

The Bopyridae (Crustacea: Isopoda) parasitic on thalassinideans (Crustacea: Decapoda) from China

Jianmei An, Jason D. Williams*, and Haiyan Yu

(JA) School of Life Science, Shanxi Normal University, Linfen, 041004, P. R. China,
e-mail: anjianmei@hotmail.com;

(JDW) Department of Biology, Hofstra University, Hempstead, New York 11549, U.S.A.,
e-mail: Jason.D.Williams@hofstra.edu;

(HY) Institute of Oceanology, Chinese Academy of Sciences, Qingdao 266071, P. R. China,
e-mail: yhy@ms.qdio.ac.cn

Abstract.—Eight species among six genera of bopyrid isopods (representing the subfamilies Pseudioninae and Ioninae) infesting thalassinideans from China are reported. Of these, four species are new to science: *Gyge fujianensis* n. sp., *Progebiophilus elongatus* n. sp., *Upogebione bidigitatus* n. sp., and *Procepon liuruiyui* n. sp., infesting *Upogebia major* (de Haan), *Nihonotrypaea japonica* Ortmann, *Upogebia carinicauda* (Stimpson), and *Austinogebia wuhsienweni* (Yu). One species, *Ione cornuta* Bate, 1864, is recorded for the first time from Chinese waters and from a new host. *Pseudione longicauda* Shiino, 1937, *Gyge ovalis* (Shiino, 1939), and *Progebiophilus sinicus* Markham, 1982, previously known from Hong Kong or Taiwan, are recorded for the first time from mainland China, extending their range north.

The epicaridean family Bopyridae currently contains about 590 described species, approximately one tenth of which are parasites of thalassinidean decapods (Markham 2001, Boyko & Williams 2009), commonly known as ghost or mud shrimp. Bopyrids from thalassinideans belong to four subfamilies: two subfamilies (Pseudioninae and Ioninae) contain species that are ectoparasites, infesting the branchial chamber of hosts, the monotypic Phyllofurinae is represented by a species that is an ectoparasite on the abdomen of hosts, and the subfamily Entophilinae contains one species that is endoparasitic in the abdomen of host ghost shrimp (Markham 2005, Markham & Dworschak 2005). Although the Indo-West Pacific contains the highest number of thalassinideans (Dworschak 2000,

2005), China has been less well sampled than other regions and thus likely holds many new records and new species of bopyrid parasites. Examination of thalassinidean decapods deposited in the Institute of Oceanology of the Chinese Academy of Sciences (IOCAS) yielded eight branchial bopyrid species belonging to six genera within the Pseudioninae and Ioninae. Among the eight species, four are new to science, one is recorded for the first time from Chinese waters, and three are recorded for the first time from mainland China from new hosts.

Materials and Methods

Materials for this study came from National Comprehensive Oceanographic Survey (1958–1960) and a series of investigations of marine fauna and flora along the Chinese coast by the Institute of

* Corresponding author.

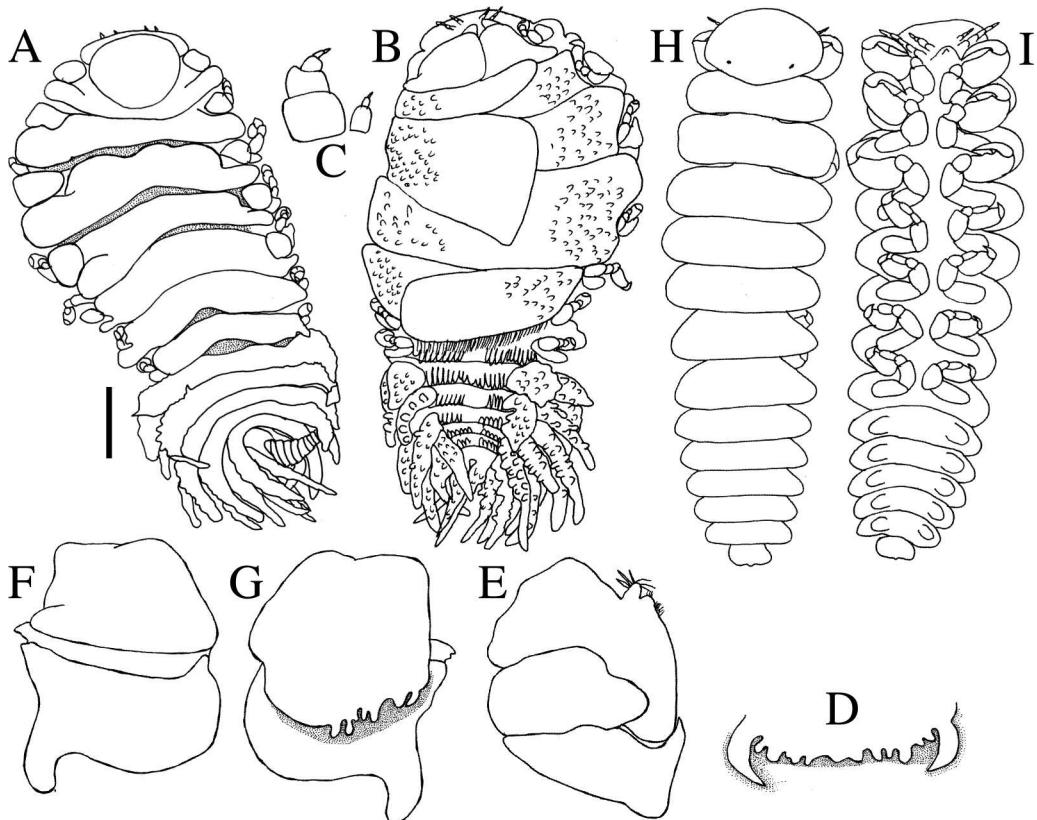


Fig. 1. *Pseudione longicauda* Shiino, 1937. Female (A–G, CIET510301). A. Dorsal view. B. Ventral view. C. Right antennae. D. Barbula. E. Right maxilliped, external view. F. Right oostegite 1, external view. G. Right oostegite 1, internal view. Male (H, I, CIET510302). H. Dorsal view. I. Ventral view. Scale bars: 1 mm (A, B); 0.52 mm (D, F, G); 0.38 mm (E); 0.50 mm (H, I).

Oceanology, Chinese Academy of Sciences (IOCAS). All materials examined are deposited in the IOCAS, Qingdao, China. The specimens were viewed and drawn with a Zeiss Stemi SV II Apo. Males for scanning electron microscope study were fixed in 2.5% glutaraldehyde in 0.2 M Millonig's phosphate buffer at pH 7.4 for 1.5 h and postfixed in 1% osmium tetroxide in 0.2 M Millonig's buffer for 1 h. The specimens were dehydrated through a graded series of ethanol, followed by critical point drying. After sputter coating with colloidal gold, the specimens were examined with a KYKY2800B scanning electron microscope.

Taxonomy

Family Bopyridae Rafinesque-Schmaltz, 1815

Subfamily Pseudioninae Codreanu, 1967

Genus *Pseudione* Kossmann, 1881

Pseudione longicauda Shiino, 1937

Fig. 1

Pseudione longicauda Shiino, 1937:479–482, figs. 1, 2 [type locality Seto, Japan; infesting *Nihonotrypaea japonica* Ortmann].—Shiino, 1952:41, 43.—Shiino, 1958:30–31, fig. 1.—Shiino, 1964:242.—Shiino, 1972:7.—Danforth, 1963:849.—Bourdon, 1968:150, 172, 214–215.—Restivo, 1970:314.—Bourdon, 1981a:628.—Bourdon et al., 1981:498.—

Markham, 1992a:281–282, figs. 4, 5 [Hong Kong; infesting *Nihonotrypaea petalura* (Stimpson)].—Huang, 1994: 530.—Adkison & Heard, 1995:108.—Saito et al., 2000:37.—Huang, 2001:326.—Markham, 2001, tables 1, 2.—Li, 2003:155, tables 1, 3.—Itani, 2004:37–41, tables 3, 4.—Saito & Kinoshita, 2004:1–7, figs. 3, 4, tables 1, 3.

Material examined.—Infesting *Nihonotrypaea japonica* Ortmann. Cangkou, Jiaozhou Bay, Shandong province, 36°04'N, 120°19'E, 8 Mar 1951, CIET510301, 1 female, CIET510302, 1 male; 4 Aug 1955, CIET550801, 1 female; Yantai, Shandong province, 37°30'N, 121°24'E, 30 Jun 1957, CIET570601, 2 females, CIET570602, 2 males; Dongwo, Hainan province, 19°00'N, 110°10'E, 16 Mar 1957, coll. Zhengang Fan & Jieshan Xu, CIET570301, 1 female. No. 1 sea beach of Qingdao, Shandong province, 36°00'N, 120°18'E, 3 Nov 1963, coll. Zhengang Fan, Chen Mu & Xiubin Fang, CIET631101, 1 female, CIET631102, 1 male. Cangkou, Jiaozhou Bay, Shandong province, 36°04'N, 120°19'E, 9 Apr 1954, coll. Xiuji Zhang, CIET540401, 1 female, CIET540402, 1 male. Shazikou, Jiaozhou Bay, Shandong province, 36°04'N, 120°19'E, 24 Apr 1964, coll. Zhengang Fan & Haokui Lu, CIET640401, 1 female, CIET640402, 1 male. Lianjiang, Fujian province, 26°20'N, 119°53'E, 1 Jun 1964, coll. Guangzong Wu & Fuzeng Sun, CIET640601, 2 females, CIET640602, 2 males. Cangkou, Jiaozhou Bay, Shandong province, 36°04'N, 120°19'E, 4 Jun 1954, CIET540601, 2 females, 2 males.

Remarks.—*Pseudione longicauda* has been thoroughly described and illustrated by Shiino (1937, 1958) and Markham (1992a). This is the northernmost record of the species from China; the species was previously found in Hong Kong. Differences between the Chinese specimens (Fig. 1) and those of Shiino (1937) and Markham (1992a) are minor. The Chinese females possess tubercles on the

external surfaces of oostegites 2–5 (Fig. 1B), and have setose maxilliped palps on the maxillipeds (Fig. 1E); Hong Kong females lack tubercles and the palps are composed of two setose articulating sections. The Chinese males have weakly developed tuberculate pleopods (Fig. 1I); Markham (1992a) and Shiino (1937) indicated the males lacked pleopods, but Shiino (1958) described juvenile males with tuberculiform pleopods, suggesting this character is variable depending on development of the males.

There has been considerable debate on the taxonomy of the host *Nihonotrypaea japonica*. Sakai (1999, 2001, 2005) considered the genus *Nihonotrypaea* Manning & Tamaki, 1998, to be a synonym of *Callianassa* and synonomized *N. japonica* with *N. harmandi* (Bouvier) (Sakai 2001). However, other researchers (see Dworschak 2000, 2005; Lin et al. 2007) have convincingly supported the erection of the genus *Nihonotrypaea* by Manning & Tamaki (1998), and morphological analyses have shown *N. japonica* and *N. harmandi* to be distinct (Wardiatno & Tamaki 2001, Tamakai 2003). Interestingly, Manning & Tamaki (1998) indicated that these host species could be separated on the basis of their parasites; unfortunately, they did not identify the species of parasites and, to our knowledge, no one has done so since. The biology and natural history of *N. japonica* and *N. harmandi* have been studied in detail (Tamaki & Suzukawa 1991, Tamaki et al. 1992a, b, 1996, 1997, 1999; Tamaki & Ingole 1993, Tamaki & Ueno 1998, Tamaki & Miyabe 1999), including their parasite fauna and mechanisms for removal of parasites (Batang & Suzuki 2003, Itani 2004).

Distribution and hosts.—Japan, on *Nihonotrypaea japonica* (Ortmann); China, Hong Kong, on *Nihonotrypaea petalura*; China, Shandong Province, Fujian Province, Hainan Province, on *Nihonotrypaea japonica*.

