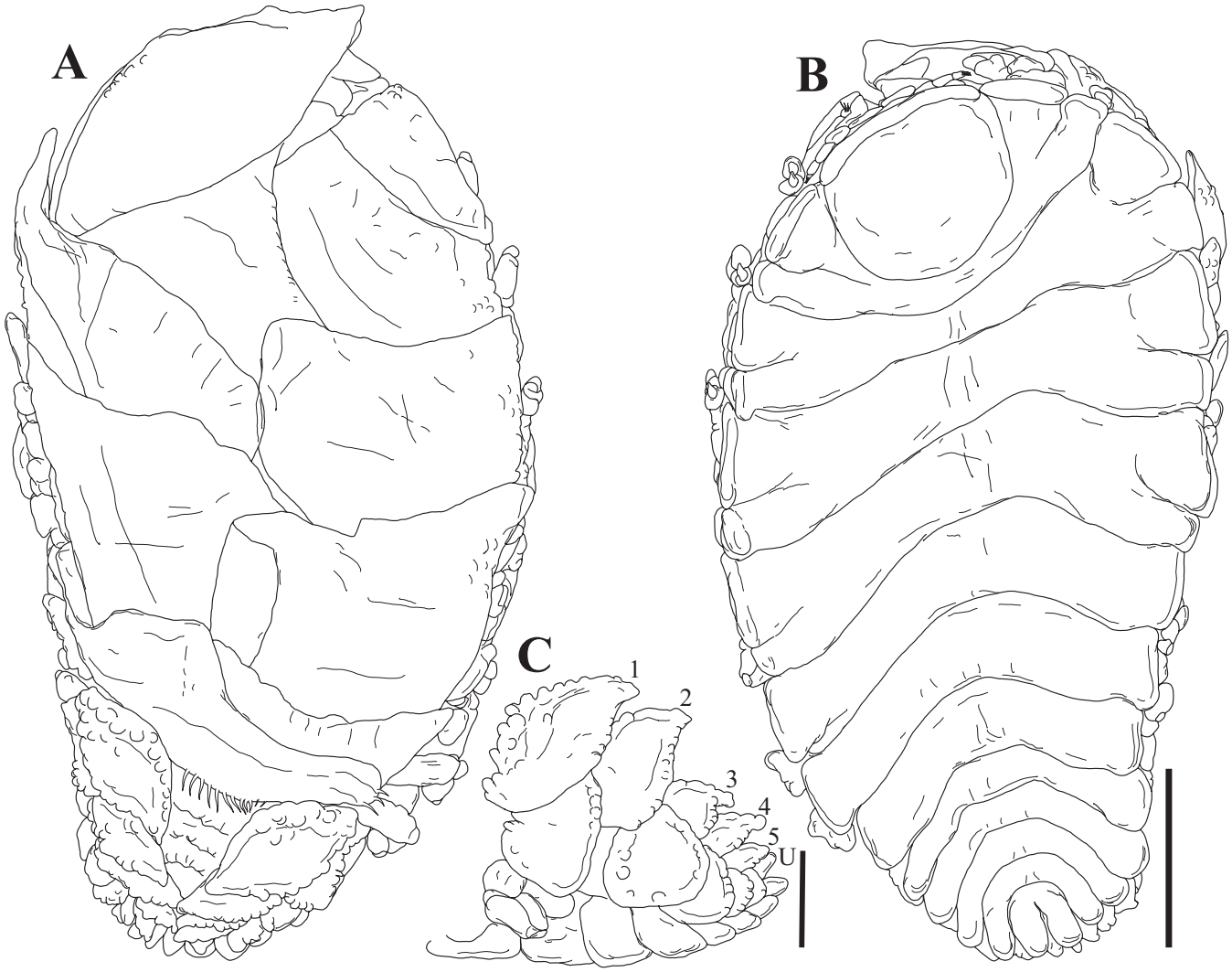

Fig. 7. *Bopyrissa marami*, new species, female paratype, USNM 1493972. A, ventral view; B, dorsal view; C, pleon, lateral view. Numbers indicate pleopods, U = uropods. Scale bars = 1.0 mm (A, B); 500 μm (C).

C. gaimardii (3.3 mm SL), Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; 1 dextral ovigerous ♀ (4.4 mm), 1 ♂ (1.4 mm) (USNM 1493933), from right branchial chamber of ♂ *C. gaimardii* (3.1 mm SL), Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; 1 dextral ovigerous ♀ (3.66 mm), 1 ♂ (1.30 mm), from right branchial chamber of ♂ *Calcinus minutus* (2.7 mm SL), host also parasitised by an entoniscid (JDW pers. coll.), Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; 1 dextral ovigerous ♀ (3.7 mm), 1 ♂ (1.3 mm) (USNM 1493934), from right branchial chamber of ♂ *C. gaimardii* (2.9 mm SL), host also infested with *Eremitione clibanaricola*, new combination (USNM 1493999), Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; 1 dextral ovigerous ♀ (4.3 mm), 1 ♂ (1.4 mm) (USNM 1493935), from right branchial chamber of ♂ *C. minutus* (3.2 mm SL), Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; 1 dextral ovigerous ♀ (4.6 mm), 1 ♂ (1.6 mm) (USNM 1493936), from right branchial chamber of ♂ *C. gaimardii* (3.3 mm SL), Batangas, Sombrero Island, coll. JDW, 30 January 1999; 1 dextral ♀ (3.4 mm), 1 ♂ (1.1 mm) (USNM 1493937), from right branchial chamber of ♂ *C. gaimardii* (2.5 mm SL), Batangas, Sombrero Island, coll. JDW, 30 January 1999; 1 dextral ovigerous ♀ (3.9 mm), 1 ♂ (1.4 mm) (USNM 1493938) from right branchial chamber of ♂ *C. gaimardii* (3.1 mm SL), Batangas, Anilao, coll. JDW, 13 February 1999; 1 dextral ovigerous ♀ (4.3 mm), 1 ♂ (1.3 mm) (USNM 1493939), from right branchial chamber of ♀ *C. gaimardii* (3.0 mm SL), Batangas, Anilao, coll. JDW, 13 February 1999; 1 dextral ovigerous ♀ (5.5 mm), 1 ♂ (1.7 mm) (USNM 1493940), from right branchial chamber of ♂ *C. gaimardii* (3.8 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (3.4 mm), 1 ♂ (1.3 mm) (USNM 1493941), from right branchial chamber of ♂ *C. gaimardii* (2.7 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (4.6 mm), 1 ♂ (1.2 mm) (USNM 1493942), from right branchial chamber of ♀ *C. gaimardii* (3.2 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (5.9 mm), 1 ♂ (1.6 mm) (USNM 1493943), from right branchial chamber of ♂ *C. gaimardii* (4.9 mm SL), host also parasitised by a peltogastrid rhizocephalan (host and parasite sent to R. Yoshida), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (3.0 mm), 1 ♂ (1.1 mm) (USNM 1493944), from right branchial chamber of ♀ *C. gaimardii* (2.1 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (2.60 mm), 1 ♂ (1.19 mm)

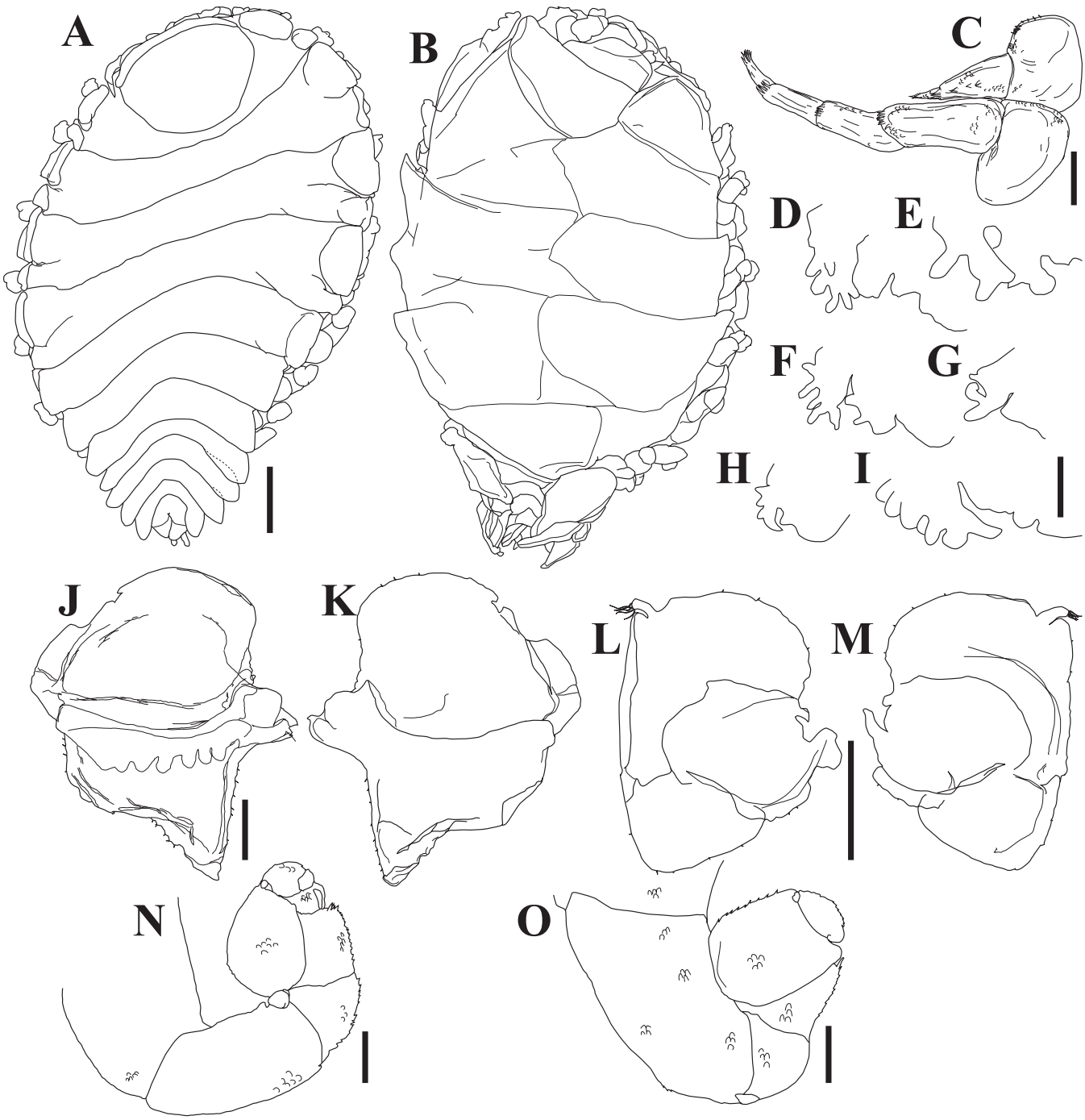

Fig. 8. *Bopyrissa marami*, new species, female holotype, USNM 1493918 (A, B), and female paratypes, USNM 1493933 (C), USNM 1493970 (D), USNM 1493934 (E), USNM 1493978 (F), USNM 1493925 (G), USNM 1493974 (H), USNM 1493973 (I), USNM 1493944 (J-M), USNM 1493966 (O, N). A, dorsal view; B, ventral view; C, right antennule (top) and antenna (bottom); D–I, variation in barbular morphology; J, left oostegite 1, inner view; K, left oostegite 1, external view; L, right maxilliped, inner view; M, right maxilliped, external view; N, right pereopod 1; O, right pereopod 7. Scale bars = 500 µm (A, B); 200 µm (C); 250µm (D–M); 50 µm (N, O).

(USNM 1493945), from right branchial chamber of ♂ *C. gaimardii* (2.5 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (2.9 mm), 1 ♂ (1.2 mm) (USNM 1493946), from right branchial chamber of ♂ *C. gaimardii* (2.5 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (5.2 mm), 1 ♂ (1.8 mm) (JDW pers. coll.), from right branchial chamber of ♀ *C. gaimardii* (3.2 mm SL), host also parasitised by a peltogastrid rhizocephalan, Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (4.6 mm), 1 ♂ (1.5 mm) (USNM 1493947), from right branchial chamber of ♀ *C. gaimardii* (3.2 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (3.6 mm), 1 ♂ (1.2 mm) (USNM 1493948), from right branchial chamber of ♂ *C. gaimardii* (3.0 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (not measured, dried), 1 ♂ (not measured, dried) (JDW pers. coll.), from right branchial chamber of ♀ *C. gaimardii* (2.1 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral mature ♀ (4.7 mm), 1 ♂ (1.5 mm) (USNM 1493949), from right branchial chamber of ♀ *C. gaimardii* (3.9 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous

