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Parasitic bopyrid isopods of hermit crabs (Anomura, Paguridae) from the Atlantic coast of Mexico, with notes on their reproduction and distribution

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Abstract. Six species of bopyrids were detected from the examination of hermit crabs collected along the Atlantic coasts of Mexico and deposited in the Colección Nacional de Crustáceos housed at the Universidad Nacional Autónoma de México. *Asymmetrione tuxtlaensis* sp. nov., the third species of the genus from the west Atlantic, is described. The occurrence of *Asymmetrione desultor*, *Pseudostegias atlantica* and *Stegias clibanarii* are recorded for the first time from the Mexican Atlantic coasts and the distribution range of the last two species is extended. Both a new host and three new localities for Mexico are reported for *Anathelges hyptius* and *Bopyrissa wolffi*, respectively. Distribution and reproductive data are provided for all six species examined. A key to genera and species of bopyrid isopods that parasitize hermit crabs in the Mexican Atlantic is provided.

Keywords. Epicaridea, ectoparasite, embryo size, fecundity, host-parasite association.

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Introduction

The superfamily Paguroidea contains more than 800 described species of hermit crabs, nearly all of which are marine (McLaughlin 2003). They are best known from intertidal areas where they can be scavengers or predators being important ecologically as allogenic engineers, i.e., those engineers that transform living or non-living material from one physical state to another (Williams & McDermott 2004). Hermit crabs, with a non-calcified abdomen, obtain protection from predation by inhabiting empty gastropod shells, promoting the association with a wide variety of symbionts, including strict parasites, of which bopyrid isopods make up a substantial proportion (McDermott *et al*. 2010; Williams *et al*. 2019).

Bopyrid isopods are obligate parasites of other crustaceans since they need two different groups of crustacean hosts to complete their life-cycle: typically, decapods act as definitive hosts and copepods as intermediate hosts (Cericola & Williams 2015). Bopyrids can negatively impact the host biology and ecology by causing metabolic, behavioral, physiological and reproductive alterations (Román-Contreras 2008).

Their females are large, with distorted bodies, so much so that in some species they are barely recognizable as isopods, whereas males are small and similar to free-living isopods (see Román-Contreras 2008). The region from North Carolina, USA, through the Gulf of Mexico to the Caribbean has the third greatest number of recorded bopyrid species (79) after the northwest Pacific (123 species) and the East Asia Sea (116 species) (Williams & Boyko 2012). Despite this high diversity, the natural history of many of these species is poorly known and many undescribed species remain (Williams *et al*. 2011). Worldwide, McDermott *et al*. (2010) recorded 83 species of bopyrids infesting hermit crabs, although by now this number has increased to 95 (see Boyko & Williams 2010; Markham 2010; An *et al*. 2013, 2016; Williams & Boyko 2016; Williams *et al*. 2019). Felder *et al*. (2009) recognized 191 species of anomurans inhabiting along the Gulf of Mexico coasts, distributed into three superfamilies: Galatheoidea (89 species), Paguroidea (91 species) and Hippoidea (11 species). However, only two species belonging to Paguroidea have been recorded as hosts of bopyrids from the Mexican coasts of the Gulf of Mexico and the Caribbean hitherto (see Román-Contreras 2008). A recent examination of hermit crab samples from the Atlantic coasts of Mexico deposited in the Colección Nacional de Crustáceos (CNCR), housed at the Instituto de Biología of the Universidad Nacional Autónoma de México (UNAM), revealed specimens bearing bopyrids. The present study reports the results of that examination including the description of a new species, and new distributional and reproductive data on these parasitic isopods.

Material and methods

The abdomen and cephalothorax of 3831 hermit crabs deposited in the CNCR belonging to the families Diogenidae (n = 3529) and Paguridae (n = 302) were examined for bopyrid isopods. Sixty-three individuals were parasitized by bopyrids; their size, considered as shield length (SL), and sex were recorded. The parasites were removed from the hosts in order to recognize their specific identities and to record their total length (TL), following Romero-Rodríguez & Álvarez (2020). The total length of asymmetric females was measured from the anterior margin of the second or third thoracic somite of the longer side to the posterior margin of the pleon. Fecundity was estimated for all the ovigerous females by direct counting of eggs, in both hosts and parasites. Bopyrid embryos were classified as egg, embryo I, embryo II and epicaridium larvae following to Romero-Rodríguez & Álvarez (2020). For each bopyrid species, prevalence was considered as the total number of hermit crabs divided by the number of parasitized individuals, expressed as percentage. For each brood pouch, the width (d^1) and length (d^2) of 10 embryos were measured, and their volume (V) was calculated using the formula $V = \pi(d^1)^2 \times (d^2)/6$ (Romero-Rodríguez & Román-Contreras 2013; Cericola & Williams 2015). The measurements were made to the nearest 0.1 mm using an ocular micrometre attached to a compound microscope. Drawing sketches made with a camera lucida were used to construct the figures using Adobe Illustrator. References are not provided for host species.

Results

Taxonomy

Suborder Cymothoida Wägele, 1989
Family Bopyridae Rafinesque, 1815
Subfamily Athelginae Codreanu & Codreanu, 1956
Genus *Anathelges* Bonnier, 1900

Anathelges hyptius (Thompson, 1902)
Figs 1, 2A, 3, Table 1

Stegophryxus hyptius Thompson, 1902: 53–56, pls. 9–10.

Stegophryxus hyptius – Richardson 1904: 59; 1905: 532–535, 537, figs 578, 579. — Rathbun 1905: 48. — Sumner *et al*. 1913a: 136; 1913b: 661. — Kunkel 1918: 236. — Reinhard *et al*. 1947: 70–72. — Reinhard 1949: 17, 18, 20, 21, 27, 29, 30; 1956: 101. — Caullery 1950: 97. — Reinhard & Buckeridge 1950: 131. — Caullery 1952: 76. — Reverberi 1952: 292. — von Brand 1952: 256, 271, table 41; 1966: 222, table 38. — Szidat 1959: 504. — Florkin 1960: 405. — Danforth 1963: 11, 20. — Bowman 1964: 105, 107–109, pl. 14, fig. 22. — Noble & Noble 1964: 392–393, figs XVI-5a, 5b, 5c. — Smith 1964: 105. — Oguro 1967: 67 (in table 3). — Bourdon 1968: 133. — Schultz 1969: 322, fig. 513. — Kaestner 1970: 463. — Gosner 1971: 476. — Markham 1972: 73; 1974: 33, 35, 38, 40, figs 1–3; 1978: 102, 111, 114, 116, table 1; 1988: 3, 45–46, 57, table 1; 2003: 73–74. — Adkison & Heard 1978: 408. — García-Gómez 1983: 22, 37. — Overstreet 1983: 225. — Adams *et al*. 1987: 127. — Greenwood & Adams 1987: 106. — Anderson 1990: 290. — Korpelainen 1990: 165. — McDermott 1998: 1042–1044; 2001: 629, 634–635; 2002: 39. — Boyko & Williams 2003: 796, 797, 798. — Meconcelli *et al*. 2015: 43.
Stegophrixus hyptius – Nierstrasz & Brender à Brandis 1931: 197–198.
Stegophryxus hyptias (sic) – Miner 1950: 450, 453, pl. 145.
Stegophryxus sp. – Baffoni 1953: 447. — Reinhard 1956: 93. — Kaestner 1967: 1161; 1970: 425, 463.
?"Male bopyrid isopod" – Lemaitre *et al*. 1982: 697, fig. 7C.
Anathelges hyptius – Boyko & Williams 2003: 798–800, figs 2–3; 2004: 361, 369; 2009: 203. — Román-Contreras & Martínez-Mayén 2011: 1145–1147, 1150. — Romero-Rodríguez & Román-Contreras 2013: 646 (in table 3). — Cericola & Williams 2015: 238 (in table 1). — Ewers-Saucedo 2019: 225. — Romero-Rodríguez & Álvarez 2020: 226 (in table 1). — Aguilar-Perera 2022: 115 (in table 1).
Anathelges hyptuis (sic) – Schotte *et al*. 2009: 981.
Anathelges cf. *hyptius* – Diaz & Roccatagliata 2006: 331–340, figs 1–6. — Pardo *et al*. 2009: 2041–2042, 2052–2053, table 1.

Material examined
MEXICO • 1 ovigerous ♀ (2.45 mm TL), 1 ♂ (1.64 mm TL); Campeche, Laguna de Términos, Estero Pargo; 18º38′05.64″ N, 91º46′16.39″ W; 6 Jun. 1981; V. Solís *et al*. leg.; host ♀ of *Pagurus maclaughlinae* García-Gómez, 1982 (2.50 mm SL); J. Romero det. host; CNCR-36504 • 1 ovigerous ♀ (3.80 mm TL), 1 ♂ (1.98 mm TL); same locality as for preceding; 14 Nov. 1984; same collector; same host data as for preceding (2.97 mm SL); CNCR-36507 • 1 ovigerous ♀ (3.00 mm TL), 1 ♂ (1.31 mm TL), same locality as for preceding; 20 May 1987; same collector; host ♂ of same species as for preceding (2.25 mm SL); CNCR-36524-A • 1 ovigerous ♀ (3.70 mm TL), 1 ♂ (1.53 mm TL); same collection data as for preceding; same host data as for preceding (3.60 mm SL); CNCR-36524-B • 19 ovigerous ♀♀ (3.88 ± 0.62 mm TL), 19 ♂♂ (1.89 ± 0.28 mm TL), 2 cryptoniscus larvae (0.63 ± 0.07 mm LT); same locality; 8 Dec. 1987; same collector; host 10 ♀♀, 9 ♂♂ of same species as for preceding (3.47 ± 0.65 mm SL); CNCR-36525 • 1 ovigerous ♀ (3.17 mm TL), 1 ♂ (1.78 mm TL); Campeche, Laguna de Términos, La Bayoneta; 18°46′42.0″ N, 91°29′14.7″ W; 3 Oct. 1981; same collector; host ♀ of same species as for preceding (3.17 mm SL); J. Romero det. hosts; CNCR-36505-A • 1 cryptoniscus larva (0.56 mm TL); same locality; same host data as for preceding (3.17 mm SL); CNCR-36505-B • 1 ♀ (4.25 mm TL), 1 ♂ (2.00 mm TL); same locality; 3 Nov. 1981; same collector; detached from host; CNCR-36527 • 1 ovigerous ♀ (2.13 mm TL), 1 ♂ (1.31 mm TL); Campeche, Laguna de Términos, Punta Zasnath; 18º46′20.77″ N, 91º19′39.16″ W; 1 Aug. 1984; same collector; host ♀ of same species as for preceding (2.40 mm SL); CNCR-36506-A • 1 ovigerous ♀ (2.00 mm TL), 1 ♂ (1.30 mm TL); same locality; same host data as for preceding (2.03 mm SL); CNCR-36506-B • 1 ovigerous ♀ (4.00 mm TL), 1 ♂ (1.96 mm

Table 1. Some reproductive traits of the bopyrid isopods that parasitize hermit crabs at SW Atlantic coasts of Mexico.

Species	TL female (mm)	Fecundity (embryos)	Stage of development	Average sizes (± standard deviation)		
				Length (mm)	Width (mm)	Volume (mm^3)
Anathelges hyptius	2.13 – 4.00	480 – 2615	Egg	0.128 ± 0.010	0.116 ± 0.009	0.0009 ± 0.0002
	3.60 – 4.65	1566 – 2516	I	0.146 ± 0.010	0.117 ± 0.013	0.0011 ± 0.0003
	3.00 – 5.53	1092 – 4572	epicaridium	0.172 ± 0.014	0.123 ± 0.012	–
Asymmetrione desultor	4.90	741	I	0.231 ± 0.017	0.200 ± 0.009	0.0049 ± 0.0006
Asymmetrione tuxtlaensis sp. nov.	1.69 – 4.85	110 – 606	Egg	0.146 ± 0.016	0.167 ± 0.11	0.0019 ± 0.0005
	3.20	762	I	0.162 ± 0.16	0.193 ± 0.015	0.0027 ± 0.0007
	2.93 – 3.07	293 – 811	epicaridium	0.115 ± 0.15	0.253 ± 0.014	–
Bopyrissa wolffi	3.32 – 4.95	1601 – 4507	Egg	0.127 ± 0.009	0.118 ± 0.0012	0.0009 ± 0.0002
	4.90 – 4.50	3917	I	0.158 ± 0.010	0.140 ± 0.10	0.0016 ± 0.0003
	2.18 – 4.10	1305 – 1543	epicaridium	0.180 ± 0.009	0.126 ± 0.008	–
Pseudostegias atlantica	3.92	177	Egg	0.214 ± 0.010	0.200 ± 0.011	0.0045 ± 0.0007
	3.30 – 4.00	205 – 267	I	0.192 ± 0.015	0.163 ± 0.017	0.0027 ± 0.0007
Stegias clibanarii	3.80	1892	Egg	0.137 ± 0.009	0.131 ± 0.009	0.0012 ± 0.0002

TL); Campeche, Laguna de Términos, Isla Pájaros; 18º38′08.22″ N, 91º41′45.72″ W; 10 Mar. 1981; same collector; same host data as for preceding (3.33 mm SL); CNCR-36526 • 1 ♀ (3.40 mm TL), 1 ♂ (1.55 mm TL); Campeche, Laguna de Términos, Punta Gorda; 18º43′18.34″ N, 91º33′50.17″ W; 14 Nov. 1984; same collector; detached from host; CNCR-36528.

