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Axiidea (Crustacea: Callianassidae, Callichiridae and Ctenochelidae) and Gebiidea (Upogebiidae) collected during the Comprehensive Marine Biodiversity Survey of Singapore

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Abstract. Sampling during the Comprehensive Marine Biodiversity Survey of Singapore yielded 102 specimens of Axiidea and Gebiidea belonging to 12 species in seven genera. Axiidea were represented by one to two specimens each of *Gourretia sinica* Liu & Liu, 2010 (Ctenochelidae), *Aquaballianassa brevirostris* (Sakai, 2002) (Callianassidae), *Michaelcallianassa sinica* Liu & Liu, 2009 and *Karumballichirus karumba* (Poore & Griffin, 1979) (Callichiridae). The Gebiidea are represented by only the family Upogebiidae with six species from three genera, the most common being *Upogebia hexaceras* (Ortmann, 1894) with 34 specimens, followed by *U. ancylodactyla* de Man, 1905 with 25 specimens, *U. darwinii* (Miers, 1884) with 11 specimens, and *U. carinicauda* Stimpson, 1860 with nine specimens. The genus *Paragebicula* Sakai, 2006 is placed in synonymy of *Neogebicula* Sakai, 1982, and the latter genus is redefined. Four specimens belong to a new species, *U. singaporensis*, new species, which differs from its morphologically most similar congener *U. srilankaensis* Sakai, 2006, by the protruding lateral ridges of the carapace, the presence of a ventral spine on the first article of the antennal peduncle, and the cheliped with a dorsal median spine on the merus and a fully developed fixed finger. Five specimens represent a further species new to science, *Neogebicula johorensis*, new species, which differs from the very similar *N. leptomorpha* (Sakai, 2006) by having only one postocular spine, the presence of a ventral spine on the proximal article of the antennular peduncle, the third and fourth articles of the antennal peduncle with ventral spine each, and the posterior margin of the telson with a small median spine. *Wolffogebia phuketensis* Sakai, 1982 and *W. inermis* Sakai, 1982 are represented by two and one specimens, respectively. Five of these species are recorded from Singapore for the first time.

Key words. Axiidea, Callianassidae, Ctenochelidae, Gebiidea, Upogebiidae, taxonomy, new species, Southeast Asia

INTRODUCTION

The Comprehensive Marine Biodiversity Survey of Singapore (CMBS), organised by the National University of Singapore (NUS), Tropical Marine Science Institute (TMSI) of NUS, and National Parks Board of Singapore, was carried out in three overlapping phases between 2010 and 2015 to obtain specimens from as many marine habitats as possible (Tan et al., 2015, 2016). During this survey, numerous decapod crustaceans, including ghost- and mud-shrimps (infraorders Axiidea and Gebiidea) were collected at various shallow- and deep-water stations. Examination of the collected material has revealed that it includes 12 species in seven genera from both infraorders. The present report deals with these species, including descriptions of two new species, one each in the upogebiid genera *Upogebia* Leach, 1814 and *Neogebicula* Sakai, 1982.

MATERIAL AND METHODS

CMBS collection data is typically given as CMBS station (IT – intertidal, SW – shallow-water, DW – deep-water, SD – scuba diving, SB – coral rubble brushing, TB – beam trawl, and DR – rectangular dredge); for dredge and trawl stations, a position relative to the nearest land area (coast, island, etc.) is provided; field collection numbers are listed at the end for each specimen between parentheses. Collectors of the material are listed under "coll."; CMBS stations are abbreviated as "sta."; ovigerous females are indicated as "ov.".

Material is deposited in the Zoological Reference Collection, Lee Kong Chian Natural History Museum (former Raffles Museum of Biodiversity Research), National University of Singapore (ZRC), and the Naturhistorisches Museum Wien, Vienna, Austria (NHMW).

All drawings were made by PCD using a camera lucida mounted on a stereomicroscope, digitised and then inked and

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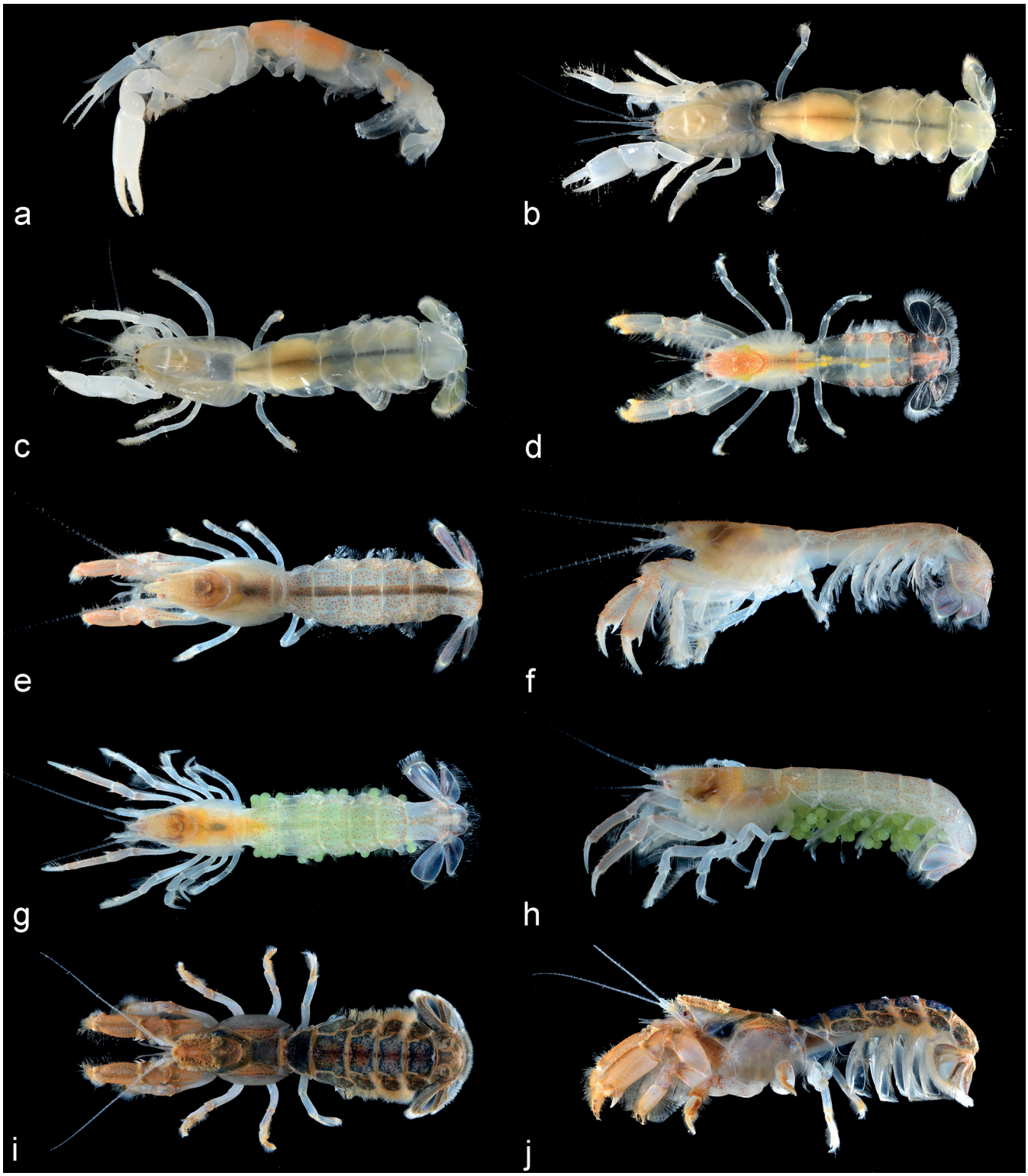

Fig. 1. Specimens, habitus (dorsal and/or ventral views), showing colouration in life: a, *Gourretia sinica* Liu & Liu, 2010, female (23/5.3) (ZRC 2017.0947); b, *Karumballichirus karumba* (Poore & Griffin, 1979), female (32/7.6) (ZRC 2018.0526); c, *Aqaballianassa brevirostris* Sakai, 2002, ovigerous female (28/5.6) (ZRC 2017.0948); d, *Upogebia singaporensis*, new species, female holotype (16/5.4) (ZRC 2017.0951); e, f, *Neogebicula johorensis*, new species, male holotype (18/5.6) (ZRC 2017.0956); g, h, same, ovigerous female paratype (21/6.3) (ZRC 2017.0955); i, j, *Wolffogebia phuketensis* Sakai, 1982, male (37/10.3) (NHMW 26036). Not to scale. [Photographs by AA].

composed in Adobe Illustrator (Coleman, 2003). Photographs of living specimens were taken by AA using a Nikon D90 digital camera set-up.

Size (in mm) is given as total length (TL) and carapace length (CL) in the form (TL/CL). Other abbreviations used in the text include: NHMUK, Natural History Museum, London, UK; TMSI, Tropical Marine Science Institute, NUS, Singapore; SMF, Senckenberg-Museum, Frankfurt, Germany; Mxp1–3, first to third maxillipeds; coll., collector. Terminology for the orientation of the appendages follows Poore (1997), where "upper" is used to describe the extensor (or anatomically anterior/dorsal) margin and "lower" the flexor (or posterior / ventral) margin. Terminology of arthrobranchs follows Ngoc-Ho (1981).

Only restricted synonymies are provided, mainly referring to the original description and major revisions with more extensive synonymy listings. Species of *Upogebia* are listed in chronological order of their description.

TAXONOMY

Axiidea de Saint Laurent, 1979

Ctenochelidae Manning & Felder, 1991

Gourretia de Saint Laurent, 1973

Gourretia sinica Liu & Liu, 2010
(Figs. 1a, 3–5)

Gourretia sinica Liu & Liu, 2010a: 750, figs. 5–10; — Poore et al., 2019: table 1; — Robles et al., 2020: suppl. tables 1, 2.
Paragourretia zarenkovi Sakai, 2010a: 1457, fig. 8; new synonym.
Ruiyuliugourretia sinica. — Sakai, 2017: 1132, 1133, fig. 3.
G.[*ourretia*] *zarenkovi*. — Sakai, 2017: 1129.

CMBS material. 1 female (23/5.3) (ZRC 2017.0947) [DNA voucher GenBank MN237905, MN237707, MN238386, MN238112], sta. TB096, Straits of Singapore near E Bunkering A, 1°18.140′N 104°04.221′E, clay, beam trawl, 22.4–25.1 m, coll. B Richer de Forges et al., 29 May 2013 (SS-3222); 1 female (18/4.5) (ZRC 2018.0560), sta. TB120, Straits of Singapore, NE of Sentosa Cove, MPA grid 5115, beam trawl, 7.2–18.0 m, coll. TMSI team, 21 March 2013 (5115TB1-120).

Description. See Liu & Liu (2010a).

Distribution. Beibu Gulf, South China Sea (type locality, Liu & Liu, 2010a), Tonkin Gulf, Vietnam (Sakai, 2010a), Singapore (this study).

Habitat. Muddy sand at depth of 27–50 m (Liu & Liu, 2010a); clay at depth of 7–25 m (this study).

Remarks. Four Indo-Pacific species of *Gourretia* possess a strong curved spine or projection on the ventro-proximal surface of the third maxilliped ischium, viz. *G. manihinae* Sakai, 1984b, *G. sinica* Liu & Liu, 2010a, *G. zarenkovi* (Sakai, 2010a) and *G. qeshmensis* Sepahvand, Pouyani & Momtazi, 2016. This character was variable in the present material, with one female (ZRC 2017.0947) bearing this spine on only one side (Fig. 3a, b). The second female (ZRC 2018.0560) lacks one of the third maxillipeds, but the attached one does have this spine, suggesting that it may be the more typical condition in the species. The CMBS material is tentatively assigned to *G. sinica* because of the strong spines on the cutting edges of the second pereopod (Figs. 4g, 5e) (lacking in *G. manihinae*). However, it differs from both *G. manihinae* and *G. sinica* by the presence of a setal row on the anterior carapace (Fig. 3a) and a spiniform seta on the propodus of the third pereopod (Fig. 3g). The species is recorded from Singapore for the first time.

There is apparently no difference between *G. sinica* and *G. zarenkovi* except for the male first pleopod, consisting of 2 or 4 articles in the former taxon, according to Liu & Liu (2010a) and Sakai (2017), respectively, vs. 3 articles in the latter taxon (Sakai, 2010a). A male first pleopod consisting of 3 or 4 articles is certainly an artefact as K. Sakai often misinterpreted folds as articulations (see Felder & Dworschak, 2015; Poore & Dworschak, 2017). Since *G. sinica* has priority by two months (14 October 2010 vs. 13 December 2010), *G. zarenkovi* is herein synonymised with the former taxon.

Callichiridae Manning & Felder, 1991

Michaelcallianassa Sakai, 2002

Michaelcallianassa sinica Liu & Liu, 2009
(Fig. 6)

Michaelcallianassa sinica Liu & Liu, 2009: 40, figs. 1–5; — Poore et al., 2019: table 1; — Robles et al., 2020: suppl. tables 1, 2.

CMBS material. 1 ov. female (24/5.7) (ZRC 2017.0957) [DNA voucher GenBank MN238003, MN237806, MN238459, MN238241], sta. DR235, east of Pulau Tekong, MPA grid 0524, sand-mud, rectangular dredge, 13.1–14.7 m, coll. TMSI team, 11 May 2013 (SEA-1943).

Comparative material. *Michaelcallianassa indica* Sakai, 2002: 1 male, 1 female (NHMW 24989), Iran, Persian Gulf, Bandar-Khamir, coll. V. Sepahvand, 2009.

Description. See Liu & Liu (2009).

Distribution. Beibu Gulf, South-China Sea (Liu & Liu, 2009), Singapore (this study).

Habitat. "Sediment" at depth range of 31–50 m (Liu & Liu, 2009); sand-mud bottom, 13–15 m (this study).

Remarks. The present specimen represents a new record of *Mi. sinica* for Singapore.

Fig. 2. Specimens, habitus (dorsal and ventral views), showing colouration in life: a, *Upogebia carinicauda* (Stimpson, 1860), male (21/6.1) (NHMW 26035); b, same, male (23/6.6) (NHMW 26034); c, d, *U. darwinii* (Miers, 1884), ovigerous female (44/12.6) (NHMW 26038); e, *U. hexaceras* (Ortmann, 1894), male (23/7.0) (ZRC 2018.0557); f, same, ovigerous female (22/6.1) (NHMW 26042); g, *U. ancylodactyla* de Man, 1905, female (40/11.3) (ZRC 2018.0551); h, same, male (29/8.4) (ZRC 2018.0549). Not to scale. [Photographs by AA].

Karumballichirus Poore, Dworschak, Robles, Mantelatto & Felder, 2019

Karumballichirus karumba (Poore & Griffin, 1979)
(Fig. 1b)

Callianassa (*Callichirus*) *maxima* — Kemp, 1915: 252, pl. 13, figs. 1–5 [not *Callianassa maxima* A. Milne-Edwards, 1870].
Callianassa karumba Poore & Griffin, 1979: 266, figs. 30, 31.
Neocallichirus karumba. — Sakai, 1999: 101; — Sakai, 2005: 180; — Dworschak, 2008: 76, figs. 1–6 (includes extended synonymy); — Sakai, 2011a: 459; — Sakai & Türkay, 2014: 181 (key).
Neocallichirus kempi Sakai, 1999: 101, fig. 24a–e; — Sakai, 2005: 180; — Sakai, 2011a: 459 — Sakai & Türkay, 2014: 180 (list).
Karumballichirus karumba. — Poore et al., 2019: table 1; — Robles et al., 2020: suppl. tables 1, 2.
Not *N*[*eocallichirus*] *kempi*. — Sakai & Türkay, 2014: 181 (key) [=*Neocallichirus thalesapensis* Sakai & Lheknim, 2014].

