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First Zoeal Stage of 15 Species of Fiddler Crabs (Crustacea: Brachyura: Ocypodidae) from Taiwan

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Fiddler crabs (Brachyura: Ocypodidae: Gelasiminae) in Taiwan consist of 5 genera and 15 species, but knowledge of their larval development is limited to just 3 species, namely *Austruca lactea*, *Tubuca arcuata*, and *Xeruca formosensis*. In our study, the morphology of the first zoeal stage (zoea I) of the 15 species is described and compared to previous studies. The results show that the characters of zoea I can be used to distinguish the five studied genera and most species (except three groups, "*Gelasimus borealis*, *G. jocelynae* and *G. vocans*", "*Paraleptuca crassipes* and *P. splendida*" and "*Tubuca arcuata*, *T. coarctata* and *T. paradussumieri*"). The lateral spines on the carapace in zoea I are suggested to be a unique character in the Ocypodinae because they are absent in the Gelasiminae and Ucidinae, which supports the current systematics of the Ocypodidae.

Key words: Larva, Morphology, Systematics, *Austruca*, *Gelasimus*, *Paraleptuca*, *Tubuca*, *Xeruca*.

BACKGROUND

The larval morphology of brachyuran crabs plays an important role in brachyuran systematics because it is less influenced by convergence and environmental adaptation than adult morphology (Rice 1980). Some characters of larval morphology have already been used in the diagnosis of the superfamily Majoidea Samouelle, 1819 (Hultgren and Stachowicz 2008), family Xenograpsidae N.K. Ng, Davie, Schubart & Ng, 2007 (NK Ng et al. 2007), genera *Eriocheir* De Haan, 1835 *sensu lato* (NK Ng et al. 1999) and *Scandarma* Schubart, Liu & Cuesta, 2003 (Schubart et al. 2003), and even species, such as *Hemigrapsus penicillatus* (De Haan, 1835) and *H. takanoi* Asakura & Watanabe, 2005 (Landeira et al. 2019).

Fiddler crabs (family Ocypodidae Rafinesque, 1815) are brachyuran crabs that inhabit intertidal areas. There are 107 described species encompassing 11 genera, including all members in the subfamily Gelasiminae Miers, 1886, as well as the genera *Afruca* Crane, 1975 and *Uca* Leach, 1814 in the subfamily Ocypodinae Rafinesque, 1815 (Shih et al. 2016a 2018 2019; Shih and Poupin 2020). Many studies have focused on the adult morphology of fiddler crabs (*e.g.*, Crane 1975; Shih et al. 2016a), whereas the comparatively fewer reports on the larval morphology cover only 23 species within 9 genera (Table 1). Among these species, 19 are in the Gelasiminae (five in *Austruca* Bott, 1973, *Cranuca inversa* (Hoffmann, 1874), and *Gelasimus hesperiae* (Crane, 1975); four in *Leptuca* Bott, 1973; six in *Minuca* Bott, 1954; three in *Tubuca* Bott, 1973 and *Xeruca formosensis* (Rathbun, 1921) and two in the Ocypodinae (*Afruca tangeri* (Eydoux, 1835) and *Uca maracoani* (Latreille, 1803)), but none in the genera *Paraleptuca* Bott, 1973 and *Petruca* Shih, Ng

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& Christy, 2015 (Table 1). In addition, the characters of the first zoeal stage (zoea I) of *Austruca occientalis* (Naderloo, Schubart & Shih, 2016) (as *Au. annulipes*), *G. hesperiae*, *Paraleptuca chlorophthalmus* (H. Milne Edwards, 1837), and *T. urvillei* (H. Milne Edwards, 1852) were included in the key in Bento and Paula

Table 1. Studies of the larval morphology of fiddler crabs. ZI–VI, larval stages of zoea; M, megalopa; *, species identified by Apel (2001)

Species	Original species names	Stages described	References
Subfamily Gelasiminae			
Austruca albimana		ZI–IV, M	Kumar and Al-Aidaroos 2022
Austruca annulipes	*Uca annulipes*	ZI–V, M	Feest 1969
	Uca annulipes	ZI	Ghory and Siddiqui 2006
Austruca iranica	*Gelasimus annulipes**	ZI–II	Hashmi 1968
Austruca lactea	*Uca lactea*	M	Muraoka 1976
	Uca lactea	ZI–V	Terada 1979
		ZI	this study
Austruca perplexa		ZI	this study
Austruca triangularis		ZI	this study
Austruca variegata (Heller, 1862)	*Uca triangularis*	ZI–V, M	Feest 1969
Cranuca inversa	*Uca* (*Cranuca*) *inversa*	ZI	Al-Aidaroos 2013
Gelasimus borealis		ZI	this study
Gelasimus hesperiae	*Gelasimus marionis*	ZI	Hashmi 1968
Gelasimus jocelynae		ZI	this study
Gelasimus tetragonon		ZI	this study
Gelasimus vocans		ZI	this study
Leptuca cumulanta		ZI	Rosário et al. 2021
Leptuca pugilator (Bosc, 1802)	*Gelasimus pugilator*	ZI–IV, M	Hyman 1920
Leptuca subcylindrica (Stimpson, 1859)	*Uca subcylindrica*	ZI–II, M	Rabalais and Cameron 1983
Leptuca thayeri	*Uca thayeri*	ZI–V, M	Anger et al. 1990
	Uca thayeri	ZI	De Souza et al. 2013
Leptuca uruguayensis	*Uca* (*Celuca*) *uruguayensis*; *Uca uruguayensis*	ZI–VI, M	Rieger 1996; Armendariz 2005
Minuca burgersi	*Uca* (*Minuca*) *burgersi*	ZI–VI, M	Rieger 1998
Minuca minax (LeConte, 1855)	*Gelasimus minax*	ZI	Hyman 1920
Minuca mordax (Smith, 1870)	*Uca* (*Minuca*) *mordax*	ZI–VI, M	Rieger 1997
Minuca pugnax (Smith, 1870)	*Gelasimus pugnax*	ZI–II	Hyman 1920
Minuca rapax	*Uca rapax*	ZI	Serbino 2008a
	Uca rapax	ZI	De Souza et al. 2013
Minuca vocator	*Uca* (*Minuca*) *vocator*	ZI–VI, M	Rieger 1999
	Uca vocator	ZI	Serbino 2008c
Paraleptuca crassipes		ZI	this study
Paraleptuca splendida		ZI	this study
Tubuca alcocki	*Uca urvillei*	ZI	Ghory and Siddiqui 2006
Tubuca arcuata	*Uca arcuata*	ZI–V, M	Ko and Kim 1989
		ZI	this study
Tubuca acuta		ZI	this study
Tubuca coarctata		ZI	this study
Tubuca dussumieri		ZI	this study
Tubuca paradussumieri		ZI	this study
Tubuca urvillei	*Uca urvillei*	ZI	Serbino 2008b
Xeruca formosensis	*Uca formosensis*	ZI–V	Hsieh and Chen 2008
		ZI	this study
Subfamily Ocypodinae			
Afruca tangeri	*Uca tangeri*	ZI–V, M	Rodriguez and Jones 1993
	Uca tangeri	ZI–V	Spivak and Cuesta 2009
Uca maracoani	*Uca* (*Uca*) *maracoani*	ZI, M	Negreiros-Fransozo et al. 2009
		ZI	De Souza et al. 2013

(2018), but there was no drawing and description.

In Taiwan, 15 species of fiddler crabs have been reported, including the endemic *X. formosensis* (Shih et al. 2015 2016b; Ng et al. 2017). However, the larval morphology of only three species, namely *Austruca lactea* (De Haan, 1835), *T. arcuata* (De Haan, 1835), and *X. formosensis* have been described (Terada 1979; Ko and Kim 1989; Hsieh and Chen 2008). Our study describes the morphology of zoea I of the 15 species from Taiwan, with a key based on more reliable characters. The important characters among species and genera are also discussed, according to the current systematics and phylogeny of fiddler crabs (Shih et al. 2016a).

MATERIALS AND METHODS

Ovigerous females of the 15 fiddler crab species from Taiwan were collected from Hsinchu City (Yangang R.), Taichung (Dajia R.), Changhua (Siansi), Tainan (Bajhang R.), and Pingtung (Baoli R. and Wanlitong) in Taiwan main island, as well as its adjacent islands, Penghu, Kinmen, and Dongsha (Table 2). The specimens of ovigerous females and released larvae were deposited into the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL). Ovigerous females were measured for carapace width (cw) (Table 2) and identified by Shih et al. (2015) and, if necessary, by analysis of the cytochrome oxidase subunit I (*COI*; unpublished). However, because the *COI* marker cannot distinguish *G. borealis* (Crane, 1975) and *G. vocans* (Linnaeus, 1758) (Shih et al. 2010), these species were identified by their ITS-1 sequences (Chu et al. 2015; HT Shih unpublished).

Each ovigerous female was kept in an opaque container (bottom dimensions of 20 × 12 or 50 × 31 cm) with 30‰ seawater (ratio of natural to artificial seawater = 1:1) changed once every 2 days. The water was 2 cm high, and the bottom of the container was covered with sediment from the specimens' habitat, with a portion of the sediment above the water surface. After the larval release, the zoeae were attracted by a flashlight and collected by a plastic dropper. Some zoeae were preserved in 70% ethanol directly. The remaining zoeae were first preserved in 4% buffered formalin, which was changed once every 1 h for 3 h, then preserved in 70%

Table 2. The ovigerous females used in this study

Species	Catalogue no. (NCHUZOOL)	Locality in Taiwan	cw (mm)	Date of collection
Austruca lactea	16768	Changhua: Siansi	11.9	12 Jul. 2018
	16769	Changhua: Siansi	11.8	12 Jul. 2018
Austruca perplexa	16770	Pingtung: Wanlitong, Kenting	9.9	13 Mar. 2021
Austruca triangularis	16771	Pingtung: Baoli River estuary	13.8	16 Oct. 2020
	16772	Pingtung: Baoli River estuary	11.4	16 Oct. 2020
Gelasimus borealis	16773	Taichung: Dajia River estuary	23.1	9 Sep. 2018
	16774	Taichung: Dajia River estuary	22.0	9 Sep. 2018
Gelasimus jocelynae	16775	Penghu: Chihsi, Siyu	16.4	31 Jul. 2020
	16776	Penghu: Chihsi, Siyu	18.1	31 Jul. 2020
	16777	Penghu: Chihsi, Siyu	17.2	31 Jul. 2020
Gelasimus tetragonon	16778	Dongsha Island	32.6	17 Jun. 2019
Gelasimus vocans	16779	Penghu: Chihsi, Siyu	23.9	31 Jul. 2020
	16780	Penghu: Chihsi, Siyu	21.3	31 Jul. 2020
	16781	Penghu: Chihsi, Siyu	23.9	31 Jul. 2020
Paraleptuca crassipes	16782	Dongsha Island	18.2	17 Jun. 2019
Paraleptuca splendida	16783	Penghu: Cingluo	13.5	3 Aug. 2020
Tubuca acuta	16784	Kinmen: Cihti	15.9	18 Aug. 2020
Tubuca arcuata	16785	Tainan: Bajhang River estuary	24.9	17 Apr. 2020
Tubuca coarctata	16786	Pingtung: Baoli River estuary	19.2	8 Nov. 2018
Tubuca dussumieri	16787	Pingtung: Baoli River estuary	21.9	8 Nov. 2018
Tubuca paradussumieri	16788	Kinmen: Cihti	18.8	20 Aug. 2020
Xeruca formosensis	16789	Changhua: Siansi	15.0	12 Aug. 2018
	16790	Hsinchu County: Yangang River estuary	26.4	18 Sep. 2020

ethanol for final fixation.

For each species, 1–3 ovigerous females were used (Table 2), and 20 zoeae were selected from each female. Each zoea was put in glycerin and dissected under a stereoscope using tiny needles. To enhance observation, the sample was either dyed with eosin or immersed in lactic acid (Rice 1981; Schoeman and Cockcroft 1996) for imaging under a phase-contrast microscope. Multiple images were stacked using Helicon Focus 5.0 stacking software into a focus-stacking image for illustration, and the morphological character states were described. The characters were measured for 20 zoeae using AxioVision Rel. 4.8 software. We found that the characters examined were stable within a species.

The terminology of larval description followed Bookhout and Costlow (1974), Pohle and Telford (1981), Clark et al. (1988), Anger et al. (2015), Clark and Cuesta (2015), Landeira et al. (2019) and Colavite et al. (2021) and included the carapace, antennule, antenna, maxillule, maxilla, first maxilliped, second maxilliped, pleon, and telson. Based on Pohle (1991), the measurements provided (in millimeters) are of the carapace length (cl), rostro-dorsal length (rdl), dorsal spine length (dsl), and rostral spine length (rsl) (Fig. 1).

RESULTS

Description of the first zoeal stage *Austruca* Bott, 1973

Austruca lactea (De Haan, 1835)

(Fig. 2, Table 3)

Material examined: zoea I (from ♀ 11.9 mm, NCHUZOOL 16768, Siansi, Changhua, coll. Y.-C. Zhang et al., 14 Aug. 2018); zoea I (from ♀ 11.8 mm, NCHUZOOL 16769, Siansi, Changhua, coll. Y.-C. Zhang et al., 14 Aug. 2018).

Size: cl. 0.35 ± 0.008 mm, rdl. 0.58 ± 0.016 mm, dsl. 0.11 ± 0.008 mm, rsl. 0.14 ± 0.008 mm.

Carapace (Fig. 2A): Lateral spines lacking, dorsal spine curved, relatively short, rostral spine straight, dorsal spine and rostral spine with pointed termination. Eyes round and sessile.

Antennule (Fig. 2B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 2C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod and endopod absent.

Maxillule (Fig. 2D): Epipod seta absent; coxal

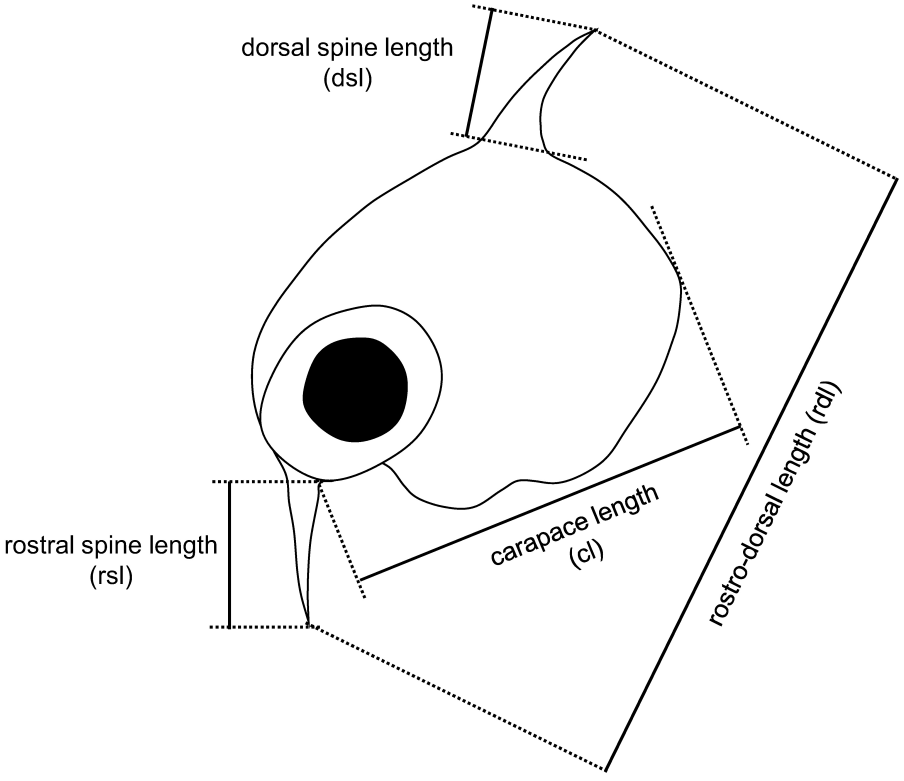

Fig. 1. The measurements of the first zoeal stage used in this study.

endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article; exopod seta absent.