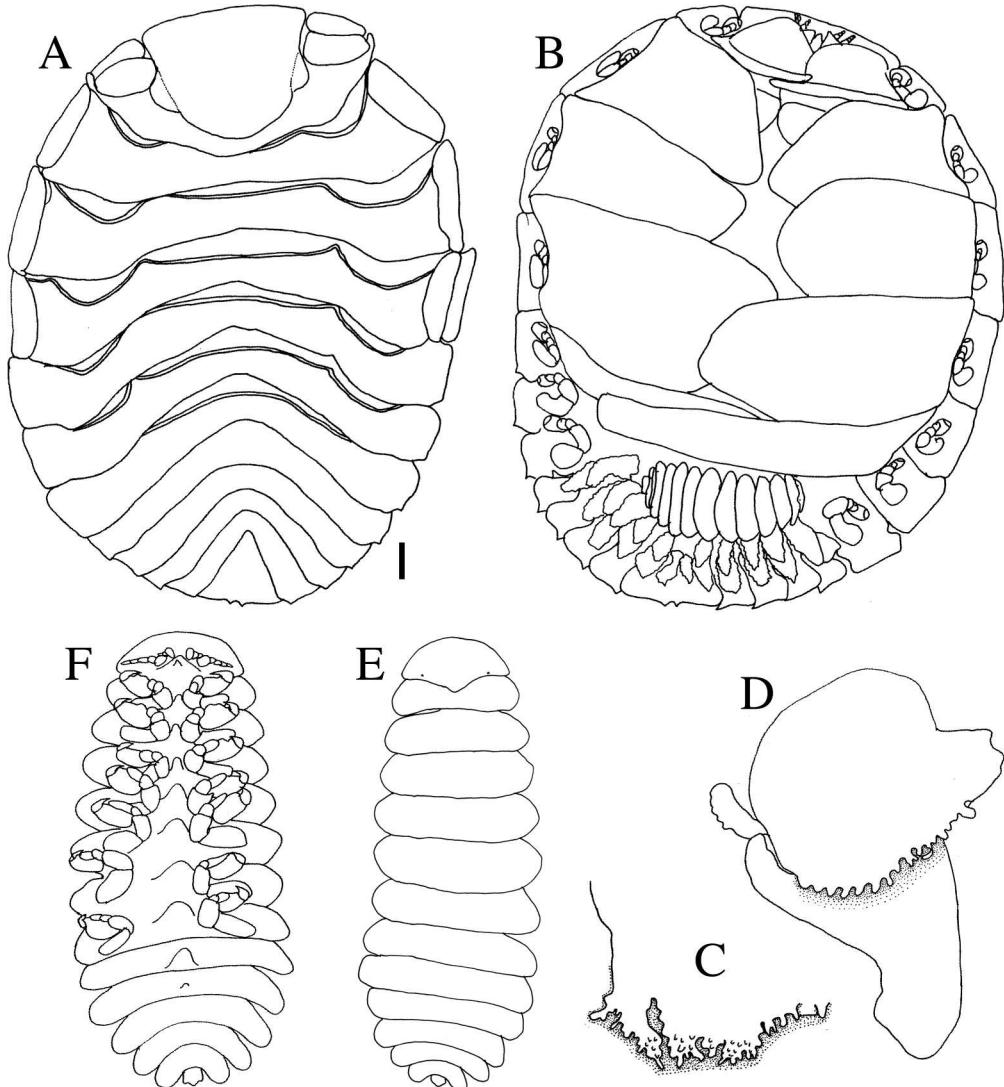


Fig. 2. *Gyge ovalis* (Shiino, 1939). Female (A–D, CIET560601). A. Dorsal view. B. Ventral view. C. Right side of barbula. D. Right oostegite 1, internal view. Male (E, F, CIET560602). E. Dorsal view. F. Ventral view. Scale bars: 1 mm (A, B); 0.36 mm (C, E, F); 0.50 mm (D).

Genus *Gyge* Cornalia & Panceri, 1861

Gyge ovalis (Shiino, 1939)

Fig. 2

Abbreviated synonymy. (See Markham 2004, for complete synonymy to 2004.)

Metabopyrus ovalis Shiino, 1939a:88–91, figs. 7, 8 [Hakata Bay, Kyūsyū, Japan; infesting *Upogebia major* (de Haan)].

Gyge ovalis: Markham, 2004:195–197, fig. 6 [Chang-Hua County, southwest Tai-

wan, infesting *Austinogebia edulis* (Ngoc-Ho & Chan)].

Material examined.—Infesting *Upogebia major* (de Haan). Cangkou, Jiaozhou Bay, Shandong province, 36°04'N, 120°19'E, 9 Apr 1954, CIET540403, 2 females, CIET540404, 2 males; 11 Feb 1960, CIET600201, 4 females, CIET-600202, 4 males; 26 Jun 1956, coll. Yiqing Liu, CIET560601, 3 females, CIET-560602, 3 males; 5 Nov 1956, coll.

Zhengang Fan & Jieshan Xu, CIET-561101, 2 females, CIET561102, 2 males; 9 Oct 1956, coll. Xiuji Zhang, CIET-561003, 2 females, CIET561004, 2 males; 3 Sep 1957, coll. Xiutong Ma, CIET-570901, 10 females, CIET570902, 10 males; 10 Nov 1957, coll. Yongliang Wang, CIET571102, 5 females, CIET-571103, 4 males; 9 Sep 1949, CIET-490901, 1 female; 13 Jul 1957, coll. Yaxi Yang, CIET570701, 1 female, CIET-570702, 1 male; 29 Sep 1954, CIET-540901, 1 female, CIET540902, 1 male; 20 Sep 1956, CIET560901, 1 female, CIET560902, 1 male; 20 Oct 1955, CIET-551001, 3 females, CIET551002, 2 males; 29 Mar 1955, CIET550301, 1 female; 18 Jul 1958, CIET580701, 1 female, CIET-580702, 1 male; 23 Dec 1957, CIET-571201, 1 female, CIET571202, 1 male; 18 Oct 1951, CIET511001, 2 females, CIET-511002, 1 male; 9 Oct 1956, CIET561001, 1 female. Cangkou, Jiaozhou Bay, Shandong province, 36°04'N, 120°19'E, 7 May 1951, CIET510505, 1 female, CIET-510506, 1 male. Xunjia Island, Jiaozhou Bay, Shandong province, 35°58'N, 120°17'E, 27 Apr 1951, CIET510403, 1 female, CIET510404, 1 male.

Infesting *Austinogebia wuhsienwensi* (Yu). Cangkou, Jiaozhou Bay, Shandong province, 36°04'N, 120°19'E, 12 Apr 1953, CIET530401, 1 female, CIET530402, 1 male.

Remarks.—Bourdon (1968) and Page (1985) suggested that *Metabopyrus* Shiino, 1939 should be united with *Gyge* Cornalia & Panceri, 1861, but they did not formalize this synonymy. Markham (2004) incorporated *Metabopyrus* into *Gyge*, which then included four species, and redescribed *Gyge ovalis* from Taiwan. Our specimens of *Gyge ovalis* from Jiaozhou Bay, China (Fig. 2) correspond very closely to the original description (Shiino 1939a). Whereas females of *G. ovalis* from Taiwan and Korea lack maxilliped palps (Kim & Kwon 1988, Markham 2004), those from China and

Japan have small palps (Shiino 1939a, 1958). Male specimens of *G. ovalis* from China have prominent midventral projections on all pereomeres and the first pleomere (Fig. 2F); midventral projections were found on the last four pereomeres and first pleomere in Shiino's males (Shiino 1939a) but were not noted in Markham's males (Markham 2004). *Gyge ovalis* is abundant in Jiaozhou Bay, China, where *Austinogebia wuhsienwensi* is a new host record for the parasite. We consider *G. ovalis* to be widely distributed in Asia and the degree of morphological variation (e.g., presence/absence of minute palp on maxilliped) to represent intraspecific variation.

Distribution and hosts.—Japan, on *Upogebia major* (de Haan); southwest Korea, on *Upogebia major* (de Haan); southwest Taiwan, on *Austinogebia edulis* (Ngoc-Ho & Chan); China, Jiaozhou Bay, Shandong province, on *Upogebia major* (de Haan) and *Austinogebia wuhsienwensi* (Yu).

Gyge fujianensis, new species

Fig. 3

Material examined.—Infesting *Upogebia major* (de Haan). Holotype: Fujian province, 26°05'N, 119°18'E, 7 Jun 1964, coll. Daoyuan Sun, CIET640603, 1 female. Allotype: same collection data as holotype, CIET640604, 1 male.

Description of holotype (CIET640603).—Length 6.12 mm, maximal width 4.98 mm across pereomere 3, head length 1.28 mm, head width 1.86 mm, pleon length 1.78 mm. All body regions and segments distinct. Dextral rotation <11°. No pigmentation except for eyes. Body outline smoothly oval (Fig. 3A, B).

Head pentagonal, deeply set into pereon and not extending beyond body margin, without frontal lamina. Eyes small, near anterolateral corners of head. Antennule of 3 articles, antennae of 4 articles, both with terminal setae (Fig. 3C). Maxilliped lacking palp, posterior lobe produced anteromedially into

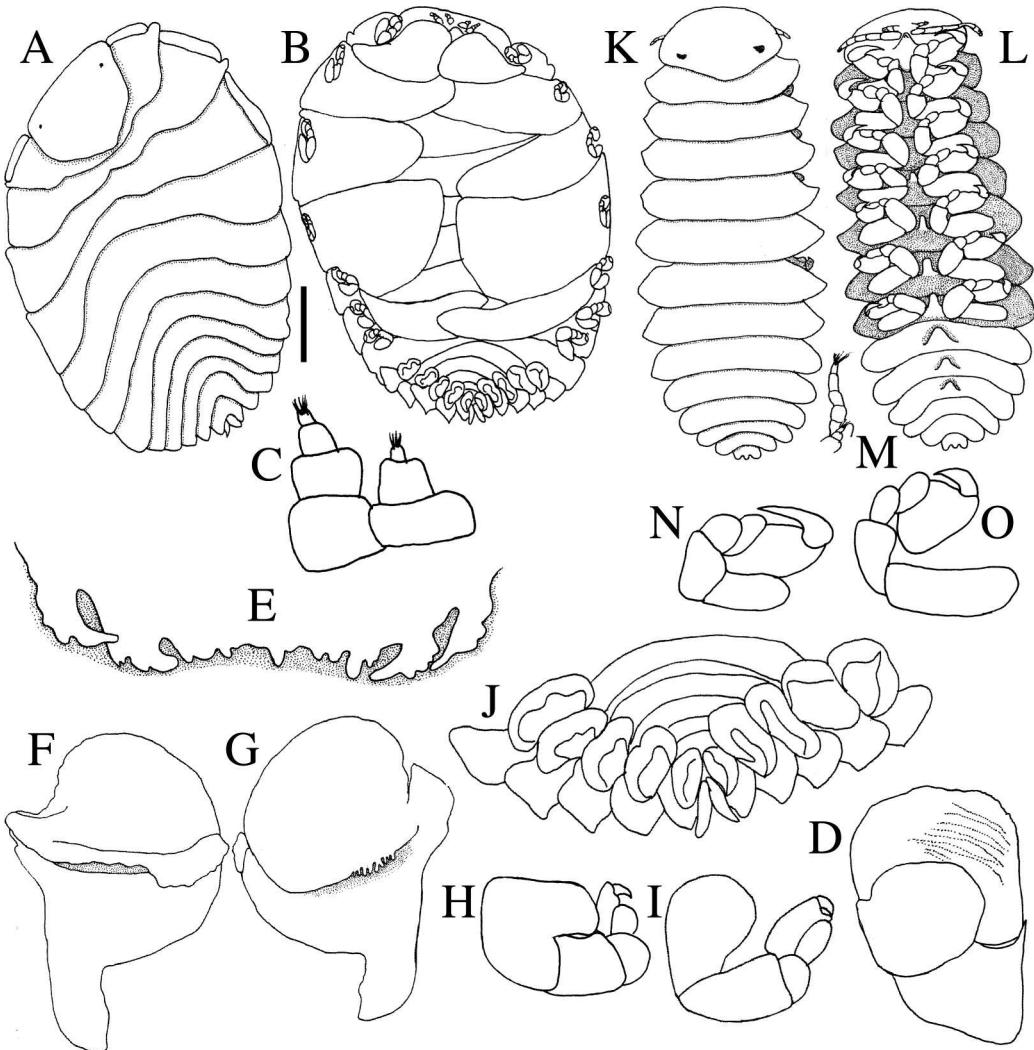


Fig. 3. *Gyge fujianensis*. Female (A–J, CIET640603). A. Dorsal view. B. Ventral view. C. Right antennae. D. Right maxilliped, external view. E. Barbula. F. Right oostegite 1, external view. G. Right oostegite 1, internal view. H. Right pereopod 1. I. Right pereopod 7. J. Ventral view of pleon. Male (K–O, CIET640604). K. Dorsal view. L. Ventral view. M. Left antennae. N. Left pereopod 1. O. Left pereopod 7. Scale bars: 1 mm (A, B); 0.19 mm (C, L, M–O); 0.45 mm (D); 0.33 mm (E); 0.56 mm (F, G); 0.29 mm (H, I); 0.53 mm (J); 0.50 mm (K, L).

sharp plectron (Fig. 3D). Barbula with two large digitate processes with digitate margins on each side, digitate margin in center (Fig. 3E).

