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Parasites (Isopoda: Epicaridea and Nematoda) from ghost and mud shrimp (Decapoda: Axiidea and Gebiidea) with descriptions of a new genus and a new species of bopyrid isopod and clarification of *Pseudione* Kossmann, 1881

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Table of contents

Abstract	252
Introduction	252
Methods and materials	253
Taxonomy	253
Isopoda Latreille, 1817	253
Bopyroidea Rafinesque, 1815	253
Ionidae H. Milne Edwards, 1840	253
<i>Ione</i> Latreille, 1818	253
<i>Ione cornuta</i> Bate, 1864	254
<i>Ione thompsoni</i> Richardson, 1904	255
<i>Ione thoracica</i> (Montagu, 1808)	256
Bopyridae Rafinesque, 1815	260
Pseudioninae Codreanu, 1967	260
<i>Acobelione</i> Bourdon, 1981	260
<i>Acobelione halimedae</i> n. sp.	260
Key to females of species of <i>Acobelione</i> Bourdon, 1981	262
<i>Gyge</i> Cornalia & Panceri, 1861	262
<i>Gyge branchialis</i> Cornalia & Panceri, 1861	262
<i>Gyge ovalis</i> (Shiino, 1939)	264
<i>Ionella</i> Bonnier, 1900	265
<i>Ionella agassizi</i> Bonnier, 1900	265
<i>Ionella compressa</i> (Shiino 1964) n. comb.	266
<i>Orthione</i> Markham, 1988	266
<i>Orthione furcata</i> (Richardson, 1904)	266
<i>Progebiophilus</i> Codreanu & Codreanu, 1963	268
<i>Progebiophilus bruscai</i> Salazar-Vallejo & Leija-Tristan, 1990	268
<i>Progebiophilus upogebiae</i> (Hay, 1917)	269
<i>Pseudione</i> Kossmann, 1881	273
<i>Pseudione callianassae</i> Kossmann, 1881	274
<i>Pseudione longicauda</i> Shiino, 1937	278
<i>Robinione</i> n. gen.	278
<i>Robinione overstreeti</i> (Adkison & Heard, 1995) n. comb.	279
Rhabditida Chitwood, 1933	282
Physalopteridae Railliet, 1893	282
<i>Heliconema</i> Travassos, 1919	282
<i>Heliconema</i> sp.	282
Acknowledgements	284
References	284

Abstract

Ghost and mud shrimps in Axiidea and Gebiidea are hosts to parasitic epicaridean isopods, including species in Bopyridae and Ionidae. These isopods can reach high prevalence levels on their mud shrimp hosts and may strongly influence host ecology and biology. Currently, 54 species of bopyrids and eight species of ionids are known to parasitize ghost and mud shrimps. We present new taxonomic data on three species of ionids and ten species of bopyrids (nine previously described and one new to science), as well as on an undescribed species of nematode from an axiidean host. New locality and host records are given for all species. Our analysis of new material and review of museum specimens includes the description of the new species *Acobelione halimeda* n. sp. from *Austinogebia spinfrons* (Haswell, 1881). We also provide an improved definition for the genus *Pseudione* Kossmann, 1881, based on morphological characters found in both sexes, and resolution of the type species, *P. callianassae* Kossmann, 1881. In our revision of *Pseudione* we erect a new genus, *Robinione*, and placed two species therein: *R. overstreeti* (Adkison & Heard, 1995) and *R. brattstroemi* (Stuardo, Vega & Cespedes, 1986). In addition, two other species are removed from *Pseudione*: *P. compressa* (Shiino, 1964) is moved to *Ionella* Bonnier, 1900, and *P. panopei* Pearse, 1947 is considered a synonym of *Progebiophilus upogebiae* (Hay, 1917). Bopyrid isopods represent a large, diverse taxon and our findings help clarify the taxonomy of those species found on ghost and mud shrimps.

Key words: Bopyridae, Ionidae, Physalopteridae, taxonomy

Introduction

Ghost and mud shrimps in the families Axiidea and Gebiidea have body forms adapted for burrowing in soft benthic substrates. For many years, these two taxa were united under Thalassinoidea, but recent studies have shown this taxon is not monophyletic (e.g., Robles *et al.* 2009, and review in Poore *et al.* 2014). Nevertheless, the similarity in body shape and habitats of species in these two groups appears to be so similar as to allow species of parasitic isopods (e.g., members of Bopyridae and Ionidae), and in some cases even individuals of the same species, to switch from hosts in one infraorder to the other. Therefore, although Axiidea+Gebiidea is a paraphyletic grouping, it is useful to consider their constituent species as a morphologically homogenous host assemblage from the perspective of their bopyrid parasites. Ecologically, bopyrids are known to infest mud shrimps at some of the highest reported prevalence levels for these parasitic isopods, having the potential to dramatically impact host populations, and thus their hosts' potential for bio-engineering of soft bottom ecosystems (Griffen 2009; Ubaldo *et al.* 2014; Pascal *et al.* 2016; Dairain *et al.* 2017). Mud shrimps are also host to the only documented case of an introduced epicaridean parasite (Williams & An 2009; Chapman *et al.* 2012; Hong *et al.* 2015). This parasite, *Orthione griffenis* Markham, 2004, has had profound impacts on populations of their ecosystem engineer hosts (Chapman & Carter 2014).

Taken together, axiideans and gebiideans make up the fourth largest group of decapods parasitized by bopyrid isopods, after caridean shrimp, anomurans, and brachyurans (Boyko & Williams 2009). Three of the 10 subfamilies of Bopyridae (Keponinae, Phyllodurinae, Pseudioninae) contain species that parasitize ghost and mud shrimp, as do all of the species in the monogenic Ionidae. Currently, 54 species of bopyrids and all species of *Ione* Latreille, 1818, are known from host species in these two infraorders. This represents 8.5% of bopyrid species (54/639) and all of the ionid species (8/8) (Boyko 2013). Species in Keponinae and Pseudioninae are known to occur on hosts in both infraorders, whereas the sole species in Phyllodurinae is known only from gebiidean hosts. Only 7% (7/100) of keponine species are found on axiidean and gebiidean hosts, whereas 19% (47/233) of pseudionines are found on them. Of the 17 bopyrid genera that contain species parasitizing axiidean and gebiidean hosts, only two, *Acobelione* Bourdon, 1981, and *Progebiophilus* Codreanu & Codreanu, 1963, contain species reported from hosts in both infraorders. Lastly, there is an entoniscid reported from *Gebiacantha acutispina* (de Saint-Laurent & Ngoc-Ho, 1979) but it was never described and its identity and affinities remain unknown (de Saint-Laurent & Ngoc-Ho 1979).

In the present paper, we report on three species of ionids and nine species of bopyrids, all previously described, as well as on an undescribed species of nematode from an axiidean host. We provide new locality and host records for all of these species, and describe a new species of *Acobelione* Bourdon, 1981, from Singapore. The genus *Pseudione* Kossmann, 1881, is clarified by resolving the identity of its poorly described type species: *Pseudione callianassae* Kossmann, 1881. Finally, four species are removed from *Pseudione*: 1) *Pseudione overstreeti*

Adkison & Heard, 1995, is made the type species of *Robinione* **n. gen.** and *P. brattstroemi* Stuardo, Vega & Cespedes, 1986 is also moved to that genus, 2) *Pseudione compressa* Shiino, 1964, is moved to *Ionella* Bonnier, 1900, and 3) *Pseudione panopei* Pearse, 1947, is relegated to synonymy with *Progebiophilus upogebiae* (Hay, 1917).

Methods and materials

Subsequent to The Crustacean Society summer meeting in Galveston, Texas (June 2008), two of the authors (CBB, JDS) travelled to the University of Louisiana, Lafayette (ULLZ: University of Louisiana-Lafayette Zoological Collections) to study the extensive collection of ghost and mud shrimp (Axiidea and Gebiidea) present there. Approximately 220 lots were examined, containing in excess of 1000 specimens belonging to at least 30 species. Specimens of *Callichirus islagrande* (Schmitt, 1935), *C. santarosaensis* Sakai and Türkay, 2012, *Lepidophthalmus louisianensis* (Schmitt, 1935), *Neotrypaea gigas* (Dana, 1852), *N. uncinata* (H. Milne Edwards, 1837), *Nihonotrypaea japonica* (Ortmann, 1891), *N. cf. petalura* (Stimpson, 1860), *Upogebia dawsoni* Williams, 1986, and *U. felderii* Williams, 1993 parasitized by either epigarideans or nematodes were found in the collection and borrowed for morphological study and molecular analysis. All parasites were identified as far as practicable based on morphological characters. All epigaridean specimens were sampled for DNA analysis, although only DNA from the parasite of *N. japonica* was successfully amplified (see Boyko *et al.* 2013).

In addition to the ULLZ collections, the authors examined specimens from the following collections: Florida Museum of Natural History (UF); Museum National d'Histoire Naturelle, Paris, France (MNHN); National Museum of Victoria, Melbourne, Australia (NMV), National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); National Science Museum of Tokyo (NSMT); Naturhistorisches Museum Wien, Austria (NHMW); Yale Peabody Museum of Natural History, Invertebrate Zoology collection (YPM IZ); and the Zoological Reference Collection, Lee Kong Chian Natural History Museum (formerly the Raffles Museum) (ZRC).

Line drawings were made with a camera lucida drawing tube attached to Olympus compound or dissecting microscopes. Final images were created by tracing a scanned copy of the original sketch with a Wacom Cintiq pen display using Adobe Illustrator. In addition to conventional light micrographs, some specimens were imaged with a Macropod Pro kit (MacroscopicSolutions) and resulting pictures were aligned and stacked with the focus stacking software Zerene Stacker (10–65 images from bottom to top of specimens). For scanning electron microscopy (SEM), specimens were dehydrated in an ascending ethanol series and run through a critical point drier (SAMDRI-795). After drying, the specimens were attached with double-sided sticky tape to aluminum stubs and coated with gold in an EMS-550 sputter coater. Images were taken using a FEI Quanta 250 SEM.

Carapace length (CL) is provided as an indicator of size for the hosts. Isopod size is given as total body length (anterior margin of head to posterior margin of pleotelson). Measurements were made to 0.1 mm using an ocular micrometer or micro-scale tool (Electron Microscopy Services). Maximal length measurements of nematode specimens were recorded from light micrographs and ImageJ software.

In areas of the text where abbreviation of generic names might cause confusion (e.g., *Pseudione* and *Progebiophilus*) we have spelled the names out in full. Bibliographic references are provided for authors and dates of all parasite taxa but not for those of host species.

Taxonomy

Isopoda Latreille, 1817

Bopyroidea Rafinesque, 1815

Ionidae H. Milne Edwards, 1840

Ione Latreille, 1818

Ione cornuta Bate, 1864

Ione cornuta Bate, 1864: 668 (type locality: east side of Vancouver Island, British Columbia, Canada, infesting *Callianassa longimana* Stimpson, 1856 = *Neotrypaea gigas* (Dana, 1852)).—Bate & Westwood, 1862: 253 (mention).—Giard & Bonnier, 1887a: 41, 63 (list), 77 (list).—Perrier, 1893: 1021 (mention).—Richardson, 1899a: 869 (list).—Richardson, 1899b: 338 (list).—Bonnier, 1900: 48, 61, 62, 222, 245–247 (discussion of characters).—Richard, 1900: 71 (list).—Richardson, 1900: 308 (key).—Gerstaecker & Ortmann, 1901: 185 (list), 266 (list).—Giard, 1904: 592 (mention).—Richardson, 1904: 75 (list), 77–78 (comparison with other *Ione* species).—Richardson, 1905: 504–505 (repeat of the description by Bate, 1864), 510 (mention).—Giard, 1913: 420 (mention).—Nierstrasz & Brender à Brandis, 1923: 80 (list).—Nierstrasz & Brender à Brandis, 1931: 180–182, figs. 57–59 (Vancouver, British Columbia, Canada, infesting unknown host).—Hiraiwa, 1933: 55 (mention).—Caspers, 1939: 243 (list).—Shiino, 1939a: 13–16, fig. 2, 3 (Seto, Japan, infesting *Nihonotrypaea japonica* (Ortmann, 1891)).—Hatch, 1947: 164 (list), 225 (characters, host list, distribution), pl. 9, figs. 113–115 (figures after Richardson, 1905).—Codreanu & Codreanu, 1956a: 577, 580, 583 (mention).—Codreanu & Codreanu, 1956b: 120 (mention).—Gooding, 1957: 698 (Hammond Bay, Nanaimo, British Columbia, Canada, first mention of this species infesting *Callianassa californiensis* Dana, 1854 = *Neotrypaea californiensis* (Dana, 1854)).—Danforth, 1963a: 8, 33, 43 (list), pl. 8, figs. 1–3.—Shiino, 1964a: 30, 32 (mention).—Schultz, 1969: 316 (mention; erroneous statement that the species was never illustrated).—Danforth, 1970b: 10, 17, 47 (list), 79–80 (translation of description from Bonnier, 1900), 147 (key), fig. 22a–c.—Shiino, 1972: 8 (list).—Miller, 1975: 285, 286 (key), 305 (list), pl. 64, fig. 19.—Rudy & Rudy, 1979: 152 (mention).—Bird, 1982: 52, 54, 55 (mention).—Hart, 1982: 32 (mention).—Kozloff, 1983: 301 (mention).—Austin, 1985: 587 (list).—Rafi, 1985: 12 (list).—Bourdon, 1987: 342 (key, list).—Kim & Kwon, 1988: 205–207, 220, fig. 4 (South Korea, infesting *N. japonica*).—Markham, 1992a: 3, table 1 (list).—Kozloff, 1993: 301 (mention).—Markham, 1995: 86 (mention).—Brusca *et al.*, 2001: 7 (key), 20 (list), pl. 6, fig. 32.—Saito *et al.*, 2000: 42 (list).—Markham, 2001: 197, 199, 200 (list).—Sadro, 2001: 176 (list).—Saito, 2002: 223 (list).—Itani, 2004b: 37, table 3 (Japan, infesting *Nihonotrypaea harmondi* (Bouvier, 1901), *N. japonica*, *N. petalura* (Stimpson, 1860)).—Saito & Kinoshita, 2004: 1–6, fig. 3 (prevalence in Tokyo Bay, Japan infesting *N. japonica*).—Espinosa-Pérez & Hendrickx, 2006: 237 (list).—Brusca *et al.*, 2007: 512 (key), pl. 236B.—Pernet *et al.*, 2008: 1127–1129, 1133–1134, 137–1140 (Oregon, infesting *N. californiensis*).—Yu & An, 2008: 692 (list).—An *et al.*, 2009: 235–237, fig. 6 (Shandong, Liaoning, and Zhejiang Provinces, China, infesting *N. japonica*, *N. petalura*, *N. harmondi* and *Upogebia major* (De Haan, 1841)).—Campos *et al.*, 2009: 1255 (List), 1256 (mention).—Espinosa-Pérez *et al.*, 2009: 229 (list).—Williams & An, 2009: 121–122 (mention).—Passarelli, 2010: 7, 8, 14, 20, 32, 35–38, 41, 45, 50, 52–54, 5–60 (California, infesting *N. californiensis*).—Dumbauld *et al.*, 2011: 346 (prevalence in Washington, U.S.A. infesting *N. californiensis*).—Chapman *et al.*, 2012: 1223, 1229, 1230 (mention).—Cohen, 2012: 2, 32, 46, 48 (mention).—Rudy and Rudy, 2013: 288 (mention).—Boyko *et al.*, 2013: 499 (placement on phylogenetic tree).—Chapman & Carter, 2014: 351–352 (mention).—Miura *et al.*, 2014: 31 (table), 34–35, fig. 1 (Japan, infesting *N. japonica*).—Saito, 2016: 146 (mention).

Ione cornutus—Bate, 1866: 283–284 (repeat of information from Bate, 1864).—Stebbing, 1893: 414 (list).

Ione [sic] *cornuta*—Kossmann, 1881b: 171, 181 (mention).

Ione brevicauda Bonnier, 1900: 48, 61, 222, 248–250, pl. 4 (type locality: San Francisco, California, U.S.A., infesting “*Callianassa*” sp.).—Giard, 1904: 592 (mention).—Richardson, 1905: 504–507, fig. 553 (translation of the description of Bonnier, 1900).—Giard, 1913: 419 (mention).—Fee, 1927: 36–37 (British Columbia, infesting *N. gigas*; placement into synonymy with *I. cornuta*).—Nierstrasz & Brender à Brandis, 1931: 182 (mention).—Caspers, 1939: 243 (list).—Menzies & Miller, 1954: 141, fig. 65 (illustration).—Danforth, 1963a: 43 (list).—Shiino, 1964a: 32 (mention).—Schultz, 1969: 316 (list; figure from Bonnier, 1900).—Román-Contreras, 2008a: 382 (mention).

Ione sp. Menzies & Miller, 1954: 141 (key), 153 (list).—Carlton & Kuris, 1975: 408 (mention).—Haig & Abbott, 1980: 580 (mention).—Lee & Miller, 1980: 543, fig. 21.10 (“British Columbia to California,” infesting *N. californiensis*).—Kuris *et al.*, 2007: 635 (mention).—Campos *et al.*, 2009: 1255 (list).

“parasitic isopods occur on *Callianassa*” Kozloff, 1973: 232 (occurrence in Puget Sound region on *C. californiensis* = *N. californiensis*).

“bopyrid isopod parasites” Poore, 2000: 151 (Japan, infesting *Grynaminna tamakii* Poore, 2000).

“another species of bopyrid isopod” Anonymous, 2003: 4, 3.

? “parasit bopyrid” Wardiatno, 2004: 81–84 (Japan, infesting *N. japonica*; see Remarks).

not *Ione* sp. Lamb & Hanby, 2005: 280, fig. AR19.A (= *Orthione griffenis* Markham, 2004, infesting *Upogebia pugettensis* (Dana, 1852)).

not *Ione* sp. Lamb & Hanby, 2005: 280, fig. AR19.B (= gen. et sp. indet., infesting *Acantholithodes hispidus* (Stimpson, 1860)).

Material examined. Mexico: Mature female (7.2 mm), mature male (3.3 mm), ex left branchial chamber of female *Neotrypaea gigas* (5.7 mm CL), ovigerous female (11.0 mm), mature male (6.0 mm), ex right branchial chamber of intersex *N. gigas* (8.0 mm CL), ovigerous female (9.0 mm), mature male (4.0 mm), ex left branchial chamber of female *N. gigas* (9.2 mm CL), ovigerous female (8.0 mm), mature male (4.5 mm), ex left branchial chamber of female *N. gigas* (6.0 mm CL), Bahia de Los Angeles, Baja California Norte, coll. F. Mantelatto, J. Cuesta & R. Robles, 6 Dec 2001 (ULLZ 10196 [3 pairs]; USNM 1437637 ex ULLZ 10196 [1 pair; female incomplete, tissue

removed for molecular analysis]. **Japan**: Ovigerous female (10.2 mm), mature male (5.2 mm), *ex* left branchial chamber of female *Grynaminna tamakii* (12.0 mm CL), Minami-Arima-cho sandflat, near south end of Shimabara Peninsula, Nagasaki Prefecture, Kyushu (32°37'N, 130°13'E), coll. A. Tamaki, 8 Jul 1998 (NSMT-Cr 12529).

Distribution. Japan, South Korea, China; British Columbia, Canada to California, U.S.A., and Gulf of California, Baja California Norte, Mexico.

Hosts. *Grynaminna tamakii* Poore, 2000, *Nihonotrypaea harmondi* (Bovier, 1901), *N. japonica* (Ortmann, 1891), *N. petalura* (Stimpson, 1860), *Neotrypaea californiensis* (Dana, 1854), *N. gigas* (Dana, 1852) (type host), *Upogebia major* (De Haan, 1841).

Remarks. The records of this species from an upogebiid host (An *et al.* 2009) may seem questionable as *I. cornuta* is otherwise only known from callianassid hosts but the congener *I. thoracica* (Montagu, 1808) has been reported to infest both callianassid and upogebiid hosts in the Mediterranean (Markham 2001). However, there are no records of *I. cornuta* from the west coast of the United States on any upogebiid host. Many early records had the host cited as *Callianassa longimana*, a synonym of *N. gigas*. Although Campos *et al.* (2009) listed *I. cornuta* as a parasite of *N. gigas* (based on data from Richardson 1905) and “*Ione* sp.” as a parasite of *N. californiensis* (based on data from Haig & Abbott 1980), they did not find infested hosts of either species from the Gulf of California. The Mexican specimens reported here therefore represent the first record of *I. cornuta* from the Gulf of California. The specimens from *Grynaminna tamakii* are the first bopyrids recorded from this host species.

The inclusion of “Nobuhiro & Kyoko 2004” in the synonymy list for this species by An *et al.* (2009) is an error as these are the first names of the authors Saito and Kinoshita (2004). The specimens studied by Wardiatno (2004) were never named or figured; they are likely either this species or *Pseudione longicauda* Shiino, 1937, as these are the only species known from *Nihonotrypaea japonica*.

Ione thompsoni Richardson, 1904

Fig. 1A–C

Ione thompsoni Richardson, 1904: 75–78, figs. 64–68 (2 specimens, type locality: North Falmouth, Massachusetts, infesting *Callianassa stimpsoni* Smith, 1873 = *Gilvossius setimanus* (DeKay, 1844)).—Giard, 1904: 592 (mention).—Rathbun, 1905: 49 (list).—Richardson, 1905: 508–510, figs. 554–558 (repeat of 1904 text; no new material).—Giard, 1913: 420 (mention).—Sumner *et al.*, 1913: 661 (list).—Kunkel, 1918: 192 (mention of specimens examined herein in a footnote).—Chopra, 1923: 437 (mention).—Nierstrasz & Brender à Brandis, 1923: 80 (list).—Miner, 1950: 451, pl. 145 (list; brief description with figures from Richardson, 1904).—Danforth, 1963a: 8 (list).—Shiino, 1964a: 32 (mention).—Smith & Bowman, 1964: 105, 107, 108, pl. 14, fig. 20 (list, figure after Richardson, 1904).—Schultz, 1969: 316, fig. 502 (list, figure after Richardson, 1904).—Danforth, 1970b: 10, 47 (list), 147 (key), fig. 22d–f (after Richardson, 1905).—Kaestner, 1970: 462–463 (mention occurrence “on *Callianassa* on the eastern North American coast”).—Gosner, 1971: 476 (list).—Lawler, 1978: 309 (list).—Markham, 1988: 56 (list).—Adkison & Heard, 1995: 108 (mention).—Markham, 1995: 86 (mention).—Markham, 2001: 199, 200 (list).—Heard *et al.*, 2007: 22 (mention of specimens from Georgia and Florida). “Crustacean lice” Pimentel, 1967: 89, 2 unnumbered figures (after Richardson, 1904).

Material examined. United States: Mature female (17.9 mm), mature male (5.3 mm) (YPM IZ 089393), *ex* left branchial chamber of female *Gilvossius setimanus* (15.6 mm CL) (YPM IZ 005658.CR), Long Island Sound, outer island, Thimble Islands, Branford, New Haven County, Connecticut, 4–6 ft (1.2–1.8 m), coll. A. E. Verrill, 17 May 1910.