♀ (4.5 mm), 1 ♂ (1.2 mm) (USNM 1493950), from right branchial chamber of ♀ *C. gaimardii* (2.9 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (5.2 mm), 1 ♂ (1.9 mm) (USNM 1493951), from right branchial chamber of ♀ *C. gaimardii* (3.6 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (3.0 mm), 1 ♂ (1.2 mm) (USNM 1493952), from right branchial chamber of ♂ *C. gaimardii* (2.6 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (2.6 mm), 1 ♂ (1.1 mm) (USNM 1493953), from right branchial chamber of ♂ *C. gaimardii* (2.3 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral mature ♀ (4.8 mm), 1 ♂ (1.5 mm) (USNM 1493954), from right branchial chamber of ♀ *C. gaimardii* (3.0 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 dextral ovigerous ♀ (4.6 mm), 1 ♂ (1.5 mm) (USNM 1493955), from right branchial chamber of ♀ *C. gaimardii* (3.6 mm SL), Bataan, Morong, coll. JDW, 28 February 1999; 1 dextral ovigerous ♀ (3.72 mm), 1 ♂ (1.25 mm) (USNM 1493956), from right branchial chamber of ♂ *C. gaimardii* (2.6 mm SL), Bataan, Morong, coll. JDW, 28 February 1999; 1 dextral ♀ (5.6 mm), 1 ♂ (1.3 mm) (USNM 1493957; male on SEM stub, JDW pers. coll.), from right branchial chamber of ♂ *C. gaimardii* (3.4 mm SL), Bataan, Morong, coll. JDW, 28 February 1999; 1 dextral juvenile ♀ (1.4 mm), 1 ♂ (0.6 mm) (JDW pers. coll.), from right branchial chamber of ♀ *C. gaimardii* (1.8 mm SL), Bataan, Morong, coll. JDW, 28 February 1999; 1 dextral mature ♀ (5.1 mm), 1 ♂ (1.8 mm) (USNM 1493958), from right branchial chamber of ♀ *C. gaimardii* (3.4 mm SL), Bataan, Morong, coll. JDW, 28 February 1999; 1 dextral juvenile ♀ (2.8 mm), 1 ♂ (1.0 mm) (USNM 1493959), from right branchial chamber of ♀ *C. gaimardii* (2.3 mm SL), Bataan, Morong, coll. JDW, 28 February 1999; 1 dextral ovigerous ♀ (4.1 mm), 1 ♂ (1.3 mm) (USNM 1493960), from right branchial chamber of ♀ *C. gaimardii* (2.7 mm SL), Bataan, Morong, coll. JDW, 28 February 1999; 1 dextral ovigerous ♀ (5.3 mm), 1 ♂ (1.7 mm) (USNM 1493961), from right branchial chamber of ♀ *C. gaimardii* (3.5 mm SL), Bataan, Morong, coll. JDW, 28 February 1999; 1 dextral mature ♀ (3.0 mm), 1 ♂ (1.1 mm) (USNM 1493962), from right branchial chamber of ♀ *C. gaimardii* (2.4 mm SL), Bataan, Morong, coll. JDW, 28 February 1999; 1 dextral ovigerous ♀ (3.1 mm), 1 ♂ (1.1 mm) (USNM 1493963), from right branchial chamber of ♀ *C. gaimardii* (2.62 mm SL), Bataan, Morong, coll. JDW, 28 February 1999; 1 dextral ovigerous ♀ (4.0 mm), 1 ♂ (1.4 mm) (USNM 1493964), from right branchial chamber of ♀ *C. gaimardii* (2.6 mm SL), Bataan, Morong, coll. JDW, 28 February 1999; 1 dextral ovigerous ♀ (2.5 mm), 1 ♂ (1.0 mm) (USNM 1493965), from right branchial chamber of ♂ *C. gaimardii* (1.9 mm SL), Puerto Galera, Lalaguna Beach, coll. JDW, 27 March 1999; 1 dextral ovigerous ♀ (4.2 mm), 1 ♂ (1.5 mm), 1 cryptoniscus larva of unidentified *Cabirops* sp. (0.8 mm) (JDW pers. coll.), from right branchial chamber of ♀ *C. gaimardii* (3.4 mm SL), Puerto Galera, Lalaguna Beach, coll. JDW, 27 March 1999; 1 dextral ovigerous ♀ (4.0 mm), 1 ♂ (1.4 mm) (USNM 1493966), from right branchial chamber of ♀ *C. gaimardii* (2.7 mm SL), Boracay, White Beach, coll. JDW, 15 April 1999; 1 dextral ovigerous ♀ (5.5 mm), 1 ♂ (1.6 mm) (USNM 1493967), from right branchial chamber of ♂ *C. gaimardii* (3.8 mm SL), Bataan, Morong, coll. JDW, 25 April 1999; 1 dextral ovigerous ♀ (4.4 mm), 1 ♂ (1.3 mm) (USNM 1493968), from right branchial chamber of ♂ *C. gaimardii* (3.1 mm SL), Bataan, Morong, coll. JDW, 25 April 1999; 1 dextral ♀ (2.7 mm), 1 ♂ (1.0 mm) (USNM 1493969), from right branchial chamber of ♂ *C. gaimardii* (2.3 mm SL), Bataan, Morong, coll. JDW, 25 April 1999; 1 dextral ovigerous ♀ (5.6 mm), 1 ♂ (1.8 mm) (USNM 1493970), from right branchial chamber of ♂ *C. gaimardii* (4.2 mm SL), Bataan, Morong, coll. JDW, 25 April 1999; 1 dextral ovigerous ♀ (4.3 mm), 1 ♂ (1.3 mm) (USNM 1493971), from right branchial chamber of ♂ *C. gaimardii* (3.2 mm SL), Bataan, Morong, coll. JDW, 25 April 1999; 1 dextral ovigerous ♀ (5.0 mm), 1 ♂ (1.4 mm) (USNM 1493972), from right branchial chamber of ♂ *C. gaimardii* (3.7 mm SL), Bataan, Morong, coll. JDW, 25 April 1999; 1 dextral ovigerous ♀ (6.1 mm), 1 ♂ (2.0 mm) (USNM 1493973), from right branchial chamber of ♂ *C. gaimardii* (4.4 mm SL), Bataan, Morong, coll. JDW, 25 April 1999; 1 dextral ovigerous ♀ (6.2 mm), 1 ♂ (1.6 mm) (USNM 1493974), from right branchial chamber of ♂ *C. gaimardii* (4.3 mm SL), Bataan, Morong, coll. JDW, 25 April 1999; 1 dextral ovigerous ♀ (5.3 mm), ♂ (1.6 mm) (USNM 1493975), from right branchial chamber of ♂ *C. gaimardii* (3.5 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 dextral ovigerous ♀ (4.0 mm), 1 ♂ (1.2 mm) (USNM 1493976), from right branchial chamber of ♂ *C. gaimardii* (2.7 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 dextral ovigerous ♀ (5.1 mm), 1 ♂ (1.6 mm) (USNM 1493977), from right branchial chamber of ♂ *C. gaimardii* (3.5 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 dextral ovigerous ♀ (5.0 mm), 1 ♂ (2.1 mm) (USNM 1493978), from right branchial chamber of ♂ *C. gaimardii* (3.8 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 dextral mature ♀ (4.7 mm), 1 ♂ (1.8 mm) (USNM 1493979), from right branchial chamber of ♀ *C. gaimardii* (3.5 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 dextral ovigerous ♀ (3.8 mm), 1 ♂ (1.3 mm) (USNM 1493980), from right branchial chamber of ♂ *C. gaimardii* (2.7 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 dextral ovigerous ♀ (4.5 mm), 1 ♂ (1.4 mm) (USNM 1493981), from right branchial chamber of ♂ *C. gaimardii* (3.2 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 dextral ovigerous ♀ (3.9 mm), 1 ♂ (1.2 mm) (USNM 1493982), from right branchial chamber of ♀ *C. gaimardii* (2.9 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 dextral ovigerous ♀ (3.5 mm), 1 ♂ (1.0 mm) (USNM 1493983), from right branchial chamber of ♂ *C. gaimardii* (2.7 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 dextral ovigerous ♀ (3.9 mm), 1 ♂ (1.3 mm) (USNM 1493984), from right branchial chamber of ♂ *C. gaimardii* (2.8 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 dextral ovigerous ♀ (3.7 mm), 1 ♂ (1.3 mm) (USNM 1493985, on SEM stub), from right branchial chamber of ♀ *C. gaimardii* (3.3 mm SL), Puerto Galera, Lalaguna Beach, coll. JDW, 18 June 2000; 1 dextral ovigerous ♀ (5.6 mm), 1 ♂ (1.8 mm) (ZRC 2018.0818), from right branchial chamber of ♂ *C. gaimardii* (3.9 mm SL), Puerto Galera, Lalaguna Beach, coll. JDW,

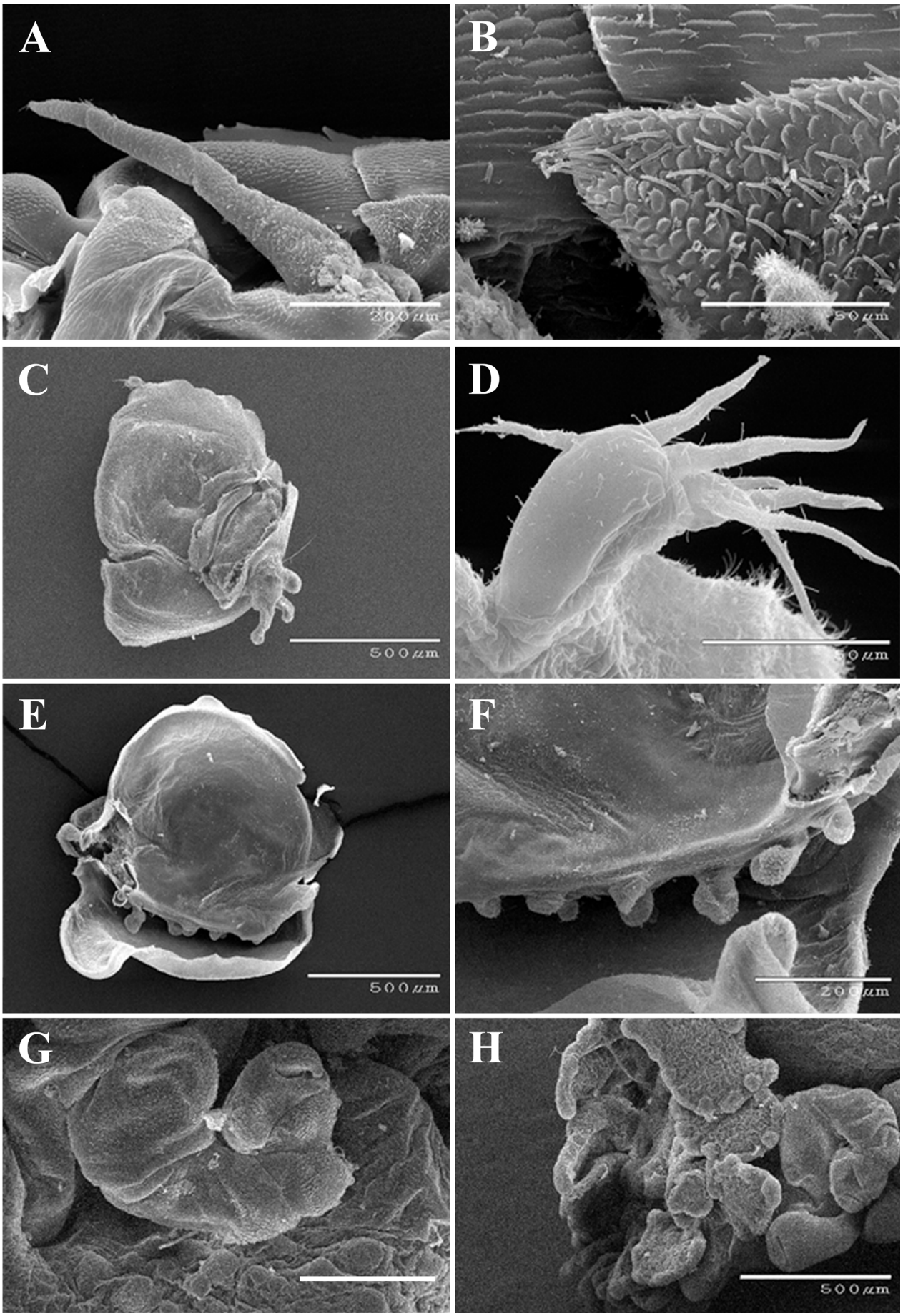

Fig. 9. *Bopyrissa marami*, new species, female paratype, USNM 1493920. A, left antenna; B, Left antennule, terminal article; C, left maxilliped, outer view; D, palp of maxilliped; E, right oostegite 1, internal view; F, right oostegite 1, digitate inner ridge; G, left pereopod 1; H, pleopods, lateral view. Scale bars = 200 µm (A, F, G); 50 µm (B, D); 500 µm (C, E, H).

18 June 2000; 1 mature ♀ (4.5 mm) (ZRC 2018.0820), from right branchial chamber of ♀ *C. gaimardii* (3.1 mm SL), host also parasitised by an entoniscid (host in JDW pers. coll.), Puerto Galera, Lalaguna Beach, coll. JDW, 18 June 2000; 1 mature ♀ (4.3 mm), 1 ♂ (1.53 mm) (ZRC 2018.0821), from right branchial chamber of ovigerous ♀ *C. minutus* (3.2 mm SL), Puerto Galera, Lalaguna Beach, coll. JDW, 18 June 2000; 1 ovigerous ♀ (4.9 mm), 1 ♂ (1.8 mm) (ZRC 2018.0823), from right branchial chamber of ♀ *C. gaimardii* (3.2 mm SL), Puerto Galera, Lalaguna Beach, coll. JDW, 18 June 2000; 1 mature ♀ (3.9 mm), 1 ♂ (1.4 mm) (ZRC 2018.0825), from right branchial chamber of ♂ *C. minutus* (2.9 mm SL), Puerto Galera, Lalaguna Beach, coll. JDW, 18 June 2000.

Description. Female body length 4.10 mm, maximal width 2.41 mm, head length 0.66 mm, head width 1.01 mm, pleon length, 0.9 mm. Mean length of female specimens was 4.39 ± 0.93 mm and mean maximal width was 2.57 ± 0.52 mm (n=48). Head dextrally deflexed with ~40° distortion angle. Body pyriform, all body regions and segments distinct (Figs. 7A, B, 8A, B). Head suboval, deeply set into pereon; frontal lamina semicircular, notched slightly in middle, covered in scales (Figs. 7B, 8A); eyes absent. Antennules of 3 articles each, article 1 of right and left antennules fused; setae at distal tip of antennules and scattered on ventral surface and margins of article 1; scales covering entire surface (Figs. 8C, 9B). Antennae of 5 articles each, covered in scales, tuft of setae at distal tip and setae on lateral surface and at margins of articles (Figs. 8C, 9A). Maxilliped with acute spur, slender palp with ~7 setae present, posterior margin of maxilliped setose (Figs. 8L, M, 9C, D). Barbula with two lateral projections with variable digitation, medial projection most variable, sometimes as a low rounded nub (Fig. 8D–I). Oostegites completely enclosing brood chamber; setae on posterior margin of fifth oostegite; oostegite 1 with rounded anterior lobe, triangular posterior lobe with short setae along edge, inner ridge of oostegite 1 with 6–7 large digitate projections (Figs. 8J, K, 9E, F). Pereon of 7 distinct pereomeres, broadest across pereomere 4, tapering towards pleon posteriorly. Prominent dorsolateral bosses and coxal plates on segments 1–4, tergal projections half length of dorsolateral bosses on segments 1–4; segments 5–7 with dorsolateral bosses continuing whole length of segment, tergal projections absent (Figs. 7A, 8A). Pereopods 1–5 subequal in size, 6 and 7 slightly smaller, setae on anterior tip of propodi, directly underneath dactyli, no large gap between pereopods, scales on all pereopodal articles (Figs. 8N, O, 9G). Pleon of 6 distinct pleomeres, sixth pleomere ventrally displaced, first 5 pleonal segments with lateral plates. Five pairs of biramous pleopods, tuberculate on margins; small pair of lanceolate, distally rounded, uniramous uropods present on pleomere 6, uropods mostly hidden in dorsal view (Figs. 7B, C, 8A, 9H).

