Nauplius
THE JOURNAL OF THE BRAZILIAN CRUSTACEAN SOCIETY

e-ISSN 2358-2936
www.scielo.br/nau
www.crustacea.org.br

ORIGINAL ARTICLE

Rediscovery and redescription of *Entoniscus creplinii* Giard and Bonnier, 1887 (Isopoda: Bopyroidea: Entoniscidae) parasitizing *Polyonyx gibbesi* Haig, 1956 (Decapoda: Anomura: Porcellanidae), a symbiotic crab from the tubes of *Chaetopterus* cf. *variopedatus* (Annelida), from North Carolina and Florida, U. S. A.

John J. McDermott[1] (In Memorian)
Jason D. Williams[2] orcid.org/0000-0001-5550-9988
Christopher B. Boyko[2, 3] orcid.org/0000-0002-2205-1488

1 formerly Department of Biology, Franklin and Marshall College. Lancaster, PA 17604, United States of America (deceased); posthumous submission (see Williams, 2018)

2 Hofstra University, Department of Biology. Hempstead, New York 11549, United States of America.
JDW E-mail: jason.d.williams@hofstra.edu
CBB E-mail: christopher.b.boyko@hofstra.edu

3 American Museum of Natural History, Division of Invertebrate Zoology. New York, New York, 10024, United States of America.
CBB E-mail: cboyko@amnh.org

ZOOBANK: http://zoobank.org/urn:lsid:zoobank.org:pub:B547AB26-3989-47E2-BE52-A06CBF2DE105

ABSTRACT

The porcellanid crab *Polyonyx gibbesi* Haig, 1956, an obligate symbiont of *Chaetopterus* cf. *variopedatus* ([Renier], [1804]) in the western Atlantic, is parasitized by a rare entoniscid isopod. Crabs from coastal North Carolina and Florida, U.S.A., were dissected and examined for this internal parasite in 1966 and 1967. Two of 83 crabs (2.4 %) and 3 of 100 (3.0 %) crabs from North Carolina and Florida, respectively, were parasitized. Only female parasites were found, including five immature and three mature specimens; one host was parasitized by three immature entoniscids simultaneously. One of the mature parasites was liberating epicaridium larvae and the others had developing eggs or larvae. Parasitized female crabs were all ovigerous; the parasites did not castrate the hosts. The parasite is identified as *Entoniscus creplinii* Giard and Bonnier, 1887, previously known only from Brazil, and the female is redescribed.

KEYWORDS

Atlantic, Chaetopteridae, isopod, parasitism, symbiosis

Corresponding Author
Jason D. Williams
jason.d.williams@hofstra.edu

SUBMITTED 23 July 2021
ACCEPTED 11 November 2021
PUBLISHED 24 June 2022

DOI 10.1590/2358-2936e2022010

Introduction

The symbiotic porcellanid crab *Polyonyx gibbesi* Haig, 1956 inhabits the tubes of the marine benthic polychaete worm *Chaetopterus* cf. *variopedatus* ([Renier], [1804]) [author and date cited per ICZN Opinion 479 (ICZN, 1857)] from Woods Hole, Massachusetts to Uruguay (Williams, 1984; McDermott, 2005; Mantelatto *et al.*, 2021). The crab's biology and relationship with the other major symbiont of *Chaetopterus* cf. *variopedatus*, the pinnotherid brachyuran *Pinnixa chaetopterana* Stimpson, 1860, is relatively well known (Enders, 1905; Pearse, 1913; Gray, 1961; Gore, 1968; Grove and Woodin, 1996; McDermott, 2005; Sandford, 2006). However, *Polyonyx gibbesi* has been reported to host an entoniscid isopod in Brazil (Müller, 1871), a seemingly rare parasite considering it has not been reported on again in 150 years.

There are several taxonomic and nomenclatural issues involving all three species in the hypersymbiosis between *C.* cf. *variopedatus*, *P. gibbesi*, and the entoniscid isopod. The host in this symbiotic web (see Boyko and van der Meij, 2018), *Chaetopterus* cf. *variopedatus*, is likely part of a species complex with the type locality for the species located in the Mediterranean; specimens in the western Atlantic probably belong to an undescribed species, possibly identical with "*Chaetopterus* '*variopedatus*' 2" of Tilic and Rouse (2020). Primary symbionts within the tubes of this polychaete include pinnotherid and porcellanid crabs and investigations have revealed poorly known secondary symbionts living on or in these decapods, including hyperparasites such as endoparasitic isopods (McDermott, 2009).

The taxonomic history of *P. gibbesi* is a bit complicated but necessary to understand the distribution of the species. Haig (1956) discussed the nomenclatural issues surrounding the western Atlantic *Polyonyx* Stimpson, 1858 species formerly known as *Porcellana macrocheles* Gibbes, 1850 (= *Polyonyx macrocheles*) but showed it was a junior homonym of *Porcellana macrocheles* Poeppig, 1836, and introduced *Polyonyx gibbesi* as a new name for the taxon. Haig (1956) considered the range of this species to be from Massachusetts, U.S.A. to Panama but she considered the record of Müller (1871) to possibly refer to the same species. Ejchel (1965) subsequently described *Polyonix* (*sic*) *creplinii* (also as "*creplini*" in the same paper) from Brazil but this name has also been regarded as a synonym of *P. gibbesi* (Gore, 1974). The range of the species has further been extended southward to Argentina (Belleggia *et al.*, 2010; Mantelatto *et al.*, 2021).