Pereon broadest across pereomere 3. Coxal plates on first three pereomeres of right side, but only on first pereomere of left side. Oostegites incompletely enclosing brood pouch. Oostegite 1 smoothly

rounded anteriorly, with simple digitate internal ridge (Fig. 3F, G). Basis carinae of pereopods 1–7 progressively smaller posteriorly (Fig. 3H, I), carina of pereopod 1 almost reaching propodus (Fig. 3H), basis of pereopod 7 with reduced carina (Fig. 3I).

Pleon of 6 pleomeres, lateral plates absent, pleomeres 1–5 bearing uniramous

pleopods, without tubercles on ventral surface of pleon; pleomere 6 min, with median indentation and slender finger-like uniramous uropods extending from center (Fig. 3J).

Description of allotype (CIET640604).—Length 2.27 mm, maximal width 1.0 mm across pleomere 6, head length 0.24 mm, head width 0.63 mm. All body segments distinct (Fig. 3K, L).

Head suboval, posterior margin triangular, dark eyes near posterolateral margins. Antennule of 3 articles, antennae of 5 articles, both with terminal setae (Fig. 3M).

All pereomeres almost equal in width, with pointed mediolateral edge (Fig. 3K). Pereomeres 4–7 and pleomeres 1–3 with prominent midventral projections. Pereopods all similar in structure and size, dactyli of first two pereopods larger than others (Fig. 3N, O).

Pleon of 6 pleomeres, with rounded mediolateral edge. Pleomere 1 slightly less wide than pereomere 7, pleomeres diminishing rapidly in width posteriorly. Pleomeres without pleopods, pleotelson produced into two short posterior projections and anal cone, no uropods (Fig. 3L).

Etymology.—The specific name *fujianensis* refers to the locality of the type specimens.

Remarks.—Including the new species, the genus *Gyge* presently contains five species. *Gyge fujianensis* is most similar to *G. branchialis* Cornalia & Panceri, 1861, which has been reported many times from Britain through the Mediterranean to the Black Sea (Bonnier 1900, Bourdon 1968). However, females of *G. fujianensis* have distinct eyes, pentagonal head, coxal plates on the long side of pereomeres 1–3, and lack tubercles on the ventral surface of the pleon and pleopods, whereas females of *G. branchialis* have no eyes, have a trapeziform head, coxal plates on the long side of pereomeres 1–4, and possess many tubercles on the ventral surface of pleon and pleopods. Males of *G.*

fujianensis possess a triangular posterior margin of the head, midventral projections on pereomeres 4–7 and pleomeres 1–3, has pereopods with all segments distinct, and lacks pleopods; in contrast, males of *G. branchialis* have a straight posterior margin of the head, midventral projections present on pereomeres 2 or 3 to 7, fused carpi and meri of pereopods, and pleopods on pleomeres 1–5. In addition, the males of *G. fujianensis* have a more slender pleon than males of *G. branchialis*.

Distribution and hosts.—China, Fujian province, on *Upogebia major* (de Haan).

Genus *Progebiophilus* Codreanu & Codreanu, 1963

Progebiophilus sinicus Markham, 1982
Fig. 4

Abbreviated synonymy.

Progebiophilus sinicus Markham, 1982: 336–340, 385, figs. 8–10, table 1 (type locality Hong Kong; infesting *Upogebia* sp. = *U. major*).—Salazar-Vallejo & Leija-Tristan, 1989:428, table 1.—Markham, 1990:556, fig. 1.—Kazmi & Bourdon, 1997:62.—Markham, 1988: 12.—Markham, 2001:tables 1, 2.—Li, 2003:153, tables 1, 3.—Markham, 2005: 92.

Material examined.—Infesting *Upogebia major* (de Haan). Shajiang, Fujian province, 26°05'N, 119°18'E, 3–4 Mar 1957, CIET570303, 1 female, CIET-570304, 1 male.

Remarks.—This species has been thoroughly described and illustrated by Markham (1982, 1990) from Hong Kong. The present specimens (Fig. 4) are from Fujian province near the previously recorded range. Females of the Chinese specimens have obscure dorsolateral bosses on the short side of pereomeres 5–7 and the lateral plates are longer than previously reported specimens (Fig. 4A) (Markham 1982, 1990).

Distribution and hosts.—Hong Kong, China, on *Upogebia* sp. [= *U. major*] (de

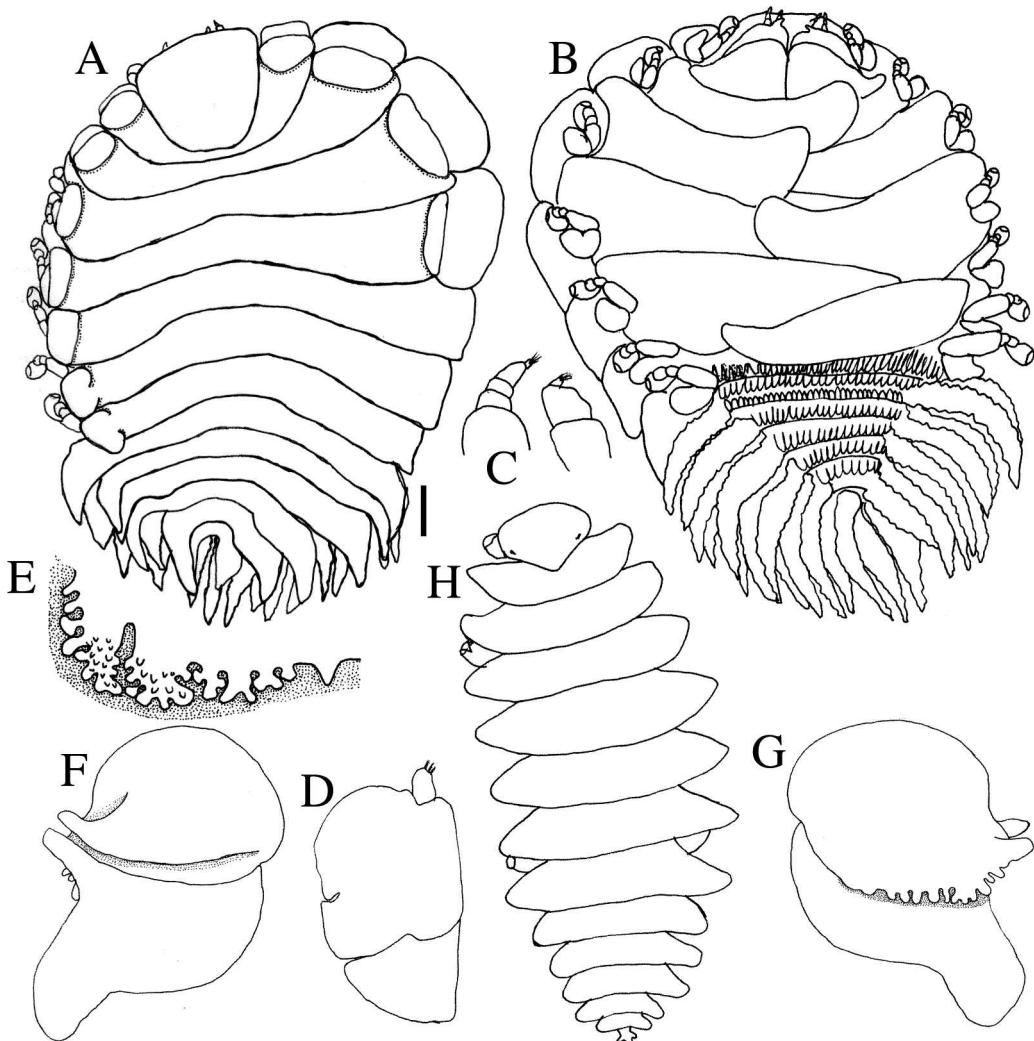


Fig. 4. *Progebiophilus sinicus* Markham, 1982. Female (A–G, CIET570303). A. Dorsal view. B. Ventral view. C. Right antennae. D. Right maxilliped, external view. E. Right side of barbula. F. Right oostegite 1, external view. G. Right oostegite 1, internal view. Male (H, CIET570304). H. Dorsal view of male. Scale bars: 1 mm (A, B); 0.15 mm (C); 0.50 mm (D); 0.33 mm (E); 0.58 mm (F, G); 0.39 mm (H).

Haan]; Fujian province, China, on *U. major*.

***Progebiophilus elongatus*, new species**
Fig. 5, Table 1

Material examined.—Infesting *Nihonotrypaea japonica* (Ortmann). Holotype: Cangkou, Jiaozhou Bay, Shandong province, 36°04'N, 120°19'E, 7 May 1951, CIET510501, 1 female. Allotype: same collection data as holotype, CIET510502,

1 male. Paratypes: Chejia Village, Dalian, Liaoning province, 38°54'N, 121°38'E, 29 May 1950, coll. Ruiyu Liu, CIET500501, 2 females, CIET500502, 2 males. Yantai, Shandong Province, 37°30'N, 121°24'E, 30 Jun 1957, ET570603, 1 female, ET570604, 1 male.

