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Probynia ramiroromani, new species (Isopoda: Bopyridae) and new occurrences of bopyrid isopods parasitizing decapod crustaceans from Mexican Atlantic waters

Jesús Romero-Rodríguez and Fernando Álvarez*

(JRR, FA) Colección Nacional de Crustáceos, Instituto de Biología, Universidad Nacional Autónoma de México (UNAM). Apartado Postal 70–153, Ciudad de México 04510, México

Abstract.—Six species of bopyrids were detected by inspection of crustaceans of diverse taxa collected in the Gulf of Mexico and the Mexican Caribbean that were deposited in two scientific collections housed in the Universidad Nacional Autónoma de México. *Probynia ramiroromani*, new species is described, becoming the first species of the genus from the American continent. The occurrence of *Pseudione* cf. *crenulata* is recorded for the first time in the west Atlantic coast, the distribution ranges of *Orthione furcata*, *Parabopyrella thomasi*, and *Robinione overstreeti* are extended, and *O. furcata* and *Urobopyrus processae* are reported for the first time in Mexican waters. *Munida valida*, *Periclimenaeus perlatus*, *Processa bermudensis*, and *Upogebia vasquezi* are now recognized as hosts of *P.* cf. *crenulata*, *P. ramiroromani*, *U. processae*, and *O. furcata*, respectively.

Keywords: branchial parasite, Epicaridea, host-parasite association, isopods, western Atlantic coast.

Within the Crustacea, a large number of species of amphipods, barnacles, copepods, and isopods establish parasitic relationships with invertebrate and vertebrate hosts. Parasitic species comprise ~7.7% of the described isopods grouped in the superfamilies Bopyroidea and Cryptoniscoidea, usually referred to as epicarideans, which use other crustaceans both as intermediate and definitive hosts (Williams & Boyko 2012). Sexual dimorphism in epicarideans is extreme, with dwarf males being similar to free-living isopods, whereas females are larger, with distorted bodies, so much so that in some species they are barely recognizable as isopods (see Román-Contreras 2008). These parasites can negatively impact the hosts in various ways, affecting their reproduction, activity levels, growth rates, or population structure (Oliveira & Masunari 1998, McGrew & Hultgren 2011, Romero-Rodríguez et al. 2016).

The first record for a bopyrid on the American continent was made by Dana (1853) for *Argeia pugettensis* found in Puget Sound, northwest coast of the U.S.A., parasitizing *Metacrangon munita* (Dana, 1852) (as *Crangon munitus*). Shortly after, Leidy (1855) reported *Leidya distorta* (as *Cepon distortus*) parasitizing the fiddler crab *Leptuca pugilator* (Bosc, 1801) (as *Gelasimus pugilator*) in New Jersey, U.S.A. (Markham 1974a). Since then, the number of described species has increased gradually, especially during the 20th century (Markham 1985). Along the northwestern Atlantic and Caribbean coasts, Markham (1985) reported 37 species of bopyrids parasitizing carideans. Subsequently, in a broader revision, Wil-

* Corresponding author.
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liams & Boyko (2012) accounted for 91 species occurring on a wider variety of hosts, although considering epicarideans included in Cryptoniscoidea, Dajidae, and Entoniscidae the number is increased to 102 species; most of these bopyrids (87 species) inhabit the region between North Carolina, U.S.A., through the Gulf of Mexico to the Caribbean.

Román-Contreras (2008) published the only compilation of bopyrid isopod records from Mexico so far, recognizing 17 species from Mexican Atlantic waters (plus two Entoniscidae and one Dajidae species), omitting the report of *Robinione overstreeti* (Adkison & Heard 1995). Further reports increased this number to 28 bopyrid species (Román-Contreras & Martínez-Mayén 2011, Romero-Rodríguez & Martínez-Mayén 2017, 2018, Romero-Rodríguez et al. 2017, Romero-Rodríguez & Álvarez 2020a, 2020b). However, the bopyrid diversity along the western Atlantic, and particularly in Mexican waters, remains poorly known, as they are frequently omitted from studies on the taxonomy or ecology of their hosts (Boyko & Williams 2009). In this contribution we present a report on specimens deposited in two collections housed at Universidad Nacional Autónoma de México (UNAM).

Materials and Methods

Crustaceans of diverse taxa parasitized by bopyrid isopods were detected by examination of the biological material deposited in the Colección Nacional de Crustáceos (CNCR), Instituto de Biología, and the Colección de Crustáceos de Yucatán (YUC–CC), Unidad Multidisciplinaria de Docencia e Investigación, UMDI–Sisal, both housed at UNAM. Size, taken as carapace length (CL) measured from the postorbital margin to the posterior mid-dorsal margin of the cephalothorax, and sex were recorded for each host. The parasites were removed from the hosts in order to recognize their specific identities and to record total lengths (TL), following Romero-Rodríguez & Álvarez (2020a). The measurements were made to the nearest 0.1 mm using an ocular micrometer attached to a compound microscope. Digital photographs of each parasitic species were taken with a Leica DFC490 camera mounted on a Leica Z16APOA stereomicroscope. Drawing sketches made with a camera lucida were used to construct the figures using Adobe Illustrator. References are not provided for host species.

Systematics

Suborder Cymothoida Wägele, 1989
Family Bopyridae Rafinesque, 1815
Subfamily Bopyrinae Rafinesque, 1815
Genus *Parabopyrella* Markham, 1985
Parabopyrella thomasi (Nierstrasz & Brender à Brandis, 1929)
Fig. 1A, Table 1

Bopyrella thomasi Nierstrasz & Brender à Brandis 1929:32–33, Figs. 41–42 (type-locality St. Thomas, Virgin Islands; parasitizing *Tozeuma carolinense* Kingsley, 1878).—Shiino 1936:159.—Shiino 1939:12.—Markham 1974a:193–195, 316, 323.—Bourdon 1980:210–212, Fig. 11a–d.

Parabopyrella thomasi: Markham 1985:66 (in key), 71–73, Fig. 31.—Markham 1988:57.—Kensley & Schotte 1989:112.—Boyko 2006:43.—An et al. 2015:47–48, 61 (in key), 65.—Romero-Rodríguez & Martínez-Mayén 2018:1183–1194, Figs. 1–4, Tables I, II (Bahía de la Ascensión and Bahía del Espíritu Santo, Quintana Roo, Mexico; parasitizing *T. carolinense*).