Distribution. North Falmouth, Massachusetts to Long Island Sound; and possibly to St. Augustine, Florida.

Host. *Gilvossius setimanus* (DeKay, 1844) (type host).

Remarks. The specimens from Long Island Sound match the original description of *Ione thompsoni*, with females possessing highly digitate lateral plates, five pairs of biramous pleopods, and large, slightly curled, uniramous uropods (Fig. 1A, B); the oostegites are covered in short, thin cuticular extensions (Fig. 1B). Males are found attached between the pleopods (Fig. 1B) and have long, lanceolate lateral plates (Fig. 1C). *Ione thompsoni* is a rare bopyrid, with the pair of specimens reported herein first being mentioned without description or illustration in a footnote in Kunkel (1918) and only now having their identity verified, nearly 100 years later. This rarity is surprising considering the relatively large size of the host, *Gilvossius setimanus*, and its distribution in the well-studied fauna of the shallow water, northeastern American coastal region. The range of the host is from Nova Scotia to southern Georgia (Heard *et al.* 2007), whereas that of *I. thompsoni* is apparently from Cape Cod,

Massachusetts to northern Florida. However, the only records of *I. thompsoni* from outside Massachusetts (type locality) and Long Island Sound (present specimens) are from Georgia and Florida but with both as “pers. observ.” cited in Heard *et al.* (2007); these specimens are not known to have been deposited in any museum collection and are not described or illustrated. Although Heard *et al.* (2007) stated that the southern end of the range of the host was Georgia, they also mentioned a parasitized host from St. Augustine, Florida, without comment that such a record would extend the known host range somewhat farther south. Williams (1984) gave the host range as extending to Franklin County, Florida, but this locality is in the Florida panhandle; Manning and Felder (1991) suggested that specimens from the northeastern Gulf of Mexico might belong to an undescribed species of *Gilvossius*. No bopyrids have been reported from specimens of *Gilvossius* from the Gulf of Mexico.

Richardson (1904) described the species based on “two specimens... collected by Mr. G. M. Gray at North Falmouth, Massachusetts” and listed the “type” as USNM 29091. However, it is clear that Richardson (1904) had at least three specimens on hand because she described both the male and female of the species, but also mentioned a “young female” and an “adult female” (p. 75, footnote). USNM 29091 is the female holotype, whereas USNM 29230, also labeled as being collected from the type locality by Gray, contains one female and one male, both of which are paratypes.

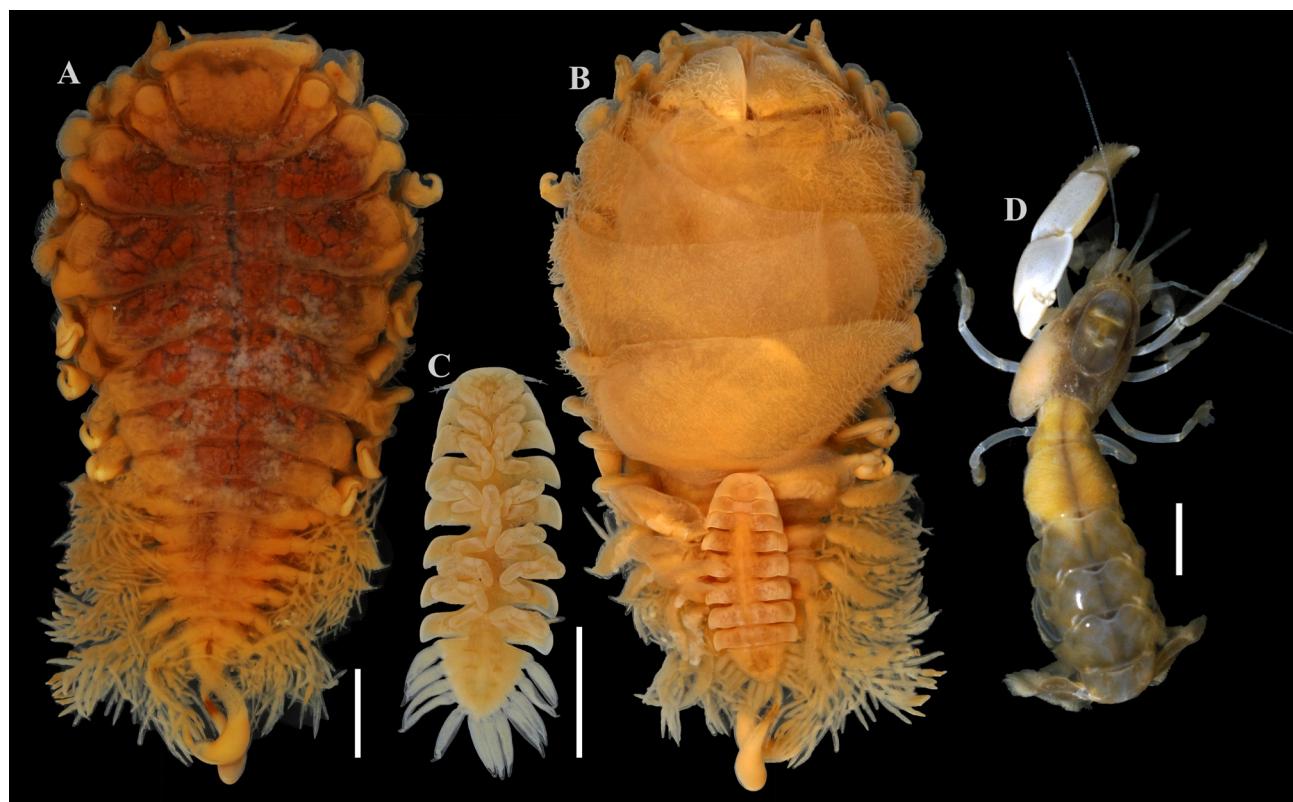


FIGURE 1. A–C, *Ione thompsoni* Richardson, 1904 (YPM IZ 089393) ex *Gilvossius setimanus* (DeKay, 1844)). A, dorsal overview of female; B, ventral overview of female with male *in situ*; C, ventral overview of male. D, photograph of live male *Callianassa truncata* Giard & Bonnier, 1890 (NHMW 20514) from Croatia bearing *Ione thoracica* (Montagu, 1808) (NHMW 25810) in left branchial chamber. Scale bars: A–C = 2 mm; D = 5 mm. D courtesy of Peter Dworschak.

Ione thoracica (Montagu, 1808)

Figs 1D, 2

Oniscus thoracicus Montagu, 1808: 103–104, pl. 3, figs. 3–4 (type locality: Devonshire, England, infesting *Cancer subterraneus* = *Callianassa subterranea* (Montagu, 1808)).—Leach, 1813–1814: 405–406 (description of Montagu, 1808, repeated).—Latreille, 1817: 54 (list).—Duvernoy, 1841: 113 (mention).

Oniscus (Ione) thoracicus—Latreille, 1818: pl. 336, fig. 46.

Ione thoracica—Lamarck, 1818: 170–171 (list).—Guérin-Méneville, 1836: 22 (list), pl. 26, figs. 1–2.—White, 1857: xi (figure caption), 254–255, pl. 14, fig. 8a–b.—McAndrew, 1861: 225 (list).—Bate & Westwood, 1867: 255–256 (discussion),

unnumbered fig. (copied from H. Milne Edwards, 1840).—Carus, 1885: 453 (list).—Giard & Bonnier, 1886: 890 (mention).—Norman, 1886: 13 (list).—Giard & Bonnier, 1887a: 23, 29, 36, 63, 76–77 (list), fig. 6.II.—Giard, 1887: 1115 (mention).—Giard & Bonnier, 1887b: 1309 (mention).—Groult, 1887: 165–166 (brief discussion), pl. 11, fig. 13.—Giard, 1888: 28 (mention).—Lo Bianco, 1888: 410 (list).—Giard & Bonnier, 1889: 259 (mention).—Giard & Bonnier, 1890b: 376, 377, 381, 385, 387, 388 (discussion, list).—Ide, 1892: 100, 148, 149, pl. 7, figs. 95–97 (structure of male and female digestive tracts).—Perrier, 1893: 1021 (list).—Bonnier, 1900: 8, 152, 164, 166–167, 238–245, 247, 273, 381, pls. 1, 2, 3, figs. 1–6, text fig. 43.—Richard, 1900: 71 (list).—Gerstaeker & Ortmann, 1901: 153 (mention), 156–157 (mention), 185 (list), 254, 256–258 (list).—Richardson, 1904: 78 (mention).—Norman, 1905a: 17 (list).—Norman, 1905b: 86, 93 (list).—Norman & Scott, 1906: vii, 52 (list).—Sinel, 1906: 224 (list).—Norman, 1907: 363 (list).—Lo Bianco, 1909: 594, 603 (list).—Giard, 1913: 408, 419 (mention).—Guilart, 1913: 3 (list).—Nierstrasz & Brender à Brandis, 1923: 80 (mention).—Caroli, 1928: 321–326 (larval development).—Caroli, 1929b: 501 (mention).—Popov, 1929: 6, 10, 11, 17, 25 (occurrence in Kilen Bay on *C. subterranea*).—Tucker, 1930: 7–8 (mention).—Caroli, 1931: 316, 319, 320 (mention).—Schmitt 1931: 159, fig. 31 (figure after Bonnier, 1900).—Tattersall, 1931: 187 (list).—Caspers, 1939: 243 (list).—Reverberi, 1941: 187, 197, figs. 3, 4 (Naples, infesting *Callianassa laticauda* Otto, 1828 = *Pestarella tyrrhena* (Petagna, 1792)).—Reverberi, 1942b: 91–93, 98, 99 (Naples, infesting *C. laticauda* = *P. tyrrhena*).—Carayon, 1943: 47 (mention).—Reverberi & Pitotti, 1943: 111–184 (biology, development), figs. 1–27.—Reverberi, 1943a: 2, 42, 48, 72, 76, 94, 96, 101 (mention).—Reverberi, 1943b: 231, 233, 277–289, 296–298, 303, 309, 311, table 18–29, 42 (effects on *C. laticauda* = *P. tyrrhena*).—Reverberi, 1945: 227, 230, 237–240, fig. 7 (development; effects on *P. tyrrhena*).—Veillet, 1945: 297 (mention).—Reverberi, 1947b: 81–85, 87, 90, 91 (Naples, infesting *C. laticauda* = *P. tyrrhena* and *Upogebia littoralis* (Risso, 1816) = *U. pusilla* (Petagna, 1792) (experimental infestation)).—Baffoni, 1948: 134 (mention).—Baffoni, 1950: 213, 216, 218–222 (Naples, infesting *C. laticauda* = *P. tyrrhena*).—Holthuis, 1950: 15 (North Sea on *C. subterranea*).—Caullery, 1952: 70, 75–76 (discussion of sex change).—Reverberi, 1952: 292 (mention).—Baffoni, 1953: 438–442 (Italy, infesting *C. laticauda* = *P. tyrrhena*).—Pike, 1953: 235 (occurrence at Jersey, England on *C. stebbingi* = *P. tyrrhena*).—Attardo, 1955: 125 (mention).—Reinhard, 1956: 89, 90, 101 (effects on hosts).—Spooner, 1957: 205 (list).—Charniaux-Cotton, 1960: 434–435 (mention).—Tuzet *et al.*, 1960: 505 (mention).—Holme, 1961: 453 (list).—Holme, 1966: 475 (list), 490, fig. 53 (distribution).—Bourdon, 1964: 3 (list).—Noble & Noble, 1964: 561 (mention).—Shiino, 1964a: 30 (mention).—Schmitt, 1965: 96, fig. 39 (figure after Bonnier, 1900).—Cals, 1966: 132 (mention).—Codreanu, 1967: 204 (mention).—Bourdon, 1968: 82–94, fig. 1–8, 9b (synonymy list, redescription, biological data), 95 (comparison with *I. vicina*), 121, 124, 128, 133, 134, 147, 157, 217, 408 (synonymy of *I. gebiae*), 410.—Field, 1969: 1273 (discussion of larvae).—Sadoglu, 1969: 175, 194–196, 201, 203, 206, figs. 17, 18, 20, 23B, 25B (eye development).—Danforth, 1970b: 19, 20 (mention).—Kaestner, 1970: 425 (mention).—Noble & Noble, 1971: 475 (mention).—Rioja, 1971: 511 (mention).—Bourdon, 1972: 101 (mention).—Naylor, 1972: 69 (list), 73 (characters), fig. 23j–l.—Cheng, 1973: 715–716 (review of life cycle).—Beck, 1980a: 148 (mention).—Bourdon, 1980: 1, 2 (Roscoff, France, infesting *C. tyrrhena* = *P. tyrrhena*).—Adema, 1981: 61–62, fig. 1 (Netherlands, infesting *C. subterranea*).—Anderson & Dale, 1981: 143, 153 (larval host preferences discussed).—Bourdon, 1981b: 120 (mention).—Bourdon *et al.*, 1981: 497, 500 (mention).—Adema & Huwae, 1982: 33, 46–47, fig. 5 (record from Netherlands).—Ross, 1983: 167, table 1 (list).—Anderson & Dale, 1989: 16 (mention).—Müller, 1989: 43 (mention).—Wägele, 1989: 214–215, fig. 98 (life cycle, phylogeny).—Isaac *et al.*, 1990: 402–404 (list; species characters), fig. 9.15.—Owens & Rothlisberg, 1991: 785 (mention).—Brandt, 1993: 126 (mention).—Raibaut & Trilles, 1993: 374, 375, 429–431 (review of life cycle), figs. 11c, 50.—Janssen & Brandt, 1994: 9–11, fig. 1 (review of life cycle).—Legrand & Juchault, 1994: 684–685 (mention).—Rowden & Jones, 1994: 623, 625, 629, 633, table 4 (prevalence levels on *C. subterranea* from the North Sea).—Hayward *et al.*, 1995: 358–360 (list), fig. 8.25.—Markham, 1995: 86 (mention).—Astall *et al.*, 1996: 822 (mention).—Dworschak, 1998: 1536, 1536, 1543, 1545, table 1 (prevalence levels in *P. tyrrhena* from the Adriatic Sea).—Markham & Boyko, 1999: 3 (mention).—Trilles, 1999: 288, 293, 295, 296, 305, 323, 330, 334, 335, figs. 8.8F, 8.12B, 8.14D, 8.16D.—Mariappan *et al.*, 2000: 305 (mention).—Dreyer & Wägele, 2001: 172, 175, fig. 10 (life cycle).—Markham, 2001: 196 (mention), 197 (in part, not material from Nigeria), 199–201 (list, in part, not material from Nigeria).—Van der Land, 2001: 322 (list).—Torres Jorda & Roccatagliata, 2002: 725 (mention).—Junoy & Castelló, 2003: 303 (list).—Wardiatno, 2004: 83 (mention).—Legrand & Juchault, 2006: 421 (mention).—Román-Contreras, 2008a: 282 (mention).—Meconcelli *et al.*, 2015: 43 (mention).—Subramoniam, 2017: 7 (table), 17 (mention).

Jone [sic] thoracicus—Brébisson, 1825: 254 (brief discussion).—Desmarest, 1825: 286, pl. 46, fig. 10.—Audouin & H. Milne Edwards, 1826: 359–361, pl. 49, figs. 10–11.—H. Milne Edwards, 1840a: 279–280 (list).—H. Milne Edwards, 1840b: pl. 59, fig. 1.—Verril, 1869: 243 (mention).—Stalio, 1877: 1386 (240 in separately paginated reprint volume) (list).

Iona [sic] thoracica—Bosc & Desmarest, 1830: 129 (list).—Lamarck, 1838: 293 (list).—H. Milne Edwards, 1840a: pl. 33, figs. 14–15.

Ione thoracique—Bosc & Desmarest, 1830: 129 (list), pl. 15bis, fig. 5.

Ione thoracicus—Lucas, 1840: 246, pl. 19, figs. 2–3.—H. Milne Edwards, 1843: 174–175 (discussion).—White, 1847: 111 (list).—Van der Hoeven, 1849: 746 (list).—White, 1850 (81 (list).—Gosse, 1855: 133 (list), fig. 227.—Lucas, 1883: LXXVIII–LXXIX (Mediterranean, infesting *C. subterranea*).—Stebbing, 1893: 414 (list).—Tattersall, 1905: 86 (list).

Jone [sic] thoracica—Cornalia & Panceri, 1861: 115–116 (list).—Heller, 1866: 749–750 (list).—Nardo, 1868: 268 (list).—Fraisse, 1877: 52 (Naples, infesting *Gebia littoralis* Risso, 1816 = *U. pusilla*).—Fraisse, 1878a: 290 (same data as Fraisse, 1877).—Fraisse, 1878b: 405, 417 (mention).—Stossich, 1880: 229 (list).—Kossmann, 1881a: 653, 665, pl. 33, figs. 14–16 (illustration of head appendages).—Kossmann, 1881b: 170–181, pl. 10, figs. 1–9.—Walz, 1882: 178, 193 (mention).—

Gerstaeker & Ortmann, 1901: pl. 11, figs. 1–3.—Giard & Bonnier, 1887a: 176 (mention).—Giard & Bonnier, 1889: 259 (mention).—Giard, 1899: 497 (47 in alternately paginated edition) (list).—Giard, 1913: 129 (list).—Reverberi, 1942a: 58 (Italy, infesting *C. laticauda* = *P. tyrrhena*).—Reverberi, 1945: 235, 237–239, figs. 6, 8, 9 (development; effects on *P. tyrrhena*).—Reverberi, 1947a: 345–347 (development; effects on *C. laticauda* = *P. tyrrhena*).—Kaestner, 1967: 1161 (mention).—Restivo, 1968: 505 (Naples, infesting *C. laticauda* = *P. tyrrhena*).

Iones [sic] *thoracicus*—Van Beneden, 1876: 145 (mention).

“a parasite... makes its home within the thoracic plate of the burrowing crab (*Callianassa subterranea*)” Wood & Holder, 1885: 478 (mention).

Ione vicina Giard & Bonnier, 1890b: 376, 385, 387 (*nomen nudum*) (Naples, infesting *Callianassa truncata* Giard & Bonnier, 1890).—Stebbing, 1893: 414 (list).—Reverberi, 1943a: 42–43 (mention) (new synonymy).

Ione gebiae Giard & Bonnier, 1890b: 377, 398 (*nomen nudum*) (Naples, infesting *Gebia stellata* = *Upogebia stellata* (Montagu, 1808).—Stebbing, 1893: 414 (list).—Bonnier, 1900: 222, 248 (*nomen nudum*).—Richard, 1900: 71 (list).—Nierstrasz & Brender à Brandis, 1923: 80 (mention).—Shiino, 1964a: 30, 32 (mention).—Bourdon, 1968: 408 (list).

Ione vicina Bonnier, 1900: 48, 61, 222, 247–248, 294, pl. 3, figs. 7–15 (type locality: Naples, Italy, infesting *C. truncata*).—Richard, 1900: 71 (list).—Richardson, 1905: 505, 507 (mention).—Nierstrasz & Brender à Brandis, 1923: 80 (mention).—Caroli, 1929b: 501 (mention).—Caroli, 1931: 320–321 (mention).—Caspers, 1939: 243 (list).—Reverberi, 1943b: 233, 297–299, 301, figs. 47, 50, 51 (effects on *C. truncata*).—Baffoni, 1949: 237 (mention).—Shiino, 1964a: 30, 32 (mention).—Bourdon, 1968: 82 (mention), 94–95, fig. 9A (after Bonnier, 1900).—Restivo, 1970: 305, 314 (mention).—Argano *et al.*, 1995: 23 (list).—Markham, 1995: 86 (mention).—Abed-Navandi & Dworschak, 1997: 568 (first report from Croatian *C. truncata*).—Trilles, 1999: 296, 334 (mention), fig. 8.16C.—Markham, 2001: 199–200 (list).—Van der Land, 2001: 322 (list) (new synonymy).

Jone [sic]—Reverberi, 1947b: fig. 1 (Naples, infesting *C. laticauda* = *P. tyrrhena*).

Ione—Reveberi, 1947b: figs. 2–7, 9 (Naples, infesting *C. laticauda* = *P. tyrrhena* and *U. littoralis* = *U. pusilla* [experimental infestation]).

Ione Thoracica—Brezeanu & Elian, 1958: 1181 (mention).

Jone [sic] *vicina*—Restivo, 1968: 505 (none found at Naples on *C. truncata*).

Jone [sic] *gebiae*—Restivo, 1968: 506, table 3 (none found at Naples on *Upogebia littoralis* = *U. pusilla*).

“a bopyrid parasite” Hughes, 1998: 60–61 (summary of data from Rowden & Jones, 1994).

not *Ione thoracica*—Olaosebikan, 1986: iv, vi, vii, viii, 9, 27–32, 39, 40, fig. 13 (Nigeria, infesting *Callianassa balssi* Monod, 1933 = *Callichirus balssi* (Monod, 1933)) (= *Ione* undescribed sp.).

Material examined. Croatia: Mature female (11.8 mm), mature male (4.5 mm) (NHMW 25382), ex branchial chamber of *Pestarella tyrrhena* (sex and size unknown), Volosko, coll. D. Abed-Navandi, 18 May 2000; mature female (5.5 mm), mature male (2.2 mm) (NHMW 25807), ex branchial chamber of female *Callianassa truncata* (4.9 mm CL) (NHMW 14779/K6), Kvarner, Volosko, coll. D. Abed-Navandi, 15 Jul 1996; mature female (9.4 mm), mature male (3.3 mm) (NHMW 25810), ex left branchial chamber of male *N. truncata* (9.0 mm CL) (NHMW 25014, Fig. 1D), Volosko, Croatia, coll. D. Abed-Navandi, Apr 2003. **Italy:** Mature female (12.0 mm), mature male (5.7 mm) (NHMW 25231), ex branchial chamber of female *P. tyrrhena* (13.2 mm CL) (NHMW 25853), Lido di Staranzano, coll. P. Dworschak, 11 May 1988; 4 ovigerous females (8.7–11 mm), 2 mature males (5.1–5.3 mm), 1 partial mature male (posterior end only), ex unknown host, Naples Aquarium, coll. unknown, 17 Nov 1890 (NMV J62892). **Tunisia:** Mature female (4.8 mm), mature male (2.5 mm) (NHMW 25809), ex branchial chamber of male *C. truncata* (6.4 mm CL) (NHMW 18819/7), Hammamet, ca. 2 m, coll. P. Dworschak 15 Jan 2000.

Distribution. Northwestern Atlantic (Netherlands, Belgium, United Kingdom, France); Mediterranean (Spain, Tunisia, Italy); Adriatic Sea (Croatia); and Black Sea.

Hosts. *Callianassa subterranea* (Montagu, 1808) (type host), *C. truncata* Giard & Bonnier, 1890, and *Pestarella tyrrhena* (Petagna, 1792).