Description of holotype (CIET510501).—Length 6.21 mm, maximal width 3.27 mm, head length 1.0 mm, head width 1.49 mm, pleon length 1.87 mm. All body regions

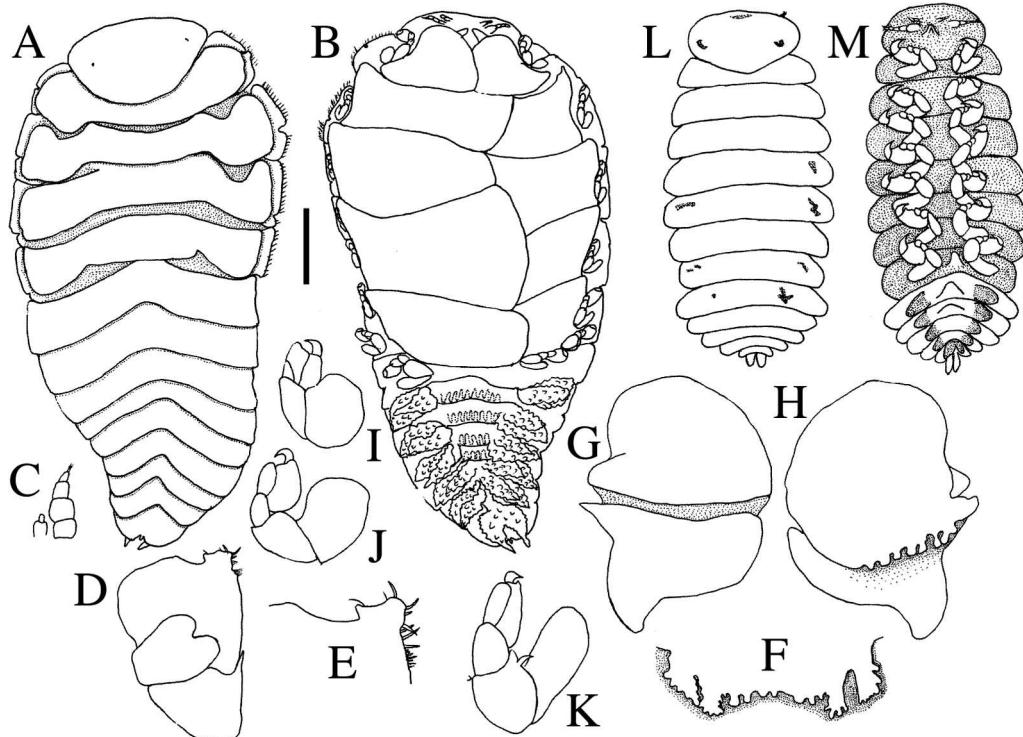


Fig. 5. *Progebiophilus elongatus*. Female (Holotype: A–K, CIET510501). A. Dorsal view. B. Ventral view. C. Left antennae. D. Right maxilliped, external view. E. Palp of right maxilliped. F. Barbula. G. Right oostegite 1, external view. H. Right oostegite 1, internal view. I. Right pereopod 1. J. Right pereopod 2. K. Right pereopod 7. Male (Allotype: L, M, CIET510502). L. Dorsal view. M. Ventral view. Scale bars: 1 mm (A, B); 0.28 mm (C, E, I, J, K); 0.56 mm (D, F, G, H); 0.20 mm (L, M).

and segments distinct. Nearly symmetrical, slight dextral rotation $<5^\circ$, no pigmentation (Fig. 5A, B). Body broadest across pereomeres 2–3, gradually tapering posteriorly, pleon elongate, weakly S-shaped.

Head ovate, wider than long, without frontal lamina. Eyes small. Antennule of 2 articles, antenna of 4 articles, few setae except for second antennae with terminal setae (Fig. 5C). Maxilliped with short, stout, non-articulated, setose palp with shallow notch in middle, posterior lobe produced anteromedially into sharp plectron (Fig. 5D, E). Barbula with two large falcate processes and digitate margins on each side, digitate margin in center (Fig. 5F).

Pleon broadest across pereomeres 2–3, gradually tapering posteriorly. Coxal

plates on first four pereomeres, with setae on right side of first four pereomeres. Dorsolateral bosses and tergal projections absent. Oostegites completely enclosing vaulted brood pouch. Oostegite 1 smoothly rounded anteriorly, with simple digitate internal ridge, blunt posterolateral point (Fig. 5G, H). Basis carinae of pereopods 1–7 progressively smaller posteriorly (Fig. 5I, K), carina of pereopod 1 overlapping propodus (Fig. 5I), basis of pereopod 7 with reduced carina, and with a spine on the ischium (Fig. 5K).

Pleon of 6 pleomeres, lateral plates absent, pleomeres 1–5 bearing biramous pleopods, endopods and exopods similar, margins almost smooth, with small tubercles on surface; pleomere 6 with middle indentation. Uropods uniramous,

Table 1.—Described species of *Progebiophilus* with locality and host data.

Species of <i>Progebiophilus</i>	Locality	Host
<i>P. assisi</i> Kazmi & Bourdon, 1997	Pakistan	<i>Upogebia assisi</i> Barnard
<i>P. backeri</i> (Hale, 1929)*	South Australia	<i>Upogebia bowerbankii</i> (Miers)
<i>P. brevis</i> Bourdon, 1981b	Sierra Leone	<i>Paragebicula contigua</i> (Božić & de Saint Laurent)
<i>P. bruscai</i> Salazar-Vallejo & Leija-Tristan, 1989	Gulf of California, Mexico	<i>Upogebia dawsoni</i> Williams
	Gulf of California, Mexico	<i>Upogebia dawsoni</i> Williams
	Gulf of California, Mexico	<i>Upogebia macginitieorum</i> Williams
	Gulf of California, Mexico	<i>Pomatogebia rugosa</i> (Lockington)
	Zaire	<i>Upogebia furcata</i> (Aurivillius)
<i>P. chapini</i> (Van Name, 1920)**	Black Sea	<i>Upogebia pusilla</i> (Petagna)
<i>P. euxinicus</i> (Popov, 1927)**	Mediterranean Sea	<i>Upogebia pusilla</i> (Petagna)
	Mediterranean Sea	<i>Upogebia deltaura</i> (Leach)
	Adriatic Sea	<i>Upogebia pusilla</i> (Petagna)
<i>P. filicaudatus</i> (Shiino, 1958)**	Japan	<i>Upogebia issaeffi</i> (Balss)
<i>P. insperatus</i> Markham, 2005	Brazil	<i>Upogebia paraffinis</i> Williams
<i>P. kensleyi</i> Markham, 2005	South Africa	<i>Upogebia africana</i> (Ortmann)
<i>P. sinicus</i> Markham, 1982	Hong Kong	<i>Upogebia</i> sp.
<i>P. upogebiae</i> (Hay, 1917)**	North Carolina, USA	<i>Upogebia affinis</i> (Say)
	Brazil	<i>Upogebia omissa</i> Gomes Corrêa
	Mexico	<i>Upogebia felderii</i> Williams
	Florida, USA	<i>Upogebia affinis</i> (Say)
<i>P. villosus</i> (Shiino, 1964)**	Japan	<i>Upogebia pugnax</i> (de Man)
<i>P. elongatus</i> n. sp.	China	<i>Nihonotrypaea japonica</i> (Ortmann)

* Originally in the genus *Cryptione* (Hansen, 1897).

** Originally in the genus *Pseudionae* Kossmann, 1881.

similar in structure to pleopods, extending slightly beyond margin of pleomere 6 (Fig. 5B).

Description of allotype (CIET510502).—Length 1.18 mm, maximal width across pleomere 4, 0.51 mm, head length 0.26 mm, head width 0.38 mm. All body segments distinct, scattered pigment on dorsal surface of anterior margin of head, pereomeres 4–7 and pleomere 1.

Head oval, posterior margin triangular, dark eyes near posterolateral regions. Antennule of 3 articles, antenna of 5 articles, with few setae.

Pereomeres 4–5 broadest, body tapering slightly from pleomere 3, pereomeres rounded laterally (Fig. 5L). Pereomeres 1–6 without midventral projections, pereomere 7 and pleomeres 1–2 with prominent midventral projections. Pereopods all similar in structure and size (Fig. 5M).

Pleon of 6 pleomeres, pleomere 1 wider than pereomere 7. Pleomeres 1–5 with

tuberculiform pleopods, pleotelson produced into two long symmetrically extending posterior projections. No uropods (Fig. 5M).

Etymology.—The specific name *elongatus* refers to the long body of the holotype female.

Remarks.—With the newly described species included, the genus *Progebiophilus* presently contains 13 species (Table 1), most of which parasitize mud shrimp of the genus *Upogebia*. *Progebiophilus elongatus* is the only member of the genus found on hosts in the genus *Nihonotrypaea*, and the new species is distinguished from all other species in the genus by its long sinusoidal body. *Progebiophilus elongatus* is most similar to *P. villosus* (Shiino, 1964) but differs by having a nearly symmetrical, elongate body, whereas females of *P. villosus* have extensive head rotation (~30–40°) and a short pleon. Females of both *P. villosus* and *P. elonga-*

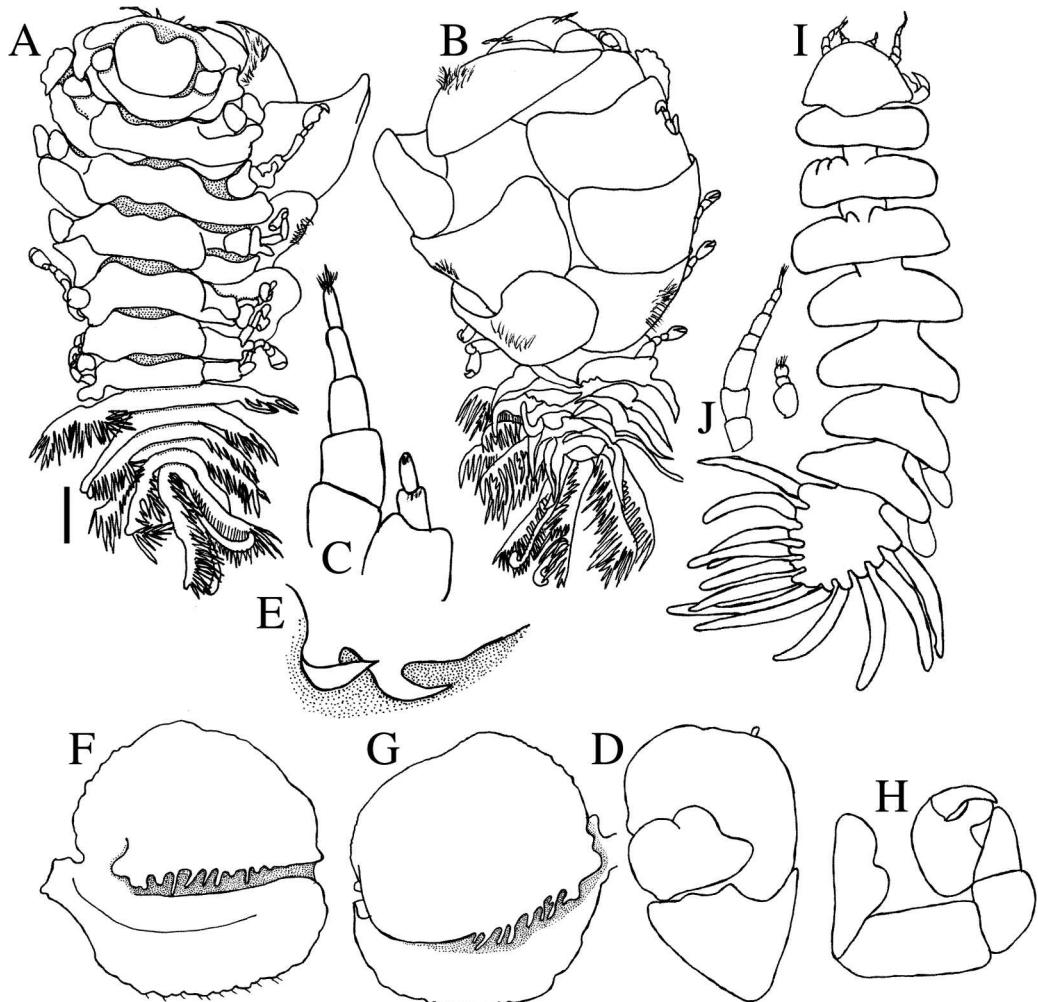


Fig. 6. *Ione cornuta* Bate, 1864. Female (A–H, CIET570501). A. Dorsal view. B. Ventral view. C. Right antennae. D. Right maxilliped, external view. E. Right side of barbula. F. Right oostegite 1, external view. G. Right oostegite 1, internal view. H. Left pereopod 6. Male (I, J, CIET570502). I. Dorsal view of male. J. Right antennae. Scale bars: 1 mm (A, B); 0.10 mm (C, H, J); 0.40 mm (D, F, G); 0.30 mm (E); 0.47 mm (I).

tus possess setae on coxal plates 1–4; however, *Progebiophilus villosus* also has setae on the last 3 pereomeres and pleomeres. In addition, females of *P. elongatus* have a much more elongate body and the pleopods are not as round as in *P. villosus* but are more triangular with tubercles on the surface, and the uropods of the females are not rod-like in shape as in *P. villosus* but similar to the shape of the pleopods. Females of *P. elongatus* possess a spine on the ischium of pereopod 7, a feature lacking in *P. villosus*.

Distribution and hosts.—China, on *Ni-honotrypaea japonica* (Ortmann).

