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ORIGINAL PAPER

Resurrection of the parasitic isopod genus *Cryptione* Hansen, 1897 (Epicaridea: Bopyridae) and description of a new species of parasitic isopod (Epicaridea: Bopyridae) from the deep-sea shrimp *Notostomus gibbosus* (Caridea: Acanthephyridae) with an analysis of its phylogenetic position based on molecular data

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Abstract

A new species of pseudionine parasite is described from the deep-sea shrimp *Notostomus gibbosus* A. Milne-Edwards, 1881, collected in the Gulf of Mexico, the first record of a bopyrid parasitizing any member of the family Acanthephyridae Spence Bate, 1888. Morphological and molecular data are provided to support the inclusion of the new species and 12 other branchial ectoparasites of caridean shrimps in the genus *Cryptione* Hansen, 1897 that is resurrected herein. *Cryptione* is sister to the genus *Pseudione* sensu stricto, ectoparasites of axiid and callianassid shrimps as well as nephropid lobsters. The new species *Cryptione grandis* can be distinguished from its closest congeners including *C. parviramus* (Adkison, 1988) from the Gulf of Mexico by several female and male characters. The epicaridium larvae of *C. grandis* were examined with scanning electron microscopy (SEM), only the second description of this stage for any species in the genus. A table listing all species in *Cryptione* and taxonomic notes on some species are provided.

Keywords Bopyrid · Ectoparasite · Epicaridium larva · New species · Pseudioninae

Introduction

As presently defined, the bopyrid isopod subfamily Pseudioninae (~240 species; Boyko et al. 2024) contains species that parasitize a wide range of definitive hosts, with most being found on members of Anomura but also Achelata, Astacidea, Axiidea, Brachyura, Caridea, and Gebiidea. All pseudionines are ectoparasites, with most of the species (in 52 genera) being found within the branchial chambers of their definitive hosts, but some (in 3 genera) occurring under the pleon of definitive hosts (Boyko and Williams 2024). However, the breadth in host usage among pseudionines may be an artifact due to lack of phylogenetic resolution. In fact, the subfamily and some of its genera have long been noted as likely being non-monophyletic and in need of extensive revision (see Bourdon

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1968). Female pseudionines produce broods of epicaridium larvae that are released into the water column and seek out a copepod intermediate host upon which that they attach and form microniscus larvae prior to transforming into cryptoniscus larvae that are responsible for seeking out and settling on definitive hosts. All pseudionines are assumed to be ectoparasites of copepod intermediate hosts; however, little is known of this portion of their life cycle, especially host specificity (Pike 1960; Williams and Boyko 2012; Williams et al. 2022).

The genus *Pseudione* Kossmann, 1881, has been particularly problematic (see Boyko et al. 2017; Brito et al. 2018; Horch et al. 2018; Williams et al. 2019; Pereira et al. 2021) and previously consisted of a large (> 80 species) heterogenous group. Boyko et al. (2017) redescribed the type species of *Pseudione* and defined *Pseudione* sensu stricto which presently contains 9 species that parasitize axiid and callianassid shrimps, as well as nephropid lobsters. Other species described in *Pseudione* have been moved into new genera (e.g., *Asymmetrione* Codreanu, Codreanu & Pike, 1965, *Eremitione* Williams & Boyko, 2019, *Orthione* Markham, 1988, *Parione* Richardson, 1910, *Robinione* Boyko, Williams & Shields, 2017). Thus, at present, nearly 30 species in *Pseudione* sensu lato have uncertain taxonomic affiliation. Pereira et al. (2021) described a new species of *Pseudione* sensu lato from a squat lobster host and discussed the evidence that the *Pseudione* "crénelés" (all parasites of galatheoid hosts; see Bourdon 1972, 1976; Kazmi and Boyko 2005) form a monophyletic group; however, they did not propose a new genus for this group.

Hansen (1897) proposed the new genus *Cryptione* for his new species *C. elongata* discovered on the deep-sea shrimp *Nematocarcinus agassizii* Faxon, 1893 from ~1636 m depth near the Galapagos Islands. Later, Markham (1999) redescribed the species based on specimens from the Chesterfield Islands and followed Nierstrasz & Brender à Brandis (1923) in concluding that the genus *Cryptione* was a synonym of *Pseudione*. Some authors (e.g., Schultz 1969; Rioja 1971; Brusca 1987) were not aware of or did not follow this synonymy, and it is now apparent that *Cryptione* is distinct from *Pseudione sensu lato*. Herein, we resurrect the genus *Cryptione*, based on findings from a new species parasitizing shrimp from the Gulf of Mexico that match the key characters of the genus.

Within the Gulf of Mexico, two species exist within the deep-sea shrimp genus *Notostomus.* Both species participate in diel vertical migration, which describes a predator avoidance behavior in which animals migrate to shallow waters to feed and mate at night. The species *N. gibbosus* A. Milne-Edwards, 1881, can be easily recognized by its bright red color and distinctive enlarged carapace which is filled with a fluid that allows them to control buoyancy in the water column (Sanders and Childress 1988). Collections of *N. gibbosus* from the Gulf of Mexico led to the finding of a new species of branchial bopyrid, the first record of a pseudionine parasitizing a member of the family Acanthephyridae Spence Bate, 1888. Upon examination, the species was found to morphologically closely match the characters of the type species of *Cryptione*, a genus that presently includes 11 other species of pseudionines known to parasitize caridean hosts (see Table 1). The purpose of the present work was to describe the female, male, and epicaridium (first larval) stage of this new species. In addition, molecular analyses were completed to examine the phylogenetic relationships of this new species, supporting *Cryptione* as distinct from other pseudionine genera.

Materials and methods

Sample collection

Samples were collected on the R/V Point Sur in the northern Gulf of Mexico in May 2023 (DP09) using a multiple opening-closing net and environmental sensing system (MOC-10) ranging from 0 to 1500 m in depth as part of the DEEPEND/RESTORE project funded by NOAA (National Oceanic and Atmospheric Administration). Parasitic isopods (one male and one female) were removed from the gill chamber of a deep-sea acanthephyrid shrimp, *Notostomus gibbosus*, and preserved in 80% ethanol at − 20 °C. Isopods were cataloged into the Florida International Crustacean Collection (FICC) at Florida International University-Biscayne Bay Campus. Larvae from the female isopod were removed from the brood chamber of the female isopod and preserved separately for molecular work and scanning electron microscopy (SEM) study, whereas the adult specimens were retained for morphological analyses.

Morphological examination

Measurements of hosts and parasites were made with dial calipers and a micro-scale tool (Electron Microscopy Sciences); host shrimp size is given as carapace length (CL); adult parasitic isopod size is given as maximal length (from anterior border of head to terminus of pleon or posterolateral extensions of final pleomere). Camera lucida sketches of isopod specimens were made with an Olympus compound scope (CX41) or dissecting scope (SZX-12); sketches were scanned and then traced using a Wacom drawing tablet (Wacom Cintiq 22HDT pen display) and Adobe Illustrator. Adult isopods were imaged with a Macropod Pro kit (Macroscopic Solutions), and resulting pictures were aligned and stacked with the focus stacking software Zerene Stacker (~ 20 images from bottom to top of specimens).

