

# Bopyrid isopods of the genus Aporobopyrus infesting porcellanid crabs (Decapoda: Anomura) in the Gulf of California, Mexico: new host and parasite records

Authors: Romero-Rodríguez, Jesús, and Álvarez, Fernando

Source: Proceedings of the Biological Society of Washington, 132(1):

99-118

Published By: Biological Society of Washington

URL: https://doi.org/10.2988/19-00005

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <a href="https://www.bioone.org/terms-of-use">www.bioone.org/terms-of-use</a>.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Bopyrid isopods of the genus *Aporobopyrus* infesting porcellanid crabs (Decapoda: Anomura) in the Gulf of California, Mexico: new host and parasite records

Jesús Romero-Rodríguez\* and Fernando Álvarez

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

Abstract.—Based on examination of porcellanid crabs from the Gulf of California, Mexico, deposited in the Colección Nacional de Crustáceos of the Instituto de Biología, Universidad Nacional Autónoma de México, we document Petrolisthes crenulatus, P. hirtispinosus and P. galapagensis as hosts of bopyrid isopods belonging to the genus Aporobopyrus for the first time. The new records increase to 42 the number of known hosts for these ectoparasites. Further, this report provides the first record of Aporobopyrus curtatus for the coasts of Mexico and the eastern Pacific, becoming the second species of the genus with an Amphiamerican distribution. The distribution ranges of A. bourdonis, A. muguensis and A. trilobatus are extended and morphological remarks and a key to the four bopyrid species are provided.

**Keywords:** Bopyridae, eastern Pacific coast, Epicaridea, host-parasite association, Isopoda

The infraorder Anomura is one of the most abundant and diverse groups of decapods in the Gulf of California, and the crabs of the family Porcellanidae are a numerically dominant group in the intertidal zones due in part to their high diversity (Villalobos & Álvarez 2002). Anomurans are the group second most commonly infested by bopyrid isopods, after caridean shrimps (Boyko & Williams 2009). Within Anomura, porcellanid crabs are mainly parasitized by members of the genus Aporobopyrus Nobili, 1906 (Williams & Madad 2010), but also by species of the pseudionine genera Anuropodione Bourdon, 1967, Aporobopyrina Shiino, 1934, Parionella Nierstrasz & Brender à Brandis, 1923, Pleurocrypta Hesse, 1865 and Pseudione Kossmann, 1881 (Boyko et al. 2012). All of them live ectoparasitically

in their hosts' branchial chambers and can partially or completely inhibit their hosts' growth and reproduction (Van Wyk 1982, Oliveira & Masunari 1998). *Aporobopyrus* currently contains 20 described species worldwide (Boyko et al. 2008 onwards), of which only *A. gracilis* Nierstrasz & Brender à Brandis, 1929 and *A. retrorsa* (Richardson, 1910) parasitize non-porcellanid hosts (Williams & Madad 2010).

Markham (1992) pointed out that there are relatively few species of bopyrid isopods known from the Pacific coast of the Americas, a pattern that becomes evident when the number of species reported for the Western Pacific (166) and those reported for the eastern Pacific (37) are compared (Williams & Boyko 2012). Twenty species of bopyrids are recognized from the Pacific coast of Mexico, five belonging to the subfamily Pseudioninae and only three to *Aporobopyrus*: A. bourdonis Markham, 2008 on

<sup>\*</sup> Corresponding author. DOI: 10.2988/19-00005

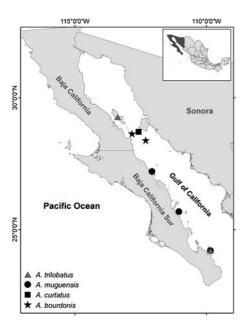


Fig. 1. Sampling sites of porcellanid crabs parasitized with bopyrids (*Aporobopyrus* spp.) in the Gulf of California, Mexico.

Petrolisthes edwardsii (de Saussure, 1853), A. muguensis Shiino, 1964 parasitizing Pachycheles rudis Stimpson, 1859 and A. trilobatus (Nierstrasz & Brender à Brandis, 1925) parasitizing Petrolisthes hians Nobili, 1901 (Markham 2008, Román-Contreras 2008), but no bopyrids on porcellanids have so far been recorded in the Gulf of California. Only three species of pseudionines are known from the Gulf of California: Pseudione galacanthae Hansen, 1897 on Galacantha diomedae Faxon, 1893, Progebiophilus bruscai Salazar-Vallejo & Leija-Tristan, 1990 on Upogebia dawsoni Williams, 1986 and Ione cornuta Bate, 1865 on Neotrypaea gigas (Dana, 1852) (Román-Contreras 2008, Boyko et al. 2017).

Notwithstanding the fact that taxonomic or ecological data on diverse potential hosts of bopyrids is abundant in the literature, their associated parasites are often overlooked (Boyko & Williams 2009), hence the reappraisal of material already deposited in museums or institutional collections can provide an opportu-

nity to increase the records and the knowledge about this group of parasites (Markham 2008). The present study is based on material collected during the "Conservación de las islas en un mar en el desierto, Golfo de California" project, which was conducted from 1985 to 1987 to create an inventory of the plant and animal species that inhabit the islands of the Gulf of California (Villalobos et al. 1992). All crustaceans collected were deposited in the Colección Nacional de Crustáceos (CNCR) of the Instituto de Biología, Universidad Nacional Autónoma de México, in Mexico City. We present herein the results of a study of the porcellanid crabs parasitized by bopyrids, with notes on their morphological variability, distribution and host specificity.

### Materials and methods

Porcellanid crabs were collected every 3 months by hand, between May 1985 and May 1987, from beneath rocks and coral rubble in the intertidal zones of 23 islands in the Gulf of California, Mexico. Twelve islands are in the northern gulf and 11 are situated along the east coast of the Baja California Peninsula in the southern portion; the sampling sites were located in the protected zone of the islands (Fig. 1). The crabs were preserved in 70% ethanol, identified to species, sexed, and deposited in the CNCR. For more details on the methods and a description of the sampling sites see Villalobos et al. (1989) and Villalobos & Álvarez (2002).

Measurements taken from each host were carapace length (CL), from the anterior margin of the rostrum to the posterior margin of the carapace, and carapace width (CW), as the maximum distance between the lateral margins of the carapace (Britto-Mata et al. 2017). The parasites were removed from the hosts' branchial chambers and the total length

(TL) of males and symmetrical females were measured from the anteromedial margin of the head to the posterior margin of the pleon; in asymmetrical females TL was considered as the anterior margin of the first peromere of the longer side to the posterior margin of the pleon. The width (W) was measured across the widest pereomere (Romero-Rodríguez & Martínez-Mayén 2018). Length and width of the head and pleon of each specimen are also provided (Table 1). Measurements were made using an ocular micrometer attached to a compound microscope with a 0.1 mm precision. Comments on morphological variation or on characters that were not mentioned in previous studies are provided for all species.

### Results

Systematics.—
Suborder Cymothoida Wägele, 1989
Infraorder Epicaridea Latreille, 1825
Superfamily Bopyroidea Rafinesque, 1815
Family Bopyridae Rafinesque, 1815
Subfamily Pseudioninae Codreanu, 1967
Genus Aporobopyrus Nobili, 1906
Aporobopyrus bourdonis Markham, 2008
(Figs. 2A, 3A, 4; Table 1)

"a bopyrid" Haig 1968: 61.

"Pseudioninae sur *Petrolisthes edwarsi* (de Saussure)" Bourdon 1976: 236–238, 241 (in table), fig. 43.

"Bopírido indeterminado" Campos & Campos 1989: table 2.

"Pseudioninae, gen. sp.?" Salazar-Vallejo & Leija-Tristán 1990: 430 (appendix 1).

*Aporobopyrus bourdonis* Markham 2008: 146–148, 154, fig. 1.—Boyko et al. 2012: 5, 22 (in table).

Material examined.—1 adult female (host: Petrolisthes galapagensis Haig, 1960, CNCR 4161) Isla San Pedro Mártir, Sonora, Mexico (28°22'49"N, 112°18'25"W), J.C. Nates and A. Cantú

coll.; 04 May 1985, CNCR 19408. 1 juvenile female, 1 male (host unknown; parasite detached); Isla San Lorenzo, Baja California, Mexico (28°37′44″N, 112°49′34″W), J.C. Nates and E. Lira coll., 14 Feb 1986, CNCR 19446.