Maxilla (Fig. 2E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 2F): Basis with 2+2+3+2

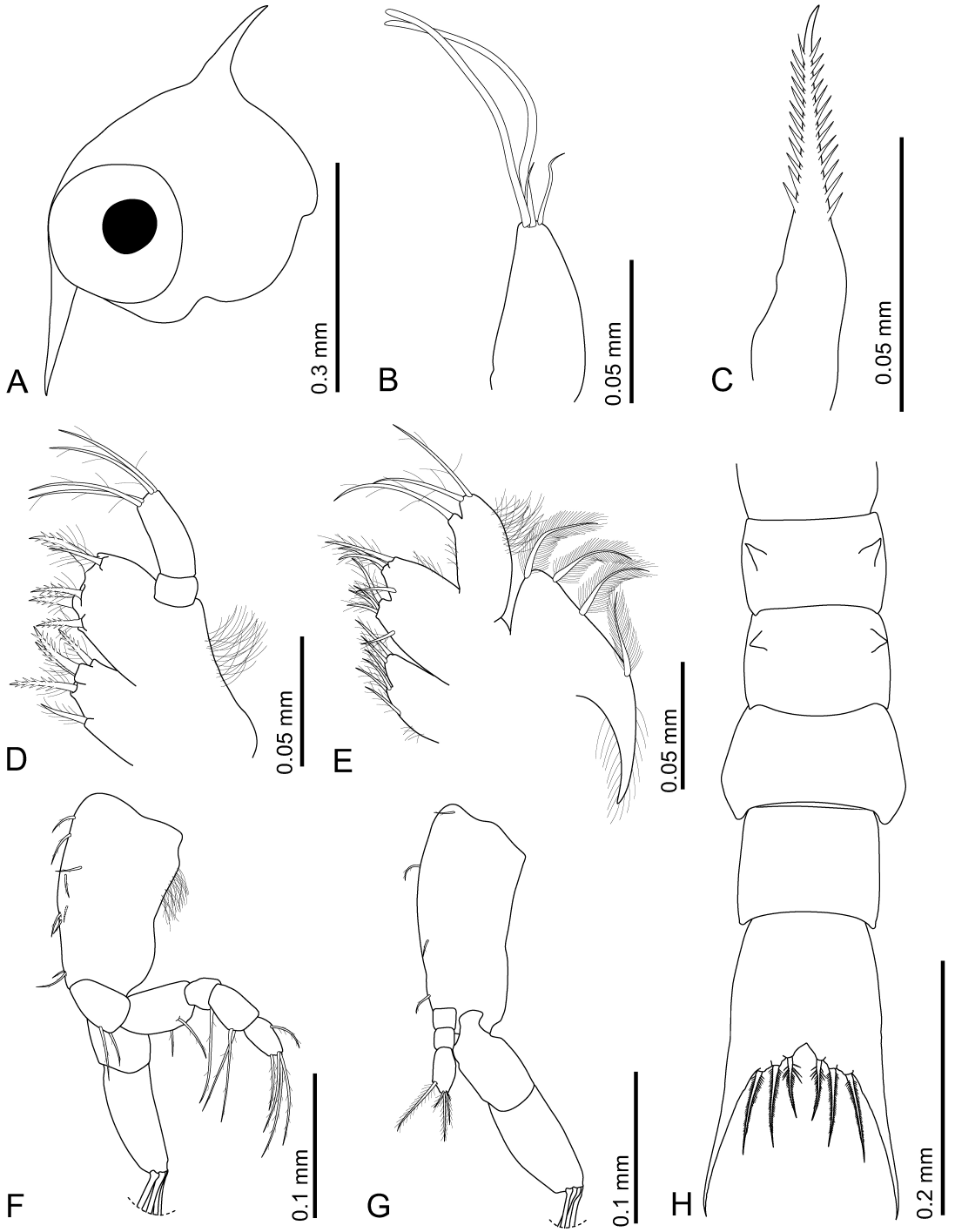

Fig. 2. *Austruca lactea*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 2G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 2H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 2H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

Austruca perplexa **(H. Milne Edwards, 1852)**

(Fig. 3, Table 3)

Material examined: zoea I (from ♀ 9.9 mm, NCHUZOOL 16770, Wanlitong, Pingtung, coll. Y.-C. Zhang et al., 13 Mar. 2021).

Size: cl. 0.46 ± 0.014 mm, rdl. 0.88 ± 0.024 mm, dsl. 0.20 ± 0.008 mm, rsl. 0.23 ± 0.008 mm.

Carapace (Fig. 3A): Lateral spines lacking, dorsal spine slightly curved, relatively short, rostral spine straight, dorsal spine and rostral spine with pointed termination. Eyes round and sessile.

Antennule (Fig. 3B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 3C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod short, with 1 terminal simple seta, seta not reaching tip of protopod. Endopod absent.

Maxillule (Fig. 3D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article; exopod seta absent.

Maxilla (Fig. 3E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 3F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 3G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 3H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 3H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

Austruca triangularis **(A. Milne-Edwards, 1873)**

(Fig. 4, Table 3)

Material examined: zoea I (from ♀ 13.8 mm, NCHUZOOL 16771, Baoli River estuary, Pingtung, coll. Y.-C. Zhang et al., 18 Oct. 2020); zoea I (from ♀ 11.4 mm, NCHUZOOL 16772, Baoli River estuary, Pingtung, coll. Y.-C. Zhang et al., 20 Oct. 2020).

Size: cl. 0.42 ± 0.011 mm, rdl. 0.67 ± 0.029 mm, dsl. 0.13 ± 0.007 mm, rsl. 0.16 ± 0.013 mm.

Carapace (Fig. 4A): Lateral spines lacking, dorsal spine curved, relatively short, rostral spine straight, dorsal spine and rostral spine with pointed termination. Eyes round and sessile.

Antennule (Fig. 4B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 4C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod short, with 2 terminal simple setae, setae not reaching tip of protopod. Endopod absent.

Maxillule (Fig. 4D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article; exopod seta absent.

Maxilla (Fig. 4E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 4F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 4G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 4H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a

pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 4H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

***Gelasimus* Latreille, 1817**
***Gelasimus borealis* (Crane, 1975)**
(Fig. 5, Table 3)

Material examined: zoea I (from ♀ 23.1 mm, NCHUZOOL 16773, Dajia River estuary, Taichung,

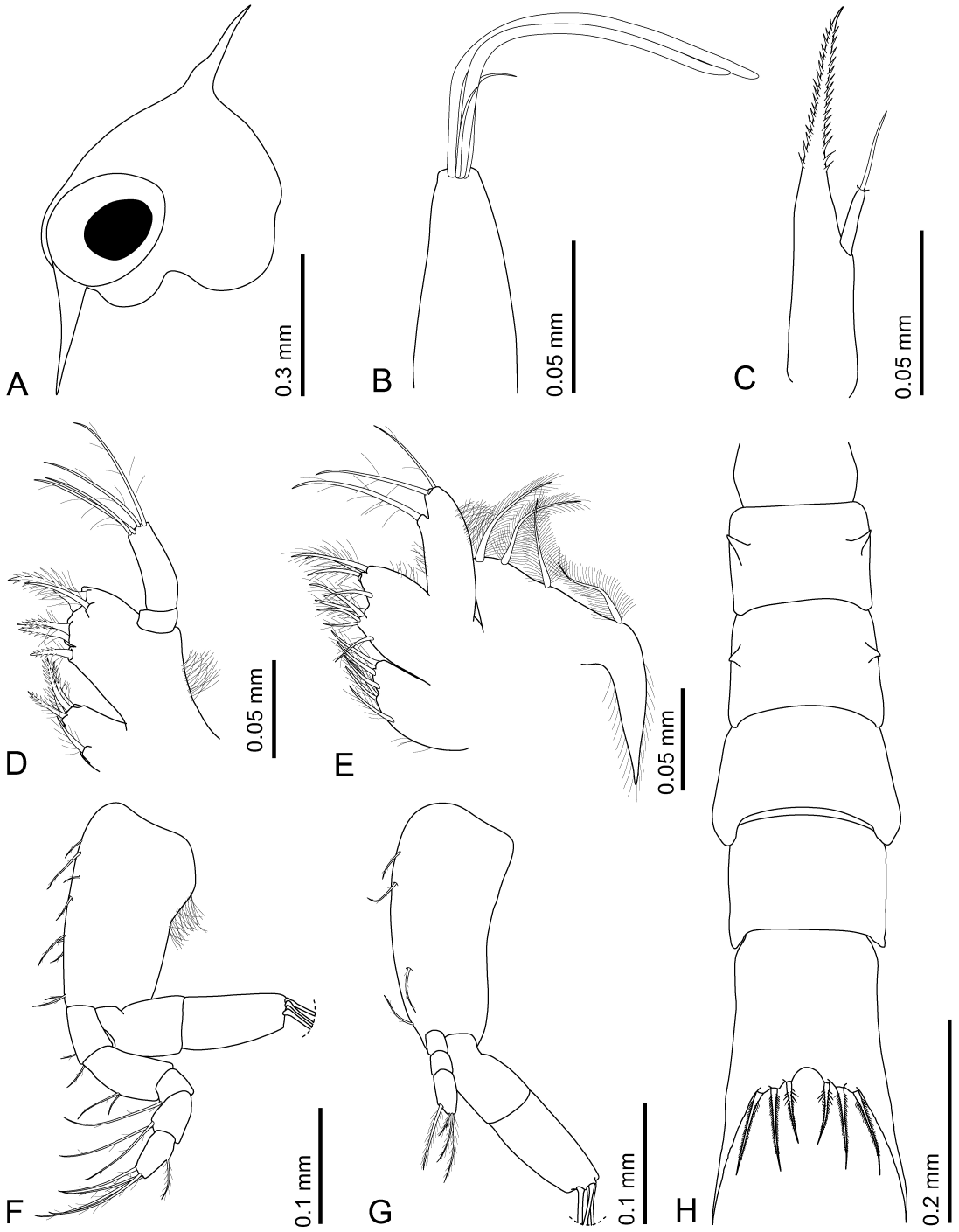

Fig. 3. *Austruca perplexa*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

coll. Y.-C. Zhang et al., 11 Sep. 2018); zoea I (from ♀ 22.0 mm, NCHUZOOL 16774, Dajia River estuary, Taichung, coll. Y.-C. Zhang et al., 13 Sep. 2018).

Size: cl. 0.32 ± 0.011 mm, rdl. 0.41 ± 0.015 mm, dsl. 0.04 ± 0.006 mm, rsl. 0.06 ± 0.008 mm.

Carapace (Fig. 5A): Lateral spines lacking, dorsal spine curved and very reduced, rostral spine straight and very reduced, dorsal spine as long as rostral spine and pointed termination. Eyes round and sessile.

Antennule (Fig. 5B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 5C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod short, with 1 terminal simple seta, seta not reaching tip of protopod. Endopod absent.

Maxillule (Fig. 5D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article; exopod seta absent.

Maxilla (Fig. 5E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 5F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 5G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 5H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral

Table 3. The setation of different appendages in zoea stage I of 15 species of fiddler crabs from Taiwan. See figures 2–16

Structure		*Au. lactea*	*Au. perplexa*	*Au. triangularis*	*G. borealis*	*G. jocelynae*	*G. tetragonon*	*G. vocans*
antennule	exopod	2 aes+2 ss	2 aes+2 ss	2 aes+2 ss	2 aes+2 ss	2 aes+2 ss	2 aes+2 ss	2 aes+2 ss
antenna	exopod	–	1 ss	2 ss	1 ss	1 ss	2 ss	1 ss
maxillule	coxal endite	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps
	basial endite	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps
	endopod	4 ps	4 ps	4 ps	4 ps	4 ps	4 ps	4 ps
maxilla	coxal endite	3 ps+3 ps	3 ps+3 ps	3 ps+3 ps	3 ps+3 ps	3 ps+3 ps	3 ps+3 ps	3 ps+3 ps
	basial endite	5 ps+4 ps	5 ps+4 ps	5 ps+4 ps	5 ps+4 ps	5 ps+4 ps	5 ps+4 ps	5 ps+4 ps
	endopod	1 ps+2 ps	1 ps+2 ps	1 ps+2 ps	1 ps+2 ps	1 ps+2 ps	1 ps+2 ps	1 ps+2 ps
	scaphognathite	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps
first maxilliped	basial endite	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)
	endopod	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)
	exopod	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps
second maxilliped	basial endite	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)
	endopod	0, 0, 5 ps	0, 0, 5 ps	0, 0, 5 ps	0, 0, 5 ps	0, 0, 5 ps	0, 0, 5 ps	0, 0, 5 ps
	exopod	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps

Structure		*P. crassipes*	*P. splendida*	*T. acuta*	*T. arcuata*	*T. coarctata*	*T. dussumieri*	*T. paradussumieri*	*X. formosensis*
antennule	exopod	2 aes+2 ss	2 aes+2 ss	2 aes+2 ss	2 aes+2 ss	2 aes+2 ss	2 aes+2 ss	2 aes+2 ss	2 aes+2 ss
antenna	exopod	–	–	2 ss	1 ss	1 ss	2 ss	1 ss	2 ss
maxillule	coxal endite	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps
	basial endite	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps	4 pds+1 ps
	endopod	4 ps	4 ps	4 ps	4 ps	4 ps	4 ps	4 ps	4 ps
maxilla	coxal endite	3 ps+3 ps	3 ps+3 ps	3 ps+3 ps	3 ps+3 ps	3 ps+3 ps	3 ps+3 ps	3 ps+3 ps	3 ps+3 ps
	basial endite	5 ps+4 ps	5 ps+4 ps	5 ps+4 ps	5 ps+4 ps	5 ps+4 ps	5 ps+4 ps	5 ps+4 ps	5 ps+4 ps
	endopod	1 ps+2 ps	1 ps+2 ps	1 ps+2 ps	1 ps+2 ps	1 ps+2 ps	1 ps+2 ps	1 ps+2 ps	1 ps+2 ps
	scaphognathite	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps
first maxilliped	basial endite	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)	2, 2, 3, 2 (ps)
	endopod	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)	2, 2, 1, 2, 5 (ps)
	exopod	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps
second maxilliped	basial endite	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)	1, 1, 1, 1 (ps)
	endopod	0, 0, 5 ps	0, 0, 5 ps	0, 0, 5 ps	0, 0, 5 ps	0, 0, 5 ps	0, 0, 5 ps	0, 0, 5 ps	0, 0, 5 ps
	exopod	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps	4 dps

