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CHRISTOPHER B. BOYKO, JASON D. WILLIAMS,  
AHMET ÖKTENER

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**Redescription of the Mediterranean endemic parasitic isopod *Anuropodione amphiandra* (Codreanu, Codreanu & Pike, 1966) n. comb. (Crustacea: Isopoda: Bopyridae) from *Munida rutllanti* Zariquiey Alvarez, 1952, with new records from Turkey and a review of the genus *Anuropodione* Bourdon, 1967**

**CHRISTOPHER B. BOYKO<sup>1,2</sup>, JASON D. WILLIAMS<sup>2</sup> and AHMET ÖKTENER<sup>3</sup>**

<sup>1</sup> Division of Invertebrate Zoology, American Museum of Natural History, Central Park West @ 79th St., New York, New York 10024, U.S.A.

<sup>2</sup> Department of Biology, Hofstra University, Hempstead, New York 11549, U.S.A.

<sup>3</sup> Department of Fisheries, Sheep Research Institute, Çanakkale Street 7km., 10200, Bandırma, Balıkesir, Turkey

Corresponding author: [cboyko@amnh.org](mailto:cboyko@amnh.org)

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## Abstract

Seven species of bopyrid isopods were previously known from Turkish Mediterranean waters; a purported eighth species, *Orthione griffenis* Markham, 2004, is based on incorrect identification and likely represents *Epipenaeon ingens ingens* Nobili, 1906, a species already known from the area. In the present study, we report on specimens referable to *Pleurocrypta amphiandra* Codreanu, Codreanu & Pike, 1966, infesting *Munida rutllanti* Zariquiey Alvarez, 1952, collected from the southern Aegean Sea off Turkey; this species was formerly known only from the Mediterranean off Algeria and the Adriatic Sea. The species is redescribed and illustrated for the first time and transferred to *Anuropodione* Bourdon, 1967, which is reviewed and *A. australiensis* Bourdon, 1976, is transferred to *Allorbmorphus* Bourdon, 1976. A key to all species of *Anuropodione* and a list of all bopyrids found on squat lobsters and porcelain crabs in the Mediterranean are provided.

**Keywords:** Aegean Sea; bopyrid; endemic; Epicaridea; squat lobster; Turkey.

## Introduction

The parasitic isopod family Bopyridae contains over 600 species (Boyko *et al.*, 2008 onwards), all of which are parasitic on calanoid copepods as larvae and decapod crustaceans as adults (Boyko & Williams 2009; Williams & Boyko 2012). Seven of these species have been reported from Turkish waters in the Mediterranean region: *Bopyrina ocellata* (Czerniavsky, 1868) from *Hippolyte inermis* Leach, 1816 (Artüz, 2017; Sea of Marmara); *Bopyrus squillarum* Latreille, 1802, from *Palaemon adspersus* Rathke, 1837, *P. elegans* Rathke, 1837, and *P. serratus* (Pennant, 1777) (Geldiay and Kocataş, 1972; Kirkim *et al.*, 2008); *Epipenaeon ingens ingens* Nobili, 1906, from *Penaeus aztecus* Ives, 1891 (a western Atlantic species introduced into the Mediterranean) (Korun *et al.*, 2013); *Pleurocrypta galathea* Hesse, 1865, from *Galathea squamifera* Leach, 1814 (Geldiay and Kocataş, 1972); *P. longibranchiata* (Bate & Westwood, 1867) from *Galathea nexa* Embleton, 1834, and *G. squamifera* (Geldiay and Kocataş, 1972; Kirkim *et al.*, 2008); *P. microbranchiata* G. O. Sars, 1898, from *Galathea intermedia* Lilljeborg, 1851 (Geldiay and Kocataş, 1972; Kirkim *et al.*, 2008);

*P. porcellanaelongicornis* Hesse, 1876, from *Pisidia* cf. *bluteli* (Risso, 1816) and *Pisidia* sp. (Geldiay and Kocataş, 1972; Kirkim *et al.*, 2008).

Mediterranean records of a purported eighth species of bopyrid, *Orthione griffenis* Markham, 2004, found infesting *Penaeus kerathurus* (Forskål, 1775) (Uluköy *et al.*, 2008, cited by Ceyhan *et al.*, 2009) are obvious misidentifications. Although *Orthione griffenis* has been documented as an invasive species in mud shrimp (Decapoda: Gebiidea) along the west coast of the US (Williams & An 2009; Hong *et al.*, 2015; Boyko *et al.*, 2017), no species of *Orthione* infest penaeid shrimp (Markham, 2004). It is most likely that these bopyrids are actually *Epipenaeon ingens ingens* Nobili, 1906, originally described from the Red Sea but which entered the Mediterranean before 1968 and was first reported from Turkey on the host *P. semisulcatus* De Haan, 1844 (Bourdon, 1968; An *et al.*, 2014). This bopyrid is now also known in the Mediterranean from the introduced shrimp hosts *P. aztecus* and *P. stylirostris* (Stimpson, 1871) (Korun *et al.*, 2013; An *et al.*, 2014). Owens and Rothlisberg (1991) suggested that *E. ingens ingens* might eventually infest the Mediterranean endemic host *P. kerathurus* and this

prediction appears to have been born out; this is the first record of *E. ingens ingens* on any Mediterranean endemic shrimp host.