Entoniscid isopods are endoparasitic in a wide range of decapod hosts, including pinnotherid crabs along the east coast of the United States (McDermott *et al.*, 2019), but only the four species in the genus *Entoniscus* Müller, 1862 are known from porcellanid crabs (Shiino, 1942; Boyko *et al.*, 2008 onwards). Müller (1871) reported an entoniscid from *Porcellana* (*Polyonyx*) *creplinii*, but the parasite was incompletely described and was not named. Giard and Bonnier (1887) introduced the available name *Entoniscus creplinii*, based on the cursory description from Müller (1871) but examined no specimens and added no additional information on the species.

It is the purpose of this paper to provide the first report of *E. creplinii* since its original discovery, the first full description of females of *E. creplinii* from *P. gibbesi*, and to document its prevalence in host crab populations in North Carolina and Florida.

Material and Methods

Crabs were collected by the first author from the tubes of *C.* cf. *variopedatus* in June and October, 1966 in the vicinity of Beaufort, NC (34°43'N 76°40'W), and in November and December 1966 and February 1967 on Virginia Key, Miami, FL (25°40'N 80°10'W). For a review of the environmental conditions at these two locations see McDermott (2005). Crabs were isolated in seawater in the laboratory in order to detect the possible emergence of epicaridium larvae, indicating the presence of one or more mature female parasites. All crabs were then dissected and observed for isopods. Vernier calipers were used to measure crab carapace width (CW) in millimeters. Female isopods and epicaridium larvae were observed with dissecting and compound microscopes; isopod size is given as maximal length of female body. Figures were produced using Adobe Illustrator to trace original drawing tube sketches or drawings that were made with a

dissecting microscope. All specimens are deposited in the United States National Museum of Natural History, Smithsonian Institution (USNM).

Systematics

Order Isopoda Latreille, 1817

Suborder Epicaridea Latreille, 1825

Superfamily Bopyroidea Rafinesque, 1815

Family Entoniscidae Kossmann, 1881

Subfamily Entoniscinae Kossmann, 1881

Genus *Entoniscus* Müller, 1862

***Entoniscus creplinii* Giard and Bonnier, 1887**
(Figs. 1–2)

Entoniscus 3 Müller, 1871: 54 (brief description; see below).
"*Entoniscus*…im *Porcellana Creplinii*" Fraisse, 1878: 25, 387 (mention).
"L'*Entoniscus* de *Porcellana Creplinii*" Giard, 1878: 683 (mention).— Giard and Bonnier, 1887: 89 (mention).
Entoniscus Creplinii Giard and Bonnier, 1887: 231 (table), 236 (after Müller, 1871).— Stebbing, 1893: 406 (mention).— Bonnier, 1900: 227, 380 (lists).
"*Entoniscus*… *creplinii*" Lucas, 1905: 1048 (list).
Entoniscus creplinii— Shiino, 1942: 51 (mention).— Adkison, 1990: 23, 51, 54 (mention; list).— Brasil Lima, 1998: 640 (list).— Boos *et al.* 2012: 1036 (list).

Material examined herein (subset of specimens originally examined by JJM). North Carolina: 3 immature females, all parasitizing a single female *Polyonyx gibbesi* (13.3 mm CW) associated with *Chaetopterus* cf. *variopedatus*, Beaufort, coll. J.J. McDermott, 21 June 1966 (specimens fixed 3 July 1966) (USNM 1660598; specimens in pieces and combined in one lot). Florida: 2 mature females, 1 each parasitizing separate male specimens (7.8 and 8.5 mm CW) of *P. gibbesi* and 1 immature female parasitizing an ovigerous female (10.1 mm CW) *P. gibbesi* associated with *C.* cf. *variopedatus*, Miami, coll. J. J. McDermott, 9 November 1966 (USNM 1660599; specimens in pieces and combined in one lot).

Type locality. Desterro (= Florianópolis, state of Santa Catarina), Brazil.

Type host. *Porcellana* (*Polyonyx*) *creplinii* Müller, 1871 (*nomen nudum*) (= *Polyonyx gibbesi* Haig, 1956).

Description of female (Figs. 1, 2). Mature specimens occupying most of host hemocoel, laying under host stomach, pleon extending dorsally through digestive gland of host to an opening on pereopods 2–4, such as the merus-carpus articulation of right fourth pereopod (Fig. 1D), or unidentified positions in the antero-lateral dorsal quarter of the crab; brood chambers of ovigerous specimens extending into spaces of host pleon. Sheath formed by host surrounds entire parasite. Body of mature parasites orange color due to gonad extending as 2 bands along length of body.

Pereon approximately straight from cephalon to posterior end (Figs. 1A–C, 2A). Cephalon rounded, dorsally divided into 2 bulbous lobes (Figs. 1A–C, 2A, D–G), ventrally undivided, bearing 2(?) pairs of fused flattened antennae (Fig. 2D–G), maxillipeds not observed. Pereon lacking ovarian processes, pereopods apparently absent. Five pairs of subequal oostegites, margins highly crenulate (Figs. 1A–C, 2A). Oostegite 1 not subdivided in lobes. Oostegites 2–5 not fused, not covering oostegite 1 (Figs. 1A–C, 2A).