(aes) aesthetasc, (dps) densely plumose seta, (pds) plumodenticulate seta, (ps) plumose seta, (ss) simple seta, (–) absent.

spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 5H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

***Gelasimus jocelynae* (Shih, Naruse & Ng, 2010)**

(Fig. 6, Table 3)

Material examined: zoea I (from ♀ 16.4 mm, NCHUZOOL 16775, Chihsi, Siyu, Penghu, coll. Y.-C. Zhang et al., 1 Aug. 2020); zoea I (from ♀ 18.1 mm,

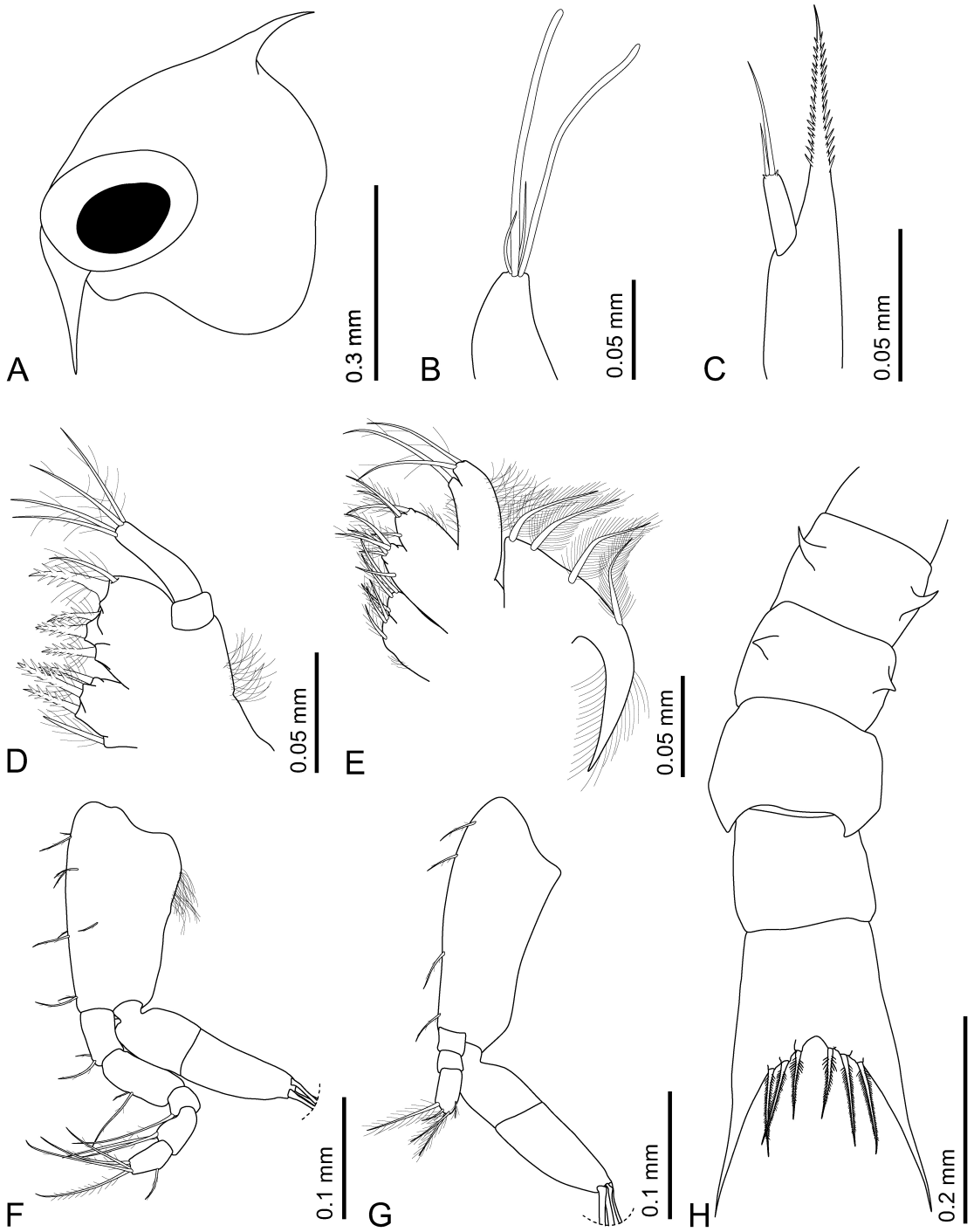

Fig. 4. *Austruca triangularis*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

NCHUZOOL 16776, Chihsi, Siyu, Penghu, coll. Y.-C. Zhang et al., 2 Aug. 2020); zoea I (from ♀ 17.2 mm, NCHUZOOL 16777, Chihsi, Siyu, Penghu, coll. Y.-C. Zhang et al., 10 Aug. 2020).

Size: cl. 0.36 ± 0.009 mm, rdl. 0.43 ± 0.011 mm, dsl. 0.04 ± 0.000 mm, rsl. 0.04 ± 0.000 mm.

Carapace (Fig. 6A): Lateral spines lacking, dorsal spine curved and very reduced, rostral spine straight, dorsal spine as long as rostral spine and pointed termination. Eyes round and sessile.

Antennule (Fig. 6B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2

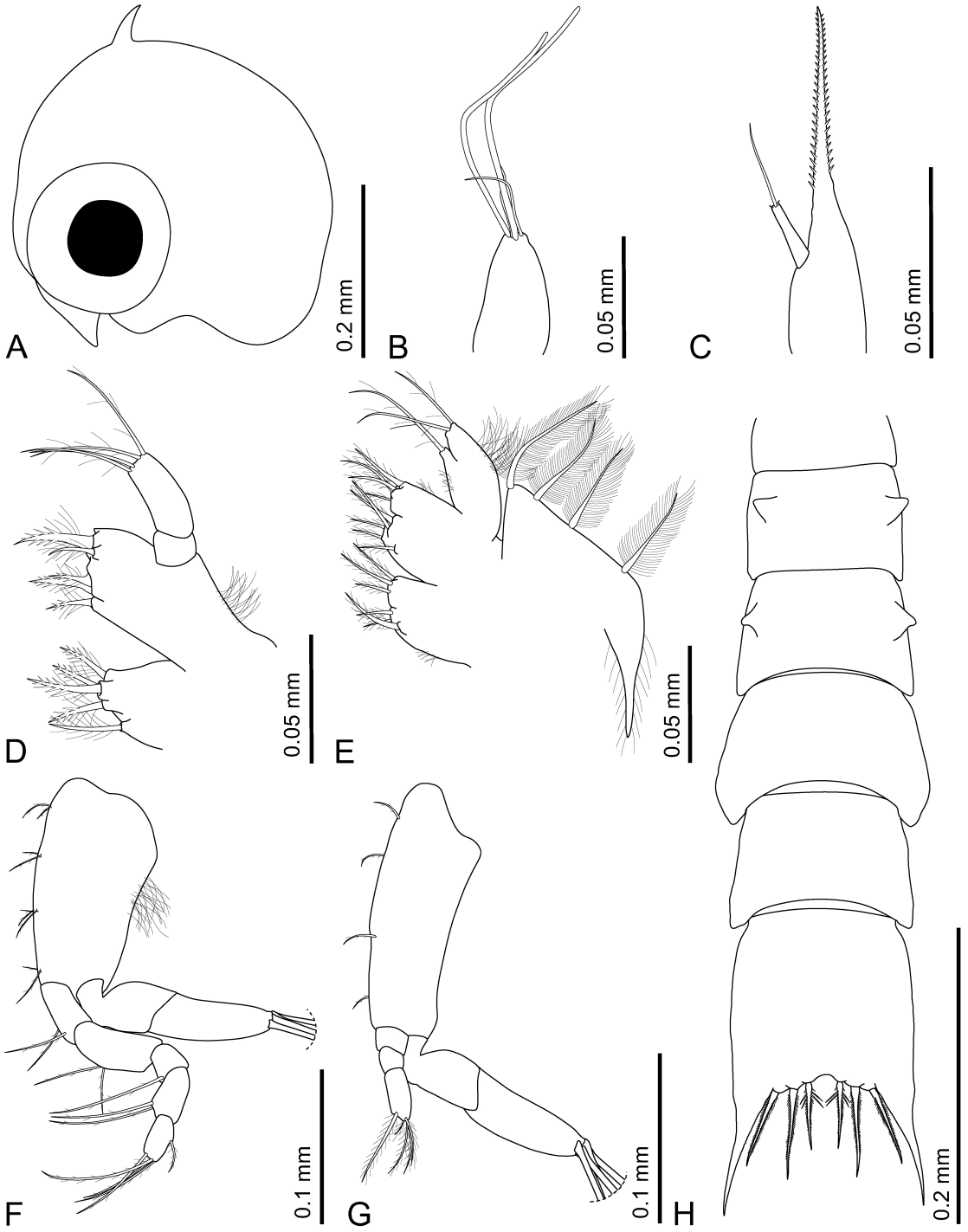

Fig. 5. *Gelasimus borealis*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

simple setae terminally.

Antenna (Fig. 6C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod short, with 1 terminal simple seta, seta not reaching tip of protopod. Endopod absent.

Maxillule (Fig. 6D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article; exopod seta absent.

Maxilla (Fig. 6E): Coxal endite bilobed with 3+3

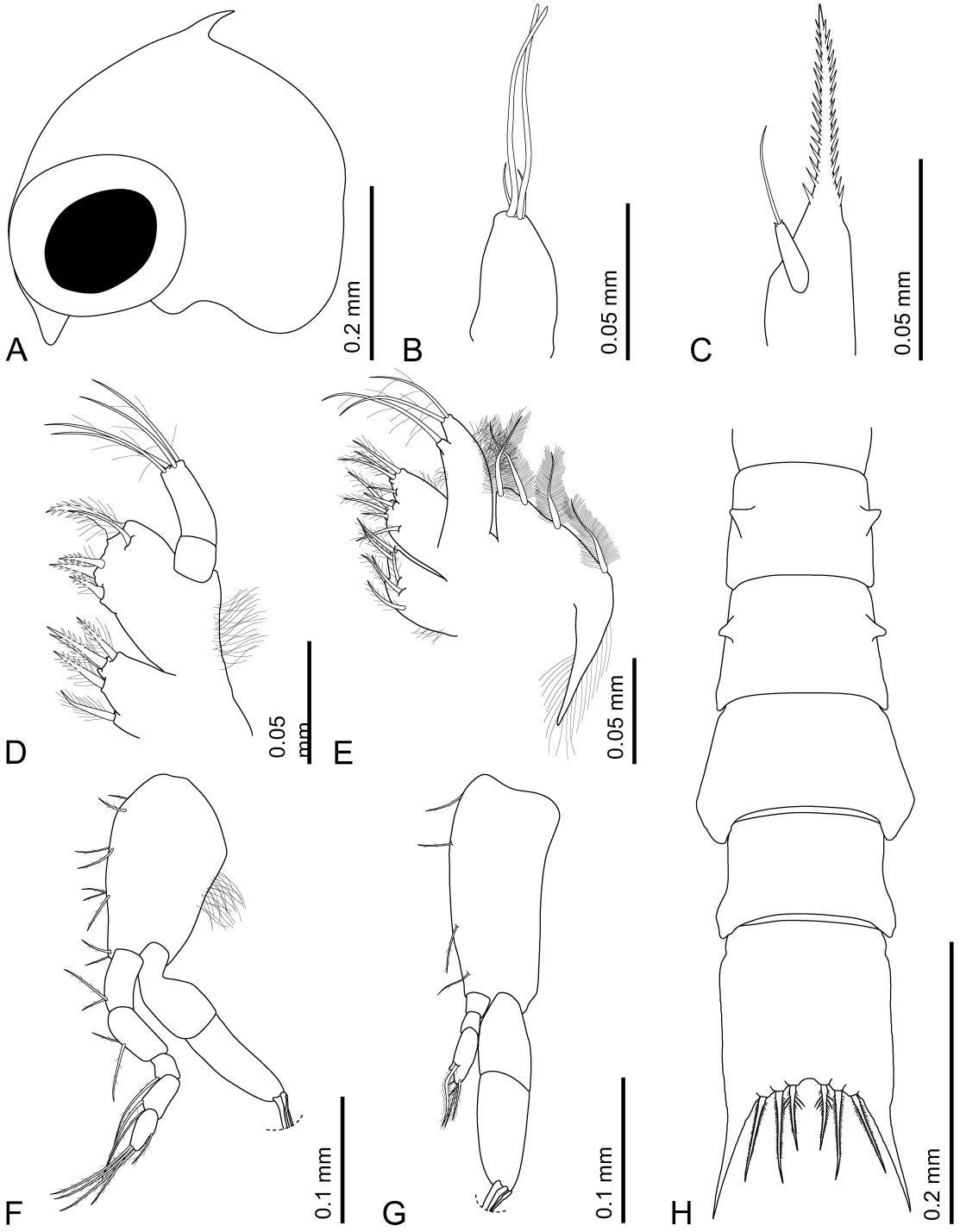

Fig. 6. *Gelasimus jocelynae*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 6F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 6G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 6H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 6H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

Gelasimus tetragonon (Herbst, 1790)

(Fig. 7, Table 3)

Material examined: zoea I (from ♀ 32.6 mm, NCHUZOOL 16778, Dongsha Island, Kaohsiung, coll. Y.-C. Zhang et al., 20 Jul. 2019).

Size: cl. 0.41 ± 0.015 mm, rdl. 0.51 ± 0.028 mm, dsl. 0.06 ± 0.022 mm, rsl. 0.06 ± 0.005 mm.

Carapace (Fig. 7A): Lateral spines lacking, dorsal spine curved and very reduced, rostral spine straight, dorsal spine as long as rostral spine and pointed termination. Eyes round and sessile.

Antennule (Fig. 7B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 7C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod short, with 2 terminal simple setae, setae not reaching tip of protopod. Endopod absent.

Maxillule (Fig. 7D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article; exopod seta absent.