The squat lobster *Munida rutllanti* Zariquiey Alvarez, 1952, lives on muddy bottoms in depths between 130 and 540 m and is historically distributed in the eastern Atlantic from northwestern Spain south to Mauritania, including the Canary and Cape Verde Islands, as well as in the western Mediterranean and Aegean Sea (Fransen, 2014). However, the species has spread eastward into the eastern Mediterranean and the Adriatic Sea (Frogia *et al.*, 2010; Petric *et al.*, 2010). *Munida rutllanti* has potential as a fishery due to its relatively large size (carapace length, excluding rostrum, up to 22 mm) and ability to be caught in large quantities (Kocak *et al.*, 2008; Frogia *et al.*, 2010; Fransen, 2014) but does not currently have commercial value and is not a target species (Kocak *et al.*, 2008).

Four squat lobster species in the genus *Munida* Leach, 1820 (*M. intermedia* A. Milne Edwards & Bouvier, 1899, *M. rugosa* (Fabricius, 1775), *M. rutllanti*, and *M. tenuimana* G. O. Sars, 1872) have been reported from Turkish waters (Bakir *et al.*, 2014), all of which have been recorded bearing bopyrids elsewhere in the Mediterranean (Table 1) but no bopyrids have previously been reported on any Turkish specimens belonging to these species of *Munida*. Three species of *Pleurocrypta* have been reported from squat lobster hosts collected off Turkey, but

all were on hosts in the genus *Galathea* Fabricius, 1793 (Galatheidae) (Table 1; see also Boyko *et al.*, 2012; Bakir *et al.*, 2014).

The present paper reports for the first time the presence of *Anuropodione amphiandra* (Codreanu, Codreanu & Pike, 1966) n. comb., parasitic on *M. rutllanti* from Turkish waters. Examination of a large series of specimens allowed us to determine that this species does not belong to *Pleurocrypta* Hesse, 1865, the genus to which it was originally assigned, and to quantify the variability in the pleon morphology of males.

## Material and Methods

Squat lobsters were collected at depths from 60 to 400 m with a commercially used bottom trawl (mesh size: 44 mm; time of haul period: 08:00-12:00 and 13:00-17:00; engine power of the commercial trawler: 700 hp; bottom type: muddy), off Babakale Port, North Aegean Sea, Turkey (39°25'2.32"N-39°28'11"N; 26°03'39.46"E-26°20'18"E) in March 2017 (93 specimens) and August 2018 (150 specimens).

Hosts and parasites were placed in 70% ethanol and parasites were subsequently removed from the host branchial chambers; male parasites were firmly attached to the ventral pleon region of females in all cases. Select parasites were dissected using a Wild M5 and an Olympus XZS12 stereomicroscope. Dissected parts were mounted

**Table 1.** List of bopyrid species known from squat lobsters and porcelain crabs (Anomura: Galatheaidea) in the Mediterranean Sea.

Bopyrid Species	Hosts	Mediterranean Localities	References
<i>Anuropodione amphiandra</i> (Codreanu, Codreanu & Pike, 1966) n. comb.	<i>Munida rutllanti</i> Zariquiey Álvarez, 1952	Algeria; Adriatic Sea	Codreanu, Codreanu & Pike, 1966; Petric <i>et al.</i> , 2010
<i>Pleurocrypta galathea</i> Hesse, 1865	<i>Galathea dispersa</i> Bate, 1859 <i>Galathea nexa</i> Embleton, 1834 <i>Galathea squamifera</i> Leach, 1814	France, Monaco, Turkey	Bourdon, 1968; Geldiay & Kocataş, 1972
<i>Pleurocrypta longibranchiata</i> (Bate & Westwood, 1867)	<i>Galathea nexa</i> Embleton, 1834; <i>Galathea squamifera</i> Leach, 1814	France, Turkey	Geldiay & Kocataş, 1972
<i>Pleurocrypta microbranchiata</i> G. O. Sars, 1898	<i>Galathea intermedia</i> Lilljeborg, 1851	Spain, Turkey	Bourdon, 1968; Geldiay & Kocataş, 1972
<i>Pleurocrypta piriformis</i> Bourdon, 1968	<i>Galathea strigosa</i> (Linnaeus, 1761)	Spain	Bourdon, 1968
<i>Pleurocrypta porcellanaelongicornis</i> Hesse, 1876	<i>Pisidia longicornis</i> (Linnaeus, 1767)	Turkey	Geldiay & Kocataş, 1972
<i>Pleurocrypta strigosa</i> Bourdon, 1968	<i>Galathea strigosa</i> (Linnaeus, 1761)	Spain, Italy	Bourdon, 1968
<i>Pseudione crenulata</i> G. O. Sars, 1898	<i>Munida intermedia</i> A. Milne Edwards & Bouvier, 1899 <i>Munida rugosa</i> (Fabricius, 1775) <i>Munida tenuimana</i> G. O. Sars, 1872	Spain, Italy	Zariquiey Alvarez, 1958; Castriota <i>et al.</i> , 2010