Distribution

Anathelges hyptius has one of the largest geographical ranges for any bopyrid species in the western Atlantic (Fig. 1), from Massachusetts, USA, to Curaçao and the Bahamas (Boyko & Williams 2004), which may be related to the eight species of pagurids used as hosts throughout its range (Markham 1978; Boyko & Williams 2004): *Iridopagurus caribbensis* (A. Milne-Edwards & Bouvier, 1893; *I. margaritensis* García-Gómez, 1983; *Pagurus annulipes* (Stimpson, 1860); *P. brevidactylus* (Stimpson, 1859); *P. longicarpus* Say, 1817; *P. maclaughlinae*; *P. provenzanoi* Forest & de Saint Laurent, 1968 and *P. stimpsoni* (A. Milne-Edwards & Bouvier, 1893). It has been suggested that its geographical distribution extends to Argentina and Chile parasitizing two more hosts (Diaz & Roccatagliata 2006; Pardo *et al*. 2009): *P. comptus* (White, 1847) and *P. villosus* Nicolet in Gay, 1849, respectively.

In Mexico it has only been recorded in Laguna de Términos parasitizing a single female of *P. longicarpus* (Román-Contreras & Martínez-Mayén 2011), so this record does not represent a new locality for this bopyrid but *P. mclaughlinae* is recorded as new host in the area.

Remarks

Our material (Figs 2A, 3A, F) conforms well with the characters proposed for *A. hyptius* by Thompson (1902), but some variations were observed. The barbula of adult females consists of a single slightly acute and curved projection on each side and two foliaceus plates in the medial margin (Fig. 3B). The barbula of this species was described with three curved processes on each side but only two lateral projections were illustrated (Thompson 1902: plate 9, fig. 7). However, the observed specimens agree

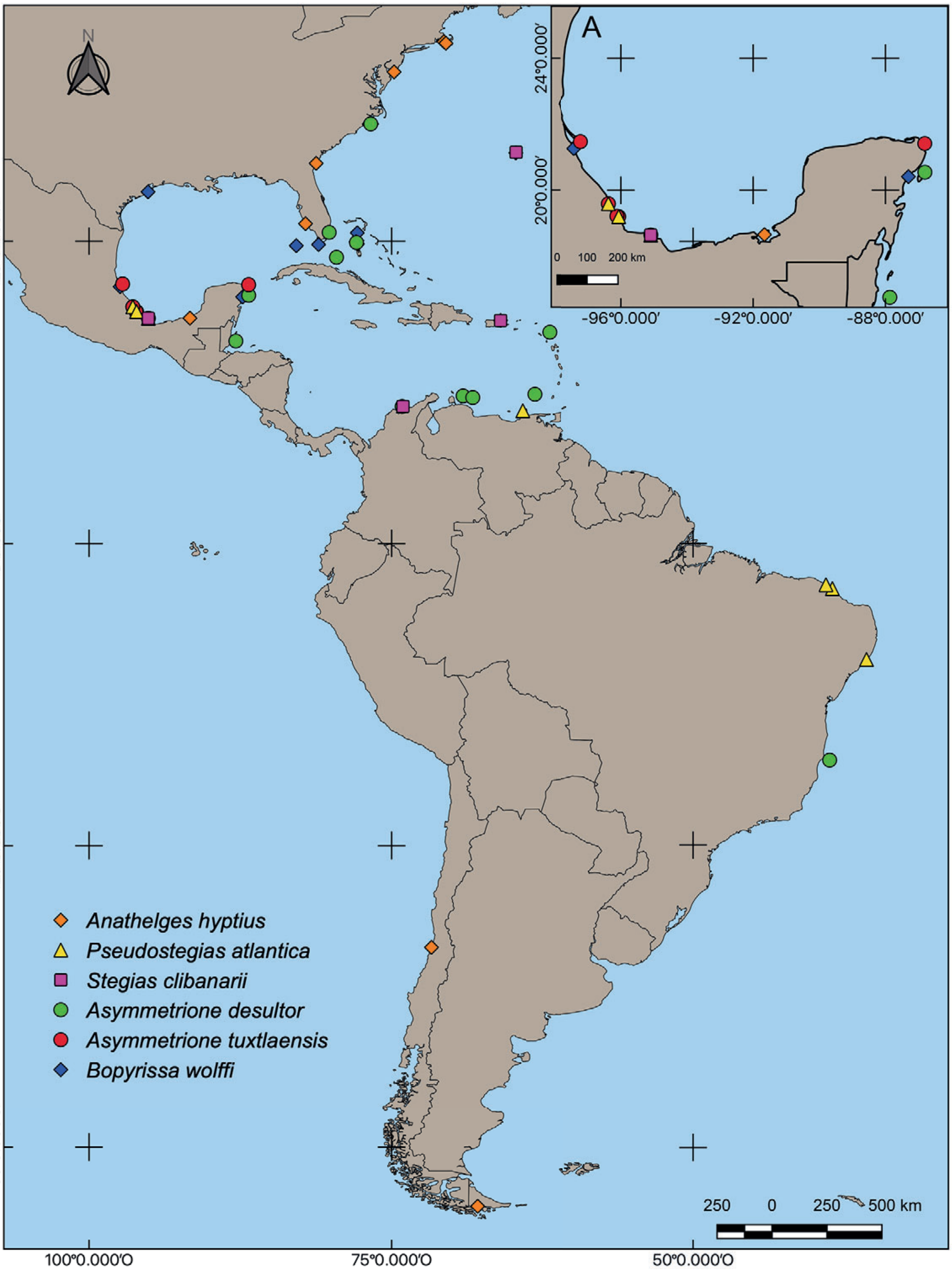

Fig. 1. Distribution along the American continent of five bopyrid species that parasite hermit crabs recorded in the Mexican Atlantic. **A**. Detail of the Atlantic coast of Mexico.

with the subsequent illustrations and description of the barbula provided by Markham (1974: fig. 1d) and Diaz & Roccatagliata (2006: fig. 4b).

Overall, the first pair of oostegites of the adult females examined (Fig. 3C–D) are similar to those described by Thompson (1902), although this author did not define the internal ridge. Markham (1974: fig. 1e) illustrated it smooth and almost straight, contrasting with the inner ridge thickened in the middle portion and bearing one small digitation proximally recorded in our adult females (Fig. 3D), which coincides with what Diaz & Roccatagliata (2006: fig. 5g) reported for an adult female of *A.* cf. *hyptius* parasitizing the abdomen of *P. comptus* in Argentina. Likewise, an ovigerous female (36525-Q) had no uropods thus the last segment of pleon had a round appearance. The maxilliped was similar to that noted by Thompson (1902: pl. 9, fig. 5) but the anterior segment was somewhat rectangular in outline when the external lateral margin, that tends to bend inwards, is extended; the surface of both anterior and posterior segments has a rough appearance (Fig. 3E).

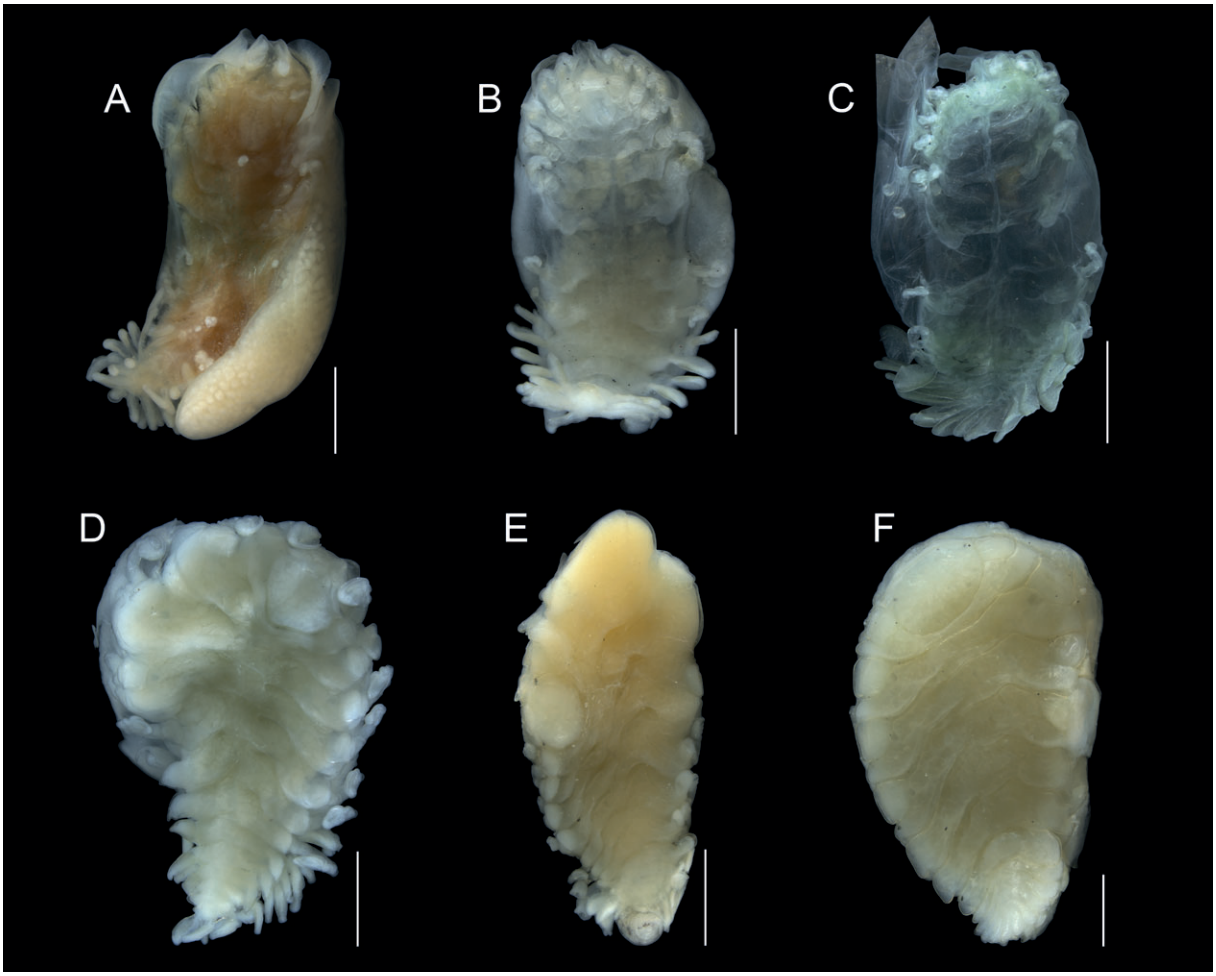

Fig. 2. Dorsal view of ovigerous females of bopyrid isopods that parasites hermit crabs in Atlantic Mexican coasts. **A**. *Anathelges hyptius* (Thompson, 1902) (CNCR-36525-C). **B**. *Pseudostegias atlantica* Lemos de Castro, 1965 (CNCR-36483). **C**. *Stegias clibanarii* Richardson, 1904, stained with methylene blue (CNCR-36487). **D**. *Asymmetrione desultor* Markham, 1975 (CNCR-36488). **E**. *Asymmetrione tuxtlaensis* sp. nov., with male ventrally attached to pleon (CNCR-36495). **F**. *Bopyrissa wolffi* Markham, 1978 (CNCR-36502-A). Scale bars: A–E = 1.0 mm; F = 0.5 mm.

Reproduction

Sizes of the two adult females without embryos in the marsupium were 3.40 and 4.25 mm TL, both paired with a male but detached from the host. Average TL of the ovigerous females (n = 23) was 3.65 ± 0.73 mm and ranged from 2.13 to 5.53 mm TL (Table 1), which are smaller than the range of females carrying embryos (5.98–6.56 mm long) reported by McDermott (1998); however, the overall average fecundity calculated (1906.67 ± 1021.51 embryos) is close to the average number of embryos (2462.33 ± 1,181, calculated from original data) reported by McDermott (1998). The lowest (480 embryos) and highest (4572 embryos) fecundities were recorded from the ovigerous females with the minimum and maximum TL, respectively. The latter could be explained by the significant ($\tau_{16} = 5.74$, $p < 0.05$) and positive ($r = 0.67$) relationship calculated between fecundity and the size of the ovigerous females: fecundity = 1808 + 1031.10 (TL). The highest number of embryos recorded (Table 1) was higher than the maximum fecundity (3437 embryos) reported by McDermott (1998) in a 6.56 mm female.

The average length and width of embryos of *A. hyptius* by stage of development and epicaridium larvae are shown in Table 1. Sizes of embryos in egg stage ranged from 0.11 to 0.15 mm of length and between 0.09 and 0.13 mm of width, whilst the length of embryos in stage I varied from 0.13 to 0.16 mm and their width was between 0.09 and 0.15 mm. These sizes are smaller than those reported by McDermott (1998) for embryos in an early stage (0.172 ± 0 mm long and 0.144 ± 0.4 mm wide), this difference may be due to the low number of embryos examined by the latter author (n = 10). Volumes of embryos in egg stage ranged from 0.0005 to 0.0013 mm^3, and for embryos in stage I varied between 0.0006 and 0.0019 mm^3. The average volume of both stages of development (Table 1) is similar to those reported for other bopyrids of comparable sizes (see Romero-Rodríguez & Álvarez 2020). The epicaridium larvae length ranged from 0.15 to 0.20 mm and the width between 0.09 and 0.15 mm.