Remarks. Bourdon (1968) compared *Ione thoracia* with *I. vicina* based on Bonnier’s (1900) data as he did not have any bopyrids from *Callianassa truncata* available to examine. Bourdon (1968) concluded that the only apparent differences between the two species were in the shapes of the endopods and lateral plates of the first pleopods (Fig. 2). We examined five pairs of *Ione* from *C. truncata* and *Pestarella tyrrhena*, including: three from Croatia (Figs 1D, 2C, E), one from Italy (Fig. 2D), and one from Tunisia (Fig. 2F). Whereas the Croatian females show near identical morphology to the Italian specimen illustrated by Bonnier (1900; repeated by Bourdon 1968: fig. 9A; Fig. 2A herein) in the morphology of the first pleopod endopods, lateral plates, and appearance of short endopods (Fig. 2C, E), the Tunisian (Fig. 2F) and newly examined Italian females (Fig. 2D) have first pleopods that are identical to that of the “typical” *I. thoracica* (Bourdon 1968: fig. 9B; Fig. 2B herein) in possessing long endopods. The specimen Bonnier (1900) identified as *I. thoracica* came from an unspecified locality that was most likely Wimereux, France. In other respects the females are essentially identical, as are the males. This leads us to

conclude that there is no good reason to maintain *I. vicina* as distinct from *I. thoracica*; therefore, we herein synonymize the two species. Interestingly, specimens occurring on *Pestarella tyrrhena* from Italy and Croatia both show “typical” *I. thoracica* morphology for the first pleopod, suggesting there may be a population on *C. truncata* around Italy and Croatia that show the “*vicina*” morphology of the first pleopod, perhaps due to isolation from other populations on these hosts in the Mediterranean. Note that several spellings of *Ione thoracica/thoracicus* were incorrectly given by Bourdon (1968) in his synonymy list and are corrected herein.

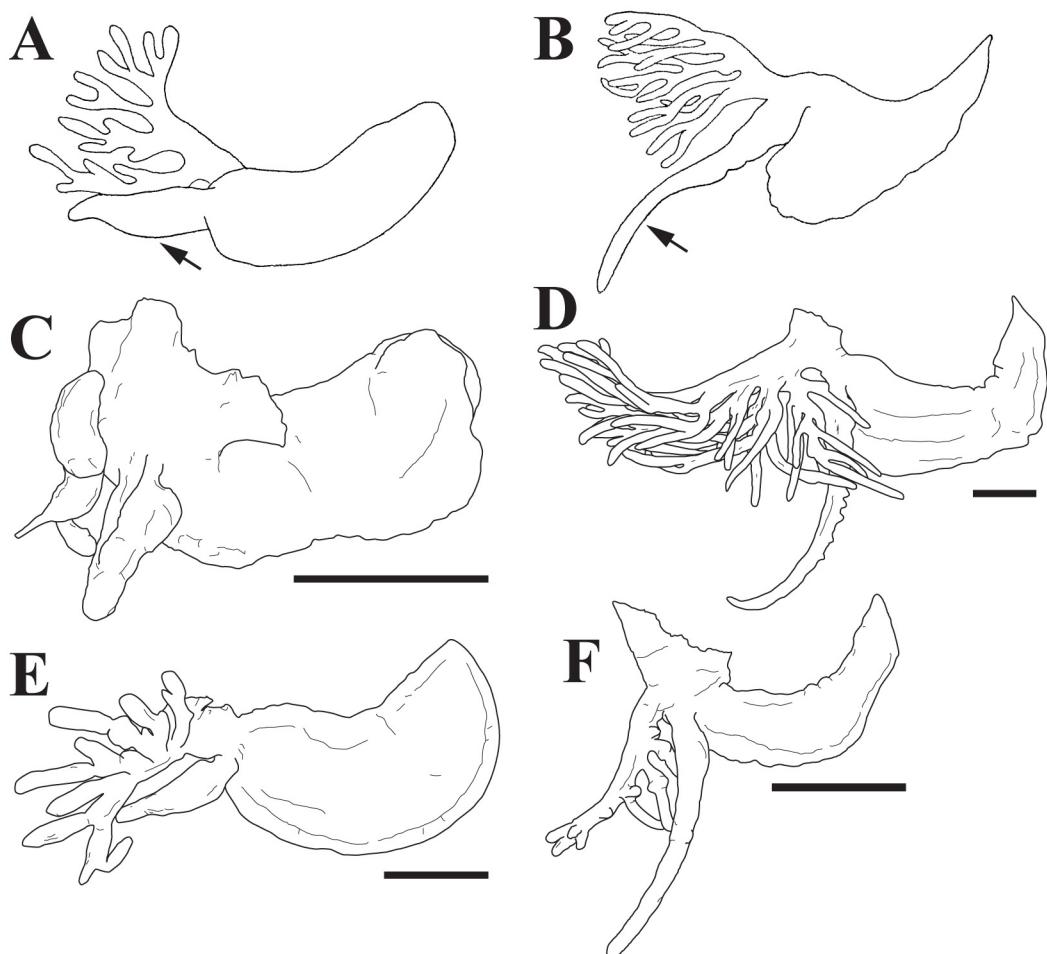


FIGURE 2. Variation in pleopod morphology of *Ione thoracica* (Montagu, 1808). A, pleopod 1 of specimen identified by Bonnier (1900) as *Ione vicina* Bonnier, 1900 from Naples, Italy, note short endopod (arrow); B, pleopod 1 of specimen identified by Bonnier (1900) as *I. thoracica* from unspecified locality, but most likely Wimereux, France, note long endopod (arrow); C, pleopod 1 of specimen from Volosko, Croatia (NHMW 25807 ex *Callianassa truncata* Giard & Bonnier, 1890); D, pleopod 1 of specimen from Lido di Staranzano, Italy (NHMW 25231 ex *Pestarella tyrrhena* (Petagna, 1792)); E, pleopod 1 of specimen from Volosko, Croatia (NHMW 25810 ex *C. truncata*); F, pleopod 1 of specimen from Hammamet, Tunisia (NHMW 25809 ex *C. truncata*). A, B from Bourdon 1968; not to scale. Scale bars: C–F = 0.5 mm.

Boyko *et al.* (2013) erred when they stated that *Ione* spp. were unlikely to occur on gebiid hosts and also in their agreement with Bourdon (1968) in discounting the earlier report by Fraisse (1877; 1878a) of *I. thoracica* from *Upogebia pusilla* (Petagna, 1792) (not *U. stellata* (Montagu, 1808)). In addition, data from An *et al.* (2009) strongly support the rare occurrence of *Ione* spp. on gebiid hosts.

We consider the material from Nigeria reported by Olaosebikan (1986) to be distinct from *Ione thoracica*. The form of the females’ uropods is very different from that seen in any specimens of *I. thoracica* (based on material examined in this study, as well as illustrations from other papers, e.g., Reverberi & Pitotti 1943; Bourdon 1968) and the coxal plates of the first two pereomeres are not elongated as in true *I. thoracica*. Additionally, the host, *Callichirus balssi* (Monod, 1933), and locality occur well outside of the range of *I. thoracica*. *Callianassa balssi*

Monod, 1933 is the type species of *Balsscallichirus* Sakai, 2011, but is better left in *Callichirus* Stimpson, 1866, pending revision of these and related genera (Poore, pers. commun.).

Bopyridae Rafinesque, 1815

Pseudioninae Codreanu, 1967

Acobelione Bourdon, 1981

Acobelione halimedae n. sp.

Fig. 3

Material examined. Singapore: Mature non-ovigerous **holotype** female (7.5 mm), *ex* right branchial chamber of female *Austinogebia spinfrons* (8.6 mm CL), Sta. 6, Pulau Tekong (type locality) (ZRC 1990.4330).

Etymology. This species is named for the tapered and marginally constricted lateral plates and pleopods that are reminiscent of the “segmented” appearance of species in the algal genus *Halimeda* J. V. Lamoroux, 1812 (e.g., *H. cylindracea* Descaisne, 1842) with subquadrate or cylindrical plates. In Greek mythology, *Halimeda* was a Nereid, the daughter of Nereus and Doris.

Distribution. Singapore.

Host. *Austinogebia spinfrons* (Haswell, 1881) (type host).

Description. Female (Fig. 3A, B), body length 8.0 mm, maximal width 6.4 mm, head length 1.5 mm, head width 1.9 mm. No body pigmentation. Pereon weakly sinistral (15°) with coxal plates and pereomeres of right side slightly larger on segments 1–4 (Fig. 3A). Head slightly wider than long, with thin frontal lamina (Fig. 3A), deeply embedded medially in first pereomere; eyes lacking.

Antennules of three articles each, antennae of four articles each (Fig. 3C).

Maxilliped with rounded distal end and subacute recurved spur; palp present as setose, non-articulated lobe (Fig. 3E).

Barbula with 2 pairs of irregular lateral projections with numerous short, finger-like marginal lobes; medial margin with few finger-like, short fleshy projections (Fig. 3D).

First *oostegite* anterior lobe rounded, external posterior face with patch of irregular low, fleshy lobes, inner ridge with numerous small rounded projections along $\frac{3}{4}$ of length; distal lobe subtriangular, slightly recurved (Fig. 3F, G). Fourth and fifth oostegites with fringe of setae on posterior margin (Fig. 3B).

Pereon composed of 7 pereomeres (Fig. 3A), first 2 markedly curved and rounded at lateral margins, third and fourth nearly laterally straight, rounded at lateral margins except for one side of pereomere 7 which has a posterolateral point (Fig. 3J), last 3 slightly curved posteriorly at truncate lateral margins; broadest across pereomere 4, gradually tapering anteriorly and posteriorly; Pereomere 1 with convex posterior margin; posterior margins of pereomeres 2 and 3 nearly straight; posterior margins of pereomeres 4–7 convex (Fig. 3A). Pereomeres 1–4 with rounded coxal plates, no dorsolateral bosses. Pereomere 4 bilobed laterally, remainder undivided with rounded coxal plates.

First pair of *pereopods* near anterolateral margin of head; pereopods evenly spaced. Pereopods subequal in size (Fig. 3H, I), carpi and meri fused, small tubercles present on lateral faces of some ischia; basis with ridge of larger tubercles (Fig. 3H, I).

Pleon with 5 distinct pleomeres plus small pleotelson (Fig. 3A), pleomeres resembling posterior three pereomeres, but with tapered lateral plates. Lateral plates present distally on pleomeres as elongate, tapered lobes with numerous constrictions along length (Fig. 3A, J, K); lateral region of pleomeres with few, low warty lobes on margins and surface (Fig. 3A, K). First five pleomeres with pair of tapered, elongate, biramous pleopods with lateral constrictions as seen in lateral plates (Fig. 3L); pleopods extending beyond lateral plates and visible in dorsal view, mostly on left side of body (Fig. 3A), all endopods and exopods subequal in size and shape (Fig. 3B).

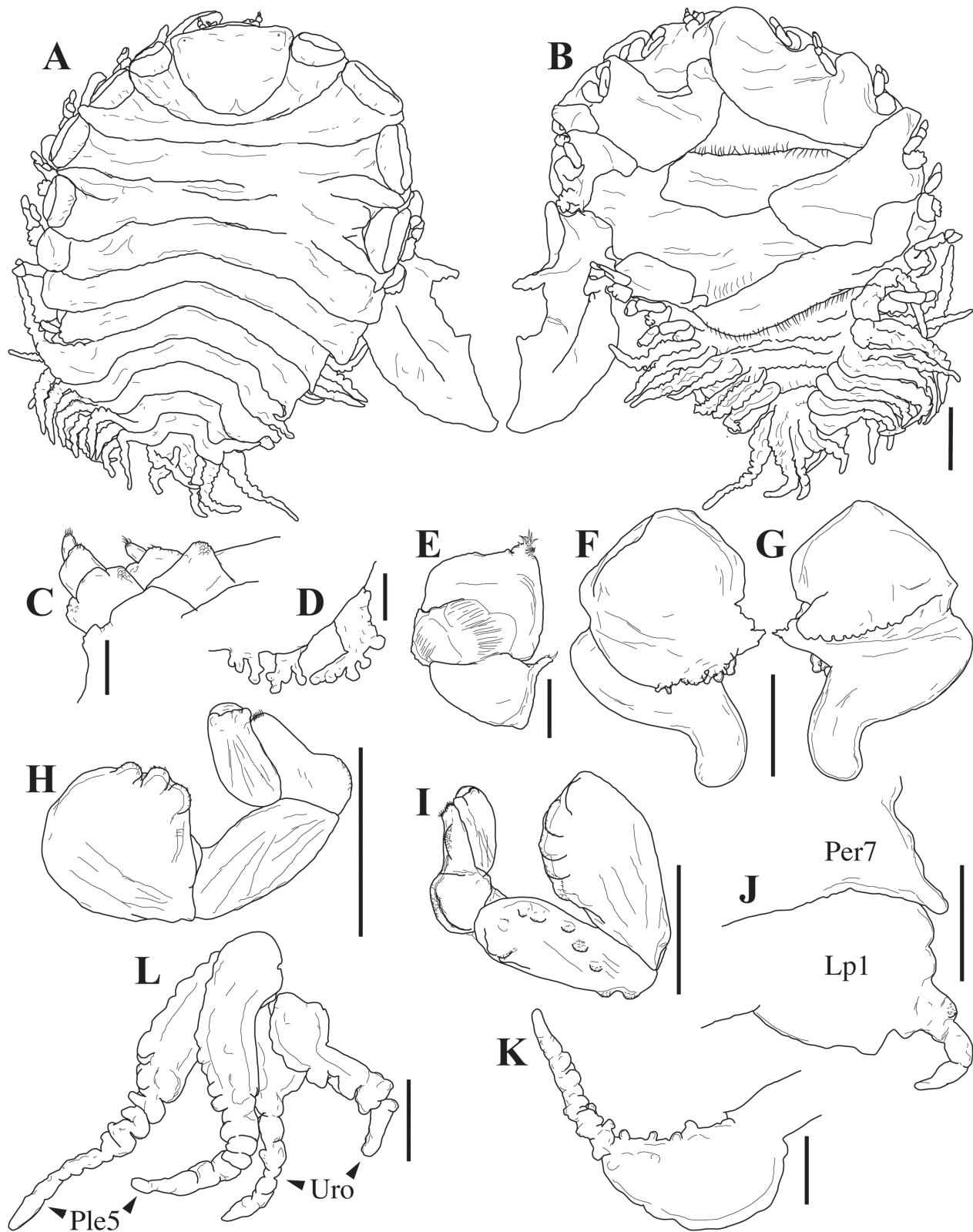


FIGURE 3. *Acrobelinea halimedae* n. sp., mature holotype female (ZRC 1990.4330), ex *Austinogebia spinfrons* (Haswell, 1881). A, dorsal overview of female; B, ventral overview of female; C, right antennule and antenna; D, left barbula; E, right maxilliped, outer view; F, right oostegite 1, internal view; G, right oostegite 1, outer view; H, right pereopod 1; I, left pereopod 7; J, right pereomere 7 (Per7) and right lateral plate 1 (Lp1); K, left lateral plate 1; L, ventral view of fifth pleopods (Ple5) and uropods (Uro). Scale bars: A, B, E, F = 1 mm; C = 125 µm; D = 250 µm; G–L = 500 µm.

Pleotelson not easily seen in dorsal view (Fig. 3A), bearing pair of uniramous uropods with endopod and exopod subequal in size, both resembling lateral plates and pleopods in having numerous marginal constrictions (Fig. 3A, L).

Male unknown.

Remarks. All species of *Acobelione* have females with the barbula possessing lateral projections with numerous short, finger-like lobes on the margins, and lateral plates and pleopods with numerous constrictions along their lengths, as well as pereopods with scattered tubercles on the ischia and a ridge of pronounced tubercles on the bases. This new species is most similar to *A. langi* (Van Name, 1920) (see also Bourdon 1981b) but differs from it in the shape of the female's head (flat frontal margin in *A. halimedae n. sp.* vs. distinctly medially produced in *A. langi*) and the overall body shape (nearly circular in *A. halimedae n. sp.* vs. ovate in *A. langi*). The material (2 females and 2 males) of *A. langi* examined by Bourdon (1981b) came from hosts collected at the same time and from the same locality as the unique holotype but were not seen by Van Name (1920) and are not type specimens. *Acobelione anisopoda* Bourdon, 1981b was described from an immature female and mature male (type host and locality: *Gebiacantha talismani* (Bouvier, 1915) from off Príncipe, Gulf of Guinea); both show characters of species in *Acobelione*, but the female does not have well developed tubercles on the pereopods nor laterally constricted lateral plates or pleopods. However, these differences may be due to the specimen's immaturity. A key to species in the genus based on mature females is given below, including type host and type locality data.

Although not common, *Acobelione* has species known from both gebiidean and axiidean hosts (An *et al.* 2009). However, Bourdon (1981b) erred when he listed *Acobelione reverberii* (Restivo, 1970) as occurring on *U. pusilla* because the 66 individuals said by Bourdon (1981b: 120, footnote) to be from this upogebiid host are clearly stated by Restivo (1968) to be from *C. truncata*. Likewise, the listing by Markham (2001) of *A. reverberii* occurring on *U. pusilla* is erroneous; his supposed source for that data (Restivo, 1970) does not list any host other than *Callianassa truncata*. Restivo (1968), although listing a "nuova specie" from *U. pusilla*, also lists one from *C. truncata*, and this is the correct data that should be associated with *A. reverberii*.

Key to females of species of *Acobelione* Bourdon, 1981b

(*A. anisopoda* Bourdon, 1981b is excluded because it is only known from an immature female)

- | | | |
|-----|---|--|
| 1a. | Coxal plate margins smooth | 2 |
| 1b. | Coxal plate margins acute | <i>A. reverberii</i> (Restivo, 1970)
[type locality: Naples, Italy; type host: <i>Necallianassa truncata</i> (Giard & Bonnier, 1890)] |
| 2a. | Frontal margin of head convex, produced | <i>A. langi</i> (Van Name, 1920)
[type locality: Banana, Democratic Republic of the Congo (06° S, 12° 20' E); type host: <i>Upogebia furcata</i> (Aurivillius, 1898)] |
| 2b. | Frontal margin of head straight | <i>A. halimedae n. sp.</i>
[type locality: Pulau Tekong, Singapore; type host: <i>Austinogebia spinfrons</i> (Haswell, 1881)] |

Gyge Cornalia & Panceri, 1861

Gyge branchialis Cornalia & Panceri, 1861

Gyge branchialis Cornalia & Panceri, 1861: 90–111, pls. 1, 2 (type locality: "della magica laguna su cui sorge Venezia, non lungi dall'isola di S. Giorgio", Italy, infesting *Gebia littoralis* = *U. pusilla*).—Hesse, 1861: 102 (mention).—Heller, 1866: 749 (list).—Bate & Westwood, 1867: 228–229 (comparison with *Gyge galathea* Bate & Westwood, 1867).—Nardo, 1868: 251, 268, 316 (mention).—Norman, 1869: 262 (list).—Fraisse, 1877: 52 (mention).—Stalio, 1877: 241 (list).—Fraisse, 1878a: 290 (mention).—Fraisse, 1878b: 396, 405, 412, 423 (mention).—Stossich, 1880: 229 (list).—Kossmann, 1881a: 653 (mention), pl. 22, figs. 12, 13, 20, 22, 26.—Walz, 1881: 159, 160, 164 (mention).—Walz, 1882: 127, 128, 132, 142–147, 149, 156, 158, 162–164, 167, 172, 176, 189, 190, pl. 2, figs. 9–12, 14, 16, 17, pl. 3, figs. 18, 23B, 24, pl. 4, figs. 29, 30, 32, 33 (Trieste, infesting *Gebia littoralis* [sic] = *U. pusilla*).—Carus, 1885: 452 (list).—Norman, 1886: 13 (list).—Giard, 1887: 1113, 1115 (mention).—Giard & Bonnier, 1887a: 18, 26, 36, 43, 62, 176 (mention).—Groult, 1887: 164 (list).—Giard, 1888: 24, 29 (mention).—Giard & Bonnier, 1888a: 305 (mention).—Giard & Bonnier, 1888b: 63 (mention).—Giard, 1889: 169–170 (mention).—Giard & Bonnier, 1889: 259 (mention).—Giard & Bonnier, 1890b: 377 (mention), 384 (list).—Ide, 1892: 100, 148, 150 (study of digestive tract).—Perrier, 1893: 1021 (list).—Stebbing, 1893: 412 (list).—Giard, 1896: 96, 249 (mention).—Bonnier, 1900: 353–356, pl. 34, figs. 1–11 (France, infesting *Upogebia stellata* (Montagu, 1808)).—Richard, 1900: 71 (list).—Bohn, 1901: 325–326, 331 (France, infesting *U. stellata*).—

