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A new species of endoparasitic isopod, *Portunion sinensis* sp. nov. (Isopoda: Entoniscidae), found in the mud crab *Scylla paramamosain* in China

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Portunion (Isopoda, Epicaridea, Entoniscidae) is an extremely rare endoparasitic isopod genus that is found mainly in the blood cavity of decapod crustaceans, such as true crabs and hermit crabs. The mud crab (*Scylla paramamosain*) is one of the most economically important crab species in south China and Asia. In this study, we identified a new endoparasitic isopod species, *Portunion sinensis* sp. nov., from the hemocoel of *S. paramamosain*. *Portunion sinensis* sp. nov. is similar to *Portunion conformis* in having the anterior vertical to thorax, the posterior directed backwards for Female's ventral processes. However, the new species can be distinguished from *Portunion conformis* by the rudimentary abdominal spines present on segment III-IV in males. Herein we describe a detailed morphological description of this new species and conduct an extensive comparison with related species. This study marks the first description *Portunion sinensis* sp. nov. of an endoparasitic isopod species found in *Scylla paramamosain* in China. The findings expand the known biodiversity of parasitic isopods and contribute to understanding the host-parasite associations within this commercially significant crab species in the region.

KEYWORDS

endoparasite, Isopoda, *Portunion sinensis* sp. nov., *Scylla paramamosain*, taxonomy

1 Introduction

Bopyrid isopods infesting *Scylla paramamosain* belong to the superfamily Bopyroidea, family Entoniscidae, subfamily Entoninae. Species in the superfamily Bopyroidea are known for their holoparasitic behaviors. They mainly parasitize the gill cavity or abdomen of crustaceans (Jianmei, 2011) and can affect the reproduction and development of the host (Williams and Boyko, 2012). One member of this superfamily is the family Entoniscidae, which contains 53 species and includes the genus *Portunion*. These are rare isopod parasites

that inhabit the hemocoel of decapod crabs. Only seven valid *Portunion* species were recognized in the latest WoRMS list (Table 1). Species of *Portunion* have been reported in various areas, including the North Atlantic (Association, 1957; Blakeslee et al., 2009; Cornelius et al., 2019; Perkins, 1925; Zetlmeisl et al., 2011), the northeast Pacific (Kuris et al., 1979; Shields and Kuris, 1985), and the southwest Pacific (Brockerhoff, 2004; Koehler and Poulin, 2010) (Table 2). We summarize the characteristics that differentiate the new species from other *Portunion* species. A key to the genera of the Entoniscidae is also provided. Prior to this study, however, there was no description of *Portunion* spp. from the mud crab *S. paramamosain*.

2 Materials and methods

2.1 Sample collection and prevalence survey

We collected specimens of *S. paramamosain* from 2019 to 2024 from five provinces in China: Beihai, Guangxi Zhuang Autonomous Region (21° 33' 10.86" N, 109° 40' 16.11" E); Huizhou, Guangdong province (22° 40' 4.38" N, 114° 44' 17.12" E); Zhangpu, Fujian province (23° 52' 58.15" N, 117° 33' 43.39" E); Taizhou, Zhejiang province (29° 06' 49" N, 121° 23' 13" E); and Haikou, Hainan province (18° 54' 6.82" N, 110° 31' 27.37" E) (Figure 1). Crab specimens were collected from natural aquatic environments and transported to the laboratory within a period not exceeding 2 days. Upon arrival at the laboratory, the crabs were humanely euthanized by exposure to freezing conditions at 0°C, achieved through the use of an ice-water mixture, prior to dissection. The carapace of each *S. paramamosain* specimen was meticulously removed by making precise incisions along the suture with a medical scalpel. In instances where present, the female parasite was examined and delicately dissected to separate it from the host's visceral mass. Marsupium dissection of the females yielded eggs, embryos, epicaridium larvae, and dwarf males.

TABLE 1 Seven valid *Portunion* species in the WoRMS list.

Entoniae	Localities	References
<i>Portunion bourdoni</i> Chaix and Veillet, 1981	France	Chaix and Veillet (1981)
<i>Portunion conformis</i> Muscatine, 1956	San Francisco Bay	Muscatine (1956)
<i>Portunion flavidus</i> Shiino, 1942	Japan	Shiino (1942)
<i>Portunion kossmanni</i> Giard and Bonnier, 1886	French Exclusive Economic Zone	Giard and Bonnier (1886)
<i>Portunion maenadis</i> Giard and Bonnier, 1886	French Exclusive Economic Zone	Giard and Bonnier (1886)
<i>Portunion moniezii</i> Giard and Bonnier, 1886	French Exclusive Economic Zone	Giard (1878)
<i>Portunion salvatoris</i> Giard and Bonnier, 1887	Naples	Giard and Bonnier (1887)

2.2 Morphological analysis

The morphological characteristics of the parasites were documented, and specimens were imaged using a stereoscopic microscope (SteREO Discovery.V12, Zeiss, Oberkochen, Germany). For scanning electron microscopy (SEM) analysis, adult parasites were fixed in SEM fixation buffer (G1102, Servicebio, Wuhan, China), meticulously washed, and dehydrated for 10 minutes, followed by critical point drying. Parasite embryos and epicaridium larvae were similarly fixed in SEM fixation buffer, washed, and post-fixed with osmium tetroxide for 30 to 60 minutes, and then dehydrated for 5 minutes prior to critical point drying. Upon completion of sample preparation, the parasites were examined and photographed using a FESEM SU 8100 SEM (Hitachi, Tokyo, Japan).