The three cryptoniscus larvae recorded, one attached dorsally to the posterior limit of the host's cephalothorax and two more attached to the female's marsupium (see below), matched well the

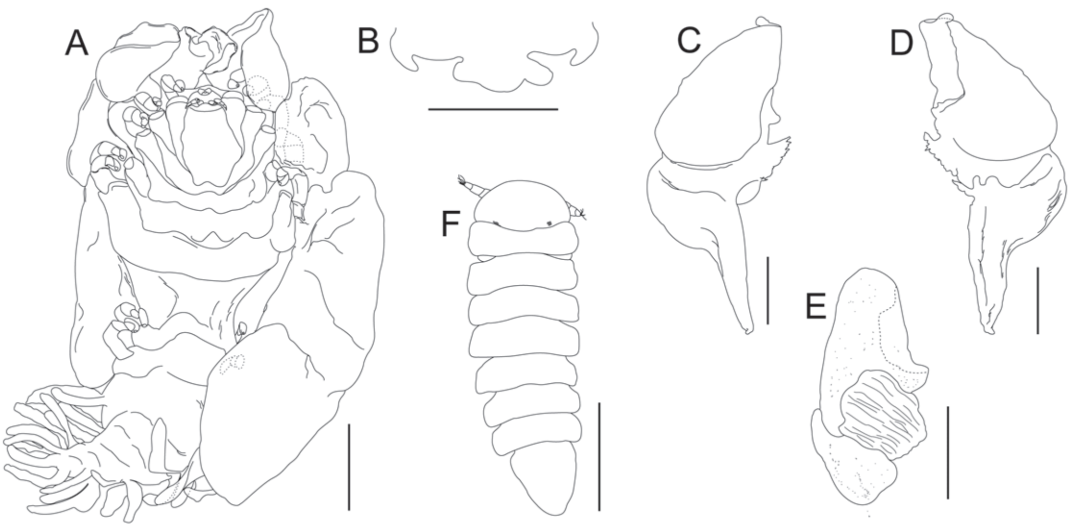

Fig. 3. *Anathelges hyptius* (Thompson, 1902). **A**. Ovigerous ♀, dorsal view (CNCR-36525-F). **B**. Barbula. **C**. First oostegite, external view. **D**. Same, internal view. **E**. Maxilliped. **F**. ♂, dorsal view (CNCR-36525-E). Scale bars: A = 1.0 mm; B–F = 0.5 mm.

description but were smaller (0.63 ± 0.07 mm TL, 0.25 ± 0.02 mm width) than the length of 0.7 mm provided by Thompson (1902).

The average TL of males was 1.80 ± 0.30 mm, and varied from 1.33 to 2.25 mm TL which is similar to that recorded by McDermott (1998) and Boyko & Williams (2003), but smaller than the 3 mm males reported by Thompson (1902). Except for one male, that was attached transversally between pleomeres 1–2 of the female, all males were inside the females' brood pouch between pereomeres 6–7, transversely aligned with their head directed towards the right side of the female and attached to the last oostegites. Although this is the typical position reported for males of *A. hyptius*, Markham (1974) registered during live observations that males can get out from the brood pouch and crawl all over the female's body.

The number and average size by sex of individuals of *P. mclaughlinae* parasitized by *A. hyptius* were rather similar, 14 females (3.28 ± 0.58 mm SL) and 13 males (3.32 ± 0.72 mm SL) were recorded. No statistical differences by sex were found ($\chi^2 = 0.08$, df = 1; $P < 0.05$).

The abdomen of a *P. mclaughlinae* male of 3.36 mm SL was simultaneously parasitized by *A. hyptius* and an undetermined rhizocephalan; one externa with two lobes of different sizes; were located below the bopyrid female, this last one was tightly attached to the host abdomen, with its head directed towards the host pleon, while one of its pereomeres was holding the largest externa. The male of *A. hyptus* was inside the marsupium of this female, additionally two cryptoniscus larvae were observed attached to the inner side of the oostegites of this bopyrid female, one on the lateral margin of the left oostegite 5 and another one on the anterior margin of the oostegite 3 of the right side.

A total of 475 hermit crabs were counted in the samples, of which 29 were parasitized by *A. hyptius*, this represents a prevalence of 6.11 %.

Genus *Pseudostegias* Shiino, 1933

Pseudostegias atlantica Lemos de Castro, 1965
Figs 1, 2B, 4, Table 1

Pseudostegias atlantica Lemos de Castro, 1965: 105–108, figs 1–9.

Pseudostegias atlantica – Markham 1978: 115; 1982: 373; 2003: 72. — Page 1985: 203. — Brasil-Lima 1998: 640. — Williams & Boyko 1999: 720 (in key). — Boyko 2004: 701. — McDermott *et al*. 2010: 11 (in table 1). — Figueredo *et al*. 2013: 92–93. — Ribeiro *et al*. 2019: 1–3, 6, figs 2–3.

Material examined

MEXICO • 1 juvenile ♀ (2.60 mm TL); Veracruz, Los Tuxtlas, Montepío; 18º38′35.23″ N, 95º05′54.43″ W; 19 Feb. 1996; R. Robles leg.; host ♀ of *Clibanarius antillensis* Stimpson, 1859 (3.40 mm SL); C. Hernández det. host; CNCR-36482 • 1 ovigerous ♀ (4.00 mm TL), 1 ♂ (1.65 mm TL); same locality as for preceding; 19 Feb. 1996; same collector; detached from host; CNCR-36486-A • 1 ovigerous ♀ (3.76 mm TL), 1 ♂ (1.67 mm TL); same collection data as for preceding; detached from host; CNCR-36486-B • 1 ovigerous ♀ (3.92 mm TL), 1 ♂ (1.67 mm TL) Veracruz, El Morro de la Mancha; 19º35′22.79″ N, 96º22′45.21″ W; 19 May 1998; F. Álvarez and R. Robles leg.; host ♀ of *Calcinus tibicen* (Herbst, 1791) (2.54 mm SL); C. Hernández det. host; CNCR-36483 • 1 juvenile ♀ (3.88 mm TL), 1 ♂ (1.15 mm TL); same locality; 20 Apr. 2006; J.L. Villalobos *et al*. leg.; host ♂ of same species as for preceding (4.90 mm SL); Y. de los Santos det. host; CNCR-36484 • 1 ovigerous ♀ (3.30 mm TL), 1 ♂ (1.53 mm TL); Veracruz, Isla Verde; 19º11′59.18″ N, 96º04′01.28″ W; 30 Jul. 1965; J. Cabrera leg.; Detached from host (possibly *C. antillensis*); CNCR-36485.

Distribution

Pseudostegias atlantica is recorded for the first time in Mexico, previously known from Ceará and Alagoas, Brazil (Lemos de Castro 1965; Ribeiro *et al*. 2019) and Isla Margarita, Venezuela (Figueredo *et al*. 2013), its distribution range is now extended to the southwestern Gulf of Mexico (Fig. 1). Similarly, the number of known hosts for *P. atlantica* increases to three: *Calcinus tibicen*, *Clibanarius antillensis*

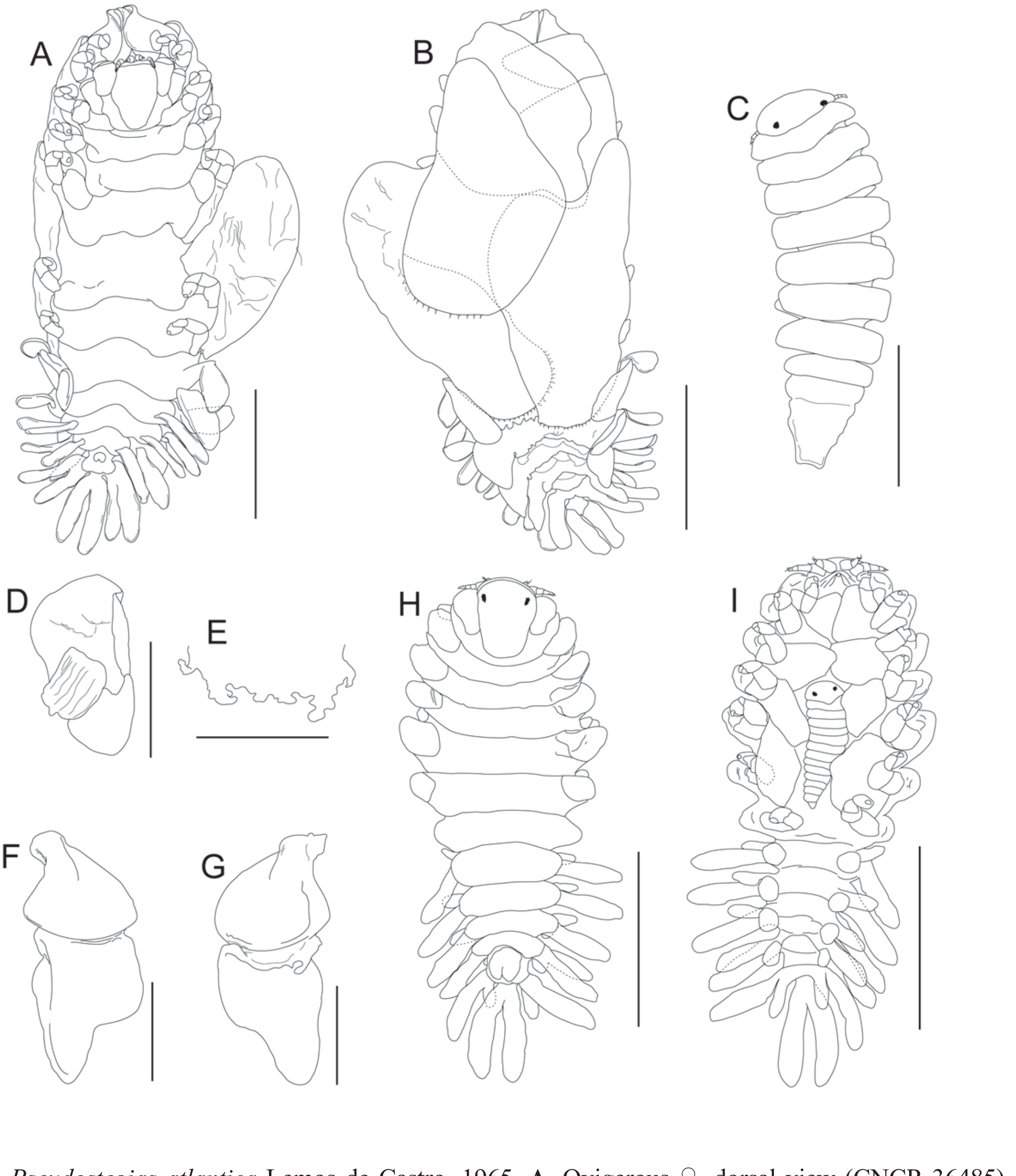

Fig. 4. *Pseudostegias atlantica* Lemos de Castro, 1965. **A**. Ovigerous ♀, dorsal view (CNCR-36485). **B**. Same ventral view. **C**. ♂, dorsal view (CNCR-36485). **D**. Maxilliped. **E**. Barbula. **F**. First oostegite, external view. **G**. Same, internal view. **H**. Juvenile ♀, dorsal view (CNCR-36482). **I**. Same, with cryptoniscus larva attached between oostegites, ventral view. Scale bars: A–B, H–I = 1.0 mm; C–G = 0.5 mm.

and *Paguristes tortugae* Schmitt, 1933. In Montepío, Veracruz, *P. atlantica* co-occurs with the brachial bopyrid *Asymmetrione tuxtlaensis* sp. nov.

Remarks

The bopyrids examined are morphologically similar to *Pseudostegias atlantica* (Figs 2B, 4A–C) described by Lemos de Castro (1965). Ribeiro *et al*. (2019) defined traits not provided in the original description such as the antennae of both sexes and the first pair of oostegites; the maxilliped and barbula are described below.

Maxilliped with anterior segment much larger than posterior one, rounded in shape and lacking palp, posterior segment semi-triangular in shape with rounded borders and round spur (Fig. 4D). Barbula bearing two lateral projections of sinuated outlines on each side; external projection smaller, narrow and bent up; internal one larger, stout and curved; medial margin with two small rounded projections directed to opposite sides (Fig. 4E).

The following variations were observed: in females, the endopods of the five pairs of pleopods were wider than exopods and directed backward (Fig. 4B), in contrast, Lemos de Castro (1965) noted that endopod of pleopods 1–3 is wide and folded inwards, while in pleopods 4–5 is elongated and directed outwards. The first pair of oostegites contrasts with those reported by Ribeiro *et al*. (2019), the anterior segment is drop-shaped due to the anterior margin extending rather upwards, the posterior segment is larger than the anterior one, rectangular in shape and with posterolateral projection wide, bearing small setae on posterior distal margin (Fig. 4F); the inner margin is thickened in the middle section, similar to that reported by Ribeiro *et al*. (2019) but bears two projections in the proximal section, one small and triangular in shape and another larger and curved (Fig. 4G). Males (Fig. 2C) were more similar to those illustrated by Lemos de Castro (1965: fig. 5) and only differ from those described by Ribeiro *et al*. (2019) in the lack of setae in the distal margin of carpus of pereopods 1 and 7.

Two juvenile females were recorded, one of 2.60 mm TL with a cryptoniscus larva between their oostegites (Fig. 4H–I) and another one of 3.88 mm TL paired with a male attached in the marsupium. Both females with dorsolateral bosses scantly developed in pereomeres 1–4 on both sides, oostegites not completely developed and ovoid in shape and pleopods with round endopods that increase in size backwards (Fig. 4I).

Reproduction

The average size of ovigerous females (n = 4) was 3.75 ± 0.31 mm TL; their range sizes are shown in Table 1. The average fecundity of *P. atlantica* was 217 ± 37.63 embryos, the minimum (177 embryos) and maximum (267 embryos) fecundities were recorded in females of similar sizes (3.92 and 4.00 mm TL, respectively), but carrying embryos of different developmental stages (Table 1). Sizes of embryos in egg stage were larger than those in stage I, the first ones ranged from 0.20 to 0.23 mm of length and between 0.18 and 0.23 mm of width, whilst the length of embryos in stage I varying from 0.15 to 0.22 mm and their width between 0.13 and 0.18 mm. Table 1 shows the average length, width and volume of *P. atlantica* embryos, which are larger than those recorded for other bopyrids (see Romero-Rodríguez & Álvarez 2020).

Males were recorded inside the females' marsupium, and their average size was 1.63 ± 0.07 mm TL, with a range from 1.53 to 1.67 mm TL. Both female and male sizes were smaller than those reported by Lemos de Castro (1965) in Brazil (5.5 and 3.0 mm, respectively).

One hundred and sixty-two hermit crabs were counted in the samples, of which six were parasitized by *P. atlantica*, thus prevalence of this bopyrid was of 3.70%.

Genus *Stegias* Richardson, 1904

Stegias clibanarii Richardson, 1904
Figs 1, 2C, 5, Table 1

Stegias clibanarii Richardson, 1904: 59–60, fig. 34.