For SEM preparation of epicaridium larvae, specimens were dehydrated in an ascending ethanol series and drying was completed with a Samdri 795 Critical Point Dryer. Larvae were then mounted on aluminum stubs, coated with gold using an EMS-550 Sputter coater, and viewed with a FEI Quanta

Table 1 Described species in *Cryptione*, with data on their type localities (including longitude and latitude where known), host genera and families they are found to parasitize, and the maximum length of females and males of the parasites

Species of *Cryptione*	Type locality	Long/Lat	Host genera	Host family(s)	Female max length (mm)	Male max length (mm)	References
C. affinis (G. O. Sars, 1882)	Norway	Not provided	*Plesionika, Notopandalus, Nauticaris, Pandalus, Dichelopandalus*	Pandalidae, Hippolytidae	8.3	1.9	G. O. Sars 1883
C. chiloensis (Román-Contreras & Wehrtmann, 1997)	Chile	42°25′S, 73°43'W	*Nauticaris*	Hippolytidae	4	0.96	Román-Contreras and Wehrtmann 1997
C. clevai (Boyko, 2004)	New Caledonia	23°02.09′S, 166°56.61′E	*Stylodactylus*	Stylodactylidae	7.2	2.3	Boyko 2004
C. cognata (Markham, 1985)	Gulf of Mexico	27°37′N, 84°13′W	*Philocheras*	Crangonidae	2.02	0.72	Markham 1985
C. elongata africana (Kensley, 1968)	South Africa	33°26′S, 16°33′E	*Nematocarcinus*	Nematocarcinidae	15.2	5.5	Kensley 1968
C. elongata elongata Hansen, 1897	Galapagos	0°4′S, 90°24′30″W	*Nematocarcinus*	Nematocarcinidae	13	4.1	Hansen 1897
C. indica (Chopra, 1930)	Andaman Is	Not provided	*Pontophilus, Plesionika*	Crangonidae, Pandalidae	2	–	Chopra 1930
C. magna (Shiino, 1951)	Japan	Not provided	*Heterocarpus*	Pandalidae	20.2	6	Shiino 1951
C. parviramus (Adkison, 1988)*	Gulf of Mexico	28°44′N, 89°38′W; 24°23′N, 83°22′W	*Plesionika; Heterocarpus*	Pandalidae	11.5	3.7	Adkison 1988
C. pontocari (Page, 1985)	New Zealand	37°19.5′S, 176°16.5′E	*Pontocaris*	Crangonidae	5.2	2.6	Page 1985
C. stylopoda (Boyko, 2004)	Vanuatu	15°41.52′S, 167°02.67′E	*Stylodactylus*	Stylodactylidae	8.1	3.2	Boyko 2004
C. tattersalli (Nierstrasz & Brender à Brandis, 1923)	Indonesia	7°15′S, 115°15.6′E	*Plesionika*	Pandalidae	12	5	Nierstrasz and Brender à Brandis 1923
C. grandis sp. nov	Northern Gulf of Mexico	28°55′58.8″N, 87°57′00.0″W	*Notostomus*	Acanthephyridae	20.1	5.9	Present study

**C. parviramus* (Adkison 1988) is considered the senior synonym of *P. ampla* Markham 1988 (see “Remarks”)

250 SEM. Measurements of larvae (maximal length) were made from SEMs using ImageJ software; Adobe Photoshop was used to produce final figures from SEM images.

Specimens were deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

DNA extraction and sequencing

Total genomic DNA (gDNA) was extracted from the larvae (HBG 13202a-13202d) using DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA). One nuclear gene and one protein-coding gene were selected to evaluate the phylogenetic position including the small ribosomal subunit (18S rRNA) and cytochrome c oxidase subunit I (COI), respectively. The targeted genes have previously been used to investigate the phylogenetic relationship within isopods and COI can be used for species-level identification (Boyko et al. 2013). Selection of these genes was also suitable as GenBank sequences from previous studies could be included in the phylogenetic analysis. Forward and reverse primers used for this analysis were the same as indicated by Machida and Knowlton (2012) (Supplementary Table 1, primer pairs #1 and #5_RC).

DNA was amplified using polymerase chain reaction (PCR) and carried out in 25 µL reaction volumes on a Thermo Cycler (Applied Biosystems, PCR System). Each PCR mixture contained 12.5 µL of GoTaq Green, 8.5 µL of UV-sterilized deionized water, 1 µL of each (forward and reverse) primer, and 2 µL of DNA per sample. The thermal profile began with initial denaturation at 94 °C for 3 min followed by 25 cycles of 94 °C for 30 s, primer specific annealing temperature (42–72 °C) for 30 s, 72 °C extension for 1 min, and a final extension of 72 °C for 7 min.

After amplification, 3 µL of PCR products was visualized on a 25-well precast using 2% agarose gel electrophoresis stained with 0.5 µL of GelRed nucleic acid gel stain (Biotium) and ran at 100 V for 40 min. Gels were imaged under UV light and final PCR products were purified and sequenced by TACGen (Richmond, CA, USA).

Phylogenetic analyses

Outgroup taxa from the genus *Anilocra* were selected based on previous studies (Boyko et al. 2013). For ingroup selection, we included 1 sample (HBG 13202a) of the target species with an additional 35 epicaridean species (Supplementary Tables 2–4) to ensure diversity was captured across the group. Single gene (18S or COI) and concatenated (18S/COI) phylogenetic trees were used to investigate the identity and phylogenetic placement of the new parasitic isopod. Sequences (18S and COI) for additional species were downloaded from NCBI's GenBank database when available (Supplementary Tables 2–4) and uploaded into the Geneious Prime software (ver. 11.0.20.1). DNA sequences were aligned using a multiple sequence alignment tool (MAFFT) and concatenated for our 18S and COI alignments. In some cases, 18S and COI sequences were available for different individuals of the same species, and these were concatenated in the concatenated sequence alignment.

Both single-gene trees (18S and COI) and concatenated tree (18S + COI) were constructed in the IQ-TREE 2.3.1 program using a maximum likelihood (ML) approach. ModelFinder was used to determine the model of evolution and partitioning. The best model of evolution and partitioning was determined based on the Bayesian Information Criterion (BIC) implemented within IQ-TREE. Confidence in the resulting topologies was assessed using ultrafast bootstrapping (UFBoot) and Shimodaira-Hasegawa-like approximate likelihood ration test (SH-aLRT) with 1000 replicates and the search parameter for the best-scoring tree was selected. Trees were visualized in FigTree v1.4.4. All support values are listed on the corresponding branch and presented on the final phylogeny; high support values are indicated by values of > 95 (UFBoot) and > 80 (SH-aLRT). Any values under 70 were not presented on the branches.

Results

Systematics

Order Isopoda Latreille, 1816
Suborder Epicaridea Latreille, 1825
Superfamily Bopyroidea Rafinesque, 1815
Family Bopyridae Rafinesque, 1815
Subfamily Pseudioninae Codreanu, 1967
***Cryptione* Hansen, 1897**

Diagnosis

Female elongate, body nearly straight to distorted (< 55°); head not bilobed; frontal lamina present, narrow to wide. Maxilliped with setose palp, some species with setose region below palp. Barbula with one or two lateral projections. Five pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distolateral projection, smaller than anterior lobe; internal ridge smooth or digitate. Pereopods generally increasing in size posteriorly; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; five pairs of biramous pleopods decreasing in size posteriorly, endopods smaller than exopods; uropods uniramous or reduced. **Male** approximately 4–7 times as long as wide, head subobvate, as wide as pereon, pereomeres not narrower posteriorly. Eyes present or absent. Maxillipeds absent (see also "Remarks"). Pereopods subequal. Pleon of six pleomeres; five pairs of uniramous pleopods present; posterolateral corners of pleomere 6 extended; uropods absent. Definitive hosts caridean shrimp.

