

Abdominal bopyrid parasites (Crustacea: Isopoda: Bopyridae: Athelginae) of diogenid hermit crabs from the western Pacific, with descriptions of a new genus and four new species

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Abstract. Diogenid hermit crabs (Decapoda: Anomura: Diogenidae) from localities in the western Pacific (Philippines, Papua New Guinea, Australia, and Taiwan) were examined for abdominal bopyrid parasites. Over 2000 hermit crabs were collected from various localities in the Philippines between December 1996 and June 2000. Fifty-seven of these crabs harboured abdominal bopyrid parasites, no species of which have ever been previously reported from the Philippines. In addition, samples from expeditions to Papua New Guinea, newly collected material from Taiwan, and museum specimens from Australia were studied. Based on this material, examination of type specimens, and a review of the literature, we report seven species of athelgine bopyrids from eight species of Philippine hermit crabs. Three of these Philippine species are new to science and are described herein: *Allathelges alisonae* n. sp., *Falsanathelges mariae* n. sp., and *Pseudostegias trisagitta* n. sp. *Parathelges aniculi* (Whitelegge, 1897) (synonyms: *P. whiteleggei* Nierstrasz & Brender à Brandis, 1931 and *P. weberi* Nierstrasz & Brender à Brandis, 1923) is redescribed based on Philippine and Australian material and two male forms are recognised. Characters are provided to distinguish *Pseudostegias setoensis* Shiino, 1933 and *P. dulcilacuum* Markham, 1982. Material from Australian localities yielded *Claustrathelges macdermotti* n. gen., n. sp., from a stone-inhabiting hermit crab, as well as *Athelges ankistron* Markham, 2010, previously known only from the type series. Papua New Guinea specimens were all identified as *Athelges takanoshimensis* Ishii, 1914. Specimens from Taiwan belong to *F. mariae* n. sp., *P. aniculi*, *P. dulcilacuum*, and *P. setoensis*. A revised key to all athelgine bopyrid genera is provided.

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

INTRODUCTION

The parasitic isopod family Bopyridae presently contains nine subfamilies (Boyko & Schotte, 2015), all members of which are obligate parasites of mostly marine but a few freshwater crustaceans throughout the world. Approximately 1/4 of the nearly 800 described bopyrid species are known from areas in the East Asian Sea and Indian Ocean; however, researchers have predicted that areas of the Indo-Malay-Philippines Archipelago contain much undescribed diversity (Markham, 1986; Williams & Boyko, 2012), and this region is known as a center for diversity of many taxa, including potential crustacean hosts for bopyrids (Carpenter & Springer, 2005). Whereas most bopyrids occur in the branchial chamber of hosts, those in three subfamilies, including species in Athelginae, attach to the abdomen of hosts. All athelgines are parasites of anomurans and their impacts on hermit crabs,

as well as their life cycles have been reviewed (McDermott et al., 2010; Cericola & Williams, 2015).

Hermit crabs act as hosts for a wide range of symbionts (Williams & McDermott, 2004), including bopyrid parasites (Markham, 2003; McDermott et al., 2010). As part of ongoing studies on the symbionts of hermit crabs from the Indo-West Pacific (Williams, 2000, 2001a, b, 2002; Williams & Boyko, 1999, 2006; Williams & Schuerlein, 2005; Madad, 2008; Williams & Madad, 2010; Murphy & Williams, 2013; Williams, 2013; Cericola & Williams, 2015), we examined a variety of hermit crab hosts collected intertidally, predominately from coral reef areas of the northern and central Philippines. Prior to this study, only approximately 34 bopyrid species were known from the Philippines (see Williams & Madad, 2010) and only one, *Bopyrophryxus branchiabdormalis* Codreanu, 1965, was known from a hermit crab host, a parapagurid (Bourdon & Boyko, 2005). Additional material from localities in the western Pacific (Papua New Guinea, Australia, and Taiwan) was also examined. Our investigations in this region have led to the discovery of new records and new species in the subfamilies Athelginae and Pseudioninae (branchial parasitic isopods). Specifically, the present study reports on nine athelgine species, including four that are new to science. A separate study (Madad & Williams, in prep.) will focus on the pseudionine species found with these hosts.

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Table 1. List of Philippine localities where hermit crabs were collected intertidally and shallowly subtidal (<5 m depth) between July 1997 to June 2000.

Province	Locality	Lat/Long	Abdominal Bopyrids Present	Branchial Bopyrids Present
Cebu	Olango Island and Sulpa Islet	10°14'15"N, 124°00'29"E	Yes	Yes
Cebu	Mactan Island, Maribago	10°17'04"N, 124°00'05"E	Yes	Yes
Palawan	Apulit Island	10°57'26.37"N, 119°37'00.54"E	No	No
Palawan	Magbautoc Island	10°59'28.25"N, 119°35'25.84"E	No	No
Aklan	Boracay, Rocky Beach	11°57'42"N, 121°55'25"E	Yes	Yes
Aklan	Boracay, White Beach	11°57'51.65"N, 121°55'20.86"E	No	No
Aklan	Boracay, Diniwid Beach	11°58'34"N, 121°54'38"E	Yes	No
Oriental Mindoro	Puerto Galera, Coco Beach	13°31'32"N, 120°57'44"E	Yes	Yes
Oriental Mindoro	Puerto Galera, La Laguna Beach	13°31'32"N, 120°58'08"E	Yes	Yes
Batangas	Sombrero and Sepok Islands	13°41'53"N, 120°49'47"E	Yes	Yes
Batangas	Anilao	13°42'14.5"N, 120°52'45.3"E	Yes	Yes
Bataan	Morong	14°39'53"N, 120°16'28"E	Yes	Yes
Bataan	Mabayo	14°44'00"N, 120°16'32"E	Yes	Yes

MATERIALS AND METHODS

Hermit crabs inhabiting gastropod shells were collected by the first author (JDW) from the intertidal and shallow subtidal zones (<5 m depth) in Philippine localities (Table 1; see Williams, 2002 for map) between July 1997 to June 2000 with three additional specimens collected by Paul Cassidy in November and December 1996. These Philippine specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), the Zoological Reference Collection of the Lee Kong Chian Natural History Museum (formerly the Raffles Museum of Biodiversity Research) (ZRC) and in the collection of the first author (see Material Examined section for each species for details).

Samples were preserved en masse in the field (relaxation in 3% magnesium chloride, fixed in 10% formalin-seawater solution and stored in 70% ethyl alcohol) or examined while live and fixed in 100% ethyl alcohol for future molecular studies. Notes on coloration and behavior were made on live specimens. Hermit crabs were removed from gastropod shells by cracking with a mortar and pestle constructed from a 7.5 cm diameter galvanised steel pipe mortar and 3 cm diameter pestle.

Papua New Guinea and Australia specimens were borrowed from the Museum National d'Histoire Naturelle, Paris (MNHN), and the Museum Victoria, Melbourne, Australia (MV), respectively. The Taiwanese specimens were provided by Ryuta Yoshida and are deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Camera lucida sketches made of specimens were scanned into a Macintosh™ computer. Images were then prepared using the programs Adobe Photoshop™ and Adobe Illustrator™.

Shield length (SL) is provided as an indicator of size for the host crabs. Isopod size is given as total body length (anterior margin of head to posterior margin of pleotelson). Measurements were made to 0.01 mm using an ocular micrometer. Taxonomic authorities of hermit crabs are provided in Table 2.

Additional specimens were borrowed from the Australian Museum (AM), Natural History Museum of Los Angeles County, California (LACM), Naturalis Biodiversity Center (formerly Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands (RMNH), Zoological Museum of Amsterdam (now incorporated into the RMNH collections) (ZMA), and Zoological Museum, University of Copenhagen (ZMUC).

Key to the genera of Athelginae

(Based on females; modified from Boyko & Williams, 2003)

1. Lateral plates present2
 - Lateral plates lacking7
2. Lateral plates on pleomeres I–V3
 - Lateral plates on pleomeres I–III only
 -*Stegias* Richardson, 1904 (3 spp.)
3. Lateral plates on pleomere V similar to other lateral plates on other pleomeres4
 - Lateral plates on pleomere V reduced, globular or scarlike....
 -*Pseudostegias* Shiino, 1933 (8 spp.)
4. Pereopods V and VI separated by wide distance (broad pereomeres)5
 - Pereopods V and VI not separated by wide distance (narrow pereomeres)6
5. Pleopods uniramous
 -*Minimatelges* Boyko & Williams, 2003 (2 spp.)
 - Pleopods biramous*Anatelges* Bonnier, 1900 (4 spp.)
6. Five pleomeres*Claustratelges* n. gen. (1 sp.)
 - Six pleomeres
 -*Falsanatelges* Boyko & Williams, 2003 (2 spp.)

Table 2. List of hermit crab species and localities examined during the present study with bopyrid species found, other localities these bopyrids are known from and other bopyrid species known to occur on these hosts but not found during the present study. N/A = not applicable as hosts were not identified to species.

Hermit Crab Species	Present Locality	Bopyrid Species Found	Other Localities	Other Bopyrid Species	References
<i>Areopaguristes tuberculatus</i> (Whitelegge, 1900)	Australia: Tasmania & Victoria	<i>Parathelges aniculi</i> (Form A male)	none	none	
<i>Aniculus aniculus</i> (Fabricius, 1787)	Tuvalu	<i>Parathelges aniculi</i> (Form unknown male)	none	none	
<i>Calcinus gaimardii</i> (H. Milne Edwards, 1848)	Philippines	<i>Falsanathelges mariae</i> n. sp.; <i>Parathelges aniculi</i> (Form A & B males); <i>Pseudostegias dulcilacuum</i>	none	none	
<i>Calcinus guamensis</i> Wooster, 1984	Taiwan	<i>Falsanathelges mariae</i> n. sp.	none	none	
<i>Calcinus laevimanus</i> (Randall, 1840)	Indonesia	<i>Parathelges aniculi</i> (Form B male)	China; Japan	<i>Pseudostegias setoensis</i> ; <i>Propseudione rhombicosoma</i> Shiino, 1933	An et al., 2011; McDermott et al., 2010
<i>Calcinus latens</i> (Randall, 1840)	Papua New Guinea	<i>Athelges takanoshimensis</i>	Japan	<i>Pseudione calcinii</i> Shiino, 1958	McDermott et al., 2010
	Philippines	<i>Falsanathelges mariae</i> n. sp.; <i>Parathelges aniculi</i> (Form A & B males)	Japan	<i>Pseudione calcinii</i>	McDermott et al., 2010
<i>Calcinus lineapropodus</i> Morgan & Forest, 1991	Indonesia	<i>Parathelges aniculi</i> (Form unknown male)	none	none	
<i>Calcinus minutus</i> Buitendijk, 1937	Philippines	<i>Bopyrissa</i> sp.; <i>Falsanathelges mariae</i> n. sp.; <i>Parathelges aniculi</i> (Form A & B males); <i>Pseudostegias trisagitta</i> n. sp.	none	none	
<i>Calcinus morgani</i> Rahayu & Forest, 1999	Taiwan	<i>Pseudostegias dulcilacuum</i>	Indonesia; Japan	<i>Pseudostegias dulcilacuum</i> ; <i>Propseudione rhombicosoma</i>	McDermott et al., 2010
<i>Calcinus pulcher</i> Forest, 1958	Philippines	<i>Parathelges aniculi</i> (Form B male)	none	none	
<i>Calcinus vachoni</i> Forest, 1958	Taiwan	<i>Parathelges aniculi</i> (Form A male)	none	none	
<i>Cancellus typus</i> H. Milne Edwards, 1836	Australia: Victoria	<i>Claustrathelges macdermotti</i> n. gen., n. sp.	none	none	

Hermit Crab Species	Present Locality	Bopyrid Species Found	Other Localities	Other Bopyrid Species	References
<i>Ciliopagurus strigatus</i> (Herbst, 1804)	Indonesia	<i>Athelges takanoshimensis</i> ; <i>Athelges</i> sp.	none	none	
	Philippines	none	Indonesia	<i>Athelges</i> sp.	McDermott et al., 2010
<i>Clibanarius englaucus</i> Ball & Haig, 1972	Philippines	none	Red Sea	<i>Asymmetrione shiinoi</i> Codreanu, Codreanu & Pike, 1965	McDermott et al., 2010
<i>Clibanarius merguiensis</i> de Man 1888	Philippines	<i>Falsanathelges mariae</i> n. sp.; <i>Pseudostegias dulcilacuum</i>	Thailand	<i>Pseudostegias dulcilacuum</i>	McDermott et al., 2010
<i>Clibanarius virescens</i> (Krauss, 1843)	Taiwan	<i>Pseudostegias setoensis</i>	Hong Kong; Australia: Queensland	<i>Pseudostegias dulcilacuum</i> ; <i>Pseudostegias setoensis</i>	An et al., 2011; herein
<i>Dardanus hessii</i> (Miers, 1884)	Indonesia	<i>Parathelges aniculi</i> (Form A male)	Australia: Queensland	<i>Pagurion tuberculata</i> Shiino, 1933	Markham, 2010
<i>Dardanus lagopodes</i> (Forskål, 1775)	Philippines	<i>Allathelges alisonae</i> n. sp.	none	none	
	Taiwan	<i>Parathelges aniculi</i> (Form unknown male)	none	none	
<i>Dardanus pedunculatus</i> (Herbst, 1804)	Philippines	none	none	none	
<i>Dardanus woodmasoni</i> (Alcock, 1905)	Philippines	<i>Athelges takanoshimensis</i>	none	none	
<i>Diogenes tumidus</i> Rahayu & Forest, 1995	Taiwan	<i>Pseudostegias dulcilacuum</i>	none	none	
<i>Diogenes</i> sp.	Papua New Guinea	<i>Athelges takanoshimensis</i>	N/A	N/A	
<i>Diogenes</i> sp.	Philippines	<i>Parathelges aniculi</i> (Form B male)	N/A	N/A	
<i>Paguristes runyanae</i> Haig & Ball, 1988	Philippines	none	none	none	
<i>Paguristes sulcatus</i> Baker, 1905	Australia: Tasmania & Victoria	<i>Parathelges aniculi</i> (Form A male)	none	none	
	Australia: Queensland	<i>Athelges ankistron</i>	none	none	Markham, 2010
<i>Pseudopaguristes monoporus</i> (Morgan, 1987)	Indonesia	<i>Parathelges aniculi</i> (Form A male)	Japan	<i>Parapagurion calcinicola</i> Shiino, 1933	McDermott et al., 2010

Table 3. List of hermit crab host species parasitised and their abdominal 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. N/A = not applicable; samples were non-quantitative. In addition to those hosts listed in the table, *Ciliopagurus strigatus*, *Clibanarius englaucus*, *Dardanus pedunculatus* and *Paguristes runyanae* were collected in small quantities (<75 specimens) but lacked any bopyrid parasites. *Ciliopagurus strigatus* is known as a host of *Athelges takanoshimensis* in Indonesia (see material examined for that species and Table 2; listed as *Athelges* sp. in McDermott et al., 2010). *Clibanarius englaucus* is not known to bear any abdominal bopyrids, although it does host one branchial species (see Table 2). *Dardanus pedunculatus* and *P. runyanae* are not known to bear any bopyrid species.

Host species	Number examined	Total Parasitized (%)	Parasite species-number (%)
<i>Calcinus gaimardii</i> (H. Milne Edwards, 1848)	994	17 (1.7)	<i>Falsanathelges mariae</i> n. sp. – 3 (0.3) <i>Parathelges aniculi</i> (Form A) – 3 (0.3) <i>Parathelges aniculi</i> (Form B) – 4 (0.4) <i>Pseudostegias dulcilacuum</i> – 7 (0.7)
<i>Calcinus latens</i> (Randall, 1840)	505	11 (2.2)	<i>Falsanathelges mariae</i> n. sp. – 1 (0.2) <i>Parathelges aniculi</i> (Form A) – 5 (1.0) <i>Parathelges aniculi</i> (Form B) – 5 (1.0)
<i>Calcinus minutus</i> Buitendijk, 1937	206	16 (7.8)	<i>Falsanathelges mariae</i> n. sp. – 3 (1.5) <i>Parathelges aniculi</i> (Form A) – 2 (1.0) <i>Parathelges aniculi</i> (Form B) – 10 (4.6) <i>Pseudostegias trisagitta</i> n. sp. – 1 (0.5)
<i>Calcinus pulcher</i> Forest, 1958	32	1 (3.1)	<i>Parathelges aniculi</i> (Form B) – 1 (3.1)
<i>Clibanarius merguensis</i> de Man 1888	N/A*	8	<i>Falsanathelges mariae</i> n. sp. – 2 <i>Pseudostegias dulcilacuum</i> – 6
<i>Dardanus lagopodes</i> (Forskål, 1775)	123	2 (1.6)	<i>Allathelges alisonae</i> n. sp. – 2 (1.6)
<i>Dardanus woodmasoni</i> (Alcock, 1905)	N/A	1	<i>Athelges takanoshimensis</i> – 1
<i>Diogenes</i> sp.	N/A	1	<i>Parathelges aniculi</i> (Form B) – 1

7. Uniramous uropods articulated with terminal pleomere.....
.....*Parathelges* Bonnier, 1900 (11 spp.)
– Uropods lacking or reduced non-segmented lobes8
8. Pleopods on pleomere V present.....
.....*Allathelges* Kazmi & Markham, 1999 (2 sp.)
– Pleopods on pleomere V lacking.....
.....*Athelges* Gerstaecker, 1862 (13 spp.)

RESULTS

Prevalence data could be determined only from samples collected in the Philippines. In total, 2175 Philippine hermit crabs were examined, of which 57 (2.6%) were parasitised by isopods. Eleven species of hermit crabs were identified among the Philippine samples (see Table 2) as well as one species identified only to genus. Four species of hermit crabs (*Calcinus gaimardii*, *C. latens*, *C. minutus*, and *D. lagopodes*) made up 84% of the collections and were the most commonly parasitised (Table 3). Seven species of parasitic isopods were found: *Allathelges alisonae* n. sp. (2 host individuals parasitised), *Athelges takanoshimensis* (1 host individual parasitised), *Falsanathelges mariae* n. sp. (9 host individuals parasitised), *Parathelges aniculi* (Form A) (10 host individuals parasitised), *P. aniculi* Form B (21 host individuals parasitised), *Pseudostegias dulcilacuum* (13 host individuals parasitised), and *P. trisagitta* n. sp. (1 host individual parasitised). None of the 128 hermit crabs from Palawan (the only locality where *Paguristes runyanae* was found) had bopyrids. Unlike the other localities sampled, Palawan is aligned with Borneo as a separate biogeographical

province from the rest of the Philippines (Spalding et al., 2007).

The Papua New Guinea hosts yielded only a single species of parasite, *Athelges takanoshimensis*, found on three individuals belonging to two identified host species and one unidentified host (Table 2). Taiwanese hermit crabs were infested with four bopyrid species on six different hosts with two bopyrids, *P. aniculi* and *P. dulcilacuum*, being found on more than a single host (Table 2). Australian hermit crabs bore three different bopyrids on three host species.