Stegias clibanarii – Richardson 1905: 536–537, fig. 580. — Verril 1908: 448, fig. 64. — Nierstrasz & Brender à Brandis 1923: 107; 1931: 200. — Menzies & Glynn 1968: 13, 18–19, 83 fig. 3. — Schultz 1969: 322, fig. 514. — Markham 1972: 64–65; 1975a: 225–230, figs 1–2; 1975b: 260, 263; 1978: 102 (in key), 103–104, 111–112, 116, fig. 10, table 1; 1979: 523 (in key), 526–527; 1988: 3, 46–48, fig. 18, table 1; 2003: 72. — McDermott 1974: 2; 2002: 34–40, figs 1–2, table 1. — Ross 1983: 167. — Schultz 1986: 371, 372, pl. 123. — Kensley 1994: 320 (in table 1). — Campos 2003: 79–80, 86. — Romero-Rodríguez & Román-Contreras 2008: 1207; 2013: 646 (in table 3). — McDermott *et al*. 2010: 12 (in table 1), 27. — Trilles & Hipeau-Jacquotte 2012: 288. — Cericola & Williams 2015: 238 (in table I). — Romero-Rodríguez & Álvarez 2020: 2226 (in table 2).

non *Stegias clibanarii* – Pearse 1932: 4–5, figs 22–26. — Schultz 1969: 323, fig. 515.

Material examined

MEXICO • 1 ovigerous ♀ (3.80 mm TL), 1 ♂ (1.64 mm TL); Veracruz, Los Tuxtlas, Montepío; 18º38′34″ N, 95º05′50″ W; Jul. 2002; A. Argüelles and M. Maldonado leg.; host ♀ of *Clibanarius tricolor* (Gibbes, 1850) (3.60 mm SL); A. Argüelles det. host; CNCR-36487.

Distribution

Stegias clibanarii has been recorded exclusively in the Caribbean region: Bermuda (Richardson 1904), San Juan, Puerto Rico (Menzies & Gynn 1968) and Magdalena, Colombia (Markham 1988); with the new records its geographic range extends to the southwestern Gulf of Mexico (Fig. 1), likewise also represents the first evidence of its occurrence in Mexican coasts. The only known host for this bopyrid species so far is *C. tricolor*.

Remarks

The material examined (Figs 2C, 5A, G) agree in most details with the descriptions given by Richardson (1904) and Markham (1975a) for *Stegias clibanarii*, only differing in the following aspects: female with small eyes on the anterolateral margins of head (Fig. 5A), the barbula's left projection more pointed than that on the opposite side (Fig. 5B), first pair of oostegites with a curved projection in the proximal end of the inner margin (Fig. 5C-D) and all five pairs of pleopods biramous (Fig. 5E). The maxilliped, not previously described, with anterior segment square in shape and much larger than posterior one, without palp but anterior and distal margin folded, converging in superior lateral margin giving it pointed appearance; posterior segment rectangular in shape (Fig. 5F). Male with the fusion of head and first pereomere not as conspicuous (Fig. 5G) as that illustrated by Markham (1975a).

Reproduction

The size of the female examined (3.80 mm TL) was similar to the average size for ovigerous females (3.55 ± 0.44 mm) previously reported (McDermott 2002) but the number of embryos counted in our female (Table 1) was almost three times as high as the maximum fecundity reported (667 embryos) for *S. clibanarii* by McDermott (2002). The average embryos' length and width recorded (Table 1) were similar to those reported by McDermott (2002) for embryos recently deposited in the marsupium

(0.157 ± 0.008 and 0.133 ± 0.016 mm, respectively) but their average volume was smaller than the 0.0015 mm^3 calculated by Romero-Rodríguez & Álvarez (2020).

The size of the male examined (1.64 mm TL) is in the range of 0.78 to 1.71 mm TL reported by McDermott (2002), although Markham (1975a) noted that males of this species can reach 2.6 mm TL.

The prevalence calculated for *S. clibanarii* was of 25%; however, the sample was only of four hermit crabs.

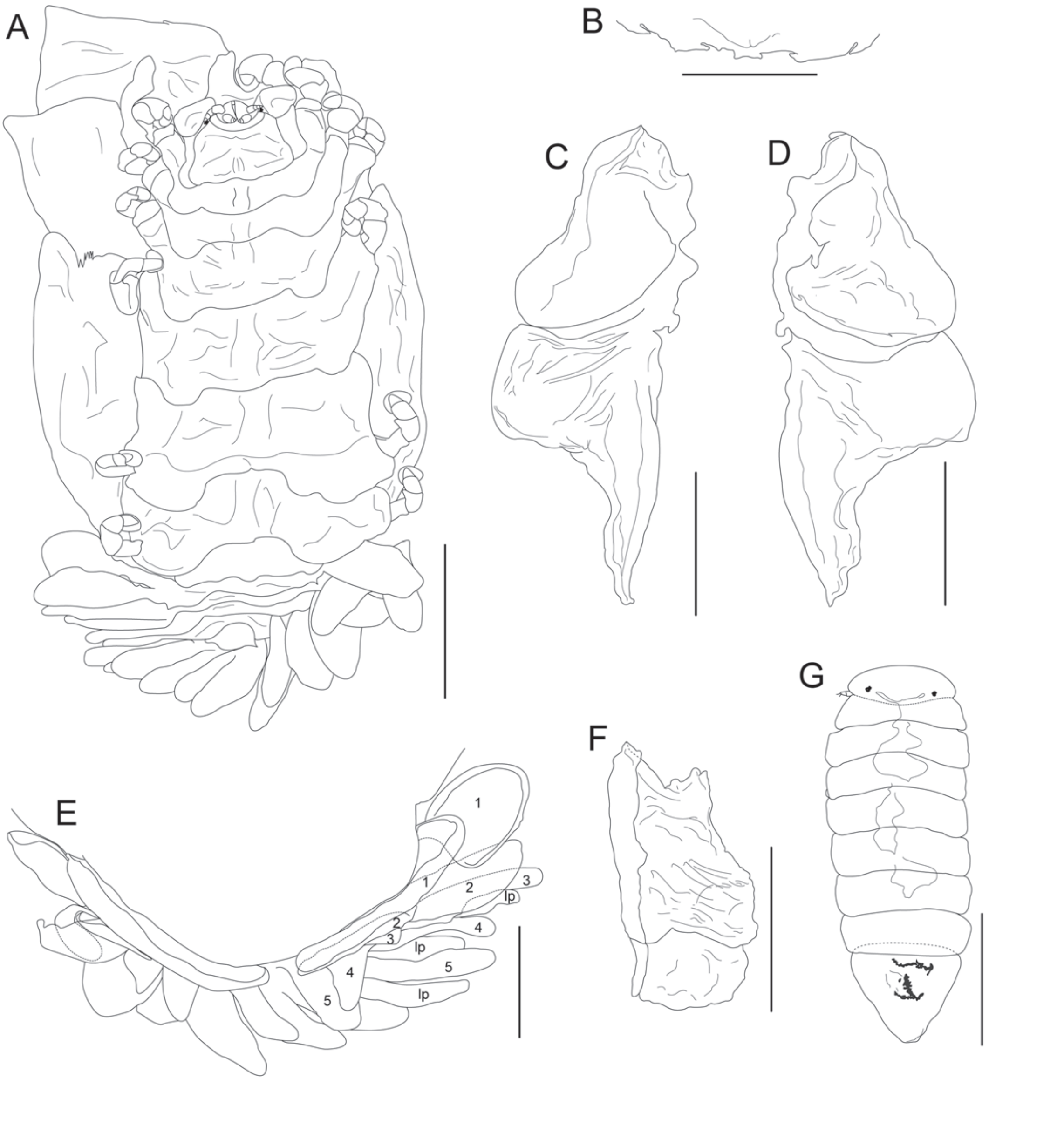

Fig. 5. *Stegias clibanarii* Richardson, 1904 (CNCR-36487). **A**. Ovigerous ♀, dorsal view. **B**. Barbula. **C**. First oostegite, external view. **D**. Same, internal view. **E**. Pleon, ventral view. **F**. Maxilliped. **G**. ♂, dorsal view. Numbers indicate pairs of pleopods. Abbreviation: lp = lateral plate. Scale bars: A = 1.0 mm; B–G = 0.5 mm.

Subfamily Subfamily Pseudioninae Codreanu, 1967
Genus *Asymmetrione* Codreanu, Codreanu & Pike, 1965

Asymmetrione desultor Markham, 1975
Figs 1, 2D, 6, Table 1

Asymmetrione desultor Markham, 1975b: 255–260, figs 1–4.

? "Bopyrien" – Forest & de Saint Laurent 1968: 74.
Asymmetrione desultor – Markham 1978: 102–103, 115–116, table 1; 1985: 108; 1988: 7, table 1; 2003: 73–74. — Adkison & Heard 1978: 408. — Bourdon 1979: 143–144. — Ross 1983: 167. — Markham & Donath-Hernández 1990: 243. — Camp 1998: 134. — McDermott 1998: 1044; 2001: 629 (in table 2), 635. — Campos 2003: 86. — Boyko & Williams 2004: 357, 359–360, 366–369, 373, 377–378. — Williams & Schuerlein 2005: 101. — Pardo *et al*. 2009: 2048–2049 (in key). — An *et al*. 2010: table 1; 2016: table 2. — McDermott *et al*. 2010: 8. — Williams *et al*. 2019: 86 (in key).

Material examined

MEXICO • 1 ovigerous ♀ (4.90 mm TL), 1 ♂ (2.50 mm TL); Quintana Roo, Cozumel; 20º32′39″ N, 86º48′21″ W; 18 Aug. 1987; J.L. Villalobos *et al*. leg.; host ♂ of *Pagurus stimpsoni* (A. Milne-Edwards & Bouvier, 1893) (7.10 mm SL); J. Romero det. host; CNCR-36488 • 1 juvenile ♀ (1.84 mm TL); Veracruz, El Morro de la Mancha; 19º35′22″ N, 96º22′45″ W; 27 May 2004; C. Hernández *et al*. leg.; detached from host; CNCR-36489.

Distribution

Asymmetrione desultor is widely distributed along the western Atlantic (Fig. 1): from North Carolina and Florida, USA, Antigua, Bahamas, Curaçao, Bonaire, Belize, Colombia to Brazil (Boyko & Williams 2004), hence its presence in Mexican waters was suggested by Markham & Donath-Hernández (1990); however, the material examined herein is the first evidence that this bopyrid parasitizes hermit crabs from the SW Gulf of Mexico and the Mexican Caribbean. *Pagurus stimpsoni* is not a new host for *A. desultor* since Markham (2003) noted that this bopyrid has a wide host range, that includes one species of Diogenidae Ortmann, 1892 (*Paguristes tortugae*) and seven species of Paguridae Latreille, 1802, one in the genus *Iridopagurus* de Saint Laurent-Dechancé, 1966 (*Iridopagurus* sp.) and five in *Pagurus* Fabricius, 1775 (*P. brevidactylus*, *P. longicarpus*, *P. provenzanoi* Forest & de Saint Laurent, 1968, *P. stimpsoni* and *P. tortugae*) and another one in *Pylopagurus* A. Milne-Edwards & Bouvier, 1893 (*Pylopagurus* sp.).

Remarks

The morphology of the adult couple examined (CNCR-36488) (Figs 2D, 6A–B) matched well with the characteristics defined for *Asymmetrione desultor* by Markham (1975b), but the following variations were observed in the female: the first pair of oostegites with inner margin slightly sinuated and with a rounded lobule in the proximal portion (Fig. 6C), Markham (1975b: fig. 1f) sketched a similar lobe in his figure but he did not refer to it in the female's description; as well, the uropods of the female examined were uniramous (Fig. 6A) instead of biramous. As far as we know, the maxilliped of this bopyrid has not been described previously thus the following is provided. Maxilliped with anterior segment much larger than posterior one, rectangular in shape with distal margin extending forward but lacking palp or setae and lateral margin folded upwards, posterior segment triangular in shape with long and pointed spur (Fig. 6D).

Although the female examined detached from the host was slightly damaged (CNCR-36489), it matched well the description of *A. desultor*, and was classified as juvenile according to the following features:

oostegites not fully developed, barely touching each other in the mid abdominal portion, only the fifth pair overlapping, the barbula had two very small projections on each side and a smooth medial margin, as well as exopods of the pleopods more developed than endopods which in most cases had a fleshy bulge shape.