Remarks

A diagnosis of this genus was not provided in the original description or in subsequent reports. *Cryptione* is morphologically similar to *Pseudione* sensu stricto species that parasitize axiideans and astacideans (Boyko et al. 2017). Females of *Pseudione* sensu stricto possess maxillipeds with two setose palps (as in *Pseudione callianassae* Kossmann, 1881; see Fig. 8C in Boyko et al. 2017) or palp with a rounded lower ridge covered with setae (e.g., *Pseudione nephropsi* Shiino 1951; see Fig. 6C in Shiino 1951). In contrast, females of *Cryptione* typically have a single broad setose palp on each maxilliped; however, in *C. indica* (Chopra 1930) the palp is accompanied by a basal, rounded setose portion but these setae are compound rather than simple setae (Markham 1994). Although *Pseudione* sensu stricto and *Cryptione* are similar based on morphology, molecular data supports the conclusion that *Cryptione* is distinct.

The study has also brought to light taxonomic issues among three species of *Pseudione* sensu lato, all from shrimp hosts collected in the Gulf of Mexico (GOM). Two of these species: *P. ampla* Markham, 1988, on the pandalid *Heterocarpus ensifer* A. Milne-Edwards, 1881, from 366 m depth in the northern GOM off the coast of Louisiana and *P. parviramus* Adkison, 1988, on *Parapandalus longicauda* Rathbun, 1902, from 133 m depth in the eastern GOM and Cay Sal Bank are morphologically indistinguishable based on their original descriptions. After re-examining the type specimens (*P. ampla* = USNM 98677 and 229,911; *P. parviramus* = USNM 172441 and 172442), we can find no characters to distinguish these taxa. The species were described in the same year and it appears that the authors were not aware of each other's work (Adkison 1988; Markham 1988). We herein synonymize *P. ampla* with *P. parviramus* based on publication dates (1 December 1988 and 13 September 1988, respectively).

In addition, the characters of *P. cognata* (Markham, 1985) described from the crangonid *Philocheras gorei* (Dardeau, 1980) collected at 78 m depth from the GOM west of Egmont Key, Florida, are in need of clarification. The species was originally reported (and shown in drawings) to lack a frontal lamina (Markham 1985); however, re-examination of type specimens (USNM 172351; USNM 181546) showed that the females possess a thin frontal lamina, as found in other members of *Cryptione*. The females of *P. cognata* have indistinct dorsolateral bosses on the long sides of pereomeres 2–5 and the maxilliped palp exhibits large setae with setules along the length. These characters and the general body form of the females (e.g., body distortion at ~ 50°) are slightly different from the other species in *Cryptione* but there are no characters that clearly place *P. cognata* outside of this genus. Thus, we have moved *P. cognata* to *Cryptione* along with all members of *Pseudione* sensu lato that parasitize caridean shrimps. We urge resampling of *P. cognata* for additional morphological and molecular work to test this placement. The distinction between the subspecies *C. elongata africana* (Kensley, 1968) and *C. elongata elongata* Hansen, 1897 is questionable, especially considering that the former was based on only one male/female pair, the female of which appears to have a malformed posterior end. New material from the west coast of the Cape Peninsula of South Africa is needed to clarify the status of this subspecies.

In addition to recognizing *Cryptione* as a valid genus with the type species of *C. elongata* Hansen, 1897, we transfer 11 species from *Pseudione* sensu lato group into *Cryptione* and below describe a new species within the genus; all of these species are restricted to caridean shrimp definitive hosts (Table 1). This leaves 16 species known from galatheoid hosts in *Pseudione* sensu lato, eight of which belong to the group of *Pseudione* "crénelés" (see Pereira et al. 2021) and another eight which have uncertain affiliation.

Type species

Cryptione elongata Hansen, 1897

Type locality

Galapagos Islands; type host: *Nematocarcinus agassizii* Faxon, 1893

Other included species and subspecies

Cryptione affinis (G. O. Sars, 1882) comb. nov., *C. chiloensis* (Román-Contreras & Wehrtmann, 1997) comb. nov., *C. clevai* (Boyko, 2004) comb. nov., *C. cognata* (Markham, 1985) comb. nov., *C. elongata africana* (Kensley, 1968) comb. nov., *C. elongata elongata* Hansen, 1897, *C. indica* (Chopra, 1930) comb. nov., *C. magna* (Shiino, 1951) comb. nov., *C. grandis* sp. nov., *C. parviramus* (Adkison, 1988) comb. nov., *C. pontocari* (Page, 1985) comb. nov., *C. stylopoda* (Boyko, 2004) comb. nov., and *C. tattersalli* (Nierstrasz & Brender à Brandis, 1923) comb. nov. See Table 1 type localities and host affiliations.

Cryptione grandis **sp. nov.** (Figs. 1, 2, 3, 4, and 5)
https://zoobank.org/10e13c8c-cdef-4c3b-86fd-a9167fd57bf8

Material examined

Holotype: ovigerous mature female (20.1 mm TL; USNM 1716194), northern Gulf of Mexico, 28°55′58.8″N 87°57′00.0″W, depth 0–1500 m, R/V Point Sur, 02 May 2023, infesting right branchial chamber of *Notostomus gibbosus* (36.3 mm CL including rostrum; DP09;

Fig. 1 *Cryptione grandis* sp. nov. from *Notostomus gibbosus* (**a**–**d** female holotype (USNM 1716194); **e** male allotype (USNM 1716195)). **a** Lateral view of *N. gibbosus* with *C. grandis* sp. nov. extending from right branchial chamber (ventral view of female with larvae in brood chamber shown); **b** lateral view of *N. gibbosus* with *C. grandis* sp. nov. removed and positioned dorsal side up (male attached to posterior pleon, shown with arrow); **c** female dorsal view; **d** female ventral view; **e** male dorsal view. Scale bars: **a**–**d** = 5 mm; **e** = 1.5 mm

MOC10-B001N-241-N0). Allotype*:* mature male (5.9 mm TL; USNM 1716195), found with holotype infesting right branchial chamber of *N. gibbosus*. Paratypes: epicaridium larvae (USNM 1716196, on SEM stub), from brood chamber of holotype.

Description of female

Holotype female (Figs. 1a–d and 2a–l): total body length 20.1 mm, maximal width 13.2 mm at pereomere 4, head length 4.7 mm, head width 6.1 mm, pleon length 6.6 mm. Body oval, longer than wide; nearly symmetrical, with slight (~17°) dextral rotation (Figs. 1c, d and 2a). All body regions and pereomeres distinct. No pigmentation.

Head suboval, deeply inset into first pereomere. Frontal lamina narrow, extending slightly beyond lateral sides. Minute eyes present posterolaterally, deeply embedded (Fig. 2b). Antennule of three articles (Fig. 2c), antenna of seven articles (Fig. 2c), each with terminal article setose, all articles covered by scales. Barbula (Fig. 2d) with two pairs of lanceolate lateral projections, outer pair longer; medial margin sinuous. Maxilliped (Fig. 2e, f) with two articles, anterior margin of largest article setose; well-developed, extended, non-articulated palp present with setae along entire length; spur long and broad, overlapping circular structure on medial posterolateral edge of anterior article.