Maxilla (Fig. 7E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 7F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 7G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 7H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 7H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

Gelasimus vocans (Linnaeus, 1758)

(Fig. 8, Table 3)

Material examined: zoea I (from ♀ 23.9 mm, NCHUZOOL 16779, Chihsi, Siyu, Penghu, coll. Y.-C. Zhang et al., 1 Aug. 2020); zoea I (from ♀ 21.3 mm, NCHUZOOL 16780, Chihsi, Siyu, Penghu, coll. Y.-C. Zhang et al., 4 Aug. 2020); zoea I (from ♀ 23.9 mm, NCHUZOOL 16781, Chihsi, Siyu, Penghu, coll. Y.-C. Zhang et al., 5 Aug. 2020).

Size: cl. 0.31 ± 0.013 mm, rdl. 0.39 ± 0.012 mm, dsl. 0.04 ± 0.005 mm, rsl. 0.04 ± 0.005 mm.

Carapace (Fig. 8A): Lateral spines lacking, dorsal spine curved and very reduced, rostral spine straight, dorsal spine as long as rostral spine and pointed termination. Eyes round and sessile.

Antennule (Fig. 8B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 8C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod short, with 1 terminal simple seta, seta not reaching tip of protopod. Endopod absent.

Maxillule (Fig. 8D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article; exopod seta absent.

Maxilla (Fig. 8E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 8F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal

long plumose setae.

Second maxilliped (Fig. 8G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 8H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 8H): Telson bifurcated, inner margin

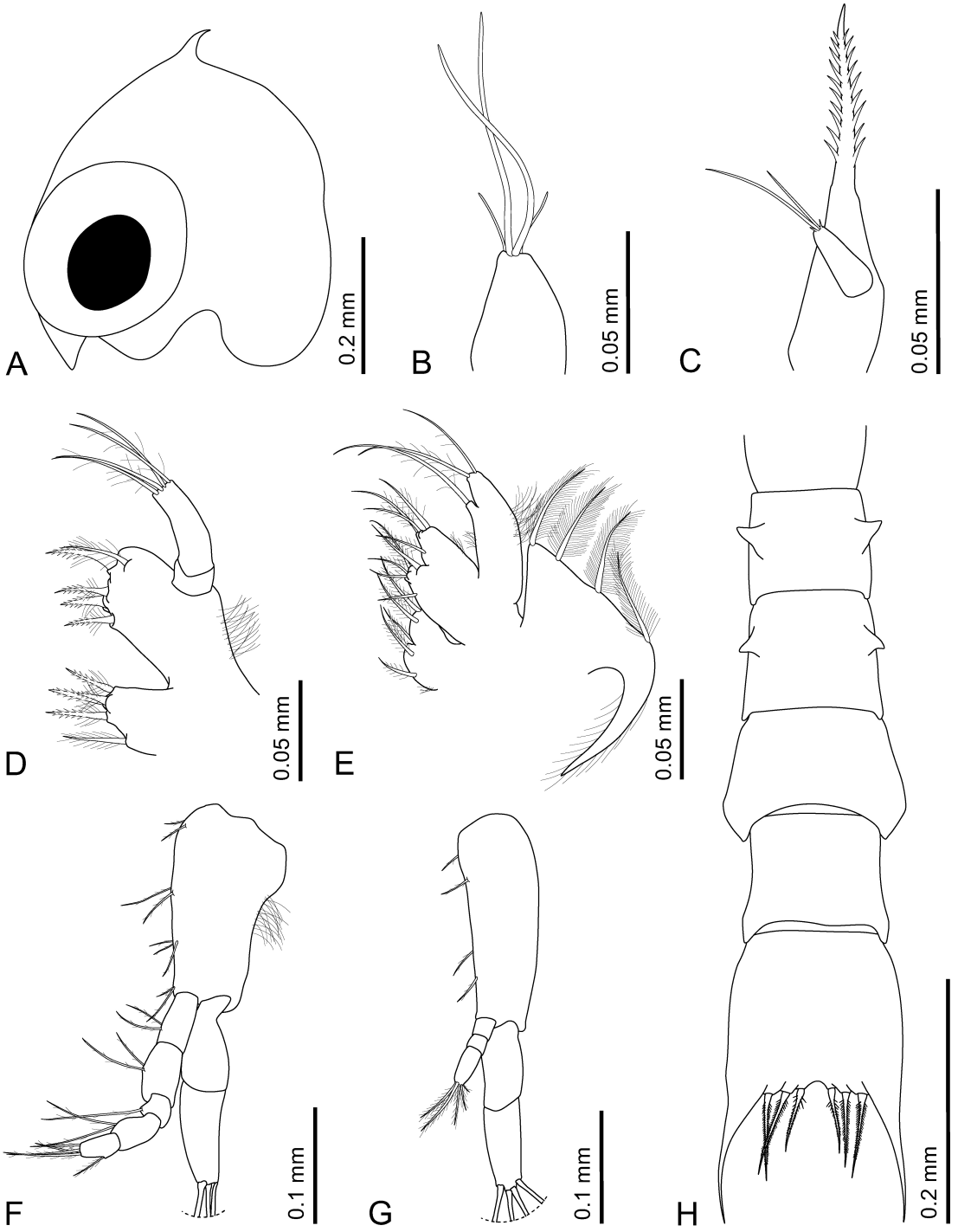

Fig. 7. *Gelasimus tetragonon*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

with 6 (3+3) serrate spines.

Paraleptuca **Bott, 1973**
Paraleptuca crassipes **(White, 1847)**
(Fig. 9, Table 3)

Material examined: zoea I (from ♀ 18.2 mm, NCHUZOOL 16782, Dongsha Island, Kaohsiung, coll. Y.-C. Zhang et al., 20 Jun. 2019).

Size: cl. 0.31 ± 0.012 mm, rdl. 0.37 ± 0.013 mm, dsl. 0.04 ± 0.000 mm, rsl. 0.04 ± 0.004 mm.

Carapace (Fig. 9A): Lateral spines lacking, dorsal spine curved and very reduced, rostral spine straight, dorsal spine as long as rostral spine and pointed

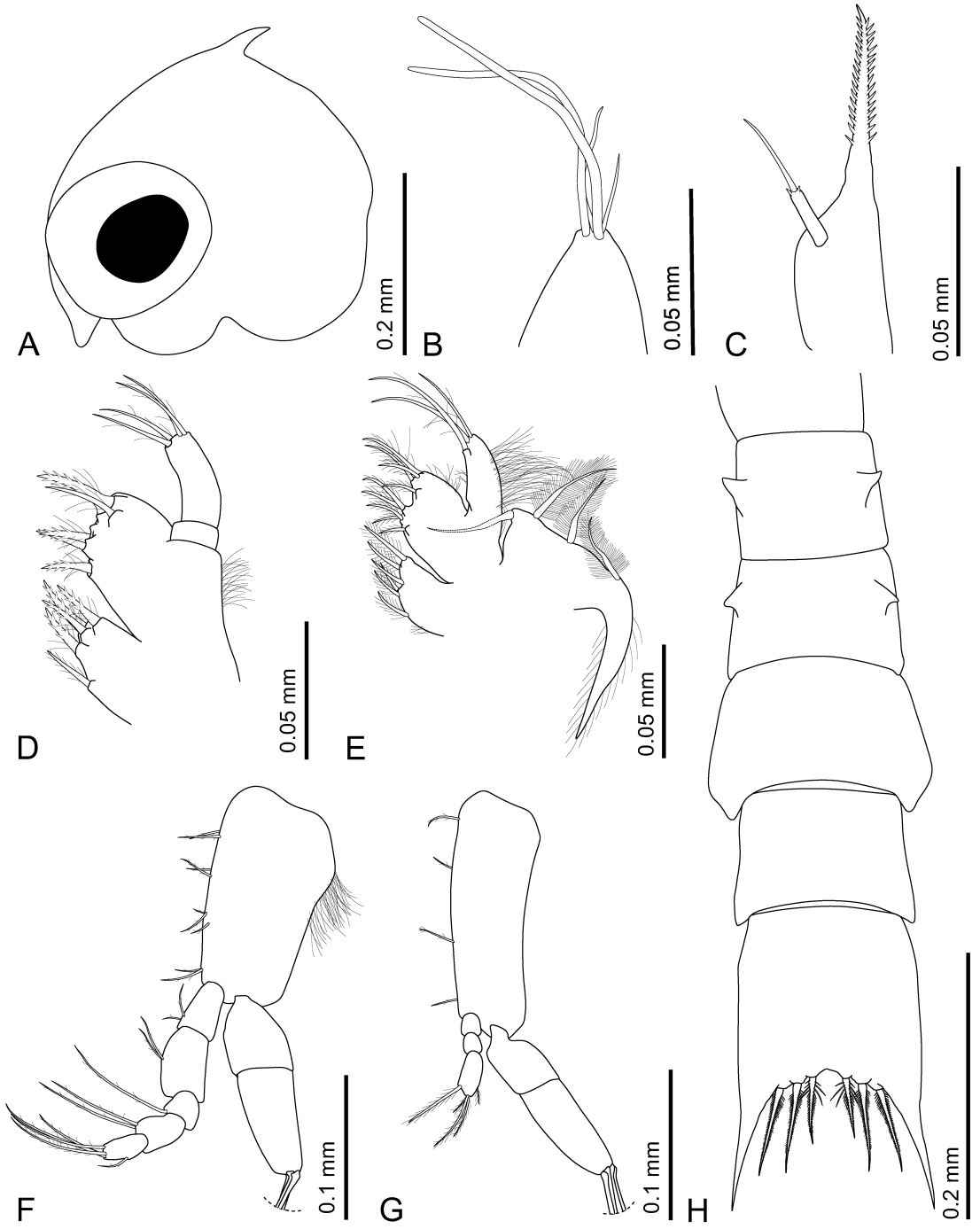

Fig. 8. *Gelasimus vocans*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

termination. Eyes round and sessile.

Antennule (Fig. 9B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 9C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod and endopod absent.

Maxillule (Fig. 9D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article;

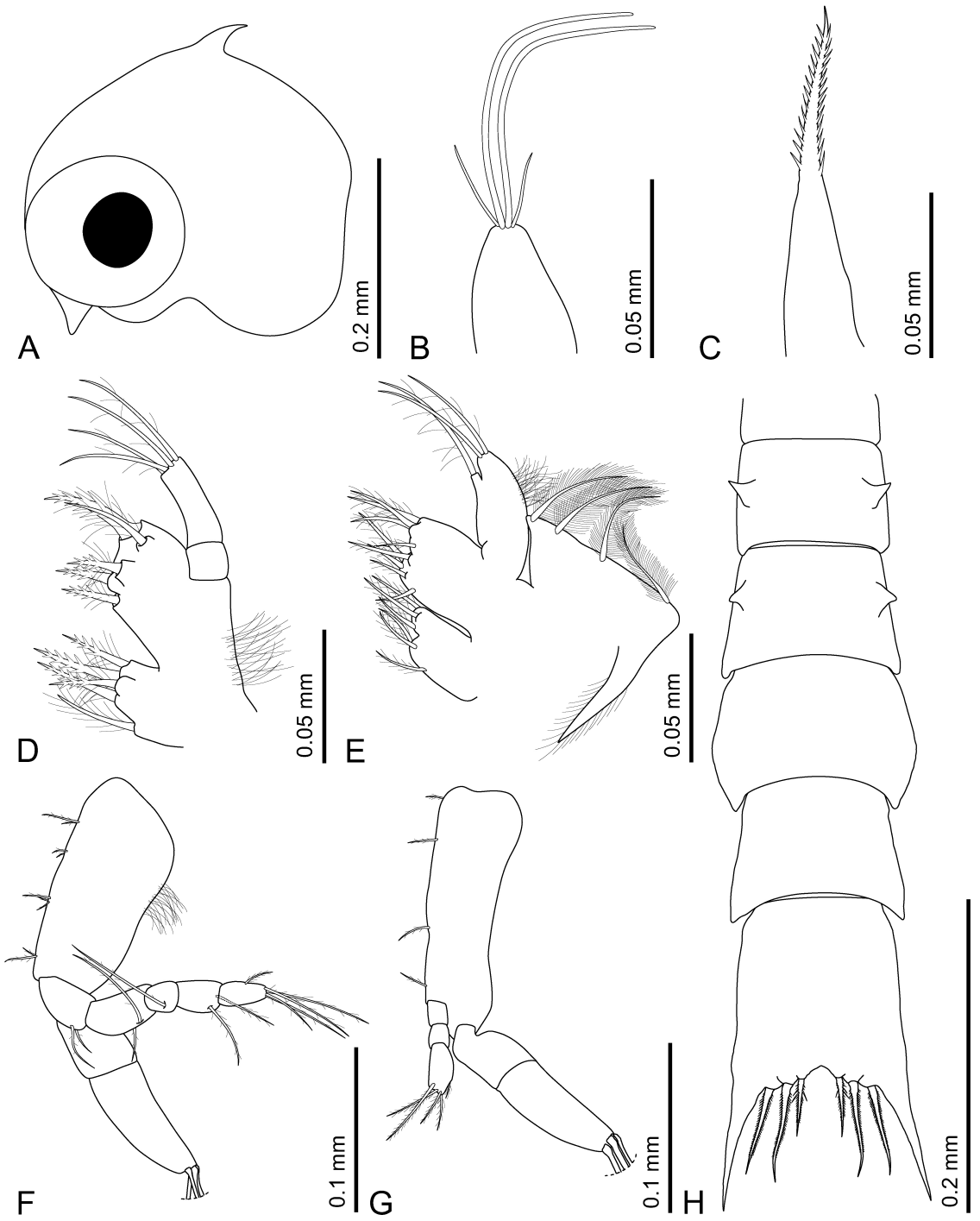

Fig. 9. *Paraleptuca crassipes*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

exopod seta absent.

Maxilla (Fig. 9E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 9F): Basis with 2+2+3, 2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 9G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 9H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 9H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

Paraleptuca splendida **(Stimpson, 1858)**

(Fig. 10, Table 3)

Material examined: zoea I (from ♀ 13.5 mm, NCHUZOOL 16783, Cingluo, Penghu, coll. Y.-C. Zhang et al., 4 Aug. 2020).

Size: cl. 0.30 ± 0.011 mm, rdl. 0.37 ± 0.015 mm, dsl. 0.04 ± 0.000 mm, rsl. 0.04 ± 0.004 mm.

Carapace (Fig. 10A): Lateral spines lacking, dorsal spine curved and very reduced, rostral spine straight, dorsal spine as long as rostral spine and pointed termination. Eyes round and sessile.

Antennule (Fig. 10B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 10C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod and endopod absent.

Maxillule (Fig. 10D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article; exopod seta absent.

Maxilla (Fig. 10E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 10F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 10G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 10H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 10H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

Tubuca **Bott, 1973**
Tubuca acuta **(Stimpson, 1858)**

(Fig. 11, Table 3)

Material examined: zoea I (from ♀ 15.9 mm, NCHUZOOL 16784, Cihti, Kinmen, coll. Y.-C. Zhang et al., 21 Aug. 2020).

Size: cl. 0.31 ± 0.010 mm, rdl. 0.49 ± 0.009 mm, dsl. 0.08 ± 0.002 mm, rsl. 0.11 ± 0.006 mm.