Distribution.—Isla San Lorenzo and Isla San Pedro Mártir, Baja California, Mexico (this study); Bahía de Chamela, Jalisco, Mexico (Bourdon 1976) and Guanacaste, Costa Rica (Markham 2008).

Remarks.—The head of both adult and juvenile females is wider than long, broadly rounded anteriorly with a narrow but well defined frontal lamina, slightly curved on its posterior end (Fig. 2A). Antennules and antennae are composed of 3 and 5 segments each, respectively. In both females, the pereomeres are distinct and bear coxal plates and tergal projections on pereomeres 1-4 on both sides, those of the adult female are more evident on the longer side (Fig. 2A), whereas in the juvenile female the coxal plates are well developed and discernible on pereomeres 1–5 but the tergal projections are barely developed, with those on percomere 1 being the most conspicuous, and becoming less prominent posteriorly to pereomere 4.

The oostegites close completely the brood pouch of the adult female, the posterior margin of oostegites 2-4 bear small setae whilst the fifth bears a row of long setae, agreeing with previous reports (Bourdon 1976, Markham 2008). Oostegites 2-5 of the juvenile female are not entirely developed, they are rectangular, do not reach the ventral midline of the female and lack setae on their posterior margins. The shape of the first pair of oostegites of the adult female matches those described by Bourdon (1976) and Markham (2008), except for a row of small setae on its posterior margin not previously reported (Fig. 4A, B); in the juvenile female the anterior and posterior lobes are ovoid and triangular, respectively. The shape of the inner ridge of oostegite 1 is variable because Bourdon (1976) described

Table 1.—Measurements (mm) of the bopyrids of the genus Aporobopyrus and their hosts recorded in the Gulf of California, Mexico: CNCR, catalogue number of the Colección Nacional de Crustáceos, IB-UNAM; TL, total length; CL, carapace length; CW, carapace width; Juv., juvenile; Ov., ovigerous.

					Head	pı	Pleon	on				
Parasite	CNCR	Sex	TL	×	Length	Width	Length	Width	Host	Sex	CL	CW
A. bourdonis	19408	Adult female	4.30	2.80	1.25	2.05	0.75	2.12	P. galapagensis	Male	6.33	8.40
	19446	Juv. female	4.00	2.63	0.93	1.70	1.00	1.86	Detached from host			
		Male	1.98	0.70	0.27	0.49	0.50	0.61				
A. curtatus	19450	Ov. female	7.10	4.30	1.62	2.87	1.48	2.70	P. hirtispinosus	Female	10.57	12.43
		Male	3.90	1.03	0.37	0.87	0.47	0.91				
A. muguensis	21876	Adult female	2.40	1.72	0.79	1.19	0.54	1.06	P. crenulatus*			
		Male	1.29	0.64	0.20	0.49	0.43	0.54				
	22189	Juv. female	2.53	1.58	0.80	1.07	0.71	1.00	P. crenulatus *			
		Male	2.17	0.70	0.26	0.50	0.56	69.0				
	22195	Juv. female	1.76	1.03	0.43	0.74	0.50	0.73	Detached from host			
		Male	1.36	0.46	0.13	0.33	0.29	0.39				
A. trilobatus	19411	Adult female	3.27	2.37	1.25	1.60	98.0	1.45	P. crenulatus	Female	6.50	7.20
		Male	2.53	0.83	0.34	0.61	09.0	0.74				
	20074	Juv. female	1.16	0.71	0.34	0.54	0.26	0.47	P. ortmanni	Male	2.73	2.63
		Male	1.09	0.34	0.11	0.26	0.27	0.29				

\* No host data measurement available, parasites were detached and none of the crabs in the lot showed a clear bulging of the carapace.



Fig. 2. Bopyrid adult females parasitic on porcellanid crabs in the Gulf of California, Mexico. A, *Aporobopyrus bourdonis* Markham, 2008; B, *Aporobopyrus curtatus* (Richardson, 1904); C, *Aporobopyrus muguensis* Shiino, 1964; *Aporobopyrus trilobatus* (Nierstrasz & Brender à Brandis, 1925). Scale bar = 1.0 mm.

it as having digitate projections, while Markham (2008) stated that it has a slightly sinuate flap overhanging a separating groove. The adult female examined herein fits Markham's (2008) description; in the juvenile female this trait is less evident.

The maxillipeds of the adult female are similar to those described by Markham (2008) but with 2 or 3 setae on the palp's anterior margin (Fig. 4C). In the juvenile female the maxillipeds are triangular with the posterior article wider than the anterior one and with a conspicuous palp. The

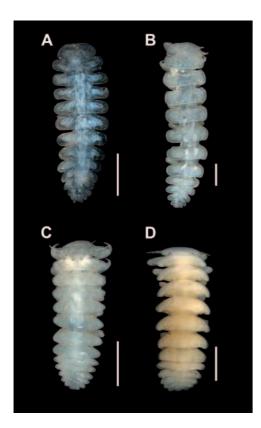


Fig. 3. Bopyrid males parasitic on porcellanid crabs in the Gulf of California, Mexico. A, *Aporobopyrus bourdonis* Markham, 2008; B, *Aporobopyrus curtatus* (Richardson, 1904); C, *Aporobopyrus muguensis* Shiino, 1964; *Aporobopyrus trilobatus* (Nierstrasz & Brender à Brandis, 1925). Scale bar = 0.5 mm.

barbula of the adult female has one sinuate lateral projection on each side and the medial margin is thick and slightly sinuate; that of the juvenile female has a tiny bulge on each side and a medial margin slightly thick but straight (Fig. 4D). The range of variation of the barbula is not defined yet, because Markham (2008) did not describe or illustrate it and our observations contrast with the barbula reported by Bourdon (1976), which have two lateral projections on each side with digitations on the margins of the external projection and the medial margin.

The pereopods in both adult and juvenile females are similar to those described

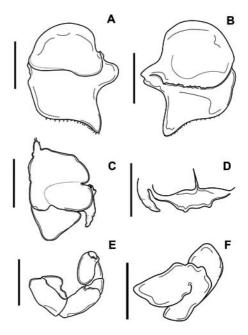


Fig. 4. Adult female of *Aporobopyrus bourdonis* Markham, 2008. A, first oostegite, external view; B, same, internal view; C, maxilliped; D, barbula; E, pereopod 7; F, left first pleopod. Scale bar = 0.5 mm.

by Markham (2008), except for the presence of a carina on the basis of each pereopod (Fig. 4E), this character was also noted by Bourdon (1976).

The pleon of both females agrees well with the original description of *A. bourdo-nis* (Markham 2008), even though that of the adult female is damaged distally. The pleopods are biramous, the endopodites are oblong and larger than the exopodites, which are ovoid in shape (Fig. 4F).

The male (Fig. 3A) that was attached to the ventral pleon region of the juvenile female agrees in size (Table 1) and morphology with Bourdon (1976) and Markham's (2008) descriptions of *A. bourdonis*, with the exception of the sixth pleomere which is not as reduced as noted by the latter author.