Gerstaeker & Ortmann, 1901: 184, 256 (list), pl. 10, figs. 1–11.—Giard, 1905: 12 (France, infesting *U. stellata*, *Gebia deltura* Leach, 1816 = *Upogebia delatura* (Leach, 1916)).—Norman, 1905a: 17 (list; synonymy with *G. galathea*).—Norman, 1905b: 86 (as senior synonym of *G. galathea*).—Tattersall, 1905: 86 (list).—Nobili, 1906: 1112 (mention).—Norman, 1907: 363 (list).—Lo Giudice, 1908: 50–80, pl. 3, figs. 2–8 (study of leg morphology).—Calman, 1909: 203, fig. 124 (figure of male and female, after Cornalia & Panceri, 1861).—Lister, 1909: 485, fig. 299 (figure of male and female after Cornalia & Panceri, 1861).—Lo Bianco, 1909: 594, 607 (list).—Chopra, 1923: 481 (mention).—Caroli, 1929a: 490–492 (effects on host, *U. littoralis* = *U. pusilla*).—Popov, 1929: 6, 10, 11, 13, 24 (Bay of Sevastopol, infesting *Gebia littoralis* = *U. pusilla*).—Tucker, 1929: 985 (mention).—Tucker, 1930: 4–14, 108 (Naples, infesting *U. littoralis* = *U. pusilla*; effects on host).—Mouchet, 1931a: 172 (mention).—Tattersall, 1931: 187 (list).—Atkins, 1933: 324, 325 (mention).—Hiraiwa & Sato, 1939: 118 (mention).—Callan, 1940: 168 (mention).—Hughes, 1940: 331–336 (Naples, effects of *U. littoralis* = *U. pusilla*).—Larwood, 1940: 50–51 (West Port, Egypt, infesting *U. littoralis* [sic] = *U. pusilla*), fig. 17 (locality map).—Reverberi, 1942a: 58 (mention).—Reverberi, 1943a: 38–41 (effects on *U. littoralis* = *U. pusilla*).—Carayon, 1944: 238–243, fig. 2A (comparison with *Gyge arcassonensis* Carayon, 1944).—Veillet, 1945: 287, 296, 297, 323 (mention).—Caroli, 1946: 62 (mention).—Reinhard *et al.*, 1947: 69–70 (mention).—Reverberi, 1947b: 85–87, 90, 91, fig. 8 (Naples, infesting *U. littoralis* = *U. pusilla*).—Morris, 1948: 6–7 (mention).—Stephensen, 1948: 116–117, fig. 34 (Denmark, infesting *U. stellata*).—Baffoni, 1950: 215 (mention).—Caullery, 1952: 204 (mention).—Von Brand, 1952: 256 (mention).—Caroli, 1953: 86–87 (mention).—Pike, 1953: 234 (United Kingdom, infesting *U. deltaura*).—Attardo, 1955: 134, 136 (mention).—Reinhard, 1956: 90 (mention).—Oguro, 1957: 32 (mention).—Spooner, 1957: 205 (list).—Florkin, 1960: 405 (mention).—Codreanu, 1961: 139–140 (mention).—Holme, 1961: 453 (list).—Bourdon, 1963: 429 (France, infesting *U. deltaura*).—Codreanu & Codreanu, 1963: 283–284 (mention).—Danforth, 1963a: 8 (list).—Reverberi & Catalano, 1963: 128–133, 138, 139 (Naples, as host of *Paracabriops marsupialis* Caroli, 1953 = *Cabriops marsupialis* (Caroli, 1953)).—Tuzet *et al.*, 1960: 505 (mention).—Houša, 1963: 107 (mention).—Bourdon, 1964: 4, 5 (Bay of Arcachon, France, infesting *U. pusilla*).—Catalano & Restivo, 1965: 204 (list).—Nielsen & Strömberg, 1965: 57 (mention).—Holme, 1966: 475 (list), 490 (distribution map).—Von Brand, 1966: 222 (mention based on data from Hughes, 1940).—Bourdon, 1967a: 283, 285 (France, infesting *U. stellata*).—Bourdon, 1967b: 847, 848 (mention).—Bourdon, 1968: 147, 151–159, 169, 322, 352, 410, 422 figs. 28–32, tables, 23, 24 (redescription, review of distribution from United Kingdom to France, Mediterranean, Adriatic, Black Sea, infesting *U. deltaura*, *U. pusilla*, *U. stellata*).—Restivo, 1968: 506 (Naples, infesting *U. littoralis* = *U. pusilla*).—Beklemishev, 1969: 353, fig. 152D (after Carus, 1885).—Sadoğlu, 1969: 173–197, 199, 201–203, 206–208, figs. 1–16, 22, 23A (study of pigmentation).—Danforth, 1970b: 3 (mention).—Kuris, 1971: 347 (mention).—Restivo, 1971: 71 (list).—Strömberg, 1971: 4, 29 (mention).—Naylor, 1972: 69, 70, 73, fig. 23H, I (summary of British records).—Kuris, 1974 (137 (mention)).—Baudoin, 1975: 344 (mention).—Restivo, 1975: 152, 153, 161–163, table 1 (Gulf of Naples, infesting *U. pusilla*; hyperparasitized by *Paracabriops marupialis* = *Cabriops marsupialis*).—Beck, 1980a: 150, 152 (mention).—Beck, 1980b: 9 (mention).—Bourdon *et al.*, 1981: 497 (mention).—Abu-Hakima, 1984: 59 (mention).—O'Brien & Van Wyk, 1985: 197 (mention).—Page, 1985: 196 (mention).—Dworschak, 1988: 68, 69, 74 (Adriatic Sea, infesting *U. pusilla*).—Markham, 1988: 17 (mention).—Müller, 1989: 44, 45, fig. 7 (mention, illustration of ventral head of male).—Anderson, 1990: 290 (mention).—Isaac *et al.*, 1990: 402–404, fig. 9.15 (morphological characters, review of British records).—Janssen & Brandt, 1994: 12 (mention).—Sassaman, 1992: 579 (mention).—Rowden & Jones, 1994: 633 (mention).—Hayward *et al.*, 1995: 358–359, fig. 8.25 (morphological characters, summary of British records).—Astall *et al.*, 1996: 821–823, table 1 (Clyde Sea, Scotland; Irish Sea; Arcachon Basin, France, infesting *U. deltaura*, *U. pusilla*, *U. stellata*).—Trilles, 1999: 305, 332 (mention).—Mariappan *et al.*, 2000: 305 (mention).—Markham, 2001: 197 (mention), 198, 200, 201 (lists).—Van der Land, 2001: 322 (list).—Junoy & Castelló, 2003: 303 (list).—Ngoc-Ho, 2003: 528 (mention).—Markham, 2004: 193–195, 197 (Adriatic Sea, infesting *U. pusilla* and *U. tipica* (Nardo, 1868)).—Le Mao, 2006: 23, 26 (list).—Román-Contreras, 2008b: 91 (mention).—Smith *et al.*, 2008: 231 (mention).—An *et al.*, 2009: 231 (mention).—Dumbauld *et al.*, 2011: 344 (mention).—Tempelman *et al.*, 2013: 17, 21, 23, figs. 8, 9 (North Sea, infesting *U. deltaura* and *U. stellata*).—Ubaldo *et al.*, 2014: 558, 561 (mention).—Pascal *et al.*, 2016: 195 (Arcachon Bay, France, infesting *U. pusilla*).—Asson *et al.*, 2017: 222 (mention).—Dairain *et al.*, 2017: 203 (Arcachon Bay, infesting *U. pusilla*).—Romero-Rodríguez *et al.*, 2017: 92 (mention).

Gyges [sic] *branchialis*—Grube, 1864: 77 [Adriatic Sea, infesting *Gebia littoralis* [sic] = *U. pusilla*].—Nardo, 1868: 263 (list).—Van Beneden, 1876: 145 (mention).

Gyge branchiale—Hesse, 1865: 236 (mention).

Gyge galathea Bate & Westwood, 1867: 225–229, unnumbered figure (type locality: Guernsey, Channel Islands, United Kingdom, infesting “*Galathea squamifera* Leach, 1814” subsequently reidentified as *U. stellata* by Norman, 1905b).—Giard & Bonnier, 1887a: 175 (list).—Stebbing, 1893: 412 (list).—Norman, 1886: 13 (list; in synonymy with *G. branchialis* without comment).—Giard & Bonnier, 1890b: 374 (mention).—Norman, 1905a: 17 (list; in synonymy with *G. branchialis* without comment).—Bonnier, 1900: 221, 356–357, 380, fig. 58 (review of data from Bate & Westwood, 1867).—Bohn, 1901: 331 (list).—Gerstaeker & Ortmann, 1901: 184, 254 (list).—Norman, 1905b: 86 (synonymy with *G. branchialis*; corrected identification of host).—Sinel, 1906: 223 (list).—Mouchet, 1931b: 504 (mention).—Pike: 1953: 234–235 (list).—Danforth, 1963a: 8 (list).

Gyge Galathea—Norman, 1869: 262 (list; in synonymy with *G. branchialis* without comment).—Giard & Bonnier, 1887b: 1309 (list).—Giard, 1896: 200 (mention).—Marine Biological Association, 1904: 245 (list).

Gyge [sp.] Parker & Haswell, 1921: 573, fig. 471.3 (figure after Gerstaeker & Ortmann, 1901).

Gige [sic] *branchialis*—Borcea, 1934: 405 (list).

Gyge galathea [sic]—Sadoğlu, 1969: 32 (mention).—Naylor, 1972: 73 (mention).

Gyge branchiatis [sic]—Owens & Glazebrook, 1985: 111 (mention).

Not *Gyge branchialis*—Pandey, 1990: 494–494, figs. 1, 2 (India, infesting *Macrobrachium birmanicum choprui* (Tiwari, 1949) = *M. gangeticum* Bate, 1868) (almost certainly a species of *Probopyrus* Giard & Bonnier, 1888).

Material examined. Italy: 2 ovigerous females (9.7–10.1 mm) not affiliated with any host, 1 ovigerous female (9.3 mm), 1 mature male (3.3 mm), *ex* right branchial chamber of female *Upogebia stellata* (14.3 mm CL), Naples Aquarium, coll. unknown, 17 Nov 1890 (NMV J71549).

Distribution. Denmark, United Kingdom, France, Spain, Portugal, Italy, Algeria, Croatia, Romania, and Russia.

Hosts. *Upogebia deltaura* (Leach, 1816), *U. pusilla* (Petagna, 1792) (type host), *U. stellata* (Montagu, 1808), and *U. tipica* (Nardo, 1869).

Remarks. Although old, these specimens are exceptionally well-preserved and match prior descriptions (e.g., Bourdon 1968).

Gyge ovalis (Shiino, 1939)

Fig. 4

Metabopyrus ovalis Shiino, 1939b: 88–91, figs. 7, 8 (Hakata Bay, Kyūshū, Japan, infesting *Upogebia major* (De Haan, 1841) (subsequently reidentified as *Upogebia issaeffi* (Balss, 1913), see Remarks).—Shiino, 1958: 48–49, fig. 10 (Japan, host unknown).—Codreanu, 1961: 140 (mention), fig. 1 (map).—Codreanu & Codreanu, 1963: 283 (mention).—Shiino, 1972: 7 (list).—Markham, 1982: 340 (mention).—Markham, 1985: 14 (mention).—Page, 1985: 196 (mention).—Kim & Kwon, 1988: 199, 201–203, 220, fig. 2 (South Korea, infesting *U. major*).—Markham, 2001: 198, 201 (list).—Itani *et al.*, 2002: 72, fig. 1a9 (Seto, Inland Sea, Japan, infesting *U. major*).—Itani, 2004a: 16, fig. 3A (mention).—Itani, 2004b: 37–39, tables 3, 5 (Japan, infesting *Austinogebia narutensis* (Sakai, 1986), *U. issaeffi*, *U. carinicauda* (Stimpson, 1860), *U. major*, *U. yokoyai* Makarov, 1938).—Nanri *et al.*, 2011: 1056 (mention).—Kwon, 2012: 1, 4, 33–34, fig. 13 (South Korea, infesting *U. major*).

“bopyrid isopods” (in part) Itani, 2001: 5 (Japan, infesting *U. yokoyai*).

Gyge ovalis—Markham, 2004: 195–197, fig. 6 (Chang-Hua County, southwest Taiwan, infesting *Austinogebia edulis* (Ngoc-Ho & Chan, 1992)).—Yu & An, 2008: 692 (list).—An *et al.*, 2009: 228–229, fig. 2 (Shandong Province, China, infesting *U. major* and *A. wuhsienweni* (Yu, 1931)).—Kinoshita *et al.*, 2010: 949–951, fig. 3 (Japan, infesting *U. yokoyai*).—Ubaldo *et al.*, 2014: 557–564 (Seto Inland Sea, Japan, infesting *U. major*).—Hong, 2013: 336–3377, fig. 6A, B (South Korea, infesting *U. major*).—Itani *et al.*, 2014: 111 (mention).—Miura *et al.*, 2014: 31 (table), 32, fig. 1C (Japan, infesting *U. yokoyai*).—Hong *et al.*, 2015: 608, 612, 613 (South Korea, infesting *U. major*).—Asson *et al.*, 2017: 222 (mention).

Material examined. Taiwan: Immature female (3.8 mm), mature male (2.1 mm), *ex* right branchial chamber of female *Austinogebia edulis* (8.0 mm CL), Yilan County, port at Tai-Chi, shallow water, coll. inland trawlers (ZRC 2016.0440)

Distribution. Japan, South Korea, Taiwan, and China.

Hosts. *Austinogebia edulis* (Ngoc-Ho & Chan, 1992), *A. narutensis* (Sakai, 1986), *A. wuhsienweni* (Yu, 1931), *Upogebia carinicauda* (Stimpson, 1860), *U. issaeffi* (Balss, 1913) (possible type host), *U. major* (De Haan, 1841) (probable type host), and *U. yokoyai* Makarov, 1938.

Remarks. The host of the types was originally reported as *Upogebia major* (De Haan, 1841) in Shiino (1939b) but was changed to *U. issaeffi* (Balss, 1913) in Shiino (1958) and back again to *U. major* in Shiino (1972). This species has been reported several times from *U. major*, including in a large-scale study of the host/parasite relationship by Ubaldo *et al.* (2014), but only once subsequently from *U. issaeffi* (Itani 2004b). The identity of the type host is therefore most likely *U. major*, but only examination of the type host can solve this question. Markham (2004) included Codreanu (1941: 140) in his synonymy list under *Metabopyrus ovalis*, but nowhere in that paper is the species mentioned and there is no p. 140 in that article; the page was probably from Codreanu (1961) where the species is mentioned and the “1941” citation is therefore a lapsus for 1961. Chapman *et al.* (2012) incorrectly stated that the record of *Gyge ovalis* from Itani (2004b) was a misidentification of *Orthione griffenis* Markham, 2004. Itani’s (2004b) identification was correct, albeit under the original combination of *Metabopyrus ovalis*. The record in Itani’s (2004b) Table 3 that is referable to *O. griffenis* is actually “*Pseudioninae* sp. 1” (Williams & An

2009; Itani *et al.* 2014). The present record (Fig. 4) is only the second from Taiwan and *A. edulis* is the only known host in Taiwan.

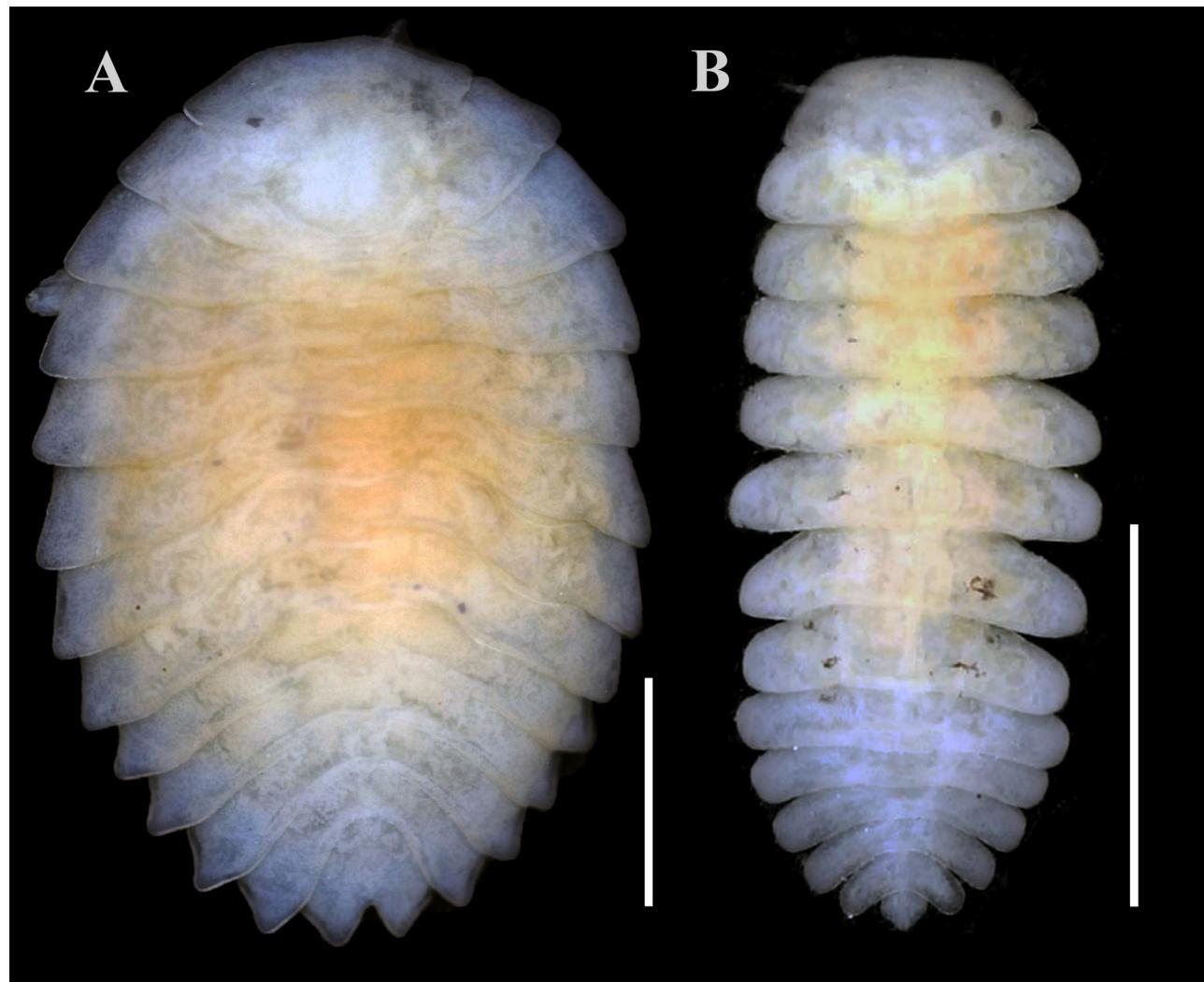


FIGURE 4. *Gyge ovalis* (Shiino, 1939) (ZRC 1997.713) ex *Austinogebia edulis* Ngoc-Ho & Chan, 1992. A, immature female, dorsal view; B, male, dorsal view. Scale bars: A, B = 1.0 mm.

Ionella Bonnier, 1900

Ionella agassizi Bonnier, 1900

Ionella agassizi Bonnier, 1900: 48, 222, 322–327, pls. 23, 24 (type locality: Talcahuano, Chile, infesting *N. uncinata* (H. Milne Edwards, 1837)).—Nierstrasz & Brender à Brandis, 1923: 87 (list).—Caspers, 1939: 243 (list).—Holthuis, 1952: 92 (mention).—Shiino, 1964a: 27–29, fig. 1 (Puerto Montt, Chile, infesting *N. uncinata*).—Danforth, 1970a: 29 (comparison with *Ionella murchisoni* Danforth, 1970).—Brusca, 1980: 259 (mention).—Page, 1985: 198 (mention).—Stuardo *et al.*, 1986a: 3 (mention).—Stuardo *et al.*, 1986b: 20–21, 24–25, 29, figs. 2a, b, 4.10–4.15, 16–18 (Dichato and Coliumo Bay, Chile, infesting *N. uncinata*).—Markham, 1992a: 3, table 1 (list).—Markham, 1994: 230 (mention).—Muñoz, 1997: 36 (Dichato, Bahía Coliumo, Chile, infesting *N. uncinata*).—Pardo, 1998: 6, table 1 (list).—Pardo *et al.*, 1998: 272 (mention).—Muñoz & George-Nascimento, 1999: 52–53 (Bahía San Vicente, Talcahuano, Chile, infesting *N. uncinata*).—Trilles, 1999: 296, fig. 8.16.F (figure after Bonnier, 1900).—Astete-Espinoza & Caceres, 2000: 244–247 (Lenga, Bahía de San Vicente, Talcahuano, Chile, infesting *N. uncinata*).—Markham, 2001: 198, 200 (list).—Muñoz, 2001: 756–760 (Lenga, Bahía San Vicente, Chile, infesting *N. uncinata*).—McDermott, 2002: 40 (mention).—Neves *et al.*, 2004: 209, 211 (mention).—Espinosa-Pérez & Hendrickz, 2006: 244 (list).—Muñoz & Olmos, 2007: 112, 119 (list).—Román-Contreras, 2008a: 383 (mention).—Smith *et al.*, 2008: 231 (mention).—Castillo-Blasco *et al.*, 2009: 715–717 (Lenga, Chile, infesting *N. uncinata*).—Pardo *et al.*, 2009: 2044, 2051–2053 (San Carlos, Valdivia, Chile, infesting *N.*

uncinata).—Thiel & Hinojosa, 2009: 681, 786, unnumbered figure (Chile, infesting *N. uncinata*).—Varisco & Vinuesa, 2011: 1684 (mention).—Stuardo & Vega, 2011: 104 (mention).—Cericola & Williams, 2015: 239 (table).

Material examined. **Panama:** Ovigerous female (6 mm; incomplete, tissue sampled for molecular analysis) (USNM 14376368 ex ULLZ 10202), ex right branchial chamber of *Neotrypaea uncinata* (6.5 mm CL, lacking gonopores) (ULLZ 10202), beach across road from NOAA/STRI lab, Panama, coll. D. L. Felder, 10 Sept 1995.

Distribution. Pacific Panama, and coast of Chile.

Hosts. *Neotrypaea uncinata* (H. Milne Edwards, 1837) (type host).

Remarks. This specimen is more similar to the female illustrated by Shiino (1964a) than that illustrated by Bonnier (1900), in that the lateral plates of the pleomeres are strongly asymmetrical, though not as strongly so as in Shiino's (1964a) specimen. This Panamanian record is a significant range extension for *Ionella agassizi*, which was previously known only from localities in Chile. However, the host, *Neotrypaea uncinata*, is known to have the broadest longitudinal range of any thalassinidean: from 34°N to 47°S (i.e., southern California to southern Chile) (Dworschak 2005). Despite the numerous records of this host from localities in Chile, Sakai (2011) inexplicably stated it was known only from the type locality. The host has been previously recorded from Panama (Ayón-Parente *et al.* 2014) but without this parasite.

***Ionella compressa* (Shiino 1964) n. comb.**

Pseudione compressa Shiino, 1964b: 240–242, fig.2 (Honohoshi, Amamioshima, Japan, infesting *Neocallichirus jousseaumei* (Nobili, 1904)).—Bourdon, 1968: 150, 172 (mention).—Danforth, 1970a: 29 (mention).—Page, 1985: 198 (mention).—Saito *et al.*, 2000: 37 (list).—Markham, 2001: 198, 200 (list).—Itani, 2004b: 37–38, table 3 (Japan, infesting *Paratrypaea bouvieri* (Nobili, 1904)).

Not *Pseudione compressa*—Shiino, 1972: 7 (Japan, infesting *Heterocarpus sibogae* de Man, 1917) (= *Pseudione magna* Shiino, 1951 *fide* Markham, 2010: 158).

Material examined. None.

Distribution. Japan.

Host. *Neocallichirus jousseaumei* (Nobili, 1904) (type host) and *Paratrypaea bouvieri* (Nobili, 1904).

Remarks. The males and females of this species appear very similar to those of *Ionella murchisoni* Danforth, 1970 and Danforth (1970a) actually compared and contrasted the two species although he did not transfer *P. compressa* to *Ionella*. Based on Shiino's (1964b) description and figures, we herein transfer *P. compressa* to *Ionella*. Examination of specimens, ideally from the vicinity of the type locality, is needed to confirm details of the morphology and to determine the relationship of *I. compressa* to other species of *Ionella*.

***Orthione* Markham, 1988**

***Orthione furcata* (Richardson, 1904)**

Fig. 5A, B

Pseudione furcata Richardson, 1904: 79, figs. 69, 70 (host unknown; type locality: eastern shore of Virginia, U.S.A.).—Richardson, 1905: 529–530, figs. 571–573 (repeat of data from Richardson, 1904).—Fowler, 1912: 523 (species entry).—Hay, 1917: 573 (mention).—Van Name, 1920: 72 (mention).—Nierstrasz & Breder à Brandis, 1923: 72 (list).—Menzies & Frankenberg, 1966: 9 (list).—Schultz, 1969: 327, fig. 524 (list; placement in key to bopyrids).—Gosner, 1971: 476 (list).—Wass, 1972: 147 (list).—Markham, 1977: 816 (mention).

Pseudione upogebiae—Pearse, 1947: 326 (in part, Beaufort, North Carolina, U.S.A., infesting *Upogebia affinis* (Say, 1818)) (not *Progebiophilus upogebiae* (Hay, 1917)).