CMBS material. 1 female (32/7.6) (ZRC 2018.0526), sta. SW117, St John's Island, DRTech, north lagoon, 1°13.116′N 103°51.079′E, silt/sand, in burrows, yabby pump, 0–0.5 m, coll. PKL Ng, JC Mendoza, R Tan, 31 May 2013 (SS-3269); 1 female (44/9.6) (ZRC 2018.0525), sta. YB188, same locality, coll. A Anker, 6 June 2013 (SS-4528).

Description. See Dworschak (2008).

Distribution. Indo-West Pacific from India to Thailand and eastern Australia (Dworschak, 2008).

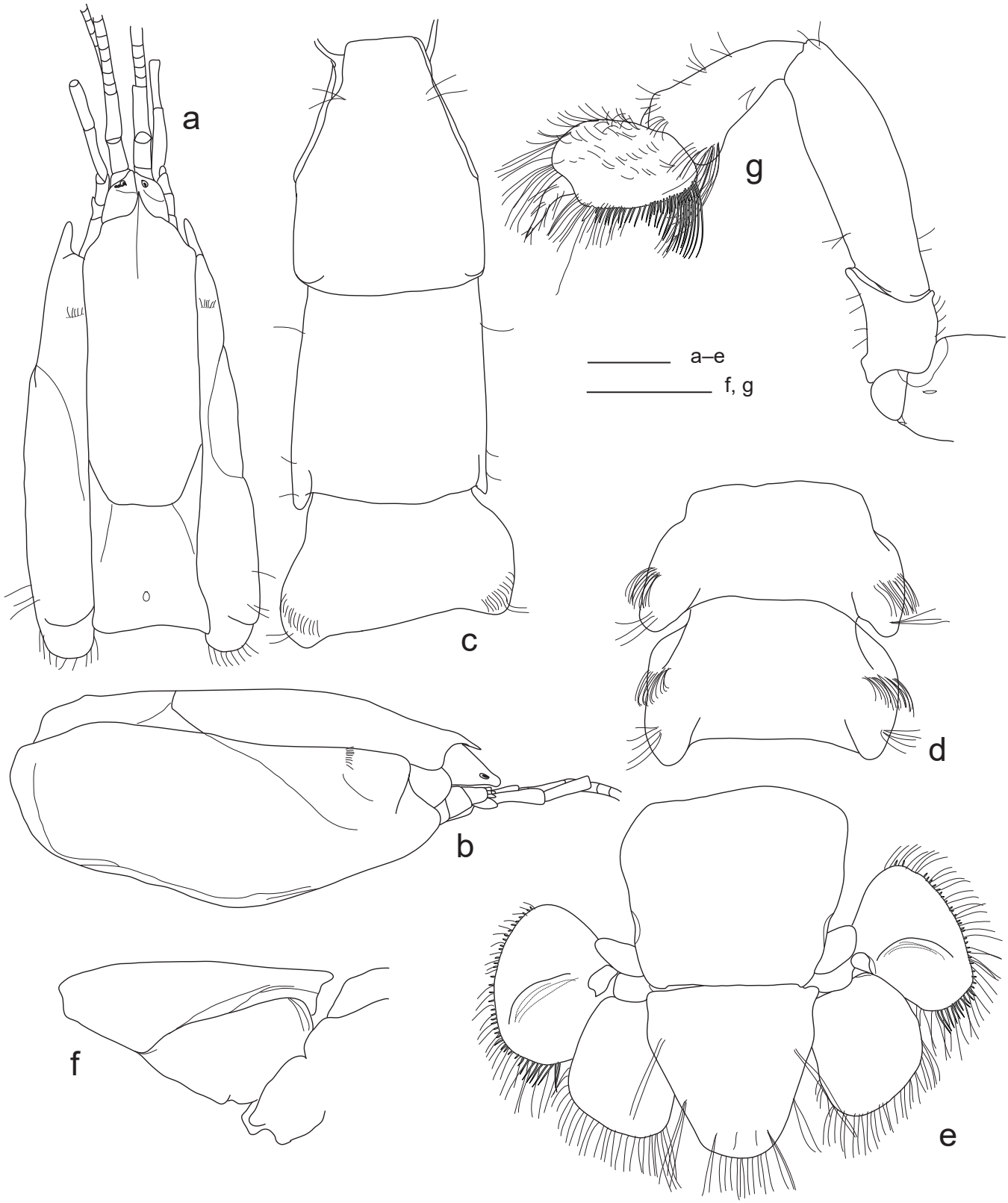

Fig. 3. *Gourretia sinica* Liu & Liu, 2010, female (23/5.3) (ZRC 2017.0947); a, carapace, dorsal view; b, same, lateral view; c, pleomeres 1–3, dorsal view; d, pleomeres 4, 5; e, pleomere 6, telson and uropods, dorsal view; f, pleomere 1, lateral view; g, second pereopod, lateral view. Scale bar = 1 mm. [Illustrations by PCD].

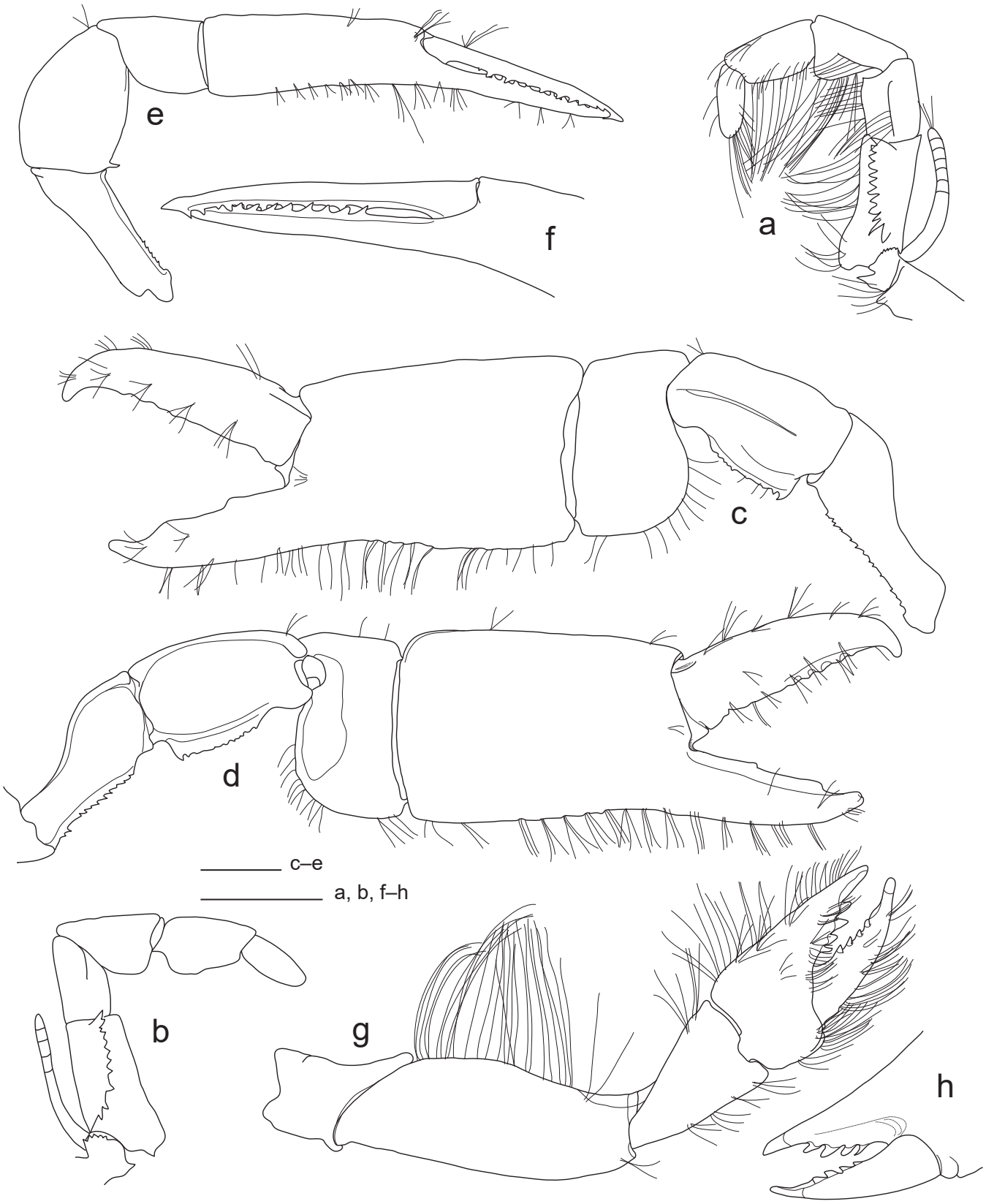

Fig. 4. *Gourretia sinica* Liu & Liu, 2010, female (23/5.3) (ZRC 2017.0947); a, right Mxp3, mesial view; b, same, left side (setae omitted); major cheliped, lateral (c) and mesial (d) view; e, minor cheliped, lateral view; f, same, fingers, mesial view; g, second pereopod, lateral view; h, same, fingers, mesial view (setae omitted). Scale bar = 1 mm. [Illustrations by PCD].

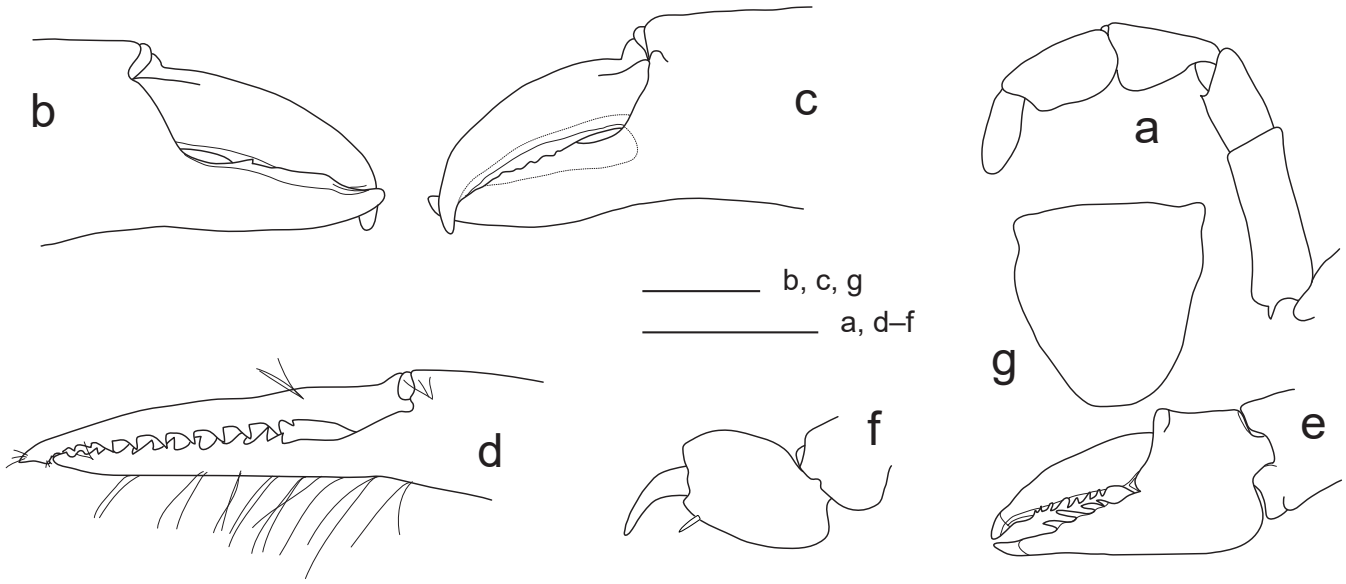

Fig. 5. *Gourretia sinica* Liu & Liu, 2010, female (18/7.5) (ZRC 2018.0560); a, left Mxp3, lateral view; major cheliped fingers, lateral (b) and mesial (c) view; d, minor cheliped fingers, lateral view; e, distal articles of pereopod 2, lateral view; f, distal articles of third pereopod, lateral view; g, telson, dorsal view. Scale bar = 1 mm. [Illustrations by PCD].

Habitat. Firm sand bottoms near mangroves (Dworschak, 2008); silt-sand bottoms in the intertidal zone or very shallow water, 0–0.5 m (present study).

Remarks. Dworschak (2008) synonymised *Neocallichirus kempi* with *N. karumba*. Sakai (2011a) considered both again as different species, however, his arguments are not convincing. The shape of the male first and second pleopods are subject to maturity as outlined by Dworschak (2008), whereas the differences in the telson shape are not obvious, as this character is quite variable (see Kemp, 1915: fig. 5; Poore & Griffin, 1979: fig. 30c; Sakai, 1999: fig. 24b; Dworschak, 2008: figs. 1a, 3a). A recent molecular study, however, indicates that two species are involved in what is identifiable as *K. karumba*, one from Singapore and a second one from Taiwan (Robles et al., 2020), thus requiring further study.

Callianassidae Dana, 1852

Aqaballianassa Poore, Dworschak, Robles, Mantelatto & Felder, 2019

Aqaballianassa brevirostris (Sakai, 2002)
(Fig. 1c)

Callianassa brevirostris Sakai, 2002: 514, figs. 30A–E, 31A–I.
Trypaea brevirostris. — Sakai, 2011a: 394.
Aquaballianassa brevirostris. — Poore et al., 2019: table 1; — Robles et al., 2020: suppl. tables 1, 2.

CMBS material. 1 ov. female (28/5.6) (ZRC 2017.0948) [DNA voucher GenBank MN237904, MN237706, MN238111], sta. SW117, St John's Island, DRTech, north lagoon, 1°13.116′N 103°51.079′E, silt/sand, in burrows, yabby pump, 0–0.5 m, coll. PKL Ng, JC Mendoza, R Tan, 31 May 2013 (SS-3267).

Description. See Sakai (2002).

Distribution. Andaman Sea (Sakai, 2002), Singapore (this study).

Habitat. Sand or mud with shell fragments at depths of 17 to 73 m (Sakai, 2002); sand/silt in the intertidal or very shallow water, 0–0.5 m (this study).

Remarks. The present ovigerous female from St John's Island represents a new record of *Aqaballianassa brevirostris* for Singapore.