3 Results and Discussion

3.1 Taxonomy

Order **Isopoda** Latreille, 1817.

Suborder **Cymothoidea** Wägele, 1989.

Superfamily **Bopyroidea** Rafinesque, 1815.

Family **Entoniscidae** Kossmann, 1881.

Subfamily **Entioninae** Codreanu, Codreanu and Pike, 1960.

3.2 Genus *Portunion* Giard and Bonnier, 1886

Diagnosis. The description below follows the terminology of the Shiino system (Shiino, 1942).

Female. Females were categorized into five developmental stages based on external morphology: the C-shaped larva (first stage), the straight juvenile (Figure 2A), the V-shaped large juvenile (Figure 2B), the mature adult (Figure 2C), and the ovigerous adult (Figure 2D).

Adult Female. The body is highly modified due to their parasitic lifestyle. Their deformed sac-like bodies have few distinguishing morphological characteristics, except for faint segmentations. The entire body is intricately intertwined with the hepatopancreas and gonads of its host. In mature and ovigerous adults, all oostegites meet each other on the opposite side and form the marsupium. The pleopods are uniramous lamellae with highly crimped margins. The first pair is much larger than the others and the pleopods get gradually smaller from front to back. Ovigerous adults have a whitish to yellowish ovary and an abdomen that is whitish to translucent. The marsupium is composed of several pairs of oostegites and the host

TABLE 2 Host and location of reported species.

Species	Host	Location	Source	
<i>Portunio sinensis</i> sp. nov.	<i>Scylla paramamosain</i>	Beihai, Guangxi	Present study	
		Huizhou, Fujian		
		Zhangpu, Guangdong		
<i>Portunio bourdoni</i>	/	/	Chaix and Veillet, 1981	
<i>Portunio conformis</i>	<i>Hemigrapsus oregonensis</i>	San Francisco Bay, California	Kuris et al., 1979	
		Bahia San Quintin		
		Estero de Ensenada		
		Agua Hedionda		
		Uper Newport Bay, California		
		Morro Bay, California		
		Elkhorn Slough, California		
		San Francisco Bay, California		
		Bodega Harbor		
		Humboldt Bay		
		Coos Bay-South Slough		
		Coos Bay-Fossil Point		
		Yaquina Bay, Oregon		
		Tacoma Narrows		
		Neath Bay		
		Strait of San Juan de Fuca		
		Argyll Lagoon		Kuris et al., 1980
		False Bay		
	Page's Lagoon			
	Amphitrite Point			
	Ucluelet			
	<i>Hemigrapsus nudus</i>	Piedras Blancas, California		
		Point Pinos, California		
		Bodega Harbor, California		
		Horseshoe Cove, California		
		Sunset Bay, Oregon		
		Coos Bay-Charleston Small Boats Mooring, Oregon		
		Yaquina Bay, Oregon		
Yaquina Head, Oregon				
Willapa Bay-Toketown				
Tacoma Narrows				
Neath Bay				
Mukkaw Bay				
Strait of San Juan de Fuca				

(Continued)

TABLE 2 Continued

Species	Host	Location	Source
		False Bay	
		Friday Harbor Laboratories	
		Page's Lagoon	
		Amphitrite Point	
		Point Richmond, Contra Costa County, California	Shields and Kuris, 1985
<i>Portunion flavidus</i>	<i>Pachygrapsus crassipes</i>	Seto	Shiino, 1942
	<i>Plagusia dentipes</i>		
<i>Portunion kossmanni</i>	/	/	Giard and Bonnier, 1886
		/	Giard and Bonnier, 1886
<i>Portunion maenadis</i>	<i>Carcinus maenas</i>	Cattewater, Plymouth	MBA (Marine Biological Association), 1957; Cornelius et al., 2019
		Exmouth	Perkins, 1924; Cornelius et al., 2019
		Plymouth	Blakeslee et al., 2009
		Firth of clyde, Scotland	Searle and Crompton, 1995
		Wimereux	Giard and Bonnier, 1886
		Saint-Pol-de-Léon	Blakeslee et al., 2009
		Bassin d'Arcachon	Bourdon, 1964
		Mira River	Blakeslee et al., 2009
		Texel	Cornelius et al., 2019
		Sylt	
		Kristineberg	
		Limfjorden	Zetlmeisl et al., 2011
		Kattegat	
<i>Portunion moniezii</i>	/	/	Giard, 1878
		/	Giard, 1878
<i>Portunion salvatoris</i>	/	Naples	Kossmann, 1881
<i>Portunion</i> sp.	<i>Cyclograpsus lavauxi</i>	Governors Bay, Lyttelton Harbor	Brockerhoff, 2004
		Kaikoura	
	<i>Hemigrapsus crenulatus</i>	Governors Bay, Lyttelton Harbor	
	<i>Helice crassa</i>	Avon-Heathcote Estuary	
	<i>Macrophthalmus hirtipes</i>	Otago Harbor, Dunedin	Dittmer et al., 2011

response sheath. It is exceedingly inflated, extending dorsally and covering the spherical cephalogaster. It is pale yellow when full of extruded eggs and developing embryos; when full of epicaridium larvae, it is brown to dark brown.

C-shaped larva. According the description in Shiino's study, it has an appearance of a caterpillar and is strongly curved ventrally, so that the cephalon almost touches the pygidium. No clear specific difference is discernible in this stage.