on slides in glycerine-gelatine mounting medium; pleopods were stained with methylene blue. Line drawings were made with a camera lucida drawing tube attached to Olympus compound or dissecting microscopes. Final images were created by tracing a scanned copy of the original sketch with a Wacom Cintiq pen display using Adobe Illustrator. In addition to conventional light micrographs, some specimens were imaged with a Macro pod Pro kit (MacroscopicSolutions) and resulting pictures were aligned and stacked with the focus stacking software Zerene Stacker (10–65 images from bottom to top of specimens).

Carapace length (CL, inclusive of rostrum) is provided as an indicator of size for the hosts. Isopod size is given as total body length (anterior margin of head to posterior margin of pleotelson). Measurements were made to 0.1 mm using an ocular micrometer, micro-scale tool (Electron Microscopy Services), or a micrometric programme (Pro-way).

Authors and dates of hosts and bopyrid parasites were verified using WoRMS (Boyko *et al.*, 2008 onwards). Bibliographic references are provided for authors and dates of all parasite taxa but not for those of host species.

Voucher specimens were deposited in the collections of the Muséum National d'Histoire Naturelle (MNHN) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

## Results

### Systematics

Family Bopyridae Rafinesque, 1815

Subfamily Pseudioninae Codreanu, 1967

Genus *Anuropodione* Bourdon, 1967

Type species: *Anuropodione senegalensis* Bourdon, 1967

### Remarks

Prior to the present study, *Anuropodione* contained five species (Boyko *et al.*, 2008 onwards) but a review of these taxa shows that *A. australiensis* Bourdon, 1976, is not properly placed in this genus, *A. dubius* (Nierstrasz & Brender à Brandis, 1929) is questionably placed here, and *Pleurocrypta amphiandra* should be transferred to *Anuropodione*. Examination of the description and illustrations of *A. australiensis* shows that this species is not correctly generically placed. The minimal development of the lateral plates on the pleon, expanded posterior lobe with acute ventral point on the first oostegite of the female, as well as the rounded, extended head and weakly projecting pleotelson and overall body proportions of the male indicate that this species is not congeneric with *A. senegalensis* Bourdon, 1967, the type species of *Anuropodione*. In many characters, *A. australiensis* is closer to *Allorbimorphus haigae* Bourdon, 1976, but it differs from that species in the females of *A. haigae* having only four pairs of biramous pleopods (four pairs biramous pleop-

ods, fifth pair uniramous in *A. australiensis*), uniramous uropods (no uropods in *A. australiensis*), and in males of *A. haigae* having all pleomeres distinct (1-3 pleomeres in *A. australiensis*). It is possible that *A. australiensis* should be placed in a new genus, but we refrain from such an action in the absence of material; however, we transfer the species to *Allorbimorphus* Bourdon, 1976, the genus to which it shares most characters, as *Allorbimorphus australiensis* (Bourdon, 1976) n. comb.

It is unclear if *A. dubius* is correctly placed in this genus. The female shows essentially no lateral plate development on the pleomeres compared to other species of *Anuropodione* and there are 5 uniramous pleopods, which contrasts with the typical 5 biramous pairs in species of *Anuropodione* (excepting *A. megacephalon*, which has 4 biramous and 1 uniramous pair). However, the pleon of the male greatly resembles that of one of the morphs found in *A. amphiandra* and the morphology of the first oostegite and maxilliped (see Bourdon, 1972) are very similar to those of other *Anuropodione* species. Bourdon (1972) compared *Probopyrus dubius*, which was clearly not correctly placed in *Probopyrus* Giard & Bonnier, 1888, to all other species known where females lacked uropods: *Parioninella obovata* Shiino, 1958 (now *Ovoionella obovata* (Shiino, 1958); see Boyko, 2004)), *A. senegalensis*, and *Bopyrissa magellanica* (Nierstrasz & Brender à Brandis, 1929) and concluded that the male and female of *P. dubius* resembled those of *A. senegalensis* more than the other species. We concur with Bourdon's (1972) conclusion, inasmuch as the male of *O. obovata* is very different from that of *P. dubius* and the female of *B. magellanica* actually does have well-developed uropods, a fact not known to Bourdon (1972; see Williams *et al.*, submitted). Unfortunately, it will be difficult to recollect *A. dubius* and garner a larger sample size, as the host was only given by Nierstrasz & Brender à Brandis (1929) as "*Galathea* spec."