Gebiidea de Saint Laurent, 1979

Upogebiidae Borradaile, 1903

Upogebia Leach, 1814

Upogebia carinicauda (Stimpson, 1860)
(Figs. 2a, b, 7)

Gebia carinicauda Stimpson, 1860: 23. — Miers, 1884: 280; — de Man, 1888: 256 (part).
Gebia barbata Strahl, 1862: 1062 (part). — Ortmann, 1891: 54, fig. 8; 1894: 22.
Gebiopsis intermedia de Man, 1888: 256 (part), pl. 16, figs. 6–8.
Upogebia (*Upogebia*) *carinicauda* var. *gracilipes* de Man, 1926: 343; — 1928: 44 (key), 65.
Upogebia (*Upogebia*) *carinicauda*. — de Man, 1928: 22 (list), 44 (key), 60, pl. 3, fig. 6–6c, pl. 4, fig. 6d–n; — Sakai, 1982: 35, figs. 6d, 8a, pls. A5, C5–6.
Upogebia (*Calliadne*) *darwini*. — Poore & Griffin, 1979: 292 (part), fig. 46 [not *U. darwinii* (Miers, 1884)].
Upogebia darwini. — Ngoc-Ho, 1977 (part): 444, fig. 4a–e [not *U. darwinii* (Miers, 1884)].
Upogebia carinicauda. — Sakai & Takeda, 1995: 204, figs. 1–3; — Sakai, 2006: 98; — Ngoc-Ho, 1979: 153, fig. 3c, d; —

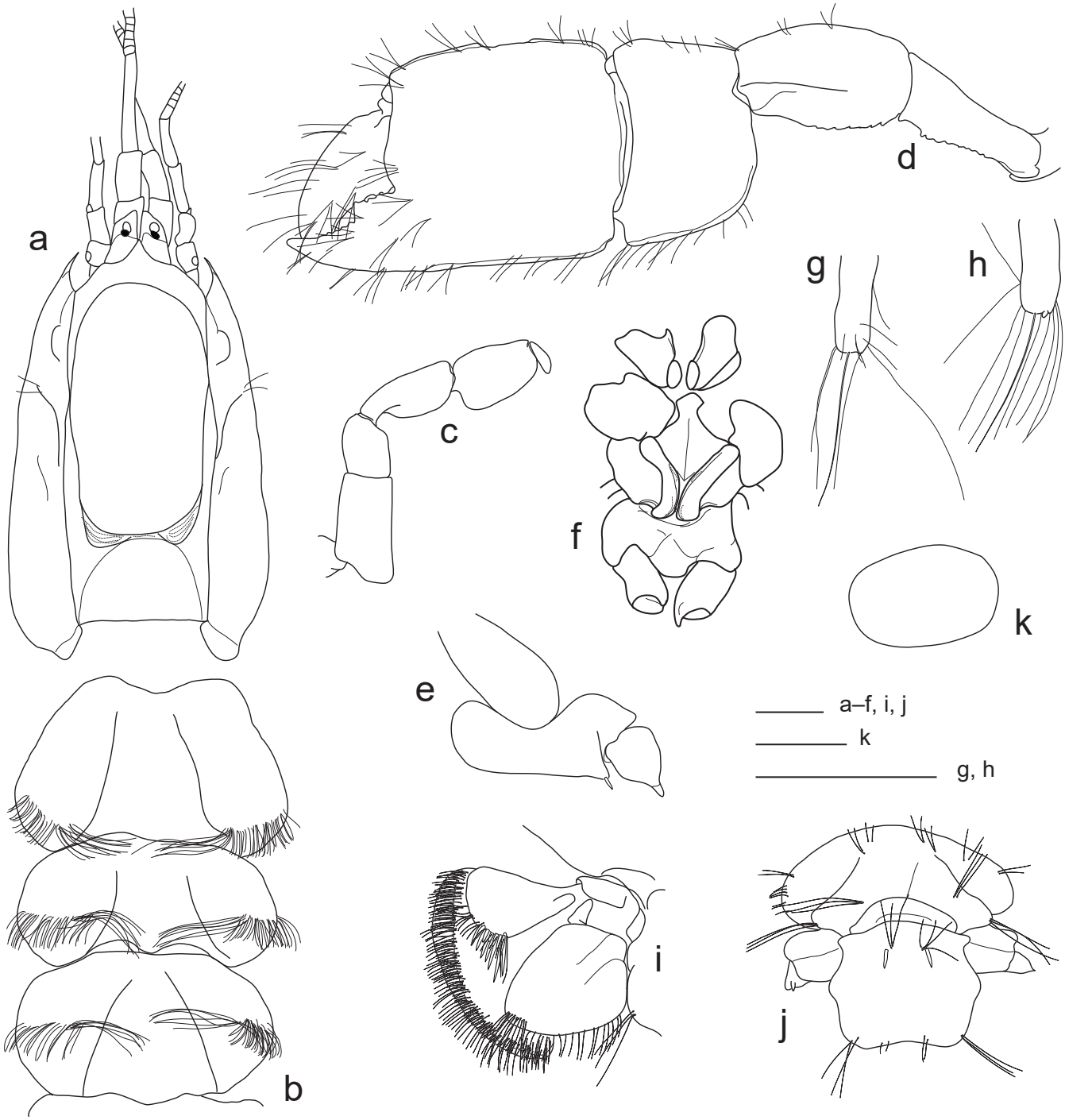

Fig. 6. *Michaelcallianassa sinica* Liu & Liu, 2009, ovigerous female (24.2/5.7) (ZRC 2017.0957); a, carapace, dorsal view; b, pleomeres 3–5, dorsal view; c, right Mxp3, lateral view (in situ, setae omitted); d, major cheliped, lateral view; e, distal articles of third pereopod, lateral view (setae omitted); f, sternites 7, 8, coxae 3–5, ventral view; g, right second pleopod, posterior view; h, left second pleopod, posterior view; i, left uropod, dorsal view; j, telson and pleomere 6, posterior view; k, embryo. Scale bar = 1 mm. [Illustrations by PCD].

Ngoc-Ho, 2008: 146, fig. 8; — Purohit & Vachhrajani, 2017: 409, fig. 1G; — Al-Kandari et al., 2020: 265, fig. 10.

Upogebia (*Upogebia*) *kempi* Sankolli, 1972: 671, figs. 9, 10; — Sakai & Türkay, 2014: 148 (list), 150 (key).

Upogebia foresti Ngoc-Ho, 1989: 870, fig. 3; — Sakai, 2006: 122; — Sakai & Türkay, 2014: 132 (list), 148 (list), 150 (key), 155.

CMBS material. 1 male (19/5.7) (ZRC 2018.0548), sta. DR031, Straits of Singapore outside Marina Bay, 1°16.415′N 103°52.838′E, mud, gravel, rectangular dredge, 19.4–19.6 m, leg. B Richer de Forges et al., 23 May 2013 (SS-1578); 1 ov. female (21/6.1) (ZRC 2018.0563), 1 male (14/4.0) (ZRC 2018.0568), sta. SB249, off Small Sister I., scuba diving, hand collection, <10 m, coll. J Teo, 26 December 2013 (SUB-0046, 0047); 1 male (21/6.3) (NHMW 26035), sta. SW001, Pulau Ubin, OBS Camp 1, 1°25′15.77″N 103°55′57.00″E, near brackish stream in secondary forest, low tide, coll. PKL Ng, JC Mendoza, HH Tan et al., 16 October 2012 (JS-0211); 1 male (23/6.6) (NHMW 26034), sta. SW032, Pulau Ubin, N side of Chek Jawa, 1°24′44.5″N 103°59′43.2″E, sand and mud flat, beach seine, 0–1 m, coll. R Tan, B Ludt et al., 19 October 2012 (JS-1386); 1 ov. female

(22/6.0) (ZRC 2018.0539), sta. SB146, W of Pulau Hantu, coral rubble brushing, 5–7 m, coll. HH Tan, S De Grave et al., 2 June 2013; 1 ov. female (17/4.7) (ZRC 2018.0537), 1 female (22/5.9), 1 male (15/4.4) ZRC 2018.0553, sta. TB172, Straits of Singapore near Kusu Island, 1°12.180′N 103°52.125′E, consolidated marine clay, 94.5–100 m, coll. B Richer de Forges et al., 5 June 2013 (SS-4521, SS-4522).

Comparative material. 3 males (CL 6.6–12.0) 2 females (CL 11.4–12.0) (NHMW 19590), Australia, Queensland, Mossman, Cooya Beach, muddy reef at low tide, coll. P. Dworschak & A. Anker, 19–20 July 2001; 1 female (21/6.1) (NHMW 26544), 1 female (20/6.1) (NHMW 26545), 1 female (18/5.3) (NHMW 26546), 1 male (17/5.3) (NHMW 26547), Indonesia, Lombok, coll. A. Anker, DL Rahayu et al., May 2014.

Diagnosis. Lateral ridges of gastric region projecting forward. Linea thalassinica (with interruption) reaching to posterior end of carapace. Rostrum longer than eyestalks, with 4 frontal teeth. Ocular spine present. Antennal peduncle longer than antennular peduncle. First pereopod usually subchelate; ischium with strong lower spine; merus with lower spines decreasing in size distally, with proximal upper spine; carpus with strong upper, moderate median and small lower spine mesially; propodus with spines on lower mesial face and proximal spine on upper border; dactylus with small tubercles proximally on mesial face, tip corneous. Second pereopod merus with proximal upper spine; propodus 1.5–1.9 times as long as high. Third pereopod merus with lower spines proximally. Pleomere 6 without lateral spines; posterior border smooth. Uropodal endopod acutely triangular. Telson 0.8–0.9 times as long as maximal width, with smooth inverted U-shaped carina. First maxilliped with epipod. Third maxilliped without epipod; exopod flagellate. Arthrobranchs of type C.

Distribution. Distributed in the Indo-Pacific, from the Red Sea to northern Australia (Sakai, 2006).

Habitat. In sand, mud, coral rubble and consolidated clay from the intertidal to 100 m depth (this study).

Remarks. The type material of *U. carinicauda* from Hong Kong is no longer extant, most probably destroyed during the Great Chicago Fire of 1871 (Evans, 1967). Stimpson's (1860) description is rather short and points to the following characters: 1) the ventral margin of the palm of the first pereopod bears a spine at the base of the fixed finger; 2) the cutting edge of the fixed finger is denticulate; and 3) the dorsal surface of the telson has a sharply elevated transverse carina near the proximal margin. Sakai (1982) considered this sufficient to differentiate it from other species known from southern China at that time. Subsequently, the species has been reported by Miers (1884) from Thursday Island, northern Australia. Part of the type material of *U. barbata* (Strahl, 1862) belongs to *U. carinicauda* as do the subsequent records of *U. barbata* by Ortmann (1891, 1894) (see Sakai, 1982).

De Man (1928) observed some variation in 18 specimens collected during the Siboga Expedition: 1) the ocular spine is sometimes very small; 2) the spine on the first pereopod palm near the base of dactylus is sometimes absent; and 3) the dactylus is only slightly longer than the fixed finger, especially in small specimens.

Ngoc-Ho (1979) compared in detail the Indian species *U. kempi* Sankolli, 1972 with *U. carinicauda* and synonymised the former with the latter. This synonymisation was followed by Sakai (1982) and Sakai & Takeda (1995). Later, Sakai (2006) considered *U. kempi* as a valid species, with *U. foresti* Ngoc-Ho, 1989 as its junior synonym, because both show a spine on the upper border of the second pereopod merus, which according to the author was absent in *U. carinicauda*. Later, *U. foresti* was again considered a valid species by Sakai & Türkay (2014). De Man (1928: 65), Ngoc-Ho (1977: fig. 4e, as *U. darwini*), Poore & Griffin (1979: fig. 46f, as *U. darwinii*) and Ngoc-Ho (2008: fig. 8F), however, indicated such a spine on the second pereopod merus for *U. carinicauda* (see comments in Ngoc-Ho, 2008: 159). In addition, *U. rupicola* Komai, 2005 has been synonymised with *U. carinicauda* by Sakai (2006), but considered as valid by Ngoc-Ho (2008) and Sakai & Türkay (2014). Another species, different from, but similar to *U. carinicauda*, is *U. saintlaurentae* Ngoc-Ho, 2008; however, two of the three characters given to discriminate the two species from each other are quite variable in the former.

The material of the CMBS attributed here to *U. carinicauda* show most of the above-mentioned variations. Consistent characters are: 1) the rostrum with four dorsal spines; 2) the prominent smooth carina on the telson; 3) the presence of a spine on the upper border of first and second pereopod merus; 4) the linea thalassinica reaching to the end of the carapace; 5) the fixed finger with a serrated cutting edge proximally; and 6) the first pereopod dactylus with a corneous tip.

On the other hand, the following characters are variable: 1) the development of the ocular spine (present in 6 of the 9 specimens); 2) the presence of either one or two spines on the mesial face of the cheliped propodus (4 of 9 specimens); 3) the chelipeds clearly subchelate with the dactylus twice as long as the fixed finger (5 specimens), barely subchelate with the dactylus only slightly longer than the fixed finger (2 specimens), or chelate with the fingers almost of the same length (2 specimens); 4) the upper border of the cheliped propodus serrated (3 specimens) or smooth; and 5) the lower border of the third pereopod with (5 specimens) or without (4 specimens) spines.

The basal antennular article with a ventral spine was figured by de Man (1928: pl. 3 fig. 6c), but either not mentioned in subsequent descriptions (e.g., Sakai, 1982; Ngoc-Ho, 2008) or described as unarmed (Sakai & Takeda, 1995: 206). Ngoc-Ho (2008) mentioned a ventral spine on the antennal peduncle. Most specimens from Singapore lack spines on the antennular and antennal peduncle, except for two specimens with the more chelate first pereopod, which possess a ventral spine on the antennular peduncle. The specimens from Australia

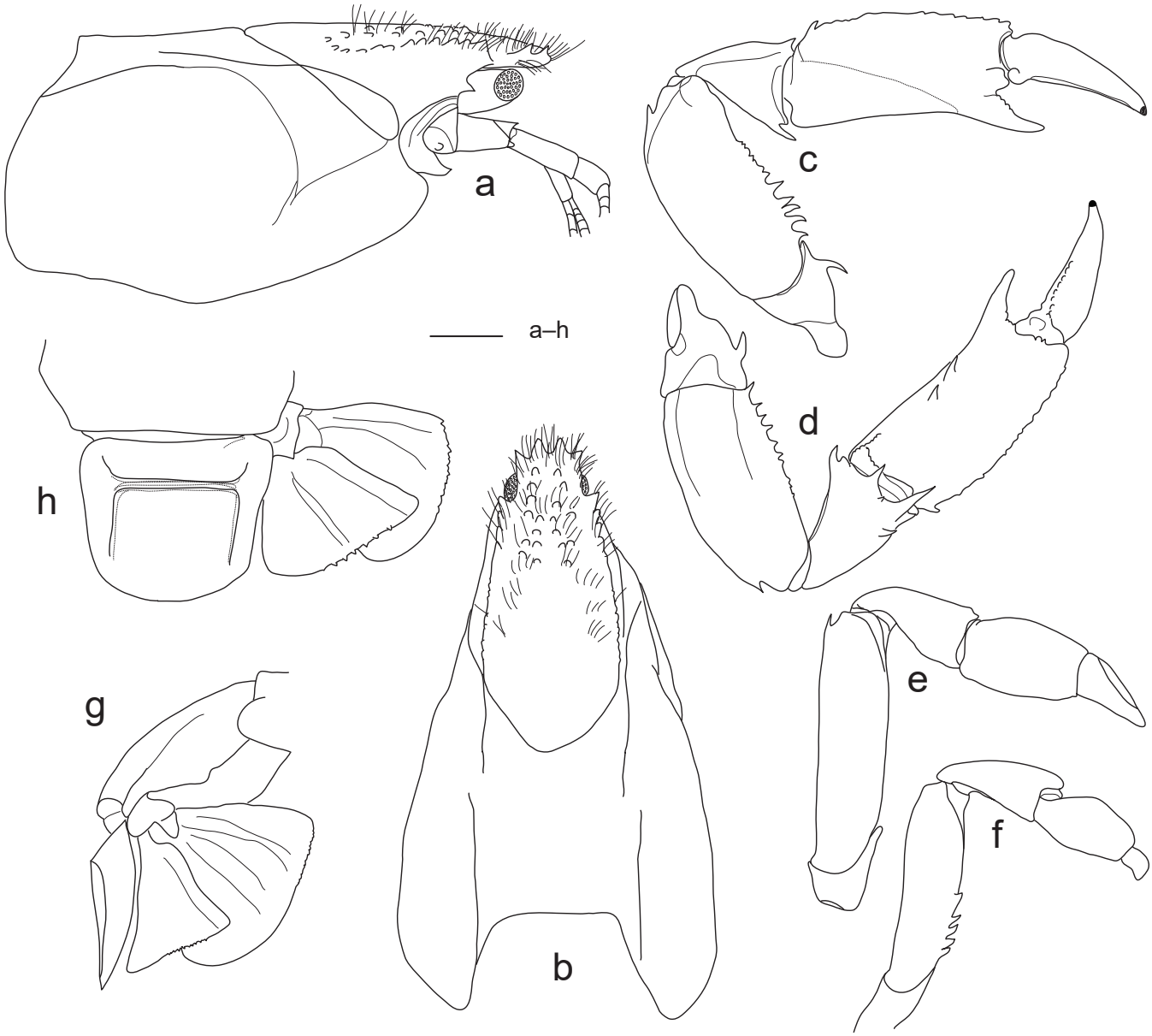

Fig. 7. *Upogebia carinicauda* (Stimpson, 1860), male (23/6.6) (NHMW 26034); a, carapace, lateral view; b, same, dorsal view; c, first pereopod, lateral view; d, same, mesial view; e, second pereopod, lateral view; f, third pereopod, lateral view; g, pleomere 6, telson and right uropod, lateral view; h, telson and right uropod, dorsal view. Setation of appendages omitted. Scale bar = 1 mm. [Illustrations by PCD].