Straight juvenile. The body is dorsally folded similar to the adult form, but it straightens when the parasite is extracted from the host, except for a slight ventral curvature in the thoraco-abdominal region. The oostegites are somewhat expanded, with the first pair extending anteriorly beyond the cephalon, forming a rudimentary "hood." The last two pairs of peraeopods are somewhat enlarged into lateral protuberances. The pleopods have begun to overlap each other, and the pleural lamellae have developed crispate margins.



FIGURE 1
Collecting sites of the *Portunus sinensis* sp. nov.

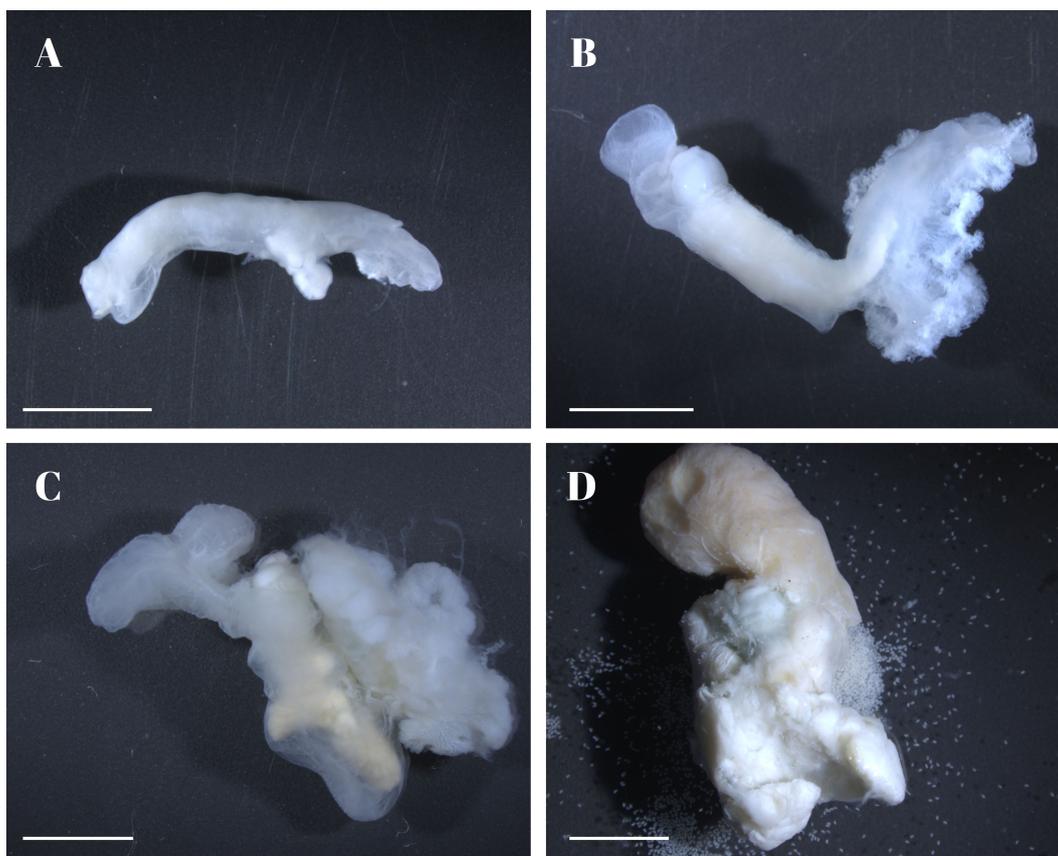


FIGURE 2
Illustration of different stages of the female *Portunus sinensis* sp. nov. (A) straight juvenile; (B) V-shaped juvenile; (C) mature adult not yet spawning; (D) ovigerous adults with eggs and developing embryos in the marsupium. Scale: 2 mm.

V-shaped large juvenile. At this stage, all major bodily organs are substantially developed. The stage is characterized by the protrusion of ovarian processes, the enlargement of oostegites, and the development of pleural folds.

Male. The male, without having any membrane enclosing it, has more or less the typical constitution of an isopod, although it has degenerated in many points; its body is normally curved ventrally. All segments are distinct. Thorax gradually narrows from the 5th segment forwards, the 1st being half as wide as the 5th; lateral parts are attenuated except in the last segment, which has a truncated margin. The limbs of the first six thoracic segments are all similar, only increasing in size posteriorly. They are scarcely prehensile in all cases. The last thoracic segment is limbless, but is provided with protuberances bearing gonopores.

Epcaridium larvae. The Epcaridea stage has a strong dorsal convexity and scattered pigment patterns. The cephalon is evenly rounded in front, bearing, on either side, a few crystallines surrounded by chromatophores. The antennules are short and two-jointed, while the antennae are long and composed of six joints of which the last two form a comparatively short flagellum. The oral cone encloses the usual piercing mandibles. Of the peraeopoda, the seventh pair is lacking. The sixth peraeopod differs in structure from others. The propodus bears a short process at the lateral end of its distal margin and merus with a very small seta on the external margin. This pair is slightly smaller than the foregoing pairs, the dactylopodite at the same time being highly degenerated, and the propodus ending in a short-pointed process.

3.3 *Portunium sinensis* sp. nov.

<https://zoobank.org/D5BB6083-114B-4D52-AF54-F79CD5604055>.

Material examined. Infesting *S. paramamosain*. Key Laboratory of Tropical Marine Ecosystem and Bioresource, Fourth Institute of Oceanography, Ministry of Natural Resources, Beihai, China. Holotype, female; Zhang pu, Fujian China. Allotype, male; Zhang pu, Fujian China. Paratype, epcaridium larvae, Zhang pu, Fujian China.