Material examined.—One adult female and one adult male in right branchial

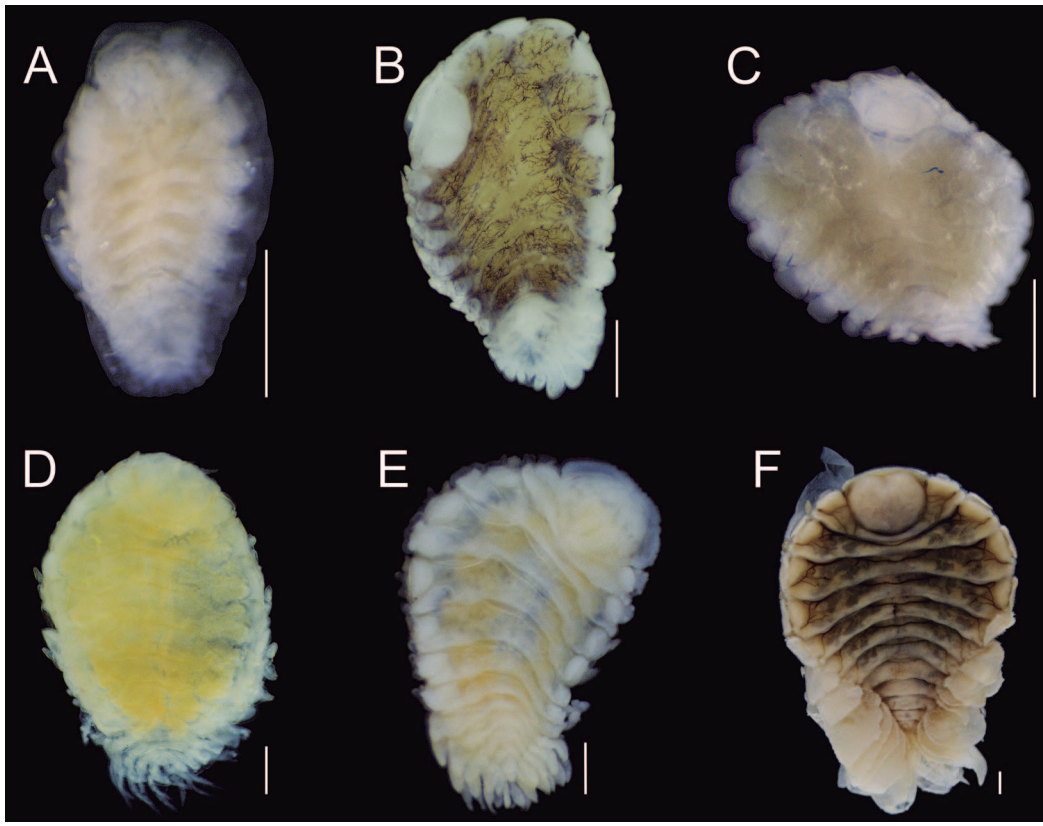

Fig. 1. Bopyrid adult females found parasitizing decapod crustaceans on the Atlantic coast of Mexico. A, *Parabopyrella thomasi* (Nierstraz & Brender à Brandis, 1929) (YUC-CC-255-11-006937); B, *Probynia ramiroromani* (CNCR-35772); C, *Urobopyrus processae* Richardson, 1904 (YUC-CC-255-11-006938A); D, *Orthione furcata* (Richardson, 1904) (CNCR-35773); E, *Pseudione crenulata* G. O. Sars, 1898 (CNCR-35774); F, *Robinione overstreeti* (Adkison & Heard, 1995) (YUC-CC-255-11-003766). Scale bars = 1.0 mm.

chamber of male *Tozeuma carolinense*, 5.28 mm CL; N. Calvo det. host; Ría Celestún, Yucatán, Mexico (20°56′59.742″N, 90°20′26.504″W); N. Calvo and Y. Reyes colls.; 12 May 2015; YUC-CC-255-11-006937 for both parasite and host.

Distribution.—From Ría Celestún, Yucatán (this study) and Bahías de la Ascensión and Espíritu Santo, Quintana Roo, Mexico (Romero-Rodríguez & Martínez-Mayén 2018) to St. Thomas, Virgin Islands (Nierstrasz & Brender à Brandis 1929).

Remarks.—The morphological features of the female (Fig. 1A) and male examined agree well with those described for *Parabopyrella thomasi* by Nierstrasz & Brender à Brandis (1929), and the length/width ratio of the pereon (1.90) and pleon (0.98) of the female are similar to those reported by Romero-Rodríguez & Martínez-Mayén (2018) of 1.84 and 0.90, respectively.

The only host known for *P. thomasi* so far is the caridean shrimp *Tozeuma carolinense*, which occurs on seagrass beds of coastal and estuarine systems of the Gulf of Mexico and Mexican Caribbean Sea and is the second most common species there, after *Hippolyte zostericola* (Smith, 1873) (Barba 2012). *Tozeuma carolinense* is distributed from Vineyard Sound, Massachusetts to São Paulo, Brazil, and from Bermuda to Saint Lucia Island and

Table 1.—Female and male sizes (mm) for some bopyrid isopods inhabiting the Gulf of Mexico and Caribbean Mexican coasts. TL, total length; WD, width; LG, length.

Species	Developmental stage	Females							Males						
			Head		Pereon		Pleon			Head		Pereon		Pleon	
		TL	WD	LG	WD	LG	WD	LG	TL	WD	LG	WD	LG	WD	LG
Orthione furcata	Adult	6.53	1.90	1.27	3.90	3.60	3.33	1.35	3.33	0.87	0.25	1.16	2.22	1.00	1.11
Parabopyrella thomasi	Adult	2.55	0.66	0.64	1.34	0.95	0.91	0.89	0.80	0.17	0.11	0.23	0.45	0.16	0.21
Probynia ramiroromani	Adult	4.79	1.36	0.76	3.10	2.15	1.65	1.42	1.14	0.29	0.20	0.42	0.76	0.33	0.31
Pseudione crenulata	Ovigerous	6.29	2.27	1.62	4.14	2.83	2.57	1.50	2.57	0.62	0.42	1.18	1.54	0.62	0.73
Robinione overstreeti	Juvenile	2.86	1.20	0.96	3.27	1.47	2.75	1.15	3.60	0.85	0.36	1.20	1.73	1.31	1.60
	Juvenile	2.94	1.00	0.73	2.37	1.29	2.80	1.20	2.86	0.73	0.38	1.14	1.62	1.00	1.18
	Adult[a]	6.57	1.96	1.32	5.11	2.76	4.08	2.25	3.46	1.04	0.58	1.47	1.82	1.67	1.20
	Adult[a]	6.00	1.96	1.47	5.00	2.42	4.00	2.12	3.54	1.67[b]	1.12	1.49	1.82	1.31	1.45
	Adult	12.31	3.26	3.00	8.30	5.00	6.79	3.67	–	–	–	–	–	–	–
Urobopyrus processae	Adult	3.52	1.07	0.66	3.27	1.70	1.27	0.87	–	–	–	–	–	–	–
	Ovigerous	2.37	0.76	0.50	2.35	1.23	1.00	0.66	–	–	–	–	–	–	–

[a] From a bilateral double infestation.
[b] Head damaged.

Curaçao (Román-Contreras & Martínez-Mayén 2009). However, despite the abundance and wide distribution of its host, this is only the third time that *P. thomasi* has been collected on the western Atlantic coasts since 1911 (Nierstrasz & Brender à Brandis 1929, Romero-Rodríguez & Martínez-Mayén 2018). The new record expands its distribution to the northwestern portion of the Yucatán peninsula, Mexico. Briggs et al. (2017) reported *Tozeuma* spp. from Florida coasts, U.S.A., devoid of parasites but with the typical deformed carapaces of recent bopyrid infestation, so it is possible that the distribution of *P. thomasi* comprises the whole Gulf of Mexico to the Caribbean coasts.

Genus *Probynia* Bourdon & Bruce, 1983
Probynia ramiroromani, new species
Figs. 1B, 2, Table 1

ZooBank LSID.—urn:lsid:zoobank.org:pub:ED298DBA-52E5-4E31-9452-B4D3495696E8.

Material examined.—One adult female, holotype, and one male, allotype (CNCR–35772) in right branchial chamber of female *Periclimenaeus perlatus* (Boone, 1930), 4.40 mm CL (CNCR–25927), inhabiting *Aplysina fistularis* (Pallas, 1766) at 4 m deep; M. Bárcenas-Cisneros det. host; Isla de Enmedio, Veracruz, Mexico (19°16′46.7″N, 95°56′51″W); S. Cházaro et al. colls.; 08 August 2007.

Description.—Female (Figs. 1B, 2A, B), body measurements are shown in Table 1. Body asymmetrical, head rotated dextrally, anterior portion broader and slightly tapered posteriorly. Dorsally, head and pleon whitish in color, pereon yellowish with thin dark brown lines, as venules, crossing throughout the surface (Fig. 1B). Ventrally, white with few thin dark brown venules.