Orthione furcata—Markham, 1988: 14–17, figs. 4–6 (Massachusetts, Virginia, and Cape Cod, infesting *U. affinis*).—Markham, 2001: 198, 200 (list).—Markham, 2004: 186 (mention).—Heard *et al.*, 2007: 26 (mention).

not *Pseudoione [sic] furcata*—Kaestner, 1970: 463 (mention occurrence on “Gulf coast” [Gulf of Mexico], infesting unknown host) (= *Progebiophilus upogebiae* (Hay, 1917)).

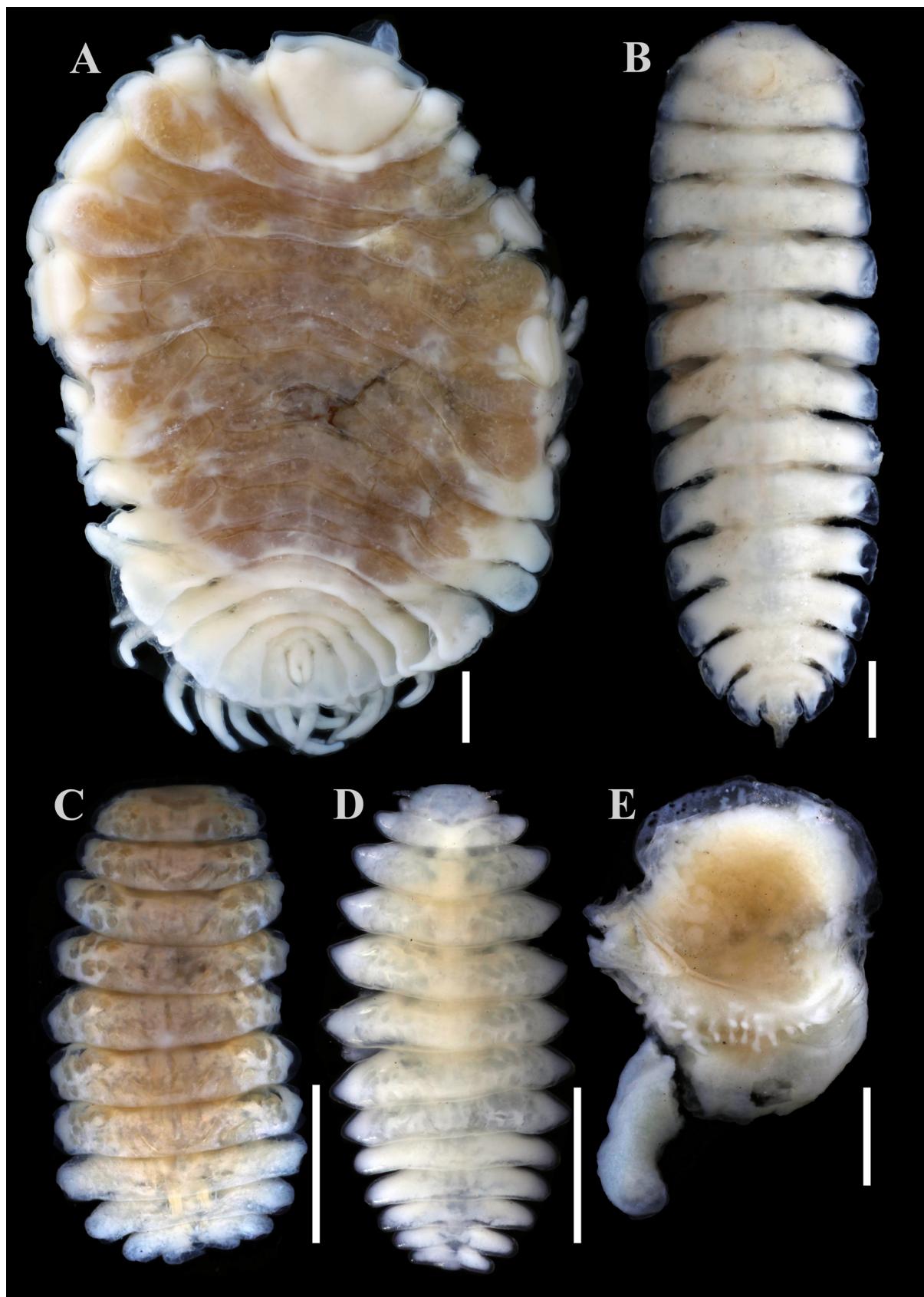


FIGURE 5. *Orthione furcata* (Richardson, 1904), *Probopyrus pandicola* (Packard, 1879), and *Progebiophilus upogebiae* (Hay, 1917). A, female dorsal view of *O. furcata* (USNM 1424906 ex USNM 84049); B, male dorsal view of *O. furcata* (USNM 84052); C, male dorsal view of *P. pandicola* (USNM 1424905 ex USNM 84047); D, male dorsal view of *P. upogebiae* (USNM 48370); E, left oostegite 1 of *P. upogebiae*, internal view (USNM 84049). Scale bars: A–E = 1.0 mm.

Material examined. United States: Ovigerous female (11.8 mm), *ex* branchial chamber of “*Panopeus herbstii*” H. Milne Edwards, 1834 [incorrect host identification; see below], Beaufort, North Carolina, coll. A. S. Pearse, 22 Aug 1946 (USNM 1424906 *ex* USNM 84049; also present in vial was a mature male (4.5 mm) and a single first oostegite of *Progebiophilus upogebiae*; both of the latter retain the USNM 84049 catalogue number); mature male (9.4 mm), *ex* branchial chamber of *Upogebia affinis* (size and sex unknown), Beaufort, North Carolina, coll. A. S. Pearse, 6 Aug 1946 (USNM 84052).

Distribution. Massachusetts to North Carolina, U.S.A.

Hosts. *Upogebia affinis* (Say, 1818).

Remarks. This species was confounded with *Progebiophilus upogebiae* (Hay, 1917) by Pearse (1947) as evidenced by the female and male examined here that were included in separate USNM lots, each labeled as being *Pseudione upogebiae*. One of these lots (USNM 84049) contained a female *Orthione furcata* (Fig. 5A), a male *P. upogebiae*, and the first oostegite of a *P. upogebiae*, whereas the other (USNM 84052) contained only a male *O. furcata* (Fig. 5B). Markham (1988) also noted that four of the six specimens originally in USNM 84051, labeled as *P. upogebiae*, were likewise actually *O. furcata*. The male specimen (USNM 84052) was misidentified on the label as “*Pseudodione* [sic] *upogebia* [sic]”. The labeling and co-mingling of two species from different genera, both otherwise only known from upogebiid hosts, in a single lot supports our conclusion that *Panopeus herbstii* is an erroneous host identification for *P. upogebiae* (see additional Remarks under that species).

Markham (1988) included Kaestner’s (1970) record of “*Pseudoione*” [sic] *furcata* from the Gulf of Mexico in his synonymy list for *O. furcata*, essentially without comment as to its validity, although he correctly noted that Kaestner (1970) gave no indication as to the source of his data. Markham (1988) logically interpreted Kaestner’s (1970) statement of the species’ occurrence on the “Gulf coast” to mean the Gulf of Mexico, but it is unusual that Kaestner, being a German researcher, would use a colloquial term such as “Gulf coast.” In fact, no mention of *Pseudione furcata* appears in the original edition of this book (Kaestner 1967). This information was added by one of the reviewers who provided “numerous suggestions and changes” when Kaestner (1967) was translated into English by H. W. and L. R. Levi (Kaestner 1970: vi–vii). Although three people (R. R. Hessler, R. J. Menzies, and S. M. Shiino) are thanked in Kaestner (1970) for contributing to the isopod section, none are identified as contributing text but the most likely source of this record of *O. furcata* is Menzies, then at Florida State University, which is in western Florida and very near to the “Gulf coast.” However, this record is almost certainly erroneous, as no other published records of *O. furcata* from south of North Carolina are known. The “Gulf coast” record is likely a misidentification of *Progebiophilus upogebiae*, a species known to occur in the northern Gulf of Mexico (see Material Examined under that species).

Progebiophilus Codreanu & Codreanu, 1963

Progebiophilus bruscai Salazar-Vallejo & Leija-Tristán, 1990

Aporobopyrus sp. Leija-Tristán & Salazar-Vallejo, 1987: 179 (Bahía de La Paz, Baja California, Sur, Mexico, infesting *Upogebia dawsoni* Williams, 1986).

Pseudione—Campos & de Campos, 1989a: 33 (Bahía Tortugas, Baja California Sur, Mexico, infesting *U. macginitieorum* Williams, 1986).—Campos & de Campos, 1989b: 177 (Bahía Tortugas, Baja California Sur, Mexico, infesting *U. macginitieorum*).

Progebiophilus bruscai Salazar-Vallejo & Leija-Tristán, 1990: 423–432, figs. 2, 3 (type locality: El Comitán, Laguna de La Paz, Bahía de La Paz, Baja California Sur, Mexico, infesting *U. dawsoni*).—Leija-Tristán & Salazar-Vallejo, 1991: 1–5 (infesting *U. dawsoni*).—Campos *et al.*, 1992: 753, 756–757 (list).—Markham, 1992a: 3 (list).—Campos & de Campos, 1998: 289–293, figs. 1, 2 (redescription, San Felipe, Baja California Norte to La Paz Bay, Baja California Sur, west coast of Baja California Peninsula at Tortugas Bay, Baja California Sur and Todos Santos Bay (Estero Punta Banda), Baja California Sur, infesting *U. dawsoni*, *U. macginitieorum*).—Kazmi & Bourdon, 1997: 62 (mention).—Trilles, 1999: 326 (mention).—Espinosa-Pérez & Hendrickx, 2001: 51 (list).—Markham, 2001: 198, 200 (list).—Brusca *et al.*, 2005 (list).—Markham, 2005: 85–86 (Coloraditos, Baja California Norte and Isla Partida, Baja California Sur, infesting *U. dawsoni* and *Pomatogebia rugosa* (Lockington, 1878)).—Espinosa-Pérez & Hendrickx, 2006: 237 (list).—Román-Contreras, 2008b: 97 (mention).—Smith *et al.*, 2008: 231 (mention).—An *et al.*, 2009: 234 (list).—Campos *et al.*, 2009: 1255 (list), 1257 (mention).—Williams & An, 2009: 121 (mention).—Dumbauld *et al.*, 2011: 337 (mention).

Material examined. Mexico: Ovigerous female (4.8 mm), mature male (1.5 mm), *ex* left branchial chamber of

female *Upogebia dawsoni* (5.0 mm CL), ovigerous female (7.0 mm), mature male (2.0 mm), ex left branchial chamber of female *U. dawsoni* (7.0 mm CL), ovigerous female (7.0 mm), mature male (2.0 mm), ex left branchial chamber of female *U. dawsoni* (6.5 mm CL), immature female (2.0 mm), mature male (1.2 mm), ex right branchial chamber of juvenile *U. dawsoni* (3.5 mm CL), immature female (3.0 mm), mature male (1.5 mm), ex right branchial chamber of juvenile *U. dawsoni* (4.5 mm CL), immature female (2.3 mm), mature male (1.3 mm), ex right branchial chamber of juvenile *U. dawsoni* (4.0 mm CL), ovigerous female (8.0 mm, sacrificed for molecular work), mature male (2.5 mm), ex right branchial chamber of female *U. dawsoni* (7.0 mm CL), sandy beach, northwest, Puerto San Carlos, Baja California Sur, coll. R. Robles, J. Cuesta & F. Mantelatto, 4 Dec 2001 (ULLZ 10195); ovigerous female (4.8 mm), mature male (2.0 mm), ex left branchial chamber of immature *U. dawsoni* (5.0 mm CL), Bahia de Los Angeles, Baja California Norte, coll. F. Mantelatto, J. Cuesta & R. Robles, 6 Dec 2001 (ULLZ 10197).

Nicaragua: mature female (6.0 mm; incomplete, sampled for molecular analysis), mature male (2.3 mm) (USNM 1437636 ex ULLZ 10194), ex right branchial chamber of male *Upogebia spinigera* (6.0 mm CL) (ULLZ 10194), Santa Julia, between Potosi and El Rosario, coll. J. A. Cuesta, R. Robles & J. T. Rodriguez, 19 Nov 2002.

Distribution. Gulf of California from San Felipe, Baja California Norte to Laz Paz, Baja California Sur; Tortugas Bay, west coast of Baja California Sur and Todos Santos Bay, Ensenada, Baja California Sur, Mexico; Nicaragua (herein).

Hosts. *Upogebia dawsoni* Williams, 1986 (type host), *U. spinigera* (Smith, 1871), *U. macginitieorum* Williams, 1986, *Pomatogebia rugosa* (Lockington, 1878).

Remarks. Although often cited as being published in 1989, the original description of this species was in an issue marked as “dépot légal 1^{er} trimestre 1990.” This species appears to be widely distributed throughout the Gulf of California, as well as on the west coast of Baja California. Its absence from the eastern coast of the Gulf of California may be an artifact of fewer hosts being collected in that region, either due to undersampling or less suitable habitats.

The Nicaraguan specimen reported on here resembles *P. bruscai* in all details of the female except that none of the bases of the pereopods have swollen dorsal knobs (e.g., Salazar-Vallejo & Leija-Tristán 1990: fig 2F; Campos & de Campos 1998: fig. 1L–M). The male likewise shows all the characters of *P. bruscai* although the pleotelson has fused rather than articulated posterolateral lobes as described and illustrated by Salazar-Vallejo & Leija-Tristán (1990: fig. 3A, C). However, the fusion of posterolateral lobes of the pleotelson in males is known to be variable in this species (see Campos & de Campos 1998).

Identification of these specimens as *P. bruscai* greatly extends the known range of the species southward from Mexico. The host, *U. spinigera*, was previously known to bear *Orthione mesoamericana* Markham, 2004, in Costa Rica and Colombia.

Progebiophilus upogebiae (Hay, 1917)

Figs 5D, E, 6, 7

Pseudionae upogebiae Hay, 1917: 572–573, pl. 100, figs. 7–12 (type locality: Beaufort, North Carolina, U.S.A., infesting *Upogebia affinis* (Say, 1818)).—Nierstrasz & Brender à Brandis, 1923: 72, 76 (list).—Brian & Darteville, 1941: 350–351 (mention).—Pearse, 1947: 326 (part) (Beaufort, North Carolina, infesting *U. affinis*).—Shiino, 1951: 32 (mention).—Catalano & Restivo, 1965: 203 (list).—Lemos de Castro, 1965: 11–14, figs. 1–11 (Ceará, Brazil, infesting *Upogebia* sp.; identified as *U. omissa* Gomes Corrêa, 1968 in Lemos de Castro, 1970).—Schultz, 1969: 325, fig. 520 (list; key).—Lemos de Castro, 1970: 3, 5, pl. 3, figs. 15–17 (Ceará, Brazil, infesting *U. omissa*).—Restivo, 1970: 314 (mention).—Restivo, 1971: 71, table 1 (list).—Wass, 1972: 147 (York River, Virginia, U.S.A., infesting *U. affinis*).—Restivo, 1975: 153, table 1 (list).—Markham, 1977: 813, 816 (synonymy of *Phyllodurus robustus* Pearse, 1953).—Kelley, 1978: 169 (list).—Lawler, 1978: 310 (list).—Bourdon, 1981b: 127 (mention), 128 (key to males of the genus).—Williams, 1984: 192 (mention).—Fox & Ruppert, 1985: 53, 196, 289, 301 (South Carolina, infesting *U. affinis*).

Pseudionae [sic] upogebiae—Hay & Shore, 1918: 408 (Beaufort, North Carolina, infesting *U. affinis*).

P. upogebiae—Van Name, 1920: 72 (mention).

P. urogebiae [sic]—Popov, 1929: 13 (mention).

Ps. urogebiae [sic]—Popov, 1929: 14 (mention).

Pseudionae [sic] upogebiae—Pearse, 1945: 305 (Beaufort, North Carolina, infesting *U. affinis*).—Williams, 1965: 104 (mention).

Pseudionae panopei Pearse, 1947: 326–328, figs. 1–11 (Beaufort, North Carolina, infesting *Panopeus herbstii* H. Milne

- Edwards, 1934, but see below).—Schultz, 1969: 328, fig. 525 (key).—Danforth, 1970b: 49, 153 (list), fig. 33E, F.—Markham, 1975: 61 (report on type material).—Kelley, 1978: 169 (list).—Markham, 1988: 56 (list) (new synonymy).
Phyllodurus robustus Pearse, 1953: 235–237, figs. 131–143 (type locality: Alligator Point, Florida, infesting *U. affinis*).—Lemos de Castro, 1965: 12 (mention).—Williams, 1965: 104 (mention).—Menzel, 1971: 76 (list).—Markham, 1977: 813, 816 (synonymy with *P. upogebiae*).—Williams, 1984: 192 (mention).
Pseudione urogebiae [sic]—Schultz, 1969: fig. 520.
Pseudoione [sic] *furcata*—Kaestner, 1970: 463 (mention occurrence on “Gulf coast” [Gulf of Mexico], infesting unknown host) (not *Orthione furcata* (Richardson, 1904)).
Progebiophilus upogebiae—Markham, 1988: 4, 9–12, 17, 56, fig. 3 (syntype and other material, Beaufort, North Carolina, U.S.A., infesting *U. affinis*).—Salazar-Vallejo & Leija-Tristán, 1990: 423, 428 (mention), 429 (key), table 1.—Williams, 1993: 37 (mention), 44 (Barra del Tordo, Mexico, infesting *Upogebia felderii* Williams, 1993).—Kazmi & Bourdon, 1997: 62 (mention).—Brasil-Lima, 1998: 636 (list).—Campos & de Campos, 1998: 288, 293 (mention).—Markham, 2001: 198, 200 (list).—Markham, 2005: 86 (Indian River Lagoon, Florida, infesting *U. affinis*).—Heard *et al.*, 2007: 26 (mention).—Román-Contreras, 2008b: 103 (mention).—An *et al.*, 2009: 234 (list).—Schotte *et al.*, 2009: 980 (list).
Progebiophilus urogebiae [sic]—Salazar-Vallejo & Leija-Tristán, 1990: 428 (mention).
“bopyrid” Williams, 1993: 44 (Barra del Tordo, Mexico, infesting *U. felderii*).
not *Pseudione upogebiae*—Pearse, 1947: 326 (in part, Beaufort, North Carolina, U.S.A., infesting *Upogebia affinis*) (= *Orthione furcata*).

Material examined. United States: Two ovigerous female paratypes of *Pseudione upogebiae* (9.8–11.1 mm), mature male paratype (3.1 mm), *ex* branchial chambers of *Upogebia affinis* (sizes and sexes unknown), Beaufort, North Carolina, coll. W. P. Hay, 17 Aug 1915, (USNM 48370); mature holotype female of *Pseudione panopei* (12.1 mm), *ex* branchial chamber of “*Panopeus herbstii*” [erroneous identification; see Remarks; size and sex of host unknown], Beaufort, North Carolina, coll. A. S. Pearse, 22 Aug. 1946 (USNM 82669; body excepting most of abdomen in EtOH, abdomen mounted on slide); mature allotype male of *P. panopei*, same data as holotype (USNM 82670; mounted on slide); paratype female of *P. panopei*, same data as holotype (USNM 82671; mounted on slide); mature female (likely ovigerous but no eggs currently present in vial) (9.9 mm), *ex* branchial chamber of “*Uca pugilator*” (Bosc, 1801) [incorrect host identification; see below], Beaufort, North Carolina, coll. A. S. Pearse, 20 Jul 1946 (USNM 84047; also present in vial was a mature male *Probopyrus pandalicola* (Packard, 1879) (3.0 mm); mature male (4.5 mm, USNM 1424905) and single first oostegite), *ex* branchial chamber of “*Panopeus herbstii*” [incorrect host identification; see below], Beaufort, North Carolina, coll. A. S. Pearse, 22 Aug 1946 (USNM 84049; also present in vial was an ovigerous female (11.8 mm) of *Orthione furcata*, now USNM 1424906); unidentifiable fragments, *ex* *U. affinis* (as per label; host not in vial), Beaufort, North Carolina, coll. A. S. Pearse, 13 Jun 1946 (USNM 84050); mature female (likely ovigerous but no eggs currently present in vial) (8.3 mm), mature male (3.2 mm), *ex* branchial chamber of *U. affinis* (as per label; host not in vial), Beaufort, North Carolina, coll. A. S. Pearse, 17 Jun 1946 (USNM 84051); ovigerous female (10.0 mm), mature male (3.3 mm), *ex* right branchial chamber of *U. affinis*, Goose Cove sand spit, Cedar Key, Levy County, Florida, 29.133°–83.037°, 0–1 m depth, coll. G. F. Paulay & UF Invertebrate Zoology class (UF 044634).

Mexico: Ovigerous female (9.0 mm, part sacrificed for molecular work), mature male (2.7 mm), *ex* right branchial chamber of female paratype of *Upogebia felderii* (8.0 mm CL), Stn 6, Barra del Tordo, mouth of Rio Carrizal, Tamaulipas, inshore of grass beds, yabby pump, coll. D. L. Felder & R. Tinnin, 24 May 1982 (ULLZ 3019); mature female (7.0 mm, ½ sacrificed for molecular work), *ex* left branchial chamber of female *U. felderii* (8.0 mm CL), Stn 6, Rio Carrizal, Barro del Tordo, Tamaulipas, coll. D. L. Felder & R. Tinnin, 24 May 1982 (ULLZ 10200); ovigerous female (7.8 mm), mature male (2.5 mm), *ex* branchial chamber of *U. felderii* (sex and CL unknown), Barra del Tordo, mouth of Rio Carrizal, Tamaulipas, oyster covered beaches near grass beds, shallow and intertidal, coll. D. L. Felder, Rabalais *et al.*, 14 Jun 1978 (USNM 1084297 *ex* ULLZ 3071).

Distribution. Virginia, U.S.A to Brazil, and northern Gulf of Mexico west to Tamaulipas, Mexico.

Hosts. *Upogebia affinis* (Say, 1818) (type host), and *U. felderii* Williams, 1993. The record of *Panopeus herbstii* H. Milne Edwards, 1834, as host of the type specimens of *Pseudione panopei* is in error; see below.

Remarks. *Pseudione panopei* has always been a puzzle because it is the only species in Pseudioninae, outside those of *Gigantione* Kossmann, 1881, that has been reported from a brachyuran host. Markham (1975) examined Pearse's type material of *Pseudione panopei* and stated that “this species is definitely assignable to *Pseudione*, but there is some reason to believe that the host was incorrectly recorded.” Markham (1975) did not, however, indicate why he thought the host was not *Panopeus herbstii* as given by Pearse (1947). We have examined all of the type material of *Pseudione panopei* (Fig. 7) and concur with Markham's (1975) conclusion that the host was recorded in

error. The morphological characters of the holotype female of *Pseudione panopei* are identical with those of *Progebiophilus upogebiae* (compare Fig. 6 herein with Fig. 3 in Markham 1988). The allotype male (USNM 82670) and the immature paratype female (USNM 82671) are both mounted on slides and in poor condition; both are highly distorted and their length cannot be measured accurately. The pleotelson of the male has lateral lobes that were folded somewhat when the specimen was mounted on a slide and Pearse (1947) inaccurately drew them as if they were segmented uropods.