Carapace (Fig. 11A): Lateral spines lacking, dorsal spine curved, relatively short, rostral spine straight, dorsal spine and rostral spine with pointed termination. Eyes round and sessile.

Antennule (Fig. 11B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 11C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod short, with 2 terminal simple setae, setae not reaching tip of protopod. Endopod absent.

Maxillule (Fig. 11D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article; exopod seta absent.

Maxilla (Fig. 11E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 11F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 11G): Basis with 1+1+1+1

sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 11H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 11H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

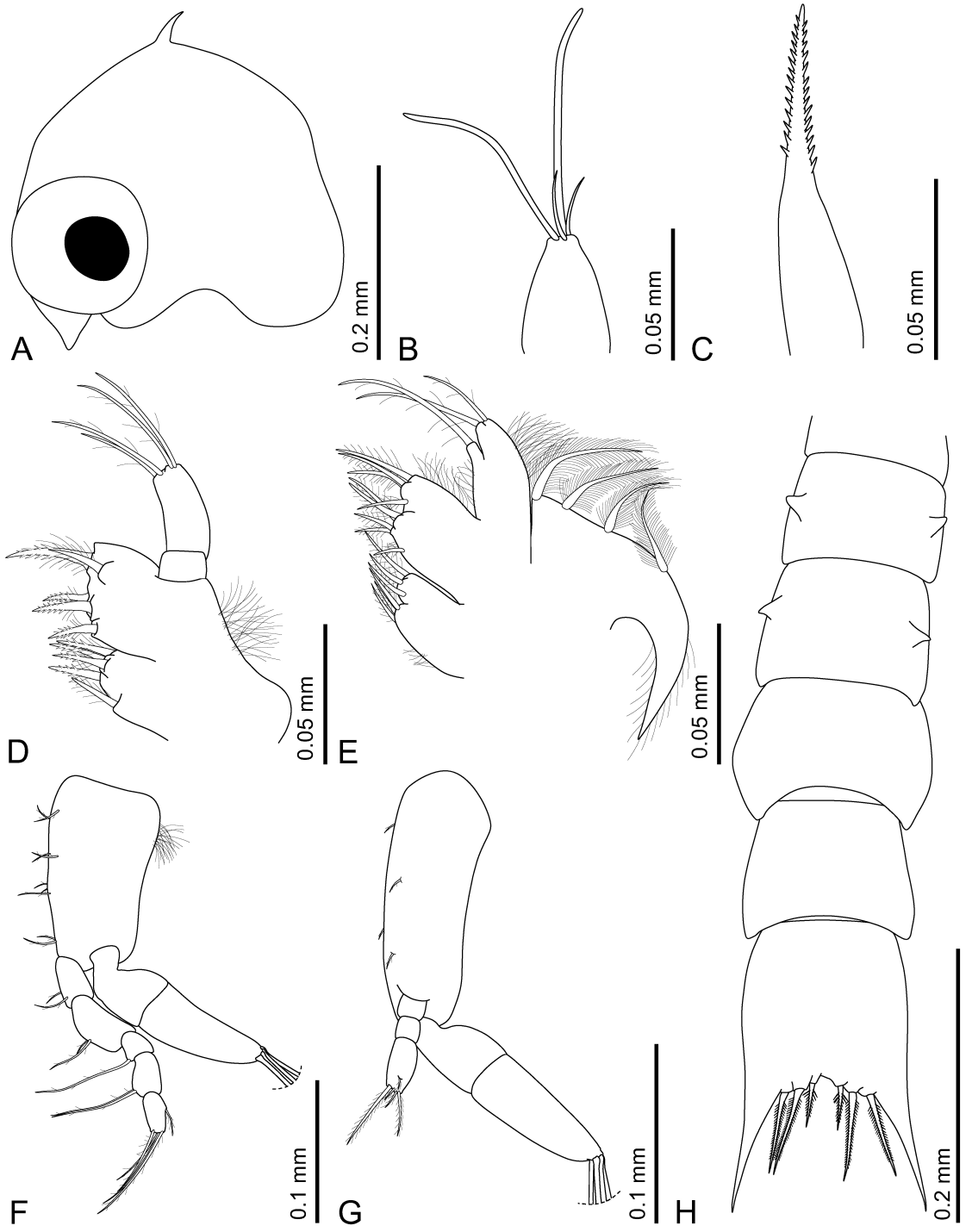

Fig. 10. *Paraleptuca splendida*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

Tubuca arcuata **(De Haan, 1835)**

(Fig. 12, Table 3)

Material examined: zoea I (from ♀ 24.9 mm, NCHUZOOL 16785, Bajhang River estuary, Tainan, coll. Y.-C. Zhang et al., 9 May. 2020).

Size: cl. 0.34 ± 0.010 mm, rdl. 0.53 ± 0.019 mm, dsl. 0.08 ± 0.004 mm, rsl. 0.11 ± 0.006 mm.

Carapace (Fig. 12A): Lateral spines lacking, dorsal spine curved, relatively short, rostral spine straight, dorsal spine and rostral spine with pointed termination. Eyes round and sessile.

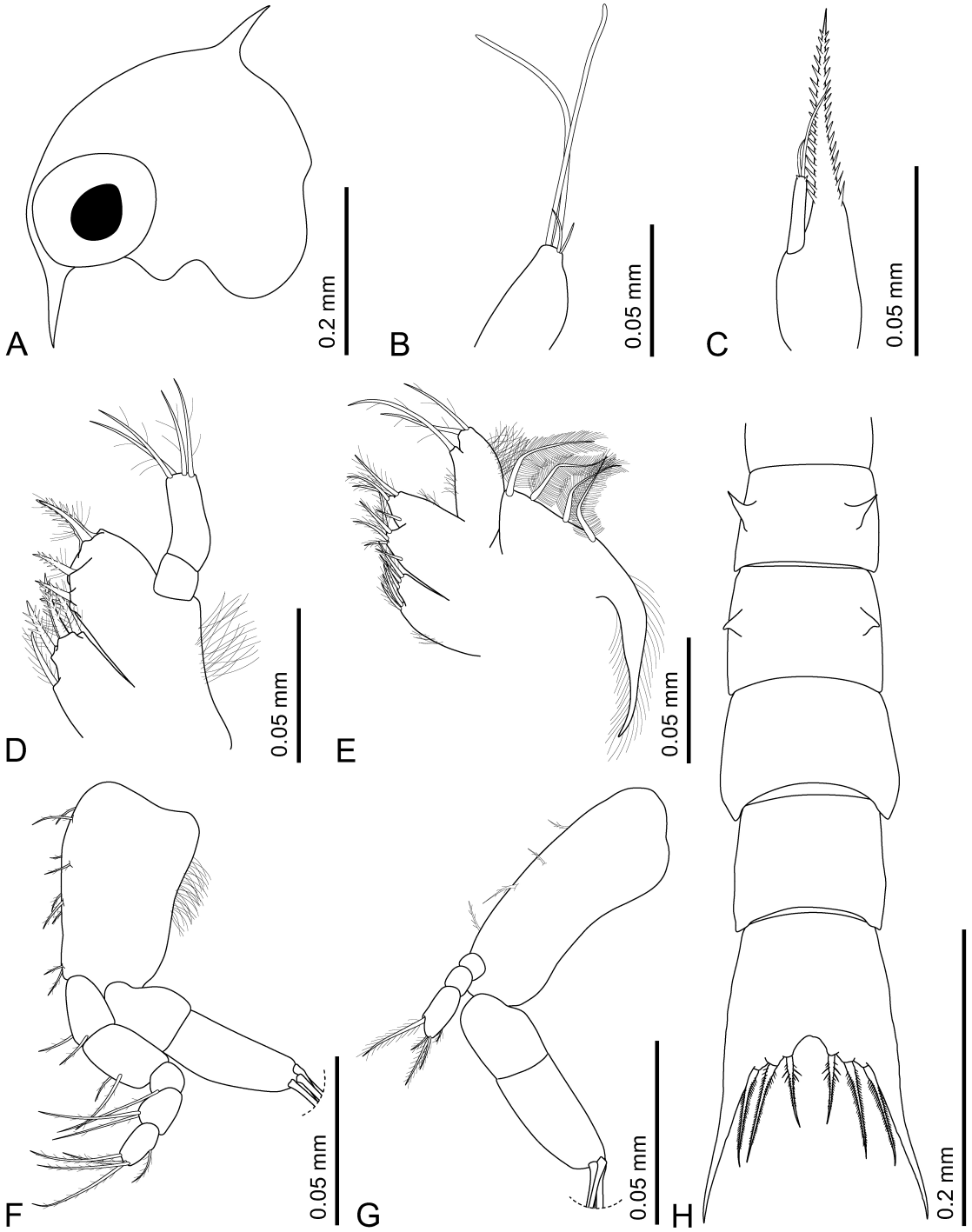

Fig. 11. *Tubuca acuta*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

Antennule (Fig. 12B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 12C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod short, with 1 terminal simple seta, setae not reaching tip of protopod. Endopod absent.

Maxillule (Fig. 12D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article;

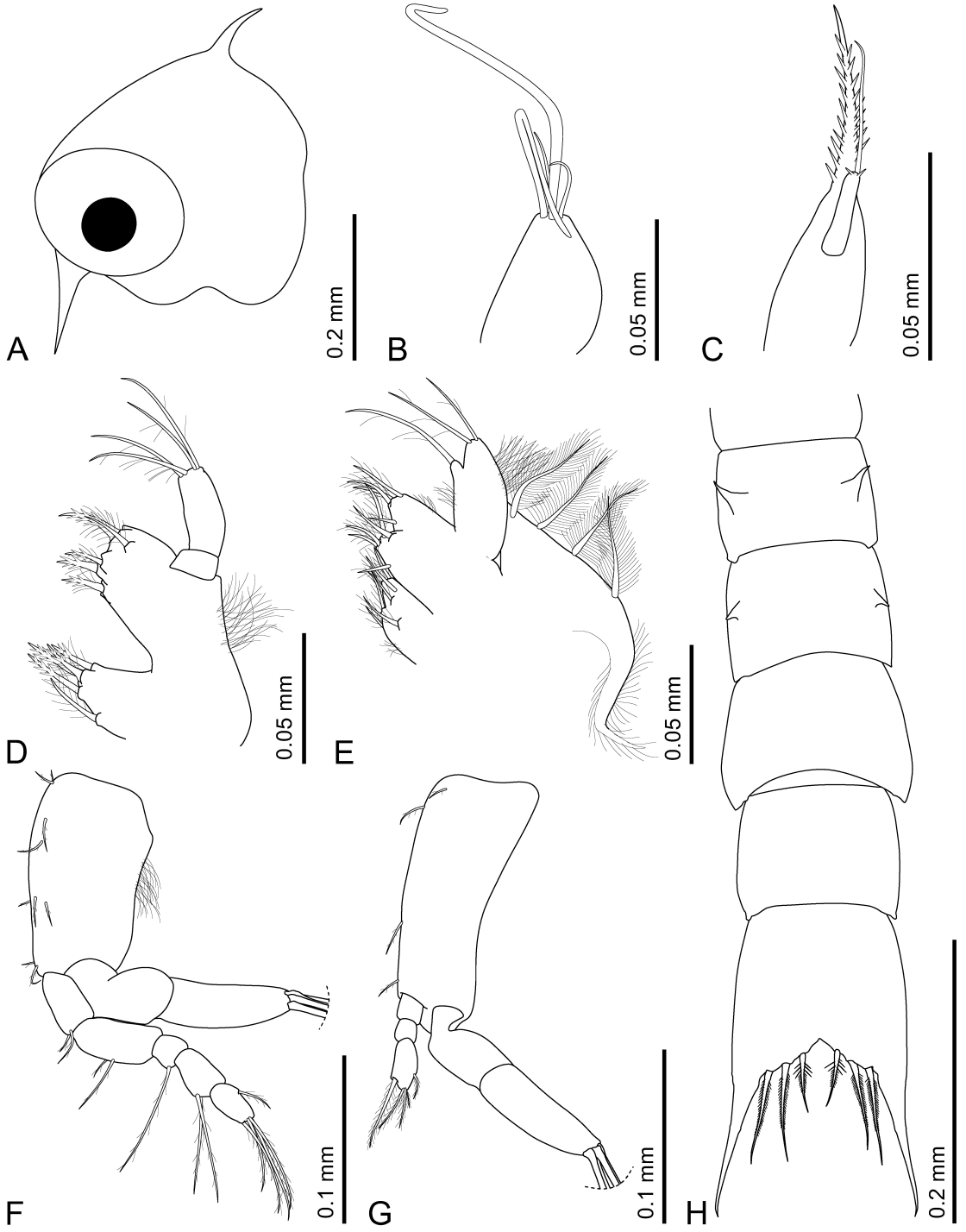

Fig. 12. *Tubuca arcuata*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

exopod seta absent.

Maxilla (Fig. 12E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 12F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 12G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 12H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 12H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

Tubuca coarctata (H. Milne Edwards, 1852)

(Fig. 13, Table 3)

Material examined: zoea I (from ♀ 19.2 mm, NCHUZOOL 16786, Baoli River estuary, Pingtung, coll. Y.-C. Zhang et al., 25 Nov. 2018).

Size: cl. 0.36 ± 0.017 mm, rdl. 0.54 ± 0.022 mm, dsl. 0.07 ± 0.007 mm, rsl. 0.11 ± 0.008 mm.

Carapace (Fig. 13A): Lateral spines lacking, dorsal spine curved, relatively short, rostral spine straight, dorsal spine and rostral spine with pointed termination. Eyes round and sessile.

Antennule (Fig. 13B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 13C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod short, with 1 terminal simple seta, seta not reaching tip of protopod. Endopod absent.

Maxillule (Fig. 13D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article; exopod seta absent.

Maxilla (Fig. 13E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 13F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 13G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 13H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 13H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

Tubuca dussumieri (H. Milne Edwards, 1852)

(Fig. 14, Table 3)

Material examined: zoea I (from ♀ 21.9 mm, NCHUZOOL 16787, Baoli River estuary, Pingtung, coll. Y.-C. Zhang et al., 25 Nov. 2018).

Size: 0.41 ± 0.012 mm, rdl. 0.61 ± 0.014 mm, dsl. 0.08 ± 0.004 mm, rsl. 0.12 ± 0.007 mm.

Carapace (Fig. 14A): Lateral spines lacking, dorsal spine curved, relatively short, rostral spine straight, dorsal spine and rostral spine with pointed termination. Eyes round and sessile.

Antennule (Fig. 14B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 14C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod short, with 2 terminal simple setae, setae not reaching tip of protopod. Endopod absent.

Maxillule (Fig. 14D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article; exopod seta absent.