(NHMW 19590) and Lombok (NHMW 26544–26547) have a spine on the antennal peduncle, but not at the antennular peduncle.

***Upogebia darwinii* (Miers, 1884)**
(Figs. 2c, d, 8)

Gebiopsis Darwinii Miers, 1884: 281, pl. 32, fig. 3.
Upogebia darwini. — Ngoc-Ho, 1977: 439 (part), figs. 1–3; — 1979: 155.
Upogebia (*Upogebia*) *darwini*. — Sakai, 1982: 17, figs. 3a, 4a–c, pls. A1–3, C3.
Upogebia darwinii. — Sakai, 2006: 101 (part), fig. 15; — Ngoc-Ho, 2008: 150, fig. 10.
Not *Upogebia* (*Calliadne*) *Darwinii*. — de Man, 1928: 84 (part), pl. 8, figs. 12, 12a, b; pl. 9, fig. 12c–f [= *U. intermedia* (de Man, 1888)].
Not *Upogebia darwini*. — Ngoc-Ho, 1977: 439 (part), fig. 4a–e [= *U. carinicauda* (Stimpson (1860)], fig. 4f–h [= *U. barbata* (Strahl, 1862)].
Not *Upogebia* (*Calliadne*) *darwinii*. — Poore & Griffin, 1979 (part): 292, fig. 46 [= *Upogebia carinicauda* (Stimpson, 1860)].
Not *Upogebia darwinii*. — Sakai, 2006: 101 (part), figs. 14A, B, 16 [= *U. hexaceras* (Ortmann, 1894)].

CMBS material. 1 male (43/12.7) (ZRC 2018.0561), 1 ov. female (47/13.4), 1 male (23/7.0) (ZRC 2018.0562), sta. DR246, north-west of Pulau Sudong, MPA grid 4213, sand, small rocks, rectangular dredge, 22.0–25.2 m, coll. TMSI team, 12 December 2013 (SEA-2684, 2581); 1 male (40/12.0) (NHMW 26037), ov. female (44/12.6) (NHMW 26038), sta. TB069, Straits of Singapore near Pulau Sudong and Pulau Semakau, 1°13.155′N 103°43.880′E, sandy bottom, beam trawl 17.9–18.9 m, coll. B Richer de Forges et al., 26

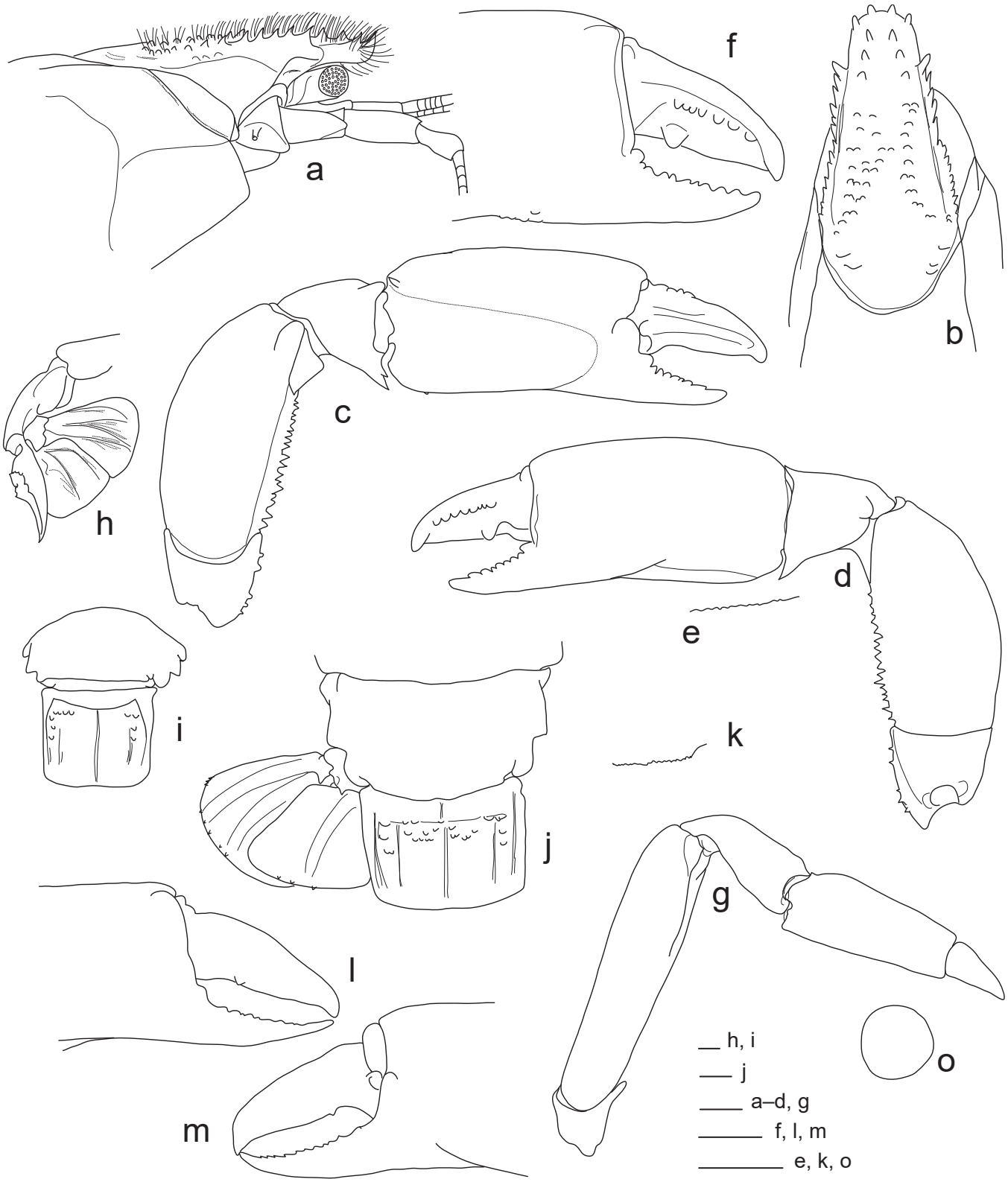

Fig. 8. *Upogebia darwinii* (Miers, 1884), a–k, male (40/12) (NHMW 26037); l–o, ovigerous female (44/12.6) (NHMW 26038); a, front, lateral view; b, same, dorsal view; c, right first pereopod, lateral view; d, same, mesial view; e, same, detail of lower border; f, left first pereopod, fingers, mesial view; g, right second pereopod, lateral view; h, pleomere 6, telson and right uropod, lateral view; i, pleomere 6 and telson, dorsal view; j, pleomere 6, telson (oblique) and left uropod, dorsal view; k, detail of posterior border of pleomere 6; l, left first pereopod fingers, mesial view; m, same, lateral view; o, outline of embryo. Setation of appendages omitted. Scale bar = 1 mm. [Illustrations by PCD].

May 2013 (SS-1654); 1 male (46/13.1) (NHMW 26039), 1 ov. female (35/10.1) (NHMW 26040), sta. TB072, Straits of Singapore, 1°13.227′N 103°45.313′E, mud, sand, beam trawl, from *Xestospongia testudinarium*, 23.1–23.6 m, coll. B Richer de Forges et al., 26 May 2013 (SS-0384); 1 male (39/11.1) (ZRC 2018.0550), sta. TB187, Straits of Singapore near Raffles Lighthouse, 1°09.239′N 103°44.674′E, sponges, rocks, gravel, beam trawl 39.5–40.2 m, coll. B Richer de Forges et al., 6 June 2013; 1 ov. female (44/12.4) (ZRC 2018.0529), sta. TB73, Straits of Singapore south of Pulau Semakau, 1°11.282′N 103°46.6321′E, sandy bottom, beam trawl 24.6–29.8 m, coll. B Richer de Forges et al., 26 May 2013 (SS-0385); 1 ov. female (30/8.6) (ZRC 2018.0535), 1 male (31/8.7) (ZRC 2018.0536), sta. DW027, Pulau Ubin, off eastern coast of Chek Jawa, 1°24.927′–1°25.273′N 103°59.980′–103°59.692′E, mud, window pane shells, beam trawl 9.9–19.1 m, coll. B Richer de Forges et al., 19 October 2012 (JS-1385).

Diagnosis. Lateral ridges of gastric region projecting forward. Linea thalassinica not reaching posterior end of carapace. Rostrum longer than eyestalks, with 4 frontal teeth. Ocular spine absent. Antennal peduncle longer than antennular peduncle. First pereopod chelate; ischium with few lower spinules; merus with small lower spines, without proximal upper spine; carpus with moderate upper spine, but without median and lower spines; propodus smooth on lower mesial face and upper border; dactylus with row of tubercles on mesial face and prominent rounded tooth proximally; fixed finger with serrated cutting edge. Second pereopod merus without proximal upper spine; propodus 2.1–2.5 times as long as high. Third pereopod merus with smooth lower border, without proximal upper spine. Pleomere 6 without lateral spines; posterior border minutely tuberculated. Uropodal endopod triangular. Telson 0.8–1.0 as long as maximal width; inverted U-shaped carina with tubercles. Third maxilliped exopod flagellate, no epipods on first and third maxilliped. Arthrobranchs of type A. Embryos 570–860 µm in diameter.

Distribution. Distributed in the Indo-Pacific, from the Red Sea to northern Australia (Sakai, 2006).

Habitat. In sand, silt, coral rubble, gravel, from the intertidal zone to 50 m; often found in sponges (Dworschak, 2000; Sepahvand et al., 2013; this study); occasionally boring in corals (Scoffin & Bradshaw, 2000).

Remarks. The syntype series of *U. darwinii* consists of 3 males and 3 females from Darwin, Australia (NHMUK 1882:7) and a male-female pair from Singapore (NHMUK 1882:24) (Ngoc-Ho, 1977). A male from Darwin with TL 20 mm was selected by Sakai (1982: 20) as lectotype, while he excluded the specimens from Singapore from the type series and attributed them to *U. ancylodactyla* de Man, 1905 (see below). Later, Sakai (2006: 94, 101, 113) attributed the Singaporean material to *U. barbata*, listing the specimens figured by Ngoc-Ho (1977) partly under *U. darwinii* (Sakai, 2006: 94) and as a synonym of *U. ancylodactyla* (Sakai, 2006: 91). It seems that the current taxonomic confusion of this species complex can only be solved by a more comprehensive revision, integrating both morphology and DNA.

***Upogebia hexaceras* (Ortmann, 1894)**
(Figs. 2e, f, 9)

Gebia (*Gebiopsis*) *hexaceras* Ortmann, 1894: 23, pl. 3 fig. 1.
Upogebia (*Calliadne*) *hexaceras*. — de Man, 1928: 24 (list), 81, pl. 8, fig. 11, 11a–f.
Upogebia (*Upogebia*) *hexaceras*. — Sakai, 1982: 23, pls. A4, C4.
Upogebia hexaceras. — Ngoc-Ho, 1990: 979, fig. 8; — Dworschak, 2019: 28 — Komai et al., 2020: 478, figs. 1–4.
Upogebia darwinii. — Sakai, 2006: 101 (part), fig. 16 [not *Upogebia darwinii* (Miers, 1884)].
Not *Upogebia* (*Calliadne*) *hexaceras*. — Poore & Griffin, 1979: 299, fig. 50 [= *Upogebia darwinii* (Miers, 1884)].

CMBS material. 2 females (17/5.1, 17/4.9) (NHMW 26048), sta. DR001, Straits of Singapore near Raffles Lighthouse, 1°10.125′N 103°45.419′E, gravel, shells, rectangular dredge, 38.3–38.5 m, coll. B Richer de Forges et al., 21 May 2013 (SS-0313); 1 female (20/5.7), 1 male (15/5.3) (ZRC 2018.0566), sta. DR013, between Pulau Hantu and Pulau Semakau, MPA grid 4513, rectangular dredge, in sponge (DR13_016), 21.1–21.9 m, coll. TMSI team, 3 July 2013 (DR13_027, DR13_028); 1 ov. female (22/6.1), 1 male (25/7.6) (NHMW 26042), sta. DR111, Straits of Singapore outside Eastern Boarding Ground A, 1°12.989′N 103°53.062′E, mostly rock bottom, rectangular dredge, 125–136 m, coll. B Richer de Forges et al., 30 May 2013 (SS-3265); 1 ov. female (25/8.3), 1 male (22/6.8) (NHMW 26041), sta. DR112, Straits of Singapore, Southern Fairway south of Sister Islands, 1°12.024′N 103°50.170′E, broken shells, rubble, rectangular dredge, 33.6–34.4 m, coll. B Richer de Forges et al., 30 May 2013 (SS-2943); 1 male (16/5.3) (ZRC 2018.0567), sta. DR114, north of Pulau Tekong, MPA grid 0226, rectangular dredge, 6.4–8.7 m, coll. TMSI team, 7 October 2013 (SEA-1276); 1 female (21/6.3), 1 male (17/5.1) (ZRC 2018.0541), 1 male (19/5.9) (ZRC 2018.0542), sta. DR125, Straits of Singapore, near Sister Islands, 1°12.416′N 103°49.858′E, laterite gravel, sand, rectangular dredge, 25.3–30.8 m, coll. B Richer de Forges et al., 31 May 2013 (SS-4002); 1 ov. female (21/6.3), 1 male (20/5.9) (ZRC 2018.0565), sta. DR222, east of Pulau Pawai, MPA grid 4411, rectangular dredge, 17.3–18.7 m, coll. TMSI team, 21 October 2013 (SEA-1613); 1 juvenile (7/2.3) (ZRC 2018.0569), sta. DR239, south of Pulau Bukom, MPA grid 4613, rectangular dredge, 24.3–27.6 m, coll. TMSI team, 11 December 2013 (SEA-2058); 1 juvenile (8/2.3) (ZRC 2018.0570), sta. DR241, north of Pulau Bukom, MPA grid 4614, rectangular dredge, 17.5–17.8 m, coll. TMSI team, 11 December 2013 (SEA-2089); 1 female (14/4.5) (ZRC 2018.0571), sta. DR257, off southwestern tip of Jurong Island, MPA grid 4013, clay, mud, rocks, rectangular dredge, 19.4–22.5 m, coll. TMSI team, 19 December 2013 (SEA-3209); 1 male (24/7.0) (ZRC 2018.0564), sta. RF353, Pulau Senang, east of jetty, intertidal, rocks, rubble, hand collection, coll. TMSI team, 30 March 2014 (INT-0849); 1 ov. female (22/6.4), 2 males (17/5.0, 18/5.0) (NHMW 26043), 1 ov. female (28/7.7) (NHMW 26045), 1 ov. female (25/7.1) (NHMW