Head distinct from first pereomere, broader than long (Table 1), anterior margin slightly curved. Frontal lamina wide, folded upwards, with rounded lateral projections that exceed lateral borders of head; posterior margin of head curved, both side margins nearly straight (Fig. 2A). Only one eye on right anterior lateral margin of head, indicated as a faint, thin, straight line. Antennule and antennae each of a single segment with chitinous line hardly visible on their middle portion, both tiny, with some distal setae (Fig. 2C). Maxilliped with anterior segment larger than posterior one, semi-rectangular

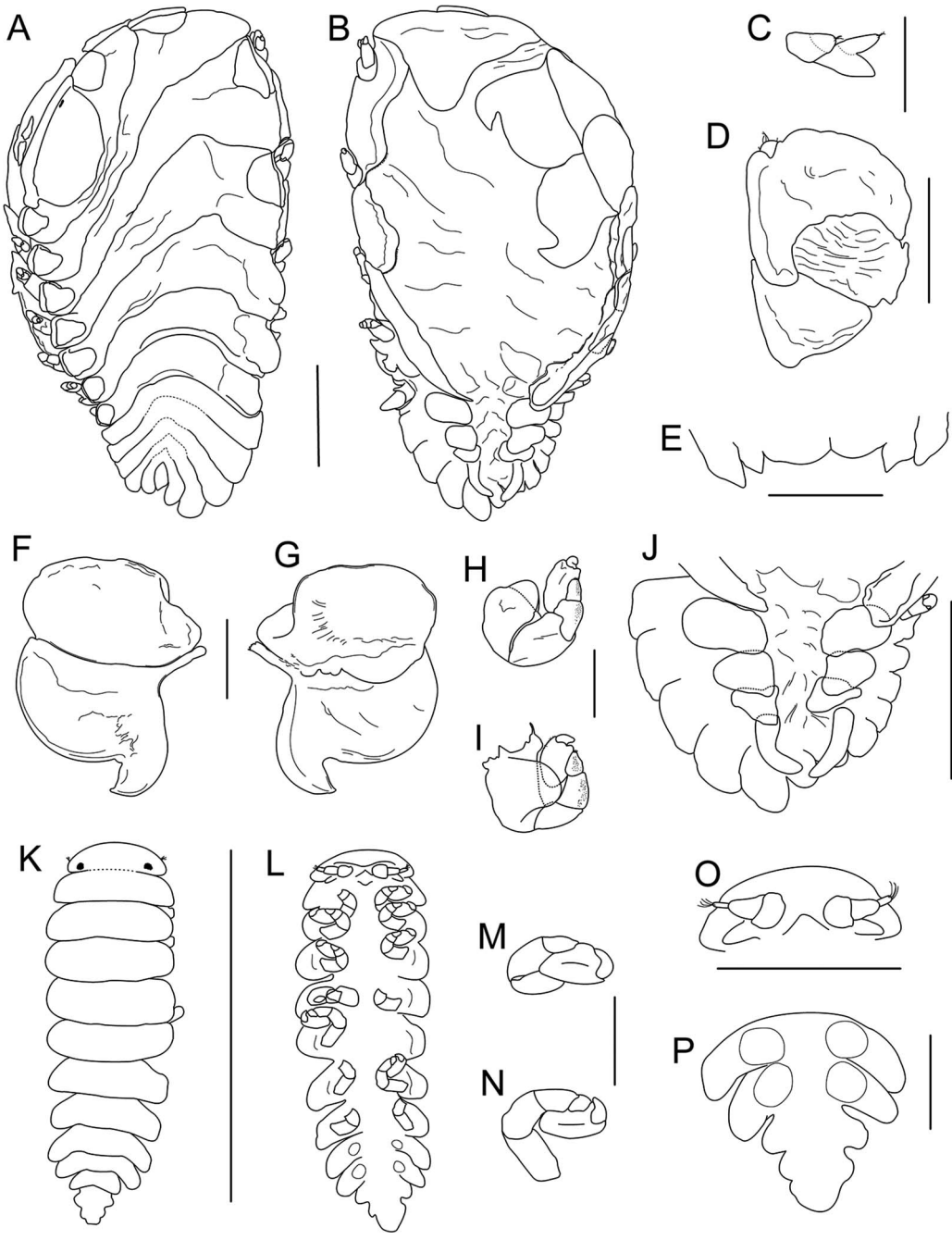

Fig. 2. *Probynia ramiroromani*, branchial parasite of *Periclimenaeus perlatus* (Boone, 1930). A–J, female; K–P, male. A, holotype (CNCR-35772), dorsal view; B, same, ventral view; C, left female antennule and antennae; D, maxilliped; E, barbula; F, first oostegite on short side of body, external view; G, same, internal view; H, pereopod 1 of long side of body; I, pereopod 7 of long side of body; J, pleon, ventral view; K, dorsal view; L, same, ventral view; M, pereopod 1 right side; N, pereopod 3 right side; O, antennules and antennae; P, pleon, ventral view. Scale bars: A, B, J–L = 1.0 mm; D–G = 0.5 mm; C, H, I, M–P = 0.25 mm.

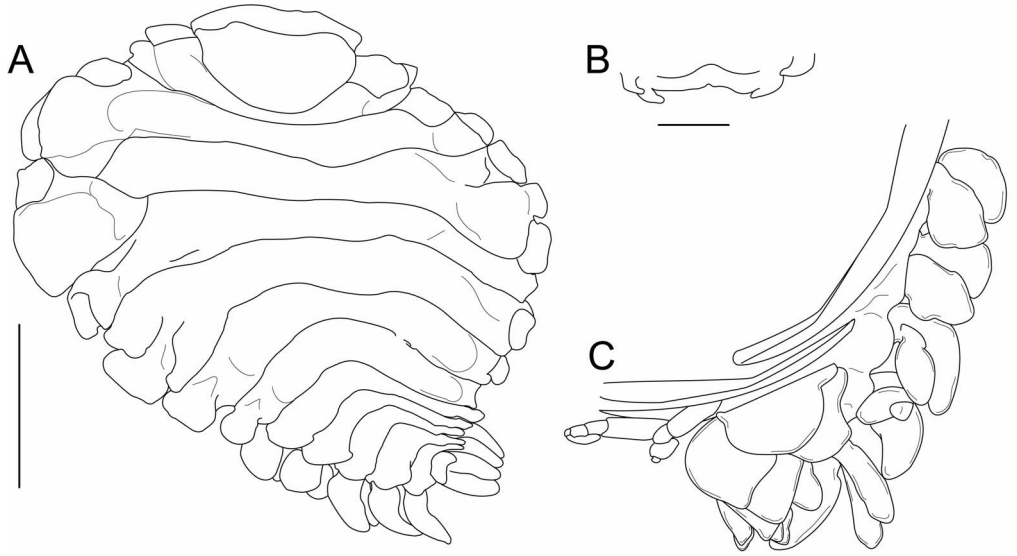

Fig. 3. Female of *Urobopyrus processae* Richardson, 1904 (YUC-CC-255-11-006938A), branchial parasite of *Processa bermudensis* (Rankin, 1900). A, dorsal view; B, barbula; C, pleon, ventral view. Scale bars: A, C = 1.0 mm; B = 0.25 mm.

with round margins, bearing a rounded unarticulated palp, with 4 or 5 setae along its distal margin, posterior segment triangular in shape with blunt spur (Fig. 2D). Barbula with two smooth and distally blunt projections on each side, with notch on medial margin giving a bilobed appearance (Fig. 2E).