Description

Holotype, adult female (Figure 2C)

Body (Figure 3A) of mature adult is curved in a U-shape, from hood to tip of posterior ventral process ca. 8.1 mm, abdomen ca. 8.8 mm in the largest specimen.

Cephalon is swollen into a double-spherical shape and is distinctly demarcated from the thorax.

Antennae, two parallel pairs of antennae, both external and internal, are inserted at the anterior part of the cephalogaster.

Maxillipeds are situated at the ventral border between the cephalon and the thorax. The exopodite of the maxilliped is broad and features a frilled surface, while the endopodite is oval-shaped and considerably smaller in comparison.

Ovarian processes. There are two ventral processes on the chest and a pair of dorsal ovarian processes. The dorsal ovarian processes arise from the anterior end of the thorax; of the two ventral processes, the anterior is shorter and makes a right angle with the posterior which projects backward.

Oostegite 1 (Figure 3B) is well developed, composed of three uniramous lobes: ascendant lobe covering the cephalogaster; transverse lobes short and blunt; recurrent lobe largest and appears slightly wrinkled, extending the entire length of pereon. Oostegites 2 to 5 are typically distinctly separated, adhering to the host membrane, enclosing a marsupium; it may adhere to the host membrane and be removed together during dissection.

Marsupium is full of ova yellowish brown to dark brown, ovary lemon-yellow, abdomen whitish.

Heart. An oval, bulbous heart is present on the dorsal surface of the pleomere.

Pleural lamellae of the initial four segments are intricately folded and exhibit crispate margins, resembling a bouquet. As one progresses posteriorly, these lamellae progressively diminish in both size and fold complexity, ultimately adopting a simple triangular form by the fifth segment.

Description.

Allotype, male (Figure 4).

Body (Figures 3C-E) of male 1.1 mm long, 0.3 mm wide at 4th thoracic segment; with scattered pigment patches, the body typically assumes a ventrally curved posture.

Cephalon is fused with the first thoracic segment; however, they can be distinguished in the lateral regions, and there is also a shallow surface groove indicating the boundary.

Antenna II absent.

Mandibles missing, maxillae and maxillipeds degenerate.

Thorax gradually narrows from the 5th segment forwards, the 1st being half as wide as the 5th; lateral parts attenuated except in the last segment which has a truncated margin. The last thoracic segment is limbless, but provided with protuberances bearing gonopores. The pleura of the thoracic segments are characterized by their abbreviated, narrow, and contorted structure, with their inferior surfaces slightly posteriorly oriented. The seventh segment is distinguishable by its absence of pleura and cylindrical morphology.

Peraeopoda (Figure 3F) are 5-jointed, with carpo-propodus as well as dactylus clad with many spinule-rows.

Ventral spine. The 1st and 2nd abdominal segments are hook-like and with a pointed tip. The spine of the 3rd and 4th segments is very rudimentary but still distinguishable.

Dot-like protrusions are present on the first four ventral spines and they also encircle segment V.

Description.