*Pleurocrypta amphiandra* Codreanu, Codreanu & Pike, 1966, belongs to *Anuropodione* on the basis of the females lacking well-developed uropods as well as maxilliped palps. Females of *Pleurocrypta* always have well-developed uropods (uniramous or biramous, depending on the species) and maxilliped palps. Codreanu *et al.* (1966) described the pleotelson of *Pleurocrypta amphiandra* as bearing "exceptionnellement des uropodes rudimentaires"; in all specimens we examined, there are small ridges on the pleotelson but they are not true uropods. Bourdon (1972), however, did report very small, poorly developed uropods on some specimens of *A. senegalensis*.

### Key to species of *Anuropodione* Bourdon, 1967, based on females

- 1a. Lateral plates of pleon weakly developed, closely adpressed ... *A. dubius* (Nierstrasz & Brender à Brandis, 1929) [Thailand, 27.4 m depth, infesting "*Galathea* sp."]
- 1b. Lateral plates of pleon forming distinct lateral ex-



tensions, not closely adpressed ... 2

2a. Head length greater than that of first four pereomeres combined ... *A. megacephalon* Markham, 1974 [28°48'N; 85°02'W, Gulf of Mexico, 54-60 m depth, infesting *Munida pusilla* Benedict, 1902]

2b. Head length less than that of first four pereomeres combined ... 3

3a. Lateral plates of pleon thin, tapered distally ... *A. carolinensis* Markham, 1974 [35°05'N 74°33'W to 37°09'N 75°11.5'W, 83-662 m depth, infesting *Munida iris* A. Milne Edwards, 1880]

3b. Lateral plates of pleon expanded distally, ovate ... 4

4a. Lateral plates of pleon non-overlapping ... *A. senegalensis* Bourdon, 1967 [Senegal to Republic of the Congo, 200-300 m depth, infesting *Munida* sp. and *M. speciosa* von Martens, 1878]

4b. Lateral plates of pleon overlapping ... *A. amphiandra* (Codreanu, Codreanu & Pike, 1966) n. comb. [Mediterranean Sea: Algeria to Turkey; Adriatic Sea, 60-400 m depth, infesting *Munida rutllanti* Zariquiey Alvarez, 1952].



**Fig. 1:** *Munida rutllanti* Zariquiey Alvarez, 1952, dorsal view of male specimen (USNM 1492241) with swollen right branchial chamber caused by *Anuropodione amphiandra* (Codreanu, Codreanu & Pike, 1966) n. comb. Scale bar = 3 mm.

***Anuropodione amphiandra* (Codreanu, Codreanu & Pike, 1966) n. comb.** (Figs. 1-4)

*Pleurocrypta* sp. Délye, 1955: 84 [Béni-Saf, west of Oran, Algeria, infesting *Munida iris* ssp. *rutllanti* [sic] = *M. rutllanti*]; Petric *et al.*, 2010: 1395-1403, fig. 7a [Adriatic Sea, infesting *M. rutllanti*].

“un bopirido sp.?” Zariquiey Alvarez, 1958: 101 [mention].

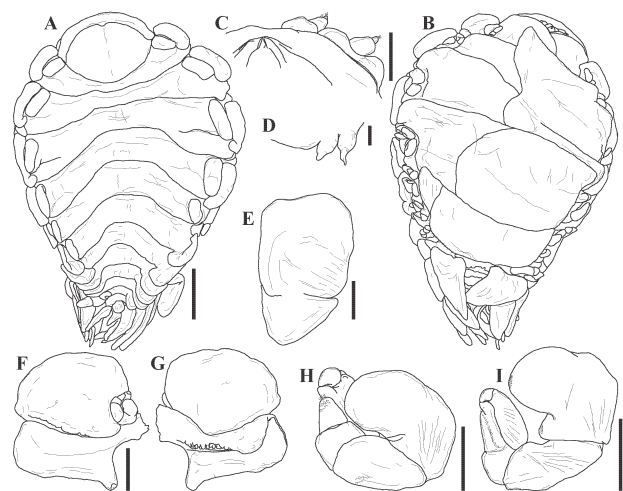
*Pleurocrypta amphiandra* Codreanu, Codreanu & Pike, 1966: 1071-1072 [type locality: Béni-Saf, west of Oran, Algeria, 205-230 m; type host: *Munida iris rutllanti* Zariquiey Alvarez, 1952 = *M. rutllanti*]; Markham, 1974: 270 [mention], 271 [table], 265 [list]; Bourdon, 1976: 366 [mention]; Boyko & Williams, 2011: 285 [mention]; Boyko *et al.*, 2012: 9, 18 [list].