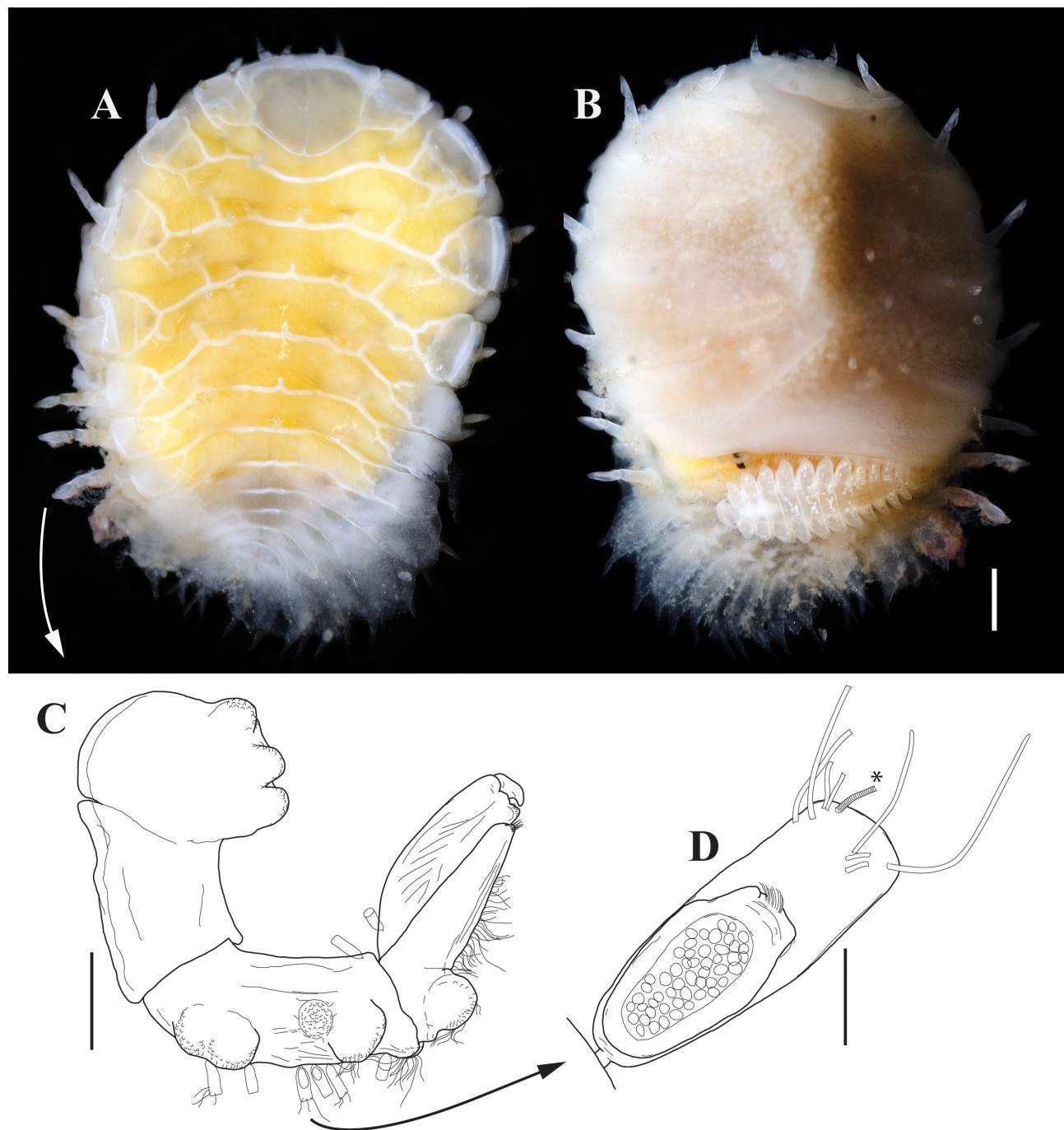


FIGURE 6. *Progebiophilus upogebiae* (Hay, 1917) (UF 044634). A, female, dorsal view; B, female, ventral view with male *in situ*; C, seventh pereopod from left side; note the *Cothurnia*-like ciliate (Vaginicolidae) and Eccrinales attached directly to the pereopod (shown only on right side) as well as on the protozoans; D, close-up of single *Cothurnia*-like sp. with attached Eccrinales (asterisk indicates only specimen of Eccrinales with septa drawn). Scale bars: A, B = 1mm; C = 250 µm; D = 25 µm. A, B courtesy of Gustav Paulay.

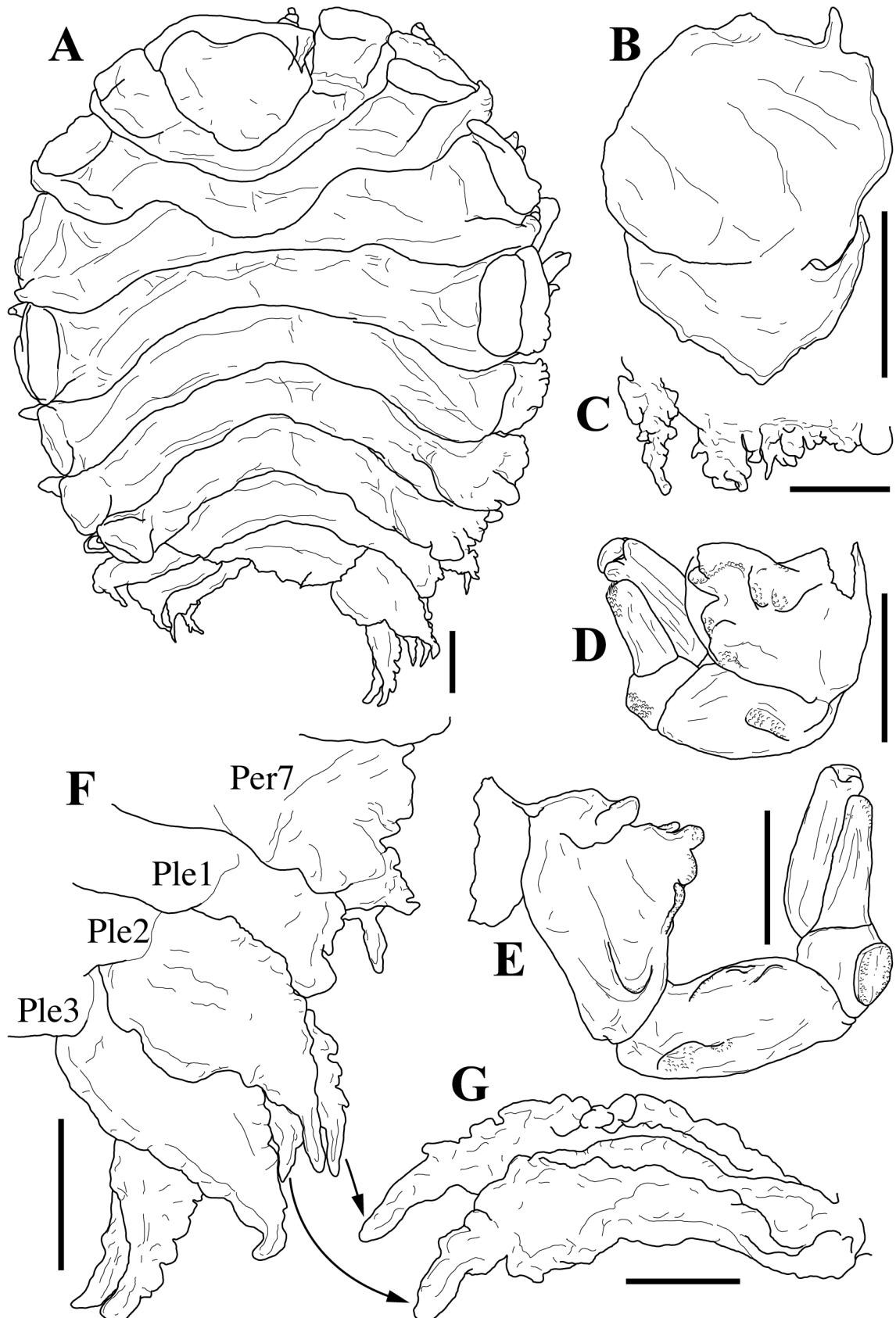


FIGURE 7. *Pseudione panopei* Pearse, 1947 (= *Progebiophilus upogebiae* (Hay, 1917)), mature female holotype (USNM 82669). A, dorsal overview of female; B, right maxilliped, outer view; C, right barbula; D, right pereopod 1; E, right pereopod 7; F, pleon, dorsal view of right side showing pereomere 7 (Per7) and pleomeres 1–3 (Ple1, 2 and 3); G, pleopod 2, ventral view of endopod and exopod. Scale bars: A, B, F = 1 mm; C–E, G = 500 µm.

Now that the identity of *Pseudione panopei* has been clarified and it is actually a species that is only known from gebiidean hosts, this leaves the following explanations for its occurrence on a brachyuran: 1) *Progebiophilus upogebiae* does, in fact, occur on *Panopeus herbstii* in Beaufort, North Carolina (and perhaps elsewhere in the host's range) and this is an unique case of a bopyrid species found on both gebiidean and brachyuran hosts or 2) the host identity was recorded in error and the types of *Pseudione panopei* were actually obtained from a *Upogebia* host. If the former is true, then it is hard to explain why no one has subsequently found this parasite on *Panopeus herbstii*, which is a common and well-studied crab. Given the clear evidence of Pearse mixing multiple bopyrid species within lots (see Material Examined above), the most parsimonious explanation is that Pearse mixed up his lots with respect to host identity as well. All of Pearse's samples except USNM 84047 (see below) include a label hand-written by Pearse (confirmed based on comparison with Pearse journals); labels include locality, date and host identification data. It is unclear why he described *Pseudione panopei* as a new species, but he may have been influenced by the now-discredited theory of Giard & Bonnier (1890b) that each parasite discovered on a novel host must be specifically distinct from all other previously described species.

USNM 84047 contains a female *Progebiophilus upogebiae* and a male *Probopyrus pandalicola* (Packard, 1879) (now USNM 1424905, Fig. 5C), a species also mentioned by Pearse (1947) and providing another example of Pearse's co-comingling of taxa and poor labeling of specimens. The host recorded on another label as "*Uca pugilator*" (now *Leptuca pugilator* (Bosc, 1801)) is also clearly in error. The original Pearse identification label for USNM 84047 is missing and the two labels in the vial indicate identification of the parasites as *Pseudione upogebiae* by Roland Bourdon. However, given that USNM 84046 and 84048 are both lots of *Leidya distorta* (Leidy, 1855) found parasitizing *L. pugilator*, we suspect that the original Pearse identification label for USNM 84047 also read *L. distorta* and this was changed when Bourdon examined the specimens. Both USNM 84046 and 84048 were cited in Bourdon & Bowman's (1970) paper on *Leidya* but 84047, conspicuously, was not. Apparently, Bourdon did not look at the male in 84047 closely as he did not notice it belonged to *Probopyrus pandalicola*, but this is perhaps not surprising as he was likely focusing on the fact that the lot did not contain any *Leidya* specimens.

The fragmentary specimen (USNM 84050) was identified on the label as "Pseudodione [sic] upogebia [sic]." Based on the poor condition of the specimen and Pearse's confusion between *Progebiophilus upogebiae* and *Orthione furcata* (Richardson, 1904) (see also Markham 1988); this vial may or may not contain fragments of *P. upogebiae*.

Although Hay & Shore (1918) misspelled the genus name and Markham (1988) correctly noted this fact, Markham's citation erroneously showed the genus name as spelled correctly. The first author to report *Progebiophilus upogebiae* from *Upogebia felderii* was Williams (1993). An additional paratype lot of *U. felderii* (ULLZ 3017) was cited by Williams (1993) as containing a host parasitized by *Progebiophilus upogebiae* and there is a note to that effect in the vial, but no parasitized specimen is present; the parasite is actually deposited as USNM 1084297 (see material examined). Both the female and male from the Florida Gulf coast show no differences from the material described and figured by Markham (1988) from North Carolina (Figs. 5D, E) except that the present male has broad midventral tubercles on pereomeres 5–7, however, these structures are rather low and can only be seen in lateral view. The specimens examined from Cedar Key, Florida (Fig. 6) are only the second record of *Progebiophilus upogebiae* under that name from the northeastern Gulf of Mexico; the first was that of Pearse (1953, as the type locality of the synonym *Phyllodurus robustus*). However, Kaestner's (1970) record of "Pseudoione" [sic] *furcata* Richardson, 1904, from the "Gulf coast" is almost certainly based on misidentified *Progebiophilus upogebiae*.

Protozoans similar in morphology to members of the genus *Cothurnia* (Vaginiculidae) were attached to the pereopods of *Progebiophilus upogebiae* from the Gulf of Mexico (Fig. 6C, D). In addition, these bopyrid specimens had mesomycetozoans (Class Mesomycetozoea, Order Eccrinales) attached to the cuticle (Fig. 6C). Such ectosymbionts have previously been reported from other bopyrids (Williams & An 2009) and their hosts (Shields *et al.* 2015).

Pseudione Kossmann, 1881

Diagnosis. Female: Body elongate; all segments distinct. Frontal lamina weakly developed, smooth. Barbula with single pair of smooth lateral projections; median region with series of low lobes. Maxilliped usually with dual palp, both lobes setose on distal margins. First oostegites with tapered posterolateral point; internal ridge with few low

projections. Coxal plates moderately developed on pereomeres 1–4 on at least one side; tergal projections not present; lateral margins of pereomeres 1–4 rounded, 5–6 tapered or rounded and resembling pleomeres. Pereopods with short carpi, smooth outer surface of meri, and relatively smooth dorsal surface of bases. Six pleomeres, first five produced into moderately to greatly developed lateral plates, directed posterolaterally; five pairs of biramous, lanceolate pleopods, edges and surfaces smooth; uropods lanceolate, uniramous or biramous, edges and surfaces smooth. Male: Body gradually tapered anteriorly and posteriorly from widest pereomere; all body regions distinct. Anterior pereopods not markedly larger than others. Pleon of six pleomeres, usually all distinct but last two or three fused in some species; pleopods uniramous, tuberculiform; posterolateral margins of pleotelson slightly to strongly produced into posterolateral lobes; no uropods. Worldwide distribution, infesting hosts in Axiidea and Astacidea (Nephropidea).

Remarks. 82 species and subspecies have been described in *Pseudione*, but after varied synonymizing and transfer to other genera, 53 currently remain in the genus (Boyko *et al.* 2011). These 53 taxa are, however, a morphologically heterogeneous assemblage, with essentially only one unifying feature: the number of pairs of pleopods. Females of all *Pseudione* species have 5 pairs of biramous pleopods and males have 5 pairs of ovate uniramous pleopods. Clearly, other morphological characters need to be examined to sort these taxa into monophyletic groupings. A significant impediment to clear delineation of this genus has always been the question of identifying the characters of the type species, *Pseudione callianassae* Kossmann, 1881, due to the poor quality of the original description. In the present work, we provide evidence that *P. dohrni* Bonnier, 1900, is identical to *P. callianassae* (see Remarks under *P. callianassae*, below), thereby providing a suite of characters that can be used to define the genus, restrict it to a group of similar taxa, and identify those species of “*Pseudione*” that belong in other existing genera or for which new genera should be established.

The characters given above in the diagnosis restrict the concept of *Pseudione* to 8 species: *P. callianassae* Kossmann, 1881 (type species, = *P. dohrni* Bonnier, 1900), *P. atlantica* Bourdon, 1971, *P. borealis* Caspers, 1939, *P. hansenii* Nierstrasz & Breder à Brandis, 1923, *P. longicauda* Shiino, 1937, *P. murawaiensis* Page, 1985, *P. nephropsi* Shiino, 1951 and *P. tanimbarensis* Markham, 1999. Of these, five (*P. callianassae*, *P. borealis*, *P. hansenii*, *P. longicauda*, and *P. murawaiensis*) parasitize hosts in Axiidea whereas three (*P. atlantica*, *P. nephropsi*, and *P. tanimbarensis*) parasitize hosts in Astacidea. Among the other 45 species previously considered to belong to *Pseudione*, none are known from astacidean hosts, whereas only three are known from axiidean hosts. Because the focus of this paper is on parasites of axiidean and gebiidean hosts, we do not deal with the 41 “*Pseudione*” species that are found on anomuran or caridean hosts. They will be arranged in natural groups as relevant material becomes available for revisionary work; we hope this will include molecular studies to test the monophyly of the groups and that *Pseudione sensu lato* can act as a testing ground for host/parasite co-evolutionary hypotheses.

We have analyzed the sole species of *Pseudione* purportedly described from a brachyuran host, *P. panopei* Pearse, 1947, because it is a synonym of a species in a genus whose other species are known from gebiidean hosts (see Remarks under *Progebiophilus upogebiae*). The three species that are found on axiidean hosts but do not share characters with *Pseudione sensu stricto* are also analyzed and transferred to other genera herein. Two of these species (*P. brattstroemi* Stuardo, Vega & Cespedes, 1986, and *P. overstreeti* Adkison & Heard, 1995) are placed in a new genus (see Remarks for *Robinione* n. gen.), whereas the third (*P. compressa* Shiino, 1964) appears to be a species of *Ionella* Bonnier, 1900 (see Remarks for *Ionella compressa*, n. comb.).

Pseudione callianassae Kossmann, 1881

Fig. 8

Pseudione callianassae Kossmann, 1881a: pl. 33, fig. 17 (type locality: Naples, Italy; type host: *Callianassa subterranea* (Montagu, 1808) (misidentification of *Callianassa truncata* Giard & Bonnier, 1890a, see Remarks).—Giard & Bonnier, 1887a: 63, 77–78, fig. 16 (list, reproduction of Kossmann’s (1881) figure).—Giard & Bonnier, 1890b: 377 (mention).—Stebbing, 1893: 411 (list).—Calman, 1898: 280 (mention).—Bonnier, 1900: 152 (mention), 168 (list), 222 (list), 248 (mention), 293 (list, discussion of identity), 381 (list).—Bohn, 1901: 330 (list).—Gerstaecker & Ortmann, 1901: 185 (list), 238 (mention), 257 (list).—Lo Bianco, 1909: 603 (mention).—Van Name, 1920: 72 (mention).—Shiino, 1937: 482 (discussion).—Pike, 1953: 225, 229 (list).—Spooner, 1957: 204 (mention).—Danforth, 1963a: 10 (list).—Catalano & Restivo, 1965: 203 (list).—Lemos de Castro, 1965: 11 (mention).—Gruner, 1966: 329 (mention).—Bourdon, 1968: 408 (discussion of identity).—Naylor, 1972: 69 (list), 75 (mention).—Bourdon, 1976: 167 (mention).—Bourdon, 1981b: 120–121 (discussion of identity).—Isaac *et al.*, 1990: 402, 404 (list).—Hayward *et al.*, 1995: 358, 360 (list).—Astall *et al.*,

- 1996: 823 (mention).—Hansson, 1998: 64 (list in possible synonymy with *P. dohrni* and *P. caspersi* Gruner, 1966).—Trilles, 1999: 335 (mention).—Markham, 2001: 196 (mention), 198 (list), 200 (list).—van der Land, 2001: 322 (list).—Boyko & Williams, 2009: 207 (mention).
- Pseudione Callianassae*—Carus, 1885: 453 (list).
- Palaegye callianassae*—Giard & Bonnier, 1890b: 374 (mention), 384–385 (list), 388 (mention).
- Palaegye Dohrni* Giard & Bonnier, 1890b: 374, 376, 377, 384–385 (*nomen nudum*).—Giard, 1905: 12 (mention).—Bouvier, 1940: 102 (mention, *nomen nudum*) (new synonymy).
- Palaegye Dohrnii* Giard & Bonnier, 1890b: 376, 377 (*nomen nudum*) (new synonymy).
- Pseudione Dohrni* Stebbing, 1893: 411 (list, *nomen nudum*) (new synonymy).
- Pseudione Dohrni* Bonnier, 1900: 48, 152, 168, 293–295, pl. 21 (type locality = Gulf of Naples, infesting *C. truncata*) (new synonymy).
- Palaegye Callianassae*—Giard, 1905: 12 (mention).
- Pseudione dohrni*—Van Name, 1920: 72 (mention).—Caroli, 1931: 320–321 (mention).—Shiino, 1937: 482 (mention).—Caspers, 1939: 236, 238, 242 (mention).—Shiino, 1951: 32, 36 (mention).—Danforth, 1963a (list).—Catalano & Restivo, 1965: 203 (list).—Shiino, 1964b: 242 (mention).—Bourdon, 1968: 173 (key), 212–215, figs. 73–75, 408 (Naples, infesting *C. truncata*).—Restivo, 1970: 305–306, 10 (key, discussion).—Bourdon, 1981a: 628 (mention).—Bourdon, 1981b: 120–121 (mention).—Hansson, 1998: 64 (list).—van der Land, 2001: 322 (list) (new synonymy).
- Pseudoione [sic] Dohrni*—Reverberi, 1943a: 42 (mention).—Reverberi, 1943b: 233, 297–299 (effects on *C. truncata*).
- Pseudojone [sic] callianassae*—Restivo, 1968: 505 (none found at Naples on *Callianassa laticauda* Otto, 1828 = *Pestarella tyrrhena* (Petagna, 1792)).
- Pseudojone [sic] dohrni*—Restivo, 1968: 505 (occurrence at Naples on *C. truncata*).
- Pseudione dorhni* [sic]—Bourdon, 1968: 150, 172, 410 (new synonymy).
- not *Pseudione callianassae*—Tattersall, 1931: 187 (Mewstone Grounds near Plymouth, England, infesting *C. subterranea*).—Pike, 1953: 225, 229 (repeat of Tattersall's (1931) record; specimen reported as lost).—Holme, 1961: 453 (English Channel, infesting *C. subterranea*).—Holme, 1966: 475, 490, fig. 53 (repeat of Holme's (1961) record); HELCOM, 2012: 140, 187 (Kattegat) (= *Pseudione borealis* Caspers, 1939).

Material examined. None; we attempted to borrow the “paratypes” (actually syntypes) of *P. dohrni* that were cited by Bourdon (1968) from MNHN but they could not be located in the collections.

Distribution. Gulf of Naples, Italy.

Host. *Callianassa truncata* (Giard & Bonnier, 1890) (type host).

Redescription (translated and modified from Bourdon, 1968). Female (Fig. 8A–E), body length 3.5 mm, maximal width 1.9 mm, head length 0.63 mm, head width 0.72 mm. No body pigmentation. Pereon weakly sinistral (8°) with coxal plates and pereomeres of left side slightly larger on segments 1–4 (Fig. 8A). Head wider than long, with thin frontal lamina (Fig. 8A), moderately embedded medially in first pereomere; eyes lacking.