Overall, these specimens agree well with the characteristics described for *A. bour-donis*. The observed morphological variability adds to what was known from the

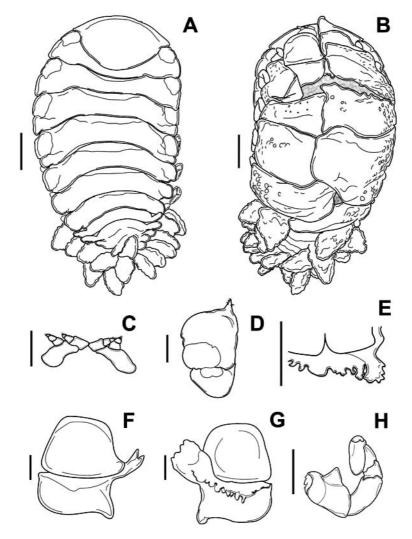


Fig. 5. Adult female of *Aporobopyrus curtatus* (Richardson, 1904). A, dorsal view: B, ventral view; C, antennules and antennae; D, maxilliped; E, barbula; F first oostegite, external view; G, same, internal view; H, barbula; E, pereopod 7; F, left first pleopod. Scale bar = 1.0 mm for A, B; 0.5 mm for C—H.

other two known females of the species, one of them had been described first as a "Pseudioninae sur *Petrolisthes edwardsi*" (Bourdon 1976) but subsequently Markham (2008) identified it as *A. bourdonis*. This is the first record of a bopyrid isopod parasitizing *Petrolisthes galapagensis*, it is also a new host record for *A. bourdonis* and extends its known geographic distri-

bution into the Gulf of California, Mexico

Aporobopyrus curtatus (Richardson, 1904) (Figs. 2B, 3B, 5, 6; Table 1)

Pseudione curtata Richardson 1904: 80–81, figs. 72–75.—Richardson 1905: 523, 530–531, figs. 574–577.—Nobili 1906: 1108.—Van Name 1920: 72.—Nierstrasz & Brender à Brandis 1923: 72,

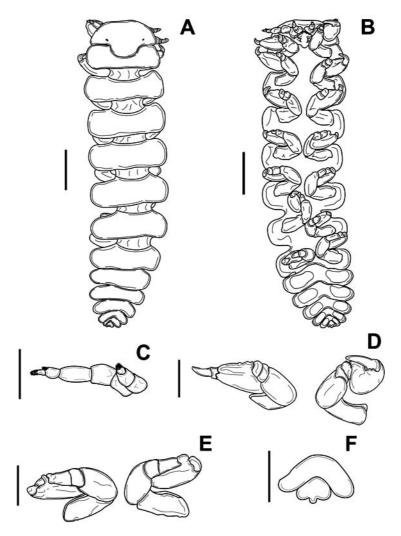


Fig. 6. Adult male of *Aporobopyrus curtatus* (Richardson, 1904). A, dorsal view: B, ventral view; C, antennule and antenna; D, pair of pleopods 1; E, pair of pleopods 7; F, pleomeres 5 and terminal in dorsal view. Scale bar = 0.5 mm for A, B; 0.2 mm for C—F.

74, 77–78.—Nierstrasz & Brender à Brandis 1925: 3, 7.—Nierstrasz & Brender à Brandis 1931: 169.—Shiino 1933: 271.—Shiino 1952: 41.—Shiino 1958: 35.—Menzies & Glynn 1968: 13.—Schultz 1969: 326, fig. 522.

Aporobopyrus curtatus Nierstrasz & Brender à Brandis 1929: 12.—Monod 1933: 227.—Shiino 1934: 267.—Shiino 1964: 22.—Markham 1975: 257–265, 269, figs. 1–3.—Menzies & Frankenberg

1966: 26.—Bourdon 1976: 166, 175–180, 188, 238, 240–241 (in table), figs. 6–9.—Camp et al. 1977: 17.—Lemos de Castro & Brasil-Lima 1980: 1–4, 6, figs. 1–15.—Duarte & Morgado 1983: 3, 5, 7, 11, fig. 10.—Markham 1988: 22–24, 56 (in table).—Markham & Donath-Hernández 1990: 242.—Boyko et al. 2012: 5, 21–24 (in table).

Aporobopyrus johannis Nierstrasz & Brender à Brandis 1929: 10–11, figs. 9–

10.—Monod 1933: 227.—Shiino 1934: 267.—Shiino 1964: 22.

Pseudione curta [sic] Behre 1950: 18. "bopyrid parasite" Haig, 1966: 355.

?Aporobopyrus gracilis Lemos de Castro 1965: 177–180, figs. 1–10.—Coelho & Koenig 1972: 256 (in table I).

Not *Pseudione curta* [sic] Menzies & Frankenberg 1966: 26 (= *Synsynella choprai* (Pearse 1932)).

?"bopyrid" Gore 1970: 963.

?"bopyrid parasites" Gore 1974: 715.

Material examined.—1 ovigerous female, 1 male (host: Petrolisthes hirtispinosus Lockington, 1878, CNCR 5411), Isla San Esteban, Sonora, Mexico (28°42′06″N, 112°34′29″W), J.C. Nates and E. Lira coll., 19 Feb 1986, CNCR 19450.

Distribution.—Along the western Atlantic coast, from North Carolina, USA, to São Paulo, Brazil (Boyko et al. 2012); in the eastern Pacific, Isla San Esteban, Sonora, Mexico (present study).

Redescription.—Female. Measurements shown in Table 1. Body larger than wide (Table 1) with outline smoothly oval and all body regions and segments distinct (Figs. 2B; 5A, B). Head almost twice as broad as long (Table 1), with narrow but well-defined frontal lamina that ends in lateral projections, rounded posteriorly and deeply embedded in pereomere 1 (Figs. 2B; 5A). No eyes. Antennules and antennae composed of 3 and 4 segments each, respectively, neither extending beyond margin of head (Fig. 5C). Terminal segment of each antenna is smallest and tipped with setae. Basal segment of antenna markedly larger than others (Fig. 5C). Maxilliped subtriangular in shape, with conspicuous non-articulated palp that bears small setae on its anterior margin (Fig. 5D). Barbula with two digitate lateral projections on each side, external one larger than internal, medial margin slightly concave with evident digitations (Fig. 5E).

Pereon widest across pereomere 3. Conspicuous dorsolateral bosses and narrow coxal plates on pereomeres 1–4 (Fig. 5A). Oostegites firmly enclosing marsupium (Fig. 5B); first pair with anterior segment oval-shaped and posterior segment rectangular with well defined falcate terminal lobe on posterolateral corner (Fig. 5F, G), digitate projections on internal ridge (Fig. 5G). Oostegites 2–4 with small setae on posterior margins, fifth one with row of larger setae. Pereopods slightly larger in size posteriorly, each with evident basal carina (Fig. 5H).

Abdomen of 6 pleomeres, each produced into lateral plates (Fig. 5A). Ventrally covered in part by five pairs of biramous, triangular and tuberculate pleopods, with margins bulging into fleshy bead (Fig. 5B). Endopodite larger than exopodite in all five pairs, both rami progressively smaller from first to fifth pleopods (Fig. 5B). Pair of uniramous uropods similar to pleopods.

Male. Measurements shown in Table 1. Body slightly tapered with all body regions and segments distinct. Head oval-shaped and twice as wide as long but narrower than first pereomere; anterior margin almost straight (Figs. 3B; 6A). Tiny eyes near posterior border (Fig. 6A). Antennules and antennae composed of three and five articles each, respectively; both tipped with setae on distal and subdistal segments (Fig. 6C).

Pereon widest on pereomeres 2 and 3, but other pereomeres not markedly narrower. All pereomeres with rounded edges and deeply separated by anterolateral indentations (Figs. 3B; 6A). Pereopods differ in size, first two pairs are largest with dactyli and propodi larger than others, all pereopods progressively decreasing in size posteriorly (Fig. 6B). Bases of all pereopods each with conspicuous carina (Fig. 6D, E).

Pleon of six distinct pleomeres, ventrally without pleopods or uropods but with faint swellings on five pleomeres (Fig. 6B).

Terminal pleomere with three-pointed structure having lateral edges directed posteriorly and partly surrounded by fifth pleomere (Fig. 6F).

Remarks.—The morphology of the female examined fits well with previous descriptions of A. curtatus (Richardson 1904, Markham 1975, Bourdon 1976), except that the palps on the maxillipeds and the lateral plates on the pleomeres are more conspicuous than those illustrated by Markham (1975: Fig. 1D and 1A, respectively). Overall, the characteristics of the male also agree with those reported for A. curtatus. The anterolateral indentation between pereomeres is an evident difference with respect to the males illustrated in the original description (Richardson 1904: Fig. 75) and redescription (Markham 1975: Fig. 3) of this species, but is similar to that noted by Markham (1988) for males of Aporobopyrus bonairensis Markham, 1988, a species that occurs in the same range of A. curtatus and infest the same host species on the western Atlantic coast (Markham, 1988). However, the indentation between pereomeres was also observed in some males of A. curtatus from the western Atlantic (Markham 1975; 1988). Moreover, the general structure of the pereopods matches with previous reports (Markham 1975; 1988) and the meri and carpi of all of them are distinct (Fig. 6D, E), as was illustrated by Markham (1975: Fig. 3D, E), which differs from the meri and carpi being fused on A. bonairensis (Markham 1988).