TAXONOMY

Family Bopyridae Rafinesque, 1815

Subfamily Athelginae Codreanu & Codreanu, 1956

Genus *Allathelges* Kazmi & Markham, 1999

Allathelges alisonae, new species (Figs. 1, 2)

Material examined. Philippines: Mature holotype female (12.5 mm), mature allotype male (3.0 mm) (USNM 1283370), infesting female *Dardanus lagopodes* (5.7 mm SL), inhabiting shell of *Conus* sp., Batangas, Sombrero Island, coll. JDW, 30 January 1999; immature paratype female (6.9 mm) (ZRC 2015.0498), mature paratype male (1.5 mm), infesting male

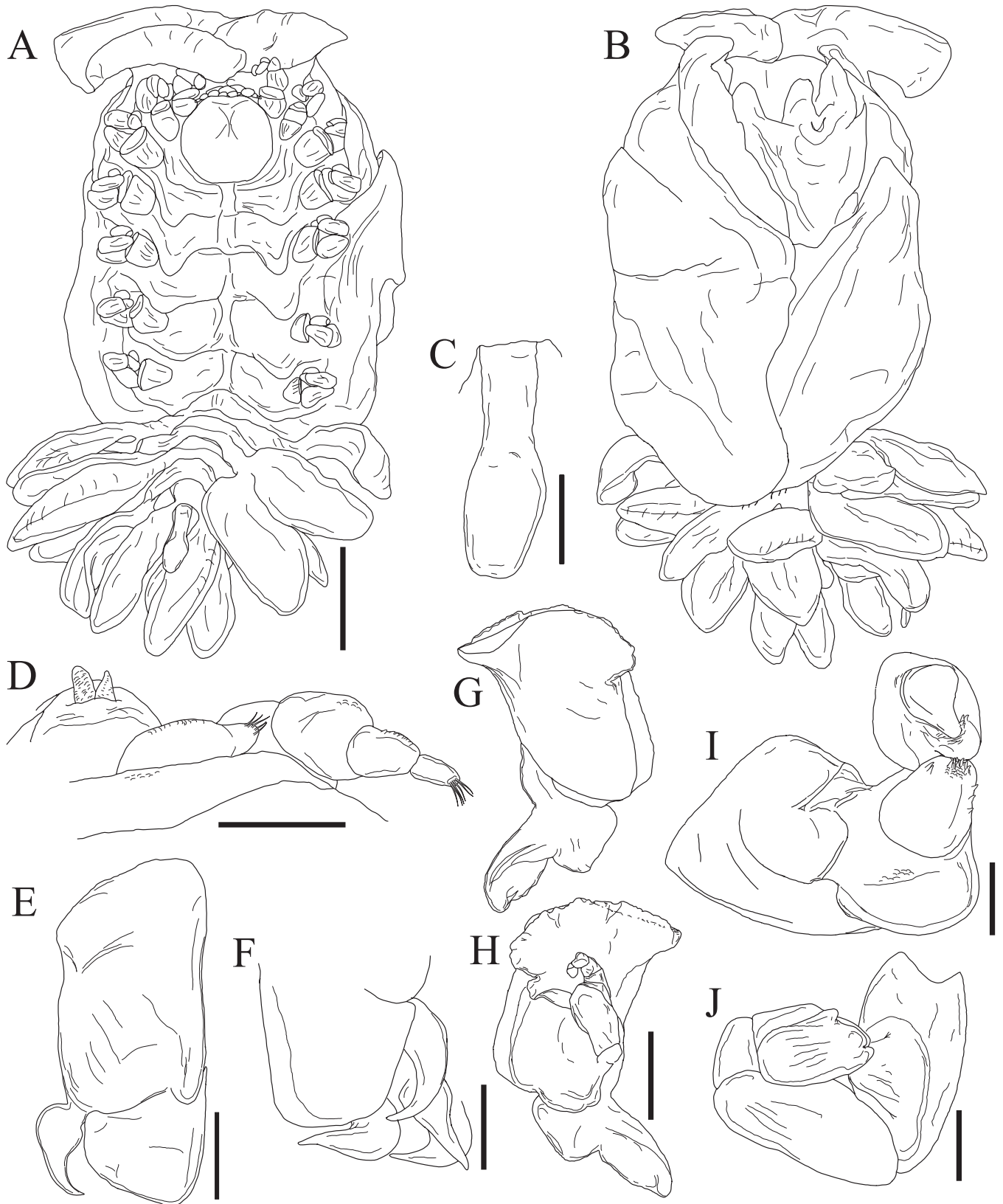


Fig. 1. *Allathelges alisonae* n. sp., female holotype, USNM 1283370 (A–J). A, dorsal view; B, ventral view; C, pleon; D, mouthparts and right antennae; E, right maxilliped, outer view; F, barbula, left side; G, right oostegite 1, outer view; H, right oostegite 1, inner view; I, right pereopod 1; J, right pereopod 7. Scale bars = 2 mm [A, B], 500 µm [C, F–H], 250 µm [D, E, J], 300 µm [I].

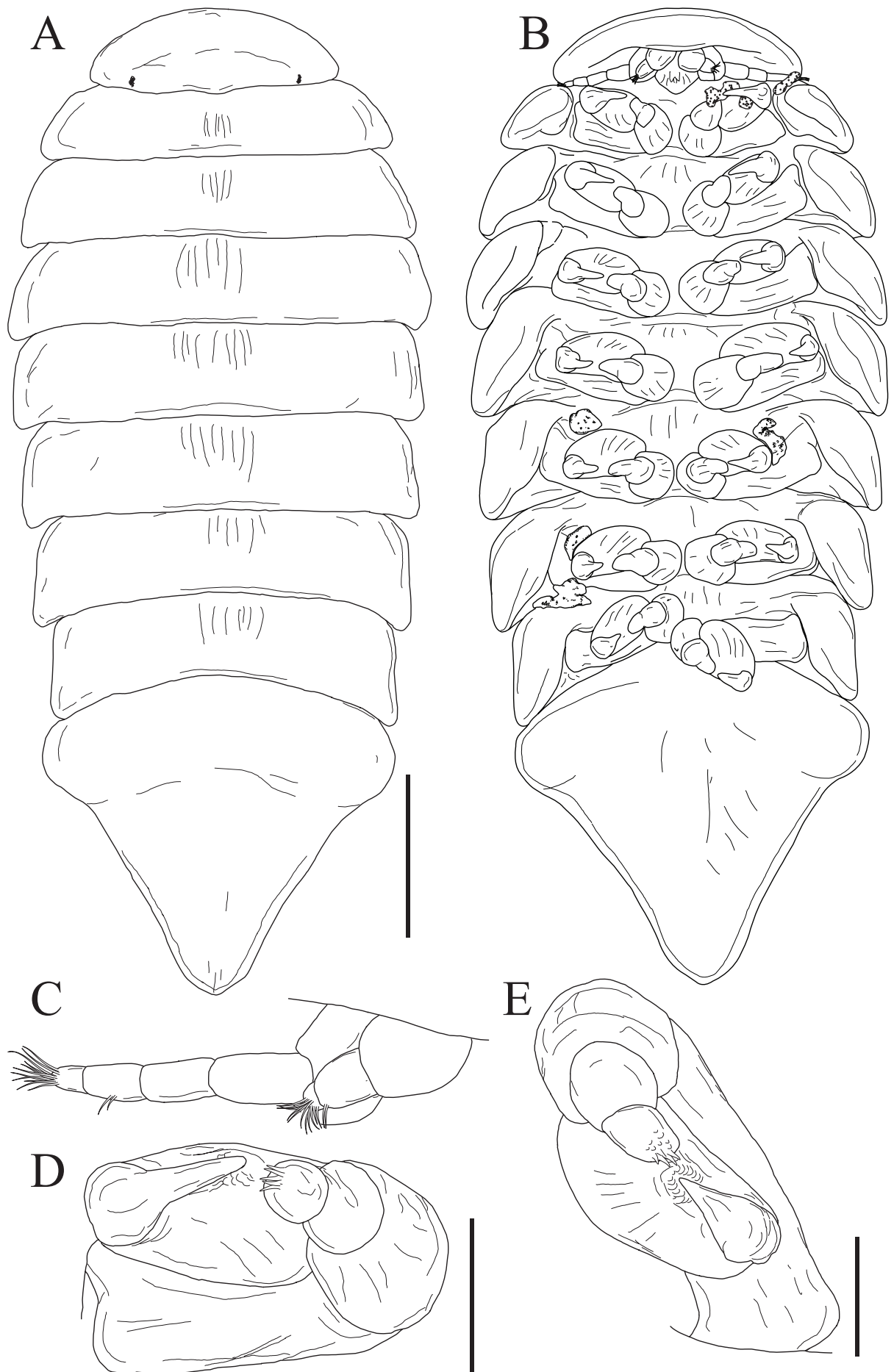


Fig. 2. *Allathelges alisonae* n. sp., male allotype, USNM 1283370 (A–E). A, dorsal view; B, ventral view; C, right antennule and antenna; D, right pereopod 1; E, left pereopod 7. Scale bars = 500 μm [A, B], 100 μm [C, D], 30 μm [E].

Dardanus lagopodes (5.4 mm SL), inhabiting shell of *Angaria delphinus* (Linnaeus), Cebu, Mactan Island, Maribago, coll. JDW, 9 July 1997.

Description. Female (Fig. 1): Body length 12.5 mm, maximal width 5.8 mm, head length 1.7 mm, head width 1.7 mm, pleon length 5.3 mm. Body longer than broad; pereon nearly symmetrical. All body regions and pereomeres distinctly segmented, except pereomeres I, II (Fig. 1A).

Head length, breadth subequal with convex lateral margins, anterior, posterior margins slightly flattened, overall shape of head circular. Eyes lacking. Antennule (Fig. 1D) of two articles, indistinctly separated; antenna (Fig. 1D) of four articles. Maxilliped (Fig. 1E) with elongate, subrectangular anterior lobe lacking palp; smaller, rounded posterior lobe bearing thin, acute spur. Barbula (Fig. 1F) with four short, smooth, distally acute lobes laterally on each side.

Pereon of five distinct pereomeres (first, second segments coalesced), broadest across pereomere IV, slightly tapering anteriorly and posteriorly. Pereomeres I, II medially anteriorly concave, posteriorly convex; pereomere III medially anteriorly concave, posteriorly sinuous with one posterolateral lobe on each side; pereomeres IV, V anteriorly and posteriorly medially sinuous with posterolateral lobes; pereomeres VI, VII anteriorly convex, posteriorly concave; pereomere VI with posterolateral lobes; pereomeres V, VI subequal in size. First oostegites extended beyond anterior margin of head (Fig. 1A, B). Oostegites completely enclosing brood pouch; posteriormost oostegite with fringe of setae on posterior margin (Fig. 1B). First oostegite anterior lobe laterally expanded and folded, posterior lobe with broad anterior region tapering to posterior rounded tip, internal ridge smooth (Fig. 1G, H). All pereopods subequal in size, dactyli slightly larger in anterior pairs, setae on distal end of carpus (Fig. 1I, J). Pereopods I–III parallel to head, evenly spaced with slightly broader gap between pereopods V, VI.

Pleon of six pleomeres, segmentation distinct. Pleomeres I–V (Fig. 1A) with elongate-ovate biramous pleopods, no lateral plates, arising from common peduncle; pleotelson narrow proximally, distally slightly expanded with rounded tip, lacking pleopods or lateral plates (Fig. 1A, C).

Male (Fig. 2): Length 3.0 mm, maximum width 1.3, head length 0.3 mm, head width 0.8 mm, pleon length 1.0 mm. Head subovate, narrow, evenly rounded distally, posterior margin nearly straight, distinct from pereomere I (Fig. 2A, B). Eye pigmentation present at lateral junction of head and first pereomere (Fig. 2A). Antennule of three articles; antenna of five articles (Fig. 2C), not extending posterolaterally beyond margin of head, distalmost article of each with tuft of long setae, penultimate article of each with few shorter setae.

Pereomere III broadest, slightly tapering anteriorly and posteriorly. All pereomeres directed posterolaterally with slightly tapered posterolateral margins. Anterior pereopods with slightly longer dactyli than posterior pairs, longer dactyli recurved and slightly twisted, touching base of propodus

anterolateral to base of raised medial region on ventral surface of propodus (Fig. 2D), posterior shorter dactyli not twisted, touching base of propodus in median of ventral surface (Fig. 2E). Propodi and other segments of all pereopods subequal; carpi with setae on distal tip (Fig. 2B, D, E).

Pleon subtriangular, anteriorly laterally expanded, tapering posteriorly, broadly rounded at tip, all pleomeres fused but with lateral indication of fusion of first pleomere with remainder of pleotelson. No midventral tubercles, pleopods, or uropods (Fig. 2B).

Type locality. Philippines, Batangas: Sombrero Island (13°42'N, 120°50'E).

Etymology. Named for Alison Carson, the wife of the first author who helped collect many of the Philippine specimens reported on herein.

Distribution. Known only from Batangas and Cebu provinces in the Philippines.

Host. Diogenidae: *Dardanus lagopodes*.

Size Range (Length). Females: to 11.75 mm, males: to 3.0 mm.

Remarks. This species has the same female pleopodal formula as the type species, *Allathelges pakistanensis* Kazmi & Markham, 1999, as well as the reflexed first oostegites that extend forward over the head. However, the female pleopods of *A. alisonae* n. sp. are large, foliose and ovate (vs. very small and slender in *A. pakistanensis*) and the pleotelson is elongated, terminally expanded and similar to the pleotelsons seen in species of *Athelges* (vs. short and terminally tapered in *A. pakistanensis*). Barbula with four pairs of projections (vs. with two pairs of projections in *A. pakistanensis*). The male of *A. alisonae* n. sp. has a lateral expansion anteriorly on the pleotelson with indication of first pleomere fusion (vs. no anterior lateral expansion and no indication of pleomere fusion in *A. pakistanensis*). *Dardanus lagopodes* has not been previously recorded as a host for bopyrids.

Genus *Athelges* Gerstaecker, 1862

Athelges ankistron Markham, 2010 (Fig. 3A–D)

Athelges ankistron Markham, 2010: 175–179, figs. 26, 27.

Material examined. Australia: Mature female (10.0 mm) (MV J62880), infesting unknown host, inhabiting unknown shell, Naracoopa, King Island, Tasmania, 39°55'11"S 144°07'35"E, coll. Marine Research Group of Victoria, 8 March 1980; mature female (17 mm), mature male (3.5 mm) (MV J62881a), no specific host or locality data [collected before 1911]; mature female (14.5 mm) (MV J62872a), 3 immature males (1–1.2 mm), 2 cryptoniscus larvae (0.8 mm), infesting *Paguristes sulcatus* (fide label), inhabiting *Phasianella ventricosa* (fide label), Naracoopa, King Island,

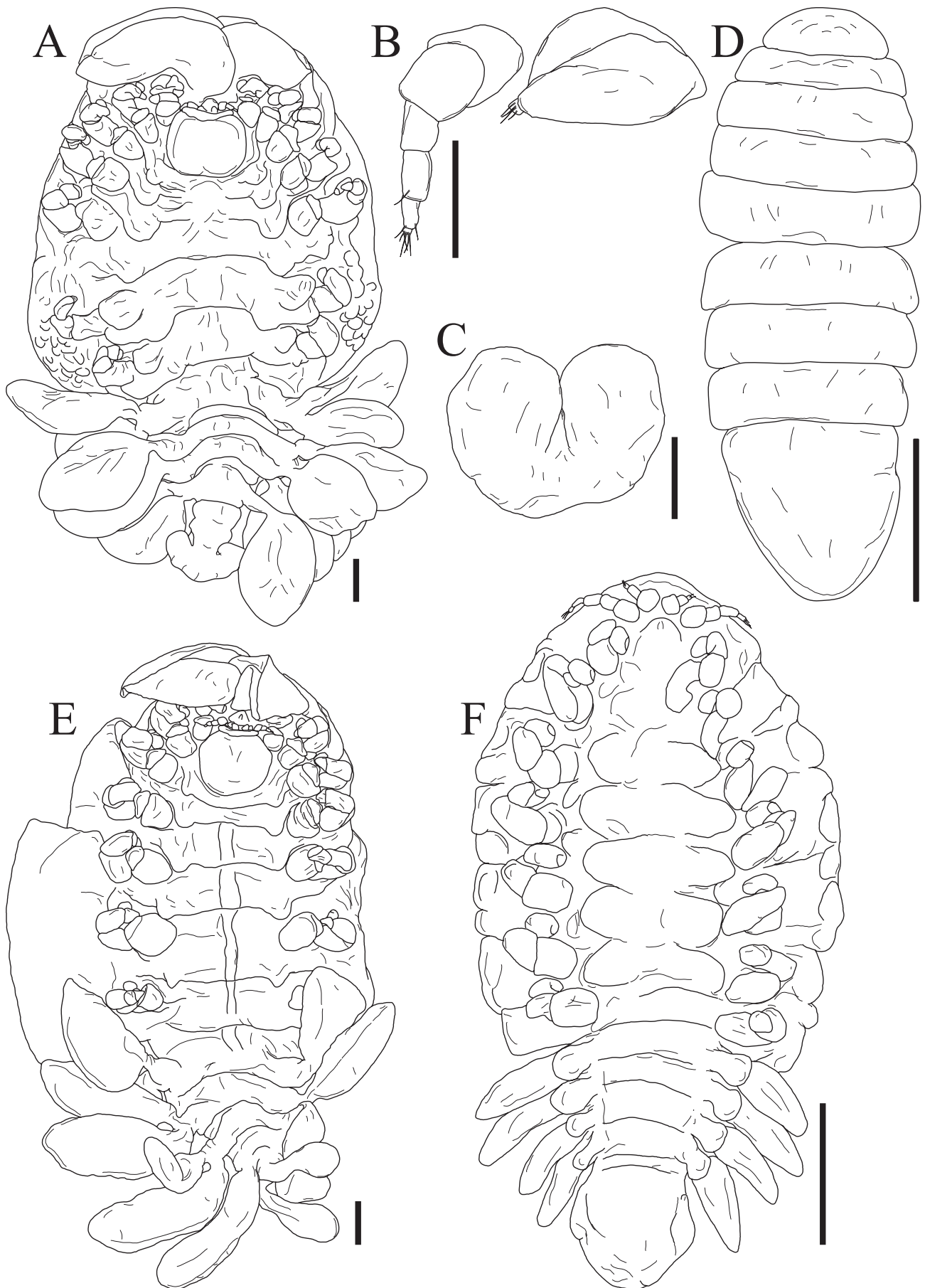


Fig. 3. *Athelges ankistrum* Markham, 2010, female, MV J62872a (A, B); MV J62881a (C); male, MV J62881 (D); *Athelges takanoshimensis* Ishii, 1914, female, USNM 1283371 (E); *Athelges* sp., immature female USNM MV J62876 (F). A, dorsal view; B, right antennule and antenna; C, en face view of pleotelson; D, dorsal view; E, dorsal view; F, ventral view. Scale bars = 1mm [A, E], 250 μ m [B, C, F], 500 μ m [D].

Tasmania, 39°55'11"S 144°07'35"E, coll. Marine Research Group of Victoria, 8 March 1980.

Type locality. Shallow water seagrass, Myora Springs, North Stradbroke Island, Queensland, 27°40.8'S, 153°24.6'E.

Distribution. Queensland (Markham, 2010); Tasmania (herein), Australia.

Hosts. Diogenidae: *Diogenes pallescens* Whitelegge, 1897 (Markham, 2010), *Paguristes sulcatus* (herein).

Size Range (Length). Females: to 17.0 mm (herein), males: to 3.5 mm (herein).

Remarks. The present specimens agree with the description of the species given by Markham (2010), although our specimens (Fig. 3A, D) are considerably larger than the types (holotype female = 5.4 mm; allotype male = 1.7 mm). Additionally, the antennae of the present specimens (Fig. 3B), although also of six segments, are much shorter and with a much stouter second segment; the female pleotelsons show a range of shape in the thickness of their recurved posterolateral lobes (Fig. 3A, C), and the males (Fig. 3D) have broader pleotelsons than that of the allotype. The range of the species is extended south to Tasmania and a new host, *P. sulcatus*, is added for the species.

Athelges takanoshimensis Ishii, 1914 (Fig. 3E)

Athelges takanoshimensis Ishii, 1914: 519–529, pl. 7; Boyko, 2004: 697–701, figs. 14, 15; Markham, 2009: 229–233, fig. 5 (full synonymy), 2010: 179; An et al., 2011: 2902–2904, fig. 1; Kwon, 2012: 28–30, fig. 11; Tudge et al., 2012, 289, 312, fig. 70.31C, D; Cericola & Williams, 2015: 236–252, figs. 1, 2–7, Tables I, II.

Athelges “undescribed species” Haig & Ball, 1988: 177.
“probably... *A. takanoshimensis*” Markham, 2010: 179.

Material examined. Indonesia: Mature female (7.14 mm, with female *Cabirops* sp. in brood chamber) (LACM CR 1975-589.4), infesting *Ciliopagurus strigatus* (unknown SL), inhabiting unknown shell, Banda Islands, Stn. 9, west end Banda Besar (04°32.6'S, 129°52'E), 0–12 m, coll. E. Ball et al., 12 April 1975. **Papua New Guinea:** Immature female (3.2 mm), mature male (1.7 mm) (MNHN-IU-2014-12733), infesting *Calcinus latens* (1.7 m SL), inhabiting unknown shell, Stn. PD35, Rempi area, south Barang Island, 05°01.3'S 145°47'E, 10–12 m, coll. Expédition Papua Niugini, 19–20 November 2012; immature female (3.0 mm) (MNHN-IU-2014-12734), infesting juvenile *Diogenes* sp. (1.4 mm SL), inhabiting unknown shell, Stn. PS19, Hargun Island, 05°01.6'S 145°48.1'E, 5 m, coll. Expédition Papua Niugini, 20 November 2012; mature female (5.0 mm) (MNHN-IU-2014-12735), infesting unknown hermit crab, inhabiting unknown shell, Stn. PB16, north Sek Island, 05°04.7'S 145°48.8'E, 5 m, coll. Expédition Papua Niugini, 13 November 2012. **Philippines:** Mature female (15.8 mm) (USNM 1283371), infesting female *Dardanus woodmasoni*

(7.46 mm SL), inhabiting unidentified shell, Cebu, Mactan Island, Maribago, coll. P. Cassidy, 2 December 1996.