Male length 1.62 mm, maximal width 0.59 mm at pereomere 4, head length 0.13 mm, head width 0.31 mm, pleon length 0.41 mm. Mean length of male specimens was 1.55 ± 0.24 mm and mean maximal width was 0.58 ± 0.08 mm (n=48). Head subovate, distinct from pereomere 1, all segments distinct (Figs. 10A, 11A); prominent eyes on posteriolateral border of head (Fig. 10A). Antennules of 2 articles each, setae on distal tip of article 2, setae on surface of article 2; antennae of 2 articles each, tuft of setae on distal tip of antennae and along ventral surface of article 2, scales on surface of article 2 (Figs. 10C, 11B). Pereon of 7 distinct pereomeres, broadest across pereomere 4, tapering posteriorly. Pereopods 3 and 4 largest, size decreasing anteriorly and posteriorly with pereopods 6 and 7 smallest, ventral surface of carpi and meri covered in scales, propodi with ridges of scales on anterior portion underneath dactyl, tuft of setae on anterior tip of propodi opposed to tip of dactyli (Figs. 10D, E, 11C, D). Pleon of 5 distinct pleomeres, tapering posteriorly, distolateral edge fringed with setae (Figs. 10A, 11E). Pleopods tuberculate, present on pleomeres 1–4 (Figs. 10B, 11E). Pleotelson with weak anterolateral projections, distolateral ends with setae; anal fissure slightly produced ventrally, midventral tubercles absent, no uropods (Figs. 10B, F–H, 11E, F).

Type locality. Coco Beach, Puerto Galera, Philippines.

Etymology. The species epithet is derived from the Filipino word *marami*, which means "many" or "numerous," reflecting the fact that this was by far the most common bopyrid found on hermit crabs from the Philippines during this study.

Distribution. Batangas, Puerto Galera, Philippines.

Hosts. Diogenidae: *Calcinus gaimardii* (H. Milne Edwards, 1848), *C. latens* (Randall, 1840), and *C. minutus* Buitendijk, 1937.

Size range (length). Females to 6.2 mm, males to 2.1 mm.

Remarks. Descriptions and diagnoses of species of *Pseudione* and closely related genera are often problematic, given the intraspecific variability and inconsistency of supposedly uniform features (Markham, 1978). The new species described herein is superficially similar to *Eremitione clibanaricola*, new combination, but it does not exhibit the marked asymmetry in female specimens that is characteristic of *E. clibanaricola*, new combination, nor does *E. clibanaricola*, new combination present a ventrally displaced sixth pleomere, which is characteristic of all *Bopyrissa* species. Females of *B. marami*, new species are most similar to those of *Bopyrissa guamensis* An, Gong, and Paulay, 2018, recently described from *Calcinus elegans* (H. Milne Edwards, 1836) collected in Guam. However, females of *B. marami*, new species are distinguished from *B. guamensis* based primarily on characters of the first oostegite, in which the posterior lobe is recurved and with smaller and more numerous projections on the inner ridge in *B. guamensis* but rounded and with fewer, larger projections on the inner ridge in *B. marami*, new species. The pleopods of the males of *B. marami*, new species are different from those of *B. guamensis* in that the former species has 4 pairs of medially situated pleopods whereas the latter has 3 pairs (lacking the pair on the fourth pleomere). The new species is also similar to *B. liberorum* Markham, 1985b, but differences between females of the two species include: two lateral lobes on the barbula in *B.*

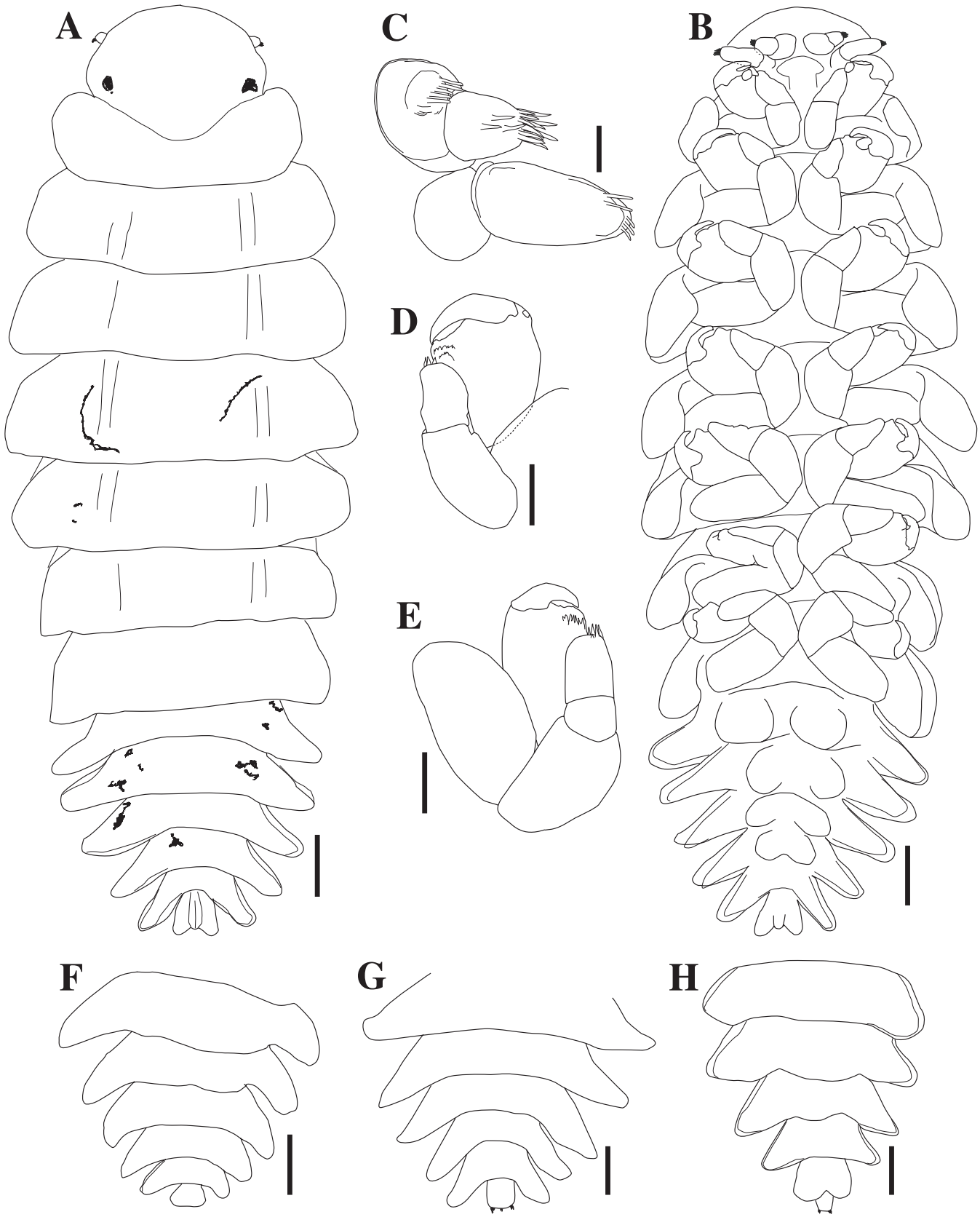

Fig. 10. *Bopyrissa marami*, new species, male allotype, USNM 1493919 (A–E) and paratypes, USNM 1493975 (F), USNM 1493933 (G), USNM 1493970 (H). A, dorsal view; B, ventral view; C, right antennule and antenna; D, right pereopod 1; E, left pereopod 7; F–H, male pleons. Scale bars = 100 μm (A, B, F–H); 20 μm (C); 50 μm (D, E).

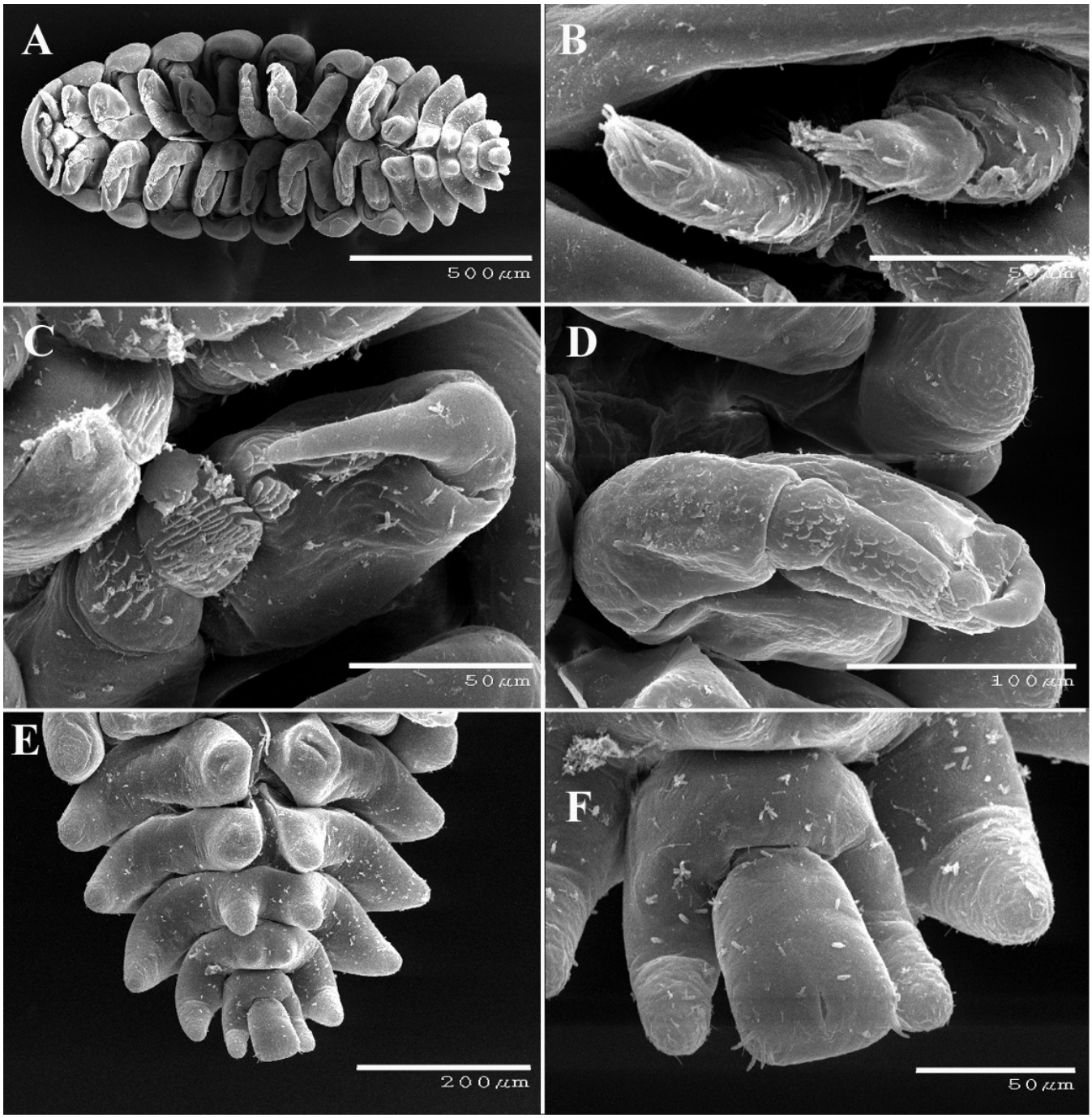

Fig. 11. *Bopyrissa marami*, new species, male paratype, USNM 1493920 (A–F). A, overview, ventral; B, left antennule and antenna; C, right pereopod 1; D, right pereopod 7; E, pleomeres; F, pleotelson. Scale bars = 500 µm (A); 50 µm (B, C, F); 0.10 mm (D); 200 µm (E).

marami, new species vs. one lobe in *B. liberorum*; inner ridge of oostegite 1 with approximately 8 large digitiform extensions in *B. marami*, new species vs. 2 or 3 low lobes in *B. liberorum*; maxilliped with extended palp in *B. marami*, new species vs. maxilliped with recessed palp in *B. liberorum*; pleopods with tubercles in *B. marami*, new species vs. smooth in *B. liberorum*. Differences between males of the two species include: pleopods large and positioned medially in *B. marami*, new species vs. pleopods low and positioned laterally in *B. liberorum*; posterolateral extentions of the pleotelson weakly extended in *B. marami*, new species vs. strongly produced in *B. liberorum*.

The position of the uniramous uropods of females of *B. marami*, new species is much like that of *B. novaeguineensis* (Danforth, 1971), new combination; however, there is no setose palp on the maxilliped of females of *B. novaeguineensis*, new combination. Males of *B. novaeguineensis*, new combination have low laterally placed pleopods and the overall body shape is much more elongate than for any specimens of *B. marami*, new species.

Ecology. Prevalence of *Bopyrissa marami*, new species over the thirteen collections of hermit crabs in which the parasite was found ranged from 0.8–19.2% (mean prevalence=6.4±6.4%, n=1,671 total hermit crabs examined).

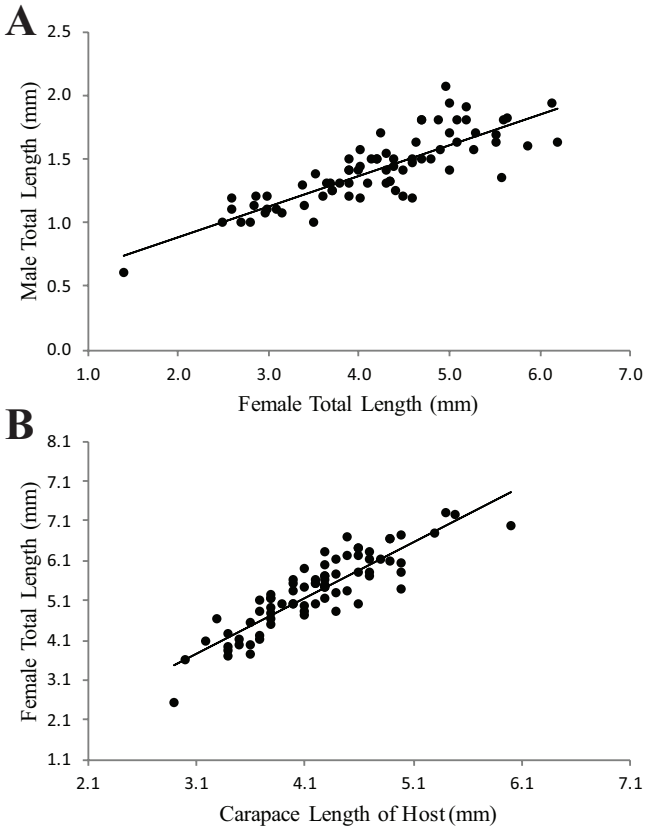

Fig. 12. A, relationship between female total body length and male total body length of *Bopyrissa marami*, new species. (linear regression: y = 0.237x + 0.421; R^2 = 0.673; df = 73; P < 0.0001); B, relationship between hermit crab host carapace length and female total body length of *Bopyrissa marami*, new species (linear regression: y = 1.40x − 0.149; R^2 = 0.785; df = 75; P < 0.0001).