Maxilla (Fig. 14E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 14F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 14G): Basis with

1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 14H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 14H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

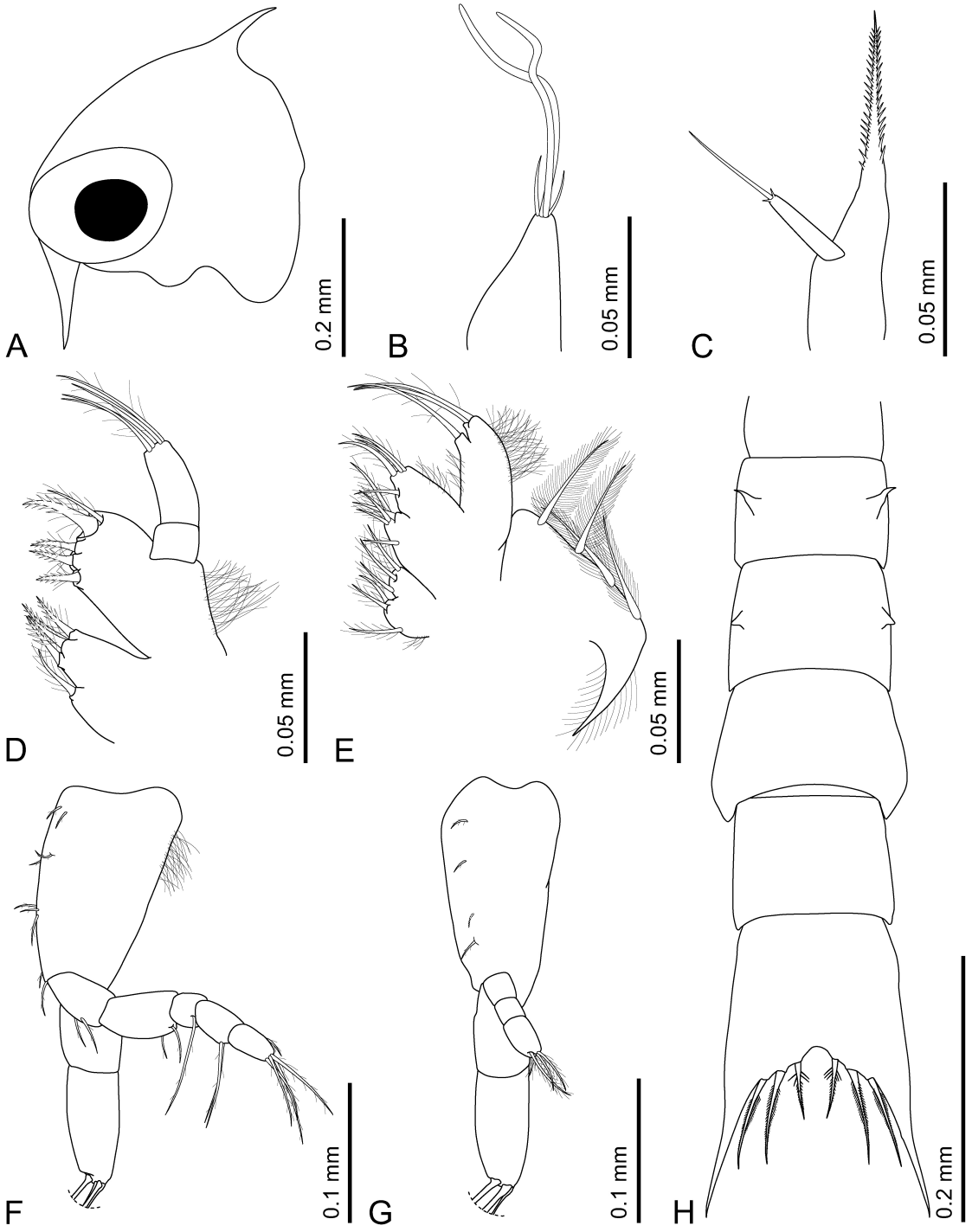

Fig. 13. *Tubuca coarctata*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

***Tubuca paradussumieri* (Bott, 1973)**

(Fig. 15, Table 3)

Material examined: zoea I (from ♀ 18.8 mm, NCHUZOOL 16788, Cihhu, Kinmen, coll. Y.-C. Zhang et al., 29 Aug. 2020).

Size: cl. 0.34 ± 0.011 mm, rdl. 0.54 ± 0.011 mm, dsl. 0.08 ± 0.003 mm, rsl. 0.12 ± 0.006 mm.

Carapace (Fig. 15A): Lateral spines lacking, dorsal spine curved, relatively short, rostral spine straight, dorsal spine and rostral spine with pointed termination. Eyes round and sessile.

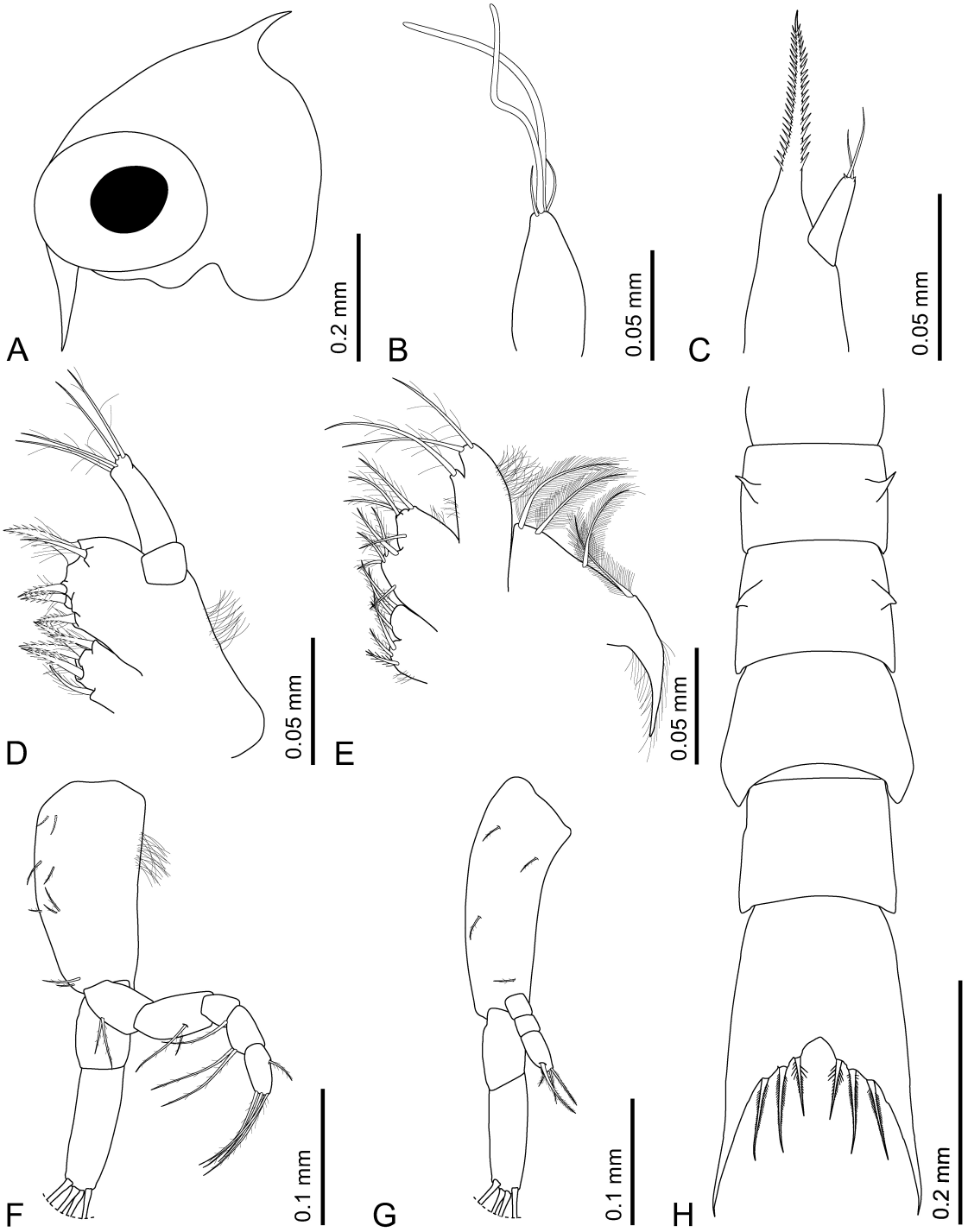

Fig. 14. *Tubuca dussumieri*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

Antennule (Fig. 15B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 15C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod short, with 1 terminal simple seta, seta not reaching tip of protopod. Endopod absent.

Maxillule (Fig. 15D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article;

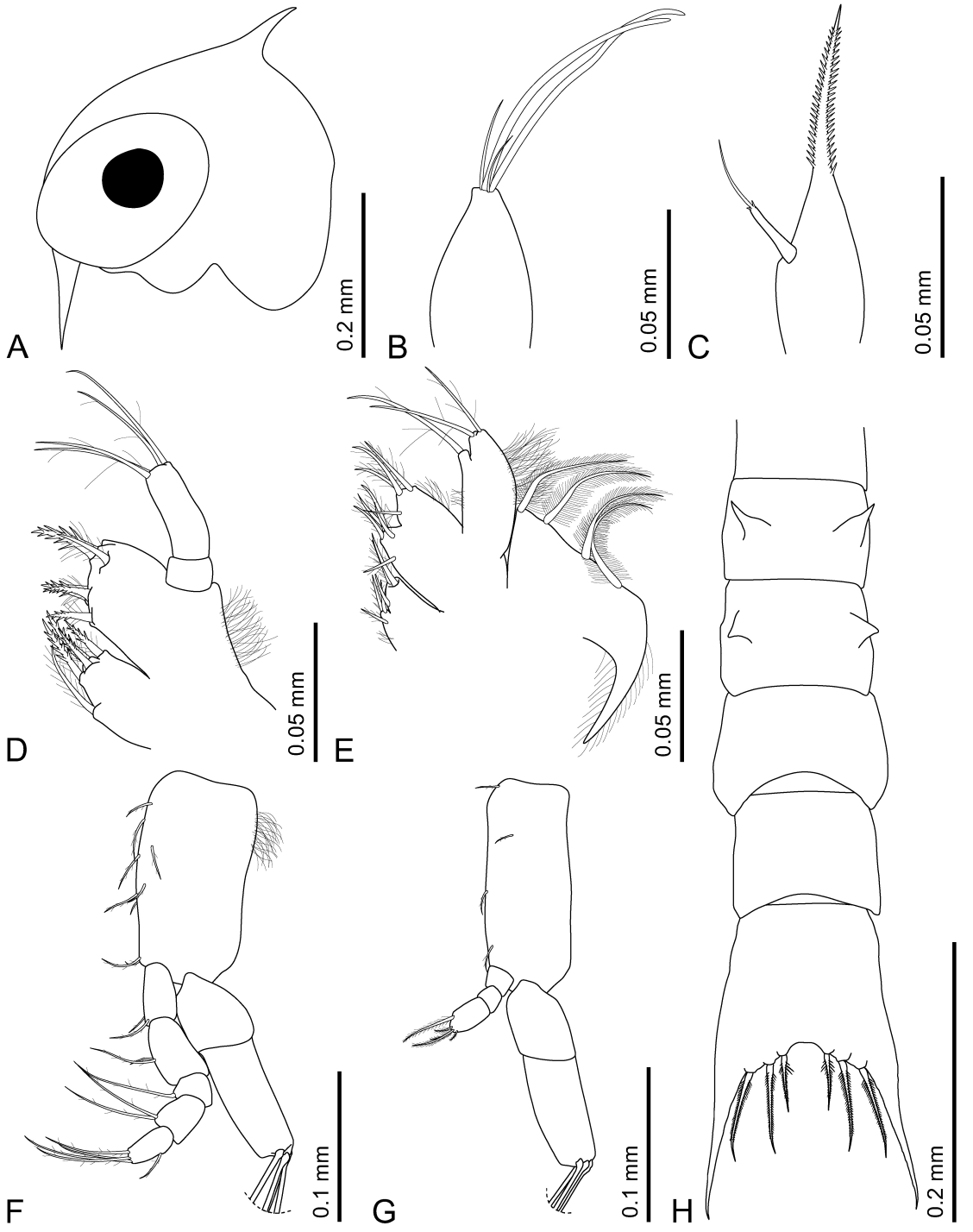

Fig. 15. *Tubuca paradussumieri*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

exopod seta absent.

Maxilla (Fig. 15E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 15F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 15G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 15H): With 5 somites, second article with a pair of relatively acute dorsolateral spines pointing anterodorsally; third article with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 15H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

Xeruca Shih, 2015
Xeruca formosensis (Rathbun, 1921)

(Fig. 16, Table 3)

Material examined: zoea I (from ♀ 15.0 mm, NCHUZOOL 16789, Siansi, Changhua, coll. Y.-C. Zhang et al., 12 Aug. 2018); zoea I (from ♀ 26.4 mm, NCHUZOOL 16790, Yangang River estuary, Hsinchu, coll. Y.-C. Zhang et al., 18 Sep. 2020).

Size: 0.35 ± 0.011 mm, rdl. 0.52 ± 0.016 mm, dsl. 0.08 ± 0.004 mm, rsl. 0.10 ± 0.004 mm.

Carapace (Fig. 16A): Lateral spines lacking, dorsal spine curved, relatively short, rostral spine straight, dorsal spine and rostral spine with pointed termination. Eyes round and sessile.

Antennule (Fig. 16B): Uniramous, endopod absent. Exopod smooth, unarticled, with 2 aesthetascs and 2 simple setae terminally.

Antenna (Fig. 16C): Protopod basal region smooth, distal end acuminate, bearing 2 rows of spines. Exopod short, with 2 terminal simple setae, setae exceeding tip of protopod. Endopod absent.

Maxillule (Fig. 16D): Epipod seta absent; coxal endite with 4 plumodenticulate setae and 1 plumose seta; basial endite with 4 plumodenticulate setae and 1 plumose seta; endopod 2-articled, proximal article without setae, 4 sparsely plumose in distal article; exopod seta absent.

Maxilla (Fig. 16E): Coxal endite bilobed with 3+3 plumose setae; basial endite bilobed with 5+4 plumose setae; endopod bilobed with 1+2 terminal sparsely plumose; scaphognathite with 4 densely plumose setae and a long acuminate posterior process with microtrichias.

First maxilliped (Fig. 16F): Basis with 2+2+3+2 sparsely plumose setae; endopod 5-articled with 2, 2, 1, 2, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Second maxilliped (Fig. 16G): Basis with 1+1+1+1 sparsely plumose setae; endopod 3-articled with 0, 0, 5 plumose setae; exopod 2-articled with 4 terminal long plumose setae.

Pleon (Fig. 16H): With 5 pleonites, second pleonite with a pair of relatively acute dorsolateral spines pointing anterodorsally; third pleonite with a pair of relatively obtuse dorsolateral spines pointing posterodorsally; fourth pleonite wider than other pleonites. Pleopods absent.

Telson (Fig. 16H): Telson bifurcated, inner margin with 6 (3+3) serrate spines.