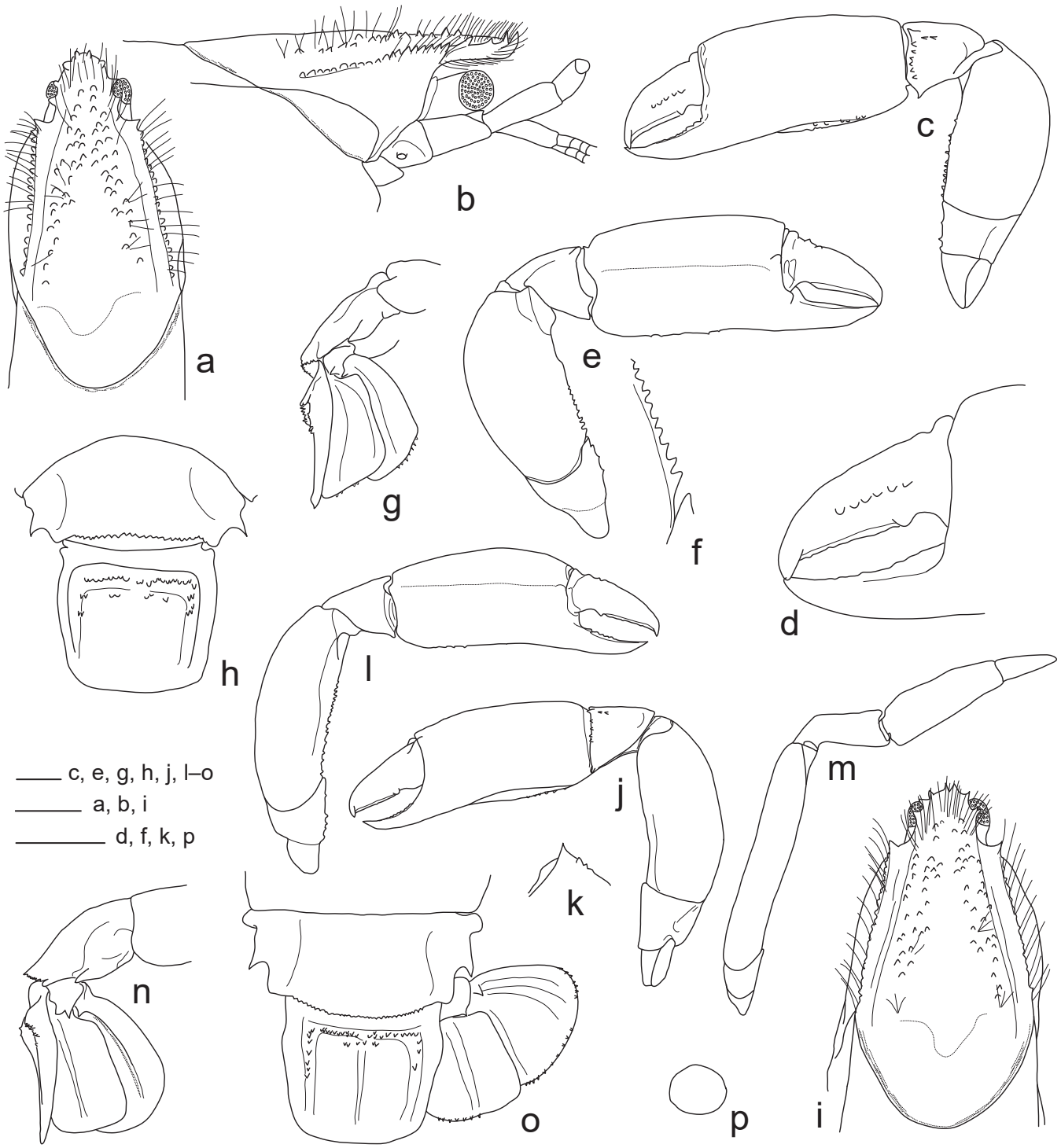

Fig. 9. *Upogebia hexaceras* (Ortmann, 1894), a–h, male (22/6.1) (NHMW 26042); i–p, ovigerous female (25/8.3) (NHMW 26041); a, i, front, dorsal view; b, same, lateral view; c, j, right first pereopod, mesial view; d, same, detail of fingers; k, same, detail of carpus; e, l, right first pereopod, lateral view; f, same, detail of lower border of merus; g, n, pleomere 6, telson and right uropod, lateral view; h, pleomere 6 and telson, dorsal view; m, right second pereopod, lateral view; o, pleomere 6, telson and right uropod, dorsal view; p, outline of embryo. Setation of appendages omitted. Scale bar = 1 mm. [Illustrations by PCD].

26046), 1 male (23/7.0) (ZRC 2018.0557), sta. SB067, Pulau Hantu, western patch reef, 1°13.6′N 103°44.8′E, coral rubble brushing 15.7 m, coll. HH Tan, S De Grave et al., 26 May 2013 (SS-1658, SS-1659, SS-1647); 1 female (27/7.6) (NHMW 26044), 1 ov. female (27/8.0) (ZRC 2018.0538), sta. SB146, west of Pulau Hantu, coral rubble brushing, 5–7 m, coll. HH Tan, S De Grave et al., 2 June 2013 (SS-2979); 1 ov. female (20/6.0), 1 male (168/5.9) (NHMW 26047), sta. TB003, Straits of Singapore near Raffles Lighthouse, Gusong Boarding Ground, 1°10.653′N 103°46.772′E, 40.7–40.9 m, coll. B Richer de Forges et al., 21 May 2013 (SS-0310); 1 male (14/4.0) (ZRC 2018.0559), sta. TB071, Straits of Singapore, south-west of Eastern Holding A, Singapore port limit, MPA grid 5414, beam trawl, 61.7–66.8 m, coll. TMSI team, 13 May 2013 (5414TB2-071); 1 male (18/5.7) (ZRC 2018.0540), sta. TB073, Straits of Singapore south of

Pulau Semakau, 1°11.282′N 103°46.6321′E, sandy bottom, beam trawl, 24.6–29.8 m, coll. B Richer de Forges et al., 26 May 2013; 1 ov. female (19/5.7), 1 male (16/4.7) (ZRC 2018.0545), sta. TB091, Straits of Singapore, Southern Fairway near St. John's Island, 1°12.926′N 103°51.647′E, beam trawl, 39.5–49.9 m, coll. B Richer de Forges et al., 28 May 2013; 1 male (19/6.0) (ZRC 2018.0527), sta. TB113, Straits of Singapore, Southern Fairway south of Sister Islands, 1°12.001′N 103°50.261′E, silt with rocks, beam trawl, 29.3–30.5 m, coll. B Richer de Forges et al., 30 May 2013; 1 female (15/4.6), 1 male (12/4.0) (ZRC 2018.0558), sta. TB128, Straits of Singapore beside Eastern Boarding Ground A, 1°12.889′N 103°52.460′E, mostly rock bottom, beam trawl, 75.2–83.7 m, coll. B Richer de Forges et al., 31 May 2013 (SS-3995); 1 ov. female (20/6.0) (ZRC 2018.0544), sta. TB185, Straits of Singapore near Pulau Senang, 1°09.942′N 103°43.458′E, thick smelly mud, laterite rocks, gravel, beam trawl, 24.3–24.5 m, coll. B Richer de Forges et al., 6 June 2013; 1 male (16/5.1) (ZRC 2018.0534), sta. TB186, Straits of Singapore off Raffles Lighthouse, 1°09.318′N 103°44.200′E, gravel, rocks, sponges, beam trawl, 35–38 m, coll. B Richer de Forges et al., 6 June 2013; 1 ov. female (17/5.1), 1 male (14/4.1) (ZRC 2018.0552), sta. TB187, Straits of Singapore near Raffles Lighthouse, 1°09.239′N 103°44.674′E, sponges, rocks, gravel, beam trawl, 39.5–40.2 m, coll. B Richer de Forges et al., 6 June 2013.

Diagnosis. Lateral ridges of gastric region projecting forward. Linea thalassinica not reaching posterior end of carapace. Rostrum rounded, as long or slightly longer than eyestalks, with 6 or more frontal teeth. Postocular spine absent. Antennal peduncle longer than antennular peduncle. First pereopod chelate; ischium smooth or with few spinules; merus with small lower spines proximally, without proximal upper spine; carpus with small upper and several small median spines, without lower spine mesially; propodus smooth on lower mesial face and upper border; dactylus with row of tubercles on mesial face and prominent rounded tooth proximally; fixed finger with serrated cutting edge proximally. Second pereopod merus without proximal upper spine; propodus 2.5–3.1 times as long as high. Third pereopod merus with smooth lower border, without proximal upper spine. Pleomere 6 with prominent lateral spines; posterior border denticulated. Uropodal endopod squarish. Telson 0.8–1.1 times as long as maximal width; inverted U-shaped carina with tubercles. First and third maxillipeds without epipods. Third maxilliped exopod flagellate. Arthrobranchs of type B. Embryos 550–750 µm in diameter.

Distribution. Known with certainty from Thursday I., Torres Strait, northern Australia (type locality), Philippines (Dworschak, 2019), Singapore (this study), Indonesia, India (Komai et al., 2020), Red Sea and Persian Gulf (Ngoc-Ho, 1990). Exact distribution (especially in Australia) uncertain due to confusion with *U. darwinii* (see below).

Habitat. Sand, silt, mud, gravel and rubble bottoms from the intertidal zone to 84 m; often associated with sponges (Komai et al., 2020; this study).

Remarks. *Upogebia hexaceras* was described based on two specimens (sex not given) from Thursday Island (Torres Strait) (Ortmann, 1894). De Man (1928: 83) studied the "single type specimen, a male" (24/8.3) deposited in what is now the Phyletisches Museum in Jena, Germany (PMJ), and provided a complementary description of the species. One specimen is still extant in the PMJ collections; however, it is a female with cl 9 mm, with the pleomere 6 bearing lateral projections and its posterior border denticulated (R. Beutel, pers. comm., 25 March 2014).

Upogebia hexaceras was treated as a valid species by Sakai (1982), although he concluded that it showed no differences from *U. darwinii*. Ngoc-Ho (1990) considered it as valid and outlined the differences between the three similar species, viz. *U. darwinii*, *U. hexaceras*, and *U. octoceras* (Nobili, 1904). Sakai (1993, 2006) considered *U. hexaceras* again as a synonym of *U. darwinii*, which was later rebutted by Ngoc-Ho (2008). Most recently, Dworschak (2019) and Komai et al. (2020) considered *U. hexaceras* a valid species.

The material of *U. hexaceras* from CMBS is very consistent in its morphological characters. All specimens display strong, sharp, lateral projections on the sixth pleomere and its posterior border is strongly denticulate. The rostrum is short, rounded, with 6–12 spines (see below), whereas the lateral projections of the carapace are prominent. It differs clearly from the CMBS material herein identified as *U. darwinii* (see above).

The number of the rostral spines is quite variable in the present material of *U. hexaceras*, with 2 specimens armed with 6 spines, 12 with 8, 1 with 9, 13 with 10, 1 with 11, and 7 with 12. These numbers exceed the range of the rostral spines (6–9) in the diagnosis of *U. hexaceras* provided by Ngoc-Ho (1990: table 1) and also that of *U. octoceras* (6–10, idem). None of the CMBS specimens, however, has a distomesial spine on the first pereopod propodus near the articulation with the dactylus, a feature typical of *U. octoceras* (Ngoc-Ho, 1990: fig. 9g, f).

Upogebia ancylodactyla de Man, 1905
(Figs. 2g, h, 10)

Upogebia (*Gebiopsis*) *ancylodactyla* de Man, 1905: 599–600.
Upogebia (*Calliadne*) *ancylodactyla*. — de Man, 1928: 24 (list), 87 (part.), pl. 9 fig. 13–13f [not pl. 9, fig. 13g, h, pl. 10, fig. 13i–j = *Upogebia baweana* Tirmizi & Kazmi, 1979].
Upogebia ancylodactyla. — Tirmizi & Kazmi, 1979: 106, fig. 1; — Sakai, 1993: 90; — Sakai, 2006: 91; — Ngoc-Ho, 2008: 143, fig. 7.
Upogebia (*Upogebia*) *ancylodactyla*. — Sakai, 1982: 27, figs. 3e, 5c; — Sakai, 1984a: 160.
[*Upogebia darwini*. — Ngoc-Ho, 1977: 439 (part), figs. 1–3b [not fig. 3c–i, = *U. darwinii* (Miers, 1884); not fig. 4f–i, = *U. barbata* (Strahl, 1862)].

CMBS material. 1 ov. female (17/5.3), 1 male (17/5.1) (ZRC 2018.0547), sta. DR174, Straits of Singapore near Kusu Island, 1°12.202′N 103°52.178′E, reddish marine clay, gravel, shells, rectangular dredge, 79.6–135 m, coll. B Richer

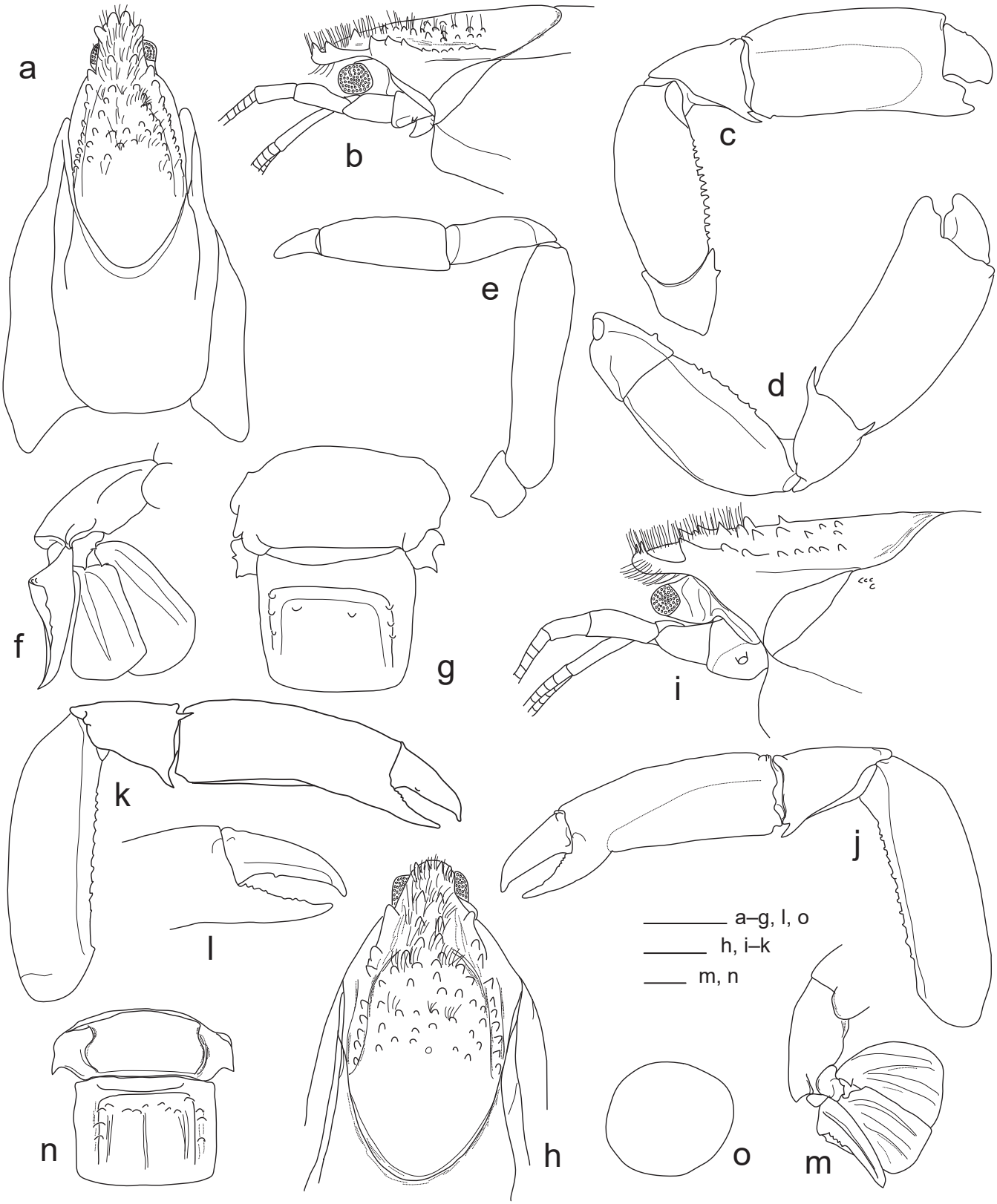

Fig. 10. *Upogebia ancylodactyla* de Man, 1905, a–g, male (15/4.9) (NHMW 26049); h–o, ovigerous female (29/8.3) (NHMW 26050); a, carapace, dorsal view; b, i, front, lateral view; h, same, dorsal view; c, k, right first pereopod, lateral view; d, j, same, mesial view; l, same as k, distal portion of chela, dorsolateral view; e, left second pereopod, lateral view; f, m, pleomere 6, telson and right uropod, lateral view; g, n, pleomere 6 and telson, dorsal view; o, outline of embryo. Setation of appendages omitted. Scale bar = 1 mm. [Illustrations by PCD].