Subfamily Ioninae H. Milne Edwards, 1840, emend. R. Codreanu, 1967

Genus *Ione* Latreille, 1817

Ione cornuta Bate, 1864

Fig. 6

Abbreviated synonymy.

Ione cornuta Bate, 1864:668.—Bate & Westwood, 1868:253, pl. 2.—Giard & Bonnier, 1887:77.—Richardson, 1899:

869.—Richardson, 1900:308.—Bonnier, 1900:245–247.—Richardson, 1904: 75.—Richardson, 1905:504.—Nierstrasz & Brender à Brandis, 1931:180–182, figs. 57–59.—Shiino, 1939b:13–16, figs. 2, 3.—Hatch, 1947.—Kim & Kwon, 1988:205–207, fig. 4.—Markham, 1992b: 3, table 1.—Saito et al., 2000:42.—Nobuhiro & Kyoko, 2004:1–7, fig. 4, table 3.—Espinosa-Pérez & Hendrickx, 2006:237.—Brusca et al., 2007:535, pl. 236B.—Pernet et al., 2008:1127–1140.
Ione brevicauda Bonnier, 1900:248–250, pl. iv.—Richardson, 1905:505–507, Fig. 553.

Material examined.—Infesting *Nihonotrypaea petalura* (Stimpson). Cangkou, Jiaozhou Bay, Shandong province, 36°04'N, 120°19'E, 29 Oct 1956, coll. Zhengang Fan, CIET561001, 1 female, CIET561002, 1 male; 10 Dec 1957, coll. Yongliang Wang, CIET571201, 1 female; 22 Aug 1957, coll. Yiqing Liu, CIET570801, 1 female, CIET570802, 1 male. Damai Island, Shandong province, 36°00'N, 120°20'E, 29 May 1957, CIET570501, 1 female, CIET570502, 1 male.

Infesting *Nihonotrypaea japonica* (Ortmann). Cangkou, Jiaozhou Bay, Shandong province, 36°04'N, 120°19'E, 7 May 1951, CIET510503, 1 female, CIET510504, 1 male. Hulu Island, Liaoning province, 40°42'N, 120°54'E, 16 Jun 1950, CIET500601, 1 female. Baoxi, Zhejiang province, 30°25'N, 120°15'E, 24 Nov 1950, CIET501101, 3 females, CIET501102, 3 males. Cangkou, Jiaozhou Bay, Shandong province, 36°04'N, 120°19'E, 26 May 1956, CIET560501, 1 female, CIET560502, 1 male. Zhanshan Bay, Shandong province, 36°00'N, 120°10'E, 9 Apr 1951, CIET510409, 1 female.

Infesting *Nihonotrypaea harmandi* (Bouvier). Cangkou, Jiaozhou Bay, Shandong province, 36°04'N, 120°19'E, 10 Nov 1957, coll. Yongliang Wang, Yaxi Yang & Jieshan Xu, CIET571101, 1 female.

Infesting *Upogebia major* (de Haan). Huiquan Bay, Shandong province, 36°05'N, 120°14'E, 16 Sep 1951, CIET510901, 1 female. Licun, Qingdao, Shandong province, 36°00'N, 120°10'E, 16 Feb 1960, CIET600203, 1 female, CIET600204, 1 male. Ye county, Shandong province, 37°52'N, 121°30'E, 5 Nov 1951, CIET511101, 1 female, CIET511102, 1 male.

Description of reference female (CIET570501, Fig. 6).—Length 8.89 mm (excluding uropods), maximal width 3.95 mm, head length 0.86 mm, head width 1.33 mm. Body axis distortion 10°, sinistral. All body segments distinct (Fig. 6A, B).

Head bilobate, wider than long, with frontal lamina extending beyond sides of head. Eyes absent. Antennae visible from dorsal side, antennule of 3 articles, antenna of 5 articles (Fig. 6C). Maxilliped (Fig. 6D) with broad, rounded anterior article and small, non-setose palp; posterior article triangular, rounded posteriorly, with long plectron ending in blunt tip. Barbula (Fig. 6E) with two smooth subequal falcate projections on each side.

Pereon broadest across third pereomere (Fig. 6A). No middorsal projections. Prominent coxal plates on all pereomeres, dorsolateral bosses on first four pereomeres. Brood pouch almost covered by oostegites. Oostegite 1 (Fig. 6F, G) rounded anteriorly, straight and setose posteriorly, without posterolateral point, internal ridge simple, with digitate margin. External surfaces of oostegites 2, 4, 5 with long setae near base (Fig. 6B). Pereopods long and slender, propodi of sixth and seventh pereopods larger than those of first five pereopods (Fig. 6H).

Pleon of six pleomeres, bearing well-developed lateral plates, posterior margins of pleopods strongly digitate, anterior margins smooth (Fig. 6A, B). Five pairs of biramous pleopods, exopodites lanceolate, about as long as corresponding lateral plates, lacking digitate mar-

gins, endopodites of first three pleopods broader than those of last two pleopods. Terminal pleomere bearing long curled uniramous uropods (Fig. 6A, B).

Description of reference male (CIET-570502).—Length 5.03 mm, maximal width across third pereomere, 1.18 mm, head length 0.58 mm. Body slender, gradually tapered posteriorly (Fig. 6I).

Head semicircular, as broad as long, posterior margin curved. Eyes absent. Head distinctly separated from first pereomere; posterior margin curved. Antennae (Fig. 6J) extending far beyond head margin; antennule of 3 articles, antenna of 7 articles, both setose distally.

Pereomeres deeply separated by lateral notches, without midventral tubercles. Pleon triangular, fused into single piece, but lateral undulations indicating six pleomeres. Six pairs of long slender lateral plates, no pleopods or uropods.

Remarks.—As indicated by Markham & Boyko (1999), the genus *Ione* currently contains seven described species. Although *Ione cornuta* has been reported many times from different geographic regions, all previous descriptions are incomplete, with some key characters not provided. This is the first record of the species from China. The present specimens are extremely similar to Shino's (1939b) specimen, but the prominent bilobate heads of the females and the curved posterior margins of the males differ from the Japanese material. The impacts of *Ione cornuta* on *Nihonotrypaea japonica* from Japan have been studied (Nobuhiro & Kyoko 2004). In addition, Pernet et al. (2008) considered its potential spread along the west coast of the United States via transport of its mud shrimp host *Neotrypaea californiensis* (Dana) sold as bait.

Distribution and hosts.—Eastern Pacific, British Columbia to California on *Neotrypaea gigas* (Dana) and *Neotrypaea californiensis* (Dana); Japan, on *Nihonotrypaea japonica* (Ortmann); Korea, on

Nihonotrypaea japonica; China, Shandong province, Liaoning province, Zhejiang province, on *Nihonotrypaea japonica*, *Nihonotrypaea petalura*, *Nihonotrypaea japonica*, *Upogebia major* (de Haan).

Genus *Upogebione* Markham, 1985

Upogebione bidigitatus, new species

Figs. 7, 8

Material examined.—Infesting *Upogebia carinicauda* (Stimpson). Holotype: Naozhou, Guangzhou province, 23°15'N, 113°27'E, 29 Nov 1954, coll. Xiutong Ma, CIET541101, 1 female. Allotype: same collection data as holotype, CIET541102, 1 male (on SEM stub). Paratypes: Infesting *Austinogebia wuhsienwensi* (Yu). Jiaozhou Bay, Stn. D7, 35°59'N, 120°25'E, 31 m, 9 Aug 2004, coll. Hongfa Wang, CIETD701, 1 female, CIETD702, 1 male.

Description of holotype (CIET541101, Fig. 7).—Length 5.08 mm, maximal width across pereomere 3, 4.48 mm, head length 1.2 mm, head width 1.35 mm, pereon length 2.57 mm, pleon length 1.15 mm. All body segments distinct, nearly symmetrical, slight sinistral distortion (Fig. 7A, B).

Head square, short frontal lamina, without eyes. Antennae (Fig. 7C) extending beyond head, antennule of 3 articles, antenna of 5 articles, terminal segments setose. Maxilliped (Fig. 7D, E) with broad anterior article bearing large articulating semicircular setose palp, its posterior article triangular with pointed plectron. Barbula (Fig. 7F) with two pairs of falcate lateral projections, middle region with three small, rounded projections.

Pereon broadest across third pereomere, first pereomere shortest and curved around head. Dorsolateral bosses absent, tergal projections present on left side of pereomeres 5–7, moderately large, similar in shape to lateral plates on pleomere 1; coxal plates on both sides of first four pereomeres and on right side of pereomeres 5, 6. Oostegites not enclosing brood pouch but almost meeting each other, first oostegite (Fig. 7G, H) with smooth

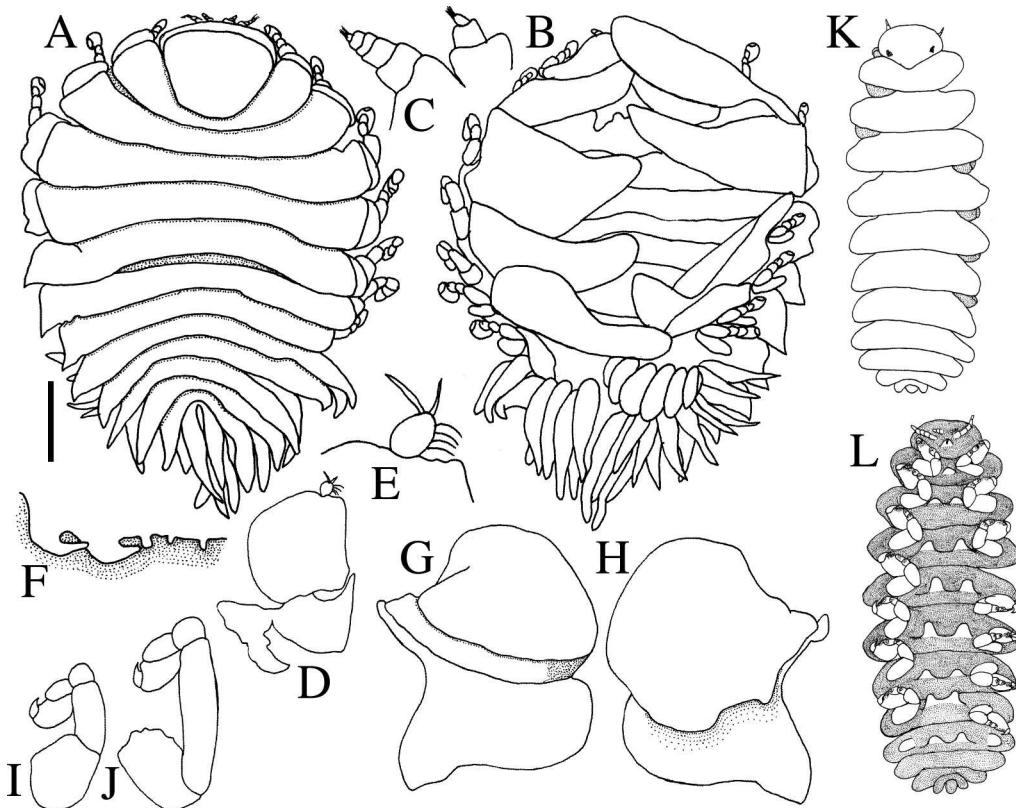


Fig. 7. *Upogebione bidigitatus*. Female (Holotype: A–J, CIET541101). A. Dorsal view. B. Ventral view. C. Right antennae. D. Right maxilliped, external view. E. Palp of right maxilliped. F. Right side of barbula. G. Right oostegite 1, external view. H. Right oostegite 1, internal view. I. Right pereopod 1. J. Right pereopod 6. Male (Allotype: K, L, CIET541102). K. Dorsal view. L. Ventral view. Scale bars: 1 mm (A, B); 0.20 mm (C, E); 0.71 mm (D); 0.44 mm (F); 0.52 mm (G, H); 0.39 mm (I, J); 0.48 mm (K, L).

unornamented internal ridge, proximal lobe ovate, distal lobe subtriangular. Pereopods (Fig. 7I, J) longer posteriorly with all articles distinct; each with stout basis and short dactyli short; ischium of seventh pereopod approximately three times longer than that of first pereopod.