Pereon broadest across pereomere 3, all pereomeres with distinct dorsal and lateral separation. On long side of body, pereomeres 1–4 with flat, semi-triangular dorsolateral bosses and, except on pereomere 1, narrow coxal plates. Tergal projection about one-half width in these pereomeres. Lateral margins of pereomeres 5–7 rounded, directed backwards, with short tergal projection decreasing in width posteriorly (Fig. 2A). On short side of body, lateral borders of all pereomeres rounded, folded on their dorsal faces, with very narrow coxal plates on each pereomere, dorsolateral bosses absent (Fig. 2A). Brood pouch open (Fig. 2B), first pair of oostegites subequal in size, of similar shape, anterior segment short, ovoid, posterior one larger with rounded margins and stout posterolateral point (Fig. 2F, G); inner ridge slightly sinuate on proximal portion, thick on distal one (Fig. 2G). Oostegites 2–5 larger on long side of body than on opposite side (Fig. 2B). On long side of body, oostegites 2–4 subtriangular in shape, directed to mid-ventral portion, with row of small setae on posterior margin; oostegite 5 rectangular, elongate, directed backwards. On short side of body, oostegites 2–4 rectangular in shape, of similar sizes, each with posterior half overlapping anterior half of succeeding one; oostegite 5 similar in form but slightly larger, directed posteriorly. Last pair of oostegites do not meet or overlap (Fig. 2B). All pereopods of similar size and form, with rounded carina at superior margin of basis, merus and carpus distinct and short with blunt dactylus (Fig. 2H, I).

Pleon nearly as wide as long (Table 1), with six segments clearly separated laterally but more or less fused medially. First pleomere approximately of same size as pereomere 7. Lateral margins of pleomeres 1 and 2 of long side and 1–3 of short side of body straight with rounded corners,

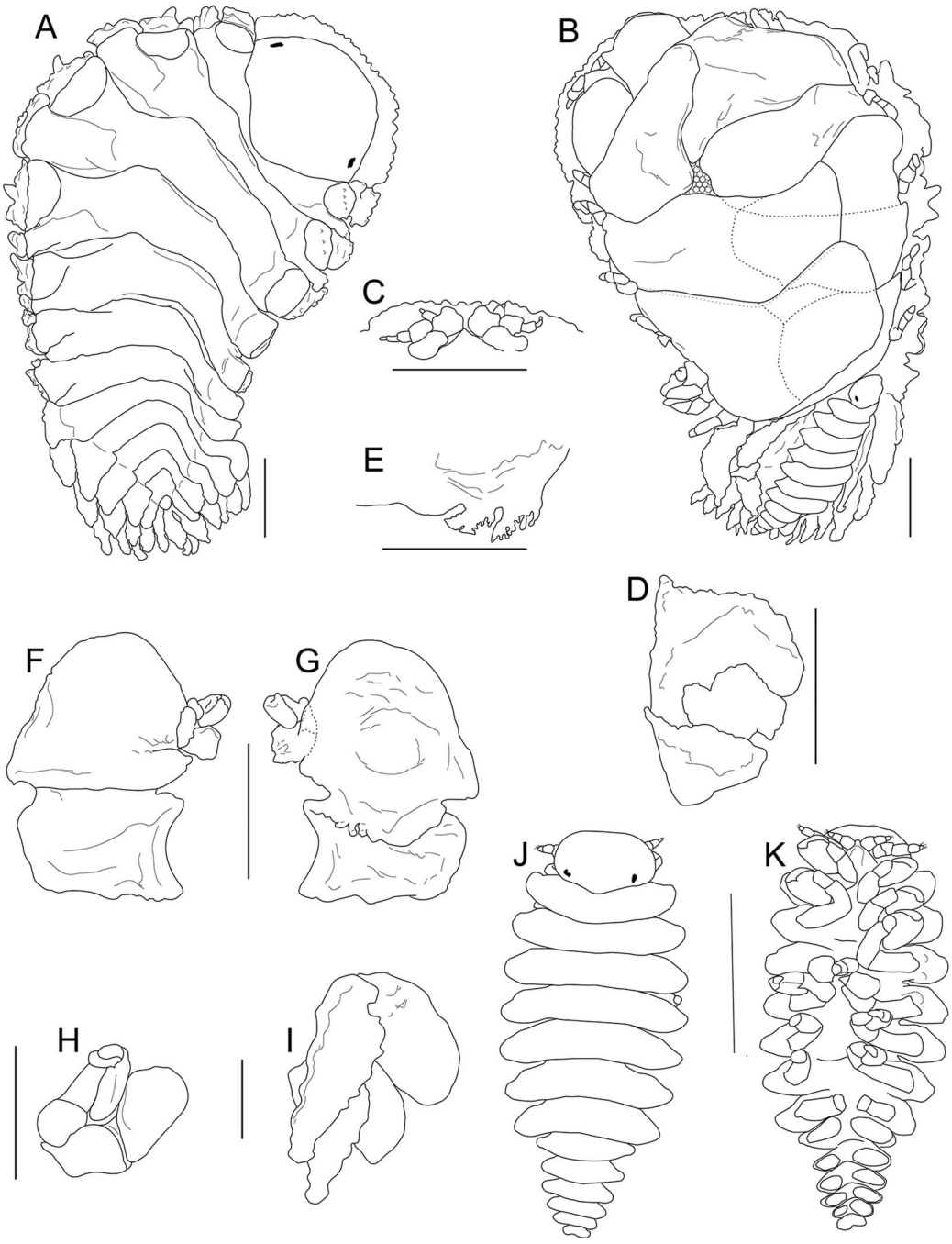

Fig. 4. *Pseudione* cf. *crenulata* G. O. Sars, 1898 (CNCR-35774), branchial parasite of *Munida valida* Smith, 1883. A–I, female; J, K, male. A, dorsal view; B, same, ventral view; C, antennules and antennae; D, maxilliped; E, barbula; F, first oostegite with pereomere 1 on long side of body, external view; G, same, internal view; H, pereopod 6 of short side of body; I, pair of pereopods 1, 2 of long side of body; J, dorsal view; K, ventral view. Scale bars: A–G, J, K = 1.0 mm; H, I = 0.5 mm.

other pleomeres with margins clearly rounded, pleomere 6 short, rhomboid in shape, partially enclosed by pleomere 5 (Fig. 2A). Four pairs of uniramous pleopods, pairs 1–3 as thick sub-rectangular plates, first pair largest, others decreasing in size posteriorly; pleopods 4 as slender, elongated flaps, directed posteriorly (Fig. 2B, J).

Male (Fig. 2K, L, Table 1), head ovoid, laterally separated but fused medially with first pereomere, slightly narrower than pereon. Conspicuous eyes on posterolateral margins of head (Fig. 2K). Antennule 3-segmented, first one larger, globular in shape; third segment with cylindrical outline, very slender, with tuft of setae on tip, barely exceeds anterior margin of head. Antennae 2-segmented, second one largest, finger-like, lacking setae (Fig. 2O). Pereon of seven pereomeres, lateral and dorsally distinct, with rounded lateral margins. Pereomeres 1–5 tightly close together, pereomeres 6 and 7 separated by anterolateral indentations, slightly directed posteriorly (Fig. 2K). Mid-ventral tubercles absent (Fig. 2L). All pereopods of similar form and size, basis long, merus and carpus fused, and dactylus short and blunt (Fig. 2L–N). Pleon with pleomeres 1–3 having rounded lateral margins, clearly separated by anterolateral indentation, dorsally distinct. Pleomeres 1 and 2 directed posteriorly, pleomere 3 laterally, other pleomeres fused into rhomboid pleotelson with sinuous outline (Fig. 2K). Pleopods as small oval bulges on pleomeres 1 and 2. Uropods absent (Fig. 2P).

Etymology.—The species is dedicated to Ramiro Román Contreras, a pioneer in the study of epicarideans in Mexico, who with dedication and enthusiasm described diverse genera and species in this group of parasites.

Type locality.—Isla de Enmedio (19°16′46.7″N, 95°56′51″W), Veracruz, Mexico.

Distribution.—Only known from the type locality in the southwestern Gulf of Mexico.