Type locality. Takanoshima, Japan (Ishii, 1914).

Distribution. Japan, Hong Kong, Korea, Taiwan (Boyko, 2004; Cericola & Williams, 2015); Singapore (Markham, 2009); Indonesia (Haig & Ball, 1988); China: Bohai Sea and Yellow Sea (An et al., 2011); Philippines (herein).

Hosts. Diogenidae: *Calcinus latens* (herein), *Ciliopagurus strigatus* (Haig & Ball, 1988), *Dardanus woodmasoni* (herein), *Diogenes edwardsii* (De Haan, 1849) (Boyko, 2004), *Diogenes pallescens* Whitelegge, 1897 (Markham, 2009), *Diogenes* sp. (herein). **Paguridae:** *Pagurodoeleinia doederleini* (Doflein, 1902), *Pagurus angustus* (Stimpson, 1858) (Cericola & Williams, 2015), *Pagurus constans* (Stimpson, 1858), *P. filholi* (de Man, 1887), *P. japonicus* (Stimpson, 1858), *P. lanuginosus* De Haan, 1849, *P. maculosus* Komai & Imafuku, 1996, *P. middendorffii* Brandt, 1851 (Boyko, 2004), *P. minutus* Hess, 1865 (An et al., 2011), *P. pectinatus* (Stimpson, 1858), *P. proximus* Komai, 2000, *P. trigonocheirus* (Stimpson, 1858) (Boyko, 2004).

Size Range (Length). Females: to 18.0 mm, males: to 4.28 mm (Boyko, 2004).

Remarks. The Indonesian specimens identified by John Markham and reported by Haig & Ball (1988) as “an undescribed species of *Athelges*” (LACM CR 1975-589.4) were examined and found to conform well to *A. takanoshimensis* with its characteristic female terminal abdominal segment (Fig. 3E). Markham (2010: 178) reported that the material from Indonesia of Haig & Ball (1988) was lost, based on a personal communication from E. E. Ball, but it was actually in the LACM collections. However, Markham (2010) correctly surmised that the material was probably *A. takanoshimensis* and not a new species. *Athelges takanoshimensis* is an oft-reported and relatively widely distributed bopyrid, known from 15 hermit crab hosts (see McDermott et al., 2010; Cericola & Williams 2015), but the parasite is apparently rare in the Philippines. Only a single female was found, although only a single specimen of the host, *Dardanus woodmasoni*, was collected. A small number of *Ciliopagurus strigatus*, the host of the Indonesian specimen reported herein, were collected from the Philippines, but none bore abdominal or branchial bopyrids. *Ciliopagurus strigatus* is known as a bopyrid host (Haig & Ball, 1988; Markham, 2010) for *A. takanoshimensis* while *Dardanus woodmasoni* is first reported here as a host for bopyrids. One female of *A. takanoshimensis* from Indonesia contained a hyperparasitic isopod (*Cabirops* sp.) in brood chamber.

Athelges sp. (Fig. 3F)

Material examined. Australia: Immature female (1.2 mm) (MV J62876), infesting juvenile *Paguristes sulcatus* (1.6 mm SL), inhabiting unknown shell, by boat ramp, Giles Point,

South Australia, 35°03'00"S 137°46'00"E, coll. G.C.B. Poore & H.M. Lew Ton, 19 March 1985.

Hosts. Diogenidae: *Paguristes sulcatus*.

Remarks. Both the female and the male are too immature to assign to species, and the South Australia locality is of little help, as no *Athelges* species are known from this state. It could be *Athelges ankistrion*, which is known from the same host in Tasmania. The juvenile female (Fig. 3F) exhibits differential development of pleopods, with elongate exopods and short rounded endopods (the adult exopods and endopods are subequal in size). The pleotelson is proportionately much larger in the juvenile compared to adult females.

***Claustrathelges* n. gen.**

Diagnosis. Female: Body longer than broad, pereon not distorted, pleon weakly distorted, head length and width subequal with nearly straight lateral margins, anterior margin weakly convex, posterior margin convex. No oostegites extended over head or produced posteriorly. Pereomeres I–IV anteriorly concave and posteriorly convex, pereomere V with margins nearly straight, pereomeres VI, VII anteriorly convex, posteriorly concave; pereomeres IV broader than other segments. Pereopod I anterior to head, pereopods II, III parallel to head, no large gaps between pereopods IV–VII. Dorsal surface of first oostegites with pattern of ridges. Pleomeres I–V with elongate-ovate biramous pleopods and uniramous lateral plates, all arising from common peduncle. Pleotelson lacking (but see Remarks in description below); pleon of five total segments.

Male: Unknown

Type species. *Claustrathelges macdermotti* n. sp. by present designation.

Etymology. The genus name is derived from *claustrum*, a Latin term referring to a prison or cloister, combined with *Athelges*, a genus of abdominal bopyrids infesting hermit crabs. The name alludes to the parasite being trapped in the stone domicile of the host hermit crab. Gender masculine.

Remarks. *Claustrathelges* n. gen. is most closely related to *Falsanathelges* Boyko & Williams, 2003, but females can be distinguished in that those of *Claustrathelges* n. gen. have only five pleomeres, all with biramous pleopods and uniramous lateral plates, while those of *Falsanathelges* have six pleomeres, with the first five bearing biramous pleopods and uniramous lateral plates and the sixth bearing biramous uropods. Additionally, the dorsal surfaces of the first oostegites of female *Claustrathelges* n. gen. bear a series of distinct ridges, while those of the first oostegites of female *Falsanathelges* are smooth.

***Claustrathelges macdermotti* n. sp.**

(Fig. 4)

Material examined. Australia: Mature holotype female (14.4 mm) (MV J62893), infesting *Cancellus typus* (fide label), inhabiting stone, San Remo Channel, Victoria, 38°32'S 145°23'E, coll. I. Kirwan, March 1978.

Description. Female (Fig. 4): Holotype body length 14.4 mm, maximal width 8.2 mm, head length 2.7 mm, head width 2.6 mm, pleon length 4.1 mm. Body longer than broad; pereon not distorted. All body regions and pereomeres distinctly segmented (Fig. 4A, B).

Head length and breadth subequal with nearly straight lateral margins, anterior margin slightly convex, posterior margin convex. Eyes lacking. Antennule (Fig. 4C) of three articles, setae on distal margin of distalmost two segments; antenna (Fig. 4C) of five articles, setae on distal margins of distalmost three segments. Maxilliped (Fig. 4G) with rounded anterior lobe, palp absent; posterior lobe subtriangular with short rounded spur. Barbula (Fig. 4D) of three lobes with highly digitate margins on each side.

Pereon of seven pereomeres, broadest across pereomere IV, tapering anteriorly and posteriorly. Pereomeres I–IV anteriorly concave and posteriorly convex, pereomere V nearly straight, pereomeres VI, VII anterior margin convex, posterior margin concave. No oostegites extended over head or produced posteriorly (Fig. 4A, B). Oostegites completely enclosing brood pouch (Fig. 4A); posteriormost oostegite with fringe of setae on posterior margin. First oostegite anterior lobe irregularly ovate with edges folded under, dorsal surface with medial region of ridges, posterior lobe with large ovate expansion and smaller, slightly tapering mesial extension, internal ridge with numerous digitations and larger digitate mesial lobe (Fig. 4E, F). All pereopods subequal, with all segments distinct (Fig. 4B, I, J). Pereopod I anterior to head, pereopods II, III parallel to head, no large gaps between pereomeres.

Pleon with five pleomeres, dorsal segmentation distinct. Pleomeres I–V (Fig. 4A, B, K) with elongate-ovate biramous pleopods and uniramous lateral plates, all arising from common peduncle; pleotelson lacking (Fig. 4K).

Male: unknown.

Type locality. San Remo Channel, Victoria, Australia.

Etymology. This species is named in honor of John J. McDermott (Emeritus Professor of Biology, Franklin and Marshall College, Pennsylvania, U.S.A.) for his considerable contributions to the biology and systematics of numerous marine invertebrates, including bopyrids. The specific name is spelled to conform to the ICZN Recommendations on the Formation of Names, Appendix D 21(a) (ICZN 1985: 197). Due to the necessity of synonymising the species we had earlier named for him, *Pseudostegias macdermotti*, in this paper, we felt it only fair to name a new species after him

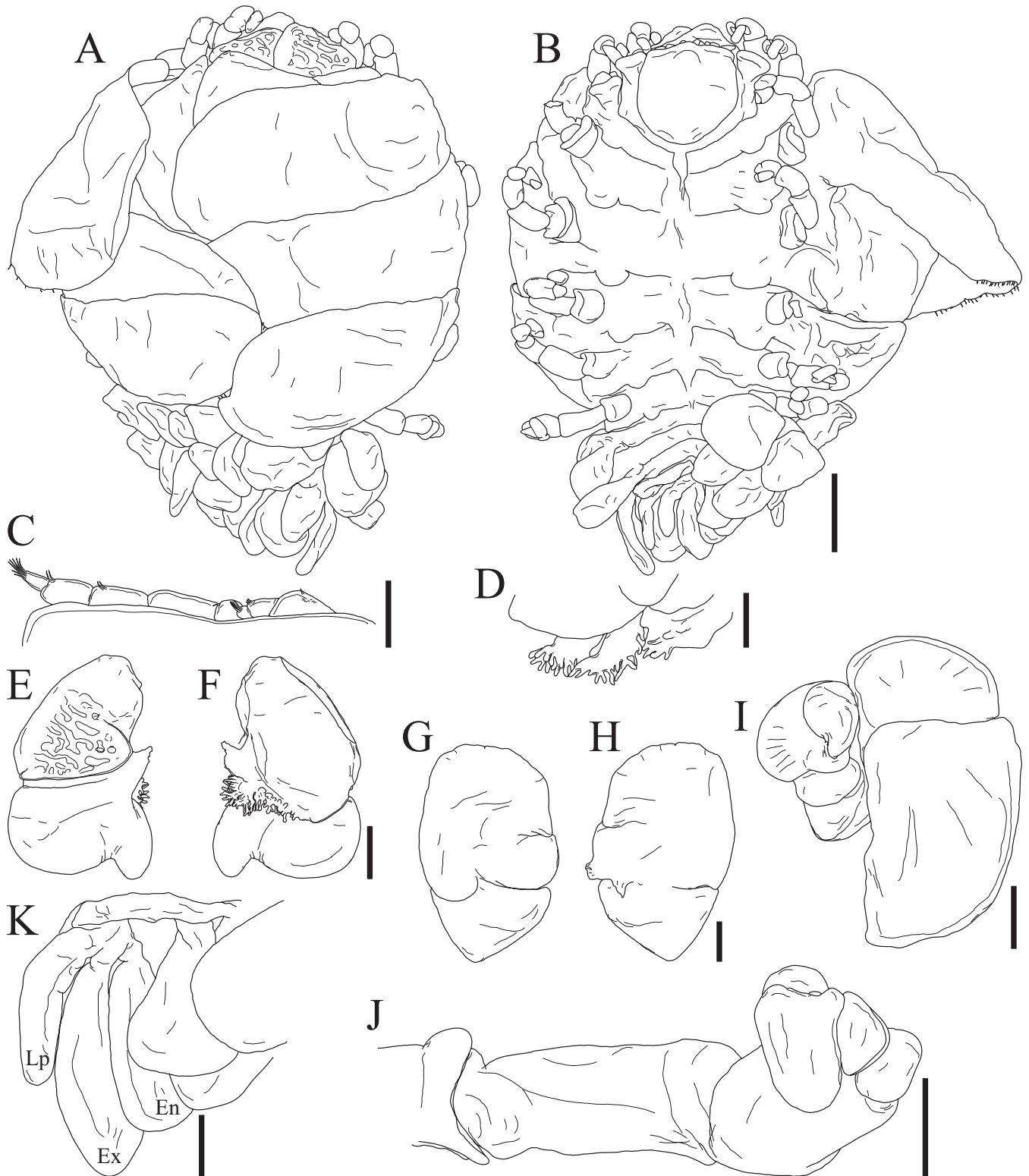


Fig. 4. *Claustrathelges macdermotti* n. sp., female holotype, MV J62893 (A–K). A, ventral view; B, dorsal view; C, left antennule and antenna, dorsal view; D, barbula, left side; E, left oostegite 1, outer view; F, left oostegite 1, inner view; G, left maxilliped, outer view; H, left maxilliped, inner view; I, left pereopod 1 and oostegite 1; J, left pereopod 7. K, terminal pleomere, dorsal view showing right endopod (En), exopod (Ex) and lateral plate (Lp). Scale bars = 2 mm [A, B], 250 μm [C, I, J], 500 μm [D, E–H, K].

to make up for it. The taxonomist giveth and the taxonomist taketh away.

Distribution. Known only from the San Remo Channel, Victoria, Australia.

Host. Diogenidae: *Cancellus typus*.

Size Range (Length). Females: to 14.0 mm, males: unknown.

Remarks. The new species can be distinguished from its closest relatives in *Falsanathelges* by the characters given in the generic diagnosis. *Cancellus* hermit crabs were previously not known to bear any bopyrids. These hermits have an unusual choice of carcinoecia in that they are typically found living in calcareous rock, pumice, and other stones (McLaughlin, 2008). These habitats would appear to be a relatively difficult type for abdominal bopyrids in regards to the high potential for scraping against the rough surface of the carcinoecia when the hermit crab abdomen is flexed.

Genus *Falsanathelges* Boyko & Williams, 2003

Falsanathelges mariae n. sp. (Figs. 5–7)

Material examined. Philippines: Mature holotype female (7.8 mm), mature allotype male (2.7 mm) (USNM 1283372), infesting male *Calcinus gaimardii* (4.4 mm SL), inhabiting unidentified shell, Oriental Mindoro, Puerto Galera, La Laguna Beach, coll. JDW, 19 July 1997; mature paratype female (5.6 mm), mature paratype male (3.1 mm) (USNM 1283373), infesting female *Calcinus latens* (3.4 mm SL), inhabiting shell of *Peristernia incarnata*, Cebu, Olango Island and Sulpa Islet, coll. JDW, 9 July 1997; immature paratype female (8.34 mm), mature paratype male (2.04 mm) (ZRC 2015.0499), infesting intersex *Clibanarius merguensis* (2.5 mm SL), inhabiting shell of *Clypeomorus* sp., Oriental Mindoro, Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; mature paratype female (5.03 mm), mature paratype male (3.47 mm) (ZRC 2015.0500), infesting female *C. gaimardii* (3.0 mm SL), inhabiting shell of *Cypraea* sp., Oriental Mindoro, Puerto Galera, Coco Beach, coll. JDW, 14 January 1999; mature female (6.33 mm) with *Cabirops* female, mature male (2.04) (pers. coll.), infesting female *Calcinus minutus* (2.8 mm SL), inhabiting shell of *Peristernia nassatula* (Lamarck), Aklan, Boracay, Rocky Beach, coll. JDW, 12 April 1999; mature female (7.74 mm) (ZRC 2015.0501), infesting male *C. merguensis* (2.26 mm SL), inhabiting unidentified shell, Puerto Galera, La Laguna Beach, coll. JDW, 17 June 2000; mature female (8.41 mm), mature male (2.53 mm) (USNM 1283374), infesting female *C. gaimardii* (3.3 mm SL), inhabiting unidentified shell, Puerto Galera, La Laguna Beach, coll. JDW, 28 July 1997; mature female (7.38 mm), mature male (2.61 mm) (USNM 1283375), infesting female *C. minutus* (1.8 mm SL), inhabiting unidentified shell, Bataan, Mabayo, coll. JDW, 21 February 1999; mature female (9.67 mm), mature male (3.0 mm on SEM stub) (USNM 1283376), infesting

male *C. minutus* (3.6 mm SL), inhabiting unidentified shell, Bataan, Mabayo, coll. JDW, 21 February 1999. **Taiwan:** Mature female (7.8 mm, damaged), mature male (2.3 mm) (USNM 1283377), infesting female *Calcinus guamensis* (3.6 mm SL), inhabiting unknown shell, Siadao, Pingtung, coll. R. Yoshida, 26 July 2011; mature female (7.4 mm), mature male (2.5 mm) (USNM 1283378), infesting female *C. guamensis* (3.7 mm SL), inhabiting unknown shell, Houwan, Pingtung, coll. R. Yoshida, 27 July 2011; mature female (6.4 mm) (USNM 1283379), infesting male *C. guamensis* (2.5 mm SL), inhabiting unknown shell, Gonggang, Green Island, coll. R. Yoshida, 24 June 2013.

Description. Female (Fig. 5): Holotype body length 7.8 mm, maximal width 2.8 mm, head length 0.9 mm, head width 0.9 mm, pleon length 3.5 mm. Body longer than broad; pereon anteriorly distorted dextrally. All body regions and pereomeres distinctly separated (Fig. 5A, B).

Head length and breadth subequal with convex lateral margins, anterior margin deeply concave, posterior strongly convex. Eyes lacking. Antennule (Fig. 5C) of three articles, setae on distal margin of distalmost two segments; antenna (Fig. 5D) of five articles, setae on distal margins of distalmost three segments. Maxilliped (Fig. 5E) with subtriangular anterior lobe, palp absent; posterior lobe subtriangular with long thin spur. Barbula (Fig. 5E, H) of two short lobes with digitate margins on each side.

Pereon of seven pereomeres, pereomeres III–VII broadest, subequal in width. Pereomeres I–III anteriorly concave and posteriorly convex, pereomeres IV–VII anteriorly convex, posteriorly concave. Oostegites I slightly extended over head; no oostegites produced posteriorly (Fig. 5A, B). Oostegites completely enclosing brood pouch (Fig. 5B). First oostegite anterior lobe irregularly ovate with edges folded under, posterior lobe with large ovate expansion and smaller, recurved mesial extension, internal ridge with numerous digitations and larger digitate mesial lobe (Fig. 5F, G). All pereopods subequal and with all segments distinct (Fig. 5B, I, J). Pereopod I anterior to head, pereopods II, III parallel to head, no large gaps between pereomeres. All pereopods with elongate bases and ischia, pronounced lobe present on each basis (Fig. 5I).

Pleon with six pleomeres, dorsal segmentation distinct. Pleomeres I–V (Fig. 5A, B) with elongate-ovate biramous pleopods and uniramous lateral plates; pleotelson with uniramous uropods (Fig. 5A).

Male (Figs. 6, 7): Body length 2.7 mm, maximum width 1.1 mm, head length 0.3 mm, head width 0.6 mm, pleon length 0.8 mm. Head subovate, widest medially, distinct from pereomere I, mediodorsal cephalic slits present (Fig. 7B). Small eyes mediolaterally. Antennule of three articles (Figs. 6D, 7A), antenna of five articles (Figs. 6D, 7A), setae on distal region of all segments except for basal antennal article, proximal two articles of antennule and antenna with marginal scales. Oral cone with scales on surface (Fig. 7C).