Of these specimens, the vast majority (91.7%) infested *Calcinus gaimardii* but the species was also found on one *C. latens* and five *C. minutus* (Table 1). Two specimens of *B. marami*, new species were hyperparasitised by cabiropid isopods (2.6%, 2 of 78). One host *C. gaimardii* was doubly infested with *Eremitione clibanaricola*, new combination and *B. marami*, new species and two *C. gaimardii* were doubly parasitised by a peltogastrid rhizocephalan and *B. marami*, new species. Two hosts (one *C. gaimardii* and one *C. minutus*) were doubly parasitised by an unidentified entoniscid and *B. marami*, new species.

The mean total body length of female *B. marami*, new species was 4.2 ± 0.9 (n=77); male *B. marami*, new species mean total body length was 1.4 ± 0.3 (n=75). The relationship between female total body length and male total body length was significantly positively correlated (P < 0.0001) (Fig. 12A). *Bopyrissa marami*, new species was found to be ovigerous in all months sampled (January through April, June, and July) and thus likely breeds throughout the year, as does its dominant host *C. gaimardii* (Litulo & Tudge, 2005). Of the 75 mature female *B. marami*, new species collected, 84% were ovigerous; the smallest ovigerous female was 2.5 mm SL.

The total body length of female B. marami, new species and host hermit crabs (as estimated by carapace length) was significantly positively correlated (P < 0.0001) (Fig. 12B). One female C. gaimardii host (USNM 1493928) was found to be ovigerous although infested with a mature female and male pair of B. marami, new species; none of the other female hosts were found with eggs.

Variation. The number of articles and characteristics of the antennules of female specimens of *Bopyrissa marami*, new species showed some variation; specifically, the specimen prepared for SEM exhibited two articles, with article 1 of the left and right antennules being fused. The antennules of this specimen were shorter and more setose over the entire surface of article 1 than in other specimens (Fig. 9A, B). The barbula was typically composed of one or two digitate projections, the size of the projections and amount of digitation was variable (Fig. 8D–I); only two female specimens (4.2%; two of 48) exhibited a barbula represented by a single, slender projection, lacking digitation, similar to that of *E. clibanaricola*, new combination (USNM 1493945, USNM 1493974). The degree of digitation of the inner ridge of oostegite 1 was variable, with some female specimens showing weaker digitation than others but with digitation always present to some degree. A maxilliped palp was present in all females, with some specimens having a much larger, more pronounced setose palp than others. The length of the uropods varied; in some specimens, they were longer than the lateral plates while in other specimens, the uropods were considerably shorter. One female specimen exhibited biramous uropods, possibly the result of a developmental abnormality (USNM 1493969); a few other female specimens exhibited some degree of abnormality such as an undeveloped pleomere 1 on one side and coalescing of one or more pleomeres. Male morphology was fairly consistent overall, although they varied in the characteristics of the pleotelson, which could be almost cordiform in morphology or slightly cylindrical (Fig. 10A, F–H).

Bopyrissa xiphidiostega, new species

(Figs. 13–15)

Bopyrissa sp. A Madad, 2008: 2, 4, 5, 28–33, 47, 49, 60, 61, 84, 85, fig. 8, table 1 [Philippines, infesting *Cacinus gaimardii* (H. Milne Edwards, 1848), *C. minutus* Buitendijk, 1937, *Dardanus lagopodes* (Forskål, 1775)].

Bopyrissa sp. Williams & Boyko, 2016: 35, 57 [Batangas, Philippines, infesting *C. minutus*].

Material examined. Philippines: Mature sinistral holotype ♀ (9.3 mm) (USNM 1493986), mature allotype ♂ (1.8 mm) (USNM 1493987) from left branchial chamber of ♀ *Dardanus lagopodes* (6.8 mm SL), Cebu, Olango Island, coll. JDW, 9 July 1997; Paratypes: 1 sinistral ♀ (6.2 mm), 1 ♂ (1.7 mm; male lost) (USNM 1493988) from left branchial chamber of ♂ *D. lagopodes* (4.4 mm SL), Cebu, Danao Beach, coll. P. Cassidy, September 1996; 1 dextral ♀ (6.6 mm), 1 ♂ (2.0 mm) (USNM 1493989) from right branchial chamber of ♀ *D. lagopodes* (4.0 mm SL), Cebu, Danao Beach, coll. P. Cassidy, September 1996; 1 sinistral ♀ (5.50 mm) (USNM 1493990) from left branchial chamber of ♂ *D. lagopodes* (3.50 mm SL), Cebu, Danao Beach, coll. P. Cassidy, September 1996; 1 sinistral ♀ (4.8 mm) (USNM 1493991)

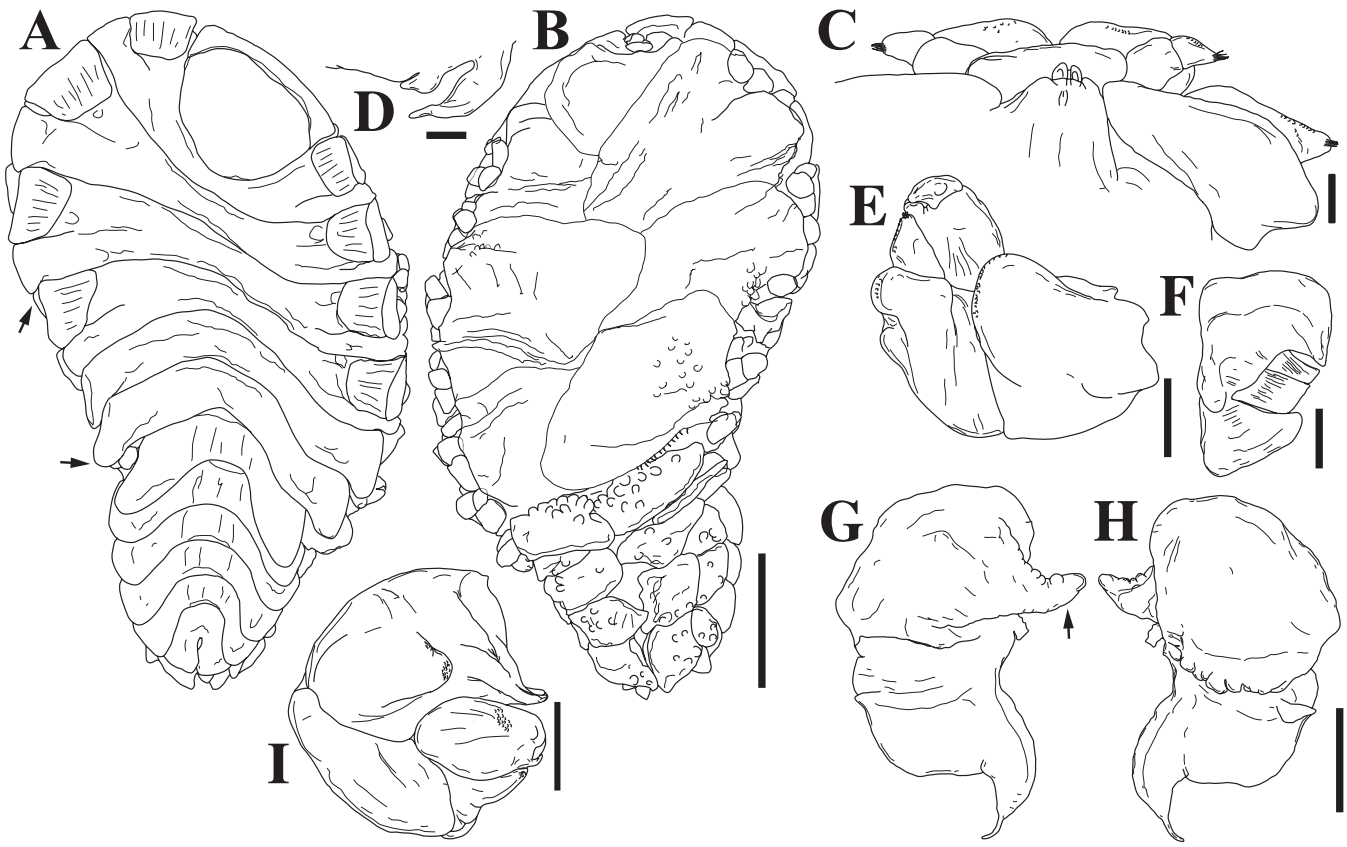

Fig. 13. *Bopyrissa xiphidiostega*, new species, female holotype, USNM 1493986. A, female, dorsal view (arrowheads show concave region that extends from pereomeres 4 to 6 when viewed laterally); B, female, ventral view; C, right and left antennule, left antenna, and mouthparts; D, right barbula; E, left pereopod 1; F, left maxilliped, outer view; G, right oostegite 1, outer view (arrowhead shows lateral extension that overlaps with basis of pereopod 1); H, right oostegite 1, inner view; I, left pereopod 7. Scale bars = 1 mm (A, B, C, G, H); 250 μm (D, I); 500 μm (E, F).

from left branchial chamber of ♂ *D. lagopodes* (3.00 mm SL), Cebu, Danao Beach, coll. P. Cassidy, September 1996; 1 sinistral ovigerous ♀ (5.8 mm), 1 ♂ (1.8 mm) (USNM 1493992) from left branchial chamber of ♂ *D. lagopodes* (3.8 mm SL) host also infested with *Asymmetrione harmoniae*, new species (USNM 1493915), Cebu, Danao Beach, coll. P. Cassidy, 6 December 1996; 1 sinistral ovigerous ♀ (4.6 mm), 1 ♂ (1.2 mm) (USNM 1493993) from left branchial chamber of ♀ *D. lagopodes* (3.3 mm SL), Cebu, Olango Island, coll. JDW, 10 July 1997; 1 sinistral ♀ (4. 7 mm), 1 unidentified elongate epicaridean cryptoniscus larva (0.9 mm) (USNM 1493994) from left branchial chamber of ♂ *Calcinus gaimardii* (3.3 mm SL), Puerto Galera, Big Lalaguna Beach, coll. JDW, 31 July 1997; 1 sinistral ovigerous ♀ (5.0 mm), 1 ♂ (1.4 mm) (USNM 1493995) from left branchial chamber of ♀ *C. gaimardii* (3.2 mm SL), Puerto Galera, Coco Beach, coll. JDW, 12-15 January 1999; 1 sinistral ♀ (3.5 mm), 1 ♂ (1.0 mm) (USNM 1493996) from left branchial chamber of ♀ *Calcinus minutus* (3.0 mm SL), Puerto Galera, Coco Beach, coll. JDW, 12-15 January 1999; 1 sinistral ovigerous ♀ (4.1 mm), 1 ♂ (1.0 mm) (USNM 1493997) from left branchial chamber of intersex *C. minutus* (3.6 mm SL), host also infested with *Parathelges aniculi* (Whitelegge, 1897) (USNM 1283393; see Williams & Boyko 2016), Batangas, Anilao**,** coll. JDW, 13 February 1999; 1 sinistral ovigerous ♀ (4.7 mm), 1 ♂ (1.1 mm) (USNM 1493998) from left branchial chamber of ♀ *C. gaimardii* (2.6 mm SL), Bataan, Mabayo, coll. JDW, 21 February 1999; 1 sinistral ovigerous ♀ (4.9 mm), 1 ♂ (1.6 mm) (ZRC 2018.0831) from left branchial chamber of ♀ *C. gaimardii* (3.5 mm SL), Bataan, Mabayo, coll. JDW, 27 March 1999; 1 sinistral ♀ (3.7 mm), 2 cryptoniscus larvae of unidentified *Cabirops* sp. (1.0 mm, 0.9 mm) (JDW pers. coll.) from left branchial chamber of ♀ *C. gaimardii* (3.4 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 sinistral ♀ (3.6 mm), 1 ♂ (0.9 mm; JDW pers. coll.), 1 cryptoniscus larva of unidentified *Cabirops* sp. (0.9 mm) (JDW pers. coll.) from left branchial chamber of ♂ *C. gaimardii* (2.6 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 sinistral ovigerous ♀ (4.0 mm), 1 ♂ (1.1 mm) (ZRC 2018.0833) from left branchial chamber of ♂ *C. gaimardii* (damaged, not measured), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 sinistral ovigerous ♀ (4.7 mm), 1 ♂ (1.3 mm) (ZRC 2018.0835) from left branchial chamber of ♀ *C. minutus* (3.6 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000; 1 sinistral ovigerous ♀ (4.3 mm), 1 ♂ (1.1 mm) (ZRC 2018.0837) from left branchial chamber of ♀ *C. gaimardii* (3.2 mm SL), Puerto Galera, Lalaguna Beach, coll. JDW, 18 June 2000.

Description. Female body length 9.38 mm, maximal width 5.31 mm, head length 1.54 mm, head width 2.08 mm, pleon length 3.23 mm. Head sinistrally deflexed with ~68° distortion angle. Body pyriform, all body regions and segments distinct (Fig. 13A, B).