de Forges et al., 5 June 2013; 1 ov. female (23/6.4), 1 male (22/6.6) (NHMW 26052), sta. IT103, Terumbu Pempang Tengah, 01°13.758′N 103°43.736′E, intertidal, coll. CS Tan, D Uyeno et al., 30 May 2013 (SS-3231); 1 male (15/4.9) (NHMW 26049), 1 ov. female (29/8.3) (NHMW 26050), 1 ov. female (25/7.7) (ZRC 2018.0530), 1 male (26/6.9) (ZRC 2018.0531), 1 male (27/8.0) (ZRC 2018.0532), 1 ov. female (24/6.9) (ZRC 2018.0533), 1 ov. female (18/5.1), 1 male (16/5.1) 1 exuvia (17/5.3) (NHMW 26054), sta. IT120, Pulau Hantu, intertidal, coll. KS Koh, TS Ahyong, K Tilbrook et al., 31 May 2013 (SS-2946, SS-2949); 1 male (26/7.7) (ZRC 2018.0528), sta. IT122, Terumbu Raya, intertidal, coll. CS Tan et al., 31 May 2013 (SS-2948); 1 male (20/6.0) (ZRC 2018.0556), sta. IT124, Terumbu Pempang Laut, 01°13.912′N 103°43.402′E, intertidal, coll. YL Lee, I Kwan et al., 31 May 2013 (SS-3981); 1 ov. female (16/5.1), 2 males (24/7.1, 18/5.1), 1 female (16/5.0) (NHMW 26053), sta. IT140, Tekukor, 1°13.899′N 103°50.265′E, intertidal, coll. YL Lee, SK Tan et al., 1 June 2013 (SS-4012); 1 male (16/4.9) (ZRC 2018.0555), sta. SB146, west of Pulau Hantu, coral rubble brushing, 5–7 m, coll. HH Tan, S De Grave et al., 2 June 2013 (SS-2979); 1 male (29/8.4) (ZRC 2018.0549), 1 female (40/11.3) (ZRC 2018.0551), sta. SD056, southern Pulau Jong, 1°12.55′N 103°47.2′E, silty rubble, hand collection by scuba diving 17 m, coll. C Messing, S De Grave, HH Tan et al., 25 May 2013 (SS-1623, SS-1624); 1 male (11/3.5) (ZRC 2018.0543), sta. SW024, Pulau Sekudu, 1°24.263′N 103°59.241′E, sand, mud, rocks, hand and yabby pump, 0 m, coll. R Tan, M Ng et al., 18 October 2012; 1 ov. female (27/7.7), 1 male (27/8.1) (NHMW 26051), sta. SW026, Tuas, West Drive 60, 1°19′45.9″N 103°37′50.9″E, intertidal, sand-mud, some corals, hand collection and beach seine, 0–0.5 m, coll. HH Ng, H Wong et al., 18 October 2012 (JS-1152); 1 ov. female (16/4.4) (ZRC 2018.0554), sta. TB172, Straits of Singapore near Kusu Island, 1°12.180′E 103°52.125′E, consolidated marine clay, 94.5–100 m, coll. B Richer de Forges et al., 5 June 2013 (SS-4522).

Diagnosis. Lateral ridges of gastric region not projecting forward. Linea thalassinica not reaching end of carapace. Rostrum longer than eyestalks, with 4 frontal teeth. Postocular spine absent. Antennal peduncle as long as antennular peduncle. First pereopod chelate, sexually dimorphic, twisted by 45° laterally; ischium with small lower spine; merus with small lower spines decreasing in size distally, without proximal upper spine; carpus with moderate upper spine, but without median and lower spines mesially; propodus smooth on lower mesial face and upper border, slender (3 times as long as high) in females, very robust (less than 2 times as long as high) in males; fingers slender in females, dactylus with rounded tooth proximally, stout (as long as high) in males. Second pereopod merus without proximal upper spine; propodus 2.1–3.0 as long as high. Sixth pleomere without lateral spines; posterior border smooth. Uropodal endopod rectangular. Telson 0.7 to 1.0 as long as wide; inverted U-shaped carina with tubercles. First and third maxillipeds without epipods. Third maxilliped exopod flagellate. Arthrobranchs of type B. Embryos 750–1430 µm in diameter.

Distribution. Ranging in the Indo-West Pacific, from the Red Sea to northern Australia (Sakai, 2006).

Habitat. Sand, mud, coral rubble and consolidated clay from the intertidal to 100 m (this study); also reported from coral rocks (Ngoc-Ho, 2008).

Remarks. De Man (1905) did not specify how many specimens were available to him from "Baingsisi, Samau-Island, near Timor", now Semau Island. Sakai (1975) first considered *U. ancylodactyla* as a junior synonym of *U. amboinensis* (de Man, 1888), but later (Sakai, 1982) corrected the identification of an illustrated specimen from Fiji Islands (Sakai, 1975: fig. 2), describing it as *U. fijiensis* Sakai, 1982.

The type material of *U. darwinii* and *U. barbata* also contained specimens of *U. ancylodactyla* according to Sakai (1982: 27). The egg diameter in gravid females of *U. ancylodactyla* seems to be somewhat variable. According to Sakai (1982), based on de Man (1928), the egg size is 0.9 mm. Ngoc-Ho (2008) listed 1.10–1.30 mm for specimens from Singapore and 1–1.1 mm for specimens from Aden; however, she earlier mentioned that the latter material, listed as *U. ancylodactyla* by Sakai (1982), was actually *U. barbata* (see also above).

Upogebia singaporensis, new species
(Figs. 1d, 11, 12)

CMBS material. Holotype: female (16/5.4) (ZRC 2017.0951), sta. IT120, Pulau Hantu, intertidal, coll. KS Koh, TS Ahyong, K Tilbrook et al., 31 May 2013 (SS-3982). Paratypes: 1 female (13/4.8) (ZRC 2017.0952), 1 juvenile (12/3.9) (ZRC 2017.0950), sta. SB055, Kusu Island, coral rubble brushing, ~4 m, coll. HH Tan, S De Grave et al., 25 May 2013 (SS-1631); 1 juvenile (11/3.6) (ZRC 2017.0953), sta. TB172, Straits of Singapore near Kusu Island, 1°12.180′N 103°52.125′E, consolidated marine clay, 94.5–100 m, coll. B Richer de Forges et al., 5 June 2013 (SS-4522).

Comparative material. *Upogebia srilankaensis* Sakai, 2006, holotype, male (24/7.4) (SMF 30213), Sri Lanka, Matara, Weligama Bay (5°59.074′N 80°19.695′E), coll. O. Löw-Beer, 3 December 1912.

Diagnosis. Rostrum elongate, with four strong dorsal spines, without infrarostral spine. Lateral ridges of gastric region weakly developed, with obtuse distal tooth and posterior to that tooth 9–11 tubercles. Postocular spine absent. Pleonal sternites unarmed. First pereopod chelate, merus lacking subdistal dorsal spine and bearing row of obtuse ventral teeth; carpus bearing 1 strong distoventral and 1 strong distodorsal spine. Meri of third to fifth pereopods unarmed.

Description of female holotype. Rostrum (Fig. 11a, b) elongate, twice as long as broad at base, setose on dorsal surface, bearing 1 pair of distal and 1 pair of subdistal dorsal spines, lacking infrarostral spine; lateral ridges of gastric region slightly protruding laterally, bearing row of 8–9 unequal tubercles; mid-dorsal area of gastric region

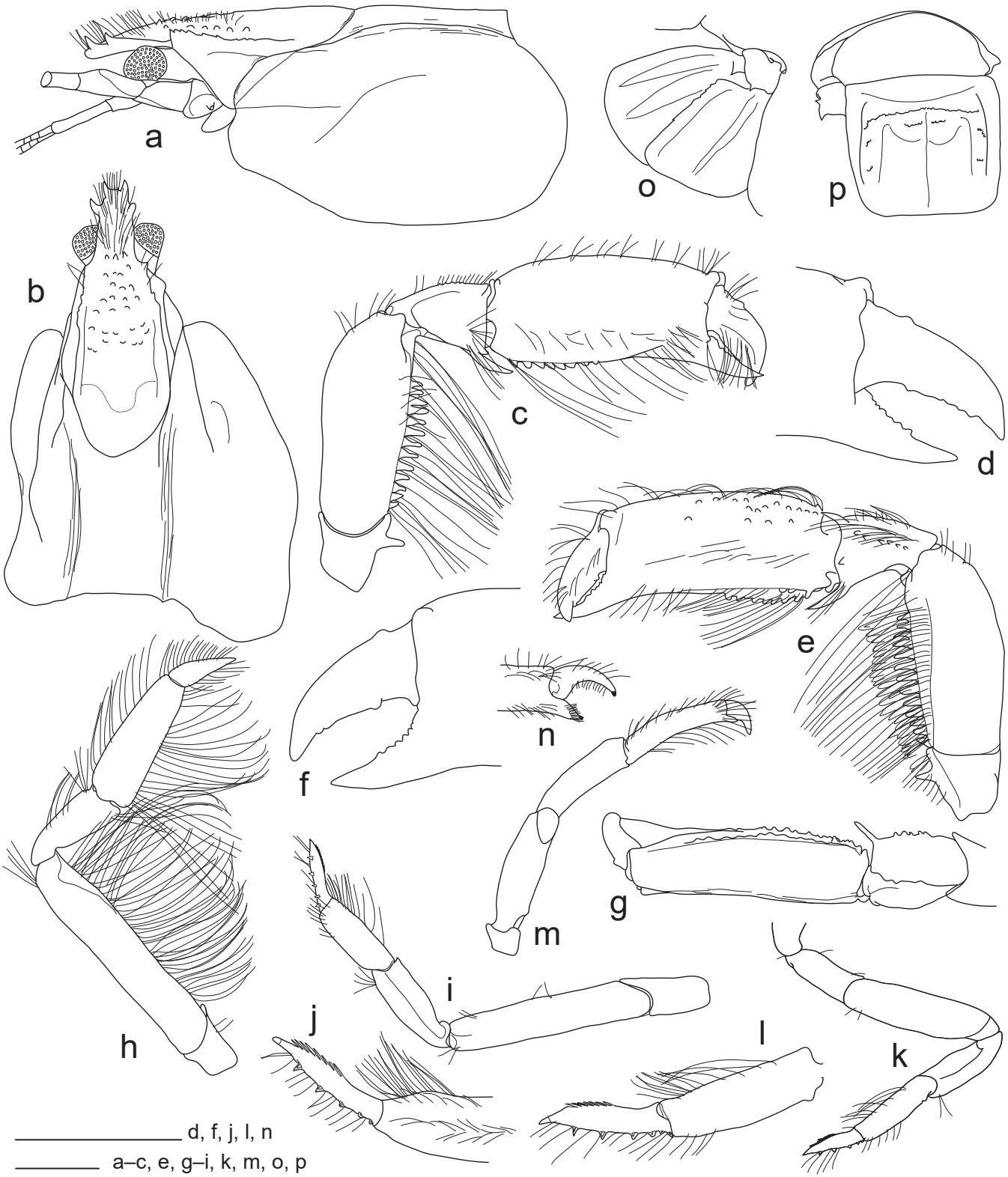

Fig. 11. *Upogebia singaporensis*, new species, holotype female (16/5.4) (ZRC 2017.0951); a, carapace, lateral view; b, same, dorsal view; c, right first pereopod, lateral view; d, same, detail of fingers (setae omitted); e, right first pereopod, mesial view; f, same, detail of fingers (setae omitted); g, left first pereopod, upper view; h, right second pereopod, lateral view; i, right third pereopod, lateral view; j, same, detail of dactylus; k, right fourth pereopod, lateral view; l, same, detail of propodus and dactylus; m, right fifth pereopod, lateral view; n, left fifth pereopod, detail; o, left uropod, dorsal view; p, telson, dorsal view. Scale bar = 1 mm. [Illustrations by PCD].