Antennules of three articles each, antennae of four articles each, basal articles enlarged, especially of antennae.

Barbula with 1 pair of lanceolate lateral projections, medial margin with series of rounded tubercles, outermost pair slightly larger (Fig. 8B).

Maxilliped with rounded distal end and subacute spur; palp present as two setose, laterally rounded, finger-like projections (Fig. 8C).

First *oostegite* anterior lobe rounded, inner ridge with 6 small rounded finger-like projections on proximal half, distal lobe subtriangular, tip with tuft of setae (Fig. 8D); fifth oostegite with fringe of setae on posterior margin.

Pereon composed of 7 pereomeres, first 4 laterally straight, last 3 wider and posterolaterally tapered to points, broadest across pereomere 6, gradually tapering anteriorly and posteriorly; pereomere 1 with convex posterior margin. Posterior margins of pereomeres 2–4 with straight to slightly concave posterior margins (Fig. 8A). Pereomeres 1–4 weakly bilobed laterally, with rounded coxal plates, no dorsolateral bosses. Pereomeres 5–7 weakly bilobed on posterior margin approximately 12% of length in from distal edge, pereomeres 5–7 similar in morphology to lateral plates of pleon, posterior indentation located more mesially in posterior pereomeres and pleomeres.

First pair of *pereopods* at anterolateral margin of head; pereopods evenly spaced. Pereopods increasing in size posteriorly, each with strong dorsal lobe on ischium.

Pleon with 5 distinct pleomeres plus pleotelson (Fig. 8A, E), pleomeres resembling posterior four pereomeres, posterolaterally tapered. Pleomeres with foliaceous, biramous pleopods, not extending beyond lateral plates and not visible in dorsal view, endopod and exopod both with tuberculate, thickened margins, tapered distally, posterior pairs decreasing in size (Fig. 8E). Uniramous lateral plates, overlapping and posterolaterally tapered (Fig. 8A); lateral plates slightly smaller posteriorly and more concave on posterior margins.

Pleotelson (Fig. 8A) rounded with pair of biramous uropods, endopod longer than exopod, exopod resembling lateral plates of pleomeres (Fig. 8A, E).

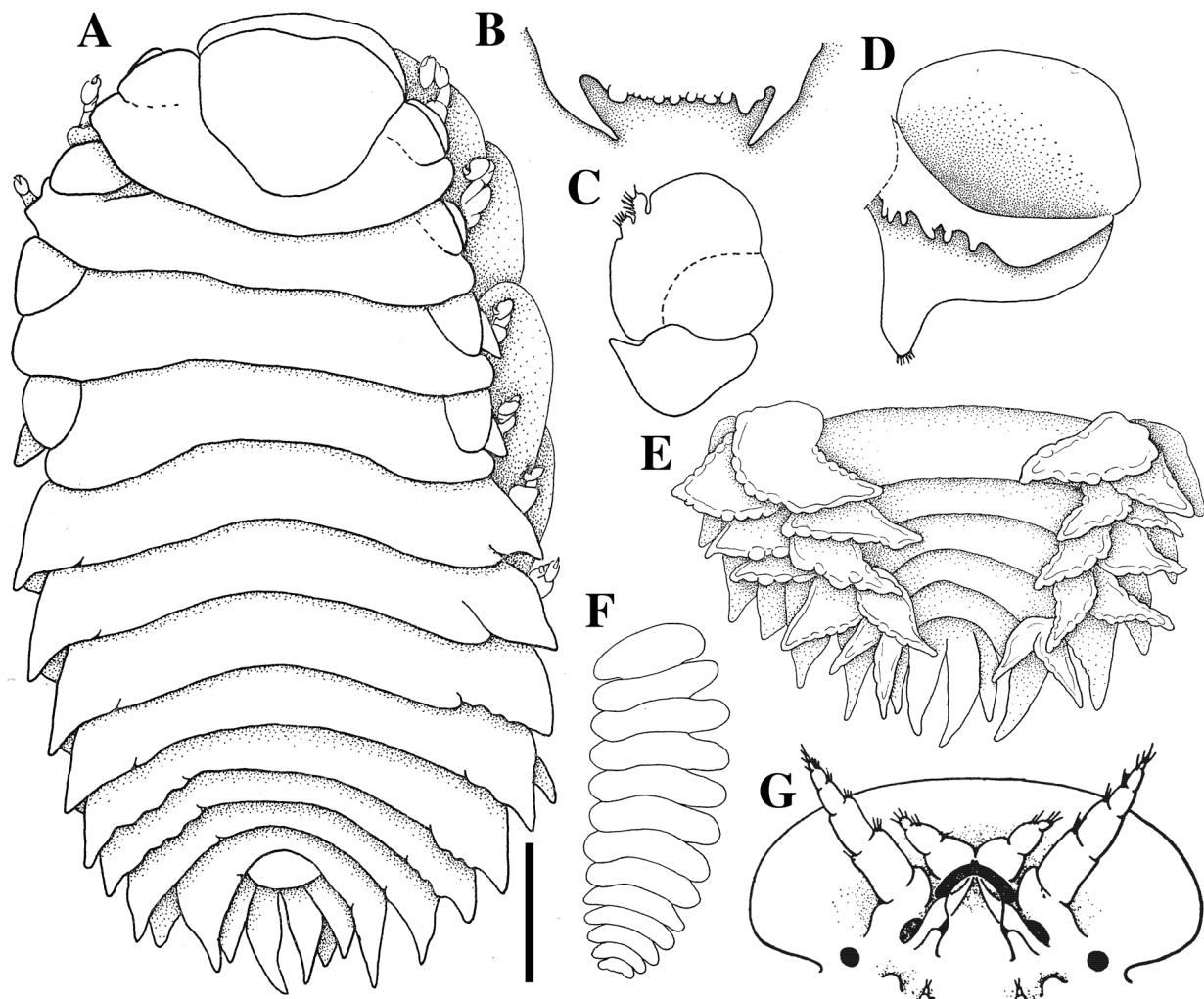


FIGURE 8. *Pseudione callianassae* Kossmann, 1881. A, female, dorsal view; B, barbula; C, maxilliped; D, first oostegite, internal view; E, pleon, ventral view; F, male, dorsal view; G, male, head, ventral view. A–F after Bourdon 1968; G after Giard & Bonnier 1887a. Scale bar: A = 0.5 mm, rest not to scale.

Male (Fig. 8F, G), length 1.5mm, maximal width 0.59 mm, head length 0.19 mm, head width 0.49 mm, pleon length 0.38 mm. Head suboval, widest medially, distinct from first segment of pereon (Fig. 8F). Eyes absent. Antennules of three articles each, antennae of four or five articles each (Fig. 8G). Small maxillipeds present, few setae on distal end (Fig. 8G).

Pereomeres 3 broadest, tapering slightly anteriorly and posteriorly (Fig. 8F). All pereomeres directed laterally, distolateral margins rounded. Pereopods not described.

Pleon with five segments plus pleotelson; segments tapering posteriorly, pleomeres directed posterolaterally (Fig. 8F). First 5 pleomeres distinctly segmented, pleotelson partly fused with fifth pleomere. First pleomere narrower than pereomeres, gradually becoming narrower posteriorly, rounded distolateral margins. Five pairs of low rounded pleopods; no midventral tubercles. Pleotelson distal margins of lobes with setae; uropods absent.

Remarks. Kossmann's (1881a) description of the type species of *Pseudione*, based on material collected from Naples on *Callianassa subterranea* (Montagu, 1808), is not only extremely brief but was entirely based on characters of the male and only the ventral surface of a male's head was figured. Markham (2001) concluded that this rendered the name a *nomen nudum*, but we consider the figure of the male's head as sufficient to make the name available (IZCN Article 12.2.7). No subsequent authors have reported a valid *P. callianassae*, although some have indicated that they collected the species (e.g., Tattersall 1931; Holme 1961), but, as shown below, these are

misidentifications of *P. borealis* Caspers, 1939. Caroli (1940) thought that the host of *P. callianassae* might be *C. truncata* Giard & Bonnier, 1890 because he could not find bopyrids on any *C. subterranea* collected from the Mediterranean. Bourdon (1968) suggested that *P. callianassae* might be identical to either *P. dohrni* Bonnier, 1900 or *P. borealis*, but refrained from synonymizing either species with the type species. Bourdon later (1981b) suggested that *P. callianassae* might be identical with either *P. dohrni* or *P. reverberii* Restivo, 1970 and that the host might not actually be *C. subterranea* but rather *C. truncata*, because that species was often found to bear both of these parasites, whereas *C. subterranea* in the Mediterranean has never been found parasitized by any bopyrid. In the same paper, Bourdon (1981b) transferred *P. reverberii* to the new genus *Acrobelione* (type species: *Pleurocrypta langi* Van Name, 1920) because females of the two species were quite similar in many characters and the males of both species lacked maxillipeds. Although Restivo (1970) described the male of *P. reverberii* as having maxillipeds, Bourdon (1981b) showed that this was an error. Kossmann's (1881a) illustration clearly shows that males of *P. callianassae* possess maxillipeds. With the elimination of *P. reverberii* as a possible synonym of *P. callianassae*, it is unclear why Bourdon (1981b) did not follow through and make *P. dohrni* a synonym of *P. callianassae* but it may be because he was unsure of the identity of the host for *P. callianassae*.

Part of the problem in determining the identity of the host of *P. callianassae* is that, for many years, the Mediterranean species of *Callianassa* were often lumped together under *C. subterranea*. Abed-Navandi & Dworschak (1997) noted that most early records of *C. subterranea* from the Mediterranean were probably misidentified *C. truncata*. In fact, there are three species of *Callianassa* occurring in the Mediterranean (*fide* Ngoc-Ho 2003): *C. acanthura* Caroli, 1946, *C. subterranea*, and *C. truncata*. *Callianassa subterranea* is found in deeper waters in the Mediterranean (35–500 m) than is typical in the rest of its range (Ngoc-Ho 2003). It is likely that Kossmann's (1881a) material came from a much shallower collection. *Callianassa acanthura* and *C. truncata* have also been at times placed in *Necallianassa* Heard & Manning, 1998, but we follow Ngoc-Ho (2003) here in retaining them in *Callianassa* Leach, 1814 *sensu stricto*, as her paper is the last to have dealt with their generic placement. Note that Giard & Bonnier (1890a) described *C. truncata* by comparing it with material they identified as *C. subterranea*. However, Ngoc-Ho (2003) showed that this comparative material was actually *Pestarella candida* (Olivi, 1792), a species from which no bopyrids have been reported. No bopyrids have been recorded from *C. acanthura* either, whereas *C. truncata* is known to bear three species of these parasites: *P. dohrni*, *Acrobelione reverberii*, and *Ione vicina* (= *I. thoracica*; see above). *Callianassa subterranea* has been reported to host three species as well: *Ione thoracia*, *P. borealis* and *P. callianassae*, but only the latter has been reported from this host in the Mediterranean, and only by Kossmann (1881a). *Pseudione dohrni*, *P. borealis*, *A. reverberii*, and *I. thoracia* are well described species that have been found on their reported hosts numerous times. *Ione vicina* is purportedly separated from *I. thoracica* by a single character (endopod of the first pleopod) that does not hold up to scrutiny and, therefore, as shown elsewhere in the present paper (see Remarks under *I. thoracica*), they are synonyms (see also Bourdon, 1968).

Pseudione callianassae has been reported from faunal surveys only twice since Kossmann's (1881a) original description. Tattersall (1931) reported it from *C. subterranea*, and this record was repeated by Pike (1953) and Spooner (1957), wherein the specimen was stated to have been lost. The second report was by Holme (1961) who reported it from "Callianassa" and this record was repeated in Holme (1966). These records are from northern European waters and it is very likely that they represent misidentified *P. borealis*, which has been reported from this region on *C. subterranea* (see Bourdon 1968; 1981a), and which is a species that was not included on any of these faunal lists. *Pseudione borealis* had been reported under the names *P. tuberculata* Caspers, 1939 (non *P. tuberculata* Richardson, 1904) and *P. caspersi* Gruner, 1966, both of which were synonymized with it by Bourdon (1981a). The record of *P. callianassae* from HELCOM (2012) is merely a checked box on a faunal list and it is unclear from where that data was obtained.

We concur with the earlier speculations of Caroli (1940) and Bourdon (1981b) that *P. callianassae* and *P. dohrni* are the same species because: 1) the only bopyrid known from *C. subterranea* in the Mediterranean is *I. thoracica*, whose males have antennae of seven articles and antennae of three articles (*P. callianassae* males with five antennal and three antennular articles), 2) *I. vicina*, herein considered a synonym of *I. thoracica* and known from *C. truncata* in the Mediterranean, also has males with seven antennal and three antennular articles and so cannot be identical with *P. callianassae*, 3) *A. reverberii*, known from *C. truncata* in the Mediterranean, has males which lack maxillipeds (present in *P. callianassae*), and 4) *P. dohrni* is found on *C. truncata* in the vicinity of Naples which is the type locality of *P. callianassae*, and has males with maxillipeds as well as five antennal and

three antennular segments. We therefore formally synonymize *P. callianassae* and *P. dohrni* herein, with the result being that *Pseudione callianassae* is now known to be restricted to the Mediterranean, currently only found in the Gulf of Naples and only on *C. truncata*.

***Pseudione longicauda* Shiino, 1937**

Pseudione longicauda Shiino, 1937: 479–482, figs. 1, 2 (type locality: Seto, Japan, infesting *Callianassa subterranea* var. *japonica* Ortmann, 1891 = *Nihonotrypaea japonica* (Ortmann, 1891)).—Shiino, 1952: 41, 43 (mention).—Shiino, 1958: 30–31, fig. 1, pl. 3, fig. 1 (Sugashima, Mie Prefecture, Japan, infesting *N. japonica*).—Danforth, 1963a: 10 (list).—Danforth, 1963b: 849 (mention).—Shiino, 1964b: 242 (mention).—Bourdon, 1968: 150, 172, 214–216 (mention).—Restivo, 1970: 314 (mention).—Shiino, 1972: 7 (list).—Bourdon, 1981a: 628 (mention).—Bourdon, 1981b: 116 (mention).—Bourdon *et al.*, 1981: 498 (mention).—Markham, 1992b: 277, 281–282, figs. 4, 5 (Hong Kong, infesting *N. petalura* (Stimpson, 1860)).—Page, 1985: 194, 196 (mention).—Huang, 1994: 530 (list).—Adkison & Heard, 1995: 108–109 (mention).—Saito *et al.*, 2000: 37 (list).—Huang, 2001: 326 (list).—Markham, 2001: 198, 200 (list).—Li, 2003: 140, 155, 158 (list).—Itani, 2004b: 38, tables 3, 4 (Japan, infesting *Nihonotrypaea harmondi* (Bouvier, 1901), *N. japonica*, *N. petalura*, *Paratrypaea bouvieri* (Nobili, 1904)).—Saito & Kinoshita, 2004: 2 (mention).—Shimoda *et al.*, 2005: (Japan, infesting *N. japonica* and *N. petalura*).—Yu & An, 2008: 693 (list).—An *et al.*, 2009: 226–227, fig. 1 (Shandong and Fujian Provinces, China, infesting *N. japonica*).—Boyko *et al.*, 2013: 499 (placement on phylogenetic tree).—Miura *et al.*, 2014: 30–32 (including table), fig. 1A (Japan, infesting *N. japonica*).—An *et al.*, 2015: 12 (list).
? “parasit bopyrid” Wardiatno, 2004: 81–84 (Japan, infesting *N. japonica*; see Remarks).

Material examined. Japan: Ovigerous female (10.5 mm, right 1/3 of body sacrificed for molecular work), mature male (2.8 mm), *ex* left branchial chamber of *Nihonotrypaea japonica* (7 mm CL, lacking gonopores), Stn 4, 32°47'N 130°36'E, Shirakawa River, Kumamoto, coll. A. Tamaki, 5 Apr 2004 (ULLZ 5471); ovigerous female (8.5 mm, left ½ sacrificed for molecular work), mature male (2.7 mm), *ex* right branchial chamber of *Nihonotrypaea* cf. *petalura* (10.6 mm CL, lacking gonopores), Sample #14, Ariakemachi, coll. A. Tamaki (ULLZ 11653).

Distribution. Japan; Hong Kong; Shandong, Fujian, and Hainan Provinces, China.

Hosts. *Nihonotrypaea harmondi* (Bouvier, 1901), *N. japonica* (Ortmann, 1891) (type species), *N. petalura* (Stimpson, 1860), and *Paratrypaea bouvieri* (Nobili, 1904).

Remarks. This species belongs to *Pseudione sensu stricto* (as defined by the resolution of the identity of the type species herein). An *et al.* (2009) included Saito & Kinoshita (2004: 1–7, figs. 3, 4) in their synonymy list for *P. longicauda*; however, Saito & Kinoshita (2004) correctly identified their material as *Ione cornuta* Bate, 1864. Both of the females discussed herein were used to generate 18S rDNA data for the phylogenetic analysis of Boyko *et al.* (2013) but were erroneously reported in the Supplemental File as being from the same lot.

The specimens studied by Wardiatno (2004) were never named or figured; they are likely either this species or *I. cornuta*, as these are the only species known from *Nihonotrypaea japonica*.

***Robinione* n. gen.**

Diagnosis. Female: Body ovate; all segments distinct. Frontal lamina weakly to moderately developed, smooth. Barbula with pair of lateral projections, either smooth or tuberculate; median region smooth or with series of low lobes. Maxilliped usually with setose palp (Fig. 9A). First oostegites with tapered posterolateral point; internal ridge with numerous fimbriate projections. Coxal plates moderately developed on pereomeres 1–4 on both sides, margins crenulate; tergal projections present; lateral margins of pereomeres 1–4 crenulate, blunt, 5–6 not distinctly different from 1–4 (Fig. 9A). Pereopods with elongate carpi, bases with large irregular, infolded mass on dorsal surface (Fig. 9C, D). Six pleomeres, first five produced into moderately to greatly developed lateral plates with crenulate edges, directed posterolaterally; five pairs of biramous pleopods, lanceolate, edges crenulate, external surfaces strongly tuberculate; uropods lanceolate, uniramous, margins crenulate and external surface tuberculate. Male: Body gradually tapered anteriorly and posteriorly from widest pereomere (Fig. 10A); all body regions distinct. Anterior pereopods not markedly larger than others (Fig. 10A–C). Pleon of six pleomeres, usually distinct but last two fused in one species; pleomeres either similar in shape to pereomeres or becoming progressively thinner and with tapered, posteriorly directed, lateral margins (Fig. 10D); pleopods uniramous, low, tuberculiform

(Fig. 10D); posterolateral margins of pleotelson slightly to strongly produced into posterolateral lobes; resembling uropods of the female in the type species (Fig. 10A, D); true uropods lacking. Currently known only from the Americas (east coast of North America, Gulf of Mexico and west coast of South America), infesting hosts in Axiidea.

Type species. *Pseudione overstreeti* Adkison & Heard, 1995.

Other included species. *Pseudione brattstroemi* Stuardo, Vega & Céspedes, 1986.

Etymology. The genus is named in honor of Dr. Robin Overstreet for his many contributions to the field of parasitology. Because the type species epithet was based on Dr. Overstreet's surname, we felt it appropriate to form the generic name based on his given name (combined with the bopyrid genus name *Ione*). The gender is feminine.

Remarks. *Robinione n. gen.* can be distinguished from *Pseudione sensu stricto* by the following character states of the females (those of *Pseudione* in parentheses): 1) body outline ovate (elongate), 2) coxal plates with crenulated and tuberculate margins (margins smooth), 3) first oostegite with numerous filamentous projections along nearly all of inner ridge (inner ridge smooth or with only a few small rounded projections in proximal region), 4) bases of pereopods with large dorsal, irregular, infolded mass, larger and more complex sculpture in posterior pereopods (pereopods without dorsal mass), and 5) lateral plates and distolateral margins of pereomeres greatly expanded, lateral plates as broad as associated pleomeres (lateral plates and pereomeres not so expanded, lateral plates narrower than their respective pleomeres).

The females of *R. overstreeti n. comb.* and *R. brattstroemi n. comb.* are nearly identical. Based on the specimens examined herein and the descriptions of Stuardo *et al.* (1986a, b), the only obvious difference between the females is that the barbula of *R. brattstroemi n. comb.* has lateral lobes with crenulate margins (barbular lobes of *R. overstreeti n. comb.* are smooth). The males of the two species, however, are remarkably different. The males of *R. brattstroemi n. comb.* have few taxonomically important features at the species level, although Stuardo *et al.* (1986b) used SEM and found setae and other morphological characters that were useful for distinguishing this species from those in other genera. The male of *R. overstreeti n. comb.* is distinct in having the lateral margins of pleomeres 2–5, as well as those of the pleotelson becoming tapered and extended posteriorly. This is reminiscent of the condition of males in *Ione*; however, in *Ione*, which belongs to a different bopyroid family than *Robinione n. gen.*, the males have all the segments of the pleon fused (separate in *R. overstreeti n. comb.*) and all the pleon segments are modified (only 2–5 modified in *R. overstreeti n. comb.*). This pleonal condition was found in all males of *R. overstreeti n. comb.* examined in this study. The males of *R. overstreeti n. comb.* have rounded medial lobes on the pleomeres (Fig. 10A, D), which may represent reduced pleopods. Finally, Stuardo *et al.* (1986b; Fig. 13) documented cephalic slits on the males of *R. brattstroemi n. comb.* and these were also found in the males of *R. overstreeti n. comb.* examined in the present study.

***Robinione overstreeti* (Adkison & Heard, 1995) n. comb.**

Figs 9, 10

Pseudioniinae [sic] sp. A. Rakocinski *et al.*, 1993: 102 (list).

Pseudione overstreeti Adkison & Heard, 1995: 105–109, figs. 1, 2 (type locality: west end of Horn Island, Mississippi, U.S.A., infesting *Callichirus islagrande* (Schmitt, 1935)).—Rakocinski *et al.*, 1996: 351 (list).—Camp, 1998: 134 (list).—Schotte *et al.*, 2009: 980 (list).—Vogt, 2016: 1409, 1410 (mention), fig. 7A (color photo of male and female).