“le Bopyridae des *Munida iris rutllanti* [sic] Zariquiey Alvarez des côtes algériennes” Bourdon, 1968: 221 [mention].

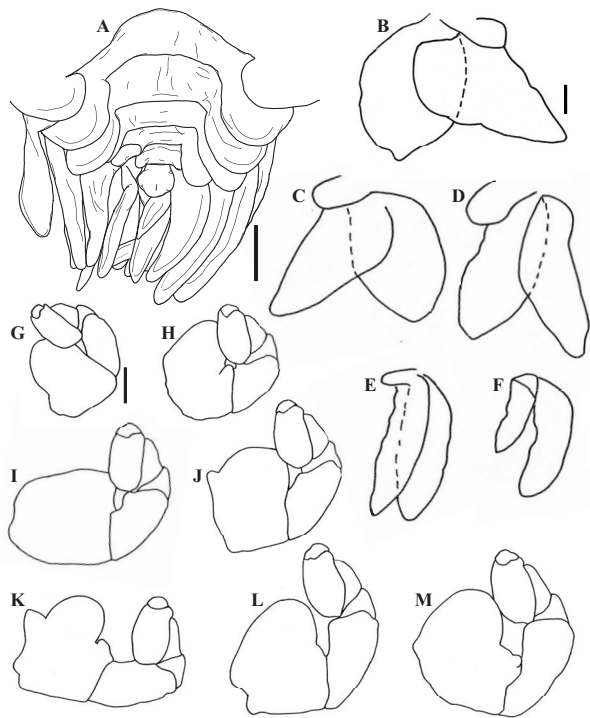
“parasite (non encore décrit à notre connaissance) des *Munida iris rutllanti* [sic]” Bourdon, 1972: 833 [mention].

#### *Material examined and used as basis for redescription*

1 dextral ovigerous female (5.5 mm), 1 mature male (1.6 mm, pleon elongate with 3 pleomeres) from right branchial chamber of unknown sex and size *Munida rutllanti* Zariquiey Alvarez, 1952, off Babakale Port (39°25'2.32"N-39°28'11"N; 26°03'39.46"E-26°20'78"E, North Aegean Sea, Turkey)



**Fig. 2:** *Anuropodione amphiandra* (Codreanu, Codreanu & Pike, 1966) n. comb., female specimen USNM 1492250 (A-I). A, dorsal view. B, ventral view. C, right antennule (top) and antenna (bottom). D, left barbula. E, left maxilliped, outer view. F, left oostegite 1, outer view. G, left oostegite 1, inner view. H, left pereopod 1. I, left pereopod 7. Scale bars = 2 mm (A, B), 250 µm (C, D, H), 500 µm (E-G, I).



**Fig. 3:** *Anuropodione amphandra* (Codreanu, Codreanu & Pike, 1966) n. comb., female specimen USNM 1492250 (A), personal collection (B-M). A, Pleon, dorsal view, B-F, pleopods 1-5, respectively, G-M, pereopods 1-7, respectively. Scale bars = 500  $\mu$ m (A), 1 mm (B-F), 250  $\mu$ m (G-M).

in March 2017 or August 2018 (USNM 1492241; Fig. 1) (all other specimens cited below with same collection data); 1 dextral ovigerous female (8.6 mm), 1 mature male (4.8 mm, pleon elongate with 5 pleomeres), from right branchial chamber of unknown sex and size *M. rutllanti* (USNM 1492244); 1 dextral ovigerous female (7.5 mm), 1 mature male (1.7 mm, pleon short with all pleomeres coalesced), from right branchial chamber of unknown sex and size *M. rutllanti* (USNM 1492250); 1 sinistral ovigerous female (7.0 mm), 1 mature male (pleon elongate with 5 pleomeres), from left branchial chamber of unknown sex and size *M. rutllanti* (USNM 1492279); 1 dextral ovigerous female (5.5 mm), 1 mature male (pleon short with all pleomeres coalesced), from right branchial chamber of male *M. rutllanti* (15 mm CL) (USNM 1492233); 1 dextral ovigerous female (7.3 mm), infesting unknown size and sex *M. rutllanti* (MNHN-IU-2017-72).