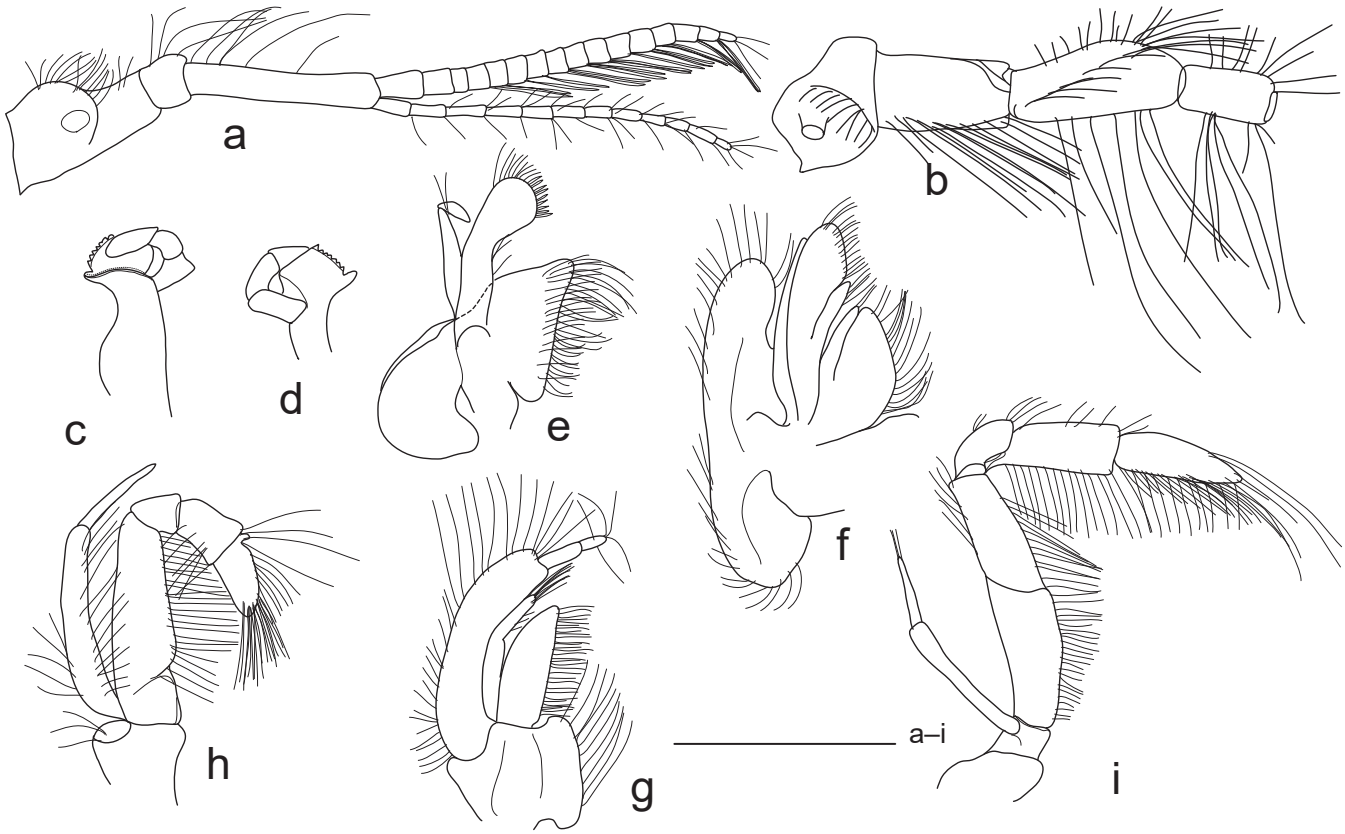

Fig. 12. *Upogebia singaporensis*, new species, holotype female (16/5.4) (ZRC 2017.0951); a, antennule; b, antenna, c, d, mandible (setation omitted); e, maxillule; f, maxilla; g, Mxp1; h, Mxp2; i, Mxp3 [a–i: all right side lateral views, except c (mesial view)]. Scale bar = 1 mm. [Illustrations by PCD].

with scattered tubercles. Cervical groove lacking spines. Postocular spine absent. Eyestalk stout, reaching to mid-length of rostrum, unarmed. Linea thalassinica reaching to posterior end of carapace.

Antennular peduncle (Figs. 11a, 12a) shorter than antennal peduncle; articles unarmed, second article short, third article elongate; flagella of same length, dorsal thicker than ventral, as long as peduncle.

Antennal peduncle (Figs. 11a, 12b) overreaching rostrum by distal margin of penultimate article; articles unarmed; scaphocerite weakly developed.

Epistome (Fig. 11a) rounded, unarmed. Mandible (Fig. 12c, d) without mesio-anterior tooth. First and second maxilla as illustrated (Fig. 12e, f). First maxilliped (Fig. 12g) without epipod. Second maxilliped (Fig. 12h) with epipod. Third maxilliped (Fig. 12i) without epipod; exopod simple (without flagellum) distally, reaching almost to end of endopodal merus.

First pereopod (Fig. 11c–f) chelate; coxa and basis unarmed. Ischium bearing 1 subterminal spine on ventral margin. Merus bearing row of 13–14 obtuse thick spines on ventral margin, increasing in size to mid-length of merus, distal ones diminishing in size; dorsal margin unarmed. Carpus triangular, lateral surface bearing longitudinal ventral carina; 1 strong, mesially directed dorsal spine, 1 small median spine, and 1 prominent dorsal spine present on distal margin; 6 small spines present on mesial surface. Palm 2.1 times as long as high; upper border unarmed, with several low tubercles on inner dorsal surface; lower border keeled with 7–8 tubercles proximally; 3 tubercles present on lower inner surface proximally. Fixed finger 0.3 times length of palm, with low denticles on cutting edge. Dactylus (Fig. 11d, f) with proximal tooth on cutting edge.

Second pereopod (Fig. 11h) unarmed; merus 5.3 times as long as wide; propodus 2.8 times as long as wide. Third and fourth pereopods (Fig. 11i, k) simple; dactylus with comb on lower border and 5 spaced corneous spines on upper border (Fig. 11j, l). Fifth pereopod (Fig. 11m) subchelate; dactylus curved, with corneous tip (Fig. 11n).

Telson (Fig. 11p) slightly longer than maximal width; dorsal surface with U-shaped concavity, latter with denticulate transverse carina. Uropodal endopod broadened, about as long as telson, with somewhat truncate, slightly convex distal margin; uropodal exopod broadened, about as long as endopod, with prominent spine proximally (Fig. 11o).

Arthrobranchs of type A, one pair each on third maxilliped, and first to fourth pereopods.

Variations. The number of spines on the lower border of the first pereopod merus ranges from 9 (juvenile 11/3.6) to 15 (female 13/4.8) on the right side and between 9 and 14 on the left side. The teeth on the lower border of first pereopod propodus differ between sides and range from 3 to 8.

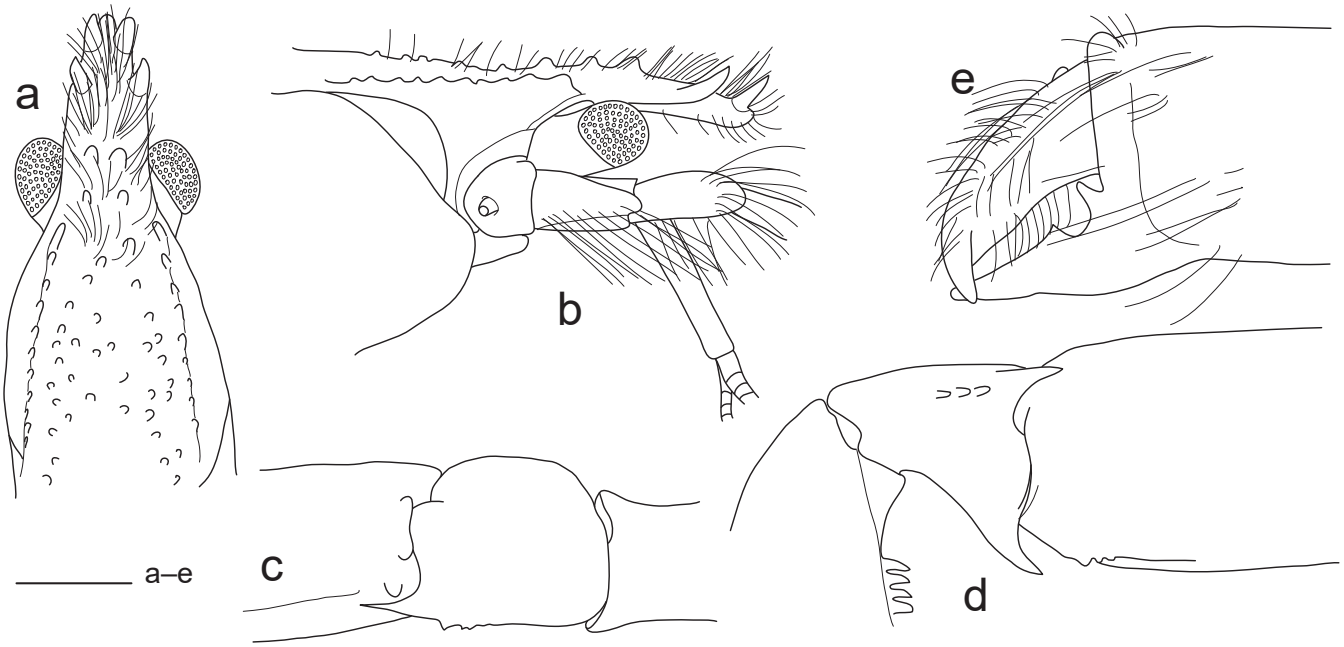

Fig. 13. *Upogebia srilankaensis* Sakai, 2006, holotype male (24/7.4) (SMF 30213); a, front, dorsal view; b, front, lateral view; c, right first pereopod, carpus, dorsal view; d, left first pereopod, carpus, mesial view; e, right first pereopod, fingers, mesial view. Scale bar = 1 mm. [Illustrations by PCD].

Etymology. Named after the type locality, the Straits of Singapore.

Distribution. Only known from the Straits of Singapore.

Habitat. *Upogebia singaporensis*, new species, has a wide bathymetric distribution: one female (16.1/5.42) was collected in the intertidal zone at Pulau Hantu (together with *U. ancylodactyla*); two specimens came from coral brushings at 4 m depth at Kusu Island, and one from consolidated clay at a depth of 94.5–100 m.

Remarks. The new species is similar to *Upogebia srilankaensis* Sakai, 2006 in possessing a long rostrum with two pairs of prominent dorsal spines (1 distal and 1 subdistal pair); in the shape of the spines on the lower border of the first pereopod merus; in having upper and lower spines on the first pereopod carpus; and in the general shape of telson and uropods. However, *U. singaporensis*, new species, differs from *U. srilankaensis* (characters in parentheses) by 1) the absence of a ventral spine on the first article of the antennal peduncle (present); 2) the slightly produced lateral ridges of the gastric carapace region (not protruding); 3) the dorsal spine on the mesial surface of the first pereopod carpus prominent (much smaller); 4) the ventral margin of the first pereopod propodus with several tubercles proximally (without tubercles); and 5) the fixed finger of the first pereopod entire (with a deep concavity on the occlusal margin).

A re-examination of the holotype of *U. srilankaensis* (Fig. 13) revealed some inconsistencies and omissions in the original description by Sakai (2006): 1) the antennal peduncle has a distinct, acute scaphocerite; 2) the first pereopod palm has a row of three tubercles proximally on the lower mesial surface (only one visible in lateral view in Sakai, 2006: fig. 23D); 3) there are two spines on the upper mesial face of the first pereopod carpus; 4) the left first pereopod has two spines ventrally on the ischium; and 5) the third and fourth pereopod dactyli have a comb on the lower border and a row of corneous spines on the upper border, as in the present new species (not illustrated nor mentioned by Sakai, 2006).

Neogebicula Sakai, 1982

Upogebia (*Neogebicula*) Sakai, 1982: 72.
Neogebicula Sakai, 1993: 95; — Ngoc-Ho, 1995: 79; — Sakai, 2006: 5; — Sakai, 2011b: 1120.
Paragebicula Sakai, 2006: 6; — Sakai, 2010b: 656; — Sakai, 2011b: 1121; new synonym.

Type species. *Upogebia* (*Neogebicula*) *alaini* Sakai, 1982.

Diagnosis. Rostrum triangular with rounded tip, longer than wide. First pereopod simple or subchelate, slender, fixed finger in females very small. Pleomere 6 longer than wide, longer than pleomere 2. Uropodal rami slender, leaf-like; exopod 3–4 times as long as wide, 2–3 times as long as telson.

Remarks. The differences between *Neogebicula* and *Paragebicula* as given by Sakai (2006, 2010b, 2011b) and Liu & Liu (2010b) are not observable over the range of morphologies of the species included and we consider *Paragebicula* a synonym of *Neogebicula*.

Species included. *Neogebicula alaini* (Sakai, 1982), *N. berggreni* (Sakai, 2015), *N. bijdeleyi* (Liu & Liu, 2010), *N. bussarawiti* (Sakai, 2015), *N. contigua* (Božic & de Saint Laurent, 1972), *N. edentata* (Lin, Ngoc-Ho & T. Y. Chan, 2001), *N. fallax* (de Man, 1905), *N. gracilis* (Ngoc-Ho, 1990), *N. holthuisi* Liu & Liu, 2010, *N. johorensis*, new species, *N. leptomorpha* (Sakai, 2006), *N. lipkei* (Sakai,

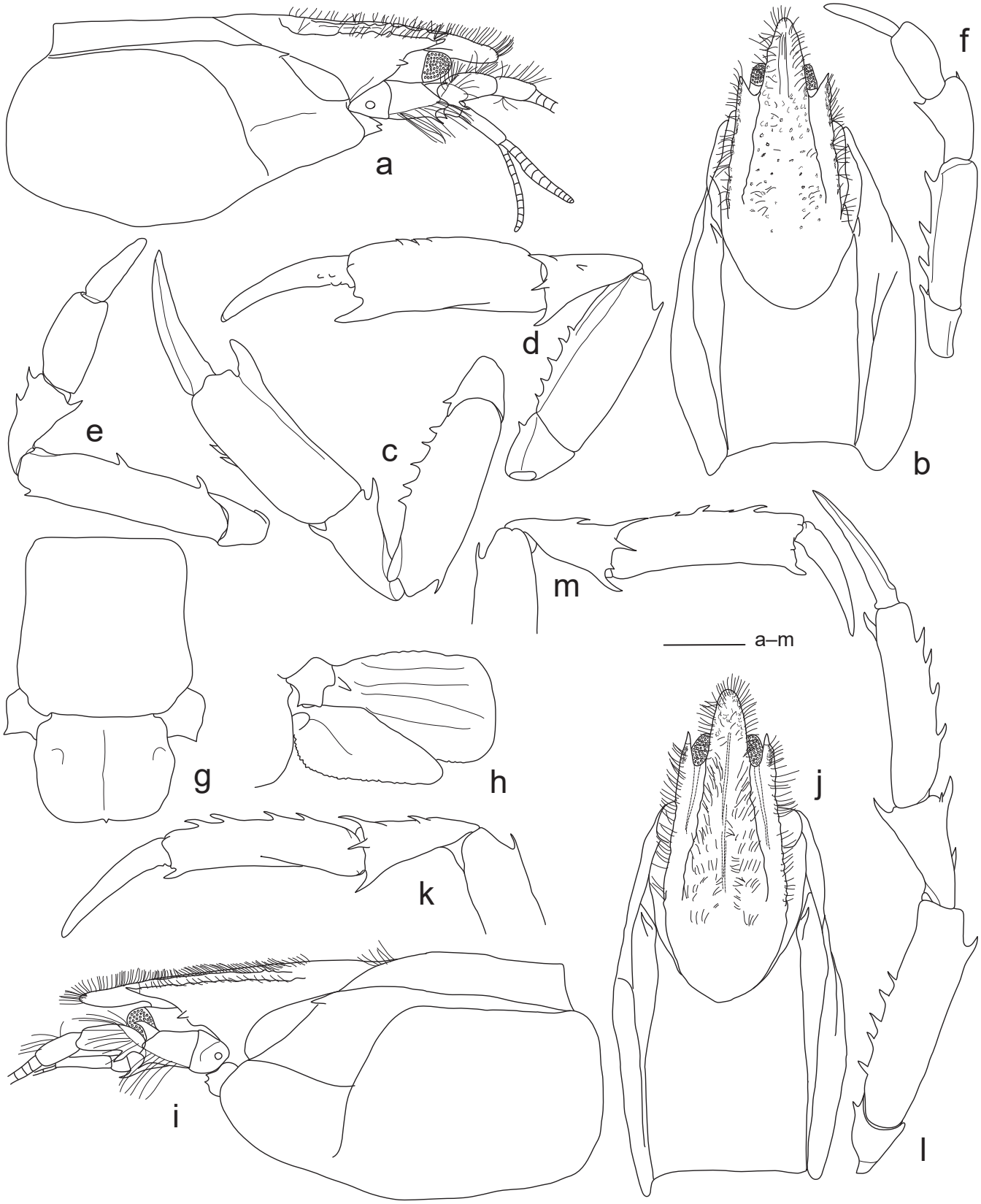

Fig. 14. *Neogebicula johorensis*, new species: a–h, holotype male (18/5.6) (ZRC 2017.0956); i–l, paratype female (21/6.3) (ZRC 2017.0955); m, paratype female (21/6.6) (ZRC 2017.0959); a, i, carapace, lateral view; b, j, carapace, dorsal view; c, l, first pereopod, lateral view; d, k, m, same, mesial view; e, second pereopod, lateral view; f, third pereopod, lateral view; g, pleomere 6 and telson, upper view; h, right uropod, dorsal view. All setae omitted, except in a, b, i, j. Scale bar = 1 mm. [Illustrations by PCD].