Pleon of six pleomeres, first five bearing slender pointed lateral plates extending posteriorly; five pairs of biramous pleopods similar to lateral plates in shape and size, all with smooth edges (Fig. 7B). Pleomere 6 with lanceolate uniramous uropods of similar structure to pleopods and lateral plates.

Description of allotype (CIET541102, Figs. 7K, L, 8).—Length 2.25 mm, head width 0.47 mm, head length 0.31 mm,

pereon length 1.48 mm, maximal width across pleon 1, 1.07 mm, pleon length 0.46 mm (Figs. 7K, L, 8A). All body regions and segments distinct, no pigmentation aside from eyes.

Head suboval, its posterior edge triangular, much narrower than first pereomere. Dark eyes near posterolateral corners of head (Fig. 7K). Antennule of 3 articles, antenna of 5 articles; distal two articles of first antennae with terminal setae, second antenna longer and extending beyond margin of head, setose terminally (Fig. 8B).

Pereon approximately 0.6 of total length; all pereomeres distinctly separated; third to seventh pereomeres almost equally wide; first pereomere with small,

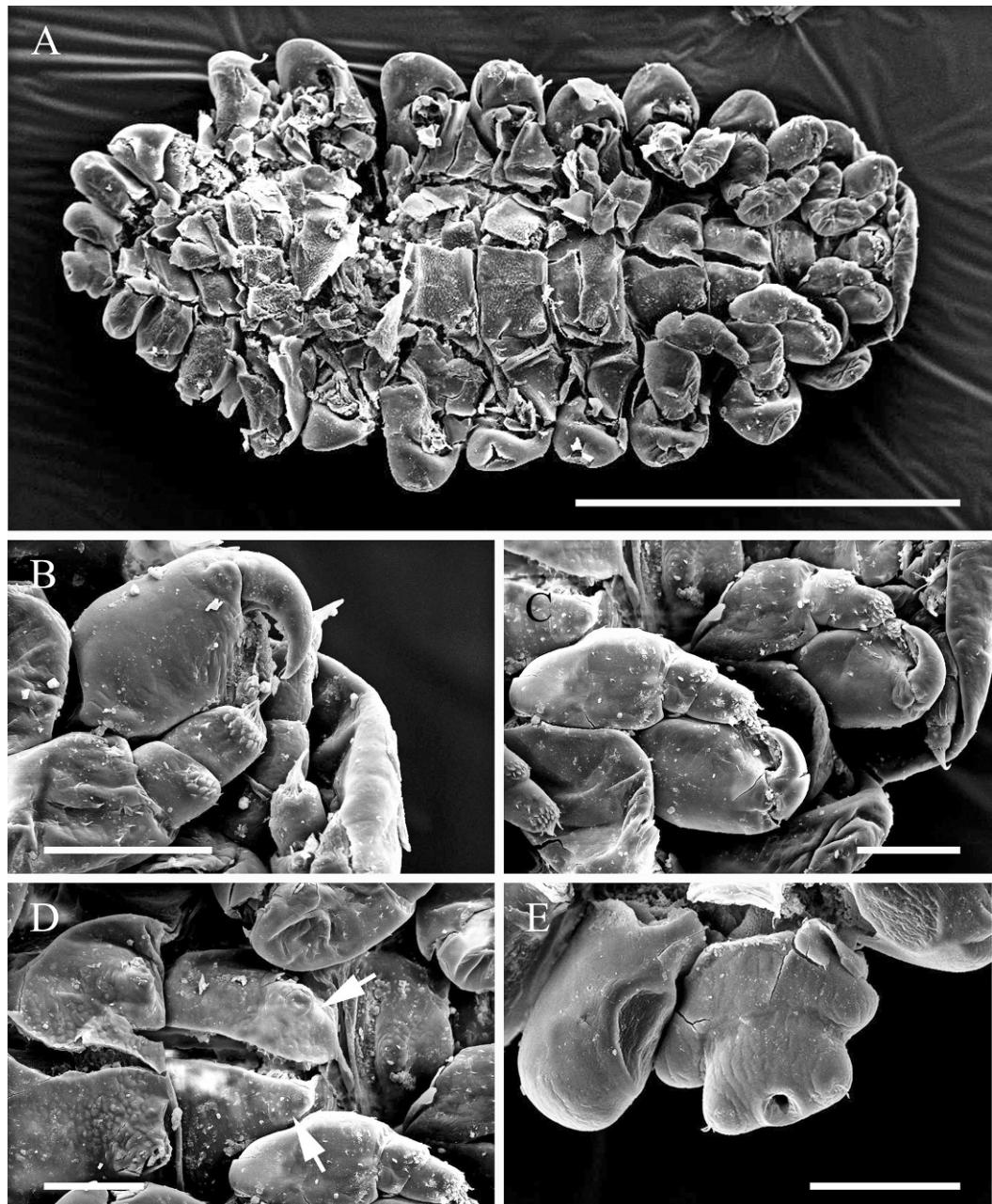


Fig. 8. *Upogebione bidigitatus*. Male (Allotype, CIET541102). SEM micrographs. A. Ventral view (damaged along pleon). B. Right antennae and pereopod 1. C. Left pereopods 1, 2. D. Ventral view of pereomeres 1–3 (arrow shows midventral projection of pereomere 2). E. End of pleon. Scale bars: 1 mm (A); 0.28 mm (B, E); 0.18 mm (C, D).

round midventral projection; second to seventh pereomeres and first pleomere with two ventral projections (Figs. 7L, 8A, D). All pereopods similar in size,

except carpi longer posteriorly; all carpi and meri with terminal setae (Fig. 8C).

Pleon of five pleomeres, first pleomere wider than pleomere 7, with two ventral

projections and sessile tuberculiform pleopods (Figs. 7L, 8A). Fourth pleomere short and concave posteriorly, fifth pleomere distinct laterally but incompletely separated dorsally and ventrally, embedded in fourth pleomere (Fig. 8E), terminal pleomere extended, posteriorly truncate, lacking uropods, distally setose (Fig. 8E).

Etymology.—The specific name *bidigitatus* refers to the male possessing two ventral projections on the second to seventh pereomeres and first pleomere.

Distribution and hosts.—China, on *Upogebia carinicauda* (Stimpson), *Austinogebia wuhsienweni* (Yu).

Remarks.—The genus *Upogebione* Markham, 1985 contains four species, including the new species, all of which parasitize hosts in the family Upogebiidae. *Upogebione bidigitatus* is similar to *U. ovalis* (Nierstrasz & Brender à Brandis, 1931), originally described as *Hypercepon ovale* by Nierstrasz and Brender à Brandis (1931) from the Gulf of Thailand. *Upogebione bidigitatus* differs from *U. ovalis* in that the females of the former lack eyes and have pleopodal endopodites nearly equal in size to the exopodites. The males of *U. bidigitatus* are similar to those of *U. ovalis*; however, males of the former can be distinguished from those of *U. ovalis* by the incomplete separation between the last two pleomeres. *Upogebione bidigitatus* is distinguished from *Upogebione phuketensis* Markham, 1985 by the nearly symmetrical body, pereomeres without dorsolateral bosses, first oostegite with smooth internal ridge, and pereopods with distinct separation between carpi and méri. In addition, the males of *U. bidigitatus* can be distinguished from those of *U. phuketensis* in having six pleomeres. *Upogebione bidigitatus* differs from *U. tropica* (Lemos de Castro & Brasil Lima, 1975), from Brazil, as males of the latter have two ventral projections only on the first pleomere and lack pleopods, whereas males of *U. bidigitatus*

have two ventral projections on pereomeres 2–7 and pleomere 1 and have tuberculiform pleopods.

Genus *Procepon* Shiino, 1937

Procepon liuruuiyi, new species

Fig. 9

Material examined.—Infesting *Austinogebia wuhsienweni* (Yu). Holotype: Naozhou, Guangdong Province, 23°15'N, 113°27'E, 29 Nov 1954, coll. Ruiyu Liu & Yongliang Wang, CIET541103, 1 female. Allotype: same collection data as holotype CIET541104, 1 male. Paratypes: same collection data as holotype CIET541105, 1 female.

Description of holotype (CIET541103, Fig. 9A–I).—Length (not including uropods) 11.61 mm, maximal width across fourth pereomere, 9.52 mm, head length 2.22 mm, head width 3.36 mm, pereon length 6.29 mm, distortion 11°, dextral. All body regions and segments distinct (Fig. 9A, B).

Head oval, wider than long, bearing short frontal lamina with setose anterior margin. Eyes absent. Antennule of 4 articles, terminal article minute, bearing setae; antenna of 5 articles, basal segments stout, with terminal setae (Fig. 9C). Maxilliped anterior article broad with stout, blunt, nonarticulating setose palp, its posterior article triangular with sharp pointed plectron (Fig. 9D). Each side of barbula bearing five lateral projections with digitate margins, projections progressively smaller toward middle, cone-shaped projection in center (Fig. 9E).

Pereon broadest across fourth pereomere, setose-margined coxal plates along sides of first four pereomeres. Tergal projections on pereomeres 5–7, small, rounded on anterior end, produced into sharp point on posterior ends. Oostegites covered with tubercles, completely enclosing highly vaulted brood pouch; first oostegite smoothly rounded anteriorly, with digitate internal ridge, long, angled,

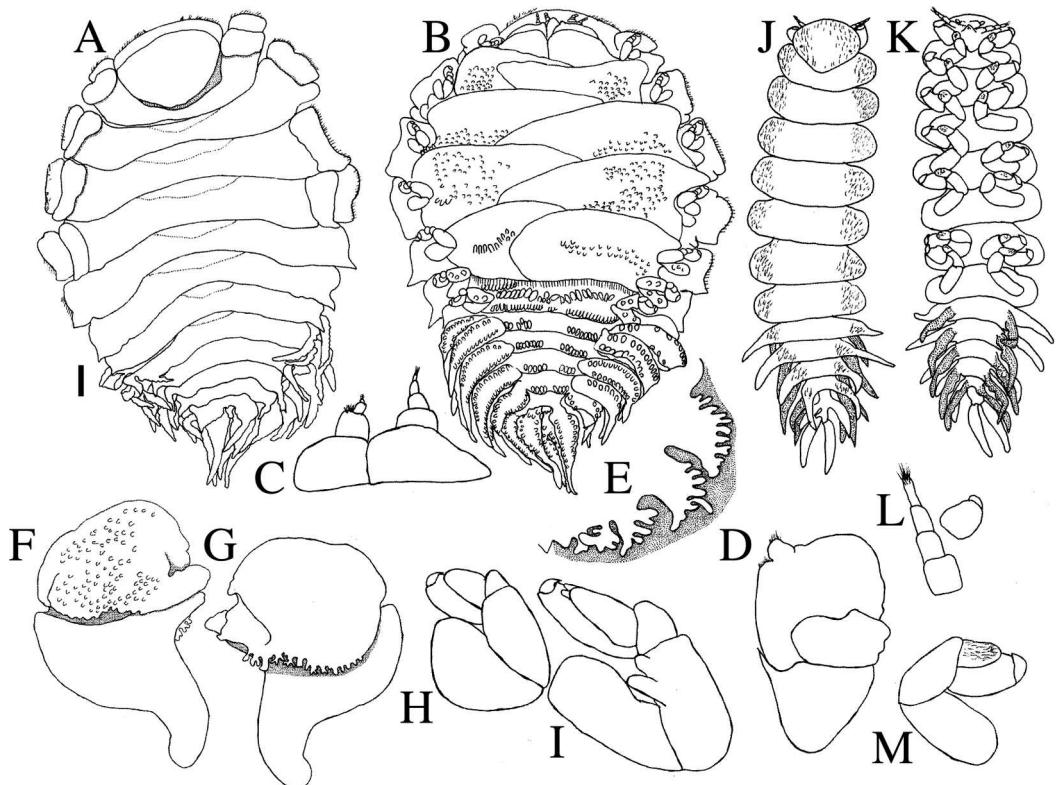


Fig. 9. *Procepion liuruuiyi*. Female (Holotype: A–I, CIET541103). A. Dorsal view. B. Ventral view. C. Left antennae. D. Left maxilliped, external view. E. Left side of barbula. F. Left oostegite 1, external view. G. Left oostegite 1, internal view. H. Right pereopod 1. I. Right pereopod 7. Male (Allotype: J–M, CIET541104). J. Dorsal view. K. Ventral view. L. Right antennae. M. Left pereopod 4. Scale bars: 1 mm (A, B); 0.14 mm (C); 0.38 mm (D); 0.26 mm (E); 0.56 mm (F, G); 0.20 mm (H, I); 0.41 mm (J, K); 0.10 mm (L, M).

round posterolateral point, posterior margin curved (Fig. 9F, G). All pereopods similar in shape, except progressively longer posteriorly (Fig. 9H, I), seventh pereopods with two large digitiform projections on ischium (Fig. 9I).