Remarks.—The morphological traits of the female of *P. ramiroromani* of a pronounced body asymmetry, head distinct from first pereomere, barbula with two pairs of lamellae, and the first pair of oostegites subequal but the other ones of different size and shape between both sides of body, as well as the attributes of the male of a head poorly demarcated from the first pereomere, subequal pereopods, and only the three first segments of pleon free, correspond to the characteristics stated for the genus *Probynia*, erected by Bourdon & Bruce (1983) for *P. obstipa* Bourdon & Bruce, 1983 found parasitizing *Periclimenaeus hecate* (Nobili, 1904) and *Typton wasini* Bruce, 1977. However, our specimens differ from the two previously described species in this genus (Boyko et al. 2008a onwards): the type species and *P. pleurocephala* (Monod, 1933). Females of *P. ramiroromani* can be distinguished from those of *P. obstipa* in that the latter does not have dorsolateral bosses on pereomeres 1–4, the posterior lobe of the first pair of oostegites is shorter and more rounded, all the pleomeres are laterally and dorsally distinct, and there are five pairs of digitiform uniramous pleopods (Bourdon & Bruce 1983). Females of *P. pleurocephala* differ from the other two species in the genus in their triangular outline of the head, the absence of frontal lamina, and the fusion of pleomeres 5 and 6 (Bourdon & Bruce 1983). A feature described and illustrated for all three species (Monod 1933, Fig. 75–3, Bourdon & Bruce 1983, Fig. 1a) but not considered within the diagnostic characters of the genus by Bourdon & Bruce (1983) is that the lateral margins of all pereomeres of the short side of the body are folded over their dorsal surfaces.

The male of *Probynia ramiroromani* is closer to the male of *P. obstipa*, but the last antennule segment is wider and the second

segment of the antenna bears two distal setae (Bourdon & Bruce 1983, Fig. 4a, b). The male of *P. pleurocephala* has the anterior margin of the head truncated, a pleon of five segments, of which the first two are dorsally distinct, and the three posterior ones have lateral undulations and the posterior extremity swollen and covered with scales (Bourdon & Bruce 1983).

Species of *Probynia* have been previously recorded in Australia (*P. obstipa*) and Egypt (*P. pleurocephala*), thus *P. ramiror-omani* is the first member of the genus recorded on the American continent. Likewise, *Periclimenaeus perlatus* is recognized for the first time as a host of bopyrids.

Genus *Urobopyrus* Richardson, 1904
Urobopyrus processae Richardson, 1904
Figs. 1C, 3, Table 1

Bopyride?: Bonnier 1900: 381 [Gulf of Marseille, parasitizing *Processa edulis* (Risso, 1816)].

Urobopyrus processae Richardson 1904:86–87, Fig. 92 (type-locality off East coast of South America 06°59′30″N, 34°47′W, parasitizing *Processa fimbriata* Manning & Chace, 1971).—Monod 1923:22 (Monaco, parasitizing *P. canaliculata* Leach, 1815).—Caroli 1934:235 (Gulf of Naples, parasitizing *P. canaliculata*).—Rouch & Taberly 1961:3–6, 8–14.—Rouch & Taberly 1962:3.—Bourdon 1968:133, 334–339, 363, 383, 409, Figs. 151–157, Tables 52–57, Graphs 22, 23 (Mediterranean coast of France, parasitizing *P. edulis*, France and Naples parasitizing *P. acutirostris* Nouvel & Holthuis, 1957).—Bourdon 1971:371 (Pointe Noire, Congo, parasitizing *Processa*, n. sp.).—Abele 1972:366.—Bourdon & Pike 1972:154.—Coelho & Koenig 1972:256, Table I.—Nöel 1976:82–84 (Banyuls, France, parasitizing *P. acutirostris*).—Anderson & Dale 1981:154–156.—Nöel 1982:651–657 (Mediterranean coast of France, parasitizing *P. edulis*).—Markham 1985:21–25, Figs. 5, 6, Table 2 [Florida, U.S.A., parasitizing *P. guyanae* Holthuis, 1959 (reported as *P. tenuipes*), *Ambidexter symmetricus* Manning & Chace, 1971 and *Ambidexter*, n. sp., Cabo de São Roque, Brazil, parasitizing *P. fimbriata*].—Markham 1986:157, Fig. 5.—Markham 1988:Table 1.—Brasil-Lima 1998:638–639.—Camp et al. 1998:134.—Oliveira & Arruda 2011:39.—An et al. 2015:23.—Rasch & Bauer 2015:89–103 (Florida, U.S.A., parasitizing *A. symmetricus*).—Rasch & Bauer 2016:1142, 1144 (Florida, U.S.A., parasitizing *A. symmetricus*).

Urobopyrus processi [sic]: Richardson 1904:87.

Urobopyrus sp.: Hutton & Sogandares-Bernal 1960:288 (Boca Ciega Bay, Florida, U.S.A., parasitizing *A. symmetricus*).—Bourdon 1963:428 (Roscoff, France, parasitizing *P. edulis*).—Hutton 1964:447.

Urobopyrus provisorius Rouch & Taberly 1961:1–23, pls. I–IV, Figs. 1–22 (Mediterranean coasts, France, parasitizing *P. acutirostris*).—Rouch & Taberly 1962:1–15, pls. I–III, Figs. 1–13.

?''Bopyrid isopod'': Coen & Heck 1983:207, 221, Table 2 (near Caribbean entrance to Panama Canal, parasitizing *A. symmetricus*).

Material examined.—One adult female (YUC-CC-255-11-006938A) in left branchial chamber of female *Processa bermudensis* (Rankin, 1900), 4.55 mm CL (YUC-CC-255-11-000593A); one ovigerous female (YUC-CC-255-11-006938B) in left branchial chamber of female *P. bermudensis* (YUC-CC-255-11-000593B), 3.52 mm CL; L. D. Santana-Moreno det. hosts; Río Bermejo, Mahahual, Quintana Roo, Mexico (18°36′32.79″N, 87°43′37.69″W), N. Simões coll., 2009.