2010), *N. monochela* (Sakai, 1967), *N. oleseni* (Sakai, 2015), *N. orlik* (Sakai, 2011), *N. setaerostrata* (Sakai, 2015), *N. vietnamensis* (Sakai, 2011), *N. waikuli* (Sakai, 2015), and *N. wistari* Ngoc-Ho, 1995.

Neogebicula johorensis, new species
(Figs. 1e–h, 14, 15)

CMBS material. Holotype: male (18/5.6) (ZRC 2017.0956), sta. DR001, eastern Straits of Johor, W of Pulau Pengerang, MPA grid 0422, rectangular dredge, 6.7–7.6 m, coll. SC Lim, A Anker, H Wong, CK Chim et al., 25 March 2014 (0326DR1-AA01). Paratypes: 1 ov. female (21/6.3) (ZRC 2017.0955), sta. DR108, eastern Straits of Johor, beside E Pulau Tekong and Pulau Pengarang, MPA grid 0422, rectangular dredge, 11.9–12.0 m, coll. SC Lim, A Anker, H Wong, CK Chim et al., 25 March 2014 (0422DR2-A108); 1 ov. female (21/6.6) (ZRC 2017.0959), sta. DR235, east of Pulau Tekong, MPA grid 0524, rectangular dredge 13.1–14.7 m, coll. TMSI team, 5 November 2013 (SEA-1944); 1 male (14/3.9) (ZRC 2017.0958), sta. DR264, Straits of Johor off Punggol, near Punggol jetty, MPA grid 5425, sand-mud, rectangular dredge, 11.2–11.3 m, coll. TMSI team, 16 January 2014 (SEA-3482); 1 female (19/5.3 left first pereopod missing) (ZRC 2017.0954), sta. DR333, W Straits of Johor, between Tuas and Pulau Merambong, MPA grid 3718, rectangular dredge, 7.2–7.5 m, coll. TMSI team, 11 February 2014 (SEA-4248).

Diagnosis. Rostrum long. Lateral ridges of gastric region strongly projecting forward. Linea thalassinica extending to end of carapace. Ocular spine present, with or without hepatic spines. Proximal antennular peduncle article with ventral spine. Antennal peduncle with articles 3 and 4 each with ventral spine. Upper border of first pereopod propodus with several spines. Sixth pleomere as long as wide. Telson with small median spine.

Description. Rostrum long, triangular, 1.7 times as long as wide at base, twice as long as eyestalks, reaching to end of fourth article of antennular peduncle, narrowing anteriorly, rounded distally (Figs. 14a, b, i, k, 15a, b); dorsal surface of rostrum and gastric region with shallow median groove and low tubercles, extending onto gastric region of carapace, covered with short serrulate setae. Ventral surface of rostrum unarmed. Carapace with lateral ridges of gastric region strongly projecting forward, almost reaching end of eyestalks, anteriorly acute, separated from median gastric region by distinct longitudinal grooves; median gastric region setose, with low tubercles, diverging posteriorly; linea thalassinica extending well beyond cervical groove, reaching posterior border of carapace; anterolateral border of carapace with prominent ocular spine (may be absent in juveniles); cervical groove with (Fig. 14a, b, i, k) or without (Fig. 15a, b) hepatic spine.

Antennule (Fig. 15c) with first article of peduncle armed with distoventral spine; second article short; third article as long as first. Dorsal flagellum longer and thicker than ventral flagellum, as long as length of second and third article combined.

Antenna (Fig. 15d) with acute scaphocerite; second article of peduncle with ventral spine; third article fused with second one; fourth article with median ventral spine.

Epistome (Figs. 14a, j, 15a) with 2–3 spines.

Mandible (Fig. 15e, f) with large mesio-anterior tooth. First and second maxilla as illustrated (Fig. 15g, h). First maxilliped (Fig. 15i) with small epipod. Second maxilliped (Fig. 15j) with small epipod; exopod simple.

Third maxilliped (Fig. 15k) without epipod; exopod without flagellum, reaching mid-length of endopod merus; ischium with single spine proximally on mesial face (not shown).

Arthrobranchs of type C; one pair each on third maxilliped, and first to fourth pereopods.

First pereopods (Figs. 14c, d, k–m, 15l, m) subchelate, equal in size and shape, sexually dimorphic. Ischium with distoventral spine. Merus about 4.4 times as long as wide, with 5 spines on lower border in proximal 0.6 of meral length, and 1 dorsodistal spine. Carpus triangular, with 3 strong distal spines, 1 dorsal, 1 mesial, and 1 ventral, 1 small spine present dorsal to strong ventral spine; mesial face with 1 small spine. Propodus 2.6 (male) or 4.6 (females) times as long as wide; ventral border unarmed; dorsal border with 2 (male) or 4 (females) spines; fixed finger small in females (Figs. 14l, m, 15l, m), distinctly larger in males (Fig. 14c, d); dactylus 0.6–0.7 times as long as propodus, with 1 low proximal tubercle on ventral border and 2 tubercles on mesial face in males only, with dorsolateral plate in males and females.

Second pereopod (Figs. 14e, 15n) with median spine on coxa; ischium unarmed; merus 4.4 times as long as wide, with 1 proximal and 1 median spine on ventral border, as well as 1 distal spine on dorsal border; carpus with 1 distal spine on ventral border, and 1 median and 1 distal spine on dorsal border; propodus unarmed, 2.3 as long as wide; dactylus 0.7 length of propodus, narrowing distally.

Third pereopod (Figs. 14f, 15o) with ischium armed with distal spine ventrally; merus 3 times as long as wide, with 3 strong spines on ventral border; carpus with 1 strong distal spine ventrally and 1 small spine dorsally; propodus twice as long as wide, unarmed; dactylus as long as propodus, slender.

Fourth pereopod (Fig. 15p) simple, unarmed. Fifth pereopod (Fig. 15q) subchelate, unarmed.

Sixth pleomere (Fig. 14g) slightly longer than wide; telson broader than long, lateral margin broadest at proximal third; distal margin broadly truncate, with median spine; dorsal surface with longitudinal median groove in distal 0.6 of segment length.

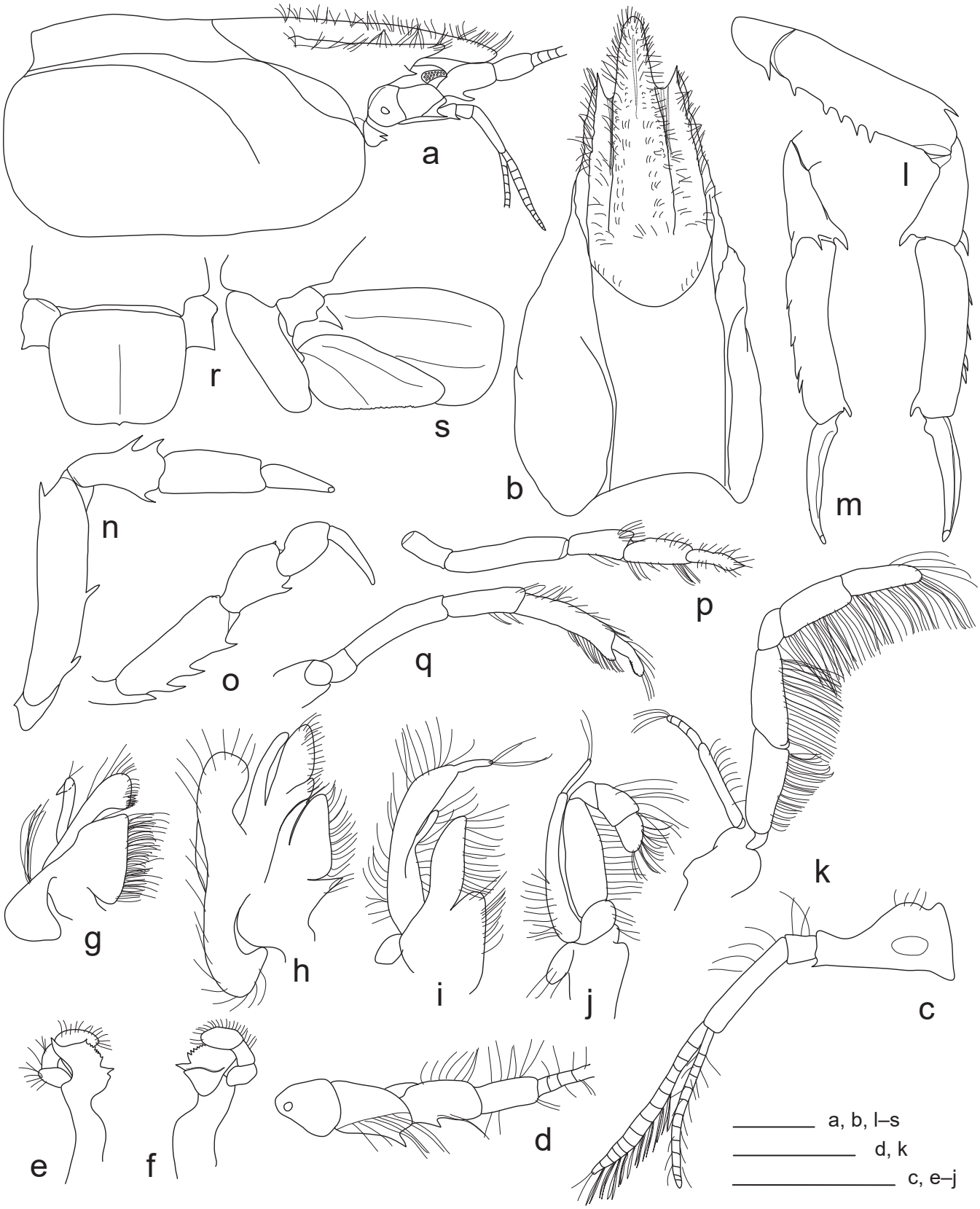

Fig. 15. *Neogebicula johorensis*, new species, paratype female (19/5.3) (ZRC 2017.0954): a, carapace, lateral view; b, same, dorsal view; c, right antennule; d, left antenna; e, f, mandible; g, maxillule; h, maxilla; i, first maxilliped; j, second maxilliped; k, third maxilliped [c–k: all right side lateral views, except d (left side lateral view) and f (mesial view)]; l, first pereopod, lateral view; m, same, distal articles, mesial view; n, second pereopod, lateral view; o, third pereopod, lateral view; p, fourth pereopod, lateral view; q, fifth pereopod, lateral view; r, telson, dorsal view; s, telson and right uropod, lateral view. Setation omitted in l–o, r, s. Scale bar = 1 mm. [Illustrations by PCD].

Pleopod 1 absent in males, uniramous in females.

Uropodal protopod (Figs. 14g, h, 15r, s) with stout spine; exopod 1.8 times as long as broad, bearing sharp proximal spine, with truncate distal margin; endopod about twice as long as broad, shorter than exopod.

Embryos 570–640 μm in diameter.

Variations. The number of spines on the upper border of the first pereopod propodus ranges from 2 to 4, one male (ZRC 2017.0958) lacks postocular spines, whereas two specimens (ZRC 2017.0954 and ZRC 2017.0958) lack the hepatic spines. One ovigerous female (ZRC 2017.0955) shows a male gonopore on the coxa of the left fifth pereopod, whilst another female (ZRC 2017.0954) has a male gonopore on the right side.

Etymology. The new species is named after the type locality, the Straits of Johor between Singapore and Johor, Malaysia.

Distribution. Presently only known from the type locality.

Habitat. Sand-mud bottoms at depths of 6.7–14.7 m.

Remarks. *Neogebicula johorensis*, new species, is most similar to *N. leptomorpha* (Sakai, 2006) from the Persian Gulf, with respect to the general shape of the rostrum and lateral ridges of the gastric region. The new species differs from *N. leptomorpha* (characters in parentheses) by 1) the presence of only one postocular spine (two postocular spines); 2) the proximal article of the antennular peduncle having a ventral spine (without spine); 3) the third and fourth articles of the antennal peduncle each armed with a ventral spine (unarmed); and 4) the posterior margin of the telson with a small median spine (without spine). The new species also shows some similarities with the eastern Atlantic *N. contigua* (Božić & de Saint Laurent, 1972), differing from it (characters in parentheses) in 1) the presence of a large mesio-anterior tooth on the mandible (absent); 2) the antennular acicle being simple distally (with bifid tip); 3) the presence of several spines on the upper border of the first pereopod propodus (only one distal spine); and 4) the sixth pleomere being as long as wide (1.2 times longer than wide). In addition, both *N. leptomorpha* and *N. contigua* lack hepatic spines, whereas in *N. johorensis*, new species, they are present in three out of five specimens of the type series.

Wolffogebia Sakai, 1982

Wolffogebia phuketensis Sakai, 1982
(Fig. 1i, j)

Wolffogebia phuketensis Sakai, 1982: 75, figs. 17a, 18c, d, 20b; — Ngoc-Ho, 1994: 213, fig. 12; — Ngoc-Ho et al., 2001: 108; — Sakai & Türkay, 2014: 157.

CMBS material. 1 male (15/4.6) (ZRC 2018.0546), sta. SW126, Sungei Buloh, 1°27.064′N 103°43.319′E, mangrove, in mud, beach seine and hand nets, intertidal (low tide), coll. KS Koh, YL Lee et al., 30 October 2012 (JS-2695); 1 male (37/10.3) (NHMW 26036), sta. SW137, Pulau Ubin, OBS Camp 1, 1°25′15.77″N 103°55′57.00″E, near brackish stream in secondary forest, low tide, coll. R Lasley, JC Mendoza, 31 October 2012 (JS-3001).

Description. See Sakai (1982) and Ngoc-Ho (1994).

Distribution. Phuket, Thailand (Sakai, 1982, type locality); Can Gio, Vietnam (Marin, 2021); Singapore (Ngoc-Ho, 1994); Sumatra, Indonesia (Sakai & Türkay, 2014).

Habitat. Intertidal, in thick mangrove mud (Ngoc-Ho, 1994; Marin, 2021; this study).

Wolffogebia inermis Sakai, 1982

Wolffogebia inermis Sakai, 1982: 81, figs. 17c, 18g, 19a, b, 20e, pl. G6; — Sakai, 1993: 109, figs. 12–14; — Ngoc-Ho, 1994: 213, figs. 10, 11; — Ngoc-Ho et al., 2001: 108.

CMBS material. 1 male (24/6.7) (ZRC 2017.0949), sta. M04, Pulau Ubin, between OBS Camp Jetty 1 and OBS Camp Jetty 2, off reservoir, near mangrove, muddy intertidal, coll. KS Tan et al., 6 March 2012.

Description. See Sakai (1982) and Ngoc-Ho (1994).

Distribution. Vietnam; Java, Indonesia; Darwin, Australia (Sakai, 2006); newly recorded from Singapore (this study).

Habitat. Intertidal, in mangrove mud (Ngoc-Ho, 1994; this study).

Remarks. Sakai (1982: fig. 18g) showed no median spine on the telson of *W. inermis*, in contrast to Sakai (1993: fig. 12C). The telson was not figured nor described by Ngoc-Ho (1994). Nevertheless, the Singaporean specimen has a blunt median spine on the telson, as figured by Sakai (1993).

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