A key to zoeal stage I of the 15 species of fiddler crabs from Taiwan

(* The cw of parental females are shown in Table 2)

1. Carapace with dorsal and rostral spines very reduced ..... 2 (*Gelasimus*)
- Carapace with dorsal and rostral spines well-developed 3
2. Antennal exopod with 1 terminal simple seta ..... *G. borealis*, *G. jocelynae*, *G. vocans*
- Antennal exopod with 2 terminal simple setae ..... *G. tetragonon*
3. Antennal only with protopod, without exopod 4
- Antenna with protopod and exopod 5
4. Carapace with dorsal spine longer (dsl/rdl > 0.18) ..... *Austruca lactea*
- Carapace with dorsal spine shorter (dsl/rdl < 0.17) ..... *Paraleptuca* (*P. crassipes*, *P. splendida*)
5. Antennal exopod with 1 terminal simple seta 6
- Antennal exopod with 2 terminal simple setae 7
6. Carapace with dorsal spine longer (dsl/rdl > 0.18), size larger (cl. > 0.4 mm)* ..... *Austruca perplexa*
- Carapace with dorsal spine shorter (dsl/rdl < 0.17), size smaller (cl. < 0.4 mm)* ..... *Tubuca arcuata*, *T. coarctata*, *T. paradussumieri*
7. Antenna with terminal simple setae longer than protopod ..... *Xeruca formosensis*
- Antenna with terminal simple setae shorter than protopod 8
8. Carapace with dorsal spine longer (dsl/rdl > 0.18) ..... *Austruca triangularis*
- Carapace with dorsal spine shorter (dsl/rdl < 0.17) 9
9. Size larger (cl. > 0.4 mm)* ..... *Tubuca dussumieri*
- Size smaller (cl. < 0.4 mm)* ..... *Tubuca acuta*

DISCUSSION

In our study the zoeal stage I of 15 species belonging to five genera of fiddler crabs from Taiwan

territory was described. The main characters of dorsal and rostral spines of the carapace, exopod of antenna, setal length of antenna and size ratios could be used to distinguish the five genera and most species from Taiwan. Species of *Gelasimus* have very reduced dorsal and rostral spines of carapace which can be distinguished from others genera. The lengths of dorsal and rostral spines in *Austruca* are longer than those in *Paraleptuca*, and the antennal exopod is absent in two species of *Paraleptuca* (see "Key"). The larval morphology is similar in *Tubuca* and *Xeruca*, but the length of terminal simple setae on antenna is exclusively

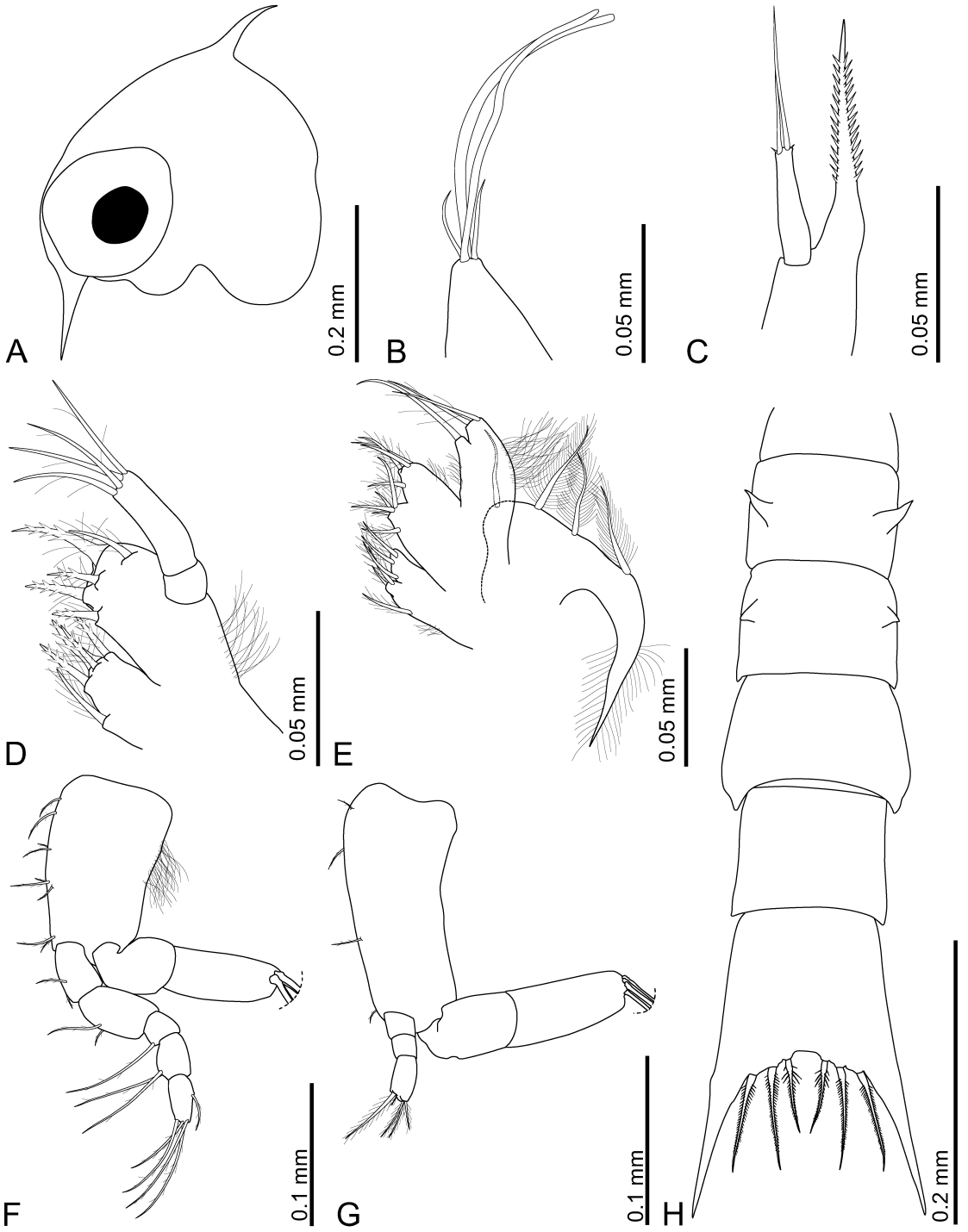

Fig. 16. *Xeruca formosensis*, zoea I. A, carapace; B, antennule; C, antenna; D, maxillule; E, maxilla; F, first maxilliped; G, second maxilliped; H, pleon and telson.

longer than the protopod in *Xeruca*.

Regarding the congeners, most could be identified by the presence of an antennal exopod and its number of terminal setae (Table 3). For the six species in *Tubuca* and *Xeruca*, they could be grouped as one terminal seta on antennal exopod (*T. arcuata*, *T. coarctata*, and *T. paradussumieri*), as well as two terminal setae on antennal exopod (*T. acuta*, *T. dussumieri*, and *X. formosensis*) (see "Key"; Table 3). Three species in *Austruca* could be separated based on their characters in zoea I. The antennal exopod is absent in *Au. lactea*, but there are one and two terminal setae on the antennal exopod of *Au. perplexa* and *Au. triangularis*, respectively (see "Key"; Table 3). Among the species examined in *Gelasimus*, only two groups could be discerned. Three species in the *G. vocans* species complex (*G. borealis*, *G. jocelynae*, and *G. vocans*) could not be separated, in agreement with their close molecular phylogeny (Shih et al. 2010 2016b). However, this species complex has one terminal seta on the antennal exopod, which is different from *G. tetragonon* which has two terminal setae. No distinct character could be found that distinguished *Paraleptuca crassipes* from *Pa. splendida*, reflecting their close phylogeny (Shih et al. 2012 2016b). Undistinguished morphology of zoea I among closely related species are also reported in other taxa, such as *Ocypode ceratophthalmus* (Pallas, 1772) and *O. stimpsoni* Ortmann, 1897 (Jiang et al. 2014).

Among 15 species of fiddler crabs from Taiwan, three species have been studied for their larval morphology (Table 4). Although the morphology of *Austruca lactea* observed in our study agrees largely with that in Terada (1979), the numbers of terminal setae on antennule and basial endite setae on maxilla are slightly different. Similarly, the number of basial endite setae on maxilla in *T. arcuata* differs from Ko and Kim (1989). This difference in the above characters could have been caused by the sample preparation process or different observation angles.

However, more differences in the characters of *Xeruca formosensis* were found between our study and Hsieh and Chen (2008), including the antenna, maxillule, maxilla, first and second maxillipeds (Table 4), which was probably caused by the lower resolution microscopy during observation. For example, only two articles in the endopod of the second maxilliped were reported in Hsieh and Chen (2008), but three articles were observed in the species we examined and in other studies (*Au. lactea* in Terada 1979; *T. arcuata* in Ko and Kim 1989). In addition, based on one terminal seta on the antennal exopod in Hsieh and Chen (2008: fig. 24a), it is also possible that their specimens were *T. arcuata* instead (Table 4) because the females of *X. formosensis* and *T. arcuata* are similar (Shih et al. 2015).

With regard to other minute structures, one pair of the dorsolateral simple setae (close to the base of dorsal spine) or one pair of the anterodorsal setae were observed on the carapace of zoea I of some fiddler crabs, *e.g.*, *Austruca iranica* (Pretzmann, 1971), *Gelasimus hesperiae* (Hashmi 1968), *Afruca tangeri* (Rodriguez and Jones 1993), and *Tubuca alcocki* Shih, Chan & Ng, 2018 (Ghory and Siddiqui 2006). However, such setae were not observed in our study and not reported in other studies, including *Austruca lactea* (Terada 1979), *Leptuca uruguayensis* (Nobili, 1901) (Rieger 1996), and *Minuca vocator* (Herbst, 1804) (Rieger 1999) which might have been caused by the microscopes used or

Table 4. Comparison of zoea stage I of *Austruca lactea*, *Tubuca arcuata*, and *Xeruca formosensis* with previous studies

Structure	*Austruca lactea*		*Tubuca arcuata*		*Xeruca formosensis*	
	Terada (1979)	this study	Ko and Kim (1989)	this study	Hsieh and Chen (2008)	this study
Antennule						
Terminal setae	2+1	2+2	–	–	4	2+2
Antenna						
Exopod setae	–	–	–	–	1	2
Maxillule						
Coxal endite setae	–	–	–	–	4	5
Maxilla						
Basial endite setae	4+4	4+5	4+4	4+5	3+3	4+5
Coxal endite setae	–	–	–	–	3+2	3+3
First maxilliped						
Setation on endopod	–	–	–	–	2, 2, 2, 2, 4+2	2, 2, 1, 2, 5
Second maxilliped						
Setation on endopod	–	–	–	–	0, 2+1	0, 0, 5

methods of specimen preparation. Similarly, the minute terminal spines on antennal exopod, the cuspidate setae on basial endite of maxillule and the minute spines on furcae of telson were reported in *Austruca iranica* (Hashmi 1968), *Tubuca alcocki* (Ghory and Siddiqui 2006), and *Afruca tangeri* (Spivak and Cuesta 2009), but not observed in our study and not reported in *Tubuca arcuata* (Ko and Kim 1989), *Leptuca thayeri* (Rathbun, 1900), *Minuca rapax* (Smith, 1870) (Anger et al. 1990, De Souza et al. 2013) and *Cranuca inversa* (Al-Aidaroos 2013). To observe these minute structures, it is suggested to use higher resolution microscopes or even scanning electron microscopy (SEM) in the future.

In our study, most of the taxa involved morpho logically similar congeners compared to species from different genera (Table 3), which agreed largely with the current systematics of fiddler crabs (Shih et al. 2016b). Although the fiddler crabs of *Afruca* and *Uca* and the ghost crabs of *Ocypode* have been included in the same subfamily Ocypodinae based on molecular evidence, some characters of their adult morphology are consistent, such as the orbital floor with a distinct tubercle at the inner corner adjacent to antennule, as well as the cornea of eyestalks presenting a distal ornament in the males of some species (Shih et al. 2016b). In addition, the character of lateral spines on carapace in zoea I appeared in *Ocypode* (Kakati 2005; Jiang et al. 2014), *Afruca* (Rodriguez and Jones 1993) and *Uca* (Negreiros-Fransozo et al. 2009), but not in other genera of the Gelasiminae (*e.g.*, the genera in our study, Table 3; *C. inversa*, Al-Aidaroos 2013; *Leptuca thayeri* (Rathbun, 1900), Anger et al. 1990; *Minuca burgersi* (Holthuis, 1967), Rieger 1998) and the Ucidinae (*e.g.*, *Ucides occidentalis* (Ortmann, 1897), Schuiteman et al. 2019). As a result, this character of larval morphology is suggested to be unique to the Ocypodinae, supporting the classification in Shih et al. (2016b).

CONCLUSIONS

Our study described the characters of zoea I in 15 fiddler crab species from Taiwan. The morphology of zoea I agrees largely with the current systematics of fiddler crabs, based on the main characters of dorsal and rostral spines on the carapace and exopod on the antenna. However, the larval morphology is indiscernible in some taxa, including *Gelasimus vocans* species complex, two species in *Paraleptuca* and three species in *Tubuca*. Molecular techniques including DNA barcoding and metabarcoding techniques can support further identification of morphologically similar larvae or larvae that have not been described before (Ueda et al. 2021; Alshari et al. 2021; Wong et al. 2021).

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Authors' contributions: YCZ performed the morphological description of larvae and drafted the manuscript. HTS participated in the discussion and drafted the manuscript. Both authors read and approved the final manuscript.

Competing interests: The authors declare that they have no conflict of interest.

Availability of data and materials: Specimens used in this study have been deposited into the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL).

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

Al-Aidaroos AM. 2013. Laboratory-hatched first zoeal stage of *Uca* (*Cranuca*) *inversa* (Crustacea: Brachyura: Ocypodidae) of the Red Sea. Mar Biodivers Rec **6:**1–6. doi:10.1017/S1755267213001036.

Alshari NFMAH, Ahmad SZ, Azlan A, Lee YH, Azzam G, Nor SAM. 2021. Metabarcoding of fish larvae in the Merbok River reveals species diversity and distribution along its mangrove environment. Zool Stud **60:**76. doi:10.6620/ZS.2021.60-76.

Anger K, Montú M, Bakker C, Loureiro Fernandes LL. 1990. Larval development of *Uca thayeri* Rathbun, 1900 (Decapoda: Ocypodidae) reared in the laboratory. Meeresforschung **32:**276–294.

Anger K, Queiroga H, Calado R. 2015. Larval development and behaviour strategies in Brachyura. *In*: Castro P, Davie PJF, Guinot D, Schram FR, von Vaupel Klein JC (eds), Treatise on Zoology – Anatomy, Taxonomy, Biology – The Crustacea, complementary to the volumes translated from the French of the Traité de Zoologie. Brill. Leiden, 9(C) (I), Decapoda: Brachyura (Part 1), pp. 317–374.