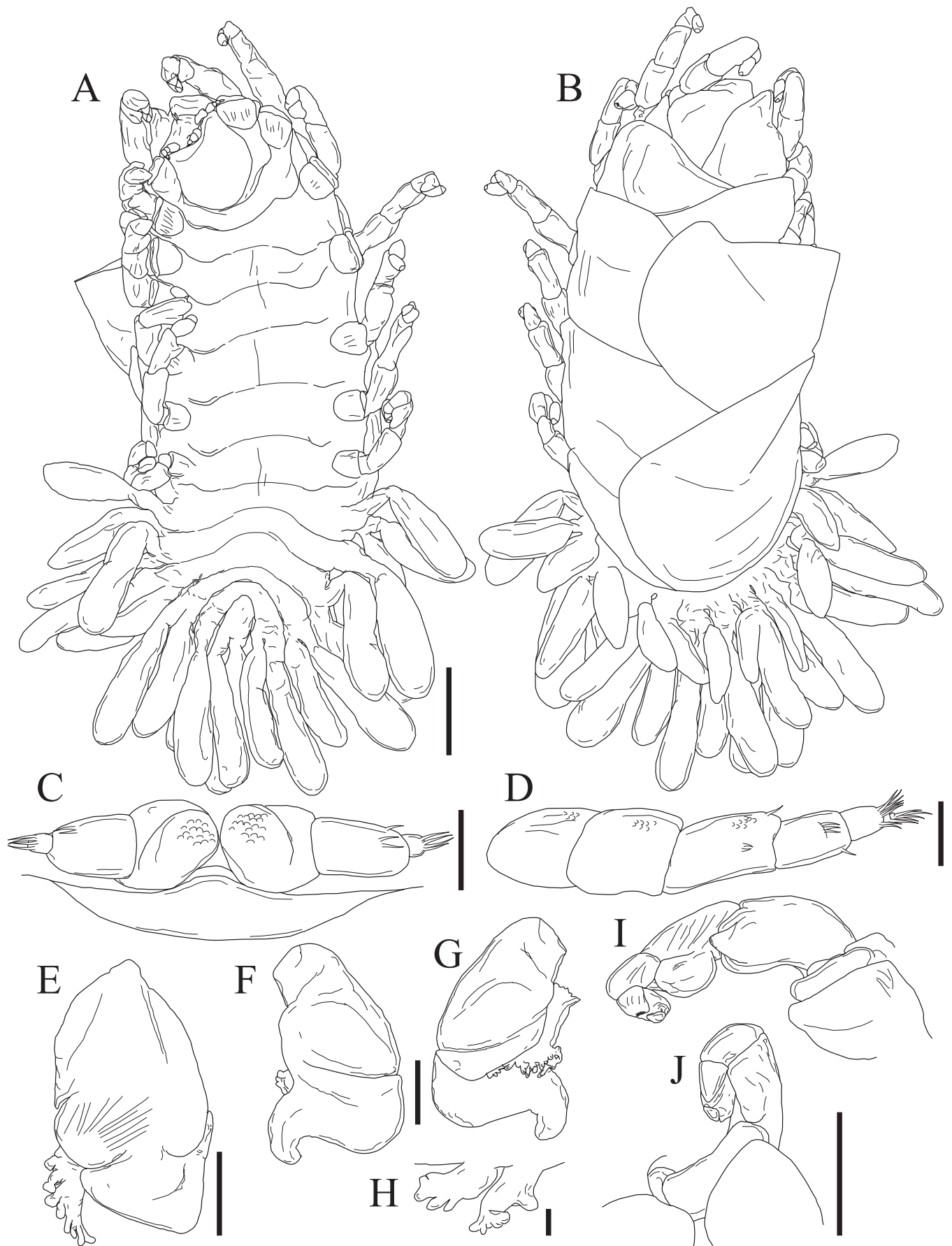


Fig. 5. *Falsanathelges mariae* n. sp., female holotype, USNM 1283372 (A, B), female paratype, USNM 1283376 (C–J). A, dorsal view; B, ventral view; C, antennules; D, right antenna; E, right maxilliped, outer view; F, right oostegite 1, outer view; G, right oostegite 1, inner view; H, barbula, left side; I, right pereopod 1; J, right pereopod 7. Scale bars = 1 mm [A, B], 50 µm [C, D, F, G], 500 µm [E, I, J], 10 µm [H].

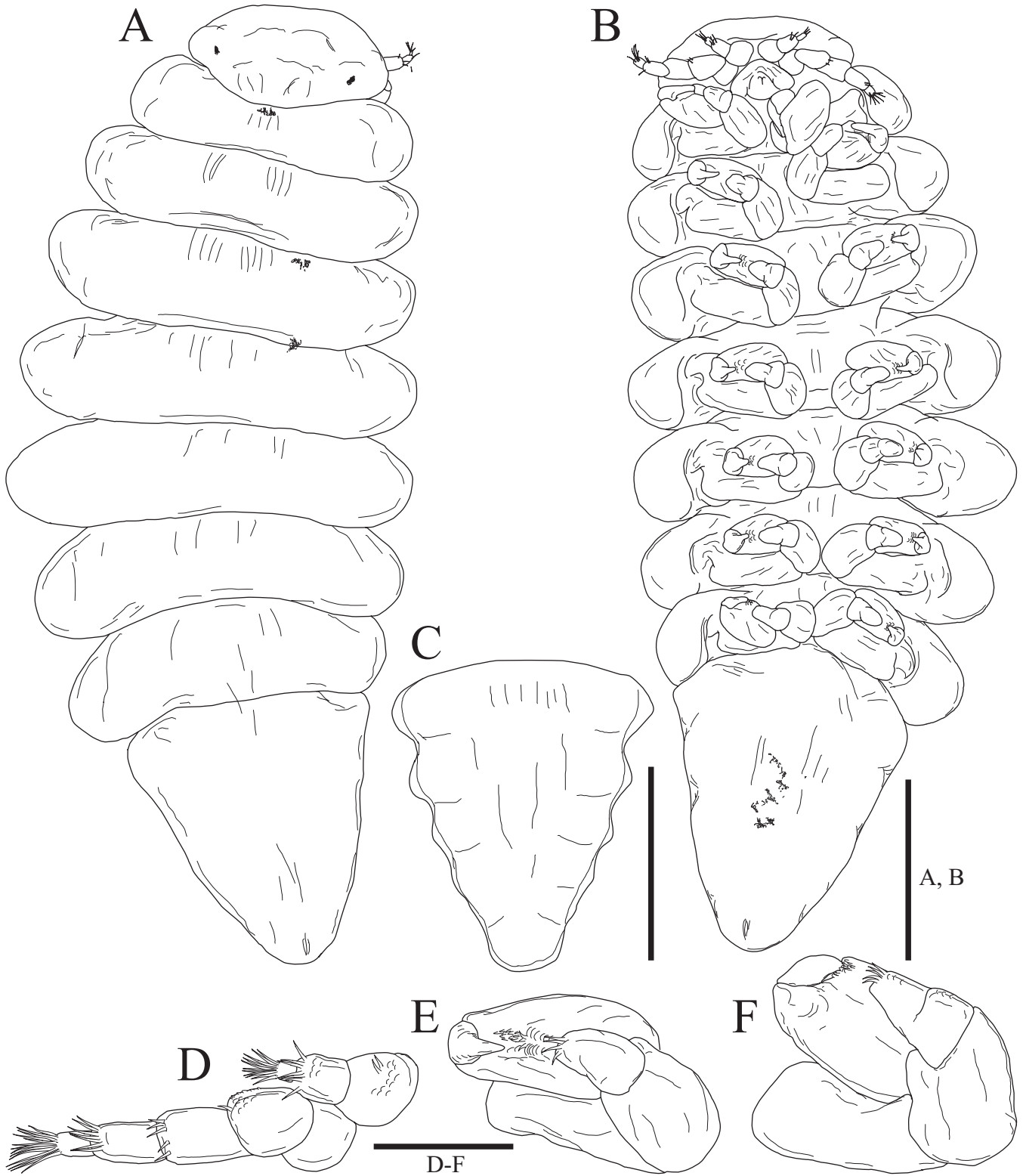


Fig. 6. *Falsanathelges mariae* n. sp., male allotype, USNM 1283372 (A, B), male paratype USNM 1283374 (C–F). A, dorsal view; B, ventral view; C, pleon, ventral view; D, left antennule and antenna; E, left pereopod 1; F, left pereopod 7. Scale bars = 500 µm [A–C], 100 µm [D–F].

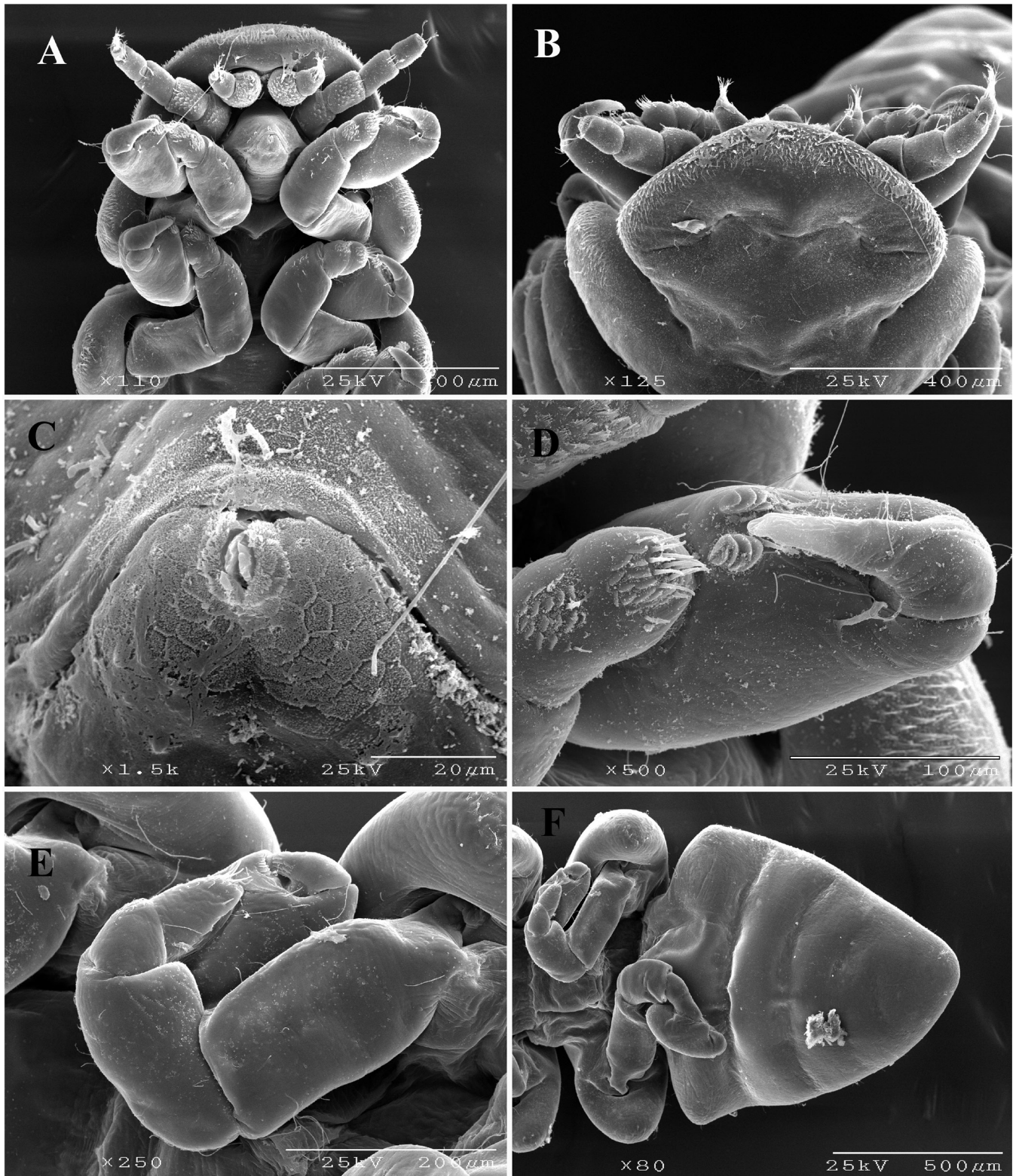


Fig. 7. *Falsanathelges mariae* n. sp. scanning electron micrographs of male paratype, USNM 1283376 (A–F). A, ventral view of anterior end; B, dorsal view of head, showing cephalic slits (presumptive sensory structure, see Bourdon et al., 1981); C, oral cone; D, left pereopod 1; E, left pereopod 7; F, seventh pereomere and pleon. Scale bars = 400 µm [A, B], 20 µm [C], 100 µm [D], 200 µm [E], 500 µm [F].

Pereomere V broadest, tapering anteriorly and posteriorly, but tapering more marked anteriorly. Pereomeres I–IV directed laterally with rounded distal margins, V–VII with slight posteriolateral curvature. Small patches of pigmentation on pereomeres I, III, IV. All pereopods (Figs. 6B, E, F, 7A, D–F), subequal in size, all articles distinctly separated, dactylus of pereopods I–II larger than those of pereopods, ventral margin of carpus, merus, and edge of propodus with few stout setae, ventral margin of carpus and edge of propodus with few low scales (Figs. 6E, F, 7D, E). Pleon tapering posteriorly, all pleomeres fused but with variable degrees of lateral indication of segmentation (Figs. 6A, C, 7F); posterior margin rounded. No midventral tubercles, pleopods, or uropods (Figs. 6B, C, 7F).

Type locality. Philippines, Oriental Mindoro, Puerto Galera: La Laguna Beach (13°30'N, 120°57'E).

Etymology. Named for Maria Spector, the wife of the second author, for her continual support and encouragement.

Distribution. Known from Oriental Mindoro and Cebu provinces in the Philippines and Taiwan.

Hosts. Diogenidae: *Calcinus gaimardii*, *C. guamensis*, *C. latens*, *C. minutus*, and *Clibanarius merguensis*.

Size Range (Length). Females: to 9.67 mm, males: to 3.47 mm.

Remarks. The genus *Falsanathelges* was erected for *Anathelges muelleri* Nierstrasz & Brender à Brandis, 1931 from Malaysia and Indonesia on the hosts *Clibanarius infraspinus* (Hilgendorf, 1869) and *Calcinus lineapropodus* Morgan & Forest, 1991, respectively. The present specimens are very similar to those of *F. muelleri*, but differ in the following characters: female uropods uniramous (biramous in *F. muelleri*), female pleopods and lateral plates slender (broadly ovate in *F. muelleri*), male pereomeres markedly broader posteriorly (all pereomeres subequal in width in *F. muelleri*). The presence of uniramous uropods in the new species, which otherwise is clearly closely related to *F. muelleri*, necessitates a modification in the key to athelgine genera given by Boyko & Williams (2003).

Calcinus gaimardii has never been reported to host bopyrids but in the present study is found to host three abdominal bopyrid species (see Table 2). One female of *Falsanathelges mariae* n. sp. from the Philippines contained a hyperparasitic isopod (*Cabirops* sp.) in the brood chamber.

Genus *Parathelges* Bonnier, 1900

Parathelges aniculi (Whitelegge, 1897)

(Figs. 8–12)

Athelges aniculi Whitelegge, 1897: 149–151, pl. 7, figs. 5a–c; Springthorpe & Lowry, 1994: 37.

Parathelges aniculi, Bonnier, 1900: 380 (list); Shiino, 1950: 164 (list); Codreanu, 1961: 137 (list); Markham, 1972: 58 (list),

76 (key); Markham, 2010: 153 (list), 179–183, figs. 28–31 (synonymy); An et al., 2011: 2906 (mention).

Parathelges weberi Nierstrasz & Brender à Brandis, 1923: 105, pl. 7, figs. 28a–d; Nierstrasz & Brender à Brandis, 1929: 302, figs. 10, 11; Nierstrasz & Brender à Brandis, 1931: 201 (list); Shiino, 1950: 164 (list); Codreanu, 1961: 137 (list); Ball & Haig, 1972: 100; Markham, 1972: 58 (list), 76 (key); Haig & Ball, 1988: 160; An et al., 2011: 2906 (mention).

Parathelges whiteleggei Nierstrasz & Brender à Brandis, 1931: 200, 201, pl. 1, fig. 4, text fig. 92; Shiino, 1950: 164 (list); Codreanu, 1961: 137 (list); Markham, 1972: 58 (list), 76 (key); An et al., 2011: 2906 (mention).

Athelges “undescribed species” Haig & Ball, 1988: 161.

Parathelges “?whiteleggei” Haig & Ball, 1988: 173.

Material examined. With Male Form A: Indonesia: Mature lectotype female (9.5 mm) and mature paralectotype male (4.7 mm) (ZMUC CRU-8616) of *Parathelges whiteleggei*, infesting “*Pagurus* sp.” [= *Dardanus hessii*] (5.9 mm SL; in vial with parasites), “Javasee” [Indonesia], coll. unknown, 4 December 1910; immature female (2.3 mm), mature male (1.4 mm) (LACM CR19755901), infesting female *Pseudopaguristes monoporus* (1.8 mm SL), inhabiting unknown shell, Indonesia, Seram, Stn. 2, around Pulau Marsegu (03°00'S, 128°02.5'E), coll. E. Ball et al., 31 March–1 April 1975. **Philippines:** Mature female (9.7 mm), mature male (3.1 mm on SEM stub) (USNM 1283380), infesting male *Calcinus gaimardii* (4.7 mm SL), inhabiting shell of *Drupella cornus* (Röding), Cebu, Olango Island and Sulpa Islet, coll. JDW, 9 July 1997; mature female (10.2 mm), mature male (2.9 mm) (pers. coll.), infesting male *Calcinus latens* (4.2 mm SL), inhabiting shell of *D. cornus*, Oriental Mindoro, Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; mature female (7.75 mm), mature male (1.77 mm on SEM stub) (USNM 1283381), infesting intersex *Calcinus minutus* (3.6 mm SL), inhabiting shell of *D. cornus*, Oriental Mindoro, Puerto Galera, Coco Beach, coll. JDW, 14 January 1999; mature female (6.0 mm), mature male (3.0 mm) (ZRC 2015.0502), infesting female *C. latens* (3.0 mm SL), inhabiting unidentified shell, Cebu, Olango Island and Sulpa Islet, coll. JDW, 9 July 1997; mature female (7.4 mm), mature male (3.6 mm) (USNM 1283382), infesting female *C. latens* (3.3 mm SL), inhabiting unidentified shell, Oriental Mindoro, Puerto Galera, La Laguna Beach, coll. JDW, 31 July 1997; mature female (7.71 mm on SEM stub), mature male (2.8 mm on SEM stub) (USNM 1283383), infesting male *C. minutus* (3.1 mm SL), inhabiting unidentified shell, Oriental Mindoro, Puerto Galera, La Laguna Beach, coll. JDW, 18 June 2000; mature female (16.1 mm), mature male (3.0 mm) (ZRC 2015.0503), infesting female *C. gaimardii* (4.0 mm SL), inhabiting unidentified shell, Oriental Mindoro, Puerto Galera, La Laguna Beach, coll. JDW, 18 June 2000. **Australia:** Mature female (13.4 mm), mature male (2.9 mm) (MV J62873), infesting unknown host, inhabiting shell of *Phasianella ventricosa* (fide label), Cape Wickham, King Island, Tasmania, 39°35'S 143°57'E, coll. Marine Research Group of Victoria, 9 March 1980; juvenile female (3.9 mm) (MV J62879), infesting *Areopaguristes tuberculosus* (fide label), inhabiting unknown shell, eastern Bass Strait, Victoria, 39°51'11"S 148°38'32"E, 51 m depth, coll. Marine Research Group of Victoria, 28 September 1980; 2 mature females

(8.2, 12.2 mm), juvenile female (6.5 mm), 2 males (1.8, 3.2 mm) (MV J62881), infesting unknown hosts, inhabiting unknown shells, Victoria, coll. unknown; 8 mature females (7.5–11.1 mm), 5 juvenile females (3.0–6.0 mm), mature male (3.0 mm) (MV J62882), infesting unknown host, inhabiting unknown shells, Flinders, Victoria, 29°S 145°02'E, coll. S. W. Fulton & F. E. Grant, 31 December 1900; mature female (9.8 mm) (MV J62895), infesting *A. tuberculosus* (fide label), inhabiting unknown shell, 5.31 nautical miles off Barracoota [oil rig], 8 nm off shore, 16.14 nm off Snapper, Victoria, 23 fms (= 42.1 m), coll. N. Coleman, early November 1987; 2 mature females (12.2, 16.2 mm), mature male (3.6 mm) (MV J62872), infesting *Paguristes sulcatus* (fide label), inhabiting *P. ventricosa* (fide label), Naracoopa, King Island, Tasmania, 39°55'11"S 144°07'35"E, coll. Marine Research Group of Victoria, 8 March 1980; mature female (10.4 mm), mature male (3.3 mm) (MV J62868), infesting female *P. sulcatus* (8.2 mm SL), inhabiting unknown shell, Shoreham, Westernport Bay, Victoria, 38°25'S 145°03'E, coll. J. A. Kershaw, 30 March 1902. **Taiwan:** Mature female (10.2 mm), mature male (3.0 mm) (USNM 1283405), infesting female *Calcinus vachoni* (3.5 mm SL), inhabiting unknown shell, Haikou, Pingtung, coll. R. Yoshida, 30 June 2011; mature female (9.0 mm), mature male (2.7 mm) (USNM 1283406), infesting male *C. vachoni* (3.6 mm SL), inhabiting unknown shell, Chuanfanshih, Pingtung, coll. R. Yoshida, 27 July 2011; mature female (10.1 mm), mature male (2.9 mm) (USNM 1283407), infesting female *C. vachoni* (3.5 mm SL), inhabiting unknown shell, Aimen Beach, Penghu, coll. R. Yoshida, 4 August 2011; mature female (8.5 mm), mature male (2.2 mm) (USNM 1283407), infesting female *C. vachoni* (3.2 mm SL), inhabiting unknown shell, Aimen Beach, Penghu, coll. R. Yoshida, 4 August 2011.