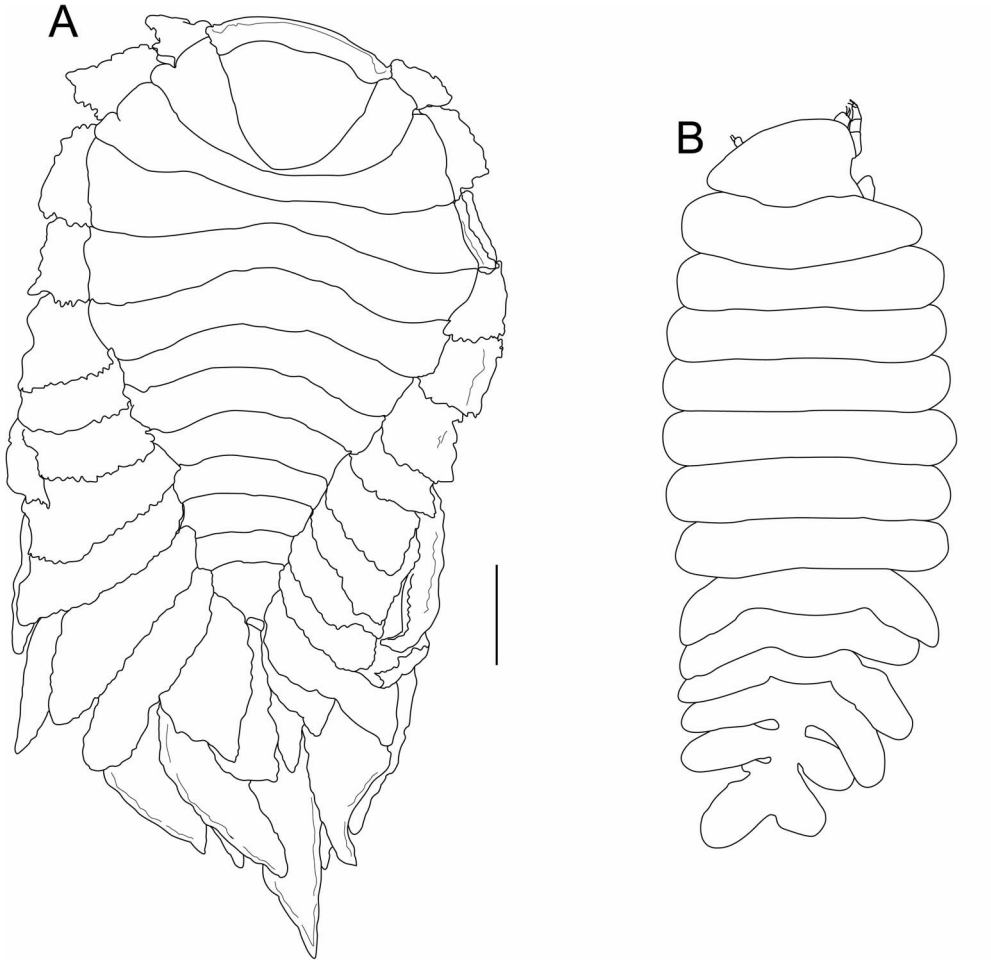

Fig. 5. Female (YUC-CC-255-11-006941A) and male (YUC-CC-255-11-006941B) of *Robinione overstreeti* (Adkison & Heard, 1995), branchial parasite of *Callichirus islagrande* (Schmitt, 1935). A, adult female, dorsal view; B, male, dorsal view. Scale bars = 1.0 mm.

Distribution.—Europe: coasts of Gulf of Marseille, Banyuls and Roscoff, France; Monaco and Gulf of Naples, Italy. Africa: coasts of Pointe Noire, Congo. West Atlantic coasts: Florida, U.S.A.; Quintana Roo, Mexico (this study); entrance to the Panama Canal, Panama; off Cabo de São Roque, Brazil and mid-Atlantic Ridge off South America (type locality) (Markham 1985).

Remarks.—Due to the limited morphological information available in the succinct description of *Urobopyrus processae* reported by Richardson (1904), Rouch & Taberly (1961) described *Urobopyrus provisorius* based mainly on three differences: the shape of the terminal segment of the pleon, their geographical distribution, and host selection. However, Bourdon (1968) considered such differences insufficient to support recognizing the latter species and considered *U. processae* as the sole member of the genus.

The morphological traits of both females examined in this study (Fig. 1C) match well with the characters described by Bourdon (1968) and Markham (1985) for *U. processae*, but some differences were

noted. The body of both females seems more oval than previously reported as the length to width ratio (1.07 in the adult female and 1.01 in the ovigerous female) was higher than that reported by Rouch & Taberly (1961), Bourdon (1968), and Markham (1985), 0.74 to 1.12 and 0.79 to 0.84, respectively (first ratio intervals calculated from original data); as well as the pleon length (Table 1), which was smaller than that reported by Bourdon (1968) and Markham (1985), 1.5 mm and 1.05 mm of length, respectively. The pleomeres on the short side of the body were more slender and longer than those on the opposite side (Fig. 3A), concurring with that described and illustrated by Rouch & Taberly (1961, Fig. 1). The pleopods from both sides clearly differ in shape and size (Fig. 3C), those on the long side are rounded and wider than long, while on the short side pairs 1 and 2 are smaller and ovoid and pairs 3–5 are lanceolate, thinner and elongated, comparable to those illustrated by Rouch & Taberly (1961, Fig. 2). The ventral surface of the pleon is not completely covered by the pleopods as noted by Markham (1985).

The barbula has two posterolateral projections on each side, the outer one is overlapping the inner one, but their medial margins varied from smooth to slightly curved forward (Fig. 3B), instead of bilobed (Rouch & Taberly 1961, Bourdon 1968, Markham 1985). Bourdon (1968, Table 52) described the change to the barbula throughout diverse female stages and pointed out the presence of the bilobed inner margin (tuberculiform) appearing in the juvenile stages. Markham (1985) also noted that the barbula middle region varied among females, but for all we know this is the first time that it is recorded as not bilobed in adult females.

Despite the fact *U. processae* has a widespread distributional range, its host selectivity is restricted to species belonging to the processid genera *Processa* Leach, 1815 (*P. acutirostris*, *P. canaliculata*, *P. edulis*, *P. fimbriata*, and *P. guyanae*) and *Ambidexter* (*A. symmetricus*) (Markham 1985). Here, *U. processae* is reported from Mexican coasts for the first time, and *P. bermudensis* as a new host of this branchial parasite.

Subfamily Pseudioninae Codreanu, 1967
Genus *Orthione* Markham, 1988
Orthione furcata (Richardson, 1904)
Fig. 1D, Table 1

Pseudione furcata Richardson 1904:79, Figs. 69–71 (type–locality eastern shore of Virginia, U.S.A., parasitizing unknown host).—Richardson 1905:529–530, Figs. 571–573.—Fowler 1912:523.—Hay 1917:573.—Van Name 1920:72.—Nierstrasz & Brender à Brandis 1923:72.—Menzies & Frankenberg 1966:9.—Schultz 1969:327, Fig. 524 (list and key).—Gosner 1971:476.—Wass 1972:147.—Markham 1977:816 [parasitizing *Upogebia affinis* (Say, 1818)].

Pseudione upogebiae (in part): Pearse 1947:326 (Beaufort, North Carolina, U.S.A., parasitizing *U. affinis*).

Orthione furcata: Markham 1988:14–17, Figs. 4–6 (Massachusetts, Virginia, and Cape Cod, U.S.A., parasitizing *U. affinis*).—Markham 2001:198, 200.—Markham 2004:186.—Heard et al. 2007:26.—Boyko et al. 2017:266–268, Fig. 5.

Pseudoione [sic] *furcata*: Kaestner 1970:463 [mention occurrence on "Gulf coast" (Gulf of Mexico), parasitizing unknown host (= *Progebiophilus upogebiae* (Hay, 1917)].

Material examined.—One adult female and one male (CNCR-35773) in left branchial chamber of female *Upogebia vasquezi* Ngoc-Ho, 1989 (CNCR-8918), 10.0 mm CL (5.0 mm shield); R. Robles det. host; Puerto Morelos, Quintana Roo, Mexico (20°53′39″N, 85°4′21″W); J. L. Villalobos et al. colls., 25 April 1988.

Distribution.—From Massachusetts to North Carolina, U.S.A. (Boyko et al. 2017), and Quintana Roo, Mexico (present study).

Remarks.—The female (Fig. 1D) and male examined agree with the features described by Richardson (1904) and Markham (1988) for *Orthione furcata*; no substantial variations were observed, but their sizes (Table 1) were smaller than those reported by Markham (1988), females of 11.0–13.7 mm TL and males of 6.0–6.8 mm TL, and Boyko et al. (2017), 11.8 mm TL and 4.5–9.4 mm TL, respectively. This branchial parasite is the type species of the genus, and even though *Orthione* Markham, 1988 currently includes two additional species, *O. griffenis* Markham, 2004 and *O. mesoamericana* Markham, 2004 (Boyko et al. 2008b onwards), *O. furcata* is the only species along the western Atlantic coast (Markham 2004). Boyko et al. (2017) established that this bopyrid did not occur south of North Carolina, U.S.A., hence our record represents the first documented evidence of the occurrence of *O. furcata* in Mexican waters, extending its distribution range to the Mexican Caribbean. As suggested by Kaestner (1970), *O. furcata* may be present in the Gulf of Mexico. Likewise, there are no previous reports of *Upogebia vasquezi* parasitized by any bopyrid, so it is here recorded as a new host of *O. furcata*, which had been previously reported parasitizing only *U. affinis* (Boyko et al. 2017).

Genus *Pseudione* Kossmann, 1881
Pseudione cf. *crenulata* G. O. Sars, 1898
Figs. 1E, 4, Table 1

Material examined.—One ovigerous female and one male (CNCR-35774) in left branchial chamber of female *Munida valida* Smith, 1883, 16.5 mm CL (CNCR-21632); A. Gaytán-Caballero det. host; Campeche bank, Gulf of Mexico (20°24.34′N, 91°34.86′W, 539 m deep), Escobar-Briones et al. colls., 27 Jun 2003.