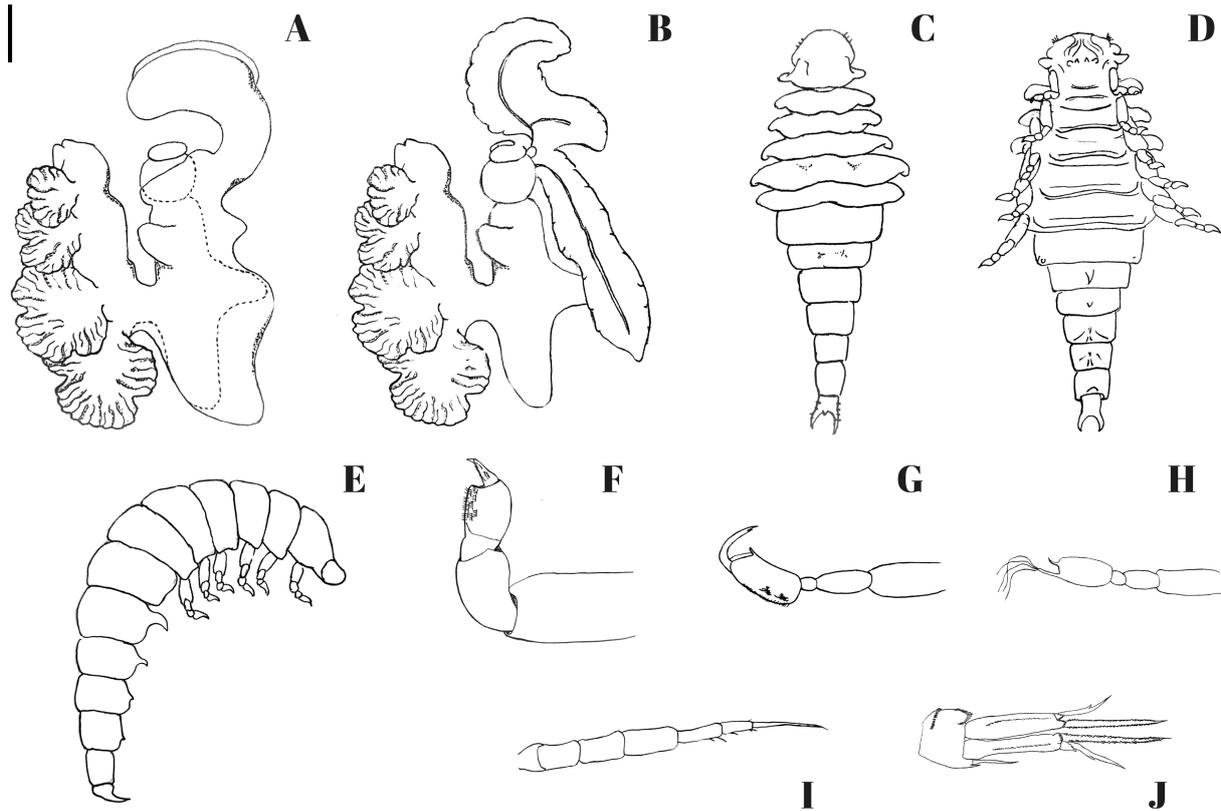


FIGURE 3

Portunion sinensis sp. nov. (A, B) holotype female; (C–F) allotype male; (G–J) Paratype, epcaridium larvae. (A) female enclosed in host membrane; (B) female with membrane removed; (C) male, dorsal view; (D) male, ventral view; (E) male, side view; (F) male, side view of pereopods; (G) epcaridium, paraeopod I; (H) epcaridium, paraeopod VI; (I) epcaridium, antenna II; (J) epcaridium, uropod. Scale: 2000 μm (A, B); 200 μm (C–E); 55 μm (F); 20 μm (G–I); 10 μm (J).

Paratype, Epcaridium larvae (Figures 5, 6).

Body is approximately 208–238 μm in length (anterior margin of head to end of telson) and has a strong dorsal convexity and scattered pigment patterns.

Cephalon presents a uniformly rounded anterior margin, with each lateral aspect bearing a small number of crystalline cones encompassed by chromatophores.

Antennule of three rounded articles, the basal article is the largest, with the second article rounded with thin seta anterior and posterior to the terminal article; the terminal article is digitiform with two long, thick setae at the terminus and two long, thick setae extending from the base.

Antennae (Figure 3I) are elongated and approximately half the length of the body; composed of six articles (four peduncular, two flagellar), the basal article the smallest, articles 2–4 progressively longer, article 4 expanded, with two setae on distolateral margin; first flagellar article slightly greater than half the width of the terminal peduncular article, second flagellar article with a thick,

long seta (subequal in length to the combined length of the first and second flagellar articles).

Mouthparts consist of an **oral cone** with a sucker-shaped structure at the terminus, composed of three plates (one anterior, two lateral). **Maxilliped** is manifested as diminutive, unsegmented lamellae.

Peraeopoda, six pairs of pereopods. Five anterior pairs of gnathopodal pereopods, subequal in size, each with a slender, slightly curved dactylus extending approximately half the length of the propodus, tip of the dactylus is hooked (Figure 3G). Pereopod 6 differs in structure from others by lacking a hook-shaped dactylus, but the end of the dactylus has a seta that is the same length as the propodus (Figure 3H).

Pleopoda, the five pairs of uniramous pleopoda are all similar in structure; the protopodite is triangular, bears two long stiff setae at its inner distal angle, and at the outer angle a quadrangular exopodite terminating in three setae.

Uropod (Figure 3J), biramous, stout cylindrical peduncle, distally with 2 slender rami.