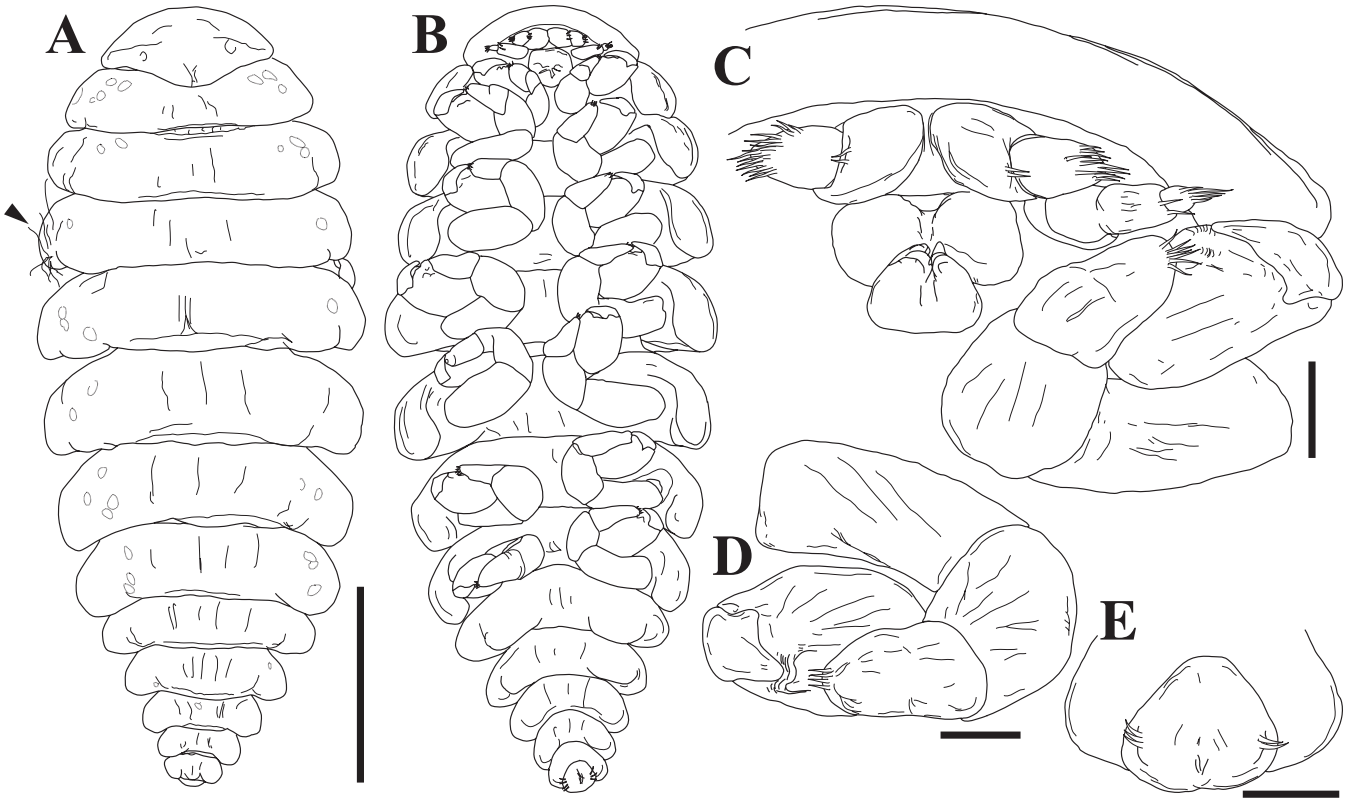

Fig. 14. *Bopyrissa xiphidiostega*, new species, male allotype USNM 1493987. A, male, dorsal view; arrowhead indicates eccrinales on left side of pereomere 3 (also found on other pereomeres but not drawn); B, male, ventral view; C, right and left antennule, left antenna, mouthparts, and left pereopod 1; D, left pereopod 7; E, terminal pleomere and pleon. Scale bars = 300 µm (A, B); 50 µm (C–E).

Head small, suboval, deeply set into pereon; frontal lamina broad, flared on lateral margins (Fig. 13A); eyes absent. Antennules of 3 articles each; basal articles appear fused, all articles covered with scales, terminal article distally setose (Fig. 13C). Antennae of 2 articles each, basal article broad, terminal article triangular, distally setose (Fig. 13C). Anterior lobe of maxilliped rounded, palp absent, spur of posterior lobe subacute (Fig. 13F). Barbula with 2 lateral projections, medial projection short (Fig. 13D). Tuberculate oostegites completely enclosing brood chamber, small round tubercles most prominent on lateral edges of oostegites, setae on posterior margin of fifth oostegite (Fig. 13B). Anterior lobe of oostegite 1 oval with lateral extension that overlaps with basis of pereopod 1 (Fig. 13G), posterior lobe triangular, curved, extending to a narrow tip; digitation on inner ridge (Fig. 13H).

Pereon of 7 distinct pereomeres, broadest across pereomere 3, tapering posteriorly; pereomeres 4–6 concave on long side (when viewed laterally) (Fig. 13A). Prominent dorsolateral bosses and reduced tergal projections on pereomeres 1–4 of concave side (Fig. 13A). Tergal projections almost as broad as dorsolateral bosses on convex side of pereomeres 1–4; pereomeres 5–7 with dorsolateral bosses continuing to midline of each segment on concave side, tergal projections absent. Pereomere 7 narrow, V-shaped and more similar to pleomere 1 than pereomere 6 (Fig. 13A). Pereopods 1–5 subequal in size, no large gap between pereopods, pereopods 6 and 7 slightly smaller (Fig. 13E, I).

Pleon V-shaped, of 6 distinct pleomeres, sixth pleomere not visible in dorsal view, pleomeres 1–5 with lateral plates, pleomere 1 deeply set into pereomere 7. Five pairs of biramous, tuberculate pleopods (Fig. 13B); small pair of distally rounded, uniramous uropods present on pleomere 6, uropods barely visible in dorsal view (Fig. 13A).

Male length 2.02 mm, maximal width 0.84 mm at pereomere 4, head length 0.21 mm, head width 0.44 mm, pleon length 0.5 mm. Head suboval, all segments distinct (Fig. 14A, B); eyes absent. Antennules of 2 articles each, setae on distal tip of article 2; antennae of 2 articles each, tuft of setae on distal tip of antennae and along ventral surface, scales on surface (Fig. 14C). Pereon of 7 distinct pereomeres, broadest at pereomere 5, tapering posteriorly (Fig. 14A). Pereopods with all articles distinct, carpus with terminal group of setae (Fig. 14D); pereopods 3 and 4 largest, size decreasing posteriorly and anteriorly with pereopods 6 and 7 smallest (Fig. 14D).

Pleon of 6 distinct pleomeres, tapering posteriorly. Midventral tubercles absent; dorsolateral pleopods present as low swellings on pleomeres 1–5 (Fig. 14B). Pleotelson rounded, no posterolateral projections present; anal fissure prominent medially, distolateral edges with setae; no uropods (Fig. 14E).

Type locality. Olango Island, Cebu, Philippines.

Etymology. The specific epithet xiphidiostega is derived from the Greek words xifidio (στιλέτο; small sword) and stegi (στέγη; cover), referring to the anterior lobe of oostegite 1

which has a dagger-like lateral extension that overlaps with the basis of pereopod 1.

Distribution. Cebu, Bataan, Puerto Galera, Batangas.

Hosts. Diogenidae: *Cacinus gaimardii* (H. Milne Edwards, 1848), *C. minutus* Buitendijk, 1937, and *Dardanus lagopodes* (Forskål, 1775).

Size range (length). Females to 9.3 mm, males to 1.8 mm.

Remarks. Markham (1978) reported that most species of *Bopyrissa* occur only in dextral or sinistral forms but not both, although noting that both forms have been recorded in *Bopyrissa diogeni* with the dextral morph predominating. *Bopyrissa xiphidiostega*, new species is unusual in that females are predominantly sinistral, although a single dextral example was found. *Bopyrissa dawydoffi* (Codreanu & Codreanu, 1963) is currently the only described species in the genus that is apparently exclusively sinistral but its generic placement is uncertain.

Females of *B. pyriforma* as described by Shiino (1958) have inconspicuous dorsolateral bosses present on pereomeres 1–4, relatively large heads deeply set into pereomere 1 that lack a pronounced frontal lamina and the uropods are completely concealed by the fifth lateral plates in dorsal view. Females of *Bopyrissa xiphidiostega*, new species have more prominent dorsolateral bosses on pereomeres 1–4 and a relatively smaller head with a well-defined frontal lamina, although *B. xiphidiostega*, new species does have reduced uropods, they are not completely concealed by the fifth pleonal plate as in *B. pyriforma*. The article counts of the antennules and antennae of females of *B. liberorum* (five and three, respectively) also differ from those of *B. xiphidiostega*, new species (three and two, respectively). Additionally, whereas *B. xiphidiostega*, new species lacks a maxilliped palp, females of *B. liberorum* have a maxilliped with a small setose palp. *Bopyrissa xiphidiostega*, new species is similar to *B. diogeni* in that females of both species possess a pronounced frontal lamina and a lateral projection on the anterior lobe of oostegite 1; however, females of *B. diogeni* have antennules of three articles each and antennae of one article each, a barbula with one lateral projection (two in *B. xiphidiostega*, new species), a smooth inner ridge on oostegite 1 (digitate in *B. xiphidiostega*, new species) and the projection on the anterior lobe of oostegite 1 is considerably broader and less tapered in B. diogeni than in *B. xiphidiostega*, new species.

Males of *B. diogeni* have antennules and antennae of three articles each, whereas those of *B. xiphidiostega*, new species, have two and three articles each, respectively. Males of *B. pyriforma* have broad, flattened pleopods; however, the pleopods seen in *B. xiphidiostega*, new species are more medially located and not as broad. The pleotelson of *B. pyriforma* has slight posterolateral projections, while those of *B. diogeni* are much larger; there are no such posterolateral projections on the telson in males of *B. xiphidiostega*, new species.

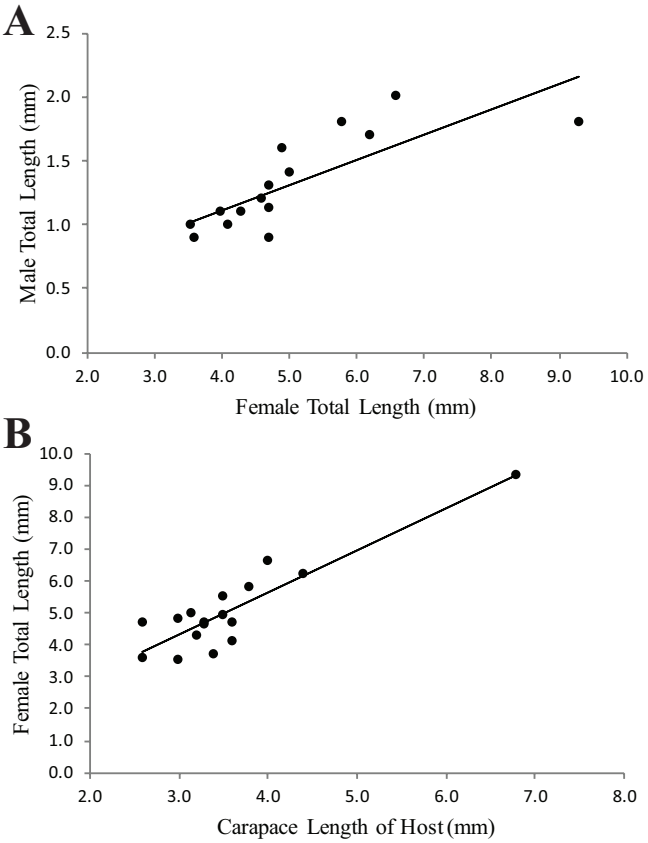

Fig. 15. A, relationship between female total body length and male total body length of *Bopyrissa xiphidiostega*, new species (linear regression: $y = 0.198x + 0.325$; $R^2 = 0.628$; df = 13; $P < 0.0004$); B, relationship between hermit crab host carapace length and female total body length of *Bopyrissa xiphidiostega*, new species (linear regression: $y = 1.322x + 0.330$; $R^2 = 0.809$; df = 15; $P < 0.0001$).

Ecology. Prevalence of *Bopyrissa xiphidiostega*, new species over the eight collections of hermit crabs in which the parasite was found ranged from 0.5–7.7% (mean prevalence=2.06 ± 2.52 %, n=1,077 total hermits examined). *Bopyrissa xiphidiostega*, new species parasitised three host species: *Calcinus gaimardii*, *C. minutus*, and *Dardanus lagopodes* in the Philippines (Table 1). One of the *D. lagopodes* was doubly infested with *B. xiphidiostega*, new species (in the left brachial chamber) and *Asymmetrione harmoniae*, new species (in the right brachial chamber). One of the *C. minutus* was doubly infested with *B. xiphidiostega*, new species and the abdominal parasitic isopod *Parathelges aniculi* (Whitelegge, 1897) (USNM 1283393; see Williams & Boyko, 2016). Two of eighteen (11.1%) female *B. xiphidiostega*, new species were found with cryptoniscus larvae of an unidentified cabiropid species and one female *B. xiphidiostega*, new species was found with an unidentified, epicaridean cryptoniscus larva. Extensions on the cuticle that we interpret as thalli of an unidentified protistan belonging to Mesomycetozoa were found on some pereomeres of males (Fig. 14A) [similar to those reported in Williams & Madad (2010)].

The mean total body length of female *B. xiphidiostega*, new species was 5.0 ± 1.4 (n=18); male *B. xiphidiostega*, new species mean total body length was 1.3 ± 0.4 (n=15). The relationship between female total body length and male total body length was significantly positively correlated

(P<0.0004) (Fig. 15A). *Bopyrissa xiphidiostega*, new species was found to be ovigerous in all months sampled (December through March, June, July, and August) and thus likely breeds throughout the year. Of the 19 mature female *B. xiphidiostega*, new species collected, 56% were ovigerous; the smallest ovigerous female was 4.0 mm. The total body length of female *B. xiphidiostega*, new species and host hermit crabs (as estimated by carapace length) was significantly positively correlated (P<0.0001) (Fig. 15B).

Variation. Female specimens conform to the typical *Bopyrissa morphology*, with the characteristic S-shaped body and five pairs of biramous pleopods and uniramous uropods; all but one individual of *Bopyrissa xiphidiostega*, new species were sinistrally distorted. Female specimens exhibited varying degrees of digitation of the inner ridge of oostegite 1, with some specimens showing pronounced digitation across the entire inner ridge whereas others showed weak digitation towards the base of oostegite 1 or no digitation at all. All female specimens had a simple, digitiform barbula varying in length, although one had several short medial protuberances. Both the pleopods and oostegites of female specimens showed tuberculation, although the tubercles were reduced in some specimens.

Eremitione Williams & Boyko, new genus

Diagnosis. Female body elongate, curved dextrally or sinistrally (straight in *E. tuberculata*, new combination); all segments distinct. Frontal lamina weakly developed, smooth. Barbula with either two lateral projections (outer more than twice as long as inner) or single elongate projection on each side meeting medially; medial region smooth or with numerous low lobes. Maxilliped with single palp, setae on projecting tip (if present). First oostegites with tapered to sharply recurved posterolateral points; internal ridge smooth or with few low projections. Coxal plates weakly developed on pereomeres 1–4 on at least one side; tergal projections not present; pereomeres 2 and 3 subequal in breadth, broader than 4; lateral margins of pereomeres 1–4 rounded, 5 and 6 tapered or rounded and resembling pleomeres; gradual transition in shape between pereomeres 1–6, 1–4 not abruptly different than 5 and 6. Pereopods with short carpi, scales on outer surface of meri, and inflated, scale-covered, dorsal surfaces of bases. Six pleomeres, first five produced into weakly developed lateral plates (greatly developed lateral plates in *E. tuberculata*, new combination), directed posterolaterally; sixth pleomere visible in dorsal view; overall pleon much narrower than pereon (except in *E. tuberculata*, new combination where they are not markedly narrower); five pairs of biramous, lanceolate pleopods, edges and surfaces relatively smooth (tuberculate in *E. tuberculata*, new combination); uropods lanceolate, uniramous, edges and surfaces smooth (tuberculate in *E. tuberculata*, new combination).