Distribution.—Eastern Atlantic: Norway and United Kingdom to Mediterranean Sea (Bourdon 1968, Boyko et al. 2012). Western Atlantic: southwestern Gulf of Mexico (present study).

Description.—Female, body measurements are shown in Table 1. Body asymmetrical, head rotated dextrally, anterior portion broader and slightly tapered posteriorly. Head with anterior margin rounded and posterior one triangular, inserted in first pereomere. Frontal lamina crenulate and slightly wider on sides. Small eyes on next to lateral margins (Fig. 4A). Antennule of three and antenna of five segments, both with wide basis and distal tuft of setae (Fig. 4C). Maxilliped with irregular outline, anterior segment sub-rectangular and small unarticulated palp lacking setae, posterior segment triangular with acute spur (Fig. 4D). Barbula with two noticeably crenulate posterolateral projections on each side, external slightly larger than internal projection, medial margin with small tubercles on each lateral side only (Fig. 4E). Pereomeres 1–4 of both sides with dorsolateral bosses and crenulate coxal plates and tergal projections, which are more conspicuous on long side of body (Fig. 4A). Pereomeres 5–7 with wider crenulate coxal plates and reduced tergal projections. First pair of oostegites with large and ovate anterior segment, posterior segment sub-rectangular, small and with rounded posterolateral point (Fig. 4F, G); internal margin with digitations on mid-proximal portion (Fig. 4G). Pereopods with conspicuous carina on upper margin of basis and on lower margin of merus (Fig. 4A, H), both decreasing in size anteriorly. Pleomeres 1–5 with triangular, uniramous and scantly tuberculated lateral plates on each side, pleomere 6 small, rounded in shape and surrounded by pleomere 5 (Fig. 4B). Five pairs of biramous, lanceolate and faintly tuberculated pleopods; endopod slightly longer and slender than exopod, both branches decrease in size posteriorly (Fig. 4B, I).

Male, body measurements are shown in Table 1, head ovoid with anterior margin more or less straight; posterior margin slightly convex and not completely fused with first pereomere (Fig. 4J). Antennule and antenna of three and five segments, respectively; antenna exceeding margin of head (Fig. 4K). All pereomeres with tapered lateral margins, first one directed forward and pereomeres 2–7 laterally directed (Fig. 4J). Pereopods of similar structure but progressively vary in size posteriorly, pairs 1–3 increase whereas pairs 4–7 decrease in size (Fig. 4K). Pleon narrower than pereomere 7. Pleomeres 1–5 triangular in shape, pleomere 6 bilobed with lateral margins rounded and bearing small tuft of setae on each lobe, visible in ventral view (Fig. 4J). Five pairs of ovoid pleopods, fleshy in appearance (Fig. 4K).

Remarks.—The crenulations and digitations on the frontal lamina, barbula and coxal plates, among other characteristics, of the examined female show their affinity with the group of eight species (one of them with two subspecies) termed the *Pseudione* "crenels," and whose differentiation is subtle (Bourdon 1972, Kazmi & Boyko 2005). This group includes: *Pseudione chiesai* Pereira, Doti, & Roccatagliata, 2021, *P. confusa confusa* (Norman, 1886), *P. confusa maxillipedis* Bourdon, 1972, *P. crenulata* G. O. Sars, 1898, *P. fibriata* Richardson, 1910, *P. itsindrae* Bourdon, 1976, *P. minimocrenulata* Nierstrasz & Brender à Brandis, 1931, *P. serejoae* Brito, Cardoso, & Boyko, 2018, and *P. subcrenulata* Nierstrasz & Brender à Brandis, 1923. Three of them have been previously reported in waters of the western Atlantic: *P. chiesai* (Mar del Plata submarine canyon, Argentina; see Pereira et al. 2021), *P. confusa maxillipedis* (St. Croix U.S. Virgin Islands; see Bourdon 1972, Kazmi & Boyko 2005), and *P. serejoae* (Campos Basin, Rio de Janeiro, Brazil; see Brito et al. 2018).

The female examined differs from *P. chiesai* and *P. serejoae* in several characters: in *P. chiesai* the frontal lamina has few shallow indentations, the two lateral projections of the barbula are smooth and oriented inward, and the maxilliped has a well-developed and setose palp (Pereira et al. 2021); in *P. serejoae* the barbula has three lateral projections, the maxilliped has no palp and the pereopods, antennules, and antennae are provided with minute scales (Brito et al. 2018).

Though the characters of our female are similar to those of *P. confusa maxillipedis* and *P. minimocrenulata*, it also differs from them in some traits. Bourdon (1972) pointed out that the frontal lamina of *P. confusa maxillipedis* is weakly crenulate and the number of digitations is extremely reduced on the internal margin of the first oostegite and the lateral projections of the barbula, characteristics that it shares with *P. confusa confusa* (Bourdon 1968, 1972). The main difference between both subspecies is the palp of the maxilliped; in *P. confusa maxillipedis* it is large, unarticulated and with long distal setae (Bourdon 1972, Fig. 6c, d, Kazmi & Boyko 2005), whereas *P. confusa confusa* has a prominent palp without setae (Bourdon 1968, Fig. 51a, 1972). These characters depart from the crenulate frontal lamina (Fig. 4A, C) and the maxilliped with a small unarticulated palp lacking setae (Fig. 4D) recorded in our specimen.

Although the female of *P. minimocrenulata* has a crenulate frontal lamina and maxillipeds with a short palp (Kazmi & Boyko 2005), it differs from our specimen in that the palp of *P. minimocrenulata* is tipped with short setae and the first pair of oostegites, the surface of the barbula and pereopods are covered with minutes scales (Kazmi & Boyko 2005), traits that were not observed in our specimen.

Nierstrasz & Brender à Brandis (1931) noted that *P. minimocrenulata* and *P. crenulata* are closely related species because their general body shape is similar; but they pointed out that *P. crenulata* can be distinguished by having a longer pleon

than *P. minimocrenulata*, coxal plates of the long side of body without thorn-shaped processes, and narrower lateral plates in the pleon without tubercles. These last two traits agree with our female specimen; additionally, the overall appearance and barbula resemble those illustrated by Bourdon (1968, Figs. 49a and 44c, respectively) for *P. crenulata*, and their maxillipeds are consistent with those described by Bourdon (1968) and illustrated by Nierstrasz & Brender à Brandis (1926, Fig. 46) and Stephensen (1948, Fig. 36–5) for the same species.

This comparison allows us to suggest that the present female is closer to *P. crenulata* than to other species reported from the western Atlantic. However, considering that we examined only a single pair and the evident discrepancy in the geographic distribution of our record, because *P. crenulata* is only known from the northeastern Atlantic and the Mediterranean Sea, we believe it best at present to designate this record as *Pseudione* cf. *crenulata*. The analysis of more material is needed to confirm the distribution of *P. crenulata* in the western Atlantic.

Munida valida has been reported as host of *Aporobopyrina anomala* Markham, 1974b and *Entophilus omnitectus* Richardson, 1903 (Boyko et al. 2012, Markham 2020) but has not previously been reported to bear any *Pseudione* specimens. *Pseudione crenulata* has been previously reported from three species of *Munida* Leach, 1820: *M. intermedia*, *M. rugosa*, and *M. tenuimana* (Bourdon 1968, Boyko et al. 2012).

Genus *Robinione* Boyko, Williams, & Shields, 2017

Robinione overstreeti (Adkison & Heard, 1995)

Figs. 1F, 5, Table 1

Pseudioniinae [sic] sp.: Rakocinski et al. 1993:102.

Pseudione overstreeti Adkison & Heard 1995:105–109, Figs. 1, 2 (type-locality: west end of Horn Island, Mississippi, U.S.A., parasitizing *Callichirus islagrande* Schmitt, 1935).—Rakocinski et al. 1996:351.—Camp 1998:134.—Schotte et al. 2009:980.—Vogt 2016:1409, 1410, Fig. 7A.