With Male Form B: Indonesia: Mature female (2.4 mm), mature male (2.0 mm) (LACM CR19755891), infesting male *Calcinus laevimanus*, inhabiting unknown shell, Indonesia, Banda Islands, Stn. 5b, north side Banda Besar, south side of Selat Lontor (04°32.2'S, 129°53'E), coll. E. Ball et al., 7 April 1975. **Philippines:** Mature female (5.5 mm) with female *Cabirops* sp., immature male (1.2 mm) (USNM 1283384), infesting intersex *C. latens* (2.7 mm SL), inhabiting shell of *D. cornus*, Batangas, Sombrero Island, coll. JDW, 5 July 1997; mature female (8.4 mm) with epicaridium larvae, mature male (2.5 mm) (ZRC 2015.0504), infesting female *Diogenes* sp. (3.4 mm SL), inhabiting shell of *Strombus* sp., Cebu, Mactan Island, Maribago, coll. JDW, 7 July 1997; mature female (6.5 mm), mature male (2.8 mm) (ZRC 2015.0505), infesting female *C. minutus* (3.3 mm SL), inhabiting unidentified shell, Oriental Mindoro, Puerto Galera, La Laguna Beach, coll. JDW, 31 July 1997; immature female (2.9 mm on SEM stub), mature male (1.8 mm on SEM stub), cryptoniscus (0.6 mm on SEM stub) (USNM 1283385), infesting female *C. gaimardii* (3.1 mm SL), inhabiting shell of *Tenguella granulata* (Duclos), Batangas, Sombrero Island, coll. JDW, 31 July 1997; mature female (7.2 mm), mature male (2.5 mm) (USNM 1283386), infesting female *C. minutus* (4.4 mm SL), inhabiting shell of *Latirolagena smaragdulus* (Linnaeus), Oriental Mindoro, Puerto Galera, La Laguna Beach, coll. JDW, 31 July 1997;

mature female (7.3 mm), mature male (2.7 mm) (USNM 1283387), infesting intersex *C. latens* (2.3 mm SL), inhabiting shell of *Tenguella granulata*, Oriental Mindoro, Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; mature female (7.0 mm), mature male (2.4 mm) (USNM 1283388), infesting male *C. latens* (3.6 mm SL), inhabiting shell of *Drupella rugosa* (Born), Oriental Mindoro, Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; mature female (9.9 mm), mature male (3.0 mm on SEM stub, pers. coll.) (USNM 1283389), infesting female *C. gaimardii* (4.0 mm SL), inhabiting shell of *D. rugosa*, Puerto Galera, Coco Beach, coll. JDW, 14 January 1999; mature female (7.4 mm), mature male (2.8 mm) (USNM 1283390), infesting male *C. minutus* (3.6 mm SL), inhabiting shell of *D. rugosa*, Oriental Mindoro, Puerto Galera, Coco Beach, coll. JDW, 15 April 1999; mature female (5.0 mm), mature male (2.2 mm) (USNM 1283391), infesting intersex *C. minutus* (3.3 mm SL), inhabiting shell of *Cypraea* sp., Bataan, Morong, coll. JDW, 25 April 1999; mature female (10.8 mm), mature male (3.9 mm) (USNM 1283392), infesting female *C. gaimardii* (3.9 mm SL), inhabiting shell of *D. cornus*, Batangas, Anilao, coll. JDW, 13 February 1999; mature female (9.4 mm), mature male (2.7 mm) (pers. coll.), infesting male *C. minutus* (3.6 mm SL), inhabiting shell of *D. cornus*, Batangas, Anilao, coll. JDW, 13 February 1999; mature female (8.1 mm), mature male (2.9 mm) (USNM 1283393), infesting intersex *C. minutus* (3.6 mm SL), inhabiting shell of *D. rugosa*, Batangas, Anilao, coll. JDW, 13 February 1999; mature female (10.7 mm), mature male (3.1 mm) (USNM 1283394), infesting female *C. latens* (2.8 mm SL), inhabiting shell of *Cypraea* sp., Bataan, Morong, coll. JDW, 28 February 1999; immature female (1.86 mm on SEM stub), mature male (1.1 mm) (USNM 1283395), infesting female *Calcinus pulcher* (2.2 mm SL), inhabiting unidentified shell, Cebu, Mactan Island, Maribago, coll. JDW, 10 July 1997; mature female (8.1 mm), mature male (3.0 mm) (USNM 1283396), infesting female *C. minutus* (3.8 mm SL), inhabiting unidentified shell, Oriental Mindoro, Puerto Galera, La Laguna Beach, coll. JDW, 28 July 1997; mature female (12.3 mm), mature male (3.3 mm) (USNM 1283397), infesting female *C. latens* (2.1 mm SL), inhabiting unidentified shell, Bataan, Mabayo, coll. JDW, 21 February 1999; mature female (7.3 mm), mature male (2.6 mm) (USNM 1283398), infesting female *C. minutus* (3.6 mm SL), inhabiting unidentified shell, Oriental Mindoro, Puerto Galera, La Laguna Beach, coll. JDW, 27 March 1999; juvenile female (4.1 mm), mature male (2.02 mm) (USNM 1283399), infesting male *C. gaimardii* (2.18 mm SL), inhabiting unidentified shell, Batangas, Sombrero Island, coll. JDW, 10 June 2000; juvenile female (2.1 mm), mature male (0.99 mm) (USNM 1283400), infesting male *C. minutus* (2.4 mm SL), inhabiting unidentified shell, Batangas, Sombrero Island, coll. JDW, 10 June 2000.

Male Form Unknown: Tuvalu: Mature holotype female of *Athelgue aniculi* (9.1 mm) (AM G-1423), infesting *Aniculus typicus* Dana, 1852 [= *A. aniculus*] (host lost), inhabiting shell of *Turbo setosus* Gmelin (fide Whitelegge, 1897) [= *T. (Marmarostoma) setosus*], Tuvalu, Funafuti [Ellice Islands, ca. 08°50'S, 177°10'E], coll. C. Hedley, between 21 May and 7 August 1896. **Indonesia:** Mature holotype female of

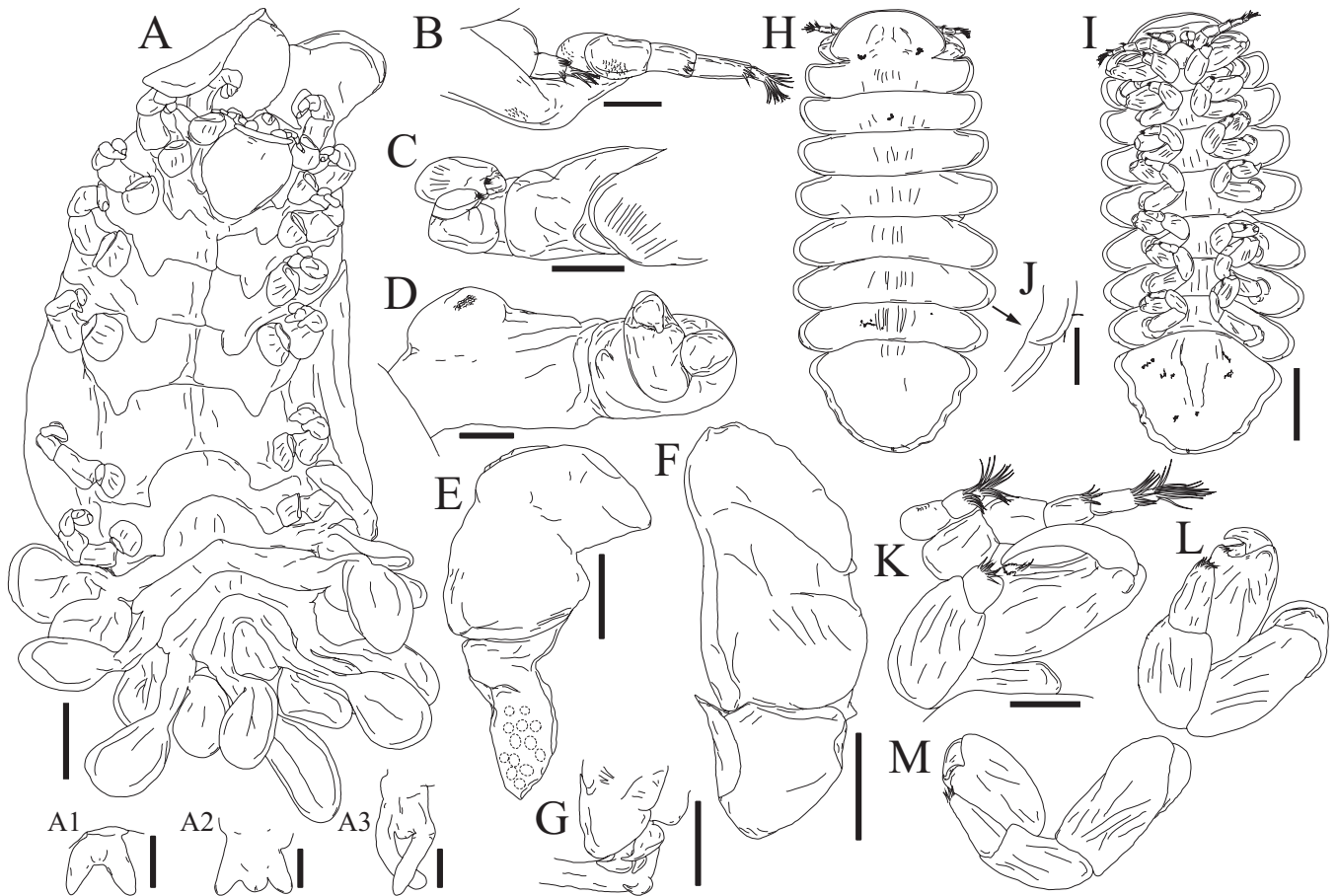


Fig. 8. *Parathelges aniculi* (Whitelegge, 1897) Form A, female (A–G), pers. coll. (A), USNM 1283382 (B–F), USNM 1283380 (G), male, pers. coll. (H–M). A, dorsal view; B, right antennule and antenna; C, left pereopod 1; D, left pereopod 7; E, left oostegite 1, outer view; F, left maxilliped, outer view; G, barbula, left side; H, dorsal view; I, ventral view; J, view of lateral notch found on pereomeres VI and VII; K, left antennulae, antenna and pereopod 1; L, left pereopod 3; M, left pereopod 7. Scale bars = 1 mm [A, E, G], 100 µm [B, K–M], 250 µm [C], 500 µm [D, F, H, I], 50 µm [J].

Parathelges weberi (11.14 mm) (ZMA), infesting unknown host (host lost), locality unknown, coll. unknown; mature female (5.0 mm) (LACM CR19755893), infesting male “*Calcinus* undescribed sp.” [= *C. lineapropodus*], inhabiting unknown shell, Indonesia, Banda Islands, Stn. 19, outside of Gunungapi (04°30.3’S, 129°52.3’E), 0–12 m, coll. E. Ball, 28–30 April 1975. **Philippines:** Immature female (3.4 mm on SEM stub) (USNM 1283401), infesting female *C. latens* (2.6 mm SL), inhabiting shell of *Peristernia* sp., Batangas, Sombrero Island, coll. JDW, 5 July 1997; mature female (13.3 mm) (USNM 1283402), infesting male *C. gaimardii* (4.4 mm SL), inhabiting unidentified shell, Cebu, Mactan Island, Maribago, coll. P. Cassidy, 29 December 1996; mature female (7.94 mm) (USNM 1283403), infesting male *C. latens* (4.84 mm SL), inhabiting unidentified shell, Cebu, Mactan Island, Maribago, coll. P. Cassidy, 29 November 1996; mature female (3.9 mm) (USNM 1283404), infesting female *C. minutus* (2.6 mm SL), inhabiting unidentified shell, Puerto Galera, Coco Beach, coll. JDW, 15 January 1999. **Taiwan:** Immature female (8.8 mm) (USNM 1283409), infesting male *Dardanus lagopodes* (7.8 mm SL), inhabiting unknown shell, Huapinyan, Shaoliuchiu, coll. R. Yoshida, 29 July 2011; mature female (7.3 mm) (USNM 1283410), infesting female *C. vachoni* (2.6 mm CL), inhabiting unknown shell, Fongguei, Penghu, coll. R. Yoshida, 4 August 2011.

Redescription. Reference female (Fig. 8A). Body length 8.8 mm, maximal width 3.9 mm, head length 1.2 mm, head width 1.2 mm, pleon length 3.6 mm. Body longer than broad; pereon slightly to moderately (~30°) recurved. All body regions and pereomeres distinctly segmented (Figs. 8A, 10A).

Head length and breadth subequal with convex lateral margins, anterior margin flattened to slightly concave, posterior margin convex (Figs. 8A, 10A). Eyes lacking. Antennule of three articles, distal ends of last two articles with setae; antenna of five articles, all articles with scales, distal ends of last three articles with setae (Fig. 8B). Maxilliped (Figs. 8F, 10B) with elongate, ovate anterior lobe lacking palp; smaller, rounded posterior lobe bearing thin, short, acute spur. Barbula (Figs. 8G, 10B) with three short, smooth tapering lobes anterolaterally; one short, smooth tapering lobe present on subsequent pereomere (see Remarks).

Pereon of seven distinct pereomeres, broadest across pereomeres V, VI, tapering anteriorly and posteriorly. Pereomere I posterior margin overlapped by head, pereomere II posteriorly convex, pereomeres III, IV posteriorly straight, pereomeres V–VII posteriorly concave; pereomeres II–VII with posterolateral flaps near base of pereopods, most pronounced on pereomeres III–V. First oostegites extended

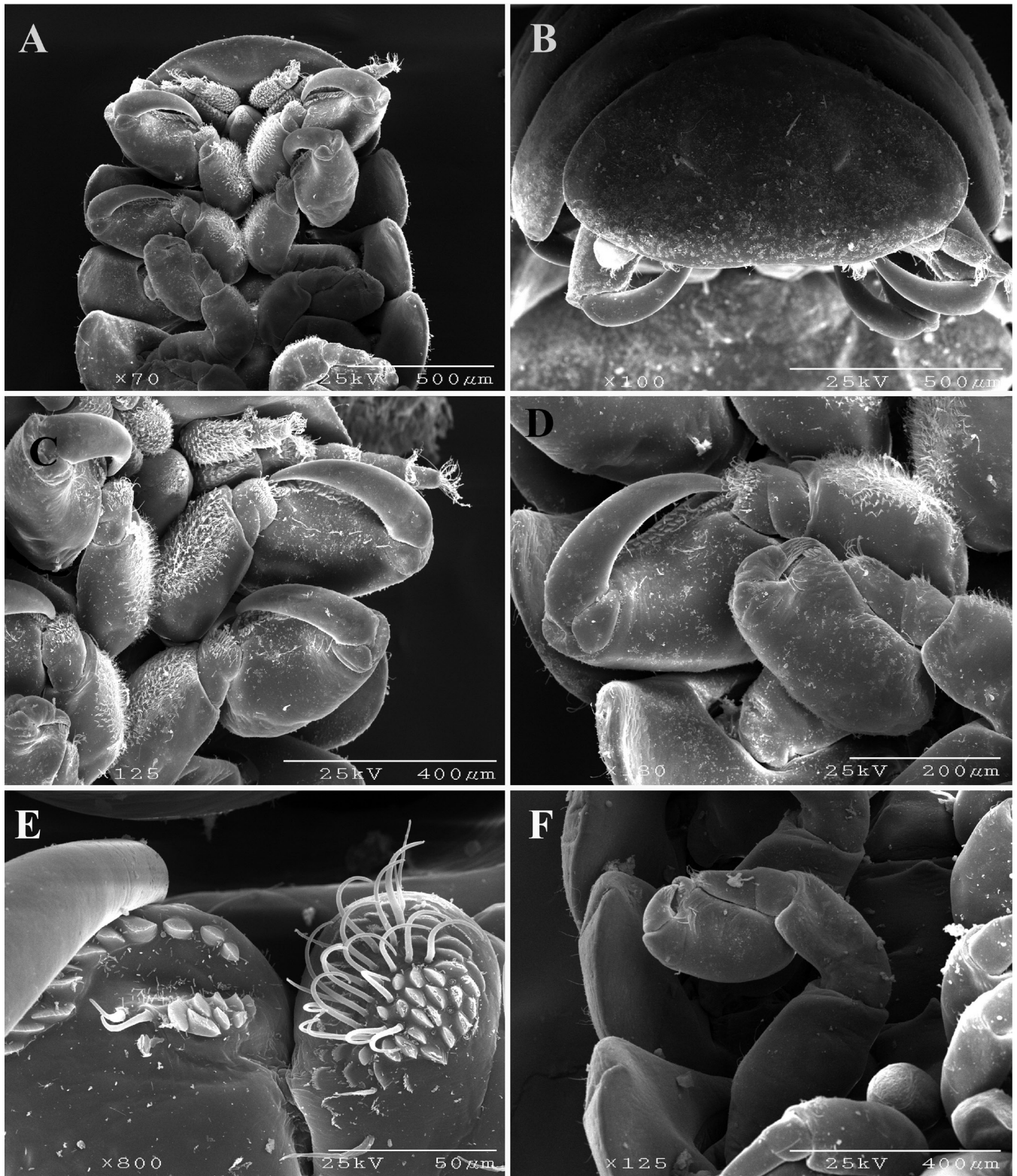


Fig. 9. *Parathelges aniculi* (Whitelegge, 1897) Form A, scanning electron micrographs of male, USNM 1283383 (A–D), USNM 1283380 6-31-87 (E, F). A, ventral view of anterior end; B, dorsal view of head, showing cephalic slits (presumptive sensory structures, see Bourdon et al., 1981); C, left antennule, antenna, pereopods 1 and 2; D, left pereopods 2 and 3; E, right pereopod 2, detail of distal end of dactyl, propodus and carpus; F, right pereopod 7. Scale bars = 500 μ m [A, B], 400 μ m [C, F], 200 μ m [D], 50 μ m [E].

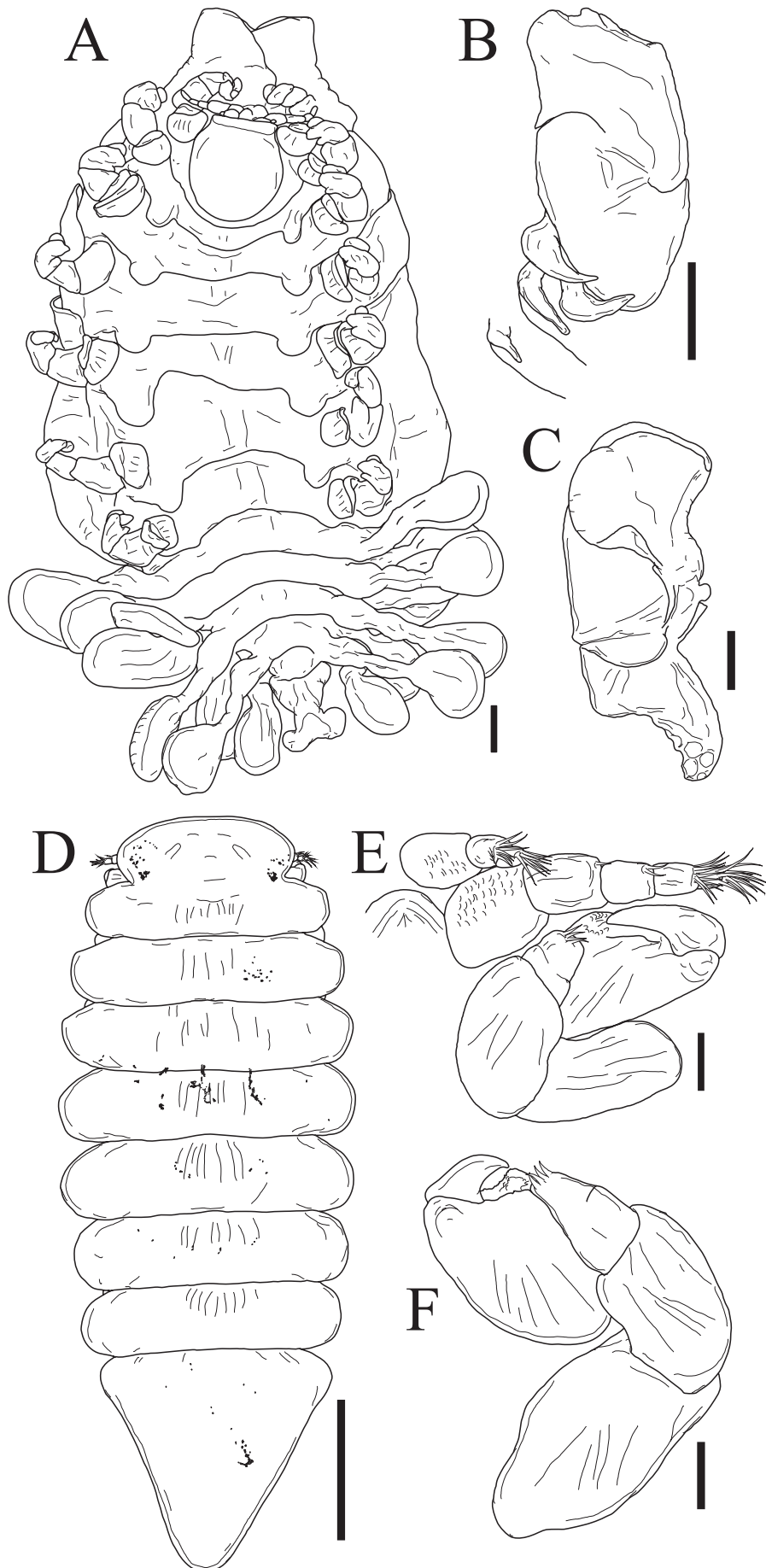


Fig. 10. *Parathelges aniculi* (Whitelegge, 1897) Form B, female (A–C), USNM 1283386 (A), USNM 1283397 (B, C), male, USNM 1283393 (D–F). A, dorsal view; B, right maxilliped, barbula and posterior digitate extension, inner view; C, left oostegite, inner view; D, dorsal view; E, left antennule, antenna and pereopod 1; F, right pereopod 7. Scale bars = 500 μ m [A–D], 50 μ m [E, F].

over head (Figs. 8A, 10A). Oostegites completely enclosing brood pouch; posteriormost oostegite with fringe of setae on posterior margin. First oostegite anterior lobe laterally expanded and folded, posterior lobe slightly recurved and tapering to rounded point, internal ridge smooth (Figs. 8E, 10C). All pereopods subequal in size, bases slightly longer and thinner in posterior pairs (Fig. 8A). Pereopod I (Figs. 8C, 10A) anterior to head, pereopod II parallel to head, slightly longer gap between pereopods V, VI, pereopods VI, VII with ovate lobe on ischium (Fig. 8D).