Male body gradually tapered anteriorly and posteriorly from widest pereomere; all body regions distinct. Anterior pereopods not markedly larger than others. Pleon of six distinct pleomeres; pleopods uniramous, tuberculiform; posterolateral margins of pleotelson slightly to strongly produced into posterolateral lobes (no posterolateral lobes in *E. tuberculata*, new combination); no uropods. Worldwide distribution in temperate and tropical waters, infesting hosts in Lithodidae and Paguroidea.

Remarks. Eighty-eight species and subspecies have been described or placed in *Pseudione* Kossmann, 1881, at one time or another; some were transferred to other genera and some were synonymised so that 53 species remained in the genus until recently (Boyko et al., 2017). These 53 taxa are a morphologically heterogeneous assemblage, with the number of pairs of pleopods being essentially the only unifying feature (females with five pairs of biramous pleopods; males with five pairs of ovate tuberculiform uniramous pleopods). Based on a study of those species of *Pseudione* found parasitising mud shrimp, ghost shrimp and lobsters, Boyko et al. (2017) defined *Pseudione* on the basis of the characters of its type species, *P. callianassae* Kossmann, 1881, and restricted the genus to contain only the seven other species which shared numerous characters with the type species and whose characters were not present in the other 45 species of *Pseudione sensu lato*. Two species were placed in a new genus (*Robinione* Boyko, Williams & Shields, 2017), *P. compressa* Shiino, 1964, was transferred to *Ionella* Bonnier, 1900, and *P. panopei* Pearse, 1947, was synonymised with *Progebiophilus upogebiae* (Hay, 1917) (Boyko et al., 2017). This left 41 species in *Pseudione sensu lato* not congeneric with the type species of *Pseudione*. In the present study, we made a detailed examination of the descriptions and illustrations of all those species of *Pseudione sensu lato* found parasitising hermit and king crabs. Nine of these previously described species appear to form a monophyletic grouping that is distinct from *Pseudione sensu stricto* and to which none of the other *Pseudione sensu lato* species found on other hosts (e.g., galatheoids, carideans) belong. Therefore, we propose a new genus to contain the species parasitising paguroid and lithodid hosts: *Eremitione* Williams & Boyko. We also provisionally place *Pseudione brandoi* Brian & Darteville, 1941, in *Eremitione*, new genus, based on the type host, even though the species was described solely from what appears to be a juvenile female and is in need of rediscovery and redescription.

Species of *Eremitione*, new genus can be distinguished from those of *Pseudione sensu stricto* (see Boyko et al., 2017) by the following characters of females: barbula of female with two lateral projections or single elongate projection on each side meeting medially (single pair of short, smooth lateral projections in species of *Pseudione s.s.*), maxilliped with single palp (usually with dual palp in species of *Pseudione s.s.*), setae on projecting tip of palp (both lobes of palp setose on distal margins in species of *Pseudione s.s.*), first oostegites with tapered to sharply recurved posterolateral point (with tapered posterolateral point in species of *Pseudione s.s.*), internal ridge of oostegites smooth or with few low projections (internal ridge with few low projections in species of *Pseudione s.s.*), coxal plates weakly developed on pereomeres 1–4 on at least one side (coxal plates moderately developed on pereomeres 1–4 on

at least one side in species of *Pseudione s.s.*), six pleomeres, first five produced into weakly developed lateral plates, except in *E. tuberculata*, new combination where the lateral plates are large but rounded (moderately to greatly developed tapered lateral plates in species of *Pseudione s.s.*), overall pleon much narrower than pereon, except in *E. tuberculata*, new combination (overall pleon as wide as or wider than pereon in species of *Pseudione s.s.*), and uropods lanceolate, uniramous (uniramous or biramous in species of *Pseudione s.s.*). Males are difficult to distinguish morphologically but in *Eremitione*, new genus males invariably have a pleon with six distinct pleomeres, whereas those of *Pseudione s.s.* usually have all pleomeres distinct but the last two or three fused in some species. *Eremitione*, new genus infests hosts in Lithodidae and Paguroidea whereas species of *Pseudione s.s.* infest hosts in Axiidea and Astacidea (Nephropidea).

Species of *Eremitione*, new genus can be distinguished from those of *Bopyrissa* by the following characters: body straight (*E. tuberculata*, new combination) or curved dextrally or sinistrally (S-shaped in species of *Bopyrissa*), sixth pleomere visible in dorsal view (sixth pleomere ventrally displaced and concealed by medially adpressed lateral plates of fifth pleomere in species of *Bopyrissa*).

Eremitone tuberculata, new combination has several differences from those of "typical" *Eremitione*, new genus: the body of the female is linear (curved dextrally or sinistrally in other species of *Eremitione*, new genus), the dorsolateral bosses on pereomeres 5–7 are greatly inflated and anterior ones overhanging posterior ones (not inflated, not overlapping in other species of *Eremitione*, new genus), the surfaces of the oostegites and pleopods are tuberculate (smooth in other species of *Eremitione*, new genus), the length of the pleon is ca. 40% of total body length (length of pleon <33% of total body length in other species of *Eremitione*, new genus), the lateral plates are much wider than the medial region of the pleomeres (lateral plates at most slightly expanded at distal margins compared to medial region of pleomeres in other species of *Eremitione*, new genus), and the male pleotelson is globular with no posterolateral extentions (posterolateral extentions in most other species of *Eremitione*, new genus, although some specimens of *E. hyndmanni*, new combination have been reported with essentially no posterolateral pleotelson extensions). However, all these differences, with the exception of the presence of tubercles, are differences of gradation in character. For example, the strong expansion of the dorsolateral bosses and lateral plates in the females of *E. tuberculata*, new combination is an expansion of structures that are present in all other species of *Eremitione*, new genus. We prefer to adopt the conservative position that *E. tuberculata*, new combination is a derived species of *Eremitione*, new genus, with morphological adaptations to its lithodid hosts (see Miranda-Vargas & Roccatagliata, 2004), especially in terms of what we interpret as secondarily-derived symmetry. It should be noted that some controversy on the evolutionary relationships of lithodoids and paguroids remain, although a "hermit to king" transition has been supported in multiple molecular analyses (see Morrison et al., 2002; Bracken-Grissom et al., 2013; Noever & Glenner, 2018; Hall & Thatje, 2018). Importantly, parasites such as bopyrids and rhizocephalans could be used as independent lines of evidence to test hypotheses on the evolutionary relationships of these anomurans (e.g., Boyko & Williams, 2009; Noever, 2017). Thus, *E. tuberculata*, new combination provides an opportunity to test (via molecular data) the hypothesis that lithodoids evolved from a hermit crab ancestor using coevolutionary studies. Alternatively, *E. tuberculata*, new combination may be found as a distinct lineage and require erection of a new genus.

Type species. *Phryxus hyndmanni* Bate & Westwood, 1867.

Type locality. Groomsport, Ireland; type host: *Pagurus* sp.

Other included species. *Pseudione biacuta* Bourdon, 1979 (type locality: 34°31′S, 53°43′W, Uruguay, 25 m depth; type host: *Paguristes robustus* Forest & de Saint Laurent, 1968); ***Pseudione brandoi* Brian & Darteville, 1941** (type locality: Landana, Angola; type host: *Clibanarius* sp. = *C. africanus* Aurivillius, 1898 *fide* Forest, 1958); ***Pseudione calcinii* Shiino, 1958** (type locality: Japan; type host: *Calcinus latens* [Randall, 1840]); ***Pseudione clibanaricola* Shiino, 1933** (type locality: Tanabe Bay, Japan; type host: *Clibanarius bimaculatus* [De Haan, 1849]); ***Pseudione giardi* Calman, 1898** (type locality: Puget Sound, Washington State, U.S.A.; type host: *Pagurus ochotensis* Brandt, 1851); ***Pseudione nobilii* Nierstrasz & Brender à Brandis, 1923** (type locality: 07°15′S, 115°15′.6′E, 289 m depth; type host: *Trizocheles spinosus* [Henderson, 1888]); ***Pseudione quasimodo* Boyko & Williams, 2004** (type locality: Andros Island, Bahamas, 24°50′47.4″N, 77°53′16.3″W, 2.1 m depth; type host: *Paguristes grayi* Benedict, 1901); ***Pseudione tuberculata* Richardson, 1904** (type locality: Port Ortway [*sic*] (= Port Otway), Patagonia (Chile), 1,050 fathoms (= 1,920.2 m); type host: *Neolithodes diomedeae* [Benedict, 1895]).

Etymology. The genus name is a combination of the generic names *Eremita* Osbeck, 1765, which, although suppressed for the purposes of the Principle of Priority (ICZN, 1990), is the oldest generic name given to a hermit crab (Morgan & Holthuis, 1988) and whose English equivalent is "hermit" and *Ione* Latreille, 1818, commonly used as a suffix for bopyrid genera. This combination of names reflects the specificity of these bopyrids on paguroid and lithodid hosts. The gender is feminine.

Key to females of *Pseudione sensu lato* from hosts in Axiioidea, Gebiidea, Nephropoidea, Paguroidea, and Lithodidae

1. Pereomere 2 narrower than 3, 3 slightly narrower or subequal to 4; lateral plates elongate, tapering..... .....*Pseudione sensu stricto* (on Axiioidea, Gebiidea, Nephropoidea)
– Pereomere 2 and 3 subequal in width, 3 wider than 4; lateral plates rounded, weakly to strongly produced..... .....*Eremitione*, new genus (on Lithodidae, Paguroidea)

Key to species of *Eremitione*, new genus, based on females
[*E. brandoi* (Brian & Darteville, 1941) not included because only juvenile female described]

1. Oostegites 2–4 and at least first pairs of pleopods tuberculate .....*E. tuberculata* (Richardson, 1904), new combination
– Oostegites and pleopods smooth 2
2. Oostegite 1 posterior lobe recurved.....3
– Oostegite 1 posterior lobe triangular 6
3. Pleopods extending well beyond lateral plates ....*E. nobilii* (Nierstrasz & Brender à Brandis, 1923), new combination
– Pleopods not or scarcely extending beyond lateral plates 4
4. Lateral lobes of barbula overlapping at medial region .... *E. giardi* (Calman, 1898), new combination
– Lateral lobes of barbula not overlapping at medial region....5
5. Body with pronounced S-shape ..... *E. clibanaricola* (Shiino, 1933), new combination
– Body weakly S-shaped..... ..*E. hyndmanni* (Bate & Westwood, 1867), new combination
6. Oostegite 1 posterior lobe longer than anterior lobe ....*E. biacuta* (Bourdon, 1979), new combination
– Oostegite 1 posterior lobe shorter than anterior lobe 7
7. Lateral plates of pleomere five overlapping much of uropods; maxilliped palp slender, extended ....*E. calcinii* (Shiino, 1958), new combination
– Lateral plates of pleomere five not overlapping much of uropods; maxilliped palp stout, not extended..... .*E. quasimodo* (Boyko & Williams, 2004), new combination

Key to species of *Eremitione*, new genus, based on males
[*E. brandoi* (Brian & Darteville, 1941), new combination and *E. calcinii* (Shiino, 1958), new combination not included because males are unknown]

1. Posterolateral lobes of pleotelson absent.....2
– Posterolateral lobes of pleotelson present 4
2. Margins of pereomeres 1–4 directed anteriorly; head laterally expanded..... .....*E. nobilii* (Nierstrasz & Brender à Brandis, 1923), new combination
– Margins of pereomeres 1–4 rounded; head subcircular.....3
3. Head fused with pereomere 1 ....*E. hyndmanni* (Bate & Westwood, 1867), new combination
– Head separate from pereomere 1..... .....*E. tuberculata* (Richardson, 1904), new combination
4. Posterolateral lobes of pleotelson as long as remainder of pleotelson; posterolateral margins of all pleomeres directed laterally ..... *E. quasimodo* (Boyko & Williams, 2004), new combination
– Posterolateral lobes of pleotelson short; posterolateral margins of all pleomeres directed posteriorly 5
5. Pleotelson not overlapped laterally by pleomere 5 .... *E. giardi* (Calman, 1898), new combination
– Pleotelson overlapped laterally by pleomere 5 6
6. Pleomere 1 much wider than head .... *E. clibanaricola* (Shiino, 1933), new combination
– Pleomere 1 approximately same width as head..... .....*E. biacuta* (Bourdon, 1979), new combination

Eremitione calcinii (Shiino, 1958), new combination
(Fig. 16A–E)

Pseudione calcinii Shiino, 1958: 36–37, fig. 4 [Seto, Japan; infesting *Calcinus latens* (Randall, 1840)]; Danforth, 1971: 101 (mention); Shiino, 1972: 7 (list); Saito et al., 2000: 37 (list); Markham, 2003: 72 (list); Boyko & Williams, 2004: 364–365 (mention); Williams & Schuerlein, 2005: 106 (mention); Madad, 2008: 5, 19, 44, 51, 82, 83, fig. fig. 7G (reexamination of holotype); McDermott et al., 2010: 9 (list); Williams & Boyko, 2016: 35 (list).

Material examined. Japan: 1 sinistral mature holotype ♀ (2.3 mm) (NSMT-Cr 14473) from left branchial chamber of *Calcinus latens* (host not in jar), Seto, Japan, coll. S. M. Shiino.

Type locality. Shiino (1958) did not state where in Japan the specimen was collected but the original data label clearly states that it was collected in Seto.

Distribution. Seto, Japan.

Host. *Calcinus latens* (Randall, 1840).

Remarks. *Eremitione calcinii*, new combination is known only from the holotype female (NSMT-Cr 14473), examination which allowed us to confirm all of the characters described by Shiino (1958), e.g., the shape of oostegite 1 (Fig. 16E). We were also able to add to the description of the species by describing and illustrating the few important parts that Shiino (1958) omitted from his description: Antennules of 2 articles each; antennae of 3 articles each, basal articles of antennae fused with each other (Fig. 16A); barbula with 2 smooth, distally rounded lateral lobes, lateralmost lobe more than two times as large as medial lobe, medial region smooth (Fig. 16B); pereopods subequal in shape and size (Fig. 16C, D).