Pleon elongate (nearly as long or even longer than rest of body in mature specimens), S-shaped, composed of 5 pleomeres, 1 and 2 indistinctly delineated, 3–5 distinct, pleomere 1 as long as remaining pleomeres combined (Figs. 1A–C, 2A, H), pleomeres 3–5 with scales (Fig. 2B). One pair of crenulate pleural lamellae on pleomere 1, similar in size and shape to oostegites, positioned immediately posterior to oostegite 5 (Figs. 1B, C, 2A). Triangular extension on pleomere 1 between pleural lamella and bulbous heart (Figs. 1A, B, 2A, H). Pleomeres 1–5 each with pair of uniramous filamentous pleopods, pleopods 1 and 2 widely separated, 3–5 overlapping (Figs. 1A–C, 2A, H), pleopods 1 and 2 laying within ventral channel on pleomeres 1 and 2. Terminal pleomere with shallow ventral notch, terminally fringed with minute setae (Fig. 2C).

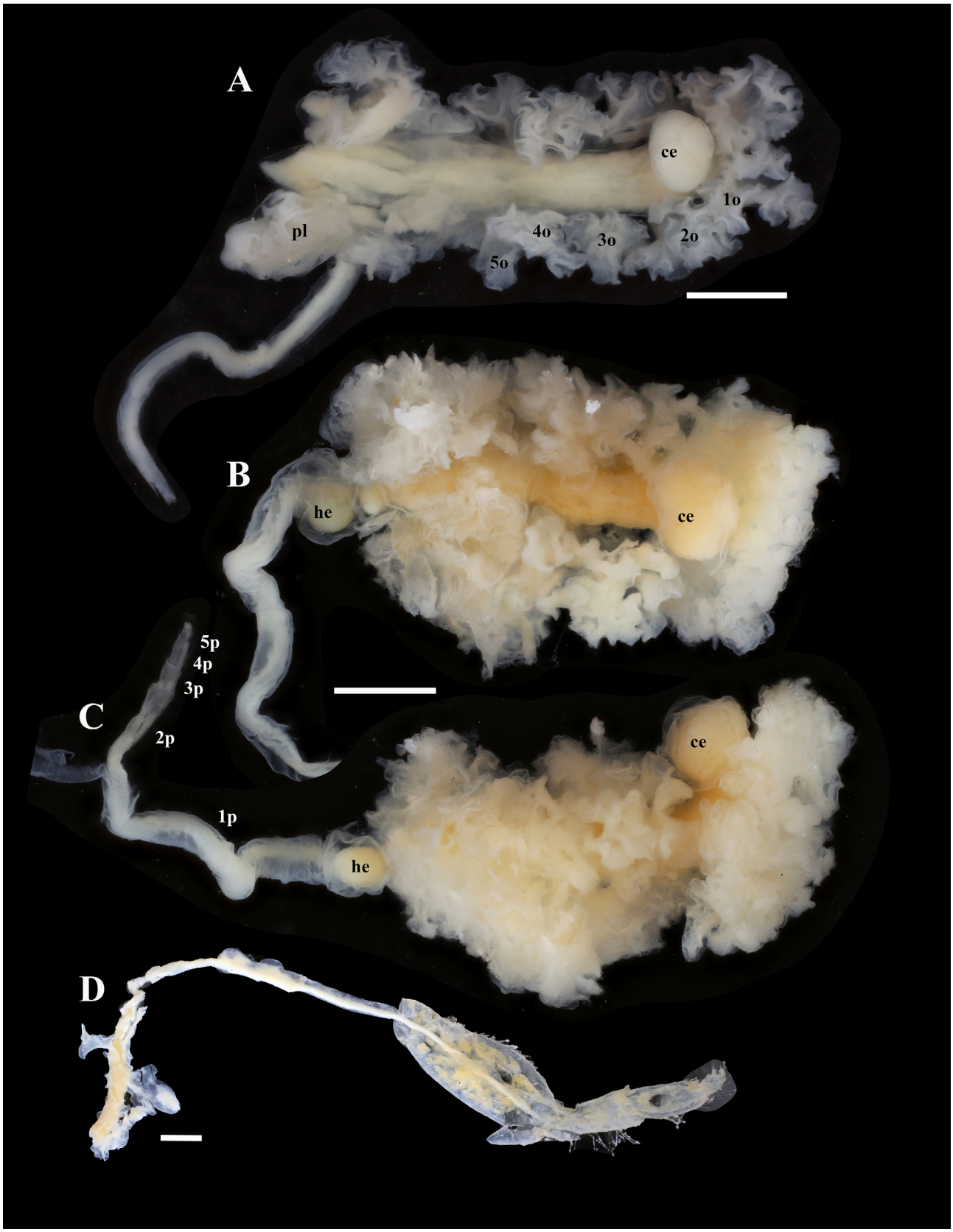

Figure 1. *Entoniscus creplinii* Giard and Bonnier, 1887 (USNM 1660598). **A**) Mature female, dorsal view. **B**) Mature female, dorsal view. **C**) Mature female, lateral view. **D**) Pleon of female extending to opening at the merus-carpus articulation of the third right walking leg of host *Polyonyx gibbesi* Haig, 1956. Abbreviations: ce = cephalon; he = heart; 1o–5o = oostegites 1 to 5; 1p–5p = pleomeres 1 to 5; pl = pleural lamellae. Scales = 0.5 mm (A); 1 mm (B–D).