Pleon with six distinct pleomeres. Pleomeres I–IV (Figs. 8A, 10A) with elongate-ovate biramous pleopods, arising from common thick peduncle, no lateral plates; pleomere V without appendages; pleotelson with uniramous, short, tapered, posterolaterally-directed uropods (Figs. 8A1–A3, 10A).

Reference Male Form A (Fig. 8H, I). Length 3.1 mm, maximum width 1.4 mm, head length 0.3 mm, head width 0.8 mm, pleon length 0.8 mm. Head subovate, widest medially, tapering posteriorly, fused with pereomere I. Eye pigmentation present at lateral junction of head and first pereomere, pronounced angled pair of cephalic slits either side of midline (Fig. 9B). Antennule of three articles (Figs. 8K, 9A, C), distalmost two articles distally setose, first and second articles covered in scales with filamentous extensions. Antenna (Figs. 8K, 9A, C) of five articles, extending posterolaterally from head, distalmost article with tuft of long setae, penultimate article with distal row of long setae, third article with ventrolateral subdistal row of short setae, second article with numerous short rows of scales with filamentous extensions, first article covered in scales with filamentous extensions.

Pereomeres IV, V broadest, tapering anteriorly and posteriorly. All pereomeres directed laterally with rounded lateral margins; pereomeres VI, VII with posterolateral small notch and setae (Fig. 8J). First two pairs of pereopods (Figs. 8K, 9D, E) with longer dactyli than posterior pairs (first and second subequal), dactyli strongly recurved and slightly twisted, touching base of propodus anterolateral to base of raised medial region on ventral surface of propodus. Dactyli of pereopods III (Figs. 8L, 9D) through VII (Figs. 8M, 9F) with broad, thin scales distally. Propodi of first and second pereopods much larger than other pairs, ventral surface with two to three medially offset rows of denticles distally reduced to one curved row proximally, short group of denticles and few short setae on opposite side forming pocket into which distal point of dactylus inserts. Carpi and meri of first and second pereopods (Fig. 9A, D, E) much shorter and stouter proportionally to other segments of other pereopods, all articles distinctly separated, distal margin of carpus with tuft of short setae and raised area of bladelike denticles, ventral surface of basis with scales with filamentous extensions.

Pleon (Figs. 8H, I) ovate with slightly expanded anterior portion, tapering posteriorly, all pleomeres fused with

lateral indication of segmentation. No midventral tubercles, pleopods, or uropods (Fig. 8I).

Reference Male Form B (USNM 1283393) (Fig. 10D). Length 2.9 mm, maximum width 1.1 mm, head length 0.2 mm, head width 0.7 mm, pleon length 0.8 mm. Head subovate, widest medially, tapering posteriorly, fused with pereomere I (Fig. 10D). Irregular eye pigmentation present at lateral junction of head and first pereomere, pronounced angled pair of cephalic slits either side of midline. Antennule of three articles (Figs. 10E, 11A, B), distalmost two articles distally setose, first and second articles covered in scales with filamentous extensions. Antenna (Figs. 10E, 11A, B) of five articles, extending posterolaterally from head, distalmost article with tuft of long setae, penultimate article with distal row of long setae, third article with ventrolateral subdistal row of setae and few scales, second article with numerous short rows of scales with short filamentous extensions, first article covered in scales with short filamentous extensions.

Pereomeres IV, V broadest, tapering anteriorly and posteriorly. All pereomeres directed laterally with rounded lateral margins. First two pairs of pereopods (Figs. 10E, 11C, E) with slightly longer dactyli (first slightly longer than second) than posterior pairs (Figs. 10F, 11D, F), moderately recurved and inserting at base of medial raised region on ventral surface of propodus (Fig. 11C), otherwise subequal in size to other pereopods. Ventral surface of propodi with two to three medially offset rows of denticles distally reduced to one curved row proximally, short group of denticles and few short setae on opposite side forming pocket into which distal point of dactylus inserts. Carpi and meri of first and second pereopods of similar proportions to other segments as in other pereopods, all articles distinctly separated, distal margin of carpus with tuft of short setae and raised area of bladelike denticles, ventral surface of bases with scales with short filamentous extensions (Fig. 11C).

Pleon subtriangular, tapering posteriorly (Fig. 10D), all pleomeres fused without lateral indication of segmentation; posterior margin rounded. No midventral tubercles, pleopods, or uropods.

Cryptoniscus larva (USNM 1283385) (Fig. 12). Length 665 μ m, maximum width 265 mm at pereomere 2; body tear-drop shaped (Fig. 12A). Cuticular surface smooth, covered with numerous thin setae (Fig. 12B, D).

Head anterior margin concave, posterior margin concave, widest at posterolateral junction with pereomere 1 (Fig. 12A). Eyes lacking. Antennule of three articles (Figs. 12C), smooth, basal article approximately three times longer than broad, distomesial region with tuft of setae, article 2 proximolateral and distolateral regions each with a tuft of setae, article 3 with distal setae and aesthetascs (Figs. 12C). Antennae of eight articles (four peduncular and four flagellar) (Fig. 12A, D), articles 1–3 cylindrical, smooth (Fig. 12D); flagellar articles much narrower than peduncular articles, proximal three with a pair of terminal setae, distalmost

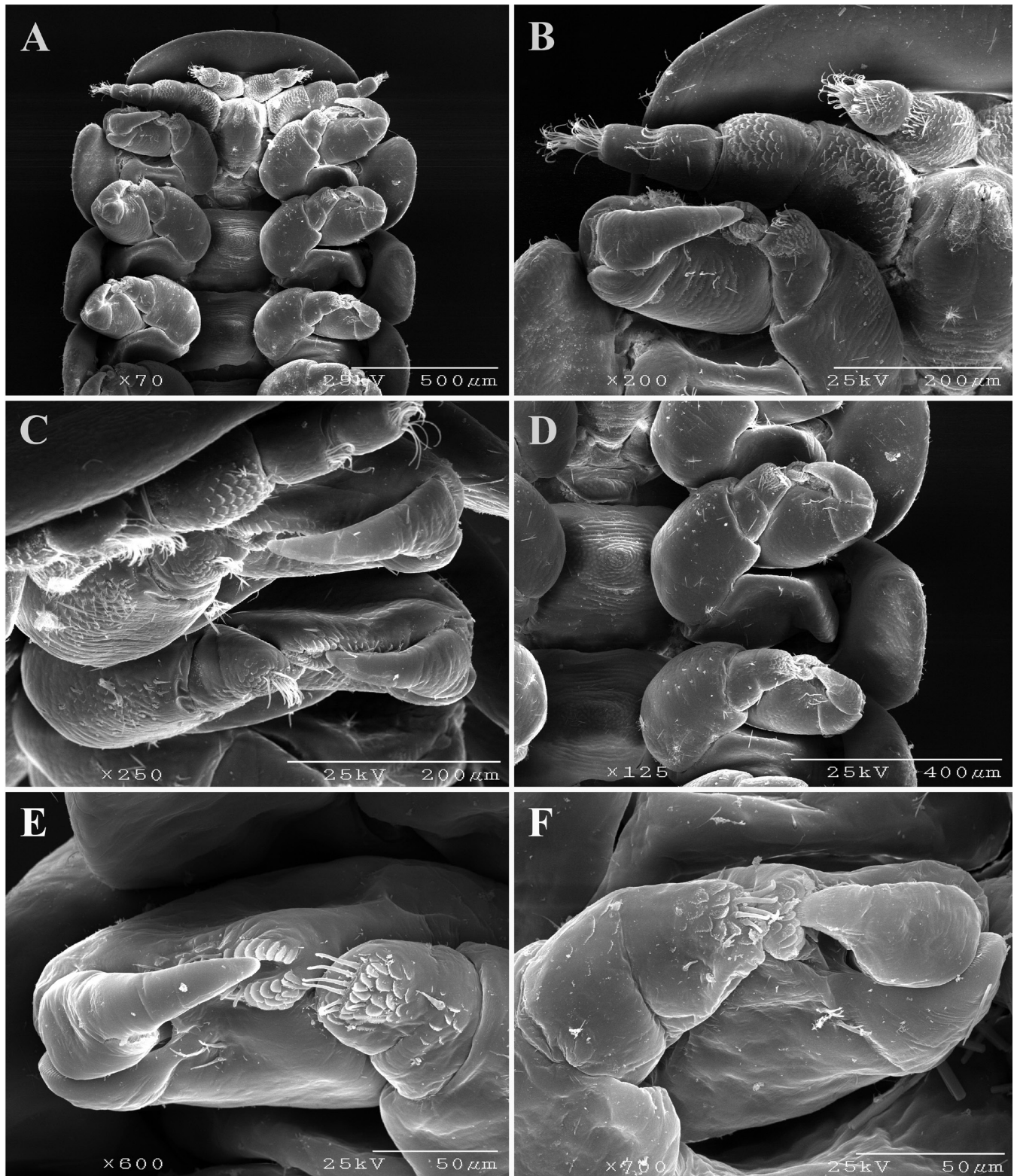


Fig. 11. *Parathelges aniculi* (Whitelegge, 1897) Form B, scanning electron micrographs of male, USNM 1283389 (A–D), USNM 1283385 (E, F). A, ventral view of anterior end; B, right antennule, antenna and pereopod 1; C, right antenna, pereopods 1 and 2, oblique view; D, right pereopods 2 and 3; E, right pereopod 2, detail of distal end of dactyl, propodus and carpus; F, left pereopod 7. Scale bars = 500 μ m [A], 200 μ m [B, C], 200 μ m [D], 50 μ m [E, F].

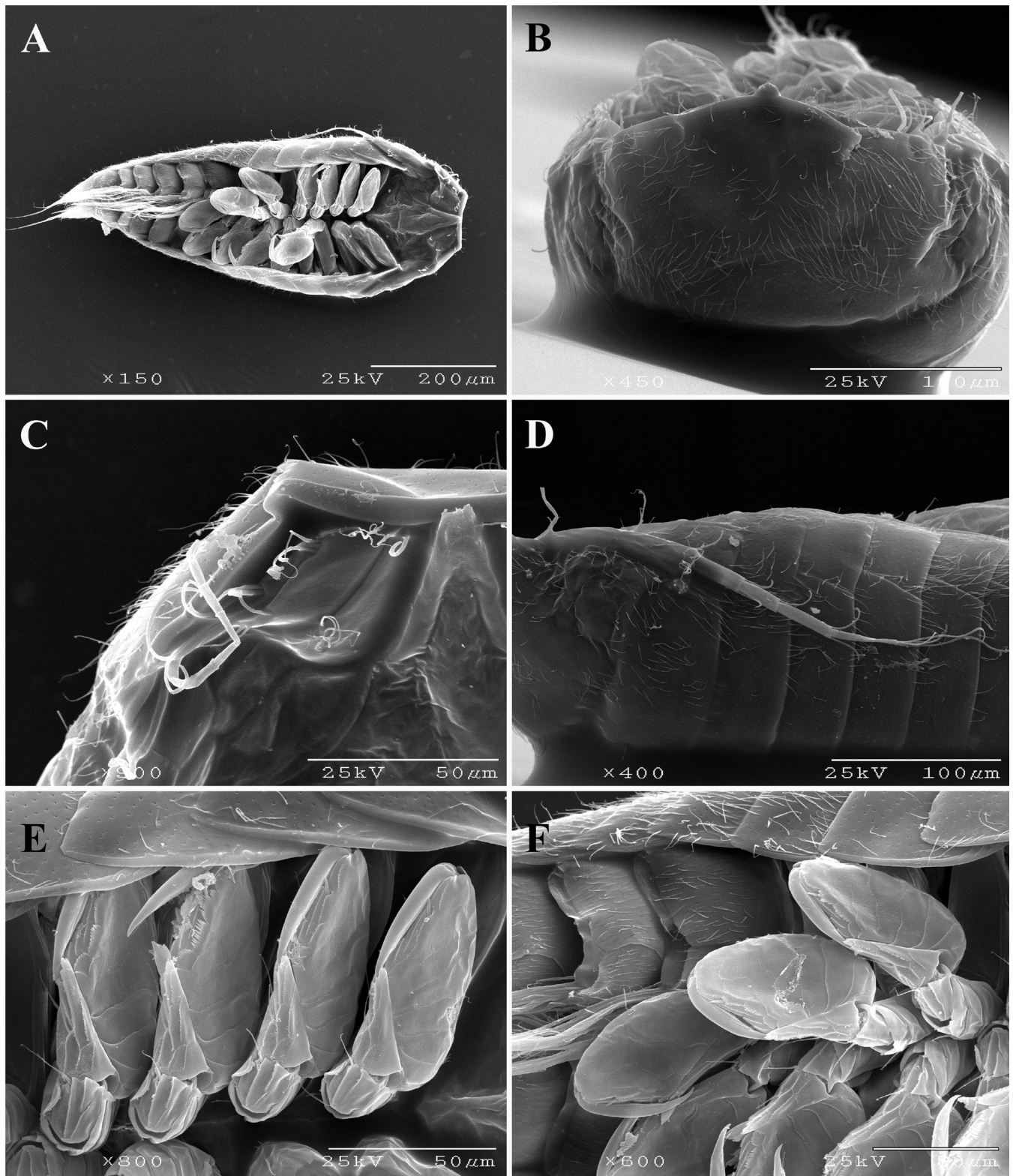


Fig. 12. *Parathelges aniculi* (Whitelegge, 1897) Form B, scanning electron micrographs of cryptoniscus larva, USNM 1283385 (A-F). A, ventral view; B, head, dorsal view; C, right antennule, ventral view; D, right antenna, laterodorsal view; E, right pereopods 1-4; F, right pereopods 5-7. Scale bars = 200 μ m [A], 100 μ m [B, D], 50 μ m [C, E, F].

article longest with distal tuft of elongate setae. Oral cone triangular, anteriorly directed (Figs. 12A, C).

Pereomere 1 broadest, tapering posteriorly. Body pigmentation lacking. Pereomeres with entire (not toothed) coxal plates 1–7 (Fig. 12A). Pereopods 1–7 isomorphic, dactyli entire (non-bifid), smooth, long and straight with ventral setal comb, stout seta 1/3 distance from base of dactylus (Fig. 12E); propodi with few cuticular ridges lined with very short setae (Fig. 12E); ventral surfaces of carpi and meri with few cuticular ridges, distoventral edge of merus with one long seta (Fig. 12E).

Pleon with 5 pleopods composed of basis (sympod), exopod, and endopod, all covered with short, thin setae (Fig. 12A). Endopods and exopods with plumose setae (Fig. 12A). Pleotelson quadrangular, endopods approximately twice as long as exopods, basis with 1 distolateral seta, endopods and exopods with terminal setae (Fig. 12A).

Type localities. *Athelgue aniculi*: Tuvalu, Funafuti (Whitelegge, 1897); *Parathelges weberi*: “unbekannt” (Nierstrasz & Brender à Brandis, 1923); *Parathelges whiteleggei*: “Javasee” [Indonesia] (Nierstrasz & Brender à Brandis, 1931).

Distribution. Tuvalu (Whitelegge, 1897), “Netherländischen-Ostindien” (Nierstrasz & Brender à Brandis, 1929), Indonesia (Nierstrasz & Brender à Brandis, 1931, Form A; Haig & Ball, 1988, Form A, B), Papua New Guinea (Ball & Haig, 1972, herein; Form A, herein), Australia: Queensland (Markham, 2010), Victoria (Form A, herein), China: South Sea (An et al., 2011), Philippines (Forms A, B, herein).

Hosts. Diogenidae: *Areopaguristes tuberculosus* (Whitelegge, 1900) (herein, Form A), *Aniculus aniculus* (Whitelegge, 1897), *Calcinus gaimardii* (herein, Form A, B), *Calcinus laevimanus* (Ball & Haig, 1972; Haig & Ball, 1988), *Calcinus latens* (herein, Forms A, B), *Calcinus minutus* (herein, Forms A, B), *Clibanarius* sp., *Dardanus hessii* (Nierstrasz & Brender à Brandis, 1931; herein, Form A), *Dardanus* sp. (Markham, 2010), *Paguristes sulcatus* (herein, Form A), *Pseudopaguristes monoporus* (Haig & Ball, 1988, Form A), *Spiropagurus* sp. (An et al., 2011), *Diogenes* sp. (herein, Form B).

Size Range (Length). With Male Form A: Females: to 16.2 mm (herein), males: to 3.6 mm (herein); with Male Form B: Females: to 12.3 mm (herein), males: to 3.9 mm (herein).

Remarks. Markham (2010) included all records of *Parathelges whiteleggei* and *P. weberi* in synonymy with *P. aniculi*. We examined the type specimens of *P. aniculi*, *P. whiteleggei* and *P. weberi* and agree with this synonymy. However, although females are indistinguishable, there are two male morphotypes that we designate as Form A and Form B. Characters that distinguish *P. aniculi* Form A and Form B are: dactyli on pereopods 1 and 2 much more elongate and recurved compared to those of pereopods 3–7

(Form A; Fig. 9A) vs. dactyli on pereopods 1 and 2 subequal in length and curvature similar to those of pereopods 3–7 (Form B; Fig. 11A), antennae and pereopods with longer setae in Form A (Fig. 9A) than in Form B (Fig. 11A). The two male morphotypes are identified separately in the material examined in the present study; prior records require re-examination. Future molecular studies are needed to determine whether the two forms represent interspecific variation or cryptic species. Unfortunately, the holotype of *Athelgue aniculi* was not accompanied by a male. In addition, *P. enoshimensis* Shiino, 1950 may be a synonym of *P. aniculi* but re-examination of topotypic material is necessary.

The barbula was defined by Markham (1988) as the processes occurring on the posteroventral border of the head of a female bopyrid. *Parathelges aniculi* exhibits a barbula with three lobes (Markham, 2010; herein); however, a fourth lobe similar in shape and appearance occurs posterolaterally to the barbula (see Figs. 8G, 10B) on what appears to be the second pereomere and as such is not part of the barbula proper. This structure does not appear to have been reported before and may be taxonomically informative. The lobes are easily overlooked unless the oostegites are fully lifted to expose the ventral side of the pereon.

Although Markham (2010) listed the type pair of *Parathelges whiteleggei* as “holotype” and “allotype,” no such designation was made by Nierstrasz & Brender à Brandis (1931) and Markham’s (2010) mention of a “holotype” is not a valid lectotype designation (ICZN, 1999; Article 74.7). We herein designate the female type specimen of *Parathelges whiteleggei* (ZMUC CRU-8616) as the lectotype. Although we did not examine the specimens reported by Ball & Haig (1972) as *P. weberi*, it is likely that this is the correct identification. The specimens identified by Markham and reported by Haig & Ball (1988) as “an undescribed species of *Athelges*” were examined and found to conform to *P. aniculi* (Form B). The pair of specimens reported by Ball & Haig (1988, as “*Parathelges ?whiteleggei*”) are confirmed to be *P. aniculi* (Form A). The type host of *Parathelges whiteleggei* was reported by Nierstrasz & Brender à Brandis (1931) and repeated by McDermott et al. (2010) as “*Pagurus* sp.” but is actually *Dardanus hessi*.