Pereon broadest across fourth pereomere (Figs. 1c and 2a). First pereomere shorter than others. Narrow coxal

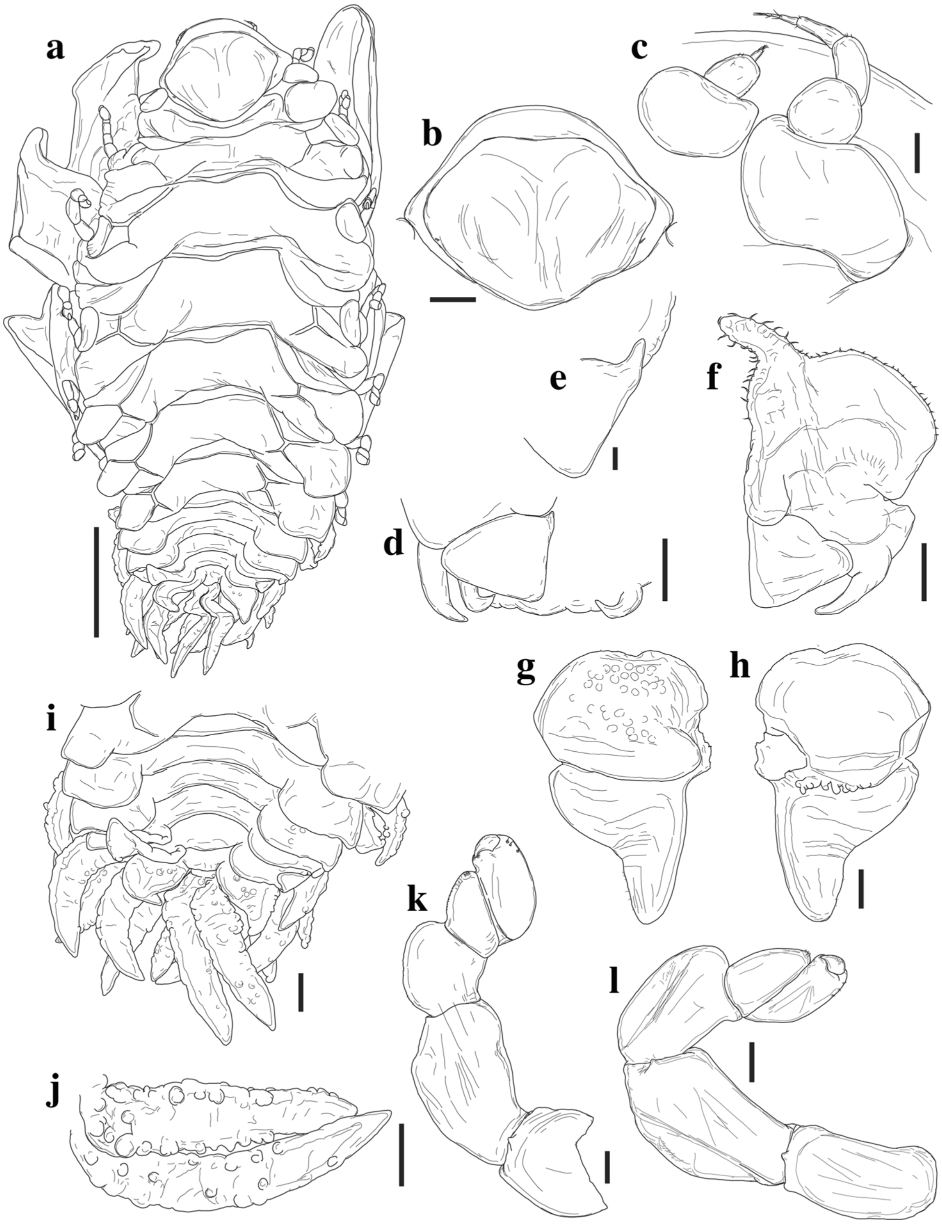

Fig. 2 *Cryptione grandis* sp. nov. a–l female holotype, USNM 1716194. **a** Female dorsal view; **b** head dorsal view; **c** left antennae (antennule to left, antenna to right); **d** barbula, with partial view of right maxilliped, only inner extension shown on left side of barbula; **e** spur of maxilliped, inner view; **f** left maxilliped, outer view; **g** left oostegite 1, outer view; **h** left oostegite 1, inner view; **i** posterior pereomeres and pleon, dorsal view; **j** fifth pleopods (endopod at top, exopod on bottom); **k** left pereopod 1; **l** left pereopod 7. Scale bars: **a** = 5 mm; **b**, **d**, **f**–**j** = 1 mm; **c**, **e**, **k**, **l** = 250 µm

plates on pereomeres 1–4. Dorsolateral bosses on pereomeres 1–7 on both sides; expanded on pereomeres 6 and 7, morphology similar to lateral plates. Oostegite 1 (Fig. 2g, h) anterior lobe rounded with small bumps; internal ridge sinuous, with irregular digitations; posterior lobe larger than anterior lobe; posterolateral point extended, inner margin with minute setae. Pereopods of six articles (Fig. 2k, l); all articles covered with scales, including dactylus; with ~ 8–9 short setae near outer margin of carpus, propodus with long setae on anterior margin near dactylus, median portion of ischium and merus expanded, set apart from article, more pronounced on posterior pereopods (Fig. 2l); posterior pereopods very slightly increasing in length.

Pleon of six segments. Pleomeres 1–5 (Fig. 2i) with triangular lateral plates, some digitate. Five pairs of biramous digitate pleopods; first pleopods slightly shorter and squatter, posterior pleopods more elongate (Fig. 2j); endopods straight, exopods curved with sickle shape. Uniramous uropods (Fig. 2a, i) of similar shape and size, slightly digitate.

Description of male

Allotype male (Figs. 1e and 3a–h): total body length 5.9 mm, maximal width 1.4 mm at pereomere 4, head length 0.51 mm, head width 0.78 mm, pleon length 2.4 mm. All body regions and segments distinct. Body elongate,