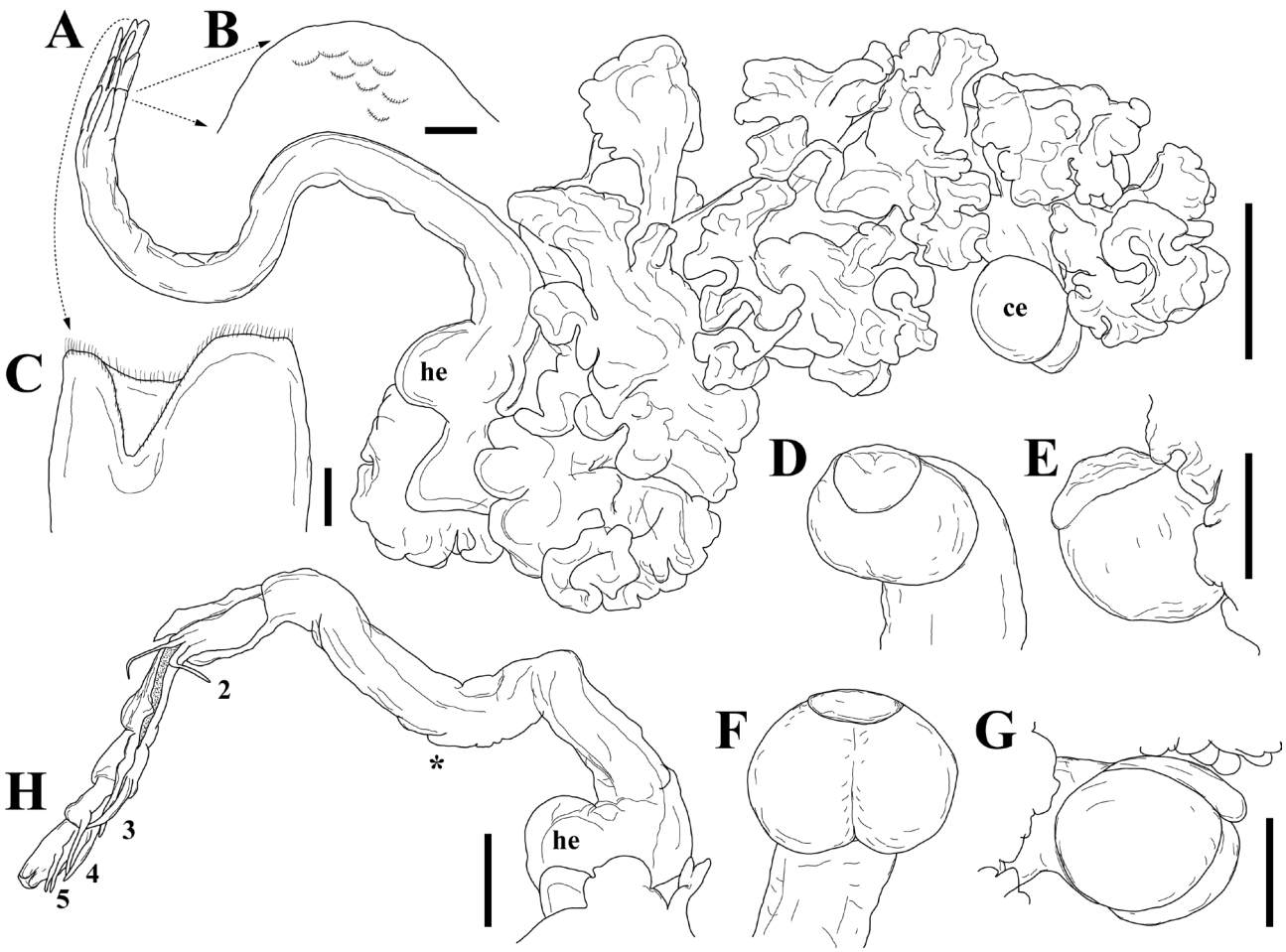

Figure 2. *Entoniscus creplinii* Giard and Bonnier, 1887 (USNM 1660598). **A**) Mature female, lateral view. **B**) Close-up of side of pleomere 3 showing scales. **C**) Terminal segment of pleon. **D**) Female cephalon with host sheath surrounding, *en face* view. **E**) Female cephalon with host sheath surrounding, lateral view. **F**) Female cephalon with host sheath removed, *en face* view. **G**) Female cephalon with host sheath removed, lateral view. **H**) Pleon of female with host sheath partially removed, asterisk showing position of first pleopods still covered by host sheath; stippled region shows channel within which second pleopods lay. Abbreviations: ce = cephalon; he = heart; 2–4 = pleopods 2 to 4. Scales = 0.5 mm (**A, D–H**); 10 μm (**B, C**).

Remarks. Müller's (1871) description of this species, which he did not name, was very short and the only characters noted were that the ovaries of the female parasites were yellow and not purple as in *Entoniscus porcellanae* Müller, 1862 and that the oostegites were less divided with smoother margins than those of the latter species. Giard and Bonnier (1887) saw no specimens but named the species based on Müller's (1871) account. Brief as Müller's (1871) description was, it was sufficient to make the name available from Giard and Bonnier's (1887) translation of Müller's (1871) text into French. Müller (1871) noted that the parasitized hosts were each found alone in the "Chätopterus" burrows, not in a pair as is typical; he speculated that the parasitized nature of the crabs made them poor choices for mates. The present material also had orange gonads and the oostegites are more compact and less divided than those of *E. porcellanae*, and so match both the characters described by Müller (1871) for *E. creplinii*.