Reproduction

The average length and width of the embryos recorded for *A. desultor* are shown in Table 1. The embryos were in stage I and their sizes ranged from 0.200 to 0.255 mm of length and between 0.182 and 0.218 mm

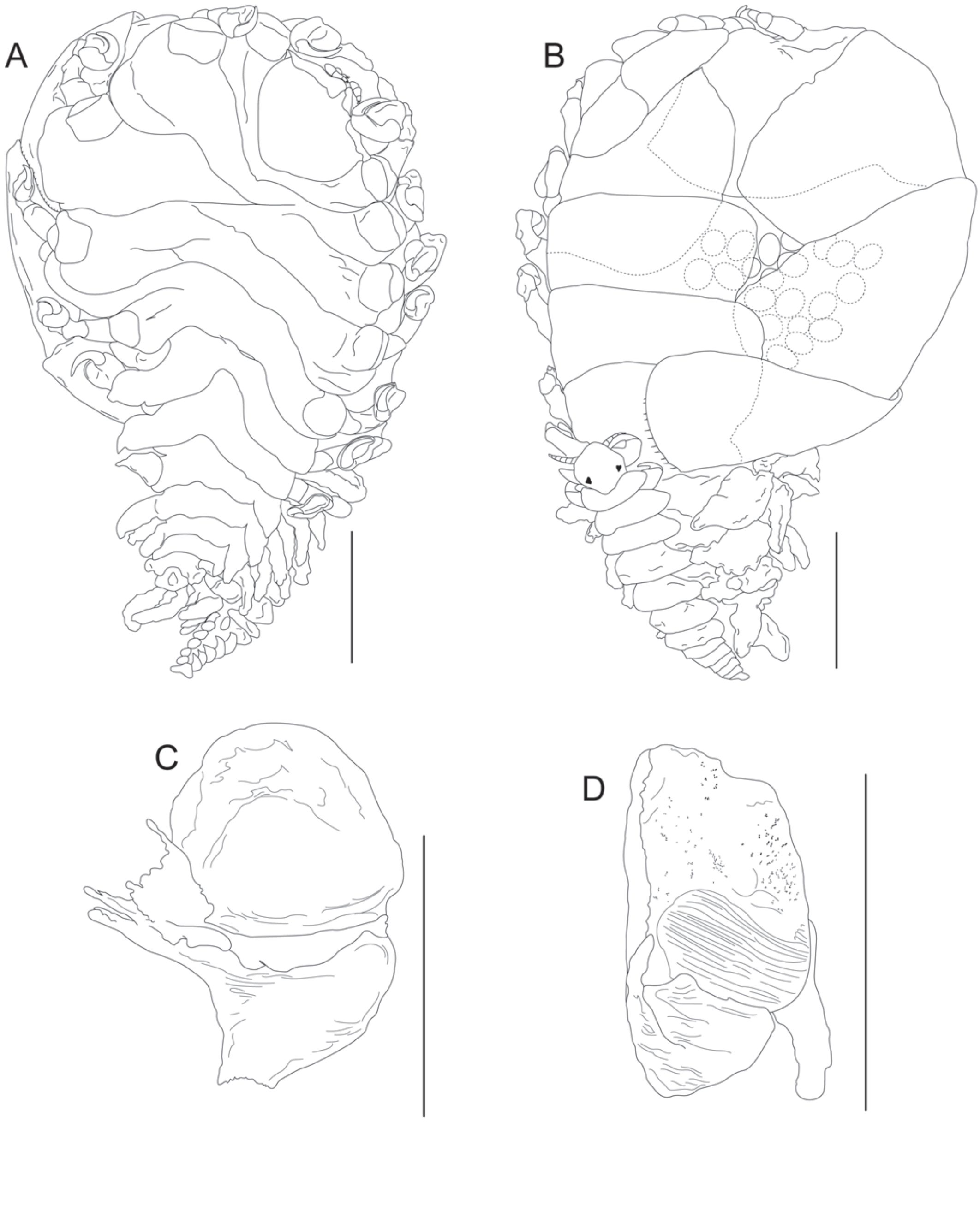

Fig. 6. *Asymmetrione desultor* Markham, 1975 (CNCR-36488). **A**. Ovigerous ♀, dorsal view. **B**. Same, with ♂ attached to pleon, ventral view. **C**. First oostegite, internal view, posterolateral point damaged. **D**. Maxilliped, with lateral projection of barbula. Scale bars = 1.0 mm.

of width. The embryo volume in this developmental stage ranged from 0.0038 to 0.0059 mm^3, thus the average volume calculated (Table 1) is greater than those reported for other bopyrids of comparable sizes (see Romero-Rodríguez & Álvarez 2020).

A prevalence of 66.67% was estimated for *A. desultor*, but this is based on a very small sample of three hosts, of which two were parasitized.

Asymmetrione tuxtlaensis sp. nov.
urn:lsid:zoobank.org:act:BF09884B-55A7-4FE6-816B-1D890D42CC7C
Figs 1, 2E, 7–8, Tables 1–2

Diagnosis

Body outline oblong, right body side longer than left one, head rotated sinistrally, margin of second right pereomere at anterior end. All body regions and segments distinct, unpigmented. First pair of pereopods clearly different in size, pleopods 1–4 biramous, 5 uniramous, uropod uniramous (Figs 2E, 7A). Male with body unpigmented, elongated, all segments clearly separated dorsally and laterally, pleon of five pereomeres plus pleotelson, globose uniramous pleopods on all pleomeres and no uropods (Fig. 8A–B)

Etymology

The specific name '*tuxtlaensis*' refers to the region where more specimens of this species were registered, Los Tuxtlas, Veracruz.

Material examined

Holotype

MEXICO • 1 ovigerous ♀ (dissected, 2.86 mm TL); Veracruz, Los Tuxtlas, Montepío; 18º38′35.23″ N, 95º05′54.43″ W; 19 Feb. 1996; R. Robles leg.; host ♀ of *Clibanarius antillensis* (3.32 mm SL); C. Hernández det. host.; CNCR-36493-A1.

Allotype

MEXICO • 1 ♂ (1.58 mm TL); same collection data as for holotype; CNCR-36493-A2.

Paratypes

MEXICO • 1 ovigerous ♀ (3.07 mm TL), 1 ♂ (1.42 mm TL); same collection data as for holotype; same host data as for preceding (3.70 mm SL); CNCR-36493-B • 1 ♀ ovigerous (3.33 mm TL), 1 ♂ (1.33 mm TL); same collection data as for holotype; same host data as for preceding (3.40 mm SL); CNCR-36493-C • 1 juvenile ♀ (2.22 mm TL), 1 ♂ (1.16 mm TL); same collection data as for holotype; host ovigerous ♀ of same species as for preceding (3.50 mm SL); CNCR-36493-D • 1 ovigerous ♀ (3.20 mm TL), 1 ♂ (1.56 mm TL); same locality as for holotype; Jul. 2002; A. Argüelles and M. Maldonado leg.; host ♂ of *C. antillensis* (3.72 mm SL); A. Argüelles det. host; CNCR-36494 • 1 ovigerous ♀ (2.93 mm TL), 1 ♂ (1.64 mm TL); same locality; 14 Jun. 2016; J.L. Villalobos *et al*. leg.; host ♀ of same species as for preceding (3.13 mm SL); J. Romero det. hosts; CNCR-36497-A • 1 ovigerous ♀ (1.69 mm TL), 1 ♂ (1.25 mm TL); same collection data as for preceding; host ♂ of same species as for preceding (2.25 mm SL); J. Romero det. hosts; CNCR-36497-B • 1 juvenile ♀ (2.07 mm TL), 1 cryptoniscus larva (1.45 mm TL); same locality; 7 Feb. 2013; F. Álvarez and J.L. Villalobos leg.; right branchial chamber of *Calcinus tibicen* ♂ (3.84 mm SL); R. Robles det. host; CNCR-36498-A • 1 cryptoniscus larva (1.47 mm TL); same collection data as for preceding; left branchial of same for preceding host; CNCR-36498-B • 1 ♀ ovigerous (1.78 mm TL), 1 ♂ (0.98 TL); Veracruz, Isla Verde; 19º11′59.18″ N, 96º04′01.28″ W; 26 Feb. 1959; A. Villalobos leg.; host ♀ of *C. antillensis* (2.90 mm SL); A.J. Provenzano det. host; CNCR-36490 • 1 cryptoniscus larva (1.20 mm TL); same locality as for preceding; 26 May 1969; I. Peña-Ramirez

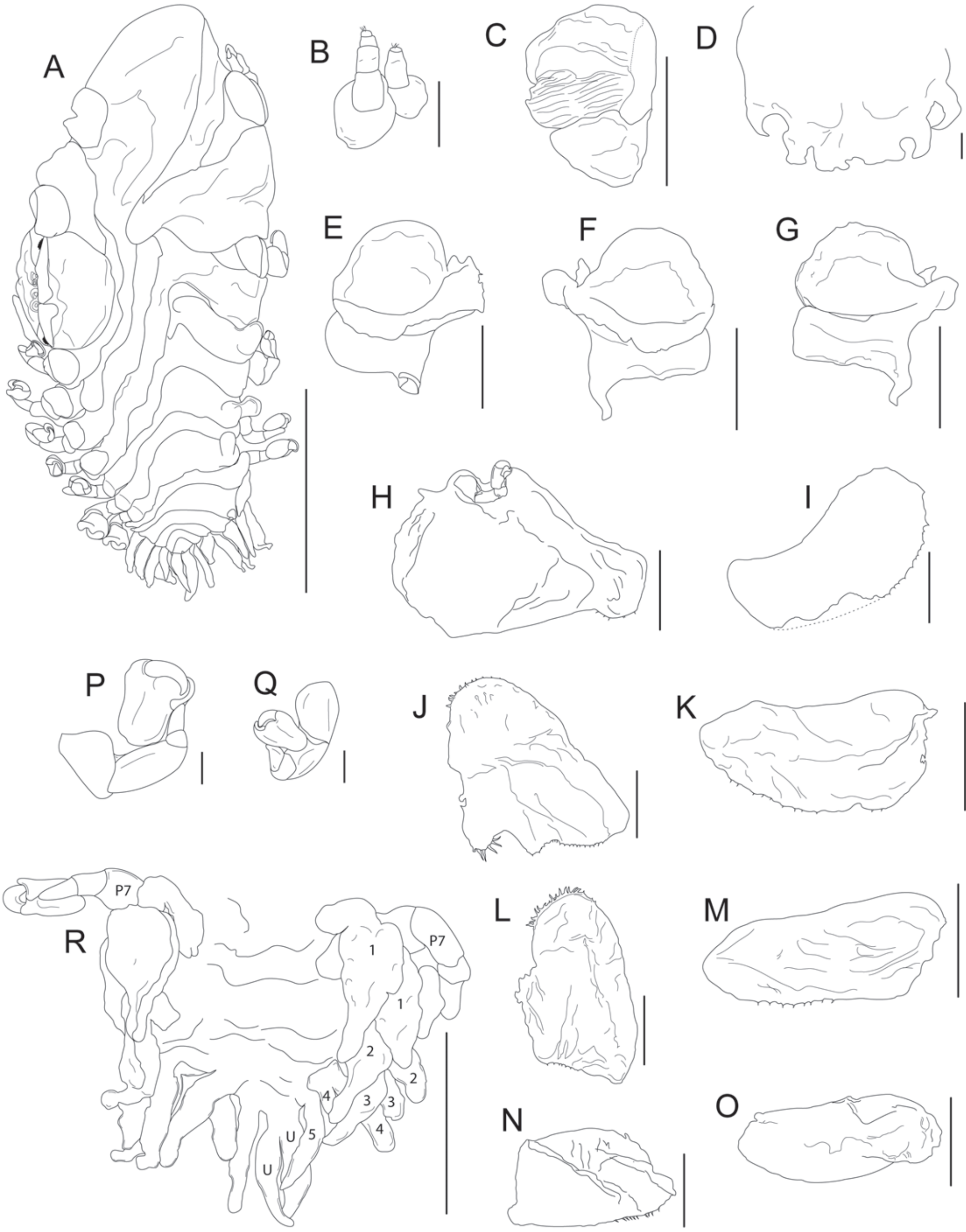

Fig. 7. *Asymmetrione tuxtlaensis* sp. nov. (CNCR-36493-A). **A**. Ovigerous ♀, dorsal view, holotype (CNCR-36493-A). **B**. Antennule and antennae. **C**. Maxilliped. **D**. Barbula. **E**. First oostegite right, internal view. **F**. First oostegite left, external view. **G**. Same, internal view. **H**. Second oostegite right, with second pereopod, external view. **I**. Second oostegite left, external view. **J**. Third oostegite right, external view. **K**. Third oostegite left, external view. **L**. Fourth oostegite right, external view. **M**. Fourth oostegite left, external view. **N**. Fifth oostegite right, external view. **O**. Fifth oostegite left, external view. **P**. First pereopod right. **Q**. First pereopod left. **R**. Pleon, ventral view. Scale bars: A = 1.0 mm; C, E–N, R = 0.5 mm; B, D, O–Q = 0.1 mm.

leg.; host ♀ of same species as for preceding (6.00 mm SL); T. Nates det. host; CNCR-36492-A • 1 bopyridium (1.49 mm TL); same collection data as for preceding; same host data as for preceding (4.75 mm SL); CNCR-36492-B • 1 ♀ (4.35 mm TL); same locality; 26 May 1969; I. Peña-Ramirez leg.; detached from host; CNCR-36500 • 1 ovigerous ♀ (2.51 mm TL), 1 ♂ (1.40 TL); Veracruz, La Blanquilla reef; 19º13′22.8″ N, 96º06′00.0″ W; 17 Apr. 1968; J. Cabrera leg.; host ♂ of same species as for preceding (5.53 mm SL); J.C. Nates det. host; CNCR-36491 • 1 ovigerous ♀ (4.85 mm TL), 1 ♂ (2.23 mm TL); Veracruz, Laguna de Tamiahua, Isla Lobos reef, 21º25′09″ N, 97º13′18″ W; 20 May 2005; J.L. Bortolini leg.; host ♀ of same species as for preceding (5.13 mm SL); G. Cervantes det. host; CNCR-36495 • 1 ovigerous ♀ (3.76 mm TL), 1 ♂ (2.02 mm TL); Veracruz, El Morro de la Mancha; 19º35′22″ N, 96º22′45″ W; 20 Apr. 2006; J.L. Villalobos *et al*. leg.; host ♂ of same species as for preceding (4.35 mm SL); Y. de los Santos det. host; CNCR-36496 • 1 ♀ (3.33 mm TL), 1 ♂ (2.09 mm TL); Quintana Roo, Ensenada Lamcom, NE border of Isla Blanca; 21º24′45.44″ N, 86º48′35.29″ W; 18 Jun. 2005; J.L. Villalobos *et al*. leg.; host ovigerous ♀ of same species as for preceding (5.00 mm SL); J. Romero det. host; CNCR-36499.

Description

Based on female holotype

Measurements. Length 2.86 mm, maximal width 2.22 mm (at second pereomere), head length 0.51 mm, head width 0.56 mm, pleon length 0.42 mm, pleon width 0.73 mm. Body distortion 88º.

Head. Ovoid, surface smooth, distinct from first pereomere. Frontal lamina broad, bent upwards with medial notch and two semi-triangular lobes, anterolateral corners rounded. Eyes at ventral anterolateral edges of head, barely visible dorsally (Fig. 7A). Antennule 3-segmented, antennae 5-segmented, both with basal article wide and rounded, second article long and cylindrical, last article smaller, rounded, tipped with tiny setae (Fig. 7B). Maxilliped with anterior segment larger than posterior one, semi-rectangular of round margins without palp, posterior segment triangular in shape bearing thin and pointed spur (Fig. 7C). Barbula with two triangular projections on each side, outer one recurved and sharp, inner projection thicker and blunt, middle margin with medial notch and one rounded projection each side (Fig. 7D).