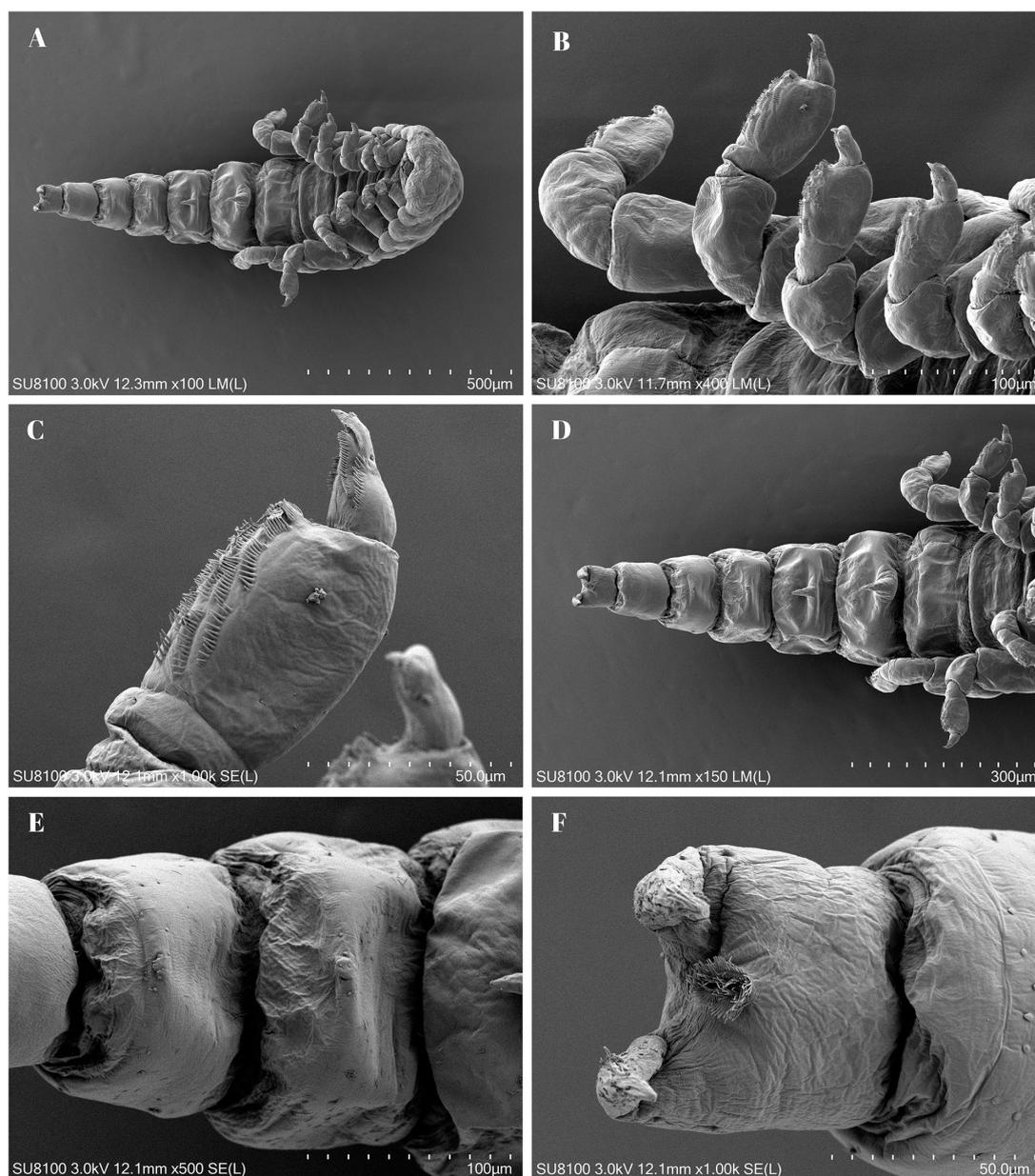


FIGURE 4

Scanning electron micrographs depicting the male of *Portunio sinensis* sp. nov. (A) ventral view of the male; (B) side view of pereopods; (C) pereopod VI; (D) close-up view of posterior region of the male showing two ventromedian hooks (white arrowhead); (E) close-up view of ventromedian hook with protuberances; (F) close-up view of telson showing anal cone and irregularly arranged protuberances.

3.4 Remarks

The *Portunio* sp. nov. differs from other closely similar species *P. maenadis*, *P. kossmanni*, *P. flavidus*, and *P. conformis* in the following way (Table 3): Female, the anterior ventral process is oriented vertically to the thorax, while the posterior process is directed backward. In contrast, both processes in *P. maenadis* are directed backward, whereas in *P. kossmanni*, the anterior process is directed forward and the

posterior backward. Male, the cephalon is fused with the first thoracic segment, the second antenna is absent, abdominal hooks are present in segments I-IV, the first two hooks with pointed tips, the spine of the 3rd and 4th segments is very rudimentary. However, in both *P. maenadis* and *P. kossmanni*, the cephalon is distinct from the thorax, and the antennae are present. In *P. flavidus*, abdominal hooks are only found in segments I-II, with the 2nd rudimentary. In *P. conformis*, abdominal spines are present in segments I-IV, the first three hooks with pointed