Ecology

North Carolina

Eighty-three crabs were collected, isolated, measured, dissected and examined for entoniscids from North Carolina; the prevalence was 2.4 % (2 of 83). Mean CW values are given in Tab. 1; females were significantly wider than males (t = 4.480; p = ≤ 0.0001). Two ovigerous female crabs (2.4 %)

were parasitized with entoniscids (Tab. 2). One crab (13.3 mm) had three immature female parasites in its hemocoel (one on the left side and two on the right); their marsupia did not contain ova, nor were males present. The elongated tubular pleon of one female was traced to an opening at the merus-carpus articulation of the third right walking leg (pereopod 4) (Fig. 1D). The other crab (14.5 mm; lost) had one immature female laying directly under the stomach with the cephalon oriented anteriorly; the elongated pleon doubled back on the body and extended toward the antero-lateral dorsal quarter of the crab and did not appear to extend into any appendage. The pleon was observed to undergo vigorous worm-like contortions; the mean heartbeat of a specimen from North Carolina was 141.7 ± 6.4 beats/min, n = 3.

Florida

One hundred specimens of *P. gibbesi* collected in Miami, Florida yielded three parasitized individuals (3.0 %) (Tabs. 1, 2), morphologically similar to those found in North Carolina. Female crabs were significantly larger than males ($t = 2.620$; $p = 0.0104$). A recently ovigerous female *P. gibbesi* (10.1 mm) with diminished gonads was parasitized with an immature female entoniscid situated in the right side of the hemocoel near the gonad. The pleon was extended anteriorly, but was damaged and could not be traced to its external opening.

Epicaridium larvae were liberated in the laboratory from a male crab host (8.7 mm). The marsupia of the mature female isopod, filled with these pigmented larvae, could be seen through the transparent ventral

Table 1. Mean carapace width (CW) measurements of male and female *Polyonyx gibbesi* examined for entoniscid isopods from North Carolina and Florida, 1966 and 1967.

Locations	Dates	Males			Females		
		n	CW ± SD	Range	n	CW ± SD	Range
North Carolina	Jun 1966	15	8.1 ± 1.4	4.9-9.2	16	11.3 ± 2.1	6.2–14.5
	Oct 1966	26	7.8 ± 2.5	2.7-10.8	26	10.7 ± 4.5	3.0–16.4
Florida	Nov 1966	18	6.8 ± 1.7	2.0-8.7	16	9.2 ± 1.5	6.0–11.1
	Dec 1966	28	6.3 ± 1.7	2.8-9.3	30	6.9 ± 2.8	1.6–12.1
	Feb 1967	4	8.1 ± 1.2	6.6-9.5	4	8.8 ± 1.1	7.3–9-7

n = number of crabs measured

Table 2. Prevalence of *Entoniscus creplinii* (Entoniscidae) in the anomuran crab *Polyonyx gibbesi* from North Carolina and Florida.

Location	Date	Crabs Examined			Infested Crabs	
		Total	Males	Females (ovig.)	Males	Females
North Carolina	Jun 1966	31	15	16 (11)	0	2
	Oct 1966	52	26	26 (15)	0	0
Totals		83	41	42 (26)	0	2
Florida	Nov 1966	34	18	16 (15)	2	1
	Dec 1966	58	28	30 (11)	0	0
	Feb 1967	8	4	4 (4)	0	0
Totals		100	50	50 (30)	2	1
Grand totals		183	91	92 (56)	2	3

ovig. = ovigerous

junction between the carapace and the abdomen. Within the host's hemocoel, the main body of the parasite enclosed in a sheath produced by the host was under the crab's heart. Its expanded marsupia filled nearly all space in the hemocoel. The anterior (cephalic) end of the parasite faced the left side and the body extended posteroventrally to the right side and under the sperm duct. The distal end of the tubular pleon entered the second right walking leg (third pereopod) exiting via an opening at the merus-carpus articulation. The gonad of the parasite was orange. The other parasitized male host (7.8 mm) harbored a mature female whose marsupia were filled with developing embryos. These were also observed at the ventral carapace-abdomen junction of the crab. The cephalic end of the female parasite was on the right side of the hemocoel. Its body crossed to the left side where the terminal pleomere passed into the first left walking leg (second pereopod) to a distinct external opening (0.105 mm diameter) in the exoskeleton of the carpus.

Discussion

Boyko *et al.* (2008 onwards) list three species of described and one unidentified porcellanid crab as hosts for the four named species of entoniscids in the genus *Entoniscus*. The female parasite found in *P. gibbesi* in the present study is superficially similar to *Paguritherium alatum* Reinhard (1945) that was described from the hermit crab host *Pagurus longicarpus* Say, 1817, collected at Woods Hole, Massachusetts, USA. The developing female of *P. alatum* is enclosed in a sheath produced by the host, and is characterized by a long, thin, tubular pleon ("respiratory tube"), which makes contact with the external environment via a pore in the exoskeleton of the eyestalks of the host, through which the epicaridium larvae are released. Reinhard (1945) recognized that this entoniscid was closely related to members of the genus *Entoniscus* but differed enough from other species in this genus so that the new genus, *Paguritherium* Reinhard, 1945, was established. Reinhard's (1945) observations were verified many years later in parasitized crabs collected in New Jersey (McDermott, 1998). Thus, *E. creplinii* from North Carolina and Florida resembles other species of *Entoniscus* and *Paguritherium* in which the elongated, tubular pleon of the female appears to be a major morphological characteristic. This structure is illustrated in the species descriptions of Shiino (1942) in *Entoniscus japonicus* Shiino, 1942 from *Petrolisthes japonicus* (De Haan, 1849), and Müller (1862) in *Entoniscus porcellanae* from an unidentified Brazilian porcellanid.