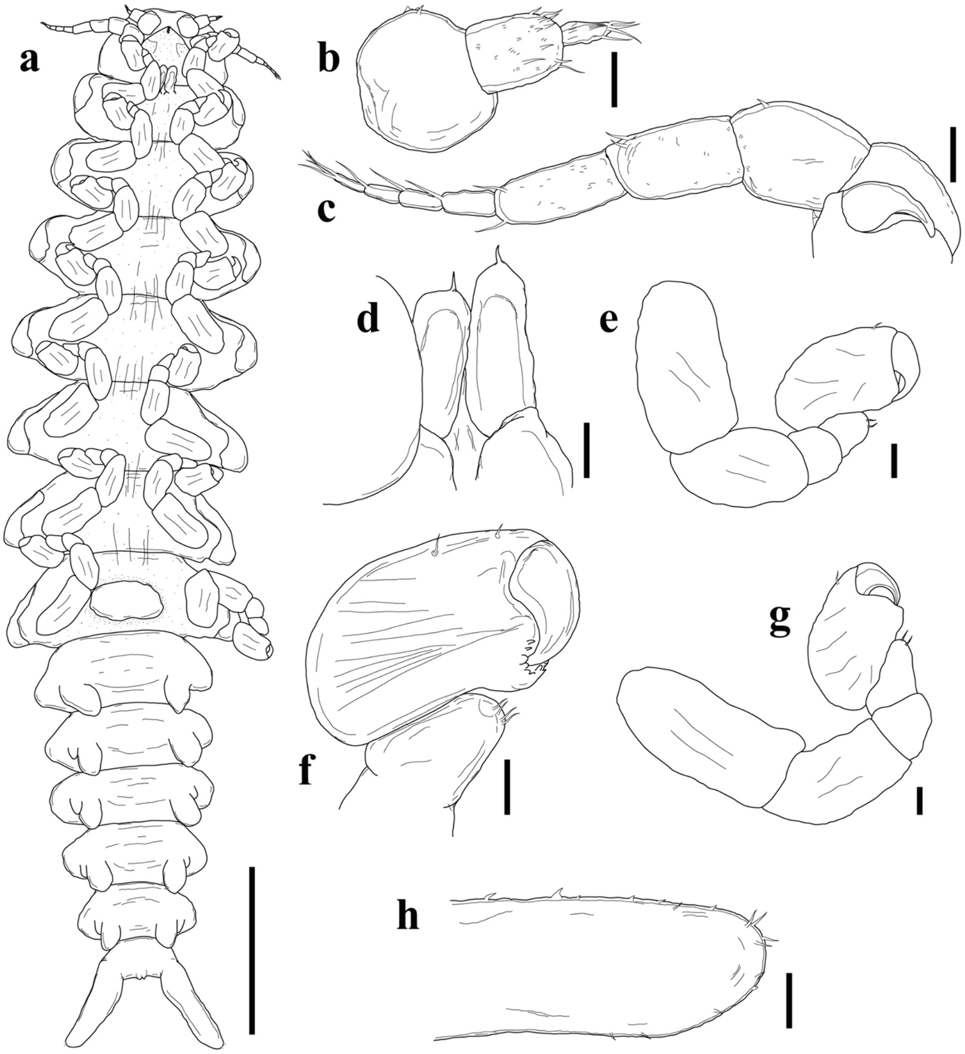

Fig. 3 *Cryptione grandis* sp. nov. **a**–**h** male allotype, USNM 1716195. **a** Ventral view; **b** left antennule; **c** right antenna (pereopod 1 obscuring part of basal segment); **d** maxillipeds; **e** left pereopod 1; **f** right pereopod 5; **g** left pereopod 7; **h** distal end of posterolateral extension of terminal pleomere. Scale bars: **a** = 1 mm; **c**–**h** = 50 μm

tapering anteriorly and posteriorly (Figs. 1e and 3a). No pigmentation.

Head rounded, slightly inset into first pereomere. Eyes absent. Antennules of three articles each (Fig. 3b); all except terminal article covered with scales; anterior margins setose. Antennae of eight articles each (Fig. 3c), first four covered with scales; all articles except basal with distal margins setose. Maxillipeds (Fig. 3d) present, with oval distal segment and terminal seta.

Pereon of seven segments, broadest at pereomere 4, tapering anteriorly and posteriorly (Fig. 1e). Pereomeres indented laterally; distolateral margins of pereomeres 1–4 directed anteriorly, and pereomeres 5–7 directed posteriorly. Broad midventral tubercle on pereomere 7 (Fig. 3a). Pereopods of six articles (Fig. 3e–g), increasing in size posteriorly. All pereopods with setae on outer margin of carpus; few large setae on anterior margin of propodus; no scales visible on any articles.

Pleon with six distinct pleomeres (Fig. 3a). Pleomeres indented laterally, and distolateral margins directed posteriorly. Pronounced cylindrical uniramous pleopods on pleomeres 1–5 (Fig. 3a). Terminal pleomere with long posterolateral extensions (see “Remarks”) covered with scales (Fig. 3a, h); lateral margins with small setae, posterodistal margin with few long setae. Uropods absent.

Description of epicaridium larvae

Approximately 830 μm in length (anterior margin of head to end of anal tube). Head curled ventrally, rounded anteriorly, nearly straight at base of antennae (Fig. 4a, b). Antennules of three articles each (Fig. 4c), basal article large, extending from oral cone to near side of head, with distal seta, branched at tip; article 2 subquadrate with distal setae, branched at tips; article 3 small, basal portion with two large setae (each divided along their length; perhaps aesthetascs), lateral digitiform lobe with two curled setae with setules along their length (Fig. 4c and inset). Antennae and terminal setae extending past length of anal tube (Fig. 4a, b, e); antennae composed of six articles