Material examined. United States: Immature female (5.5 mm), ex right branchial chamber of female *Callichirus islagrande* (10.9 mm CL), Gulf Beach, Isle Dernière, Louisiana, coll. R. B. Griffis & T. Zimmerman, 27 Jul 1993 (ULLZ 10206); immature female (5.5 mm, on SEM stub, USNM 1459847 ex ULLZ 10205), mature male (3.0 mm), ex right branchial chamber of female *C. islagrande* (8.0 mm CL), mid-intertidal pool and low intertidal, bay side, Isle Derniers, Louisiana, coll. R. B. Griffis, D. L. Felder & T. McTigue, 19 Oct 1993 (ULLZ 10205); ovigerous female (11.0 mm), mature male (4.0 mm), ex left branchial chamber of female *C. islagrande* (11.4 mm CL), Gulf side, Isle Derniers, Louisiana, coll. D. L. Felder, P. Klerks & D. Griffis, 22 Jan 1995 (ULLZ 10207); immature female (11.0 mm), mature male (4.0 mm), ex left branchial chamber of female *C. islagrande* (10.8 mm CL), Gulf side of beach, Isla Derniers, Louisiana, coll. R. B. Griffis & T. Zimmerman, 27 Jul 1993 (ULLZ 10199); female (11.0 mm), ex left branchial chamber female *C. islagrande* (10.1 mm CL), Gulf side of beach, Isle Derniers, Louisiana, coll. R. B. Griffis, D. L. Felder & T. McTigue, 19 Oct 1993 (ULLZ 10209); immature female (3.0 mm),

ex left branchial chamber of immature *C. islagrande* (5.0 mm CL), immature female (3.7 mm), mature male (2.3 mm, on SEM stub, USNM 1459848 *ex* ULLZ 10198), *ex* left branchial chamber of immature *C. islagrande* (5.0 mm CL), immature female (3.5 mm), mature male (2.0 mm), *ex* right branchial chamber of female *C. islagrande* (6.5 mm CL), immature female (3.5 mm), mature male (2.2 mm, on SEM stub, USNM 1459848 *ex* ULLZ 10198),

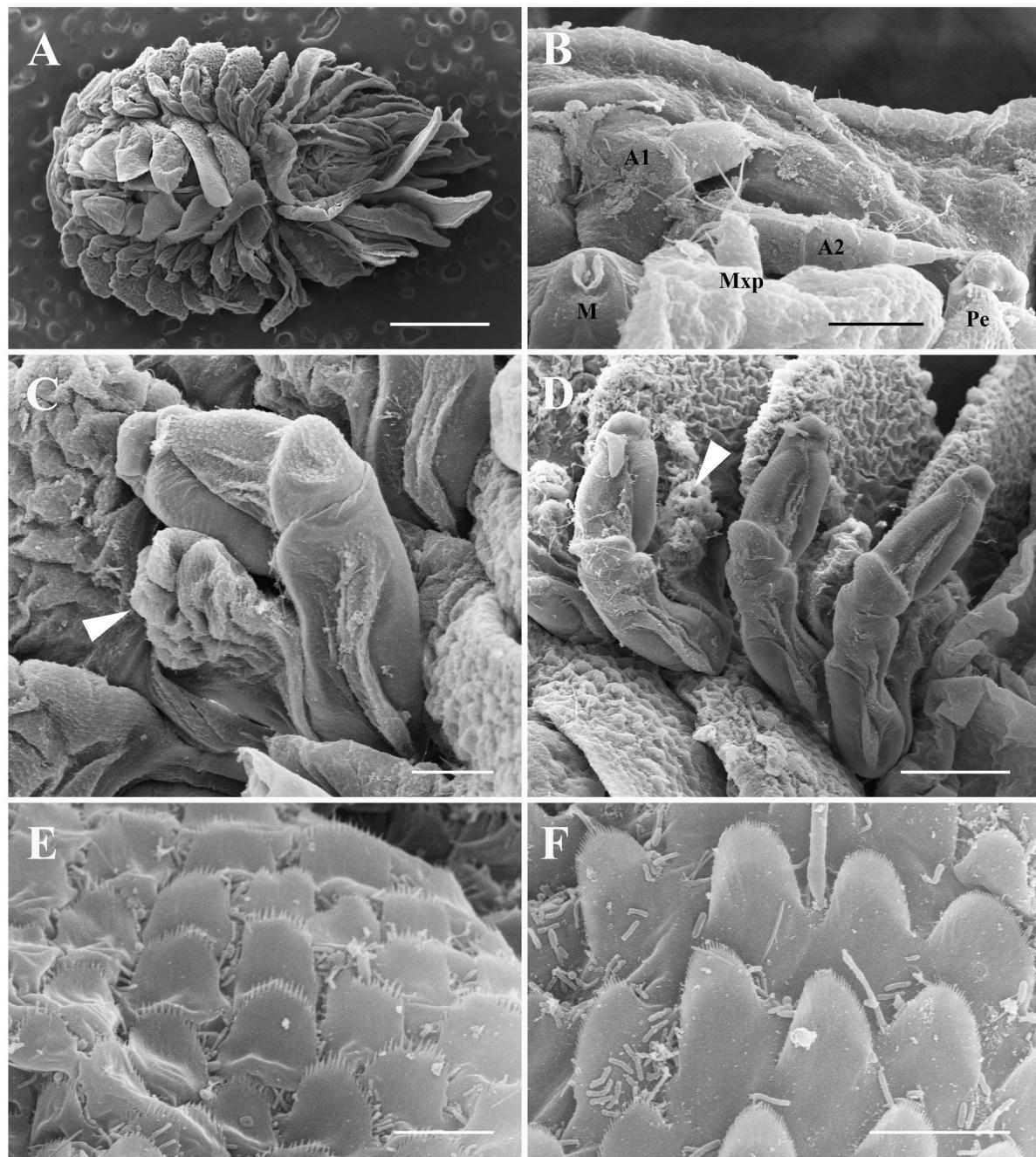


FIGURE 9. Scanning electron micrographs of *Robinione overstreeti* (Adkison & Heard, 1995), n. comb., mature female (*ex* *Callichirus islagrande* (Schmitt, 1935), ULLZ 10205). A, ventral overview of female; B, ventral view of head, left side, showing antennule (A1), antenna (A2), mouth (m), maxilliped palp (Mxp), and pereopod 1 (Pe); C, right pereopod 3, arrowhead indicates basis with dorsal mass; D, left pereopods 5–7 (left to right), arrowhead indicates basis with dorsal mass on pereopod 5; E, scales of basis of right pereopod 3; F, scales of carpus of right pereopod 3. Scale bars: A = 1 mm; B, C = 100 μ m; D = 250 μ m; E, F = 10 μ m.

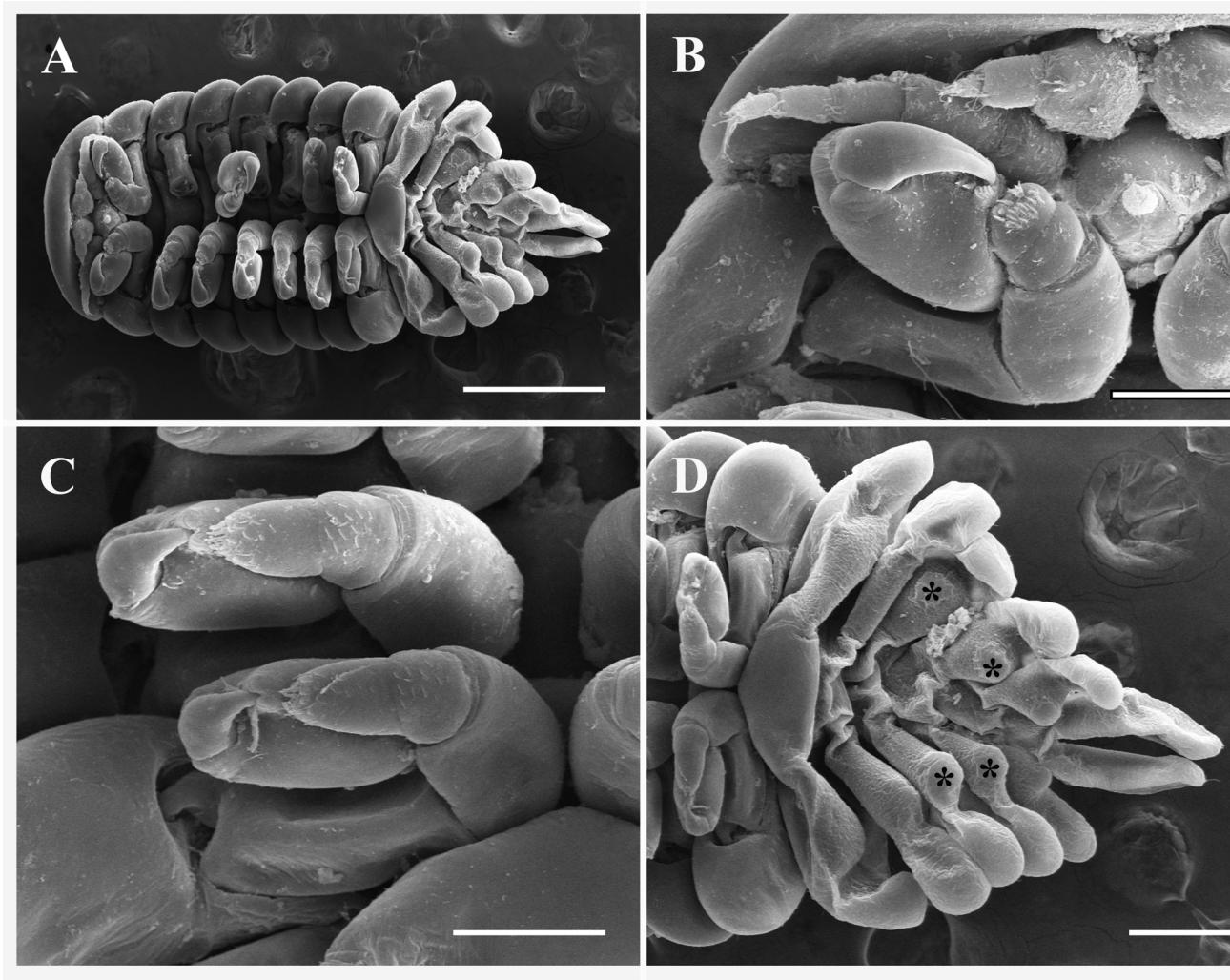


FIGURE 10. Scanning electron micrographs of *Robinione overstreeti* (Adkison & Heard, 1995), **n. comb.**, mature male (ex *Callichirus islagrande* (Schmitt, 1935), ULLZ 10198). A, ventral overview of male; B, ventral view of head, left side, showing antennule, antenna, mouth, and pereopod 1; C, left pereopods 6 and 7 (top and bottom, respectively); D, ventral view of pleon, showing pleopods with rounded medial lobes (noted on third and fourth pleopods by asterisks). Scale bars: A = 500 µm; B, C = 100 µm; D = 200 µm.

ex right branchial chamber of female *C. islagrande* (5.0 mm CL), access road #3, near Fish Pass, low tide, morning, Mustang Island, Texas, coll. D. L. Felder & L. Bilodeau, 1 Mar 2000 (ULLZ 10198); ovigerous female (12.0 mm), mature male (4.5 mm), ex *C. islagrande* (host not in vial with parasites), Gulf side, Isle Dernières, Louisiana, coll. D. L. Felder & R. B. Griffis, 24 Jul 1992 (ULLZ 10210); ovigerous female (11.0 mm), mature male (4.5 mm), ex left branchial chamber of female *C. santarosae* Sakai and Türkay, 2012 (11.4 mm CL), bay side, Isle Dernières, Louisiana, coll. A. Christian, D. Badgwill, R. B. Griffis & I. A. Griffis, 22 Jan 1993 (ULLZ 10204).

Distribution. Gulf of Mexico from west coast of Florida to Texas, U.S.A., and Tabasco, Mexico.

Hosts. *Callichirus islagrande* (Schmitt, 1935) (type species) and *C. santarosae* Sakai & Türkay, 2012.

Remarks. The present material of *R. overstreeti* **n. comb.** (Figs. 9, 10) matches that of Adkison & Heard (1995), who provided a detailed description of the species. Although they did not show the ventral view of the male, Adkison & Heard (1995) indicated that the pleopods were “vestigial or absent, represented by low mounds mesal to lateral processes of pleomeres” as we found in our samples (Fig. 10D). The male pleomeres documented in Adkison & Heard (1995; Fig. 2A) are slightly more elongate and acute than in the present specimens, but this variation is typical for pleopodal morphology in bopyrids. Each male pereopod of *R. overstreeti* **n. comb.** has a recurved dactylus, the distal end of which touches the base of the propodus and is surrounded by a low ridge of tooth-like projections (Fig. 10B, C). The female *R. overstreeti* **n. comb.** examined with SEM (Fig. 9) is not fully mature, thus has reduced oostegites and, proportionally, somewhat longer and thinner pleopods and uropods than

the holotype (Adkison & Heard, 1995; Fig. 1B). Female and male antennae (Figs. 9B, 10B) have the same numbers of articles as in the original description (3 and 4 for females; 3 and 5 for males). Female *R. overstreeti* n. comb. have pereopods with elongate carpi and a large irregular, infolded mass on the dorsal surface of each of the bases (Fig. 9C, D), all pereopodal segments covered with scales (Fig. 9C–F).

Felder & Dworschak (2015) discussed in detail the nomenclatural issues surrounding the name *C. santarosaensis*, which is now used for Gulf of Mexico populations of the *Callichirus* species formerly called *C. major* (Say, 1818), but which is distinct from that Atlantic coastal species. This is the first record of “*Pseudione*” *overstreeti* from *C. santarosaensis* (either under that name or as *C. major*). Adkison & Heard (1995) examined several hundred *C. santarosaensis* (as *C. major*) and found no bopyrids on them; it is not clear where their specimens were collected from, but based on the material examined list for *P. overstreeti*, they probably came from Alabama or Mississippi.

Rhabditida Chitwood, 1933

Physalopteridae Railliet, 1893

Heliconema Travassos, 1919

Heliconema sp.

Fig. 11

Material examined. United States: 2 worms (7.4, 8.2 mm), ex gill tissue of ovigerous female *Lepidophthalmus louisianensis* (13.0 mm CL), Grande Terre, Louisiana, coll. unknown, 25 May 1988 (ULLZ 3531); 8 worms (3 extracted: 7.5, 9.7, 11.5 mm; one specimen on SEM stub, USNM 1459849 ex ULLZ 10208), ex ventral thorax and base of third pereopods of female *L. louisianensis* (8.8 mm CL), inshore, Bay St. Louis, Mississippi, coll. unknown, 18 Jul 1990 (ULLZ 10208); 1 worm (not extracted), ex gill tissue of female *L. louisianensis* (8.9 mm CL), outer beach, Bay St. Louis, Mississippi, coll. R. Griffis & D. L. Felder, 26 Jan 1991 (ULLZ 10203).

Distribution. Mississippi and Louisiana, U.S.A.

Host. *Lepidophthalmus louisianensis* (Schmitt, 1935).

Remarks. Three specimens of *Lepidophthalmus louisianensis* (Schmitt, 1935) were parasitized by juvenile non-encysted nematodes (Fig. 11). One of the parasitized hosts (ULLZ 3531) was an ovigerous female and contained two worms extending into the gills and thorax. The other two hosts were non-ovigerous females and contained one worm (ULLZ 10203) in the gill tissue and eight worms (ULLZ 10208) in the ventral thorax and bases of third legs. The extracted nematodes ranged in length from 7.4 to 11.5 mm (8.9 ± 1.7 , n=5). Based on the morphology of the nematodes, particularly the structure of the mouth (Fig. 11B, C), they are members of Physalopteridae, most closely matching the genus *Heliconema* Travassos, 1919. The oral aperture of each of our specimens has two pseudolabia; each pseudolabium has a pair of cephalic papillae, a large median conical tooth and ridged teeth (Fig. 11B) while the amphids are indistinct. These characters are similar to those of *H. brooksi* Crites & Overstreet, 1991, which was described from the shrimp eel, *Ophichthus gomesii* (Castelnau, 1855), collected in Mississippi Sound, Gulf of Mexico. Crites & Overstreet (1991) also found a juvenile nematode in a shrimp, *Penaeus setiferus* (Linnaeus, 1767), and suggested that the juvenile specimen may also be *H. brooksi* but noted that additional research was required for verification. In addition to *H. brooksi*, an undescribed species of *Heliconema* from the sharptail eel, *Myrichthys acuminatus* (Gronow, 1854), also exists in the Gulf of Mexico (Moravec, pers. comm.).

Larvae of other *Heliconema* species are known from crustacean intermediate hosts. Those of *Heliconema anguillae* Yamaguti, 1935, are known to occur in the brachyurans *Hemigrapsus* sp. and *Perisesarma bidens* (De Haan, 1835) in Japan (Katahira & Nagasawa 2015) and it is possible that the “*Ascarophis*” third-stage larvae described by Moravec *et al.* (2003) from the brachyuran *Macrophthalmus hirtipes* (Heller, 1865) (= *Hemiplax hirtipes* Jacquinot, in Hombron & Jacquinot, 1846)) in New Zealand were also larvae of a species of *Heliconema* (Moravec, pers. comm.). Species of nematodes from other families also use callianassids as intermediate hosts and are trophically transmitted to elasmobranchs or bony fish as definitive hosts (Poinar & Thomas, 1976). For example, two unidentified species of *Ascarophis* van Beneden, 1871, were found in *Neotrypaea californiensis* (Dana, 1854) from California (Poinar & Thomas 1976).

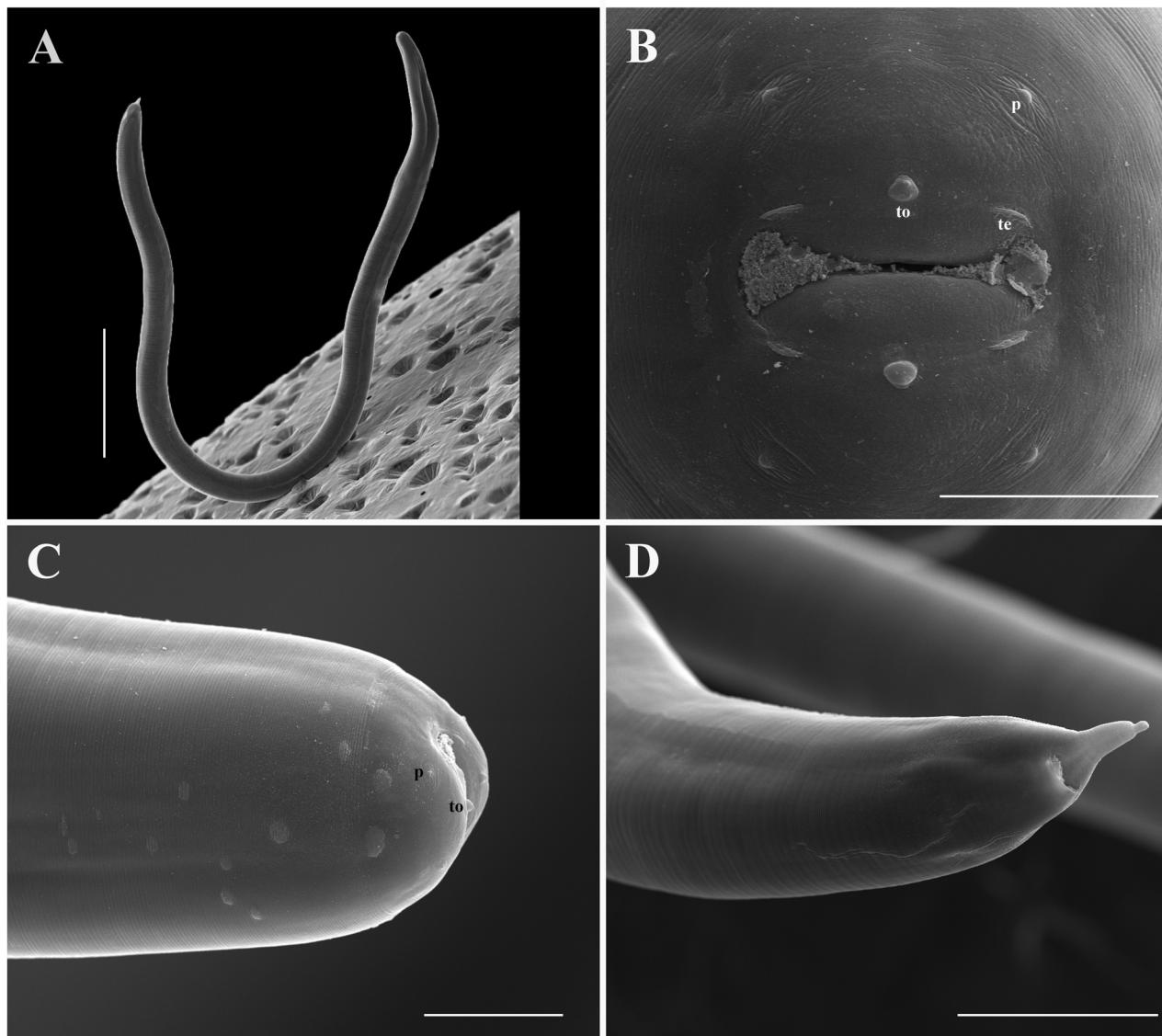


FIGURE 11. Scanning electron micrographs of *Heliconema* sp. ex *Lepidophthalmus louisianensis* (Schmitt, 1935) (USNM 1459849 ex ULLZ 10208). A, whole juvenile worm, lateral view; B, anterior end, *en face* view; C, anterior end, lateral view; D, posterior end, oblique view. P = cephalic papillae, to = median conical tooth, te = ridged teeth. Scale bars: A = 1 mm; B = 30 μ m; C = 50 μ m; D = 200 μ m.

There are no reports on the specific diet of the shrimp eel, *O. gomesii*, but it is likely an opportunistic feeder, based on the stomach contents of congeners (Casadevall *et al.* 1994) and has been reported to feed “heavily on shrimps” (Crites & Overstreet 1991); *L. louisianensis* is therefore a potential prey item. Based on stomach content analyses, potential definitive hosts in the Gulf of Mexico for this species of *Heliconema* are bottom feeding fish predators of *L. louisianensis*, including croaker (*Menticirrhus* sp., *Sciaenidae*) and unspecified catfish (Felder & Rodrigues 1993). Stingrays are also possible predators of *L. louisianensis* based on observations of their feeding habits (Felder & Rodrigues 1993).

Anguilliform fish host the highest diversity of *Heliconema* species but nematodes in this genus are also known from four other actinopterigian orders, as well as two orders of elasmobranchs (see Akram 1996; Li *et al.* 2013). Although two species of *Heliconema* have been reported from snakes, Moravec *et al.*, (2007) summarized the persistent doubts as to the identity of the type hosts for *H. longissimum* (Ortlepp, 1923). The host of this nematode was originally identified as “snakes” (in quotation marks as originally given by Ortlepp, 1923) but this species has subsequently been reported several times from eel hosts. Interestingly, only one species of *Heliconema* was ever described from adult worms extracted from a host verified as a snake: *H. serpens* Fusco & Palmieri, 1980, described from *Cerberus rynchops* (Schneider, 1799) and found in only a single host individual (Fusco & Palmieri

1980). Because these snakes are well-known consumers of eels (Gorman *et al.* 1981) it is possible that the snake picked up the nematodes through parasitized prey and thus served as a postcyclic host (*sensu* Odening 1976) for *H. serpens*; the snake was not a paratenic host because the worms were mature. If true, this would be analogous to the situation reported by Goldberg *et al.* (2002) who found mature lizard-parasitizing nematodes in the lumen of the digestive tract of snakes who preyed on parasitized lizards. Indeed, Goldberg *et al.* (2002) cautioned that any finding of adult nematodes in a snake must consider the possibility that the nematodes entered via the snake's prey, their definitive host, and not because the snake ingested an intermediate host of the parasite.

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