Entoniscus creplinii makes contact with the external environment using its terminal pleomere through openings produced in the walking legs of the host whereas *Paguritherium alatum* and *E. japonicus* produce external openings near the base of the host's compound eyes. External pores produced by most other species of entoniscids (those found in brachyuran crabs) are found in the inner wall of the crabs' branchial chambers. While none of the known species of *Entoniscus* have been recorded in multiple hosts (Boyko *et al.*, 2008 onwards), *P. paguritherium* also parasitizes the closely related hermit crab *Pagurus annulipes* (Stimpson, 1860) (Adkison and Heard, 1978).

Males of the present species were not found, possibly due to a lack of care in dissecting the female parasites in the 1960s; entoniscid males are very small (< 1mm) compared to females and easily overlooked. The males known from other *Entoniscus* spp. and *P. alatum* appear to be characteristic in that the pereopods are poorly developed unsegmented swellings.

Crabs parasitized by ovigerous female entoniscids are normally detected by observing liberated epicaridium larvae, but they are also recognized by observing oostegites with developing larvae through the thin exoskeleton at the ventral carapace-abdomen junction of the host. Reinhard (1945) and McDermott (1998) noted that mature female parasites could be detected in hermit crabs through the thin exoskeleton of their abdomens. Atkins (1933) was also able to recognize mature entoniscid females of *Pinnotherion vermiforme* Giard and Bonnier, 1887 through the poorly calcified carapace of the pinnotherid crab host *Pinnotheres pisum* (Linnaeus, 1767), a parasitic species in bivalve mollusks. Mature females of *Pinnixion sexdecennia* McDermott, Williams and Boyko, 2019 were able to be detected at the thin carapace-abdomen junction of the pinnotherid *Pinnixa chaetopterana* (see McDermott *et al.*, 2019). The carapace of the latter is

heavily calcified, unlike the pinnotherids in bivalve hosts in which the carapace is thin and translucent (McDermott, 2005).

Prevalence of the *E. creplinii* was based on a relatively small sample of 183 crabs. Crabs of both sexes were parasitized. Shiino (1942) recorded 36 parasitized individuals of *E. japonicus* among 664 host specimens (5.4 %). Reinhard (1943; 1945) recorded that *P. alatum* had a prevalence of 0.8 % (38 of 4600) in *P. longicarpus* collected in Massachusetts. Similarly, in New Jersey, only 4 of 3703 (0.11 %) of the same hermit crab were parasitized with *P. alatum* (McDermott, 1998); both sexes of crabs harbored entoniscids. Adkison and Heard (1978) found 1.0 % (3 of ~300) of the same hermit crab parasitized in North Carolina. Reinhard (1945) concluded that even if the hemocoel of crabs was more carefully examined for developing parasites and the mature females dissected in search of males, it was unlikely that the prevalence would be more than about 2 %.

Entoniscids such as *P. alatum* have been documented to cause castration of hosts and the reduction in size and morphology of the egg-bearing pleopods (Reinhard and Buckeridge, 1950; McDermott, 1998). However, in the present study, *E. creplinii* was not found to hinder host gonad development, reproduction or impact secondary sex characteristics; this is similar to the lack of such impacts on hosts caused by some other entoniscids (McDermott *et al.*, 2019). As found by Müller (1871), the parasitized hosts from North Carolina and Florida were found singly in their chaetopterid tubes; however, these porcellanids are almost always (> 90 % of the time) found as male-female pairs (McDermott, 2005). Thus, the parasites may induce changes (subtle morphological, chemical or behavioral) that make the hosts unsuitable mates. Additional studies on *E. creplinii* are needed to allow the description of male specimens of this species as well as expand our knowledge of the potential impacts of this parasite on its host and other symbiotic web members.

Acknowledgements

John McDermott appreciated the help of many individuals during several years of field studies along the Atlantic coast (C. G. Bookhout, J. D. Costlow and F. J. Vernberg at Duke University and A. A. Myrberg at University of Miami). In addition, he was thankful for assistance in the field from W. R. Belzer, J. A. Cole, J. J. McDermott III, T.M. McDermott, M. H. Taylor and F. R. Weis. This research was partially supported by funds to J. McDermott from National Science Foundation grants (G11448, G22068, and B959), post-doctoral research grants from Duke University Marine Laboratory, and Franklin and Marshall College.

References

Adkison, D.L. 1990. A review of the Entoniscinae (Isopoda: Epicaridea: Entoniscidae). New Orleans, Tulane University, Ph.D. Dissertation, 199p. [Unpublished].

Adkison, D.L. and Heard, R.W. 1978. Description of a new genus and species of Pseudioninae (Isopoda: Bopyridae) parasite of the hermit crab *Pagurus annulipes* (Stimpson) from North Carolina. *Proceedings of the Biological Society of Washington*, 91: 408–417.

Atkins, D. 1933. *Pinnotherion vermiforme* Giard and Bonnier, an entoniscid infecting *Pinnotheres pisum*. *Proceedings of the General Meetings for Scientific Business of the Zoological Society of London*, 1933: 319–363, 4 pls.

Bellegia, M.; Boschi, E.E.; Schejter, L.; Bremec, C.; Sánchez, F. and Figueroa, D. E. 2010. First record of *Polyonyx gibbesi* (Anomura: Porcellanidae) in the Argentine Sea. *Marine Biodiversity Records*, 3: e44. doi:10.1017/S175526720999100X

Bonnier, J. 1900. Contribution a l'étude des épicarides. Les Bopyridae. *Travaux de la Station Zoologique de Wimereux*, 8: 1–476, pls. 1-41.