Parathelges aniculi most commonly parasitises hermit crabs in the genus *Calcinus*, although they are known from species in eight other genera (McDermott et al., 2010; herein Table 2). One *Calcinus minutus* (USNM 1283393) with *P. aniculi* (Form B) contained a pseudionine bopyrid (*Bopyrissa* sp.) in the left branchial chamber. One female of *P. aniculi* (male Form B) from the Philippines contained a hyperparasitic isopod (*Cabirops* sp.) in the brood chamber.

Genus *Pseudostegias* Shiino, 1933

Pseudostegias dulcilacuum Markham, 1982 (Figs. 13, 14)

Pseudostegias sp. Brunenmeister, 1980: 97–98; McDermott et al., 2010: 11.

Pseudostegias dulcilaicum Markham, 1982: 370–373, figs. 25, 26; Markham, 1985: 3, 53–55, 63, figs. 26–28; Page, 1985: 201, 203; Kim & Kwon, 1988: 214–215, 220, 221, fig. 9; Markham, 1992: 299; Li, 2003: 140; Morton, 2003: 37; Markham, 2009: 230–231, fig. 6; McDermott et al., 2010: 11; Markham, 2010: 153, 183–184, figs. 32, 33; An et al., 2011: 2908; Kwon, 2012: 39–40, fig. 16.

Pseudostegias dulcilaicum [sic] Page, 1985: 203.

Pseudostegias dulcilaicum [sic] Huang, 1994: 530; Huang, 2001: 327.

Pseudostegias macdermotti Williams & Boyko, 1999: 715–719, figs. 1–4; McDermott et al., 2010: 11 (**new synonym**).

Pseudostegias setoensis — Dunbar & Coates, 2000: 49, fig. 1; Dunbar, 2001: 38.—Poore et al., 2002: 116; Markham, 2010: figs. 34, 35; An et al., 2011: 2906–2910, fig. 3 (Maozhou, material only) (not *Pseudostegias setoensis* Shiino, 1933).

Material examined. Philippines: Mature female (10.2 mm) (USNM 1283411), infesting female *Calcinus gaimardii* (3.9 mm SL), inhabiting shell of *Drupella rugosa*, Oriental Mindoro, Puerto Galera, Coco Beach, coll. JDW, 12 January 1999; mature female (7.1 mm) (ZRC 2015.0506), infesting male *C. gaimardii* (3.6 mm SL), inhabiting shell of *D. rugosa*, Oriental Mindoro, Puerto Galera, Coco Beach, coll. JDW, 14 January 1999; mature female (10.6 mm), mature male (2.6 mm on SEM stub) (USNM 1283412), infesting male *C. gaimardii* (4.6 mm SL), inhabiting shell of *Polia undosa* (Linnaeus), Bataan, Morong, coll. JDW, 28 February 1999; mature female (10.6 mm) (ZRC 2015.0507), infesting female *C. gaimardii* (4.0 mm SL), inhabiting shell of *Drupella cornus*, Aklan, Boracay, Diniwid Beach, coll. JDW, 13 April 1999; mature female (8.65 mm), mature male (2.56) (USNM 1283413), infesting female *Clibanarius merguiensis* (2.1 mm SL), inhabiting unidentified shell, Puerto Galera, La Laguna Beach, coll. JDW, 17 June 2000; immature female (8.0 mm), mature male (2.43) (USNM 1283414), infesting female *C. merguiensis* (2.1 mm SL), inhabiting unidentified shell, Puerto Galera, La Laguna Beach, coll. JDW, 17 June 2000; mature female (5.12 mm), mature male (1.65) (USNM 1283415), infesting male *C. merguiensis* (1.73 mm SL), inhabiting unidentified shell, Puerto Galera, La Laguna Beach, coll. JDW, 17 June 2000.; mature female (8.65 mm), mature male (2.45) (USNM 1283416), infesting female *C. merguiensis* (2.54 mm SL), inhabiting unidentified shell, Puerto Galera, La Laguna Beach, coll. JDW, 17 June 2000; mature female (8.38 mm), mature male (2.75) (USNM 1283417), infesting female *C. merguiensis* (2.34 mm SL), inhabiting unidentified shell, Puerto Galera, La Laguna Beaches, coll. JDW, 17 June 2000; mature female (8.69 mm), mature male (2.53 mm) (USNM 1283418), infesting female *C. merguiensis* (1.85 mm SL), inhabiting unidentified shell, Puerto Galera, La Laguna Beach, coll. JDW, 17 June 2000; mature female (5.6 mm on SEM stub) (USNM 1283419), infesting male *C. gaimardii* (3.23 mm SL), inhabiting unidentified shell, Puerto Galera, La Laguna Beach, coll. JDW, 28 July 1997; mature female (9.24 mm), mature male (2.66 mm) (USNM 1283420), infesting female *C. gaimardii* (2.9 mm SL), inhabiting unidentified shell, Bataan, Mabayo, coll. JDW, 21 February 1999; ovigerous female (8.6 mm), mature male (2.3 mm) (USNM 1283421), infesting female *C. gaimardii* (2.8 mm SL), inhabiting *D. cornus*, Puerto Galera, La Laguna Beach, coll. JDW, 18 June 2000. **Taiwan:** Mature female (12.7

mm) (USNM 1283422), infesting female *Calcinus morgani* (3.9 mm SL), inhabiting unknown shell, Haikou, Pingtung, coll. R. Yoshida, 30 June 2011; mature female (10.4 mm), mature male (2.4 mm) (USNM 1283423), infesting female *C. morgani* (4.8 mm SL), inhabiting unknown shell, Siadiao, Pingtung, coll. R. Yoshida, 26 July 2011; mature female (11.5 mm), mature male (2.5 mm) (USNM 1283424), infesting female *C. morgani* (4.2 mm SL), inhabiting unknown shell, Huapinyan, Shaoliuchiu, coll. R. Yoshida, 29 July 2011; immature female (8.0 mm) (USNM 1283425), infesting male *C. morgani* (5.5 mm SL), inhabiting unknown shell, Huapinyan, Shaoliuchiu, coll. R. Yoshida, 29 July 2011; female (1.9 mm) (USNM 1283426), infesting male *Diogenes tumidus* (4.5 mm SL), inhabiting unknown shell, Siwei, Penghu, coll. R. Yoshida, 2 August 2011.

Type locality. Tolo Harbor, Hong Kong (Markham, 1982).

Distribution. Hainan, China (An et al., 2011), Hong Kong (Markham, 1982), Thailand (Markham, 1985), South Korea (Kim & Kwon, 1988), Singapore (Markham, 2009), Australia: Queensland (Markham, 2010), Philippines (herein), Taiwan (herein).

Hosts. Diogenidae: *Calcinus gaimardii* (herein), *Calcinus morgani* (herein), *Clibanarius merguiensis* (Brunenmeister, 1980; Markham, 1985; herein), *Clibanarius taeniatum* (H. Milne Edwards, 1848), *Clibanarius virescens* (Krauss, 1843) (Markham, 2010), *Diogenes* aff. *edwardsii* (De Haan, 1849) (Markham, 1982), *Diogenes pallescens* Whitelegge, 1897 (Markham, 2009), *Diogenes* sp. (possibly aff. *edwardsii*) (Kim & Kwon, 1988), *Diogenes tumidus* (herein).

Size range (Length). Females: to 11.5 mm (herein), males: to 3.6 mm (Markham, 1985).

Remarks. *Pseudostegias dulcilaicum* (Figs. 13, 14) and *P. setoensis* (Fig. 15) are similar, but can be distinguished by the following characters of the female: barbula a pair of smooth slender lobes lateral to a broad smooth ovate medial lobe in *P. dulcilaicum* (Fig. 13B) vs. multiple (3–4) highly digitate slender lobes (no medial lobe) in *P. setoensis* (Fig. 15B); pair of large hooked lobes on ventral surface of body under 5th oostegites lacking in *P. dulcilaicum* vs. present in *P. setoensis* (Fig. 15C, see also An et al., 2011: Fig. 4B), both species have a field of digitate extensions in the region under the 5th oostegites; 5th pleomere with pair of globose lateral plates and tubular posterior extension in *P. dulcilaicum* (Fig. 13A, C) vs. pair of kidney-shaped lateral plates and no posterior extension in *P. setoensis* (Fig. 15A, D). The males of *P. dulcilaicum* (Figs. 13D, 14) and *P. setoensis* (Fig. 15E) are very similar, although the pleotelson shape is more clearly triangular and elongate with obvious lateral segmentation traces in *P. dulcilaicum* (Figs. 13D, 14A, F) vs. more rounded and with little to no segmentation traces laterally in *P. setoensis* (Fig. 15E).

Although Markham (1982) indicated that the holotype of *P. dulcilaicum* was deposited in the USNM, it was never received there and the whereabouts of the type specimen

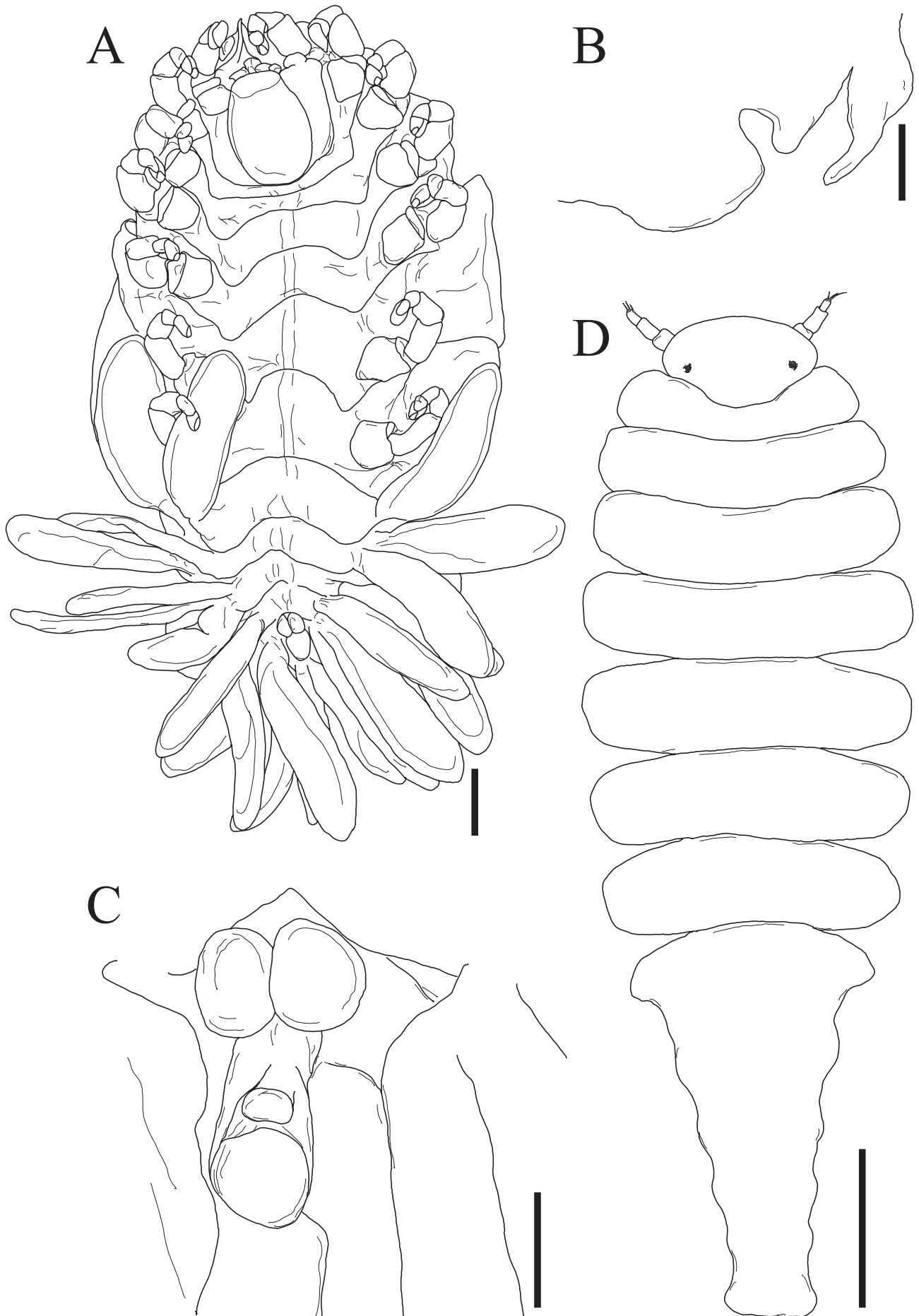


Fig. 13. *Pseudostegias dulcilacuum* Markham, 1982, female, USNM 1283412 (A, C); USNM 1283422 (B); male, USNM 1283412 (D). A, dorsal view; B, left barbula; C, fifth lateral plates; D, dorsal view. Scale bars = 1 mm [A], 250 µm [B, C], 500 µm [D].

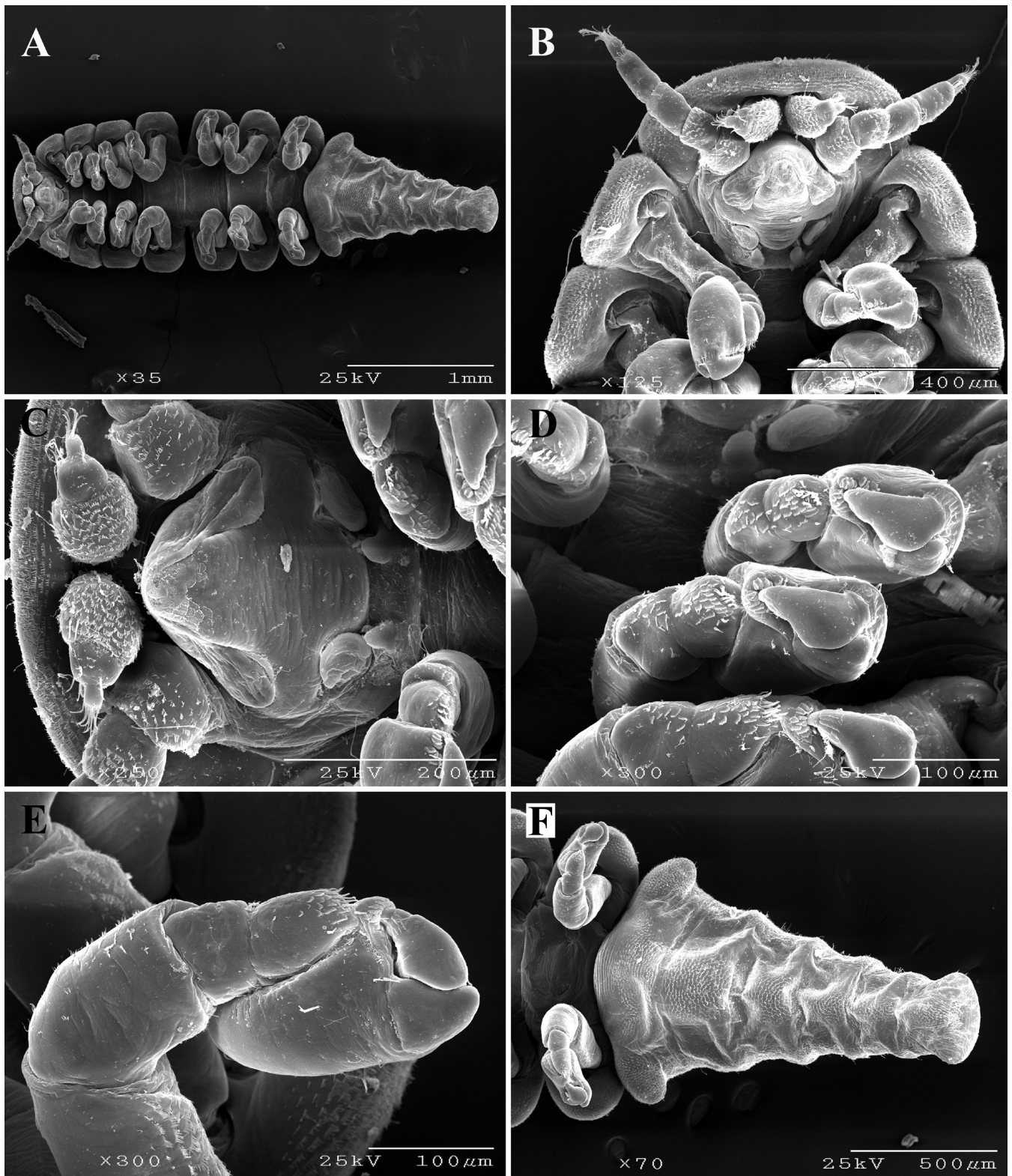


Fig. 14. *Pseudostegias dulcilacuum* Markham, 1982, scanning electron micrographs of male, USNM 1283412 (A–F). A, ventral view; B, ventral view of head, showing antennules, antennae, oral cone, and first pereopods; C, antennules and oral cone; D, left pereopods 1 and 2; E, left pereopod 7; F, pleon. Scale bars = 1 mm [A], 400 µm [B], 200 µm [C], 100 µm [D, E], 500 µm [F].

is unknown. Markham (2010) reported *P. dulcilacuum* and *P. setoensis* from Australia; however, although his figures 32 and 33 were correctly labeled as *P. dulcilacuum*, his figures 34 and 35 were incorrectly labeled as being *P. setoensis* because the material they are based on was listed by Markham (2010) under *P. dulcilacuum* and the figures match *P. dulcilacuum* in all details. Markham (2010) cited *Clibanarius* sp. as a host for *P. dulcilacuum* but Dunbar & Coates (2000) listed *C. taeniatus* and *C. virescens*, so the host “sp.” of Markham (2010) is actually *C. taeniatus*.

An et al. (2011) commented on the possible synonymy of *P. dulcilacuum* with *P. setoensis* but the present material does not support this conclusion. An et al.’s (2011) material was a mixture of *P. dulcilacuum* (Chinese mainland) and *P. setoensis* (Hong Kong).

Examination of this large series of specimens from varied localities in different stages of development has resulted in the conclusion that *Pseudostegias macdermotti* Williams & Boyko, 1999, described from Bali on *C. gaimardii*, is a junior synonym of *P. dulcilacuum* and was based (in part) on an immature female whose 5th lateral plates were likewise immature and not yet fully separated. The host of the types of *P. macdermotti* was originally identified as *C. gaimardii*, but Rahayu & Forest (1999) showed that “*C. gaimardii*” was a species complex and described *C. morgani* as a new species. The host of *P. macdermotti* matches the shield coloration of *C. morgani*. Additional specimens of *P. dulcilacuum* were obtained from *C. morgani* in Taiwan (see Material Examined).

Pseudostegias setoensis Shiino, 1933

(Fig. 15)

Pseudostegias setoensis Shiino, 1933: 290–293, fig. 16; Shiino, 1950: 161, 162; Shiino, 1952: 35, 36; Shiino, 1958: 68; Lemos de Castro, 1965: 105, 106–108; Shiino, 1972: 9; Markham, 1982: 369–373, 385; Morton & Morton, 1983: 96, 98, 201, fig. 7.5, table 10.2; Markham, 1985: 3, 51–52, 55, 63, fig. 25, table 1; Page, 1985: 201, 203; Harada, 1991: 202; Markham, 1992: 299, table 1; Huang, 1994: 530; Williams & Boyko, 1999: 720; Saito et al., 2000: 45; Kensley, 2001: 226; Kensley & Chan, 2001: 481; Poore et al., 2002: 116; Li, 2003: 140, 155, table 1; Markham, 2003: 72, 73; Boyko, 2004: 677; Markham, 2010: 184–195 (references only); McDermott et al., 2010: 11 (table); An et al., 2011: 2906–2910, figs. 4, 5 (Hong Kong specimens only).

?*Pseudostegias setoensis* — Markham, 1994: 226, 247–249, fig. 17; Markham, 2010: 185 (material examined) (see Remarks).

?*Pseudostegia* [sic] *setoensis* — Bruce, 2007: 278 (see Remarks).

Not *Pseudostegias setoensis* — Dunbar & Coates, 2000: 49, fig. 1; Poore et al., 2002: 116; Markham, 2010: fig. 34, 35; An et al., 2011: 2906–2910, fig. 3 (Maozhou material only) [= *Pseudostegias dulcilacuum* Markham, 1982].