Pleon of six pleomeres, first five bearing biramous pleopods and lateral plates, single row of tubercles on ventral surface of pleon between pleopods, with slight gap in middle. Endopodites and exopodites long, lanceolate with two regular rows of small tubercles on ventral surface of endopodites and exopodites; lateral plates similar in structure to pleopods, except more slender and lacking rows of tubercles. Uniramous uropods of same

structure as pleopods, with two rows of tubercles (Fig. 9B).

Description of allotype (CIET541104, Fig. 9J–M).—Length 6.18 mm, maximal width across pereomeres 3, 4, 1.63 mm, head length 0.71 mm, head width 0.95 mm, pleonal length 1.25 mm. All body segments distinct, patches of setae on dorsal surface of head, sides of pereomeres 1–7 and lateral plates of pleomeres 1–4 (Fig. 9J, K).

Head subcircular, eyes small, posterior edge bluntly pointed. Antennule of 2 articles, antenna of 4 articles, with setae at distal extremity of second antennae (Fig. 9L).

All pereomeres almost equally wide, with rounded margins (Fig. 9J), without

midventral projections. Pereopods similar in shape and size, dactyli small, carpi and meri fused and setose (Fig. 9M).

Pleon of six pleomeres, first five with lateral plates and uniramous pleopods, all of similar structure, long, sharply pointed, lanceolate. Final pleomere produced into long, uniramous uropods similar to pleopods (Fig. 9K).

Etymology.—The specific name *liuruiyui* is selected to express special thanks to Prof. Ruiyu Liu, for providing specimens and help in our research.

Distribution and hosts.—China, on *Austinogebia wuhsienweni* (Yu).

Remarks.—The new species belongs to the genus *Procepon* Shiino, 1937 on the basis of the females having a prominent head, lacking middorsal projections, and their pleomeres being produced into long lanceolate lateral plates and similar biramous pleopods and uniramous uropods. Males have six pleomeres with long lanceolate lateral plates and uropods. Including *Procepon liuruiyui*, there are three species in the genus *Procepon* Shiino, 1937. *Procepon liuruiyui* is most similar to *P. insolitum* Shiino, 1937, which was described by Shiino (1937, 1958) from Japan in *Upogebia major* and redescribed from Thailand in *Upogebia* sp. (Markham 1985). Females of *P. liuruiyui* differ from *P. insolitum* by the dorsolateral bosses on pereomeres 1–4 (absent in *P. insolitum*), absence of eyes (small eyes are present in *P. insolitum*), and presence of a prominent setose palp on the maxilliped (palp lacking in *P. insolitum*). Males of *P. liuruiyui* also differ from *P. insolitum* by the absence of midventral projections (small, rudimentary tubercles being present in *P. insolitum*), setose head and pereon (setae lacking in *P. insolitum*), and final pleomere without an anal cone (prominent anal cone being present between uropods in *P. insolitum*). *Procepon liuruiyui* is distinguished from *P. horridulum* Markham, 1985, from Thailand as the former has a barbula

with five pairs of projections (irregular barbula in *P. horridulum*), and tuberculated oostegites, pleopods and pleomeres (tubercles lacking in *P. horridulum*). In addition, *P. liuruiyui* can be distinguished from *P. horridulum* in that the males of *P. liuruiyui* possess five pairs of lanceolate pleopods, which are lacking in *P. horridulum*.

Acknowledgments

This study was supported by Shanxi Province Youth Science Foundation (No. 2007021041). We are grateful to Drs. John C. Markham (Arch Cape Marine Laboratory, Oregon, U.S.A.), Christopher B. Boyko (American Museum of Natural History, New York, U.S.A.), and Prof. Ramiro Román-Contreras (Universidad Nacional Autónoma de México) for their kind sharing of bopyrid literature. The authors would like to thank Prof. J. Y. Liu (Ruiyu Liu, IOCAS) and Prof. Xinzheng Li (IOCAS) for their offering of specimens and guidance in this study. Thanks also to Wenliang Liu (IOCAS) for his identification of the hosts and to Dr. Peter Dworschak (Naturhistorisches Museum Wien) for information on the current taxonomy of hosts. The helpful comments of Dr. Christopher Boyko and two anonymous reviewers are greatly appreciated. We are indebted to collectors of China/Vietnam Comprehensive Oceanographic Survey to Beibu Gulf (1959, 1960, 1962).

Literature Cited

- Adkison, D. L., & R. W. Heard. 1995. *Pseudione overstreeti*, new species (Isopoda: Epicaridea: Bopyridae), a parasite of *Callichirus isla-grande* (Decapoda: Anomura: Callianassidae) from the Gulf of Mexico.—Gulf Research Reports 9:105–110.
- Batang, Z. B., & H. Suzuki. 2003. Gill-cleaning mechanisms of the burrowing thalassinidean shrimps *Nihonotrypaea japonica* and *Upogebia major* (Crustacea: Decapoda).—Journal of Zoology, London 261:69–77.

- Bate, C. S. 1864. Characters of new species of crustaceans discovered by J. K. Lord on the coast of Vancouver Island.—Proceedings of the Zoological Society of London 1864: 661–669.
- , & J. O. Westwood. 1868. A history of the British sessile-eyed Crustacea. Vol. 1. London: John Van Voorst. 507 pp.
- Bonnier, J. 1900. Contribution à l'étude des Épicarides.—Les Bopyridae. Travaux de la Station zoologique de Wimereux 8:1–476.
- Bourdon, R. 1968. Les Bopyridae des mers Européenne.—Mémoires du Muséum National d'Histoire Naturelle de Paris, Nouvel Série (A) 50:77–424.
- . 1981a. Bopyriens nouveaux pour la faune européenne de l'Atlantique (Isopoda Epicaridea).—Bulletin du Muséum National d'Histoire Naturelle, Paris (4)3 (Section A) (no. 2):615–634.
- . 1981b. Sur cinq Bopyrides parasites de Thalassinides ouest-africaines.—Bulletin de l'Institut Français d'Afrique Noire 43 (série A, 1–2):111–134.
- , J.-L. d'Hondt, & A. Veillet. 1981. Note préliminaire sur les microsetes et les ‘fentes céphaliques’ chez les bopyriens (Crustaces epicarides).—Bulletin de la Société Zoologique de France 105(4):495–504.
- Boyko, C. B., & J. D. Williams. 2009. Crustacean Parasites as Phylogenetic Indicators in Decapod Evolution. Pp. 197–220 in J. W. Martin, K. A. Crandall and D. L. Felder, eds., Decapod Crustacean Phylogenetics (Crustacean Issues). Vol. 18. CRC Press, Boca Raton, FL, 632 pp.
- Brusca, R. C., V. R. Coelho, & S. Taiti. 2007. Isopoda. Pp. 503–542 in J. T. Carlton, ed., The Light and Smith Manual: Intertidal Invertebrates From Central California to Oregon. University of California Press, Berkeley, California, 1019 pp.
- Codreanu, R. M. 1967. Clasificarea evolutivă a bopirienilor, isopode parazite ale crustaceelor decapode și importanța lor biologică generală.—Studii Cercetări Biologie 19:203–211.
- , & M. Codreanu. 1963. Sur plusieurs bopyriens parasites branchiaux des anomoures de la Mer Noire, de la Méditerranée et du Viet-Nam.—Rapports et Procès verbaux de réunions de la Commission internationale pour l'Exploration scientifique de la mer Méditerranée 17:283–285.
- Cornalia, E., & P. Panceri. 1861. Osservazione zoologiche ed anatomiche sopra un nuovo genere di Isopodo sedentary (*Gyge branchialis*).—Accademia delle Scienze di Torino (2) 19:85–118, pls. I–II.
- Danforth, C. G. 1963. First record of a Hawaiian shore bopyrid (Isopoda, Bopyridae).—Journal of Parasitology 49(5):847–850.
- Dworschak, P. C. 2000. Global diversity in the Thalassinidea (Decapoda).—Journal of Crustacean Biology 20 (Special Number 2): 238–245.
- . 2005. Global diversity in the Thalassinidea (Decapoda): an update (1998–2004).—Nauplius 13:57–63.
- Espinosa-Pérez, M. D. C., & M. E. Hendrickx. 2006. A comparative analysis of biodiversity and distribution of shallow-water marine isopods (Crustacea: Isopoda) from polar and temperate waters in the East Pacific.—Belgian Journal of Zoology 136:219–247.
- Giard, A., & J. Bonnier. 1887. Contributions à l'étude des bopyriens.—Travaux de l'Institut Zoologique de Lille et du laboratoire de Zoologie Maritime de Wimereux 5:1–272.
- Hale, H. M. 1929. The Crustaceans of South Australia. Government Printer, Adelaide, 380 pp.
- Hansen, H. J. 1897. Reports on the dredging operations off the west coast of Central America to the Galapagos Islands, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission Steamer Albatross during 1891, Lieut. Commander Z. L. Tanner, U.S. Navy, commanding. XXII. The Isopods.—Bulletin of the Museum of Comparative Zoology, Harvard College 31(5):95–129.
- Hatch, M. H. 1947. The Chelifera and Isopoda of Washington and adjacent regions.—University of Washington Publications in Biology 10:155–274.
- Hay, W. P. 1917. A new genus and three new species of parasitic isopod crustaceans.—Proceedings of the United States National Museum 51:569–574.
- Huang, Z. 1994. Isopoda. Pp. 528–532 in Z. Huang, ed., Marine species and their distribution on China's seas. China Ocean Press, Beijing.
- . 2001. Isopoda. Pp. 325–327 in Z. Huang, ed., Marine species and their distribution on China's seas (English translation). Krieger Publishing Co, Malabar, FL.
- Itani, G. 2004. Host specialization in symbiotic animals associated with thalassinidean shrimps in Japan. Pp. 33–43 in A. Tamaki, ed., Proceedings of the symposium on “Ecology of large bioturbators in tidal flats and shallow sublittoral sediments—from individual behavior to their role as ecosystem engineers”, 1–2 November 2003. Nagasaki University, Nagasaki.