Eremitione clibanaricola (Shiino, 1933), new combination
(Figs. 16F–J, 17)

Pseudione clibanaricola Shiino, 1933: 265–268, fig. 6 [Tanabe Bay, Japan; infesting *Clibanarius bimaculatus* (De Haan, 1849)]; Dollfus *in* Neveu-Lemaire et al., 1934: 74 [list]; Shiino, 1952: 35, 42 [mention]; Codreanu & Codreanu, 1963: 285 [mention]; Bourdon, 1968: 314 [mention]; Shiino, 1972: 7 [list]; Harada, 1991: 202 [type specimen data]; Trilles, 1999: 326 [mention]; Saito et al., 2000: 37 [list]; Williams & Schuerlein, 2005: 106 [mention]; Markham, 2003: 72 [list]; Boyko & Williams, 2004: 364, 365, 383 [mention]; Saito & Kinoshita, 2004 [list]; Madad, 2008: 2, 4–6, 19, 35–37, 43–46, 48, 49, 51, 62, 63, 82, 83, fig. 7A–E [Philippines; infesting *Calcinus gaimardii* (H. Milne Edwards, 1848) and *C. minutus* Buitendijk, 1937]; McDermott et al., 2010: 9 [list].
Ps. clibanaricola, Carayon, 1943: 44 [mention].
Pseudione clibanarticola [*sic*] Danforth, 1963: 11 [list].

Material examined. Japan: sinistral ♀ lectotype (3.1 mm), 6 sinistral ♀ paralectotypes (2.9–4.3 mm), 1 ♂ paralectotype (0.6 mm) (SMBL Type #42), all infesting left branchial chambers of *Clibanarius bimaculatus* (sexes and sizes unknown), coll. S. M. Shiino, Tanabe Bay; Philippines: 1 sinistral ovigerous ♀ (3.0 mm), 1 ♂ (0.9 mm; lost) (USNM 1493999) from left branchial chamber of ♂ *Calcinus gaimardii* (2.9 mm SL), host also infested with *Bopyrissa*

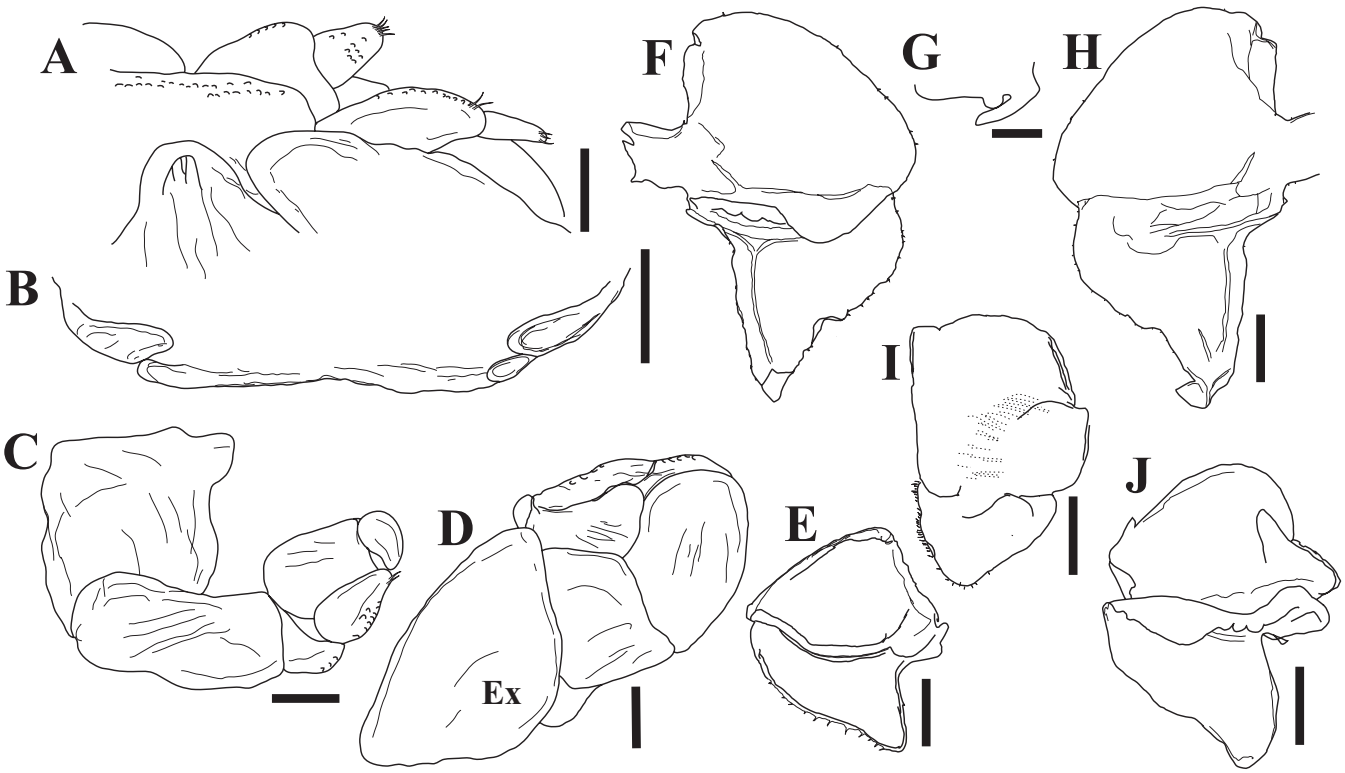

Fig. 16. *Eremitione calcinii* (Shiino, 1958), new combination, female, NSMT-Cr 14473 (A–E), *Eremitione clibanaricola* (Shiino, 1933), new combination, female, USNM 1494004 (F–I), SMBL Type No. 42 (J). A, left antennule and antenna; B, barbula; C, left pereopod 1; D, right pereopod 7 with first pleopodal exopod (Ex); E, oostegite 1, internal view; F, oostegite 1, internal view; G, barbula, left side; H, oostegite 1, external view; I, left maxilliped, external view; J, oostegite, internal view. Scale bars = 100 µm (A, C, D, E); 50 µm (B); 250 µm (F–J).

marami, new species (USNM 1493934) from right branchial chamber, Puerto Galera, Coco Beach, coll. JDW, 12-15 January 1999; 1 sinistral ovigerous ♀ (4.9 mm), 1 ♂ (0.9 mm) (USNM 1494000) from left branchial chamber of ♀ *C. gaimardii* (3.2 mm SL) Puerto Galera, Coco Beach, coll. JDW, 12-15 January 1999; 1 sinistral ovigerous ♀ (4.3 mm), 1 ♂ (1.4 mm) (USNM 1494001) from left branchial chamber of ♀ *Calcinus minutus* (3.1 mm SL), Batangas, Anilao, coll. JDW, 13 February 1999; 1 sinistral ovigerous ♀ (4.2 mm), 1 ♂ (0.9 mm) (USNM 1494002) from left branchial chamber of ♂ *C. gaimardii* (2.6 mm SL), Puerto Galera, Big Lalaguna Beach, coll. JDW, 28 March 1999; 1 sinistral ovigerous ♀ (3.5 mm), 1 ♂ (0.8 mm) (USNM 1494003) from left branchial chamber of ♀ *C. gaimardii* (2.1 mm SL), Bataan, Morong, coll. JDW, 25 April 1999; 1 ovigerous ♀ (4.5 mm), 1 ♂ (1.1 mm) (USNM 1494004) from left branchial chamber of ♂ *C. gaimardii* (3.0 mm SL), Puerto Galera, Agus Beach, coll. JDW, 18 June 2000.

Type locality. Tanabe Bay, Japan (Shiino, 1933).

Distribution. Tanabe Bay, Japan (Shiino, 1933); Puerto Galera, Bataan, and Batangas, Philippines (Madad, 2008; herein).

Hosts. *Calcinus gaimardii* (H. Milne Edwards, 1848) (Madad, 2008; herein), *C. minutus* Buitendijk, 1937 (Madad, 2008; herein); *Clibanarius bimaculatus* (De Haan, 1849) (Shiino, 1933).

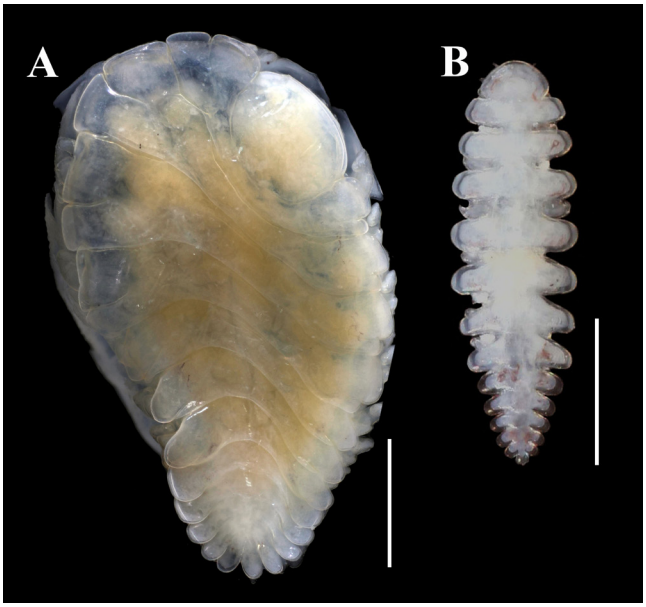

Fig. 17. *Eremitione clibanaricola* (Shiino, 1933), new combination, USNM 1494001. A, female, dorsal view; B, male, dorsal view. Scale bars = 1.0 mm (A); 500 µm (B).

Size range (length). Females to 5.3 mm, males to 1.5 mm (Shiino, 1933). Mean length of Philippine female specimens was 4.21 ± 0.68 mm and mean maximal width was 2.37 ± 0.42 mm (n=6). Mean length of Philippine male specimens was 1.16 ± 0.25 mm and mean maximal width was 0.46 ± 0.04 mm (n=6).

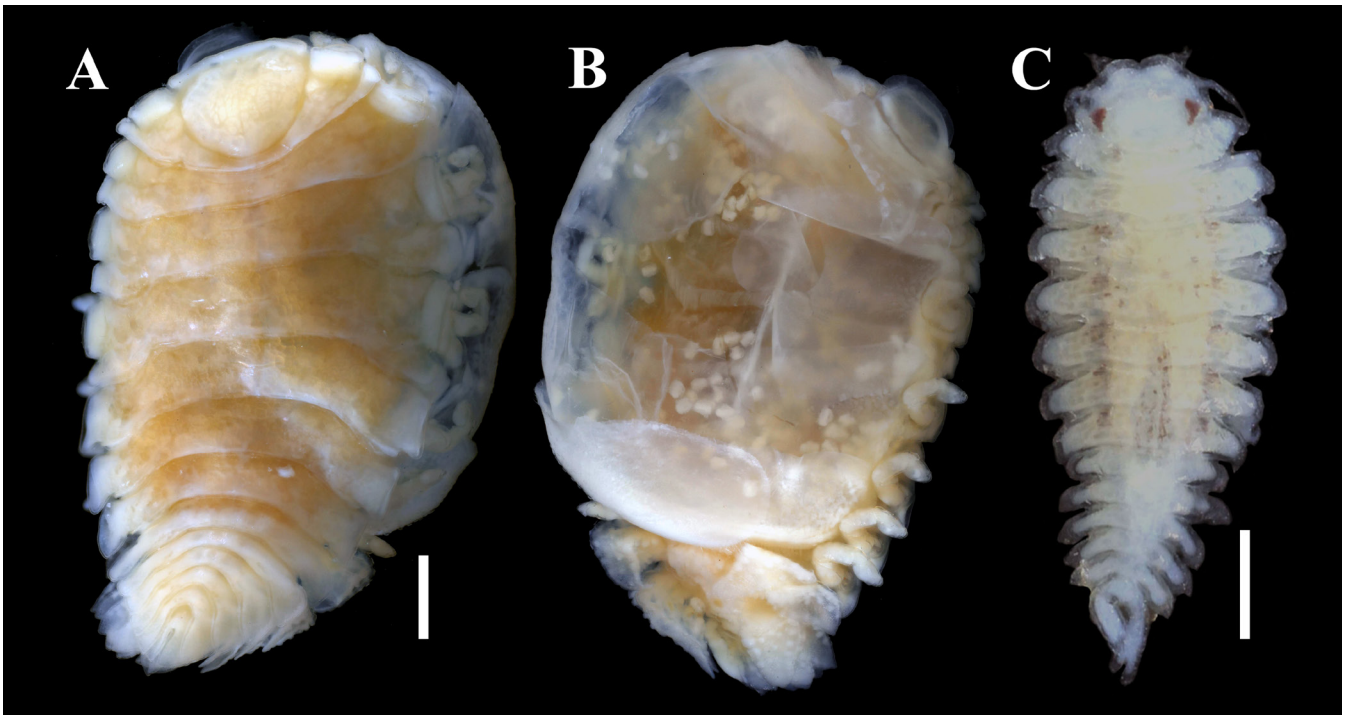

Fig. 18. *Pagurion tuberculata* Shiino, 1933, mature female, USNM 1494006 (A, B), juvenile female, USNM 1494005 (C). A, female, dorsal view; B, female, ventral view; C, juvenile female, dorsal view. Scale bars = 1 mm (A, B); 250µm (C).

Remarks. *Eremitione clibanaricola*, new combination has not been reported subsequent to Shiino's (1933) original description. One of the female specimens in the type series (SMBL Type #42) is labeled as the lectotype but such a designation was never published by any author; we formally select this specimen as the lectotype herein. Shiino (1933) noted that one of the more important characteristics of this species is the marked asymmetry of the female. Reduced development of the frontal lamina as well as reduction in the coxal plates are also characteristics that distinguish females of *E. clibanaricola*, new combination from congeneric species (Fig. 17A). Females of this species examined in the current study had very short antennae, which did not extend past the margin of their heads. The inner ridge of oostegite 1 of nearly all female specimens had slight digitation, often close to the base of attachment (Fig. 16F, H), which differs from Shiino's (1933) original description. However, examination of the types of *Pseudione clibanaricola* confirmed the presence of slight digitation (Fig. 16J) and this character was merely overlooked by Shiino. All female specimens, including the types, lack a palp on the maxilliped (Fig. 16I) and have a barbula represented by a single large lateral digitiform extension and a medial low rounded nub (Fig. 16G), which is consistent with the original description, although Shiino (1933) stated that there were two medial lobes. Uniramous uropods were seen in all of the female specimens examined; however, in certain cases the uropods were proportionally smaller than originally described. Male specimens were consistent with the original description of *Pseudione clibanaricola*, with eyes absent, a suboval head, and rounded, broad pleopods extending from the ventral surface of pleomeres 1–5 (Fig. 17B). One male specimen exhibited coalescing of some pleomeres.