Boos, H.; Bond Buckup, G.; Buckup, L.; Araujo, P.B.; Magalhães, C.; Almerão, M.P.; dos Santos, R.A. and Mantelatto, F.L. 2012. Checklist of the Crustacea from the state of Santa Catarina, Brazil. *Check List*, 8: 1020–1046.

Boyko, C.B.; Bruce, N.L.; Hadfield, K.A.; Merrin, K.L.; Ota, Y.; Poore, G.C.B.; Taiti, S.; Schotte, M. and Wilson, G.D.F. (eds). 2008 onwards. World Marine, Freshwater and Terrestrial Isopod Crustaceans database. Accessed at http://www.marinespecies.org/isopoda. Access on 07 January 2021. doi:10.14284/365.

Boyko, C.B. and van der Meij, S.E.T. 2018. A trifecta of Swiftian symbioses: stony corals, gall crabs and their parasites (Scleractinia; Brachyura: Cryptochiridae; Isopoda: Epicaridea and Cirripedia: Rhizocephala). *Zoological Journal of the Linnean Society*, 184: 304–329.

Brasil Lima, I.M. 1998. Malacostraca – Peracarida. Isopoda – Epicaridea. p. 635–644. In: P.S. Young (ed), Catalogue of Crustacea of Brazil. Rio de Janeiro, Museu Nacional.

De Haan, W. 1833–1850. Crustacea. Vol. 1. Fauna Japonica sive Descriptio Animalium, quae in itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823-1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit. Lugduni Batavorum, xvi + 244; xxi + circfl. Tab. 2 + Tab. a-q + Tab. 1–55.

Ejchel, F. 1965. Notes on crustacean decapods. *Anais da Academia Brasileira de Ciências*, 37(suppl.): 325–326.

Enders, H.E. 1905. Notes on the commensals found in the tubes of *Chaetopterus pergamentaceus*. *American Naturalist*, 39: 37–40.

Fraisse, P. 1878. *Entoniscus cavolinii* n. sp., nebst Bermerkungen über die Umwandlung und Systematik der Bopyriden. *Arbeiten aus dem Zoologisch-Zootomischen Institut in Würzburg*, 4: 382–440, pls. 20, 21.

Giard, A. 1878. Notes pour servir a l'histoire du genre *Entoniscus*. *Journal de l'Anatomie et de la Physiologie Normales et Pathologiques de l'Homme et des Animaux*, 14: 675–700, pl. 46.

Giard, A. and Bonnier, J. 1887. Contributions á l'étude des bopyriens. *Travaux de l'Institut Zoologique de Lille et du Laboratuire de Zoologie Maritime de Wimereux*, 5: 1–272, pls. 1–10.

Gibbes, L.R. 1850. On the carcinological collections of the United States, and an enumeration of species contained in them, with notes on the most remarkable, and descriptions of new species. *Proceedings of the American Association for the Advancement of Science*, 3: 167–201.

Gore, R.H. 1968. The larval development of the commensal crab *Polyonyx gibbesi* Haig, 1956 (Crustacea: Decapoda). *Biological Bulletin*, 135: 111–129.

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

Gray, I.E. 1961. Changes in abundance of the commensal crabs of *Chaetopterus*. *Biological Bulletin*, 120: 353–359.

Grove, M.W. and Woodin, S.A. 1996. Conspecific recognition and host choice in a pea crab, *Pinnixa chaetopterana* (Brachyura: Pinnotheridae). *Biological Bulletin*, 190: 359–366.

Haig, J. 1956. The Galatheidea (Crustacea Anomura) of the Allan Hancock Atlantic Expedition with a review of the Porcellanidae of the western North Atlantic. *Allan Hancock Atlantic Expedition Report*, 8: 1–45.

ICZN – International Commission on Zoological Nomenclature. 1954. Opinion 316. Rejection for nomenclatural purposes of the "Tavola Alfabetica delle Conchiglei Adriatische" and "Prospetto della Classe dei Vermi" of S. A. Renier commonly attributed to the year 1804. *Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature*, 9: 91–106.

ICZN - International Commission on Zoological Nomenclature 1957. Opinion 478. Validation undet the Plenary Powers of the generic name "Polycitor" [Renier], [1804], and of the specific name "crystallinus" [Renier], [1804], as used by the foregoing author in the combination "Polycitor crystallinus" (class Urochordata) ("Opinion" supplementary to "Opinion" 427. Opinions and Declarations Rendered by the International Commission on Zoological Nomenclature, 16(21): 353–364.

Kossmann, R. 1881. Die entonisciden. *Mittheilungen aus der Zoologischen Station zu Neapel*, 3(1/2): 149–169, pls. 8, 9.

Latreille, P.A. 1817. Les Crustacés, les Arachnides et les Insectes. In: M. le C. Cuvier (ed), Le Règne Animal Distribuè d'Après son Organisation, pour Servir de Base a l'Histoire Naturelle des Animaux et d'Introduction a l'Anatomie Comparée. Paris, Deterville. Vol. 3. i–xxix+1–653p.

Latreille, P.A. 1825. Entomologie ou Histoire Naturelle des Crustacés, des Arachnides et des Insectes. Encyclopédie Methodique. Vol. 10. Paris, Mme.Veuve Agasse, 833p.

Linnaeus, C. 1767. Systema Naturae Sive Regna Tria Naturae, Secundum Classes, Ordines, Genera, Species, Cum Characteribus, Differentiis, Synonymis, Locis. 12th Ed. v. 1 (Pt 2). Holmiae, Laurentii Salvii.