Aporobopyrus curtatus parasitizes seven species of porcellanid crabs in the western Atlantic (Boyko et al. 2012) and exhibits a certain degree of morphological variation according to the host it is found on; for example, Bourdon (1976) pointed out differences in the inner margin of the first oostegite and the basal carinae of the pereomeres between females that parasitized Petrolisthes galathinus (Bosc, 1801) and Porcellana sayana (Leach, 1820). In contrast, the female examined here agrees

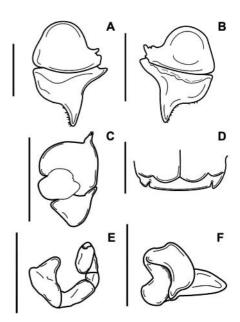


Fig. 7. Adult female of *Aporobopyrus muguensis* Shiino, 1964. A, first oostegite, external view; B, same, internal view; C, maxilliped; D, barbula; E, pereopod 7; F, left first pleopod. Scale bar = 0.5 mm.

well with the redescription presented by Markham (1975), despite that it is recorded in a new host and locality. Likewise, although the female is one of the largest reported to date (Table 1) its size is within with the body length range reported by Markham (1975) (1.7–8.9 mm TL), but the size of the male (Table 1) exceeds almost twice the size of the largest male (2.50 mm TL) previously reported (Lemos de Castro & Brasil-Lima 1980, Markham 1988). No previous records exist of A. curtatus for Mexico, and this first report from the Pacific coasts establishes an Amphiamerican distribution pattern, similar to that of A. trilobatus, the only species of the genus Aporobopyrus reported heretofore on both Atlantic and Pacific coasts (see Boyko et al. 2012). Petrolisthes hirtispinosus is a new host for A. curtatus.

Aporobopyrus muguensis Shiino, 1964 (Figs. 2C, 3C, 7; Table 1)

Aporobopyrus muguensis Shiino 1964: 20–22, fig. 1.—Schultz 1969: 315, fig. 500

b.—Markham 1975: 265 (in table).— Miller 1975: 285–286, 305, pl. 64, fig. 15.—Bourdon 1976: 166, 187.—Haig & Abott 1980: 589.—Lee & Miller 1980: 544, pl. 57, photograph 21.11.— Wallerstein 1980: 235.—Hart 1982: 32.—Van Wyk 1982: 459–471, figs. 1– 5, tables 1–3.—Sassaman et al. 1984: 651, 653.—Austin 1985: 587.—Sassaman 1985: 778, 782, 785, 787.— O'Brien & van Wyk 1985: 196, 197, fig. 2.—Campos-González & Campoy-Favela 1987: 39, 40–41, 42, 47, fig. 1.— Markham 1988: 27.—Campos & Campos 1989: 33 (in table).—Jay 1989: 75.—Salazar-Vallejo & Leija-Tristan 1990: 429 (in table).—Markham 1992: 3 (in table).—Sassaman 1992: 575, 576.—Brusca et al. 2007: 535.— Kuris et al. 2007: 654.—Román-Contreras 2008: 94 (in table).—Markham 2008: 148-150, fig. 2.—Boyko et al. 2012: 6, 21 (in table).

Aporobopyrus m guensis [sic] Bourdon 1976: 240.

Aporobopyrus muquensis [sic] Campos & Campos 1989: 30.

Aparobopyrus [sic] Raibaut & Trilles 1993: 423.

Material examined.—1 adult female, 1 male (host: Petrolisthes crenulatus Lockington, 1878, CNCR 7110), Isla San Marcos, Baja California Sur, Mexico (27°11′38″N, 112°04′08″W), E. Lira and M.D. Valle coll., 24 Jan 1987, CNCR 21876. 1 juvenile female, 1 male (host: P. crenulatus CNCR-6885), Isla Montserrat, Baja California Sur, Mexico (25°40'47"N, 111°02′43′′W), E. Lira and M.D. Valle coll., 16 Jan 1987, CNCR 22189. 1 juvenile female, 1 male (host unknown; parasite detached), Isla Cerralvo, Baja California Sur, Mexico (24°24′00′′N, 110°29′00′′W), E. Lira and M.D. Valle coll., 27 Jan 1987, CNCR 22195.

Distribution.—Central and southern coasts of California, USA (Markham 2008), Bahía Todos Santos, Baja Califor-

nia (Campos-González & Campoy-Favela 1987) and Gulf of California (present study), Mexico.

Remarks.—The anterior margin of the head in all females is wide and curved, the frontal lamina undifferentiated and the antero-lateral borders are rounded; the head is nearly of the same width as the first pereomere (Fig. 2C). The antennules and antennae are composed of four and five segments each, respectively; the antenna hardly exceeds the margin of the head in the two larger females.

The pereon has seven distinct pereomeres, in the smaller female the coxal plates are inconspicuous whilst in the two adult females they are noticeable on pereomeres 1–4 but are more developed on pereomeres 2-4 of the larger side of body. The tergal projections are visible on pereomeres 1–4, mainly on the larger side of body, but the ones on the first pereomere are the most conspicuous. Oostegites 2–5 of juvenile females are not completely developed and do not reach the medial ventral region, their shapes are rectangular with small setae on their posterior margins. Oostegites 2-4 of adult females have small setae, while the fifth one has a row of larger setae. The anterior segment of the first pair of oostegites is oval and the posterior segment is rectangular with a falcate terminal lobe on its posterolateral corner that bears a row of small setae on its distal margin (Fig. 7A,B), the inner ridge is without ornamentations (Fig. 7B).

The maxilliped of the adult female has a wider anterior region (Fig. 7C), similar to that illustrated by Markham (2008: Fig. 2G), whilst in the juvenile females this arrangement is reversed. The barbula has a smooth and straight medial margin with one projection on each side (Fig. 7D); in the juvenile female there is only a tiny bulge while the adult female carries a larger projection (Fig. 7D) but not as slender as that illustrated by Markham (2008: 149, Fig. 2F).

In all females the pereopods are slightly larger posteriorly. The first has an inconspicuous carina that increases in size posteriorly until it becomes in a blunt carina on pereopod 7 (Fig. 7E).

The first two pairs of pleopods of the larger females are broad and leaf-like (Fig. 7F), the posterior pairs have a narrow base and become wider from the middle portion to its distal end, similar to those described by Shiino (1964). Both rami of the uropods are similar in size and touch each other medially, as was noted by Markham (2008).

The pereomeres in all males are distinct, in male CNCR 22189 they are spaced with rounded borders, while in male CNCR 21876 they are closer to each other with more acute borders. The first two pairs of pereopods are the largest bearing stout and acute dactyli (Fig. 3C).

The pleon is of six pleomeres, the first one about the same length as the last pereomere; the sixth pleomere is comprised of two short lobes, with a small anal projection between the lobes.

Shiino (1964) pointed out that A. muguensis is distinguished from its congeners because it has very narrow coxal plates only on the third and fourth pereomeres of the longer side of the female, and by the bilobed pleotelson of the male: both features were observed in the specimens examined. According to Markham (2008), the known hosts for this bopyrid are Pachycheles holosericus Schmitt, 1921, P. pubescens Holmes, 1900, P. rudis Stimpson, 1859, and now, reported for the first time as a host of bopyrids, Petrolisthes crenulatus. Further, this record of A. muguensis extends its geographic range into the Gulf of California. As was noted by Markham (2008), no comments on the morphology of this species were published after its original description (Shiino 1964), despite the fact that it has been collected several times throughout its distribution range. Thus, the new geographic record, the comments on its morphological variation and the figures presented herein improve our knowledge of the species.

Aporobopyrus trilobatus (Nierstrasz & Brender à Brandis, 1925) (Figs. 2D, 3D, 8; Table 1)

Pseudione trilobata Nierstrasz & Brender à Brandis 1925: 2–3, 7, figs. 7–10.— Monod 1933: 227.—Shiino 1933: 271.—Schultz 1969: 325, fig. 519.— Bourdon 1976: 165, 167–171, 240, 241, figs. 1–3.—Markham 1978: 489.—Adkison 1988: 579.—Markham 1988: 3, 4, 17–18, fig. 7.—Campos & Campos 1989: 33 (in table).—Salazar-Vallejo & Leija-Tristán 1990: 430 (in appendix 1).