Robinione overstreeti: Boyko et al. 2017:279–282, Figs. 9, 10.—Vogt 2020:152, Fig. 6.3A.—Bortolini et al. 2021:1–13, Figs. 1B–D, 2–5, Tables I, II (Veracruz, Mexico, parasitizing *C. islagrande*).

Material examined.—One juvenile female and one juvenile male (YUC-CC-255-11-006939) in right branchial chamber of female *Callichirus islagrande*, 11.29 mm CL (8.00 mm shield) (YUC-CC-255-11-003656); O. González-Bárcenas det. host; Laguna de Tamihahua, Veracruz, Mexico (20°58′33.18″N, 97°18′31.13″W); O. González-Bárcenas coll.; 27 January 2012. One juvenile female and one juvenile male (YUC-CC-255-11-006940) in left branchial chamber of female *C. islagrande*, 8.20 mm CL (5.73 mm shield) (YUC-CC-255-11-003657); O. González-Bárcenas det. host; Tecolutla beach, Veracruz, Mexico (20°29′3.27″N, 97°0′44.35″W); O. González-Bárcenas coll.; 30 January 2012. One adult female and adult male in left branchial chamber (YUC-CC-255-11-006941A) of male *C. islagrande* (YUC-CC-255-11-003658), 13.10 mm CL (9.4 mm shield). One adult female and one adult male in right branchial chamber (YUC-CC-255-11-006941B) of same host; O. González-Bárcenas det. host; Tecolutla beach, Veracruz, Mexico (20°28′54.54″N, 97°0′32.84″W); O. González-Bárcenas coll.; 29 January 2012. One adult female (YUC-CC-255-11-003766) detached from host; Cozumel, Quintana Roo, Mexico (20°28′13.84″N, 86°58′48.4″W); J. Duarte and A. Anker colls.; 01 August 2010.

Distribution.—West coast of Florida to Texas, U.S.A., to Veracruz, Tabasco and Quintana Roo, Mexico (Boyko et al. 2017, present study).

Remarks.—The adult female detached from its host (Fig. 1F) agrees with the features described for *R. overstreeti* by Adkison & Heard (1995). The two adult females registered from a bilateral double infestation were smaller in size and showed differences such as: frontal lamina slightly wider, lateral margins rectangular to semi-triangular, resembling coxal plates (Fig. 5A); pereomeres 1–4 on both sides with coxal plates wider, slightly crenulate, with semi-triangular lateral edges, directed laterally, and tergal projections reduced (Fig. 5A); tubercles on inner ridge of first oostegite barely developed, and the two branches of pleopods 1 and 2 different in size, with the endopod smaller than the exopod, but from pleopods 3–5 progressively becoming similar in sizes. Overall, the outline of the juvenile female resembles that of the adult females of *R. overstreeti*, but they differ in having a wide frontal lamina with lateral margins varying from semi-triangular to square, more or less pointed; all pereomeres with triangular and crenulate coxal plates that do not seem to be free, all oostegites barely developed, the inner ridge of the first oostegite curved on its middle portion but smooth, barbula with one tiny bulge on each side and smooth medial margin, pereopods 1–7 with evident but not rough carina on basis, the branches of the first pairs of pleopods differ in size but become of similar size towards the last pair. Males also agree well with the characters of *R. overstreeti* (Adkison & Heard, 1995), although separation of pereomeres is variable. An adult male (YUC-CC-255-11-006941B) has the right side of the head truncate, showing the antennae in dorsal view (Fig. 5B), and the first two pairs of pereopods of the right side are similar in structure but smaller than those on the opposite side, suggesting that the male was damaged in this part of the body and the pereopods were regenerated.

The genus *Robinione* Boyko, Williams, & Shields, 2017 is comprised of two very similar species: *R. brattstroemi* (Stuardo, Vega, & Cespedes, 1986) distributed on southeastern Pacific coasts and *R. overstreeti*, considered endemic to the Gulf of Mexico (Adkison & Heard 1995, Boyko et al. 2017), hence the record of *R. overstreeti* from Cozumel, Quintana Roo, expands its distribution range to the Caribbean. Unfortunately, the host in this area remains unknown, but according to Boyko et al. (2017) only two hosts are recognized so far for this branchial parasite, *Callichirus islagrande* and *Callichirus santarosaensis* Sakai & Türkay, 2012.

Discussion

Although the geographical distribution of bopyrids is linked to the distribution of the decapods they infest (Boyko & Williams 2009), some species have only been recorded in limited areas within the wide distributional range of their hosts, as was observed for the parasite-host associations of *Pseudione thomasi*, parasitizing *Tozeuma carolinense* and *Robinione overstreeti* on *Callichirus islagrande*. In both cases, and even though *R. overstreeti* parasitizes two closely related species of the same genus, it is likely that other factors, such as the availability of intermediate hosts (pelagic copepods), are determining the reduced geographic ranges observed (Boyko & Williams 2009). Unfortunately, few studies have been dedicated to understanding the direct interactions between intermediate hosts and epicaridean larvae (see Owens & Rothlisberg 1991, 1995).

By parasitizing multiple host species, bopyrids can be distributed over larger areas, but specificity is frequently restricted to several species within one genus or to a few species belonging to closely related genera (Boyko & Williams 2009), as was observed for *Urobopyrus processae*, *Orthione furcata*, and *Pseudione* cf. *crenulata*. In particular, *U. processae* has a wider distributional range since it has been

recorded on both sides of the Atlantic, Gulf of Mexico, Brazil, the Mediterranean, and northern France (Markham 1986). If the occurrence of *P. crenulata* in the Gulf of Mexico is confirmed, its distribution will be fairly similar to that of *U. processae*.

In general, few data are available to understand how bopyrids extend their distribution. Ballast water transport has been suggested as a mechanism by which bopyrids spread to new regions or hosts. For example, *Orthione griffenis* Markham, 2004 could have been introduced to the western coast of the United States by ships arriving from China, and *Pseudione* cf. *crenulata* could have reached the western Atlantic in ballast waters from ships coming from the Mediterranean. However, at this point there is no conclusive evidence to support these hypotheses (see Williams & An 2009). Further, ballast water mediated introductions of crustaceans to new habitats has increased the number of new hosts for bopyrids. The brown shrimp *Penaeus aztecus* Ives, 1891, a native species from the western Atlantic, was introduced into the Mediterranean Sea in this way (Scannella et al. 2017). It settled and quickly spread to become an important commercial species in the Gulf of Antalya, Turkey (Gökoğlu et al. 2020). Simultaneously, *P. aztecus* became a new host for *Epipenaeon ingens* Nobili, 1906, which parasitizes other penaeid shrimps from the Red Sea, India, Hong-Kong, and Australia (Korun et al. 2013).

Therefore, it appears that the occurrence of *Pseudione* cf. *crenulata* in the western Atlantic simply had been overlooked because the prevalence of infestation by bopyrids in species of the genus *Munida* is generally low (see Varisco & Vinuesa 2011). This assumption is supported by the record of 140 specimens of *M. valida* collected in the southern Gulf of Mexico over more than a decade (1998, 2005, 2007–2009, 2011, 2012) of which only two individuals were recorded as parasitized by an unidentified bopyrid, with no further data than host sex and size (Vázquez-Bader & Gracia 2016).

This shows the importance of monitoring on the diversity of bopyrids in order to define their distributional ranges and their probable expansion to new regions, as well as the mechanisms they use to reach them.

The four new records of bopyrids for Mexican waters, including a new species presented here, brings to 32 the number of species occurring on the Atlantic coast of Mexico. Our results support the statement that this group of parasites is frequently overlooked during the taxonomic or ecological study of their hosts (Boyko & Williams 2009) and shows the enormous importance of scientific collections as sources of information.

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