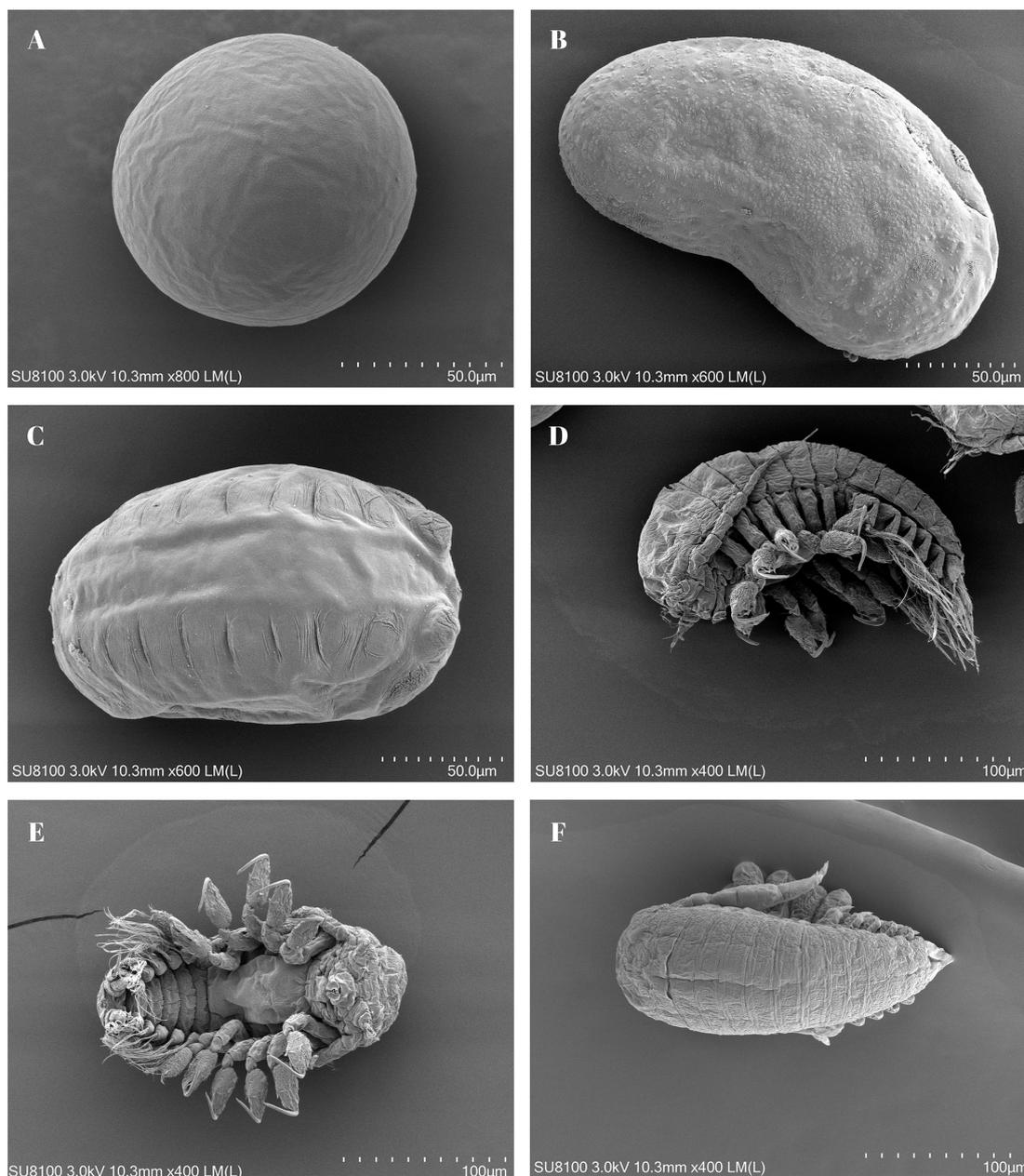


FIGURE 5 Scanning electron micrographs depicting the epicaridan of *Portunio sinensis* sp. nov. (A) extruded egg; (B, C) developing embryos; (D) side view of epicaridium larva showing 2nd antennae (white arrowhead); (E) ventral view of epicaridium larva; (F) dorsal view of epicaridium larva.

tips, and only the spine of the 4th segment is reduced. Epicaridium, the dactylus of peraeopod VI exhibits setose characteristics, whereas in *Flavidus* species, the dactylus lacks setae.

Etymology. The species name is derived from the locality, Zhangpu, located in Fujian, China.

Distribution. China (Beihai, Huizhou, Zhangpu).

3.5 Key to the genera of the Entoniscidae

- I. Female marsupium formed by host membrane alone, with all oostegites not adhering to it, and freely movable; 1st oostegite not differentiated from others; pleopoda lanceolate and pleural lamellae missing. Male peraeopoda unsegmented, tuberculiform.