"[a] bopyrid" Haig 1968: 67.

Pseudione tridentata [sic] Markham 1988: 56 (in table).

Aporobopyrus trilobotata [sic] Adkison 1988: 579.

Aporobopyrus trilobata [sic] Markham 1992: 3 (in table).—Espinosa-Pérez & Hendrickx 2001: 50.—Román-Contreras 2008: 94 (in table).

Aporobopyrus trilobatus: Markham 2008: 150–152.—Boyko et al. 2012: 7, 21–23 (in table).

Material examined.—1 adult female, 1 male (host: Petrolisthes crenulatus, CNCR 5078), Isla Ángel de la Guarda, Baja California, Mexico (29°15′36″N, 113°22′13″W), J.C. Nates and E. Lira coll.; 08 Nov 1985, CNCR 19411. 1 juvenile female, 1 male (host: P. ortmanni Nobili, 1901, CNCR 20073), Isla Cerralvo, Baja California Sur, Mexico (24°12′00″N, 109°50′53″W), J.C. Nates and E. Lira coll., 04 Aug 1986, CNCR 20074.

Distribution.—In the western Atlantic: Curaçao, Netherland Antilles (Nierstrasz & Brender à Brandis 1925, Bourdon 1976, Markham 1988); in the eastern Pacific: Gulf of California (present study), Zihuatanejo, Guerrero, Mexico (Bourdon 1976),

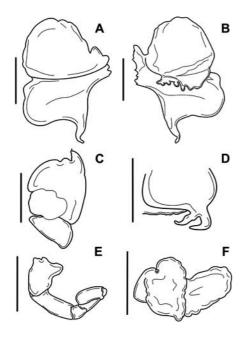


Fig. 8. Adult female of *Aporobopyrus trilobatus* (Nierstraz & Brender à Brandis, 1925). A, first oostegite, external view; B, same, internal view; C, maxilliped; D, barbula; E, pereopod 7; F, left first pleopod. Scale bar = 0.5 mm.

and Punta Arenas, Costa Rica (Markham 2008).

Remarks.—The heads of both females are wide, rounded and markedly convex, but only the adult female has a well-defined frontal lamina as well as two notches on the anterior margin of the head that gives it a trilobed shape (Fig. 2D). The antennules and antennae are composed of 3 and 6 segments each, respectively.

The pereomeres of the juvenile female are without coxal plates or dorsolateral bosses and have weakly-developed tergal projection on pereomeres 1 and 2. Pereomeres 2–4 are pigmented with a pair of tiny spots near each medial region. The adult female has narrow coxal plates and tergal projections on pereomeres 1–4 on both sides (Fig. 2D). The marsupium of the adult female is closed by well-developed oostegites, the second to fourth bearing tiny setae on their posterior margins, the fifth has a row of larger setae. The first pair

of oostegites of the adult female (Fig. 8A, B) agrees in shape with those previously described (Nierstrasz & Brender à Brandis 1925) and illustrated (Bourdon 1976: 168, Fig. 1B), and its internal ridge is slightly digitate (Fig. 8B). The juvenile female is without developed oostegites.

The maxillipeds (Fig. 8C), even those in the juvenile female, are small and not entirely developed, similar to previously published illustrations and descriptions (Bourdon 1976, Markham 1988). The barbula of the adult female has two slightly sinuate projections (Fig. 8D), similar to those illustrated by Markham (1988: 18, Fig. 7C), except that in our material the external projection is the largest and its medial margin differs from that reported by Bourdon (1976) as it is slightly sinuous. The barbula of the juvenile female has only a tiny bulge on its right corner and the medial margin is straight and smooth.

The pereopods of the juvenile female and those on the short side of the adult female each have a small basal carina, like a tiny bulge, but those on the long side of the adult female (Fig. 8E) are similar to those described by Bourdon (1976).

The pleopods of the adult female are oval-shaped (Fig. 8F), with a narrow basal section and their outlines are slightly digitate, similar to those illustrated by Markham (1988: 18, Fig. 7B), and decreasing in size posteriorly as shown by Bourdon (1976: 168, Fig. 1D–H). The exopod and endopod on the short side of the female are similar in size but those on the long side are with the exopod larger than the endopod. All pleopods of the juvenile female are similar in size, of tubular shape, with a distal region that becomes slightly wider and rounded.

The heads of both males are semicircular and narrower than percomere 1, with eyespots near the posterolateral border. The antennules and antennae are composed of 3 and 5 segments each, respectively; the antennae extend far beyond the margins of the head. All pereomeres are well separated laterally with rounded borders and narrower posteriorly (Fig. 3D). Pereomeres 2–5 of one male (CNCR 19411) are pigmented with tiny spots near their left borders; similar spots are located on the right border of pleomeres 2 and 5. Pleomeres 1 and 2 are the largest and are provided with stout and acute dactyli, pereomeres 3–7 decrease in size posteriorly, with their dactyli becoming shorter and blunter.

The pleon has five distinct pleomeres and a bilobed final pleomere, this structure in one male (CNCR 20074) has small setae on its posterior border. Each pleomere has a pair of tiny pleopods.

The differences observed in our specimens fall within the range of variation mentioned by Bourdon (1976), who noted some morphological variation between the specimens from Guerrero, Mexico, and those from Curaçao. *Petrolisthes crenulatus* is reported for the first time as host of *A. trilobatus* but *P. ortmanni* was already reported as host of a juvenile female from Punta Arenas, Costa Rica (Markham 2008). This report extends the geographical range of distribution of this bopyrid into the north of the eastern Pacific coast, now ranging from Costa Rica to the Gulf of California, Mexico.

## Discussion

Sixty-three crab species belonging to Porcellanidae are parasitized by pseudionines, of which 39 are hosts of bopyrids of the genus *Aporobopyrus* (Boyko et al. 2012), but only six host species have been documented from the Pacific coast of the Americas (see Markham 2008). Thus, the report of *Petrolisthes crenulatus*, *P. galapagensis* and *P. hirtispinosus* increase to 42 the known hosts for this group of branchial parasites, and to nine the number of hosts distributed along the Pacific coast of the continent. Boyko et al. (2012)

noted that approximately 11% of bopyrids occurring in porcellanid crabs parasitize more than one host species, but all four parasite species reported here have been reported in more than one host: A. bourdonis parasitizes two hosts, A. curtatus eight and A. muguensis and A. trilobatus four each (Boyko et al. 2012). Bopyrids increase their distribution ranges by infesting multiple hosts (Boyko & Williams 2009), for example A. curtatus occurs throughout the western Atlantic coast, from North Carolina, USA, to São Paulo, Brazil, and now is also reported for the first time in the eastern Pacific; while A. bourdonis occurs in a more restricted region since its two hosts have a similar distribution, from the Gulf of California, Mexico, to Ecuador (Villalobos et al. 1989, Hiller et al. 2004).

The extent of morphological variability in some *Aporobopyrus* species is unknown, as the number of records is limited to a few pairs of individuals for each species, which is the case for *A. bourdonis*. Even when bopyrids are reported in high numbers, no morphological notes are often given, as was the case for *A. muguensis* until Markham (2008) provided additional descriptive notes. In the present paper, we compare some morphological characters (Table 2) and provide a key of the species of *Aporobopyrus* infesting porcellanid crabs from the islands of the Gulf of California.

Key to females of the species of *Aporobopyrus* recorded in the Gulf of California, Mexico.

- 1b. Pereomeres 1–4 of both sides of body with coxal plates and tergal

Table 2.—Morphological characteristics of bopyrid females of the genus Aporobopyrus recorded in the Gulf of California, Mexico.