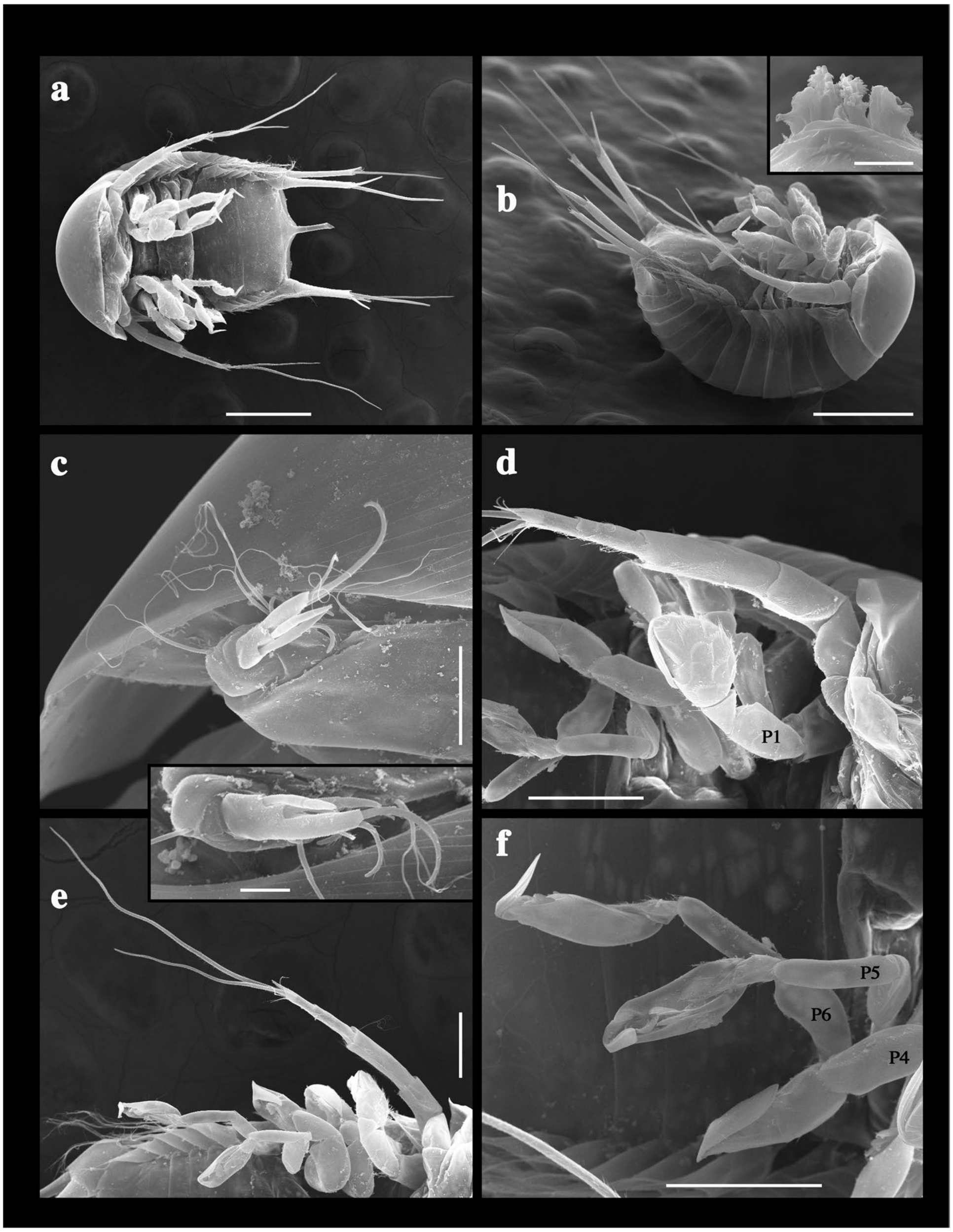

Fig. 4 *Cryptione grandis* sp. nov. **a**–**f** mature epicaridium larvae, USNM 1716196. **a** Ventral view; **b** lateral view (inset shows mouthparts, mandibles in center); **c** antennule (inset shows close-up of distal article and setae); **d** base of antenna and pereopods; **e** distal end of antennae and pereopods; **f** pereopods 4–6. Abbreviations: P1, P4–P6 = pereopods 1, 4–6. Scale bars: **a**, **b** = 250 µm; **c** = 25 µm; **d**–**f** = 100 µm; **b**, **c**, insets = 10 µm

each (four basal and two flagellar) with spinous scales, articles 1 and 2 subequal in size; articles 3 and 4 progressively longer, flagellar articles shorter than terminal basal article, flagellar article 2 with terminal spine, four short setae and two long setae, longer of which equals the length of all antennal articles (Fig. 4a, b, d, e).

Mouthparts consisting of oral cone extending between base of antennules (Fig. 4 a, b); stout mandibles with “toothed” distal end extending from oral cone (Fig. 4b inset); other mouthparts cannot be distinguished.

Six pairs of gnathopodal pereopods, progressively smaller posteriorly (Figs. 4a, b, d, e and 5a, b). Pereopods 1–3 subequal in size and form (Figs. 4d and 5a), each with thin, approximately straight dactylus, carpus completely fused with rounded propodus, with large, multifid setae to side of dactylus, merus triangular, with terminal seta, ischium ovate, basis elongate, all articles with spinous scales, most prominent on carpus/propodus. Pereopods 4–6 subequal in size and form (Figs. 4e, f and 5b); smaller than preceding pereopods; each with wide dactylus, curled along length, with large, multifid setae to side of dactylus, carpus fused with elongate propodus, merus subquadrate, with terminal setae, ischium elongate, basis broader at distal end, attenuating in width toward base, spinous scales present but not as pronounced as on pereopods 1–3.

Pleon with five pairs of pleopods (Figs. 4a, b and 5c–e), pleopods 1–4 biramous, pleopod 5 uniramous. Pleopods 1–4 (Fig. 5c, d) coxopodite and endopodite fused into triangular

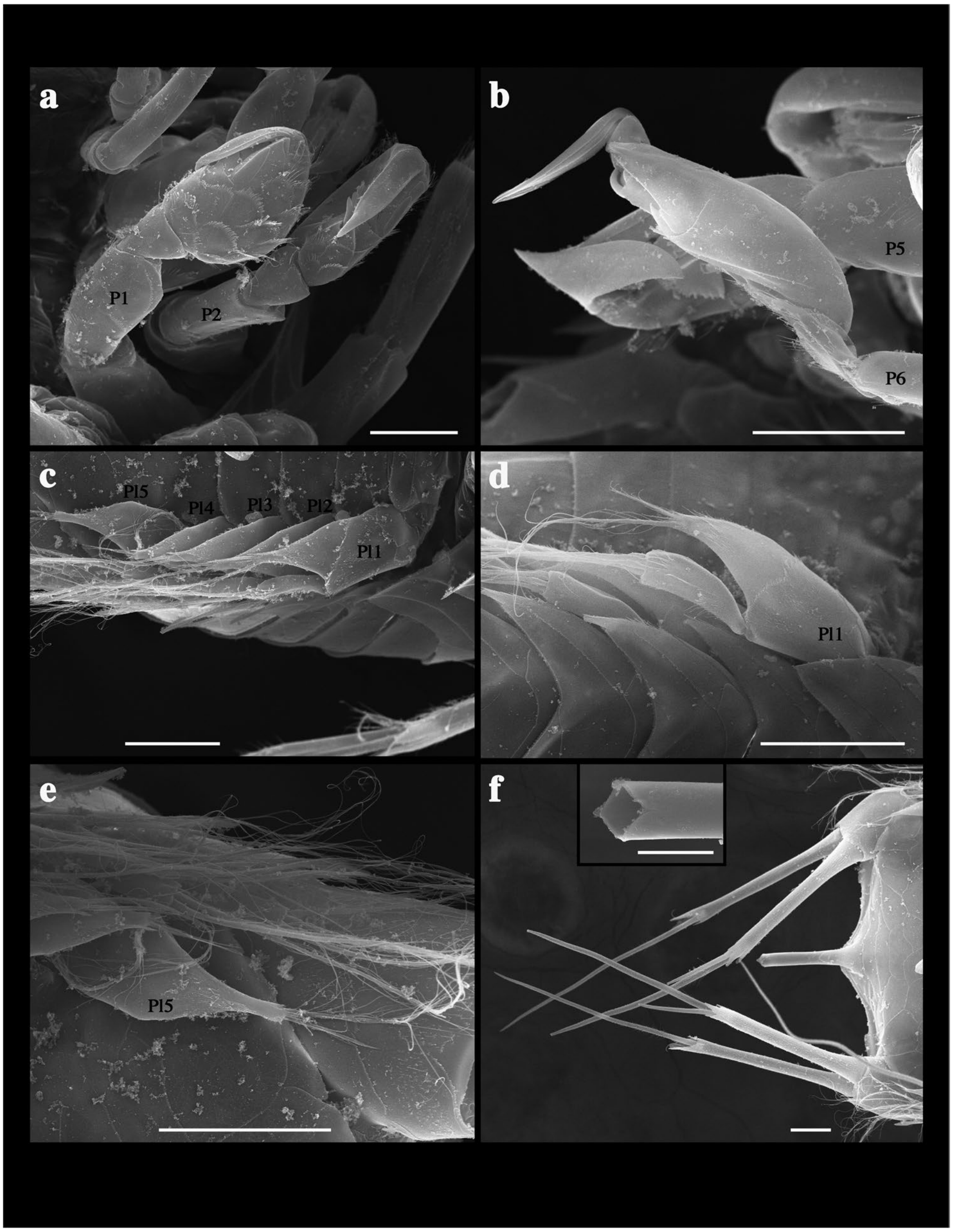

Fig. 5 *Cryptione grandis* sp. nov. **a**–**f** mature epicaridium larvae, USNM 1716196. **a** Pereopods 1, 2; **b** pereopods 5, 6; **c** pleopods 1–5; **d** pleopod 1; **e** pleopod 5; **f** ventral view of uropods and anal tube (inset shows close-up dorsal view of anal tube distal end). Abbreviations: AT = anal tube; P1, P2, P5, P6 = pereopods 1, 2, 5, 6; Pl1–5 = Pleopods 1–5. Scale bars: **a**–**f** = 50 µm; **f** inset = 20 µm

lobe with ridge of spinous scales corresponding to insertion point of endopodite, endopodite with one short and one long plumose terminal seta, exopodite cylindrical, broader at distal end, with curved inner margin, with three long, plumose terminal setae. Pleopod 5 (Fig. 5e) coxopodite and endopodite as in pleopods 1–4, exopodite absent. Uropods biramous (Figs. 4a, b and 5f), short, triangular peduncle, endopod slightly shorter than exopod, endopod ending in one long, stout and one short, stout seta with small setules along their lengths, exopod with one long, stout seta with small setules along length and minute seta at base; both exopods and endopods with terminal projections surrounding base of stout setae. Long anal tube between uropods (Figs. 4a and 5f), anal tube extending to a sharp point dorsally, and indented ventrally (Fig. 5f and inset).