Shiino (1933) reported that *E. clibanaricola*, new combination was found only in the left branchial chamber of its type host, *Clibanarius bimaculatus*, in Tanabe Bay, Japan, and this sinistral distortion is consistent with all specimens examined in the present study. *Asymmetrione asymmetrica* (Shiino, 1933) is known only from the right chamber of *C. bimaculatus*; occasionally this host bears both species of bopyrids simultaneously (Shiino, 1933). This dual-parasitism and apparent resource partitioning is similar to the occurrence noted in this study of *Bopyrissa marami*, new species in the right branchial chamber and *E. clibanaricola*, new combination in the left branchial chamber in one specimen of *Calcinus gaimardii*.

Ecology. Mean prevalence was 1.03 ± 0.40% over the five collections in which the parasite was found (n=742 total hermits examined). In total, six specimens of *Eremitione clibanaricola*, new combination. were extracted from hermit crabs collected in the Philippines, most (83.33%) infesting *C. gaimardii* (Table 1) but one was found on a female *C. minutus*.

***Pagurion* Shiino, 1933**

***Pagurion tuberculata* Shiino, 1933**
(Figs. 18, 19)

Pagurion tuberculata Shiino, 1933: 254–256, fig. 2 [Tanabe Bay, Japan; infesting *Pagurus watasei* Terao, 1913 = *Dardanus aspersus* (Berthold, 1845)]; Shiino, 1952: 41 [mention]; Danforth, 1963: 9 [list]; Shiino, 1972: 7 [list]; Harada, 1991: 201 [list]; Saito et al., 2000: 36 [list]; Markham, 2003: 72 [list]; Madad, 2008: 2, 5, 6, 17, 33–34, 46, 48, 51, 86, 87, fig. 9 [Batangas, Philippines; infesting *Dardanus lagopodes* (Forskål, 1775)]; Yu & An, 2008: 692 [list]; Markham, 2010: 151, 152,

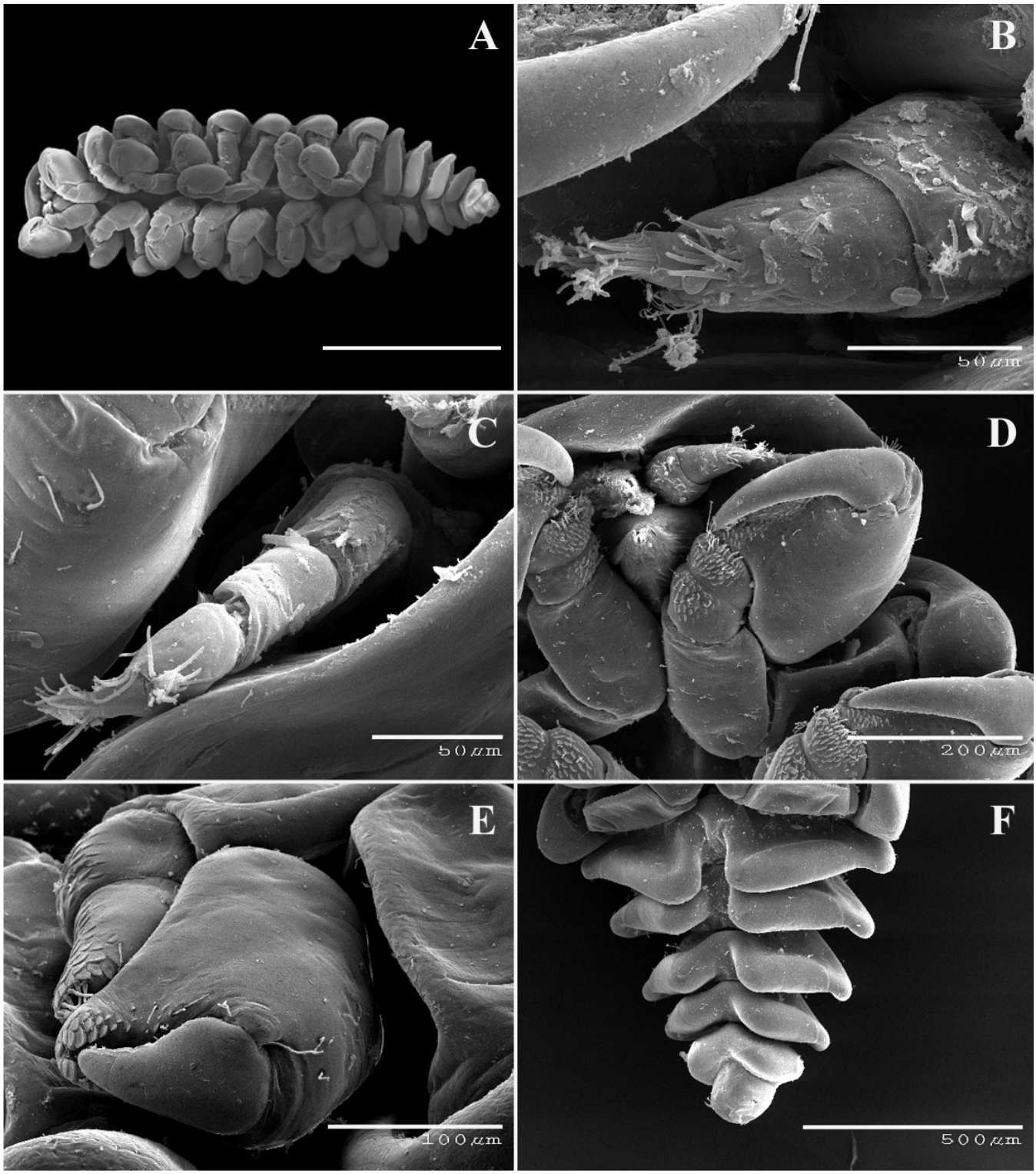

Fig. 19. *Pagurion tuberculata* Shiino, 1933, male, USNM 1494006 (A–F). A, ventral overview; B, right antennule; C, right antenna; D, right pereopods 1 and 2; E, right pereopod 7; F, pleopods. Scale bars = 500 µm (A, F); 50 µm (B, C); 200 µm (D); 100 µm (E).

156–158, figs. 6, 7 [Queensland, Australia; infesting *Dardanus arrosor* (Herbst, 1796), *D. hessii* (Miers, 1884)]; McDermott et al., 2010: 8 [list]; An et al., 2013: 561–563, fig. 1 [South China Sea; infesting *D. aspersus*]; An et al., 2016: 45 [list]; Williams & Boyko, 2016: 36 [list].

Pagurion tuberculatum [*sic*] Dollfus *in* Neveu-Lemaire et al., 1934: 74 [list].

Pagurion arrosor An, Li & Markham, 2013: 561, 563–564, fig. 2 [South China Sea, Stn. 6238, 20°00′N, 108°00′E, 83 m; infesting *D. arrosor*]; **new synonymy.**

Material examined. Philippines: 1 juvenile ♀ (1.4 mm) (USNM 1494005) from right branchial chamber of juvenile ♂ *Dardanus* sp. (1.3 mm SL), Batangas, Anilao, coll. JDW, 13 February 1999; 1 dextral ♀ (7.7 mm), 1 mature ♂ (3.00 mm) (USNM 1494006, ♂ on SEM stub) from right branchial chamber of ♀ *Dardanus lagopodes* (4.5 mm SL), Batangas, Sombrero Island, coll. JDW, 10 June 2000. Indonesia: 1 ovigerous sinistral ♀ (13.7 mm), 1 mature ♂ (3.6 mm, lost) (ZRC 2018.0829), from left branchial chamber of *Dardanus*

megistos (Herbst, 1804) (10.2 mm SL), East Lombok, Ekas, coll. 23 July 2009.

Type locality. Tanabe Bay, Japan (Shiino, 1933).

Distribution. Tanabe Bay, Japan (Shiino, 1933); Batangas, Philippines (Madad, 2008; herein), South China Sea (An et al., 2013); Queensland, Australia (Markham, 2010).

Hosts. Diogenidae. *Dardanus arrosor* (Herbst, 1796) (Markham, 2010; An et al., 2013); *D. aspersus* (Berthold, 1845) (Shiino, 1933; An et al., 2013); *D. hessii* (Miers, 1884) (Markham, 2010); *D. lagopodes* (Forskål, 1775) (Madad, 2008; herein), *D. megistos* (Herbst, 1804) (herein).

Size range (length). Females to 14.0 mm, males to 4.5 mm (Shiino, 1933).

Remarks. The mature females of *Pagurion tuberculata* examined (Fig. 18A, B) do not differ from the original type material as described by Shiino (1933) or the subsequent records of Markham (2010) and An et al. (2013). The female has five pairs of biramous pleopods, the barbula has a series of lateral projections, the inner ridge of oostegite 1 is digitate and the uropods are biramous, which are all consistent with the diagnosis provided by Shiino (1933). The Philippine male of *P. tuberculata* (Figs. 18C, 19A) exhibits the same article counts for the antennae, 3 antennular and 4 antennal (Fig. 19B, C), as described by Shiino (1933). An et al. (2013), however, illustrated 3 antennular and 5 antennal articles for this species. The original description of *P. tuberculata* did not include a detailed description of the pereopods of males (Fig. 19D, E) but their character states (first two pairs larger than others, though not markedly so) was mentioned by Markham (2010) and An et al. (2013). Markham (2010) stated that his female specimens had 2 pairs of coxal plates, not 4 as in the original description, but from his illustrations it appears that he mixed up the counts for dorsolateral bosses and coxal plates because his illustrated specimen has 2 dorsolateral bosses on each side and 4 coxal plates. Males have 5 pairs of broad pleopods (Fig. 19F); Markham (2010) noted that his male had 5 pairs of pleopods and Shiino (1933) stated there were also 5 pairs but that the posterior 2 pairs were "rather inconspicuous."

The genus *Pagurion* Shiino, 1933, monotypic until recently, is composed of *P. tuberculata* and *P. arrosor* An, Li & Markham, 2013. Genus-defining characteristics of the females include having the cephalon separated from the thorax, distinct thoracic segments, rudimentary coxal plates present on the first four segments, oostegites forming a complete marsupium with no medial gaps, distinct abdominal segments (*P. tuberculata* with a distinctly visible pleotelson, *P. arrosor* with an obscure pleotelson), lamellar lateral plates in all six segments, and five pairs of biramous pleopods as well as biramous uropods (Shiino, 1933; An et al., 2013). Males of *Pagurion* exhibit a head separated from the thorax, distinct thoracic and abdominal segments (although one specimen of *P. tuberculata* was reported with fusion between the last two pleomeres, as was the allotype of *P. arrosor*; see Markham, 2010; An et al., 2013), and uniramous tuberculate pleopods and no uropods (Shiino, 1933).

The status of *P. arrosor* as a distinct species is not supported by the evidence. An et al. (2013) stated that the differences between *P. arrosor* and *P. tuberculata* were: females lacking frontal laminae (present in *P. tuberculata*), antennae "1 and 2" (antennules and antennae) of 4 and 5 articles each, respectively (3 and 4 articles in *P. tuberculata*), pleomere 6 (pleotelson) "obscure" = dorsally not visible (the female has 6 pleomeres, but the pleotelson is covered by the fifth pleomere lateral plates) ("distinct" = dorsally visible in *P. tuberculata*), males with last two pleomeres somewhat fused (separate in *P. tuberculata*). However, most of these purported differences do not hold up under scrutiny. *Pagurion arrosor* was illustrated by An et al. (2013) with a small but present frontal lamina, contradicting the text description. An et al. (2013) also reported a female of *P. tuberculata* with 3 antennular and 5 antennal articles, not the 3 and 4 articles they indicate to be the character state for *P. tuberculata* in their comparison with *P. arrosor*, indicating that the antennal counts are variable in the species. Markham (2010) illustrated a female of *P. tuberculata* from *Dardanus arrosor* as having both pleomeres 5 and 6 "obscure" (i.e., obscured by the fourth pleomere) and the male having the last two pleomeres partially fused. These characters were used by An et al. (2013) to define, in part, *P. arrosor*; however, they included Markham's (2010) specimens as a valid record of *P. tuberculata* rather than *P. arrosor* without explanation. An et al. (2013) stated in the abstract that characters of the barbula and pleopods of the female also distinguished *P. arrosor* from *P. tuberculata*, but they did not state what these differences were, nor did they mention them in the body of the text. We can see no differences in the pleopod morphology of the females, based on the descriptions and illustrations of Shiino (1933), Markham (2010) and An et al. (2013), as well as the present material. The barbulae of the specimens of *P. tuberculata* reported by An et al. (2013) have little to no digitation in the medial regions, but the barbulae of the syntype female of *P. tuberculata* and the holotype of *P. arrosor* are virtually identical. An et al. (2013) reported the male of *P. arrosor* to have midventral tubercles on the pereomeres; these are also present in our specimens but were not previously reported from *P. tuberculata* males. However, they are small and not easily observed, and may well have been overlooked by Shiino (1933) and others. Based on the above comparison and clear indication of intraspecific variability in some characters of both males and females, we consider *P. arrosor* to be a synonym of *P. tuberculata*.

Markham (2010) gave the type host as "*Dardanus* sp." but the host was identified to species in Shiino (1933), although it was at that time usually considered a synonym of *D. scutellatus* (H. Milne Edwards, 1848) until later synonymised with *D. aspersus* by Osawa (2013). An et al. (2013) were apparently unaware of Osawa's (2013) paper and stated that their record from *D. aspersus* was the first of any bopyrid on that host.

The juvenile hermit crab host reported here (USNM 1494005) appears to also be a *Dardanus* but this is not certain and it is not identifiable to species. Markham (2010) neither described nor illustrated his specimens of *P. tuberculata* from *D. hessi* (Miers, 1884), so it is not known what the character states were for those specimens; An et al. (2013) did not include this host record in their synonymy list. An et al. (2013) incorrectly cited *Calcinus gaimardii* (H. Milne Edwards, 1848) and *Calcinus minutus* Buitendijk, 1937 as hosts of *P. tuberculata* and incorrectly credited these host records as coming from Madad (2008); no such data appears in that thesis. An et al. (2013) also incorrectly ascribed the erroneous combination "*Clibanarius gaimardii*" (= *Calcinus gaimardii*) to Madad (2008); again, no such combination appears in the thesis.

Ecology. Prevalence of parasite occurrence was 1.92% (one of 52) on *Dardanus lagopodes*; 18.9% of the collected hosts were *D. lagopodes* (n=10) and of those, 60% were female (n=6) and 40% were male (n=4).

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