- Kazmi, Q. B., & R. Bourdon. 1997. A new bopyrid isopod *Progebiophilus assisi* on the mud shrimp *Upogebia (U.) assisi* Barnard (Thalassinidea) from Pakistan.—Pakistan Journal of Marine Science 6:59–67.
- Kim, H. S., & D. H. Kwon. 1988. Bopyrid isopods parasitic on decapod crustaceans in Korea.—Korean Journal of Systematic Zoology. Special issue No 2:199–221.
- Kossmann, R. 1881. Studien über Bopyriden. I. *Gigantione moebii* und Allgemeines über die Mundwerkzeuge der Bopyriden. II. *Bopyrina virbii*; Beiträge zur Kenntnis der Anatomie und Metamorphose der Bopyriden.—Zeitschrift für Wissenschaftliche Zoologie 35:652–680.
- Latreille, P. A. 1817. Les Crustacés, les arachnides, et les insectes. In G. L. C. F. D. Cuvier. 1817. Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée, Vol. 3. Paris.
- Lemos de Castro, A., & I. M. Brasil Lima. 1975. Crustáceos isópodes epicarídeos do Brasil. VIII. Descrição de uma espécie nova do gênero *Pleurocrypta* (Isopoda, Bopyridae).—Atas da Sociedade Biologia Rio de Janeiro 17(3):129–131.
- Li, L. 2003. Hong Kong's Isopods. Pp. 137–166 in B. Morton, ed., Perspectives on marine environmental change in Hong Kong and Southern China, 1977–2001: Proceedings of an International Workshop Reunion Conference, Hong Kong, 21–26 October 2001. Hong Kong University Press, Hong Kong, 864 pp.
- Lin, F., T. Komai, & T. Chan. 2007. A new species of callianassid shrimp (Crustacea: Decapoda: Thalassinidea) from deep-water hydrothermal vents off Taiwan.—Proceedings of the Biological Society of Washington 120:143–158.
- Manning, R. B., & A. Tamaki. 1998. A new genus of ghost shrimp from Japan (Crustacea: Decapoda: Callianassidae).—Proceedings of the Biological Society of Washington 111: 889–892.
- Markham, J. C. 1982. Bopyrid isopods parasitic on decapod crustaceans in Hong Kong and Southern China. Pp. 325–391 in B. Morton and C. K. Tseng, eds., The Marine Flora and Fauna of Hong Kong and Southern China: Proceedings of the First International Marine Biological Workshop, 18 April–10 May 1980. Hong Kong University Press, Hong Kong.
- . 1985. Additions to the bopyrid fauna of Thailand.—Zoologische Verhandelingen 224: 1–63.
- . 1988. Descriptions and revisions of some species of Isopoda Bopyridae of the north western Atlantic Ocean.—Zoologische Verhandelingen (Leiden) 246:1–63.
- . 1990. Further notes on the Isopoda Bopyridae of Hong Kong. Pp. 555–566 in B. Morton, ed., The marine flora and fauna of Hong Kong and Southern China II. Volume 2: Taxonomy and ecology. Proceedings of the Second International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 2–24 April 1986. Hong Kong University Press, Hong Kong.
- . 1992a. Second list of additions to the Isopoda Bopyridae of Hong Kong. Pp. 277–302 in B. Morton, ed., The marine flora and fauna of Hong Kong and Southern China III. Volume 1: Introduction, taxonomy and ecology. Proceedings of the Fourth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 11–29 April 1989. Hong Kong University Press, Hong Kong.
- . 1992b. The Isopoda Bopyridae of the eastern Pacific: missing or just hiding?—Proceedings of the San Diego Society of Natural History 17:1–4.
- . 2001. A review of the bopyrid isopods parasitic on thalassinidean decapods.—Crustacean Issues 13:195–204.
- . 2004. New species and records of Bopyridae (Crustacea: Isopoda) infesting species of the genus *Upogebia* (Crustacea: Decapoda: Upogebiidae): the genera *Orthione* Markham, 1988, and *Gyge* Cornalia & Panceri, 1861.—Proceedings of the Biological Society of Washington 117:186–198.
- . 2005. New species and records of Bopyridae (Crustacea: Isopoda) infesting species of the genus *Upogebia* (Crustacea: Decapoda: Upogebiidae): the genus *Progebiophilus* Codreanu & Codreanu, 1963; and remarks on *Phyllo-durus* Stimpson, 1857.—Proceedings of the Biological Society of Washington 118:84–95.
- . & C. B. Boyko. 1999. A new genus for *Ione indecora* Markham, 1988, a second record for that species, and a new congeneric species from Australia (Crustacea: Isopoda: Bopyridae: Ioninae).—American Museum Novitates 3258:1–7.
- . & P. C. Dworschak. 2005. A new species of *Entophilus* Richardson, 1903 (Isopoda: Bopyridae: Entophilidae) from the Gulf of Aqaba.—Journal of Crustacean Biology 25:413–419.
- Milne Edwards, H. 1840. Histoire Naturelle des Crustaces, comprenant l'anatomie, la physiologie et la classification de ces animaux, vol 3. Roret, Paris.
- Nierstrasz, H. F., & G. A. Brender à Brandis. 1931. Epicaridea II. In Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16.—Videnskabelige Meddelelser Naturhistorisk Forening i København 91:147–225, 1 pl.

- Nobuhiro, S., & K. Kyoko. 2004. Prevalence of the bopyrid isopod *Ione cornuta* (Crustacea: Isopoda: Epicaridea) on the ghost shrimp *Nihonotrypaea japonica* (Crustacea: Decapoda: Thalassinidea) on a tidal flat of Shinhama Lagoon, northern Tokyo Bay.—Japanese Journal of Benthology 59:1–7.
- Page, R. D. M. 1985. Review of the New Zealand Bopyridae (Crustacea: Isopoda: Epicaridea).—New Zealand Journal of Zoology 12:185–212.
- Pernet, B., A. Deconinck, A. Llaban, & J. W. Archie. 2008. Evaluating risks associated with transport of the ghost shrimp *Neotrypaea californiensis* as live bait.—Marine Biology 153:1127–1140.
- Popov, V. K. 1927. [Rhizocephala and Bopyridae of the Bay of Sevastopol].—Trudy Sevastopol'skoy Biologicheskoy Stantsii Akademii Nauk SSSR 1:1–26.
- Rafinesque-Schmaltz, C. S. 1815. Analyse de la nature ou tableau de l'univers et des corps organisés.—Palermo, 224.
- Restivo, F. 1970. A new species of *Pseudione* (*Pseudione reverberii*) a parasite of *Callianassa truncata*.—Pubblicazioni della Stazione Zoológica di Napoli 38(2):305–315.
- Richardson, H. 1899. Key to the isopods of the Pacific coast of North America, with descriptions of twenty-two new species.—Proceedings of the United States National Museum 21(1175):865–869.
- . 1900. Results of the Branner-Agassiz Expedition to Brazil. II. The isopod Crustacea.—Proceedings of the Washington Academy of Sciences 2:157–159.
- . 1904. Contributions to the natural history of the Isopoda.—Proceedings of the United States National Museum 27:1–89.
- . 1905. A monograph on the Isopods of North America.—Bulletin of the United States National Museum 54:1–727.
- Saito, N., & K. Kinoshita. 2004. Prevalence of the bopyrid isopod *Ione cornuta* (Crustacea: Isopoda: Epicaridea) on the ghost shrimp *Nihonotrypaea japonica* (Crustacea: Decapoda: Thalassinidea) on a tidal flat of Shinhama Lagoon, northern Tokyo Bay.—Japanese Journal of Benthology 59:1–7.
- , G. Itani, & N. Nunomura. 2000. A preliminary checklist of isopod crustaceans of Japan.—Bulletin of the Toyama Science Museum 23:11–107.
- Sakai, K. 1999. Synopsis of the family Callianassidae, with keys to subfamilies, genera and species, and the description of new taxa (Crustacea: Decapoda: Thalassinidea).—Zoologische Verhandelingen (Leiden) 326:1–152.
- . 2001. A review of the common Japanese callianassid species, *Callianassa japonica* and *C. petalura* (Decapoda, Thalassinidea).—Crustaceana 74:937–949.
- . 2005. Callianassoidea of the world (Decapoda, Thalassinidea).—Crustaceana Monographs 4:1–200.
- Salazar-Vallejo, S. I., & A. Leija-Tristan. 1989. *Progebiophilus bruscai* n. sp., a new bopyrid isopod parasitic on the mud shrimp, *Upogebia dawsoni* Williams (Thalassinoidea), from the Gulf of California.—Cahiers de Biologie Marine 30:423–432.
- Shiino, S. M. 1937. Bopyrids from Tanabe Bay. IV. Memoirs of the College of Science, Kyoto Imperial University.—Series B 12:479–493.
- . 1939a. Bopyrids from Kyūsū and Ryūkyū.—Records of Oceanographic Works in Japan 10:79–99.
- . 1939b. Bopyrids from Tanabe Bay. V.—Annotationes Zoologicae Japonenses 18: 11–16.
- . 1952. Phylogeny of the family Bopyridae.—Annual Report, Prefectural University of Mie, sect. 2, Nat. Sci 1:33–56.
- . 1958. Note on the bopyrid fauna of Japan.—Report of Faculty of Fisheries, Prefectural University of Mie 3(1):29–74.
- . 1964. Results of Amami Expedition. 5. Bopyridae.—Report of the Faculty of Fisheries, Prefectural University of Mie 5:237–242.
- . 1972. The Epicaridea (list of species) from Japan.—Kansai Shizenkagaku 24:7–10.
- Tamaki, A. 2003. A rebuttal to Sakai (2001): “A review of the common Japanese callianassid species, *Callianassa japonica* and *C. petalura* (Decapoda, Thalassinidea).”—Crustaceana 76:115–124.
- , & B. Ingole. 1993. Distribution of juvenile and adult ghost shrimps, *Callianassa japonica* Ortmann (Thalassinidea), on an intertidal sandflat: intraspecific facilitation as a possible pattern-generating factor.—Journal of Crustacean Biology 13:175–183.
- , & S. Miyabe. 1999. Larval abundance patterns for three species of *Nihonotrypaea* (Decapoda: Thalassinidea: Callianassidae) along an estuary-to-open-sea-gradient in western Kyushu, Japan.—Journal of Crustacean Biology 20 (Special Number 2):182–191.
- , & K. Suzukawa. 1991. Co-occurrence of the cirolanid isopod *Eurydice nipponica* Bruce and Jones and the ghost shrimp *Callianassa japonica* Ortmann on an intertidal sand flat.—Ecological Research 6:87–99.
- , & H. Ueno. 1998. Burrow morphology of two callianassid shrimps, *Callianassa japonica* Ortmann, 1891 and *Callianassa* sp. (= *Callianassa*).

- nassa japonica*: De Man, 1928) (Decapoda: Thalassinidea).—Crustacean Research 27: 28–39.
- , K. Ikebe, K. Muramatsu, & B. Ingole. 1992a. Utilization of adult burrows by juveniles of the ghost shrimp, *Callianassa japonica* Ortmann: evidence from resin casts of burrows.—Researches on Crustacea 21:113–120.
- , S. Miyamoto, T. Yamakazi, & S. Nojima. 1992b. Abundance pattern of the ghost shrimp *Callianassa japonica* Ortmann (Thalassinidea) and the snake eel *Pisodonophis cancrivorus* (Richardson) (Pisces, Ophichthidae) and their possible interaction on an intertidal sand flat.—Benthos Research 43:11–22.
- , H. Tanoue, J. Itoh, & Y. Fukuda. 1996. Brooding and larval developmental periods of the callianassid ghost shrimp, *Callianassa japonica* (Decapoda: Thalassinidea).—Journal of the Marine Biological Association of the United Kingdom 76:675–689.
- , B. Ingole, K. Ikebe, K. Muramatsu, M. Taka, & M. Tanaka. 1997. Life history of the ghost shrimp *Callianassa japonica* Ortmann (Decapoda: Thalassinidea), on an intertidal sandflat in western Kyushu, Japan.—Journal of Experimental Marine Biology and Ecology 210:223–250.
- , J.-I. Itoh, & K. Kubo. 1999. Distributions of three species of *Nihonotrypaea* (Decapoda: Thalassinidea: Callianassidae) in intertidal habitats along an estuary to open-sea gradient in western Kyushu, Japan.—Crustacean Research 28:37–51.
- Van Name, W. G. 1920. Isopods collected by the American Museum Congo Expedition.—Bulletin of the American Museum of Natural History 43:42–108.
- Wardiatno, Y., & A. Tamaki. 2001. Bivariate discriminant analysis for the identification of *Nihonotrypaea japonica* and *N. hardmani* (Decapoda: Thalassinidea: Callianassidae).—Journal of Crustacean Biology 21:1042–1048.

Associate Editor: Christopher B. Boyko.