Etymology

The species epithet *grandis* is Latin for large or great, denoting the size of the female parasite.

Type locality

Northern Gulf of Mexico (28°55′58.8″N, 87°57′00.0″W); type host: *Notostomus gibbosus*.

Remarks

Two of the 13 valid species of *Pseudione* infesting carideans, now transferred to *Cryptione*, are known from the Gulf of

Mexico: *C. cognata* (Markham, 1985) on crangonid shrimp and *C. parviramus* (Adkison, 1988) on pandalid shrimp (Table 1). Of these, the new species appears most similar to *C. parviramus* in terms of overall form of the female. However, the female of the new species is more elongate and much larger (~20 mm in *Cryptione grandis* sp. nov. versus ~11 mm in *C. parviramus*) and the new species has an open brood chamber versus a brood chamber that is enclosed by oostegites as found in *C. parviramus*. In addition, the male of the new species has greatly produced posterolateral points of the terminal pleomere whereas males of *C. parviramus* lack such extensions.

The new species is similar in morphology to the females of *C. clevai* (Boyko, 2004) (parasite of stylodactylid shrimp from New Caledonia) with both possessing an elongate body with an open brood chamber; the males are also very similar in morphology. However, females of *C. clevai* have much broader uropods and a non-digitate internal ridge of oostegite 1. In terms of overall size, the new species is one of the largest within Pseudioninae and in *Cryptione* is second only to *C. magna* (Shiino, 1951) (20.2 mm TL, parasite of pandalid shrimp from Japan). However, the female of the new species is more elongate and the male has pronounced pleopods and lacks midventral tubercles on the pleomeres; the male of *C. magna* has small conical pleopods and midventral tubercles on the first three pleomeres.

Our description of the male interprets the extensions of the terminal pleomere as produced posterolateral points, not as "true" uropods, which have at least an indication of articulation at the base; "true" uropods on males appears to be restricted to species in only a few pseudionine genera (*Gigantione* Kossmann, 1881; *Parapleurocryptella* Bourdon, 1972; *Pleurocryptella* Bonnier, 1900). Other epicaridean genera show a wide range of terminal pleomere extensions (e.g., species in *Ione* Latreille, 1818, *Leidya* Cornalia & Panceri, 1861) and future comparative studies should examine the development of these and "true" uropods, testing hypotheses on whether they are homologous or convergent features. Another feature of males that should be examined in the genus is presence of maxillipeds; they are clearly visible in *Cryptione grandis* sp. nov. and *C. parviramus* (Adkison, 1988) but for the other species no comments are made on the presence/absence of the maxillipeds, although they can be seen in some figures (e.g., *C. cognata* Markham, 1985). The type specimens of one species (*C. tattersalli*) were recently re-examined and males were found to lack maxillipeds (Boyko, pers. comm.); thus, this feature appears to be variable in the genus.

Epicaridium larvae have only been examined in one other member in the genus, *C. elongata africana* (Kensley 1968), but only a single line drawing and short description were included (Kensley 1968). Certain features, such as the antennae segmentation counts and fine structure of the pereopods, were not described in sufficient detail for comparison with the new species. However, it is clear that *C. elongata africana* lacks the long anal tube that is present in *C. grandis* sp. nov. Such anal tubes have been described in other epicaridium larvae (e.g., Hansen 1895; Calman 1898; Dale and Anderson 1982) although their functional significance remains unknown.

Phylogenetic relationships

Single gene and concatenated trees were run to investigate the phylogenetic placement of the targeted individual, *Cryptione grandis* sp. nov. (Fig. 6). The 18S phylogeny included 25 sequences from GenBank and one newly generated 18S sequence, for a total of 26 sequences (Supplementary Tables 2, 4). The COI phylogeny included 19 sequences from GenBank and one newly generated COI sequence, for a total of 20 sequences (Supplementary Tables 2, 3). The final concatenated alignment length was 4656 bp, for a total of 36 sequences representing 36 species from six families.

The 18S phylogeny (Fig. 6a) recovered *C. grandis* sp. nov. on a branch falling sister to a clade including *Athelges* Gerstaecker, 1862, *Ione* Latreille, 1818, "Cyproniscidae" Giard and Bonnier, 1887, *Holophryxus* Richardson, 1905, *Zonophryxus* Richardson, 1903, *Entophilus* Richardson, 1903, *Cancrion* Giard and Bonnier, 1887, and *Portunion* Giard and Bonnier, 1886; albeit with very low support. The COI phylogeny (Fig. 6b) recovered *C. grandis* sp. nov. as sister to *Gyge ovalis* (Shiino, 1939) with low support.

Finally, the concatenated tree (Fig. 6c) was similar to the COI topology and placed *C. grandis* sp. nov. as sister to *Gyge ovalis*, but with no support. In all trees, branch lengths for the new species are similar to other congenerics. Although there is some support for a possible affinity to Pseudioninae, more investigations are needed to confidently suggest the sister relationship between *C. grandis* sp. nov. and other bopyrids.

Discussion

The finding of the new species of bopyrid parasitic isopod is the first from any member of Acanthephyridae, although crangonid and pandalid shrimp are known to be hosts of bopyrids in the Gulf of Mexico (Markham 1985, 1988, 2020; Adkison 1988). Acanthephyrid shrimp (*Acanthephyra* spp.) from the Atlantic and Pacific are known to be commonly parasitized by the "backpack" isopod *Holophryxus acanthephyrae* Stephensen, 1912 (Epicaridea: Dajidae) (Boyko and Williams 2021). This is, however, the first record of an epicaridean isopod parasitizing a species from the genus *Notostomus* A. Milne-Edwards, 1881.