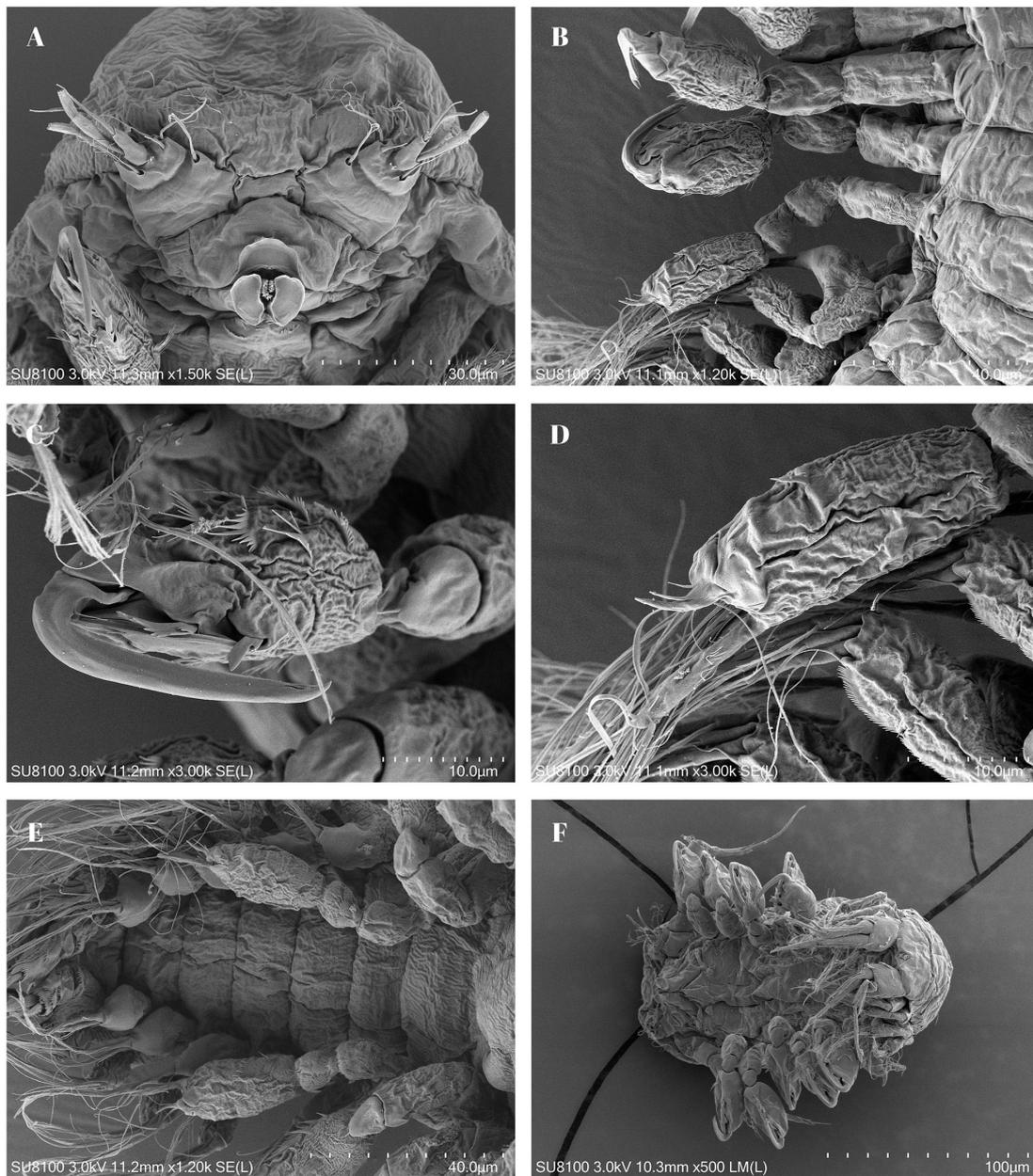


FIGURE 6

Scanning electron micrographs depicting the epicaridan of *Portunio sinensis* sp. nov. (A) cephalon, showing antennules mouthparts; (B) side ventral view, showing pereopods; (C) pereopod V; (D) pereopod VI, close-up of dactyl and propodus, with seta; (E) ventral view of posterior, showing pleopods; (F) pleon.

- A. Female without maxilliped; terminal segment of male undivided.
 1. Antenna of male projected laterally; 5th pleopod of Epicaridium dissimilar to others. (Parasitic on Anomura)
 - *Entoniscus* F. MÜLLER (5 spp.)
 2. Antenna of male not projected; 5th pleopod of Epicaridium similar to others. (Parasitic on Macrura)
 - *Synalpheion* COUTIÈRE (1 sp.)

- B. Female with maxilliped; terminal segment of male bifurcated. (Parasitic on Brachyura)
 3. *Entoniscoides* MIYASHITA (1 sp.)
- II. Female marsupium formed by close adhesion of oostegites to host membrane; 1st oostegite differentiated into three parts; pleopoda lamellar and pleural lamellae well developed. Male peraeopoda jointed. (Parasitic on Brachyura)
 - A. Marsupium complete, with 2nd pair of oostegites enclosing ascendant lamellae of 1st pair; two ventral ovarian processes present,

TABLE 3 The characteristics that differentiate the new species from other *Portunion* species.

Species	Female	Male			Epicaridium	
	Ventral process	Cephalon	Antenna II	Abdominal hooks	Dot-like protrusions	Dactylus of peraeopod
<i>Portunion sinensis</i> sp. nov.	Anterior vertical to thorax, posterior directed backward	Fused with 1st thoracic segment	Absent	In segments I - IV; Both the third and fourth reduced	On first four ventral spines; Encircles in segments V	Setose
<i>P. conformis</i>	Anterior vertical to thorax, posterior directed backward	Fused with 1st thoracic segment	Absent	In segments I - IV; Only the fourth reduced	/	Setose
<i>P. flavidus</i>	Anterior vertical to thorax, posterior directed backward	Fused with 1st thoracic segment	Absent	In segments I - II	/	Not setose
<i>P. maenadis</i>	Both processes directed backward	Distinct form thorax	Present	In segments I - IV	/	Setose
<i>P. kossmanni</i>	Anterior directed forwards, the posterior backward	Distinct form thorax	/	In segments I - IV	/	/

- a. Last peraeopod of Epicaridium shorter than others, with a simple propodite and rudimentary dactylopodite.
 - 4. Female without dorsal ovarian process.*Pinnotherion* G. & B. (2 spp.)
 - 5. Female with a pair of dorsal processes. *Portunion* G. & B. (5 spp.)**
- b. Last peraeopod of Epicaridium much longer than others, with a distally expanded propodite and well-developed dactylopodite.
 - i. Female with two pairs of dorsal ovarian processes.
 - 6. Male without penis.....*Grapsion* G. & B. (1 sp.)
 - 7. Male with penis.....*Priapion* G. & B. (1 sp.)
 - ii. Female with an unpaired dorsal ovarian process.
 - 8. *Micippion* n. gen. (1 sp.)
- B. Marsupium partly uncovered, with the 2nd pair of oostegites overlapping only the basal part of the 1st pair; ventral ovarian processes present or absent. (Last peraeopod of Epicaridium as in II, A, b)
 - a. Female with a ventral ovarian process, but without a dorsal one.
 - 9. With two ventral ovarian processes. *Tiariniinn*. gen. (1 sp.)
 - 10. With one ventral ovarian process. *Xanthion* n. gen. (1 sp.)
 - b. Female with two pairs of dorsal ovarian processes, but without ventral one.
 - 11. *Cancrion* G. & B. (4 spp.)

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding authors.

Ethics statement

The animal study was approved by ethics committee of Fourth Institute of Oceanography, Ministry of Natural Resources. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

TH: Investigation, Writing – original draft. XM: Investigation, Writing – original draft. SZ: Investigation, Methodology, Writing – review & editing. XC: Formal analysis, Investigation, Methodology, Writing – review & editing. DY: Investigation, Methodology, Resources, Writing – review & editing. JG: Formal analysis, Investigation, Methodology, Resources, Writing – review & editing. LH: Formal analysis, Investigation, Methodology, Writing – review & editing. WL: Formal analysis, Investigation, Methodology, Writing – review & editing. TP: Conceptualization, Writing – review & editing. YQ: Conceptualization, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The author(s) declare that no Generative AI was used in the creation of this manuscript.

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