Pereon. Pereomeres dorsally and laterally distinct, similar in width and shape along left side, wider with variable outline along right side. Narrow coxal plates on pereomeres left 1–7 and right 1–4. On left side dorsolateral bosses rounded, occupying nearly entire margin of pereomeres 1–4, on right side, flat and ovoid at half margin of pereomeres 1–4, thick, directed forward and decreasing in size posteriorly on 5–7 (Fig. 7A). Oostegites fully enclosing brood pouch (Fig. 8G). First pair of oostegites similar in size and shape, anterior segment large and subtriangular, posterior one short, rectangular with rounded margins bearing thin and recurved posterolateral point (Fig. 7E–G); inner ridge slightly sinuate, medially thick with rounded projection on proximal portion (Fig. 7G); oostegites 2–5 relatively ovate, those on right side larger in size, bearing marginal fringe of setae on posterior edge (Fig. 7H–O). Pereopods similar in shape, rounded carina on superior margin of basis, ischium long and cylindrical, meri subquadrate, carpi conical, propodi swollen distoventrally with deep socket for insertion of strongly recurved dactyli (Fig. 7P–Q). First pair of pereopods at both sides of head clearly different in size (Fig. 7P–Q). All pereopods on right side similar in size, left ones increasing in size backwards, 6–7 abruptly increasing in size (Fig. 7A).

Pleon. Comprised of five segments plus pleotelson, narrowing posteriorly, distinctly separated. Pleomeres 1–2 with short and rounded lateral plates, triangular pleotelson with rounded edges (Fig. 7A). Five pairs of pleopods, biramous on pereomeres 1–4 and uniramous on pereomere 5, all decrease in size posteriorly, endopod and exopod of similar sizes, pleopods on pereomeres 1–3 foliaceus with sinuated margins, on 4–5 cylindrical with smooth borders (Fig. 7R). Long, smooth and uniramous uropods (Fig. 7A, R).

Table 2. Comparison of morphological traits comparison of female of *Asymmetrione* Codreanu, Codreanu & Pike, 1965. Abbreviations: B = biramous; L = left; Lanc. = lanceolate; LP = lateral projection; Mm = middle margin; Ir = inner ridge; Perpd. = pereopods; R = right; Tubs. = tubercles; Tubte. = tuberculate; U = uniramous; * based on illustrations provided in the holotype description. Sources: 1 = An *et al*. 2010; 2 = Bourdon 1968; 3 = Bourdon 1976; 4 = Codreanu *et al*. 1965; 5 = Markham 1975b; 6 = Markham 1985; 7 = Pardo *et al*. 2009; 8 = Shiino 1933; 9 = Williams & Schuerlein 2005; 10 = Williams *et al*. 2019; 11 = this article.

Species	Body distortion	LP and Mm of barbula	Ir 1º oostegite	Perpd. on both side of body	Lateral plates of pleomeres	Pleopods	Uropods	Sources
A. aequalis	Slight R (≈ 10º)	1 pair, ondulating	Thin digitate	Similar, decreasing backward	Lacking	B 1–5, covered with Tubs.	U with swollen Tubs.	7
A. ambodistorta	Slight L (30º)	1 pair, irregular with toothed lobes	Clearly digitate	Similar, increasing backward	1–5, Lanc. with dentate margins	B 1–5, with dentate margins	B with dentate margins	6
A. asymmetrica	Heavy R (≈ 80º)	2 pairs, branched	–	Similar*	1–5	B 1–5, Tubte.	U, Tubte.	8
A. clibanarii	Heavy R (81º)	2 pairs, irregular	Thick, smooth	Similar, dactili smaller backward	1-3	B 1–5* Lanc.	B Lanc.	5
A. dardani	Heavy R (56º)	2 pairs, Tubte.	Clearly digitate	Similar	1–4	B 1–5 foliaceos	B, Tubte.	2
A. desultor	Sligth L (36º)	2 pairs, irregular margin*	Simple, with rounded lobule	Similar, 2 first pairs largest	1–3	B 1–5* Lanc.	B, Lanc.	5, 11
A. foresti	Slight R (≈ 17º)	2 pairs, with large Tubs.	Digitate and Tubte.	Similar, first two pairs largest	1–5, smooth and Lanc.	B 1–5 with Tubs.	U with few Tubs.	
A. globifera	Heavy R (98º)	2 pairs, irregular digitate	4 straight projections of digitate margins	About equal sizes	1–5 Tubte. and Lanc.	B 1–5 with Tubs.	Undescribed, smooth and globose	1
A. harmoniae	Heavy R (~65º–70º)	2 pairs, irregular digitate	Entirely lined with large digitations	Similar, ischia longer backwards	1–4 foliose with Tubs., pair 5 ovate	B 1–5 folioses with Tubs.	B folioses with Tubs.	10
A. nossibensis	Heavy R (59º)	2 pairs, entirely tuberculate	Tubte.	Similar, increasing backward	1–4 smooth dorsally with Tubs. ventrally, 5 pair short and digitiform	B 1–5 with Tubs.	B Tubte.	
A. sallyae	Heavy R (~ 65º)	1 pair, 2 rounded lobes	Smooth*	Similar, 1–5 increasing backward, 6–7 decreasing	1–5 tapering posteriorly	B 1–5 digitate with weak Tubs.	B digitate with weak Tubs.	9
A. shiinoi	Heavy R (≈ 80º)	2 pairs, smooth	Spreading backwards, with scaly Tubs.	Dissimilar, larger on long side of body	1–3 foliaceous	B 1–5, foliaceous	U Tubte.	4
A. tuxtlaensis sp. nov.	Heavy R (88º)	2 pairs, medial notch	medially thick with rounded projection	Dissimilar, larger on long side of body	1–3, decreasing in size backwards	B 1–4, fifth U	U, long and smooth	11

Female variations. Maxilliped with anterior segment rather quadrate in shape with anterior margin almost straight; the two pairs of projections on each side of the barbula ranged from both small and blunt in one female to both conspicuous and triangular in shape in most females, middle margin of one female with rectangular projection and another female with crenulations of different sizes on each side of the medial notch; the anterior segment of first oostegite ranged from triangular to ovoid, the oostegites' inner ridge medially thick in most females ranged from slightly sinuous and lacking of projections to bearing one to four projections of different sizes and shape, this variability was recorded even in the first pair of oostegites of a same female (Fig. 7E, G); one female with pleopods on pereomere 5 biramous on sinistral and uniramous on dextral; most females bears tiny scales along frontal lamina, ventral side of head, dorsolateral bosses and pereomeres.

Male description (based on allotype)

Measurements. Length 1.58 mm, maximal width 0.47 mm (at pereomeres 2–4), head length 0.16 mm, head width 0.31 mm, pleon length 0.45 mm, pleon width 0.27 mm.

Head. Ovoid with anterior margin straight, nearly fused to first pereomere medially, conspicuous eyes on posterolateral edges (Fig. 8A). Antennule 3-segmented, first one larger, quadrangular in shape, third segment small, rounded tipped with tuft of setae, barely reaches anterior margin of head. Antennae 5-segmented, distal one tipped with tuft of setae, exceeds head edges (Fig. 8B–C).

Pereon. Pereomeres with rounded lateral margins, separated by anterolateral indentations, tapering slightly backward (Fig. 8A). Midventral tubercles absent (Fig. 8B). Pereopods of similar size and shape, basis long, ischium about half size of basis, meri and carpi subquadrate, last one with cup-shaped distal margin for insertion of dactyli tip, propodi ovoid and strongly recurved dactyli; propodi and dactyli progressively smaller posteriorly (Fig. 8D–E).

Pleon. Comprised of five pleomeres plus pleotelson, first one narrower than final pereomere, others progressively narrower posteriorly, distinctly separated dorsal and laterally, lateral margins tapered, rounded and folded ventrally, resembling a conical pleon (Fig. 8A); globose uniramous pleopods on pleomere 1–5 (Fig. 8F). Pleotelson with two rounded posterolateral lobes bearing few tiny setae on each posterolateral corner, conspicuous medial anal cone. Uropods absent (Fig. 8A–B, F).

Male variations. Most variations of other examined males seem to be rather minor. One male with head rather rectangular, two males with pereomeres pigmented dorsally, pereomeres of five males slightly decrease in size backwards and pleotelson of one male with square lateral margins.

Juvenile stages

The two juvenile females examined (CNCR-36498-A and CNCR-36493-D) agreed with most characters described for the adult females but with the following traits poorly developed: body slightly asymmetrical since head is barely rotated to left side, frontal lamina wide but not bent up, barbula smooth lacking lateral projections or medial notches, flat dorsolateral bosses on pereomeres 1–4 (Fig. 8H), oostegites as small ovoid plates, in largest female barely reaching the midventral portion, first oostegite small but bearing a recurved posterolateral point and smooth inner margin, pereopods smooth or with poorly developed round carina at superior margin of basis, lateral plates in pleomeres 1–5 decreasing in size posteriorly. The individual classified as bopyridium (CNCR-36492-B) shows the following characteristics: body symmetric, all body regions and segments distinct, head rounded and small, frontal lamina wide bearing round bulges on each lateral margin and two more dorsally, conspicuous eyes at mid-lateral margin of head. Antennules and antennae similar to those described for adult females but exceeding head margin (Fig. 8I). Pereomeres laterally separate, rectangular in shape with slightly wider and rounded margins covered with tiny scales; middle portion raised as triangular projection decreasing in size posteriorly, on both sides of body large and thin pereopods of similar sizes and shape, propodi slightly swollen distoventrally with recurved dactyli, oostegites not developed. Five triangular pleomeres, first one of same size than last pereomere others decreasing in size posteriorly; five pairs of uniramous pleopods with thick and bifid tip, uropods uniramous with distal margin bifid (Fig. 8I).

Type locality

Veracruz, Los Tuxtlas, Montepío, (18º38′35.23″ N, 95º05′54.43″ W).

Distribution

Known from the north-central region of Veracruz and the NE coast of Isla Blanca, Quintana Roo, Mexico (Fig. 1A).

Calcinus antillensis Stimpson, 1859 had only been reported as host of *A. clibanarii* in Colombia (Markham 1988) and *C. tibicen* had no previous records as host for any species of *Asymmetrione* (see McDermott *et al*. 2010). In Montepío, Veracruz, *A tuxtlaensis* sp. nov. co-occurred with the abdominal bopyrid *P. atlantica*, see above, and in Isla Blanca, Quintana Roo with the branchial bopyrid *Bopyrissa wolffi*. *Asymmetrione tuxtlaensis* is the fourteenth species of the genus but only the third one recorded from the west Atlantic.

Remarks

Based on the following morphological traits, the specimens examined were included in *Asymmetrione* Codreanu, Codreanu & Pike, 1965: females with body extremely asymmetric, bilobed frontal lamina, pereopods with propodi distended distoventrally with deep ʿsocketʾ for insertion of recurved dactyli. Males with head not fully fused with first pereomere and pleon segmented, thin and bearing pleopods. According to Boyko *et al*. (2008 onwards), this genus currently comprises 13 species (*A. aequalis* Pardo, Boyko & Mantelatto, 2009; *A. ambodistorta* Markham, 1985; *A. asymmetrica* (Shiino, 1933); *A. clibanarii* Markham, 1975b; *A. dardani* Bourdon, 1968; *A. desultor*; *A. foresti* (Bourdon, 1968); *A. globifera* An, Markham & Yu, 2010; *A. harmoniae* Williams, Boyko & Madad, 2019; *A. imrai* Kazmi & Khatoon, 2016; *A. nossibensis* Bourdon, 1976; *A. sallyae* Williams & Schuerlein, 2005 and *A. shiinoi* Codreanu, Codreanu & Pike, 1965), but since *A. imrani* is considered species inquirenda (Williams *et al*. 2019) it is excluded from the following comparison.

A morphological comparison of some traits of the species of *Asymmetrione* is shown in Table 2. The strong dextral body distortion (≥ 80º), two lateral projections on each side of the barbula and biramous pleopods suggest a close relationship to *A. asymmetrica*, *A. clibanarii*, *A. globifera* and *A. shiinoi*. However, the middle margin of the barbula of *A. asymmetrica* and *A. globifera* are branched and tuberculated, respectively, also both species have tuberculated pleopods which differ from those of the examined females. Based on the distribution of the species of *Asymmetrione* the material examined is close to *A. clibanarii* since, besides *A. desultor*, it is the only other member of *Asymmetrione* reported for the Western Atlantic (Markham 1975b). However, traits described for *A. clibanarii* as the first oostegite with a more or less rectangular outline, internal ridge not ornamented and without pointed posterior border, five pairs of pleopods biramous with endopod somewhat smaller than exopod, uropods biramous and pereopods of similar size on both sides of body differ from those observed in the females examined. Females of *A. shiinoi* coincide with our material in the pereopods of dissimilar sizes, biramous pleopods and uniramous uropods but differ in that *A. shiinoi* has the inner ridge of the first oostegite with scaly tubercules as well as tubercules on the uropods. Therefore, *A. tuxtlaensis* sp. nov. can be distinguished by the first pair of oostegites with a more or less ovoid outline that bears round projections on the inner ridge and pointed posterior border, first pair of pereopods at both sides of head and clearly different in size, pleopods 1–4 biramous and fifth pair uniramous, and long and smooth uniramous uropod.