#### Additional material examined

All specimens with same collection data as USNM 1492241: 1 sinistral ovigerous female (6.48 mm), 1 mature male (1.85 mm), infesting left branchial chamber of female *M. rutllanti* (36 mm CL); 1 sinistral ovigerous female (6.89 mm), 1 mature male (1.24 mm), infesting left branchial chamber of female *M. rutllanti* (37 mm CL); 1



**Fig. 4:** *Anuropodione amphandra* (Codreanu, Codreanu & Pike, 1966) n. comb., male specimens USNM 1492250 (A-D), USNM 1492279 (E), USNM 1492241 (F). A, dorsal view. B, ventral view. C, mouthparts, left antennule (top), left antenna (bottom) and left pereopod 1. D, left pereopod 7. E, pleon with 5 segments. F, pleon with 3 segments. Scale bars = 250  $\mu$ m (A, B, E, F), 50  $\mu$ m (C, D).

dextral ovigerous female (6.94 mm), 1 mature male (1.57 mm), infesting right branchial chamber of female *M. rutllanti* (39 mm CL); 1 sinistral ovigerous female (7.09 mm), 1 mature male (1.28 mm), infesting left branchial chamber of female *M. rutllanti* (39 mm CL); 1 dextral ovigerous female (6.94 mm), 1 mature male (1.57), infesting right branchial chamber of female *M. rutllanti* (39 mm CL); 1 dextral ovigerous female (7.01 mm), 1 mature male (1.49 mm), infesting right branchial chamber of female *M. rutllanti* (39 mm CL); 1 dextral ovigerous female (7.65 mm), 1 mature male (1.76 mm), infesting right branchial chamber of female *M. rutllanti* (40 mm CL); 1 sinistral ovigerous female (7.09 mm), 1 mature male (1.72 mm), infesting left branchial chamber of female *M. rutllanti* (40 mm CL); 1 sinistral ovigerous female (7.47 mm), 1 mature male (1.56 mm), infesting left branchial chamber of female *M. rutllanti* (41 mm CL); 1 sinistral ovigerous female (7.22 mm), 1 mature male (2.47 mm), infesting left branchial chamber of female *M. rutllanti* (41 mm CL); 1 sinistral ovigerous female (7.29 mm), 1 mature male (2.65 mm), infesting left branchial chamber of female *M. rutllanti* (41 mm CL); 1 dextral ovigerous female (7.24 mm), 1 mature male (3.63 mm), infesting right branchial chamber of female *M. rutllanti*

(42 mm CL); 1 sinistral ovigerous female (7.74 mm), 1 mature male (1.82 mm), infesting left branchial chamber of female *M. rutllanti* (42 mm CL); 1 sinistral ovigerous female (7.87 mm), 1 mature male (1.74 mm), infesting left branchial chamber of female *M. rutllanti* (42 mm CL); 1 sinistral ovigerous female (7.96 mm), 1 mature male (2.10 mm), infesting left branchial chamber of female *M. rutllanti* (42 mm CL); 1 sinistral ovigerous female (6.65 mm), 1 mature male (2.31 mm), infesting left branchial chamber of female *M. rutllanti* (43 mm CL); 1 dextral ovigerous female (7.63 mm), 1 mature male (1.64 mm), infesting right branchial chamber of female *M. rutllanti* (43 mm CL); 1 sinistral ovigerous female (7.90 mm), 1 mature male (1.89 mm), infesting left branchial chamber of female *M. rutllanti* (44 mm CL); 1 sinistral ovigerous female (8.02 mm), 1 mature male (1.51 mm), infesting left branchial chamber of female *M. rutllanti* (45 mm CL); 1 sinistral ovigerous female (7.68 mm), 1 mature male (1.69 mm), infesting left branchial chamber of female *M. rutllanti* (45 mm CL); 1 dextral ovigerous female (7.67 mm), 1 mature male (2.99 mm), infesting right branchial chamber of female *M. rutllanti* (45 mm CL); 1 dextral ovigerous female (8.15 mm), 1 mature male (1.87 mm), infesting right branchial chamber of female *M. rutllanti* (46 mm CL); 1 sinistral ovigerous female (8.42 mm), 1 mature male (1.54 mm), infesting left branchial chamber of female *M. rutllanti* (47 mm CL); 1 sinistral ovigerous female (8.34 mm), 1 mature male (2.19 mm), infesting left branchial chamber of female *M. rutllanti* (50 mm CL); 1 sinistral ovigerous female (8.30 mm), 1 mature male (1.98 mm), infesting left branchial chamber of female *M. rutllanti* (52 mm CL).

#### *Additional hosts examined*

All specimens with same collection data as USNM 1492241: 1 female *M. rutllanti* (16 mm CL), with swollen left branchial chamber (parasite not present) (USNM 1492232); 1 male *M. rutllanti* (22.4 mm CL), with swollen right branchial chamber (parasite not present); host also infested with immature *Lernaeodiscus ingolfi* (1.0 x 2.5 cm) (see Remarks) (USNM 1492232).