Material examined. Taiwan: Immature female (3.6 mm), mature male (0.8 mm) (USNM 1283427), infesting female *Clibanarius virescens*, Aimen Beach, Penghu, coll. R. Yoshida, 4 August 2011; 3 mature females (9.2 mm, 8.5 mm and 7.5 mm), immature female (5.2 mm), 3 mature male

(3.8 mm, 3.0 mm and 1.5 mm) (USNM 1283427), infesting *C. virescens* (parasites detached from four female hosts (3.3 mm, 3.4 mm, 3.7 mm SL) and one male host (5.1 mm SL)), Aimen Beach, Penghu, coll. R. Yoshida, 4 August 2011.

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

Distribution. Japan (Shiino, 1933), Taiwan (Shiino, 1958), Hong Kong (Markham, 1982; An et al., 2011), Thailand (Markham, 1985), possibly Chesterfield Islands, New Caledonia (Markham, 1994, but see Remarks).

Hosts. Diogenidae: *Clibanarius bimaculatus* (De Haan, 1849) (Shiino, 1933), *C. padavensis* de Man, 1888 (Markham, 1985), *C. ransoni* Forest, 1953 (Markham, 1982), *C. striolatus* Dana, 1852 (Shiino, 1958), *C. virescens* (new host), possibly *Strigopagurus boreonotus* Forest, 1995 (Markham, 1994, see Remarks).

Size range (Length). Females: to 16.5 mm (Shiino, 1958), males: to 3.8 mm (herein).

Remarks. Based on a preliminary examination in 2002 by one of us (CBB) of the MNHN Chesterfield Islands and New Caledonia material reported on by Markham (1994; later cited by Bruce, 2007), we suspect that these specimens are not *Pseudostegias setoensis* but probably represent an undescribed species. Several attempts by MNHN museum staff to locate these specimens were unsuccessful until recently, when they were found but unfortunately arrived on loan to us after the review process was completed for the present paper. See Remarks under *P. dulcilacuum* for the characters that distinguish *P. setoensis* from *P. dulcilacuum* and for comments on the mislabeling of the Australian specimens figured by Markham (2010: figs. 34, 35) as *P. setoensis* (= *P. dulcilacuum*). The present record is the second for *P. setoensis* from Taiwan; the first was from Shiino (1958). *Clibanarius virescens* was erroneously reported as a host of *P. setoensis* by Dunbar & Coates (2000) in Australia but that material is referable to *P. dulcilacuum* (Markham, 2010: figs. 34, 35). *Pseudostegias setoensis* is now known from *C. virescens* in Hong Kong (see An et al., 2011) and Taiwan.

Pseudostegias trisagitta n. sp.

(Figs. 16, 17)

Material examined. Mature holotype female (8.9 mm), mature allotype male (2.3 mm) (USNM 1283428), infesting intersex *Calcinus minutus* (2.9 mm SL), inhabiting shell of *Drupella rugosa*, Oriental Mindoro, Puerto Galera, Coco Beach, coll. JDW, 14 January 1999.

Type locality. Philippines, Oriental Mindoro, Puerto Galera: Coco Beach (13°30'N, 120°56'E).

Description. Holotype female (Fig. 16A, B): Body length 8.9 mm, maximal width 3.8 mm, head length 1.5 mm, head width 0.9 mm, pleon length 2.7 mm. Body longer than broad;

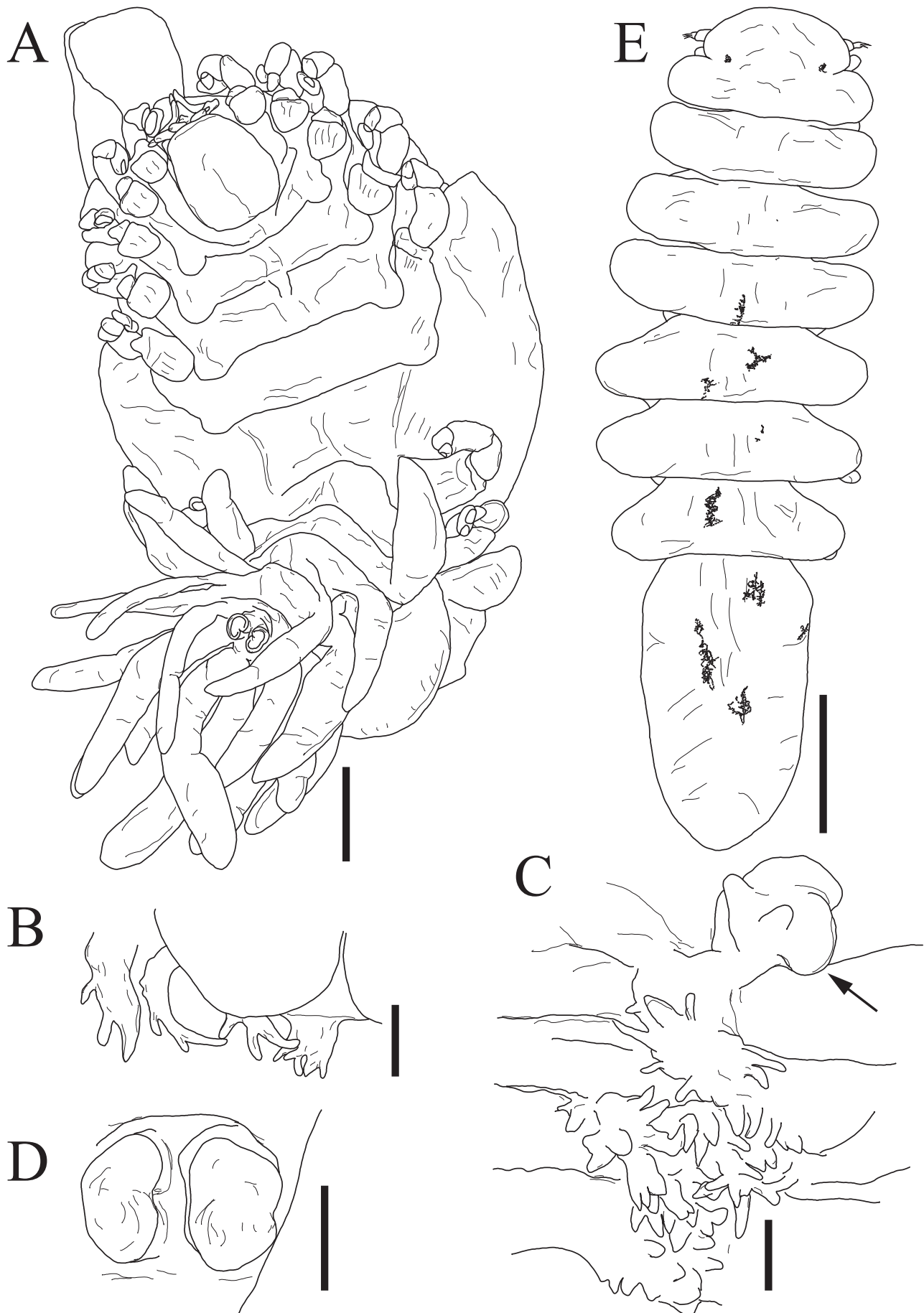


Fig. 15. *Pseudostegias setoensis* Shiino, 1993, female, USNM 1283427 (A–D); male, USNM 1283427 (E). A, dorsal view; B, barbula, left side; C, ventral surface of posterior pleonites under fifth oostegites showing large hooked lobe (arrow) and posterior field of digitate extensions; D, fifth set of lateral plates; E, dorsal view. Scale bars = 1 mm [A], 250 μ m [B–D], 500 μ m [E].

pereon straight. All body regions and pereomeres distinctly segmented but pereomeres II–V with indistinct segmentation medially (Fig. 16A).

Head 1.5 times longer than wide with weakly convex lateral margins, anterior margin convex, posterior margin weakly convex (Fig. 16A). Small eyespots anterolaterally. Antennule of three articles, distal ends of terminal article with setae; antenna of five articles, distal end of terminal article and subdistal region of third article with setae (Fig. 16C). Maxilliped (Fig. 16D) with elongate, triangular anterior lobe lacking palp; smaller, rounded posterior lobe without spur. Barbula (Figs 16E) with one short, smooth tapering lobe anterolaterally.

Pereon of seven distinct pereomeres, broadest across pereomeres IV, V, tapering anteriorly and posteriorly. Pereomere I posterior margin overlapped by head, pereomere II posteriorly convex, pereomeres III–VII posteriorly straight, pereomeres II–VII with small posterolateral flaps near base of pereopods, most pronounced on pereomeres II, III, V, VI. First oostegites not extended over head (Fig. 16A, B). Oostegites completely enclosing brood pouch; posteriormost oostegite with fringe of setae on posterior margin. First oostegite anterior lobe irregularly rounded, posterior lobe with ovate proximal region and elongate tapering posterior region, internal ridge with three short thin smooth projections mesially (Fig. 16F, G). Pereopods I–V subequal in size with ventrally projecting meral segments (Fig. 16H–J), pereopods VI, VII with distinctly more slender bases than pereopods I–V (Fig. 16A). Pereopod I (Figs. 16A, H) anterior to head, pereopods II, III parallel to head, distinctly longer gap between pereopods V, VI (Fig. 16A).

Pleon with six pleomeres, segmentation distinct. Pleomeres I–IV with elongate lateral plates approximately three times as long as wide (Fig. 16A) and weakly biramous anteroposteriorly directed pleopods (Fig. 16B). Pleomere V with pair of dorsally indented and triangular medially positioned lateral plates on either side of a small medial knob (Fig. 16J) and pair of biramous laterally directed pleopods similar in shape and proportion to lateral plates of segments I–IV (Fig. 16A). Pleomere VI with uniramous uropods, similar in shape and proportion to pleomeres I–IV lateral plates; single dorsally indented and triangular medially positioned lobe, identical to lateral plates of pleomere V (Fig. 16J).

Allotype male (Fig. 17): Length 2.3 mm, maximum width 0.8 mm, head length 0.2 mm, head width 0.4 mm, pleon length 0.6 mm. Head subovate, widest proximally, tapering anteriorly, medially fused with pereomere I (Fig. 17A). Eye pigmentation present at distal lateral junction of head and first pereomere (Fig. 17A). Antennule of three articles (Fig. 17B), all articles with distal setae. Antenna (Fig. 17C) of seven articles, extending posterolaterally from head, distalmost article with tuft of long setae, proximal four articles with distolateral setae.

Pereomeres IV, V broadest, tapering anteriorly and posteriorly. All pereomeres directed laterally with rounded lateral margins (Fig. 17A). Pereopods isomorphic (Figs. 17B, C, D), all articles distinctly separated, dactyli recurved and straight, touching base of propodus in raised medial region on ventral surface.

Pleon (Fig. 17A, B) equilaterally triangular with slightly expanded anterior portion, tapering posteriorly, all pleomeres fused with lateral indications of segmentation. No midventral tubercles, pleopods, or uropods (Fig. 17B).

Etymology. Named for the distinctive shapes of the structures on the fifth pleomere ventral surface resembling three diverging arrowheads.

Distribution. Known only from the Philippines in Oriental Mindoro province.

Host. *Calcinus minutus*.

Size range (Length). Female: 8.9 mm, male: 2.3 mm.

Remarks. In nearly all aspects, excepting the pleopod length/width proportions and the shape and proportions of the dorsal lobes on the fifth pleomere, the female of the new species resembles most closely that of *P. dulcilacuum*. The female of the new species has a much lower pleopod length to width ratio than *P. dulcilacuum*. We considered that the distinctive shape of the lobes on the fifth pleomere might represent an artifact of preservation but we can find no other altered structures on the female that would indicate this; additionally, the proportions of the lobes are quite different from those seen in the most similar species, *P. dulcilacuum*. The new species has two dorsally triangular subequal lobes on the fifth pleomere and one on the sixth pleomere while *P. dulcilacuum* has three dorsally rounded lobes with the anteriormost two being much larger than the posterior one. A fourth smaller rounded lobe is seen on the new species at the junction of the three triangular lobes; this lobe could be homologous with the fourth lobe seen in some specimens of *P. dulcilacuum* (e.g., Fig. 13C) but it has not been described from most specimens of *P. dulcilacuum*. Another character of interest is the number of lobes of the barbula which presents as a single lobe in the new species but has been variously reported without comment as one or two lobes in *P. dulcilacuum*. It is not clear whether this represents intraspecific variation. The males of the new species and *P. dulcilacuum* are very similar, albeit that most males reported for *P. dulcilacuum* have proportionally longer pleons.

Calcinus minutus has not been previously reported as a host of any *Pseudostegias* species, and we found no specimens referable to *P. dulcilacuum* on this host during the present study.

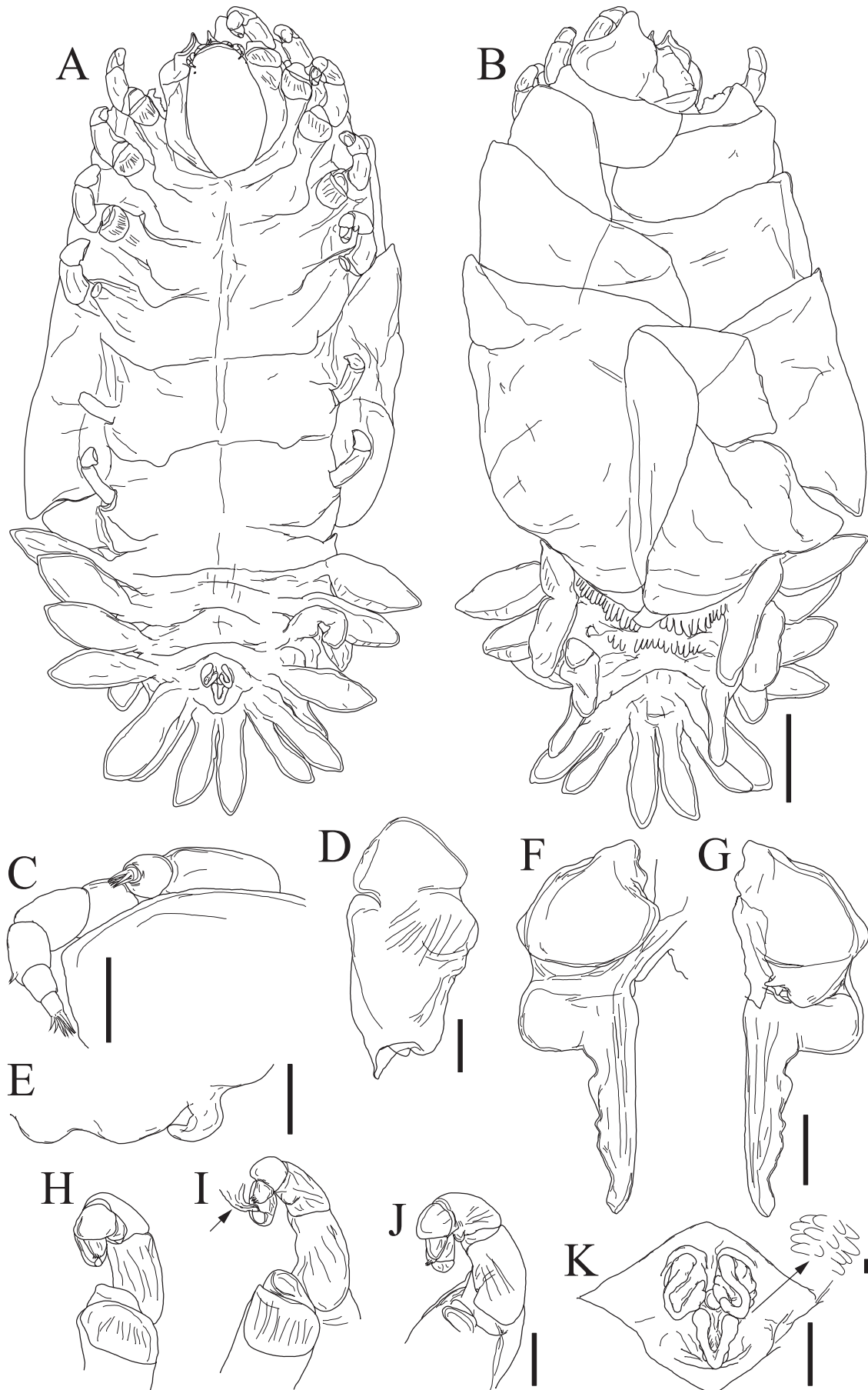


Fig. 16. *Pseudostegias trisagitta* n. sp., female holotype, USNM 1283428 (A–K). A, dorsal view; B, ventral view; C, antennae; D, left maxilliped, outer view; E, barbula, left side; F, left oostegite 1, outer view; G, left oostegite 1, inner view; H, right pereopod 1; I, right pereopod 3, host cuticle in dactyl shown by arrow; J, right pereopod 5; K, fifth lateral plates, inset showing scales. Scale bars = 1 mm [A, B], 100 μ m [C], 500 μ m [E–G], 250 μ m [D, H–K], 5 μ m [K inset].

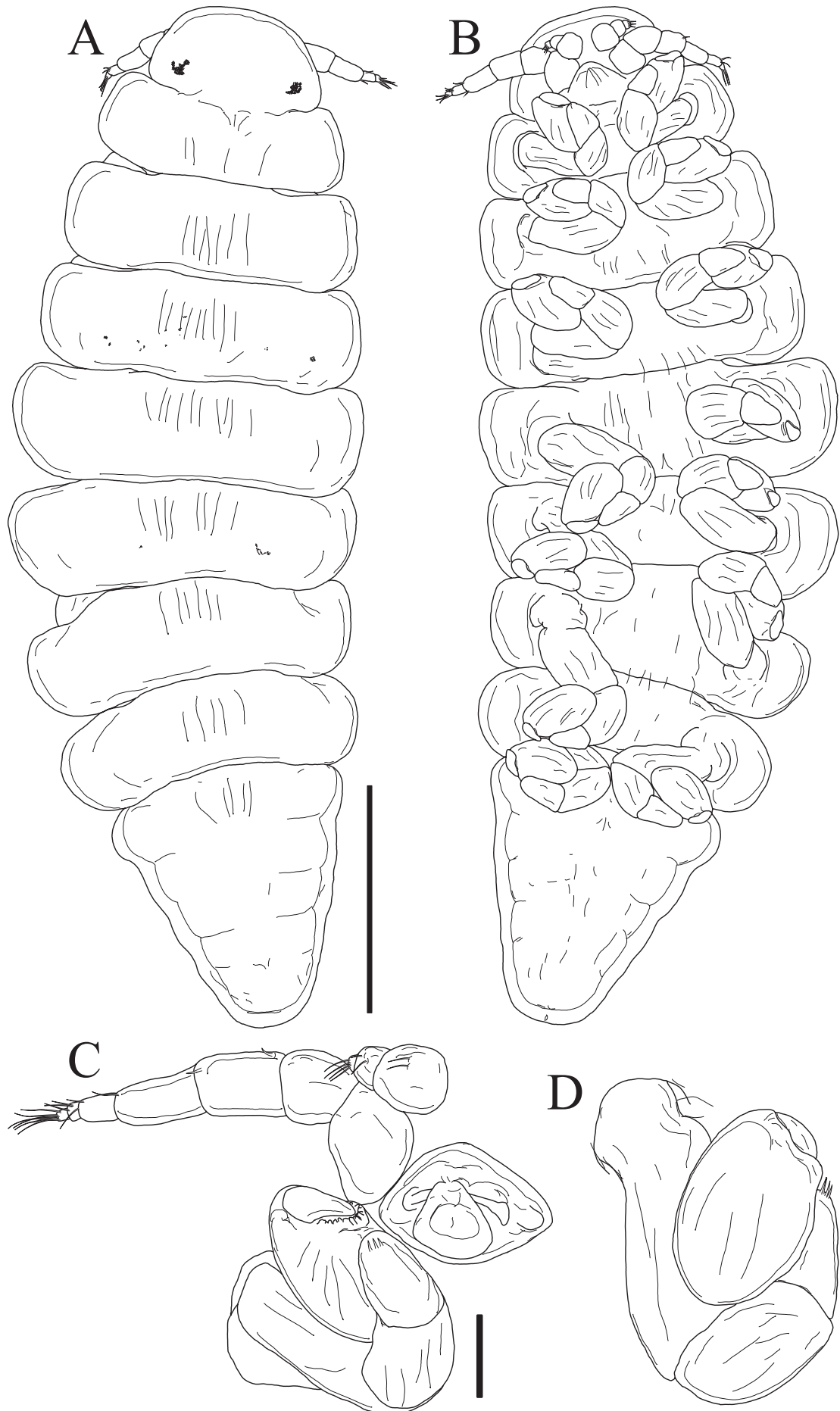


Fig. 17. *Pseudostegias trisagitta* n. sp., male allotype, USNM 1283428 (A–D). A, dorsal view; B, ventral view; C, left antennae and pereopod 1; D, right pereopod 7. Scale bars = 500 μm [A, B], 50 μm [C, D].

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