Reproduction

Sizes of the two adult females of *A. tuxtlaensis* sp. nov. without embryos in the marsupium were 3.33 and 4.35 mm TL, the former was paired with a male of 2.09 mm TL. Average TL of ovigerous females (n = 10) was 3.00 ± 0.92 mm and ranged from 1.69 to 4.85 mm TL (Table 1). The overall average fecundity

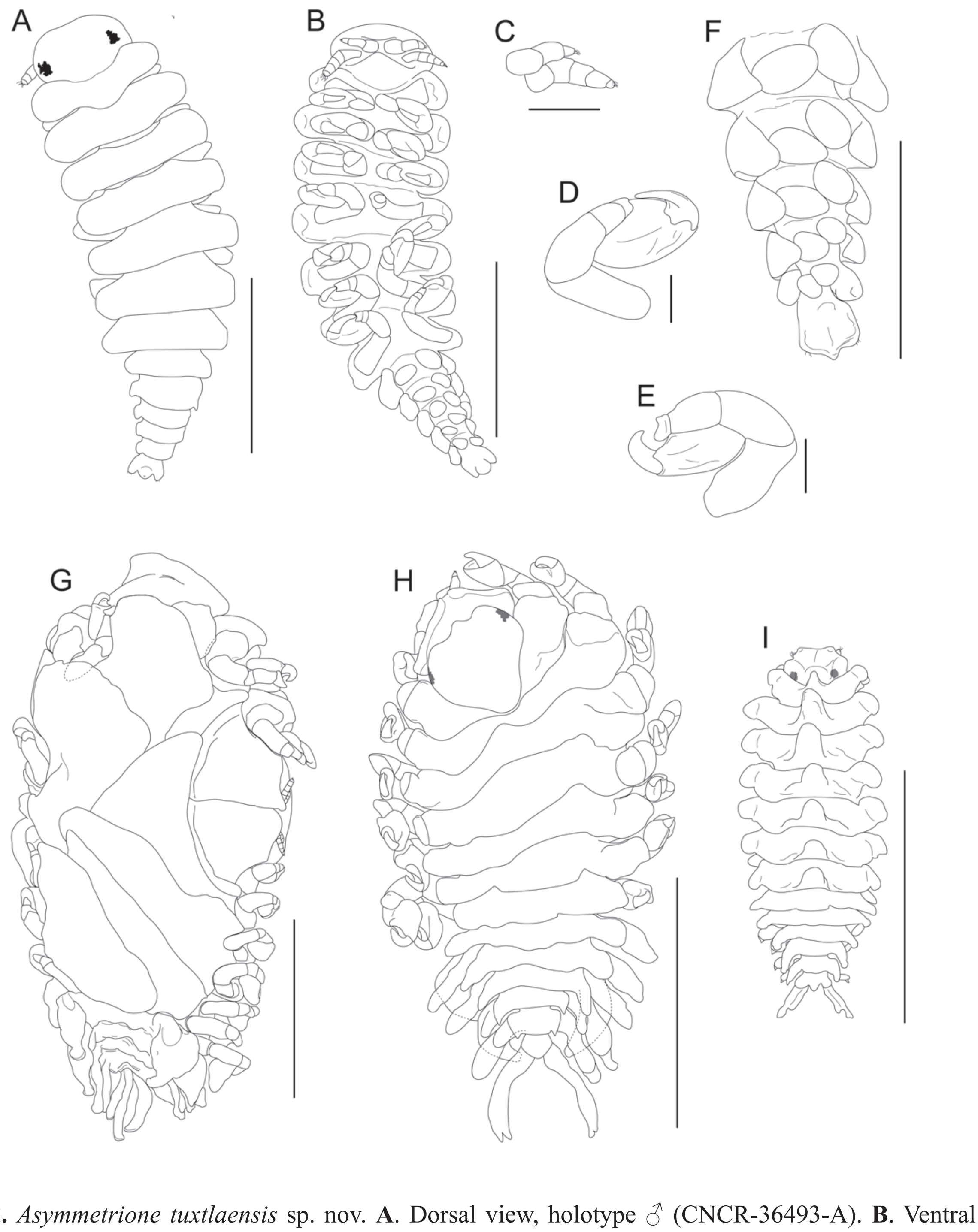

Fig. 8. *Asymmetrione tuxtlaensis* sp. nov. **A**. Dorsal view, holotype ♂ (CNCR-36493-A). **B**. Ventral view. **C**. Antennule and antennae ♂. **D**. First right pereopod of ♂, paratype (CNCR-36495). **E**. Seventh left pereopod of same ♂ paratype. **F**. Pleon of same ♂ paratype, ventral view. **G**. Adult ♀, paratype (CNCR-36499), ventral view. **H**. Juvenile ♀ (CNCR-36498-A), dorsal view. **I**. Bopyridium (CNCR-36492-B), dorsal view. Scale bars: A–B, G–I = 1.0 mm; C–E = 0.1 mm; F = 0.5 mm.

from the four ovigerous females examined was 455 ± 313 embryos, the minimum (110 embryos) was recorded in the smallest ovigerous female whilst the maximum (811 embryos) fecundity was recorded in a female of 2.93 mm TL (Table 1). The average length and width of embryos by stage of development and epicaridium larva are shown in Table 1. Sizes of embryos in egg stage ranged from 0.118 to 0.182 mm of length and between 0.145 and 0.182 mm of width, whilst the length of embryos in stage I varied from 0.145 to 0.182 mm and their width between 0.164 and 0.218 mm. Volumes of embryo in egg stage ranged from 0.0012 to 0.0031 mm^3, and for embryos in stage I between 0.0018 and 0.0038 mm^3. The average volume of both stages of development (Table 1) is similar to the range calculated for other bopyrids (Romero-Rodríguez & Álvarez 2020). The epicaridium larvae length ranged from 0.127 to 0.182 mm and the width between 0.218 mm and 0.273 mm.

Asymmetrione tuxtlaensis sp. nov. parasitized more females (n = 10) than males (n = 4) of *Calcinus antillensis*, though no statistical differences were found ($\chi^2 = 0.6$, df =1; $P < 0.05$) and both host sexes were of similar average sizes 4.05 ± 1.09 mm SL and 3.96 ± 1.37 mm SL, respectively. Two host females were ovigerous, a female of 3.50 mm SL carried 40 embryos rather circular in shape and yellowish in color with an average length, width and volume of 0.329 ± 0.013 mm, 0.314 ± 0.013 mm and 0.017 ± 0.002 mm^3, respectively. The second female of 5.00 mm SL carried 206 embryos attached on the abdomen, which were ovoid in shape and showed a thin eye line, their average length, width and volume were 0.362 ± 0.025 mm, 0.335 ± 0.013 mm and 0.021 ± 0. 002 mm^3, respectively. The number of embryos of both females was less than the average fecundity reported for *C. antillensis* (Turra & Leite 1999) but embryo size was in the range reported for this species by Turra & Leite (2007).

The 16 parasitized hosts examined were found in a 694 hermit crab sample, this represents a prevalence of 2.31%.

Genus *Bopyrissa* Nierstrasz & Brender à Brandis, 1931

Bopyrissa wolffi Markham, 1978
Figs 1, 2F, 9, Table 1

Bopyrissa wolffi Markham, 1978: 103–107, figs 1–5, table 1.

Stegias clibanarii – Pearse 1932: 4–5, figs 22–26 (in part). — Schultz 1969: 323, fig. 514 (non *stegias clibanarii*).
Pseudione sp. – Menzies & Glynn 1968: 17–18, figs 2A–B. — Markham 1972: 64; 1975a: 228. — McDermott 1974: 2.
Bopyrissa wolffi – Markham 1979: 523 (in key), 524; 1986: 154; 2003: 72. — Kensley 1994: table 1. — Markham & Donath-Hernández 1990: 243. — Markham *et al*. 1990: 416. — Camp 1998: 134. — McDermott 2002: 33–40, tables 1, 3. — Boyko & Williams 2004: 359–361, 369. — Román-Contreras, 2008: 106 (in table 2). — McDermott *et al*. 2010: 8. — Cericola & Williams 2015: table 1. — An *et al*. 2018: 579, 589 (in key), table 1. — Williams *et al*. 2019: 92 (in key), 93 (in key), 95. — Klompmaker *et al*. 2022 fig. 5.2.
Bopyrissa wolfii (sic) – Romero-Rodríguez & Martínez-Mayén 2018: 1191 (in table II).

Material examined

MEXICO • 1 ovigerous ♀ (2.18 mm TL), 1 ♂ (0.78 mm TL); Quintana Roo, Cozumel, Km 13 coastal road; 20º25′09″ N, 87º00′42″ W; 20 Apr. 1988; J.L. Villalobos *et al*. leg.; host ♀ of *Clibanarius tricolor* (3.20 mm SL); O. Valdez det. host; CNCR-36501 • 1 ovigerous ♀ (3.37 mm TL), 1 ♂ (1.15 mm TL); Quintana Roo, Ensenada Lamcom, NE border of Isla Blanca; 21º24′45.44″ N, 86º48′35.29″ W; 18 Jun. 2005; J.L. Villalobos *et al*. leg.; host ♂ of same species as for preceding (4.85 mm SL); J. Romero det. host; CNCR-

36502-A • 1 ovigerous ♀ (3.32 mm TL), 1 ♂ (1.13 mm TL); same collection data as for preceding; host ♀ of same species as for preceding (4.75 mm SL); CNCR-36502-B • 1 ovigerous ♀ (4.90 mm TL), 1 ♂ (1.47 mm TL); Veracruz, south inlet of Laguna de Tamiahua; 21º16′45″ N, 97º26′41″ W; 21 Sep. 2011; J.L. Bortolini leg.; host ♀ of *Clibanarius vittatus* (Bosc, 1801) (7.50 mm SL); G. Cervantes det. hosts; CNCR-

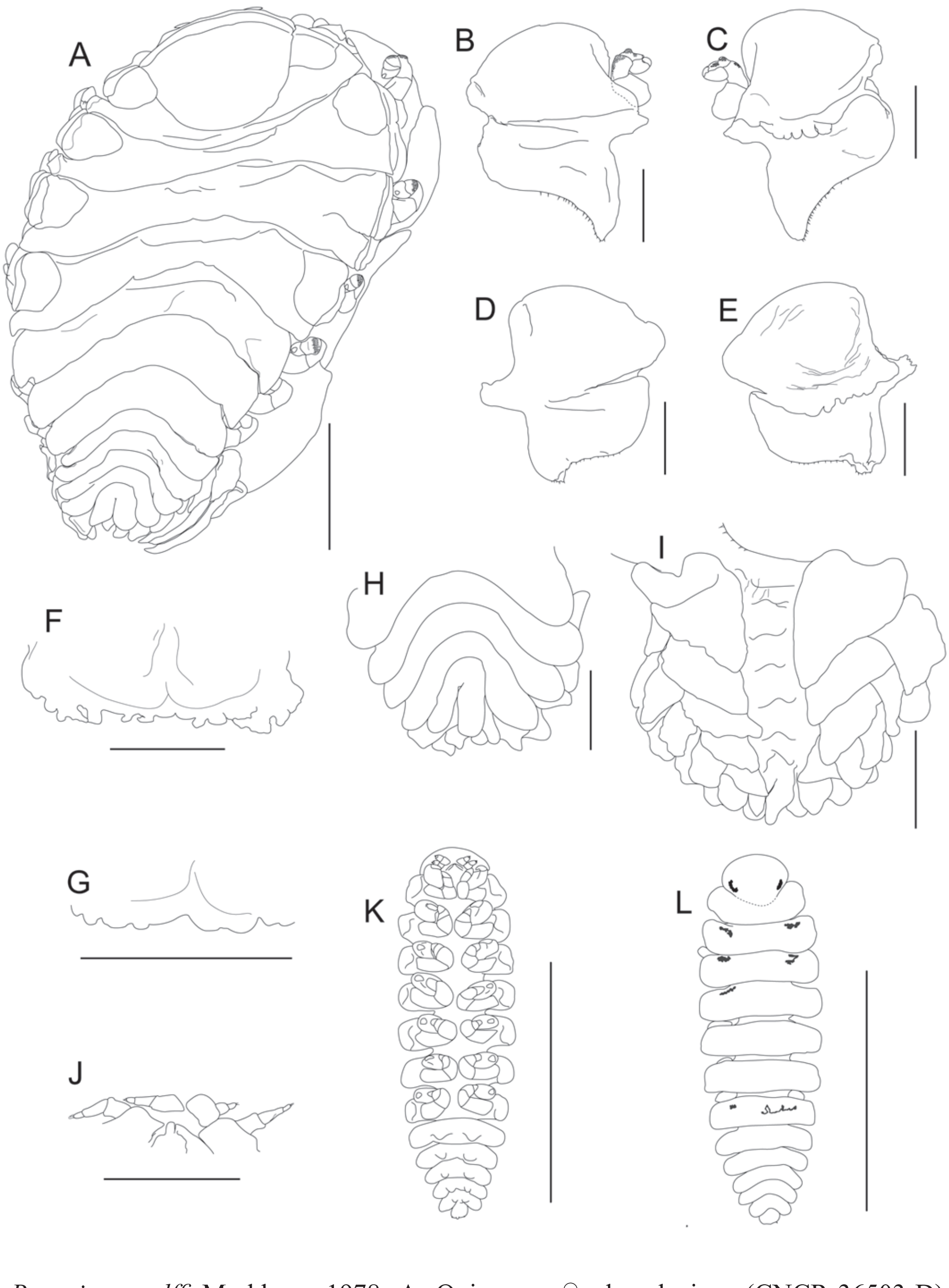

Fig. 9. *Bopyrissa wolffi* Markham, 1978. **A**. Ovigerous ♀, dorsal view, (CNCR-36503-D). **B**. First oostegite left side, external view. **C**. Same, internal view. **D**. First oostegite right side, external view. **E**. Same, internal view. **F**. Barbula. **G**. Barbula (CNCR-36501). **H**. Pleon, dorsal view (CNCR-36501). **I**. Pleon, ventral view. **J**. Antennule and antennae. **K**. ♂, ventral view. **L**. Same, dorsal view. Scale bars: A, K–L = 1.0 mm; B–G, I–J = 0.5 mm; H = 0.2 mm.