#### **Redescription**

Female (based on USNM 1492250): body length 8.9 mm, maximal width 6.1 mm, head length 1.8 mm, head width 2.6 mm, pleon length, 2.7 mm. Head dextrally deflexed with ~10° distortion angle. Body broad anteriorly, tapered posteriorly, all body regions and segments distinct (Fig. 2A, B). Head large, subovate, moderately set into pereon; frontal lamina broad, posterior margin with small median projection (Fig. 2A); eyes absent. Antennules and antennae of 3 articles each, with setae at distal tip of distal segment of both; antennae with basal segment greatly expanded, approximately 3x width of second segment (Fig. 2C). Maxilliped with short, acute spur, palp absent or as a low non-articulated lobe with few marginal setae,

no setae on margins (Fig. 2E). Barbula with two short, smooth, falcate lateral projections with tapered tips; median region smooth (Fig. 2D). Oostegite surfaces smooth, completely enclosing brood chamber; setae on posterior margin of fifth oostegite (Fig. 2B); oostegite 1 with ovate anterior lobe, narrow triangular posterior lobe with short, rounded, posterolateral extension (Fig. 2F); inner ridge of oostegite 1 with numerous low digitate projections (Fig. 2G). Pereon of 7 distinct pereomeres, broadest across pereomere 3, tapering gently towards head, markedly towards pleon. Prominent coxal plates on pereomeres 1-7, those on 1-4 elongate, recurved ovals, those on 5-7 as posteriorly expanded flattened plates, flat on longer side of body, curled on shorter side of body; elongate, ovate dorsolateral bosses on pereomeres 1-4, smaller than corresponding coxal plates (Fig. 2A). Tergal projections absent. Pereopods subequal in size, each with large smooth-edged lobe projecting from dorsal surface of basis, size of basal lobe increasing on posterior pereopods, surface of lobe with minute scales; pereopods 1-3 spaced apart, 4-7 spaced closely together (Figs. 2H, I, 3G-M). Pleon of 6 distinct pleomeres, first 5 pleonal segments with lateral plates expanded posteriorly and overlapping from pleomeres 1-5 (Figs. 2A, 3A). Five pairs of biramous pleopods, visible in dorsal view, posteriorly extending well beyond margins of lateral plates; anterior pairs triangular, posterior pairs more elongate and tapered distally, all margins smooth (Figs. 2A, B, 3A-F); pleomere 6 lacking uropods (Figs. 2A, 3A).

Male (based on USNM 1492241, 1492250, 1492279): length 1.8 mm, maximal width 0.8 mm at pereomere 4, head length 0.3 mm, head width 0.5 mm, pleon length 0.5 mm. Head subovate, distinct from pereomere 1, all body segments distinct (Fig. 4A); prominent eyes on posterolateral border of head (Fig. 4A). Antennules of 3 articles each, setae on distal tip of article 3, setae subterminally on other articles (Fig. 4C); antennae of 4 articles each, tuft of setae on distal tip of terminal article (Fig. 4C). Pereon of 7 distinct pereomeres, broadest across pereomeres 3-5, tapering slightly anteriorly and posteriorly. Pereopods subequal in size, all articles distinct; dactyli of pereopods 1-3 proportionally longer than those of 4-7, propodi with ridges of scales on anterior portion underneath dactyl, tuft of setae on anterior tip of propodi opposed to tip of dactyli (Fig. 4C, D), meri and carpi slightly larger in posterior pairs. Pleon variable, ranging from one large, triangular, posteriorly tapered segment (Fig. 4A) with faint lateral undulations to 3 distinct segments (2 narrow pleomeres plus a globose pleotelson; Fig. 4F) or 5 distinct segments (4 narrow pleomeres plus elongate pleotelson showing lateral constriction; Fig. 4E). Midventral tubercles, pleopods and uropods absent; anal cone present but not projecting (Fig. 4B, E, F).

#### *Variation*

Females occur in both dextral and sinistral forms in approximately equal numbers (~40% dextral vs. ~60%



**Table 2.** Known variation in the number pleomeres for males of species in *Anuropodione* Bourdon, 1967.

Species	Number of Pleomeres (Number of Specimens Known)					Reference(s)
<i>A. amphandra</i> n. comb.	1 (29)	2 (2)	3 (1)	5 (4***)	6 (3)	Codreanu <i>et al.</i> , 1966; Present Study
<i>A. australiensis</i>	1 (1)		3 (1)			Bourdon, 1976
<i>A. carolinensis</i>	1 (147*)		3 (2)		6 (38)	Markham, 1974; Wenner & Windsor, 1979
<i>A. dubius</i>				5 (1)		Nierstrasz & Brender à Brandis, 1929; Bourdon, 1972
<i>A. megacephalon</i>	1 (1**)					Markham, 1974
<i>A. senegalensis</i>	1 (7***)	2 (2***)		5 (3***)		Bourdon, 1967; Bourdon, 1972

\* 93 males with 1 pleomere but with lateral undulations suggesting incipient segmentation.