Apel M. 2001. Taxonomie und Zoogeographie der Brachyura, Paguridea und Porcellanidae (Crustacea: Decapoda) des Persisch-Arabischen Golfes. PhD dissertation. Johann Wolfgang Goethe-Universität, Frankfurt am Main, Germany.

Armendariz LC. 2005. Redescription of the megalopa of the fiddler

crab *Uca uruguayensis* (Decapoda, Brachyura, Ocypodidae) with special emphasis on its setae. J Nat Hist **39:**1981–1993. doi:10.1080/00222930400025920.

Bento M, Paula J. 2018. Keys and bibliography for the identification of zoeal stages of brachyuran crabs from the Western Indian Ocean. W Indian Ocean J Mar Sci **17:**13–51.

Bookhout CG, Costlow JDJ. 1974. Larval development of *Portunus spinicarpus* reared in the laboratory. Bull Mar Sci **24:**20–51.

Chu KH, Schubart CD, Shih HT, Tsang LM. 2015. Genetic diversity and evolution of Brachyura. *In*: Castro P, Davie PJF, Guinot D, Schram FR, von Vaupel Klein JC (eds), Treatise on Zoology – Anatomy, Taxonomy, Biology – The Crustacea, complementary to the volumes translated from the French of the Traité de Zoologie. Brill. Leiden, 9(C) (II), Decapoda: Brachyura (Part 2), pp. 775–820.

Clark PF, Calazans D, Pohle GW. 1998. Accuracy and standardization of brachyuran larval descriptions. Invertebr Reprod Develop **33:**127–144. doi:10.1080/07924259.1998.9652627.

Clark PF, Cuesta JA. 2015. Larval systematics of Brachyura. *In*: Decapoda: Brachyura, Treatise on Zoology-Anatomy, Taxonomy, Biology. Volume 9 Part C (2 vols) (pp. 981–1048). Brill.

Colavite J, Tavares M, de Mendonça JBJ, Santana W. 2021. The first zoeal stage of *Johngarthia lagostoma* (H. Milne Edwards, 1837) (Crustacea: Brachyura: Gecarcinidae), with comments on the validity of the genus. Thalassas **37:**767–773. doi:10.1007/s41208-021-00343-y.

Crane J. 1975. Fiddler crabs of the world (Ocypodidae: genus *Uca*). Princeton University Press, Princeton, New Jersey, 736 pp.

De Souza AS, Costa RMD, Abrunhosa FA. 2013. Comparative morphology of the first zoea of twelve brachyuran species (Crustacea: Decapoda) from the Amazon region. Zoologia (Curitiba) **30:**273–290. doi:10.1590/S1984-46702013000300004.

Feest J. 1969. Morphophysiologische Untersuchungen zur Ontogenese und Fortpflanzungsbiologie von *Uca annulipes* and *Uca triangularis* mit Vergleichsbefunden an *Ilyoplax gangetica*. Forma Functio **1:**159–225.

Ghory FS, Siddiqui FA. 2006. A comparative study of the first zoeal stage of *Uca urvillei* and *Uca annulipes* (Crustacea: Brachyura: Ocypodidae) reared in the laboratory. Turk J Zool **30:**161–166.

Hashmi SS. 1968. Study on larvae of (*Gelasimus*) (Ocypodidae) reared in the laboratory (Decapoda: Crustacea). Pak J Sci R **20:**50–56.

Hsieh HL, Chen CP. 2008. A study on the larval restoration, larval release and monitor of *Uca formosensis*. Hsinchu City Government, Hsinchu, Taiwan, 63 pp. (in Chinese)

Hultgren KM, Stachowicz JJ. 2008. Molecular phylogeny of the brachyuran crab superfamily Majoidea indicates close congruence with trees based on larval morphology. Mol Phylogenet Evol **48:**986–996. doi:10.1016/j.ympev.2008.05.004.

Hyman OW. 1920. The development of *Gelasimus* after hatching. J Morph **33:**484–525. doi:10.1002/jmor.1050330207.

Jiang GC, Liu HC, Chan T, Chan BK. 2014. First stage zoeal morphology of four ghost crabs *Ocypode ceratophthalmus* (Pallas, 1772), *O. cordimanus* Latreille, 1818, *O. sinensis* Dai, Song & Yang, 1985 and *O. stimpsoni* Ortmann, 1897 (Crustacea, Decapoda, Ocypodidae). Zootaxa **3760:**369–382. doi:10.11646/zootaxa.3760.3.4.

Kakati VS. 2005. Larval development of ghost crab *Ocypode ceratophthalma* (Pallas) under laboratory conditions. Seventh Indian Fish Forum, pp. 91–99.

Ko HS, Kim CH. 1989. Complete larval development of *Uca arcuata* (Crustacea, Brachyura, Ocypodidae) reared in the laboratory. Korean J Syst Zool **5:**89–105.

Kumar AAJ, Al-Aidaroos AM. 2022. Larval development of the mangrove fiddler crab *Austruca albimana* (Kossmann, 1877) (Crustacea: Brachyura: Ocypodidae) under laboratory conditions. Zool Stud **61:**70. doi:10.6620/ZS.2022.61-71.

Landeira JM, Cuesta JA, Tanaka Y. 2019. Larval development of the brush-clawed shore crab *Hemigrapsus takanoi* Asakura & Watanabe, 2005 (Decapoda, Brachyura, Varunidae). J Mar Biol Assoc UK **99:**1153–1164. doi:10.1017/S002531541900002X.

Muraoka K. 1976. The post-larval development of *Uca lactea* (de Haan) and *Macrophthalmus* (*Mareotis*) *japonicus* (De Haan) (Crustacea, Brachyura, Ocypodidae). Zool Mag **85:**40–51.

Negreiros-Fransozo ML, Hirose GL, Fransozo A, Bolla Jr EA. 2009. First zoeal stage and megalopa of *Uca* (*Uca*) *maracoani* (Decapoda: Brachyura), with comments on the larval morphology of South-American species of Ocypodidae. J Crustacean Biol **29:**364–372. doi:10.1651/08-3087.1.

Ng NK, Davie PJ, Schubart CD, Ng PK. 2007. Xenograpsidae, a new family of grapsoid crabs (Crustacea: Brachyura) associated with shallow water hydrothermal vents. Raffles Bull Zool, Supplement **16:**233–256.

Ng NK, Junyao G, Ng PKL. 1999. Generic affinities of *Eriocheir leptognathus* and *E. formosa* with description of a new genus (Brachyura: Grapsidae: Varuninae). J Crustacean Biol **19:**154–170. doi:10.1163/193724099X00358.

Ng PKL, Shih HT, Ho PH, Wang CH. 2017. An updated annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). J Nat Taiwan Mus **70:**1–208. doi:10.6532/JNTM.201712_70(3;4).01.

Pohle GW. 1991. Larval development of Canadian Atlantic regoniid Crabs (Brachyura, Majidae), with emphasis on *Hyas coarctatus alutaceus* Brandt, 1851, and a comparison with Atlantic and Pacific conspecifics. Can J Zool **69:**2717–2737. doi:10.1139/z91-384.

Pohle GW, Telford M. 1981. Morphology and classification of decapod crustacean larval setae: a scanning electron microscope study of *Dissodactylus crinitichelis* Moreira, 1901 (Brachyura: Pinnotheridae). Bull Mar Sci **31:**736–752.

Rabalais NN, Cameron JN. 1983. Abbreviated development of *Uca subcylindrica* (Stimpson, 1859) (Crustacea, Decapoda, Ocypodidae) reared in the laboratory. J Crustacean Biol **3:**519–541. doi:10.1163/193724083X00193.

Rice AL. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura. Trans Zool Soc Lond **35:**271–372. doi:10.1111/j.1096-3642.1980.tb00060.x.

Rice AL. 1981. The zoea of *Acanthodromia erinacea* A. Milne-Edwards; the first description of a dynomenid larva (Decapoda, Dromioidea). J Crustacean Biol **1:**174–176. doi:10.2307/1548155.

Rieger PJ. 1996. Desenvolvimento larval de *Uca* (*Celuca*) *uruguayensis* Nobili, 1901 (Crustacea, Decapoda, Ocypodidae), em laboratório. Nauplius **4:**73–103.

Rieger PJ. 1997. Desenvolvimento larval de *Uca* (*Minuca*) *mordax* (Smith, 1870) (Crustacea, Decapoda, Ocypodidae), em laboratório. Trab Oceanog Univ Fed PE **25:**227–267.

Rieger PJ. 1998. Desenvolvimento larval de *Uca* (*Minuca*) *burgersi* Holthuis (Crustacea, Decapoda, Ocypodidae), em laboratório. Rev Bras Zool **15:**727–756.

Rieger PJ. 1999. Desenvolvimento larval de *Uca* (*Minuca*) *vocator* (Herbst, 1804) (Crustacea, Decapoda, Ocypodidae), em laboratório. Nauplius **7:**1–37.

Rodriguez A, Jones DA. 1993. Larval development of *Uca tangeri* (Eydoux, 1835) (Decapoda: Ocypodidae) reared in the laboratory. J Crustacean Biol **13:**309–321. doi:10.1163/193724093X00093.

Rosário TN, Abrunhosa FA, Souza ASd. 2021. Descrição do primeiro estágio larval (zoea I) do caranguejo chama-maré *Leptuca cumulanta* (Crane, 1943) (Ocypodidae: Gelasiminae)

da Região Amazônica. *In*: Cordeiro CAM, Sampaio DS, Holanda FCAF (eds), Engenharia de Pesca: Aspectos Teóricos e Práticos. Editora Científica Digital, São Paulo, pp. 138–146. doi:10.37885/210404369.

Schoeman DS, Cockcroft AC. 1996. A description of *Ovalipes trimaculatus* (De Haan, 1833) (Brachyura: Portunidae: Polybiinae) zoeae reared in the laboratory. S Afr J Mar Sci **17:**113–134. doi:10.2989/025776196784158338.

Schubart CD, Liu HC, Cuesta JA. 2003. A new genus and species of tree-climbing crab (Crustacea: Brachyura: Sesarmidae) from Taiwan with notes on its ecology and larval morphology. Raffles Bull Zool **51:**49–60.

Schuiteman M, Pozo-Cajas M, Dominguez-Granda L, Marin Jarrin J. 2019. A description of *Ucides occidentalis* Ortmann, 1897 (Crustacea: Decapoda: Ocypodidae) zoea I. J Nat Hist **53:**1255–1261. doi:10.1080/00222933.2019.1637030.

Serbino NMB. 2008a. Descrição do primeiro estágio larval de *Uca rapax* (Smith, 1870) (Brachyura: Ocypodidae). Rev Intertexo **1:**6–15.

Serbino NMB. 2008b. Descrição do primeiro estágio larval de *Uca urvillei* (H. Milne Edwards, 1852) (Brachyura: Ocypodidae). Rev Intertexo **1:**63–73.

Serbino NMB. 2008c. Descrição do primeiro estágio larval de *Uca vocator* (Herbst, 1804) (Brachyura: Ocypodidae). Rev Intertexo **1:**74–83.

Shih HT, Chan BKK, Ng PK. 2018. *Tubuca alcocki*, a new pseudocryptic species of fiddler crab from the Indian Ocean, sister to the southeastern African *T. urvillei* (H. Milne Edwards, 1852) (Crustacea, Decapoda, Brachyura, Ocypodidae). ZooKeys **747:**41–62. doi:10.3897/zookeys.747.23468.

Shih HT, Chan BKK, Teng SJ, Wong KJH. 2015. Crustacean Fauna of Taiwan: Brachyuran Crabs, Volume II - Ocypodoidea. National Chung Hsing University, Taichung, Taiwan, 14+320 pp.

Shih HT, Lee JH, Ho PH, Liu HC, Wang CH, Suzuki H, Teng SJ. 2016b. Species diversity of fiddler crabs, genus *Uca* Leach, 1814 (Crustacea: Ocypodidae), from Taiwan and adjacent islands, with notes on the Japanese species. Zootaxa **4083:**57–82. doi:10.11646/zootaxa.4083.1.3.

Shih HT, Naruse T, Ng PK. 2010. *Uca jocelynae* sp. nov., a new species of fiddler crab (Crustacea: Brachyura: Ocypodidae) from the Western Pacific. Zootaxa **2337:**47–62. doi:10.11646/zootaxa.2337.1.4.

Shih HT, Ng PKL, Davie PJF, Schubart CD, Türkay M, Naderloo R, Jones DS, Liu MY. 2016a. Systematics of the family Ocypodidae Rafinesque, 1815 (Crustacea: Brachyura), based on phylogenetic relationships, with a reorganization of subfamily rankings and a review of the taxonomic status of *Uca* Leach, 1814, sensu lato and its subgenera. Raffles Bull Zool **64:**139–175.

Shih HT, Ng PKL, Ravichandran S, Prema M. 2019. Resurrection of *Gelasimus variegatus* Heller, 1862, a fiddler crab closely related to *Austruca bengali* (Crane, 1975) and *A. triangularis* (A. Milne-Edwards, 1873) (Decapoda, Brachyura, Ocypodidae), from the Bay of Bengal, Indian Ocean. Zool Stud **58:**12. doi:10.6620/ZS.2019.58-12.

Shih HT, Ng PKL, Wong KJH, Chan BKK. 2012. *Gelasimus splendidus* Stimpson, 1858 (Crustacea: Brachyura: Ocypodidae), a valid species of fiddler crab from the northern South China Sea and Taiwan Strait. Zootaxa **3490:**30–47. doi:10.11646/zootaxa.3490.1.2.

Shih HT, Poupin J. 2020. A new fiddler crab of *Austruca* Bott, 1973, closely related to *A. perplexa* (H. Milne Edwards, 1852) (Crustacea: Brachyura: Ocypodidae), from the South Pacific Islands. Zool Stud **59:**26. doi:10.6620/ZS.2020.59-26.

Spivak ED, Cuesta JA. 2009. The effect of salinity on larval development of *Uca tangeri* (Eydoux, 1835) (Brachyura: Ocypodidae) and new findings of the zoeal morphology. Sci Mar **73:**297–305. doi:10.3989/scimar.2009.73n2297.

Terada M. 1979. On the zoea larvae of five crabs of the family Ocypodidae. Zool Mag **88:**57–72.

Ueda K, Yanagimoto T, Chow S, Kuroki M, Yamakawa T. 2021. Molecular identification of mid to final stage slipper lobster phyllosoma larvae of the genus *Chelarctus* (Crustacea: Decapoda: Scyllaridae) collected in the Pacific with descriptions of their larval morphology. Zool Stud **60:**75. doi:10.6620/ZS.2021.60-75.

Wong KJH, Tsao YF, Tsai PC, Hsieh WP, Li HR, Machida RJ, Chan BKK. 2021. To the light side: molecular diversity and morphology of stomatopod larvae and juveniles (Crustacea: Malacostraca: Stomatopoda) from crustose coralline algal reefs in Taiwan. Mar Biodiver **51:**20. doi:10.1007/s12526-020-01150-z.