36503-A • 1 ovigerous ♀ (3.76 mm TL), 1 ♂ (1.20 mm TL); same collection data as for preceding; host ♀ of same species as for preceding (6.07 mm SL); CNCR-36503-B • 1 ovigerous ♀ (4.10 mm TL), 1 ♂ (1.04 mm TL); same collection data as for preceding; host ♀ of same species as for preceding (7.70 mm SL); CNCR-36503-C • 1 ovigerous ♀ (4.95 mm TL), 1 ♂ (1.64 mm TL); same collection data; host ♂ of same species as for preceding (8.00 mm SL); CNCR-36503-D • 1 ovigerous ♀ (4.50 mm TL), 1 ♂ (1.64 mm TL); same collection data; host ♂ of same species as for preceding (6.47 mm SL); CNCR-36503-E.

Distribution

Bopyrissa wolffi is distributed from North Carolina, Florida and Texas, USA, to the Bahamas, Bermuda, Puerto Rico and Mexico (Boyko & Williams 2004). In Mexico, this bopyrid had only been recorded parasitizing *C. tricolor* near Akumal, Quintana Roo (Markham *et al*. 1990); here, two more locations on this coast are added, Isla Blanca and Cozumel, parasitizing *C. tricolor*. Similarly, for the first time *B. wolffi* is recorded attached to *C. vittatus* in Laguna de Tamiahua, Veracruz (Fig. 1A), which is a new locality for this bopyrid in the Gulf of Mexico. McDermott *et al*. (2010) noted that only two hosts are recognized for *B. wolffi*, *C. tricolor* and *C. vittatus*.

Remarks

Both females (Figs 2F, 9A) and males (Fig. 9K–L) examined match well the description of *Bopyrissa wolffi* provided by Markham (1978); however, the following variations were observed: the marsupium of five females was partially or totally closed; first pair of oostegites differs in size, the one on the short side of the female was consistently larger than the one on the opposite side (Fig. 9B–E). Most females (n = 7) show the barbula with a single, stout and crenulated lateral projection (Fig. 9F), similar to that noted as variation and illustrated by Markham (1978: fig. 3b) but one of them (CNCR-36501) bears just a small bump on each side on the barbula (Fig. 9G), as well as pleomeres 1–3 distinct whilst pleomeres 4–5 are fused (Fig. 9H). Excepting one female (CNCR-36502-C) that had four pairs of pleopods biramous and the fifth uniramous, all other females examined had five pairs of pleopods biramous, with the endopod thinner and larger than exopod (Fig. 9I).

Markham (1978) described the antennae of *B. wolffi* as "markedly reduced", in our females the antennule was short and 3-segmented whilst the antenna was thin, long and 4-segmented, both bearing small apical setae (Fig. 9J). Likewise, in males of this species Markham (1978) noted the antennule of three segments and the antenna as "obscurely segmented (maybe of four segments)", in the males examined both antennule and antenna were 3-segmented and of similar outline and size (Fig. 9K). The pleopods in our males were a pair of small bulges at middle of each pleomere, those in first pleomere were the largest and from pleomeres 2 to 5 gradually decreasing in size (Fig. 9K).

Reproduction

The average TL of ovigerous females (3.89 ± 0.93 mm) of *P. wolffi* was more than twice that reported (1.91 mm) by McDermott (1998), since this author recorded ovigerous females between 1.73 and 2.20 mm in size and the females with embryos examined here ranged from 2.18 mm TL to 4.95 mm TL (Table 1). This noticeable difference in sizes may explain the higher overall average fecundity calculated in our samples (2182.17 ± 1660.14 embryos) compared to the mean fecundity of 314 embryos calculated by McDermott (1998). Only the smallest ovigerous female (Table 1), with an evident loss of embryos (220 embryos) was below the range reported by McDermott (1998).

The average length and width of embryos of *B. wolffi* by stage of development and epicaridium larvae are shown in Table 1. Sizes of embryos in egg stage ranged from 0.109 to 0.145 mm of length and between 0.091 and 0.127 mm of width, whilst the lengths of embryos in stage I varied from 0.145 to 0.182 mm and their width between 0.127 and 0.164 mm. Volume of embryo in egg stage ranged from 0.0005 to 0.0012 mm^3, and for embryos in stage I varied between 0.0012 and 0.0023 mm^3. The average volumes of both stages of development (Table 1) are comparable to those reported for other bopyrids of similar sizes (see Romero-Rodríguez & Álvarez 2020). The epicaridium larvae length ranged from 0.164 to 0.200 mm and the width between 0.109 mm and 0.145 mm.

In both hermit crab species parasitized by *B. wolffi* a similar number of females and males were recorded, thus no statistical differences were found (χ^2 = 0.01, df =1; $P < 0.05$), and both sexes were of similar average sizes: *C. tricolor* had an average size of 3.98 ± 1.10 mm of shield for females (n = 2) and 4.85 mm of shield for males (n = 1), whilst in *C. vittatus* the average size was 7.09 ± 0.89 mm of shield for females (n = 3) and 7.23 ± 1.08 mm of shield for males (n = 2).

The prevalence estimated for *B. wolffi* was 3.36 %, eight parasitized hosts out of 238 individuals.

Key to genera and species of bopyrids of hermit crabs from the Atlantic coast of Mexico

Based on females, modified from Boyko & Williams 2003 and Williams et al. 2019. Species non-examined here indicated by *.

1. Attached to the abdomen of the host (Athelginae) 2
– Attached to the branchial chamber of the host (Pseudioninae) 5

2. Pleomeres with lateral plates 3
– Pleomeres without lateral plates .... ***Parathelges*** (***P. occidentalis**** Markham, 1972 only species in the area)

3. Lateral plates on pleomeres 1–5 4
– Lateral plates on pleomeres 1–3 only .... *Stegias* (***S. clibanarii*** Richardson, 1904 only species in the area)

4. Lateral plates on pleomere 5 reduced, globular o scar-like .... ***Pseudostegias*** (***P. atlantica*** Lemos de Castro, 1965 only species in the area)
– Lateral plates on pleomere 5 normal .... ***Anathelges*** (***A. hyptius*** (Thompson, 1902) only species in the area)

5. Females usually greatly distorted (~ 90° or more), if not distorted with propodal sockets on pereopods .... ***Asymmetrione*** 6
– Females scantily distorted (~ 70°) or nearly symmetrical, lacking propodal sockets on pereopods .... ***Bopyrissa*** (***B. wolffi*** Markham, 1978 only species in the area)

6. Greater than 50º body asymmetry 7
– Less than 50º body asymmetry .... ***Asymmetrione desultor*** Markham, 1975

7. First pair of pereopods at both sides of head of similar size, pleopods 1–5 biramous .... ***Asymmetrione clibanarii**** Markham, 1975
– First pair of pereopods at both sides of head clearly differs in size, pleopods 1–4 biramous and 5 uniramous .... ***Asymmetrione tuxtlaensis*** sp. nov.

Discussion

Until now, only three bopyrid species had been recorded on hermit crabs from the Mexican Atlantic: *B. wolffi* and *Parathelges occidentalis* Markham, 1972 in Quintana Roo, both attached to *C. tricolor* (Markham *et al*. 1990), and *A. hyptius* in Campeche parasitizing *P. longicarpus* (Román-Contreras & Martínez-Mayén 2011). The record of four more bopyrid species in this region, with one new species, from samples of hermit crabs collected in a period of 60 years (from 1956 to 2016) and housed at the CNCR shows the importance of scientific collections as information reservoirs. Likewise, this shows that the ectoparasites information is overlooked even when probable hosts are processed to get taxonomic, biological and/or ecological data, as was noted by Boyko & Williams (2009).

From the six species examined, *A. hyptius* and *A. desultor* are widely distributed from the USA to Brazil parasitizing eight hermit crab species each. In contrast, *B. wolffi* and *S. clibanarii* are restricted from the Carolinas, USA, to the Caribbean parasitizing two and one host species, respectively (Fig. 1). This is consistent with the statement that some bopyrid species extend their geographic ranges by parasitizing multiple hosts (Boyko & Williams 2009); but does not match with the distribution range extension of *P. atlantica* reported here since only three host species have been recognized for it, though this may be due to the fact that it is only the fourth time that this parasite has been collected since it was described (Lemos de Castro 1965; Figueredo *et al*. 2013; Ribeiro *et al*. 2019; this study).

Along the Atlantic coast of Mexico, no hermit crabs bearing bopyrids were recorded for Tabasco, Tamaulipas and Yucatan, which reflects the low number of samples of hermit crabs deposited in CNCR for these areas (n = none, 5 and 2, respectively). Most hermit crab samples were from Campeche (n = 70), Quintana Roo (n = 185) and Veracruz (n = 170). Except for *A. hyptius* that has been exclusively collected in Campeche (Román-Contreras & Martínez-Mayén 2011; this study), five of six bopyrid species examined were recorded in Veracruz (Fig. 1). In this region, only three bopyrid and one entoniscid species had been recorded until 2005 (see Román-Contreras 2008) but recently four more bopyrids species were registered in the area (Romero-Rodríguez & Álvarez 2020, 2021; Bortolini *et al*. 2021) which reveals Veracruz as a high diversity area for these parasites.

In two cases, *A. tuxtlaensis* sp. nov. was found in the same sample with another bopyrid. In Montepío, Veracruz, it shared host with *P. atlantica* but in Isla Blanca, Quintana Roo, *A. tuxtlaensis* parasitized a different host than that used by *B. wolffi*. Similar co-occurrences for *A. hyptius*, *A. desultor* and *B. wolffi* were reported by Boyko & Williams (2004) from the Bahamas.

In general, bopyrid reproductive data remains scant (Cericola & Williams 2015), and for the bopyrid species discussed here are limited to those provided by McDermott (1998, 2002) for *A. hyptius*, *S. clibanarii* and *B. wolffi*. Therefore, the first reproductive data from *P. atlantica*, *A. desultor* and *A. tuxtlaensis* sp. nov. are reported here. It is important to note that the reproductive information of the individuals examined come from samples not systematically collected for isopod parasites but it provides initial data on the biological traits of these bopyrids.

Overall, sizes of ovigerous females examined varied among similar ranges but fecundity differed between species, this could be related with the embryo sizes calculated, e.g., higher fecundity of ovigerous females with embryos in egg stage was recorded in *B. wolffi* (4.95 mm LT and 4507 embryos) and *A. hyptius* (4.00 mm LT and 2625 embryos) whilst minimum fecundity was recorded in *P. atlantica* (3.92 mm LT and 177 embryos) but the average embryo size and volume of the latter were ~ 1.5 and 5 times, respectively, higher than those for *B. wolffi* and *A. hyptius* (see Table 1).

This is consistent with what has been observed in other decapod crustacean groups, where fecundity is related to the egg size, therefore some species produce few eggs but large in size while those species with small eggs have a high fecundity (Ramírez-Llodra 2002). Strömberg (1971) pointed out that bopyrid embryos rarely reach sizes of 0.2 mm since the small size and the large number of embryos agrees with the parasitic mode of life and the need of most epicarideans of two different hosts to complete their life-cycle. Steel & Steel (1975) noted that embryo sizes could be correlated with the duration of embryogenesis, hence it can provide information on the reproductive strategy of the species; e.g., *Entoniscoides okadai* Miyashita, 1940 has the largest embryos within the members of Bopyroidea (0.2 mm in diameter) and is the only known bopyrid species with no copepod host involved (Strömberg 1971). The similarity of the embryo sizes of *P. atlantica* and *A. desultor* with *E. okadai* could suggest a similar reproductive strategy, but embryo size also could be associated to other factors such as availability and quality of food or the energy content on it (Ramírez-Llodra 2002). This shows the need to improve the understanding on the reproductive biology of this group of isopods.

Castration of crustacean hosts is one of the most recognized effects of bopyrid isopods (McDermott 2002) but in some cases not all hosts are fully castrated (Calado *et al*. 2006) and ovigerous females bearing bopyrids had been reported for galatheids (Williams & Brown 1972), thalassinid shrimps (Dumbauld *et al*. 2011), alpheids shrimps (Romero-Rodríguez & Álvarez 2020) and portunid crabs (Corral *et al*. 2021). The record of two ovigerous females of *C. antillensis* parasitized by *A. tuxtlaensis* sp. nov. concurs with that observed for the hermit crabs *C. tricolor* parasitized by *S. clibanarii* (McDermott 2002), *Calcinus gaimardii* (H. Milne Edwards, 1848) and *Calcinus minutus* Buitendijk, 1937 both parasitized by *Bopyrissa marami* Williams, Boyko & Madad, 2019 (Williams *et al*. 2019).

McDermott *et al*. (2010) pointed out that the record of hosts simultaneously parasitized by both a bopyrid and a rhizocephalan is common; e.g., Williams *et al*. (2019) reported *C. minutus* simultaneously parasitized by the bopyrid *A. asymmetrica* and the rhizocephalan *Dipterosaccus* sp., and here we recorded *P. mclaughlinae* parasitized by *A. hyptius* and an undetermined rhizocephalan. Co-occurrence of bopyrids and rhizocephalans had been also recorded in lithodid crabs (Roccatagliata & Lovrich 1999) and squat lobsters (see Boyko & Williams 2009). Although the impact of both parasites on their hosts has been investigated, their impacts on host populations are still poorly understood (Boyko & Williams 2011).

Although the prevalence data presented here comes from samples that were not specific for isopod parasites, the prevalences of the branchial (*A. tuxtlaensis* sp. nov. and *B. wolffi*), and abdominal species (*A. hyptius* and *P. atlantica*) examined were within the ranges reported by Cericola & Williams (2015) for other branchial parasites (0.16–29.45 %) and abdominal parasites (0.15–7.20%). The high prevalences calculated for *A. desultor* and *S. clibanarii* are the result of the low number of specimens examined.

According to our results, the poor sampling observed for some areas and the number of probable hosts reported in the Gulf of Mexico (Felder *et al*. 2009) suggest that bopyrid diversity in this region remains underestimated. A key for the species reported in the study area hitherto is provided in order to improve the knowledge on the distribution and reproduction of these hermit crab parasites.

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