Trait	A. bourdonis	A. muguensis	A. curtatus	A. trilobatus
Head	Wider than long, broadly rounded anteriorly	Wide and curve anteriorly	Wider than long, broadly rounded anteriorly	Wide and rounded both anteriorly and posteriorly
Frontal lamina	Narrow and well defined	Undifferentiated with anterolateral borders	Narrow and well defined, ends into lateral projections	Narrow and well defined, sometimes with notches that
Barbula	l or 2 lateral projections, with or without margins digitated	l lateral projection	2 digitate lateral projections	2 lateral projections, with slightly sinuous margins
Pereomeres	Coxal plates and tergal projections in 1 to 4 of both body sides	Coxal plates and tergal projection perceptible in 1 to 4, mainly on the larger side of body.	Conspicuous dorsolateral bosses and narrow coxal plates in 1 to 4	Narrow coxal plates and tergal projection in 1 to 4 of both body sides, occasionally with dorsolateral bosses in 1 to 4
Inner ridge of first oostegite	Slightly sinuous, occasionally with digitate projections	Slightly thick, sometimes slightly ornamented	With digitate projections	Slightly digitate
Pleopods	Endopods oblongs and larger than exopods, which are ovoid	Both rami similar in size, first 2 pairs broad and leaf like shape, the following narrow and shorter	Endopods larger than exopods, of triangular shape and tuberculate	Endopods smaller than exopods, mainly in the long side of body, of oval shape with outlines faintly digitate

- projections but no dorsolateral bosses. *A. bourdonis* Markham, 2008
- 2a. Barbula with two lateral projections on each side, each one with sinuous or digitate margins ....... 3
- 3a. Pleopods triangular in shape and tuberculate, endopods larger than exopods .....
  - ..... A. curtatus (Richardson, 1904)
- 3b. Pleopods oval-shaped with outlines faintly digitate, endopods smaller than exopods ......

# Acknowledgements

The authors express their gratitude to "Programa de Becas Posdoctorales UN-AM" for the scholarship granted to the first author; to S. Guzmán-Gómez (Laboratorio de microscopía y fotografía de la biodiversidad, LANABIO/IB/UNAM) for her assistance in taking the photographs of figures 2 and 3; to J. L. Villalobos-Hiriart (Colección Nacional de Crustáceos/IB/ UNAM) for his support during the laboratory work; to E. G. Moreno-Juárez for his aid with Figure 1; to M. Martínez-Mayén (Unidad de Ecología/ICMyL/UN-AM) for the literature provided; and to the two anonymous reviewers for improving this manuscript with their comments and suggestions.

### Literature cited

- Adkison, D. L. 1988. Pseudione parviramus and Aporobopyrus collardi, two new species of Bopyridae (Isopoda: Epicaridea) from the Gulf of Mexico. Proceedings of the Biological Society of Washington 101:576–584.
- Austin, W. C. 1985. An annotated checklist of marine invertebrates of the cold temperate northeast Pacific. Khoyatan Marine Laboratory, British Columbia, 683 pp.
- Bate, C. S. 1865. Characters of new species of crustaceans discovered by J. K. Lord on the

- coast of Vancouver Island. Proceedings of the Zoological Society of London 1864:661–668.
- Behre, E. H. 1950. Annotated list of the fauna of the Grand Isle region, 1828–1946. Occasional papers of the marine laboratory. Louisiana State University 6:1–66.
- Bosc, L. A. G. 1801. Histoire naturelle des Crustacés, contenant leur description et leurs moeurs; avec figures dessinées d'après nature. Tome premier. Deterville, Paris, 258 Pp.
- Bourdon, R. 1976. Les bopyres des porcellanes. Bulletine du Muséum National d'Histoire Naturelle Zoologie 252 serie 3 (359):165–245.
- Bourdon, R. 1967. Sur trois nouveaux Bopyrides de Senegal. Bulletin de l'Institut Francaise d'Afrique Noire (A) 29:107–122.
- Boyko, C. B., N. L. Bruce, K. A. Hadfield, K. L. Merrin, Y. Ota, G. C. B. Poore, S. Taiti, M. Schotte, & G. D. F. Wilson (Eds.)(2008 onwards). World Marine, Freshwater and Terrestrial Isopod Crustaceans database. *Aporobopyrus* Nobili, 1906. Accessed through: World Register of Marine Species at: http://www.marinespecies.org/aphia.php?p=taxdetails&id=248444 on 2019-07-17.
- Boyko, C. B., & J. D. Williams. 2009. Crustacean parasites as phylogenetic indicators in decapod evolution. Pp. 197–220 *in* J. W. Martin, K. A. Crandall, & D. L. Felder, eds., Decapod Crustacean Phylogenetics (Crustacean Issues, 18), 1st edition. CRC Press, Boca Raton, 632
- Boyko, C. B., J. D. Williams, & J. C. Markham. 2012. Recent and fossil Isopoda Bopyridae parasitic on squat lobsters and porcelain crabs (Crustacea: Anomura: Chirostyloidea and Galatheoidea), with notes on nomenclature and biogeography. Zootaxa 3150:1–35.
- Boyko, C. B., J. D. Williams, & J. D. Shields. 2017.
  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. Zootaxa 4365(3):251–301.
- Brito-Mata, G. V., C. Boyko, J. D. Williams, C. Lira, & A. Figueredo. 2017. Sobre la presencia de *Aporobopyrus bonairensis* Markham, 1988 (Isopoda: Bopyridae) en *Pachycheles monilifer* (Dana, 1852) (Decapoda: Porcellanidae) de playa Cipara, península de Paria, Estado Sucre, Venezuela. Boletín del Instituto Oceanográfico de Venezuela Universidad de Oriente 56:115–122.
- Brusca, R. C., V. R. Coelho, & S. Taiti. 2007. Isopoda. Pp. 503–542 *in* J. T. Carlton, ed, The Light and Smith Manual: Intertidal Invertebrates from central California to Oregon, 4th

edition. University of California Press, Los Angeles and London, 1019 pp.

- Camp, D. K., N. H. Whiting, & R. E. Martin. 1977. Nearshore marine ecology at Hutchinson Island, Florida: 1971–1974. V. Arthropoda. Florida Department of Natural Resources, Marine Research Laboratory 25:1–63.
- Campos, E., & A. R. Campos. 1989. Epicarideos de Baja California: distribución y notas ecológicas de *Probopyrus pandalicola* (Packard, 1879) en el Pacífico oriental. Revista de Biología Tropical 37(1):29–36.
- Campos-González, E., & J. R. Campoy-Favela. 1987. Epicarideans from Baja California I. First record and bioecological notes on two Bopyridae and one Cryptoniscidae (Crustacea, Isopoda) for Mexico. Ciencias Marinas 13(3):39–48.
- Codreanu, R. 1967. Clasificarea evolutiva a bopirienilor, isopode parazite ale crustaceelor decapode si importanta lor biologica generala. Studii si Cercetari de Biologie Seria Zoologie 19(3):203–211.
- Coelho, P. A., & M. L. Koenig. 1972. A distribuiçao dos crustáceos pertenecentes ás orders Stomatopoda, Tanaidacea e Isopoda no norte e nordeste do Brasil. Trabalhos Oceanográficos da Universidade Federal de Pernambuco 13:245–259.
- Dana, J. D. 1852. Conspectus crustaceorum, &c.
   Conspectus of the Crustacea of the exploring expedition under Capt. C. Wilkes, U.S.N.
   Macroura. Proceedings of the Academy of Natural Sciences of Philadelphia 6:10–28
- Duarte, L. F. L., & E. H. Morgado. 1983. Crustáceos parasitos de invertebrados associados à esponja *Zigomicale parishii* (Bowerbank) e ao briozoario *Schizoporella unicornis* (Jhonston, 1847). Iheringia (Série Zoologia) 62:3–11.
- Espinosa-Pérez, M. C., & M. E. Hendrickx. 2001. Checklist of isopods (Crustacea: Peracarida: Isopoda) from the eastern tropical Pacific. Belgian Journal of Zoology 131(1):43–55.
- Faxon, W. 1893. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer "Albatross", during 1891, Lieut. Commander Z.L. Tanner, U.S.N., commanding. VI. Preliminary descriptions of new species of Crustacea. Bulletin of the Museum of Comparative Zoology at Harvard College 24:149–220.
- Gore, R. H. 1970. Pachycheles cristobalensis, sp. nov., with notes on the porcellanid crabs of the southwestern Caribbean. Bulletin of Marine Science 20(4):957–970.