\*\* Terminal segment with dorsal indications of 3 coalesced pleomeres.

\*\*\* Terminal pleomere with lateral undulations suggesting coalesced pleomeres.

sinistral). Male pleon morphology is highly variable (see redescription above); a similar level of variation was noted by Codreanu *et al.* (1966) for this species and is known across the genus as a whole (Table 2).

### Ecology

The rate of parasitism by *A. amphandra* on *M. rutllanti* is relatively high compared to what is known for most bopyrid species (~1-5%; Cericola & Williams, 2015). At least 9 of the 93 squat lobsters (~9.7%) collected in March 2017 bore bopyrids and at least 16 of the 150 hosts (~10.7%) collected in August 2018 contained *A. amphandra* (these prevalences are conservative estimates because six additional parasitized hosts were collected but not assignable to a specific collecting date). All of the hosts were female, except for a single male that was co-infested with a rhizocephalan.

### Remarks

Codreanu *et al.* (1966) reported that, of their nine males examined, four had all pleomeres fused into a single segment, two had two segments, and three had six segments and an overall elongate pleon. We found males with one, three, and five pleonal segments in the present material (Table 2). Codreanu *et al.* (1966) also described the pereomeres of the males as having “finement spinuleux” but these are merely small setae.

Codreanu *et al.* (1966) interpreted the variation in the number of pleomere segments as a response by males to incomplete inhibition of pleomere development by some kind of chemical secretion exuded by the female bopyrids. They labeled the males as being “néoténiques” but as that term specifically refers to the retention of larval fea-

tures in the adult, they applied it incorrectly in this situation. The assumption that male bopyrids are in some way prevented from transitioning from the male to female phase by the influence of females already present in or on the host has been mentioned in the literature (summarized in Trilles, 1999) but the mechanism is unknown and there are few studies which have experimentally demonstrated that it occurs (see Reverberi & Pitotti, 1943; Reverberi, 1947; Reinhard, 1949). Reinhard (1949) dealt with the transformation of cryptoniscus larvae, so the only studies that have shown males transforming into females are those on *Ione thoracica* Montagu, 1808 (Reverberi & Pitotti, 1943; Reverberi, 1947) and in this species the pleomeres of males are quite similar morphologically to those of the female and not variable in the number of segments, unlike in the present case with *Anuropodione* or with species of *Pleurocrypta* (Bourdon, 1965). In fact, in the case of the observed variability in the number of pleomeres of males in species of *Anuropodione*, it is unlikely that a male to female transition is occurring because if the male with one pleomere was transitioning to six pleomeres (the number possessed by the females), then that would mean the cryptoniscus larvae had all their pleomeres fused and subsequently separated again, a seemingly non-parsimonious developmental trajectory. The converse situation, that a male with six segments will transition to a male with one segment is also not probable, as females consistently present six pleomeres. It is more likely that in all species of *Anuropodione*, as with species of *Pleurocrypta*, the number of pleomeres of males is a polymorphic character lacking an evolutionary pressure for fixation at a particular number of segments. These genera provide an opportunity to test this hypothesis and examine the underlying genetic controls of the segmentation process.

One host (USNM 1492232) was doubly infested by *A.*



*amphiandra* n. comb. and an immature specimen of *Lernaeodiscus* cf. *ingolffi* Boschma, 1928. There is one prior record of a species of *Lernaeodiscus* on a *M. rutllanti* host, collected in the Ionian Sea (Øksnebjerg, 2000, who recorded the parasite as *L. ingolffi* and the host variously as *Munida iris*, *M. iris* ssp. *rutllanti* [sic], and *M. iris* ssp. *rutllanti* [sic]). However, because the host examined by Øksnebjerg (2000) bore a dried externa and the present specimen is immature, it is not certain that *M. rutllanti* hosts true *L. ingolffi*.

Petric *et al.* (2010) incorrectly stated that *M. rutllanti* was parasitized by two species of bopyrids: *Pleurocrypta amphiandra* (which they incorrectly credited Délye, 1955, with authorship of the species) and *P. intermedia* Bonnier, 1900 (which they incorrectly credited Codreanu *et al.*, 1966, with authorship and which is a synonym of *P. microbranchiata* G. O. Sars, 1898). *Pleurocrypta microbranchiata* has never been reported from *M. rutllanti*.

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