Lucas, R. 1905. Crustacea für 1904. I. Malacostraca. *Archiv für Naturgeschichte*, 71(2, pt. 2): 995–1055.

Mantelatto, F.L.; Miranda, I.; Vera-Silva, A.L.; Negri, M.; Buranelli, R.C.; Terossi, M.; Magalhães, T.; Costa, R.C.; Zara, F.J. and Castilho, A.L. 2021. Checklist of decapod crustaceans from the coast of the São Paulo State (Brazil) supported by integrative molecular and morphological data: IV. Infraorder Anomura: superfamilies Chirostyloidea, Galatheoidea, Hippoidea and Paguroidea. *Zootaxa*, 4965: 558–600.

McDermott, J.J. 1998. Prevalence of two epicaridean isopods (Bopyridae and Entoniscidae) associated with the hermit crab *Pagurus longicarpus* Say, 1817 (Anomura) from the New Jersey coast (U.S.A.). *Journal of Parasitology*, 84: 1042–1045.

McDermott, J.J. 2005. Biology of the brachyuran crab *Pinnixa chaetopterana* Stimpson (Decapoda: Pinnotheridae) symbiotic with tubicolous polychaetes along the Atlantic coast of the United States, with additional notes on other polychaete associations. *Proceedings of the Biological Society of Washington*, 118: 742–764.

McDermott, J.J. 2009. Hypersymbioses in the pinnotherid crabs (Decapoda: Brachyura: Pinnotheridae): a review. *Journal of Natural History* 43: 785–805.

McDermott, J.J.; Williams, J.D. and Boyko C.B. 2019. A new genus and species of parasitic isopod (Bopyroidea: Entoniscidae) infesting pinnotherid crabs (Brachyura: Pinnotheridae) on the Atlantic coast of the USA, with notes on the life cycle of entoniscids. *Journal of Crustacean Biology*, 40: 97–114.

Müller, F. 1862. *Entoniscus porcellanae*, ein neue Schmarotzerassel. *Archiv für Naturgeschichte*, 28: 10–18, pl. 2.

Müller, F. 1871. Bruchstücke zur Naturgeschichte der Bopyriden. *Jenaische Zeitschrift für Medicin und Naturwissenschaft*, 6: 53–73, pls. 3, 4.

Pearse, A.S. 1913. On the habits of the crustaceans found in *Chaetopterus* tubes at Woods Hole, Massachusetts. *Biological Bulletin*, 24: 102–114.

Poeppig, E. 1836. Crustacea Chilensia nova aut minus nota. *Archiv für Naturgeschichte*, 2: 133–145, pl. 4.

Rafinesque, C.S. 1815. Analyse de la Nature ou Tableau de l'Univers et des Corps Organisés. Palerme, L'Impremerie de Jean Barravecchia, 224 pp.

Reinhard, E.G. 1943. Epicaridean parasites of *Pagurus longicarpus* at Woods Hole. *Anatomical Record*, 87: 468 (abstract).

Reinhard, E.G. 1945. *Paguritherium alatum* n. g., n. sp., an entoniscian parasite of *Pagurus longicarpus*. *Journal of Parasitology*, 31: 198–204.

Reinhard, E.G. and Buckeridge, F.W. 1950. The effect of parasitism by an entoniscid on the secondary sex characters of *Pagurus longicarpus*. *Journal of Parasitology*, 36: 131–138.

Renier, S. A. 1804. Prospetto della Classe dei Vermi Nominati e Ordinati secondo il Sistema di Bosc. Padua. p. xv-xxvi. [Work No. 25 on the *Official Index of Rejected and Invalid Works in Zoological Nomenclature*; see ICZN, 1954 Opinion 316.]

Sandford, F. 2006. *Polyonyx gibbesi* (Decapoda:Anomura: Porcellanidae) and *Pinnixa chaetopterana* (Decapoda: Brachyura: Pinnotheridae), two crab commensals in tubes of the polychaete *Chaetopterus* sp., in the northern Gulf of Mexico. In: A.Asakura (ed), Biology of Anomura II. *Crustacean Research*, Special Number, 6: 23–31.

Say, T. 1817. An account of the Crustacea of the United States (continued). *Journal of the Academy of Natural Sciences at Philadelphia*, 1: 155–169.

Shiino, S.M. 1942. On the parasitic isopods of the family Entoniscidae, especially those found in the vicinity of Seto. *Memoirs of the College of Science, Kyoto Imperial University*, series B, 17(1)(2): 37–76.

Stebbing, T.R.R. 1893. A history of Crustacea Recent Malacostraca. The International Scientific Series. London, Kegan Paul, Trench, Trübner & Co. xvii + 466p., 19 pls.

Stimpson, W. 1860. Notes on North American Crustacea, in the museum of the Smithsonian Institution. No. II. *Annals of the Lyceum of Natural History of New York* 7(22): 176–246, pls. 2, 5.

Tilic, E. and Rouse, G.W. 2020. Hidden in plain sight, *Chaetopterus dewysee* sp. nov. (Chaetopteridae, Annelida) – a new species from southern California. *European Journal of Taxonomy*, 643: 1–16.

Williams, A.B. 1984. Shrimps, lobsters, and crabs of the Atlantic Coast of the eastern United States, Maine to Florida. Washington, D.C., Smithsonian Institution Press, 550p.

Williams, J.D. 2018. Obituary: Dr. John J. McDermott (1927-2017). *Proceedings of the Biological Society of Washington*, 131: 1–6.