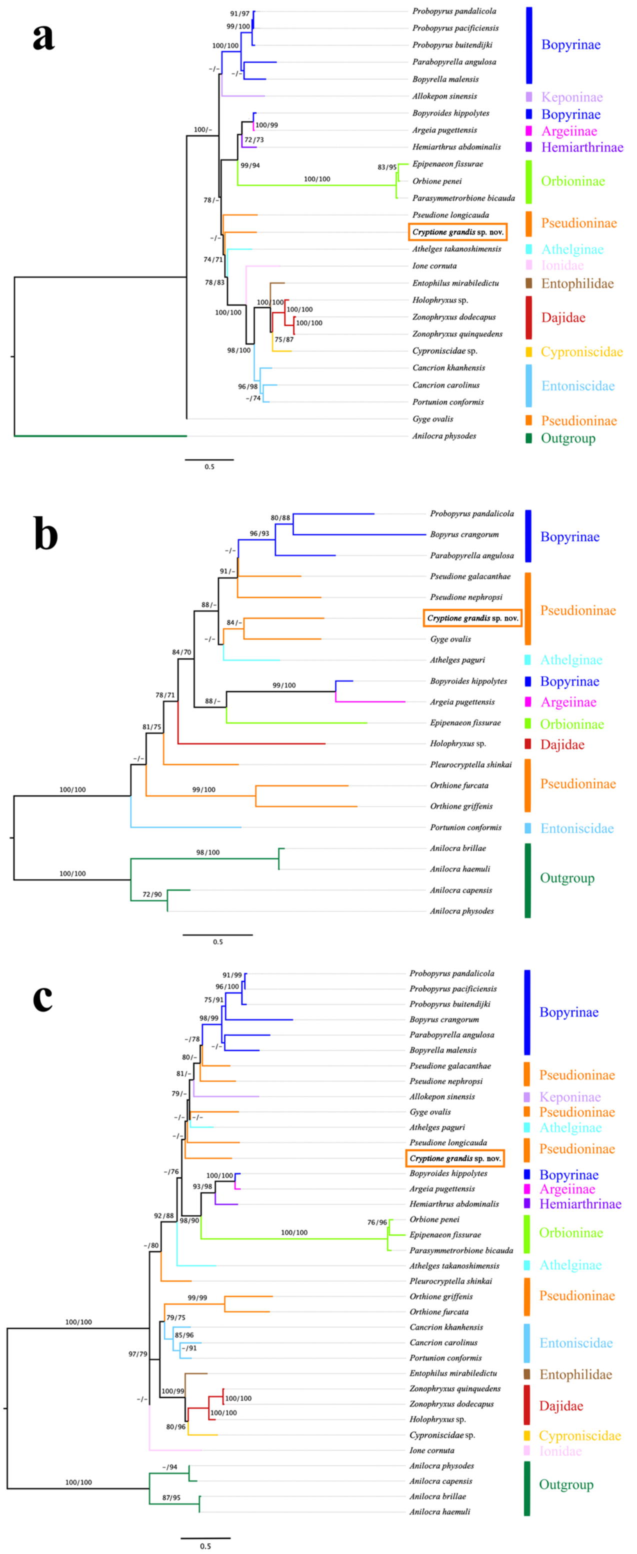

Fig. 6 Phylogenetic trees of *Cryptione grandis* sp. nov. (highlighted with orange box in **a**–**c**) and other members of Epicaridea. **a** Phylogenetic tree based on 18S data; **b** phylogenetic tree based on COI data; **c** phylogenetic tree based on combined 18S and COI data. Numbers at nodes are statistical support values for maximum likelihood (ML) ultrafast bootstrap (UFBoot) support/SH-like approximate likelihood ration test (SH-aLRT). Values less than 70% were not included in topology. Epicaridean families, subfamilies, and outgroups showed on right and in color

Bopyrid parasites are known for impacting several life history aspects of their definitive hosts, with documented cases of lowered fecundity or even castration, alteration of secondary sexual characters, damage to branchiae and reduced oxygen consumption, and reduced molt frequency, among other negative effects to parasitized individuals (see Shields 2022 and references therein). Considering only the 12 species belonging to *Cryptione*, very few studies have analyzed their effects on their shrimp hosts. *Cryptione affinis* (G. O. Sars, 1882) comb. nov. was found to damage the gill lamellae and decrease respiratory function of its host shrimps, *Plesionika* spp. (Paradiso et al. 2004). This same species has also been shown to cause negative impacts to the reproduction of *Plesionika martia* (A. Milne-Edwards, 1883), limiting the production of spermatozoa in the infested males and inhibiting oogenesis in the females (Orecchia et al. 1999). However, if the parasite is dislodged or dies, the shrimps seem to partially recover gonadal functioning although still suffering from lowered fertility (Orecchia et al. 1999). A similar impact on host reproduction was seen by Pike (1960) in the pandalid shrimp *Dichelopandalus bonnieri* Caullery, 1896 parasitized by *C. affinis*.

Penha-Lopes et al. (2011) identified a bopyrid isopod parasitizing *Palaemon concinnus* Dana, 1852, in the mangrove forests of Mozambique as *Cryptione elongata africana* (Kensley, 1968) comb. nov. (cited as *Pseudione elongata africana*) and later studied the population and reproduction of the parasite in the same locations and host (Penha-Lopes et al. 2012). Comparing the few photos of the parasite available (see Fig. 3 of Penha-Lopes et al. 2012) with the original description and illustrations by Kensley (1968), it is apparent that these bopyrids are not *C. elongata africana*. The shallow-water palaemonid host from a mangrove habitat also contradicts this identification, as the type host of *C. elongata africana* is *Nematocarcinus longirostris* Spence Bate, 1888 (Nematocarcinidae), from the deep-sea (Kensley 1968). Morphological details from the images provided in Penha-Lopes et al. (2012), such as the open marsupium of the female, indicate that the parasitic isopod from *P. concinnus* belongs to the subfamily Bopyrinae Rafinesque, 1815, possibly to the genera *Probopyrus* Giard and Bonnier, 1888, or *Parabopyrella* Markham, 1985. Identification to the species level will require new collections as no voucher specimens were deposited.

The only species in *Cryptione* that has an identified intermediate host is *C. affinis*, which parasitizes the copepod *Calanus finmarchicus* (Gunnerus, 1770) during its epicaridium larval stage (Pike 1960). Pike (1960) found that the epicaridium larvae of *C. affinis* would not attach to any other copepod species offered to it in the lab, suggesting that the presence of *C. finmarchicus* might be a limiting factor for the bopyrids' reproduction and dispersion. A literature review on the species of copepods that are known hosts of epicaridean larvae showed that species of *Calanus* are the second most parasitized group of copepods (10 records in the literature), surpassed only by *Acartia* spp. (19 records) (Williams et al. 2022). The copepod intermediate host of *Cryptione grandis* sp. nov. is currently unknown, as are many other aspects of its natural history (e.g., cryptoniscus larval morphology, definitive host specificity, impacts on hosts, geographic range).

Our results largely support recent analyses of the phylogenetic relationships of epicaridean isopods (e.g., Boyko et al. 2013; An et al. 2022; Wu et al. 2022; Williams et al. in review) and show a monophyletic Bopyridae. Within Pseudioninae, *Cryptione* is sister to *Pseudione* sensu stricto but broader sampling within the subfamily needs to be completed, especially considering that this is the largest bopyrid subfamily with 60 + genera and 240 + species. For example, the genus *Orthione* Markham, 1988, was thought to be a member of Pseudioninae but based on COI it occupies a basal position among bopyrids and may constitute its own subfamily (Wu et al. 2022; Williams et al. in review). The phylogenetic position of *Orthione* and other genera should be examined with both molecular and morphological data (including all larval stages) to provide a stronger understanding of the evolutionary relationships for these ecologically important genera and potentially provide additional taxonomically informative characters that have been previously overlooked.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No approval of research ethics committees was required to accomplish the goals of this study because experimental work was conducted with an unregulated invertebrate species.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable.

Data availability The data generated and analyzed during this study are included in the Electronic Supplementary Material files.

Author contribution Bracken-Grissom collected the specimens. Williams and Horch completed all morphological analyses (light and scanning electron microscopy) and wrote the manuscript with Ceballos and Bracken-Grissom aiding in the writing. Ceballos and Bracken-Grissom completed the molecular analyses. All authors read and approved the manuscript.

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