Gore, R. H. 1974. On a small collection of percellanid crabs from the Caribbean Sea (Crustacea, Decapoda, Anomura). Bulletin of Marine Science 24:700-721.

- Haig, J. 1960. The Porcellanidae (Crustacea Anomura) of the eastern Pacific. Allan Hancock Pacific Expeditions 24:1–440.
- Haig, J. 1966. Campagne de la Calypso au large des côtes Atlantiques de l'Amérique du sud (1961– 1962). 2. Porcellanid crabs (Crustacea Anomura). Annales de l'Institut Oceanographique du Monaco (N. S.) 44:351–358.
- Haig, J. 1968. Eastern Pacific expeditions of the New York Zoological Society: porcellanid crabs (Crustacea, Anomura) from the west coast of tropical America. Zoologica 53(5):57–74.
- Haig, J., & D. P. Abbott. 1980. Macrura and Anomura: the ghost shrimps, hermit crabs, and allies. Pp. 577–593 in R. H., Morris, D. P. Abbott, & E. C. Haderlie, eds, Intertidal invertebrates of California. Stanford University Press, California, 928 pp.
- Hansen, H. J. 1897. Reports on the dredging operations off the west coast of Central America to the Galapagos Islands, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer Albatross during 1891, Lieut. Commander Z. L. Tanner, U.S. Navy, commanding. XXII. The Isopods. Bulletin Museum of Comparative Zoology Harvard College 31(5):95–129.
- Hart, J. F. L. 1982. Crabs and their relatives of British Columbia. British Columbia Provincial Museum Handbook 40. British Columbia Provincial Museum Victoria, British Columbia, 267 pp.
- Hesse, E. 1865. Recherches sur les Crustacés rares ou nouveaux des côtes de France. (complément du troisième article). Crustacés parasites vivant dans les Ascidies phallusiennes. Annales des Sciences Naturelles, Série Zoologie et Biologie Animale 3(5):221–242.
- Hiller, A., J. F. Lazarus, & B. Werding. 2004. New records and range extensions for porcellanid crabs in the eastern Pacific (Crustacea: Anomura: Porcellanidae). Pp. 127–138 in M. E. Hendrickx, ed., Contributions to the Study of East Pacific Crustaceans 3, 1st edition. Instituto de Ciencias del Mar y Limnología, UNAM, Mexico city, 245 pp.
- Holmes, S. J. 1900. Synopsis of California stalk-eyed Crustacea. Occasional Papers of the California Academy of Sciences 7:1–262.
- Jay, C. V. 1989. Prevalence, size and fecundity of the parasitic isopod *Argeia pugettensis* on its host shrimp *Crangon franciscorum*. American Midland Naturalist 121:68–77.

- Kossmann, R. 1881. Studien über Bopyriden. Zeitschrift für Wissenschaftliche Zoologie 35:652–680.
- Kuris, A. M., P. S. Sadeghian, J. T. Carlton, & E. Campos. 2007. Decapoda. Pp. 632–656 in J. T. Carlton, ed, The Light and Smith Manual: intertidal Invertebrates from central California to Oregon, 4th edition. University of California Press, Los Angeles and London, 1019 pp.
- Latreille, P. A. 1825. Familles naturelles du règne animal, exposé succinctement et dans un ordre analytique avec l'indication de leurs genres. J. B. Baillière, Paris, 570 pp.
- Leach, W. E. 1820. Galatéadées, Galateadæ. (Crust.). Pp. 49-56 in F. Cuvier, ed., Dictionnaire des Sciences Naturelles, dans lequel on trait Méthodiquement des Différens étres de la Nature, considérés soit en eux-mêmes, d'après l'état actuel de nos connoissances, soit relativement a l'utilité qu'en peuvent retirer la Médecine, l'Agriculture, le Commerce et les Arts. Suivi d'une biographie des plus Célèbres Naturalistes. Ouvrage destiné aux médecins, aux agriculteurs, aux commerçans, aux artistes, aux manufacturiers, et à tous ceux qui ont intérêt à connoître les productions de la nature, leurs caractères génériques et spécifi ques, leur lieu natal, leurs propiétés et leurs usages, vol. 18. Levrault et Le Normant, Strasbourg et Paris.
- Lee, W. L., & M. A. Miller. 1980. Isopoda and Tanaidacea: the isopods and allies. Pp. 536– 558 *in* R. H., Morris, D. P. Abbott, & E. C. Haderlie, eds, Intertidal invertebrates of California. Stanford University Press, California, 928 pp.
- Lemos de Castro, A. 1965. Crustáceos isópodos epicarídeos do Brasil. III. Genero *Bopyrella* Bonnier (Isopoda, Bopyridae). Anais da Academia Brasileira de Ciéncias 37:283–288.
- Lemos de Castro, A., & I. M. Brasil Lima. 1980. Crustáceos isópodes epicarídeos do Brasil. XIII. Variações intraespecíficas, distribuição geográfica e hospedeiros de *Aporobopyrus* curtatus (Richardson). Boletim do Museu Nacional Nova Série Zoologia 296:1–8.
- Lockington, W. N. 1878. Remarks upon the Porcellanidea of the West Coast of North America. Annals and Magazine of Natural History 5(2):394–406.
- Markham, J. C. 1975. Bopyrid isopods infesting porcellanid crabs in the northwestern Atlantic. Crustaceana 28:257–270.
- Markham, J. C. 1978. A new genus and species of bopyrid isopod parasitic on the western Atlantic porcellanid *Pachycheles ackelianus*A. Milne Edwards. Proceedings of the Biological Society of Washington 91:483–489.

- Markham, J. C. 1988. Descriptions and revisions of some species of Isopoda Bopyridae of the northwestern Atlantic Ocean. Zoologische Verhandelingen 246:1–63.
- Markham, J. C. 1992. The Isopoda Bopyridae of the eastern Pacific, missing or just hiding? Proceedings of the San Diego Society of Natural History 17:1–4.
- Markham, J. C. 2008. New records of pseudionine bopyrid isopods, including two new species and one new genus, infesting porcellanid crabs (Decapoda: Anomura) on the Pacific coast of North and Central America. Bulletin of the Southern California Academy of Sciences 107(3):145–157.
- Markham, J. C., & F. E. Donath-Hernández. 1990. Crustacea of Sian Ka'an, including orders Nectiopoda, Stomatopoda, Thermosbaena, Myscidacea, Cumacea, Tanaidacea, Isopoda and Decapoda. Pp. 239–255 in L. D. Navarro & J. G. Robinson, eds, Diversidad boológica de la Reserva de la Biosfera de Sian Ka'an, Quintana Roo, México. Centro de Investigaciones de Quintana Roo Press, Quintana Roo, 374 pp.
- Menzies, R. J., & D. Frankenberg. 1966. Handbook on the common marine isopod Crustacea of Georgia. Athens, University of Georgia Press, Georgia, 93 pp.
- Menzies, R. J., & P. W. Glynn. 1968. The common marine isopod Crustacea of Puerto Rico: a handbook for marine biologists. Studies on the fauna of Curaçao and other Caribbean Islands 27(104):1–133.
- Miller, M. A. 1975. Phylum Arthropoda: Crustacea, Tanaidacea and Isopoda. Pp. 277–312. *in* R. I. Smith, & J. T. Carlton, eds, Light's manual: intertidal invertebrates of the central California coast. University of California Press, Berkeley and Los Angeles, 716 pp.
- Monod, T. 1933. Tanaidacea et Isopoda. Mission Robert-Ph. Dollfus en Égypt. Mémoires de l'Institute d'Égypt 21:161–264.
- Nierstrasz, H. F., & G. A. Brender à Brandis. 1923. Die Isopoden der Siboga-Expedition. II. Isopoda Genuina. I. Epicaridea. Siboga Expeditie Monographie 32:57–121.
- Nierstrasz, H. F., & G. A. Brender à Brandis. 1925. Bijdragen tot de kennis der fauna van Curaçao. Resultaten eener reis van Dr. C. J. van der Horst in 1920. Epicaridea. Bijdragen tot de Dierkunde 24:1–8.
- Nierstrasz, H. F., & G. A. Brender à Brandis. 1929. Papers from Dr. Th. Mortensen's Pacific Expedition 1914-16. 48. Epicaridea I. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kbenhavn 87:1–44.
- Nierstrasz, H. F., & G. A. Brender à Brandis. 1931. Papers from Dr. Th. Mortensen's Pacific

Expedition 1914-16. 57. Epicaridea II. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjbenhavn 91:147–225.

- Nobili, G. 1901. Viaggio del Dr. Enico Festa nella Repubblica dell'Ecuador e regioni vicine. Decapodi e Stomatopodi. Bolletino dei Musei di Zoologia ed Anatomia comparata della R. Università di Torino 415(16):1–58.
- Nobili, G. 1906. Nuovi Bopiridi. Atti della Reale Accademia della Scienze di Torino 41(11):1098-1113.
- O'Brien, J., & P. Van Wyk. 1985. Effects of crustacean parasitic castrators (epicaridean isopods and rhizocephalan barnacles) on growth of crustacean hosts. Pp. 191–281 *in* A. M., Wenner, ed., Crustacean Issues 3: factors in adult growth. Balkema, Rotterdam, 362 pp.
- Oliveira, E., & S. Masunari. 1998. Population relationships between the parasite *Aporobopyrus curtatus* (Richardson, 1904) (Isopoda: Bopyridae) and one of its porcelain crab host *Petrolisthes armatus* (Gibbes, 1850) (Decapoda: Porcelanidae) from Farol Island, southern Brazil. Journal of Natural History 32(10–11):1707–1717.
- Pearse, A. S. 1932. New bopyrid isopod crustaceans from Dry Tortugas, Florida. Proceedings of the United States National Museum 81(1):1–6.
- Rafinesque, C. S. 1815. Analyse de la nature ou Tableau de l'univers et des corps organisés. Self-published, Palermo, 224 pp.
- Raibaut, A., & J. P. Trilles. 1993. The sexuality of parasitic crustaceans. Advances in Parasitology 32:367–455.
- Richardson, H. 1904. Contributions to the natural history of the Isopoda. Proceedings of the United States National Museum 27(1305):1–89.
- Richardson, H. 1905. A monograph on the isopods of North America. Bulletin of the United States National Museum 54:1–727.
- Richardson, H. 1910. Marine isopods collected in the Philippines by the U.S. Fisheries steamer Albatross in 1907–8. Bureau of Fisheries Document 736:1–44.
- Román-Contreras, R. 2008. Estudios y registros de isópodos epicarideos de México: 1897–2005. Pp. 81–114 in F. Álvarez & G. A. Rodríguez-Almaraz, eds., Crustáceos de México: estado actual de su conocimiento, 1st edition. Dirección de Publicaciones, Universidad Autónoma de Nuevo León, Monterrey, 522 pp.
- Romero-Rodríguez, J., & M. Martínez-Mayén. 2018. Rediscovery of the bopyrid isopod *Parabopyrella thomasi* (Nierstrasz & Brender à Brandis, 1929), parasite of the arrow shrimp

- *Tozeuma carolinense* Kingsley, 1878 (Decapoda, Caridea) in the caribbean region. Crustaceana 91(10):1183–1194.
- Salazar-Vallejo, S. I., & A. Leija-Tristán. 1990. Progebiophilus bruscai n. sp., a new bopyrid isopod parasitic on the mud shrimp, Upogebia dawsoni Williams (Thalassinoidea), from the Gulf of California. Cahiers de Biologie Marine 30(4):423–432 [although usually considered as published in 1989, the issue in which this paper appeared is marked as "dépot légal 1er trimestre 1990" in printed copies].
- Sassaman, C. 1985. Cabirops montereyensis, a new species of hyperparasitic isopod from Monterey Bay, California (Epicaridea: Cabiropsidae). Proceedings of the Biological Society of Washington 98(4):778–789.
- Sassaman, C. 1992. Description of the mature female and epicaridium larva of *Cabirops monter-eyensis* Sassaman from southern California (Crustacea: Isopoda: Cabiropidae). Proceedings of the Biological Society of Washington 105(3):575–584.
- Sassaman, C., G. A. Schultz, & R. Garthwaite. 1984. Host, synonymy, and parasitic incidence of Bopyrella calmani (Richardson) from central California (Isopoda: Epicaridea: Bopyridae). Proceedings of the Biological Society of Washington 97:645–654.
- Saussure, H. de. 1853. Description de quelques crustacés nouveaux de la côte occidentale du Mexique. Revue et Magasin de Zoologie Pure et Appliquée 2(5):354–368.
- Schmitt, W. L. 1921. The marine decapod Crustacea of California with special reference to the decapod Crustacea collected by the Unites States Bureau of Fisheries steamer "Albatross" in connection with the biological survey of San Francisco Bay during the years 1912–1913. University of California Press, Berkeley, California, 470 pp.
- Schultz, G. A. 1969. The marine isopod crustaceans. Wm. C. Brown Company Publishers, Iowa, 359 pp.
- Shiino, S. M. 1933. Bopyrids from Tanabe Bay. Memoirs of the College of Science Kyoto Imperial University 8(3):249–300.
- Shiino, S. M. 1934. Bopyrids from Tanabe Bay II.

  Memoirs of the College of Science Kyoto
  University 9(4):257–287.
- Shiino, S. M. 1952. Phylogeny of the family Bopyridae. Annual Report of the Prefectural University of Mie 1(1):33–56.
- Shiino, S. M. 1958. Note on the bopyrid fauna of Japan. Faculty of Fisheries Prefectural University of Mie 3(1):27–73.

- Shiino, S. M. 1964. On three bopyrid isopods from California. Report of Faculty of Fisheries Prefectural University of Mie 5(1):19–25.
- Stimpson, W. 1859. Notes on North American Crustacea, no. 1. Annals of the Lyceum of Natural History of New York. 7(11):49–93.
- Van Name, W. G. 1920. Isopods collected by the American Museum Congo Expedition. Bulletin of the American Museum of Natural History 43:42–108.
- Van Wyk, P. M. 1982. Inhibition of the growth and reproduction of the porcellanid crab *Pachycheles rudis* by the bopyrid isopod, *Aporobopy-rus mugensis*. Parasitology 85:459–473.
- Villalobos, J. L., & F. Álvarez. 2002. Distribution of intertidal non-brachyuran decapods from the Gulf of California islands and its biogeographical implications. Pp. 241–252 in E. Escobar-Briones & F. Álvarez, eds., Modern Approaches to the Study of Crustacea, 1st edition. Kluwer Academic/ Plenum Publishers, Amsterdam, 355 pp.
- Villalobos, J. L., A. Cantú, M. D. Valle, P. Flores, E. Lira, & J. C. Nates. 1992. Distribución espacial y consideraciones zoogeográficas de los crustáceos decápodos intermareales de las islas del Golfo de California, México. Proceedings of the San Diego Society of Natural History 11:1–13.
- Villalobos, J. L., J. C. Nates, A. Cantú, M. D. Valle, P. Flores, E. Lira, & V. P. Schmidtsdorf.

- 1989. Listados Faunísticos de México. I. Crustáceos estomatópodos y decápodos intermareales de las islas del Golfo de California, México. Instituto de Biología, Universidad Nacional Autónoma de México, México D.F., 114 pp.
- Wägele, J. W. 1989. Evolution und phylogenetisches System der Isopoda. Zoologica 140:1–262.
- Wallerstein, B. R. 1980. Isopoda. Pp. 230–236. in D., Straughan, & R. W. Klink, eds, A taxonomic listing of common marine invertebrate species from southern California. Technical Reports of the Allan Hancock Foundation 3, California, 281 pp.
- Williams, A. B. 1986. Mud shrimps, *Upogebia*, from the eastern Pacific (Thalassinidea: Upogebiidae). San Diego Society of Natural History, Memoir, 14:1–60.
- Williams, J. D., & C. B. Boyko. 2012. The global diversity of parasitic isopods associated with crustacean hosts (Isopoda: Bopyroidea and Cryptoniscoidea). PLoS ONE 7(4):e35350.
- Williams, J. D., & A. Z. Madad. 2010. A new species and record of branchial parasitic isopods (Crustacea: Isopoda: Bopyridae: Pseudioninae) of porcellanid crabs from the Philippines. Experimental Parasitology 125(1):23–29.

Associate Editor: Christopher B. Boyko