

# Diversity in the Taiwanese Swimming Crabs (Crustacea: Brachyura: Portunidae) Estimated through DNA Barcodes, with Descriptions of 14 New Records

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The swimming crabs (family Portunidae) are distributed worldwide and commonly inhabit estuaries, mangroves, reefs, shallow and the deep sea. Previously, 75 species and 19 genera in this family were known to Taiwan. Our study examined specimens in Taiwanese waters, including the islands, collected between 2016 and 2020 or deposited in museums. Through the cytochrome oxidase subunit I DNA barcode marker and morphological examination, 71 species were identified. The minimum interspecific distances were greater than 4.09%, except in two unresolved groups: *Charybdis miles* (De Haan, 1835) and *Ch. sagamiensis* Parisi, 1916, as well as *Thranita pelsartii* (Montgomery, 1931) and *Thr. prymna* (Herbst, 1803). In addition, 14 species belonging to nine genera were confirmed as new records to Taiwan, viz. *Carupa ohashii* Takeda, 1993, *Lupocycclus inaequalis* (Walker, 1887), *Luu. tugelae* Barnard, 1950, *Lupocycloporus minutus* (Shen, 1937), *Monomia gladiator* (Fabricius, 1798), *M. lucida* Koch & Ďuriš, 2018, *Podophthalmus minabensis* Sakai, 1961, *Thalamita gatavakensis* Nobili, 1906, *Tha. spinifera* Borradaile, 1902, *Thalamitoides quadridens* A. Milne-Edwards, 1869, *Tho. tridens* A. Milne-Edwards, 1869, *Thr. cerasma* (Wee & Ng, 1995), *Thr. coeruleipes* (Hombron & Jacquinot, 1846) and *Xiphonectes tuberculatus* (A. Milne-Edwards, 1861). This study thus raises the total number of Portunidae species in Taiwan to 89.

**Key words:** Newly recorded species, Morphology, Mitochondrial cytochrome oxidase subunit I (COI), Barcodes.

## BACKGROUND

Portunidae is a family of over 300 species (Sasaki 2019) of swimming crab that are distributed worldwide from tropical to temperate zones, have diverse habitats (e.g., brackish estuaries, mangroves, coral reefs, shallow and deep seas), and can even be symbiotic with other animals (e.g., corals and sea urchins) (Stephenson and Rees 1968; Spiridonov 1999; Evans 2018). Some even act as keystone species in benthic communities (e.g.,

*Callinectes sapidus* Rathbun, 1896; see Boudreau and Worm 2012), whereas others have become invasive species in some regions (e.g., *Charybdis hellerii* (A. Milne-Edwards, 1867); see Dineen et al. 2001; Dessouassi et al. 2019).

The first recorded portunid from Taiwan was *Goniosoma spiniferum* Miers, 1884 (a synonym of *Ch. hellerii* (A. Milne-Edwards, 1867; see below) reported by Miers (1886)). Yu (1979) and Huang and Yu (1997) revised the Taiwanese portunids and reported 24 and

59 species, respectively. Ng et al. (2017) listed 71 species from Taiwan proper (including Penghu Islands (= Is.), Lanyu, Lyudao, Siaoliouciou Gueishan Island (= I.), Kinmen Is., Matsu Is., Diaoyutai Is., Dongsha I. and Taiping I.), but did not include three previously reported species (*Charybdis brevispinosa* Leene, 1937, *Thalamita macropus* Montogomery, 1931 and *Trierarchus corrugata* (Stephenson & Rees, 1961)) (Chou et al. 1999; Hsueh et al. 2006). Previous studies have stated that “*Thalamita poissonii*” collected from Taiwan (Balss 1922; Chou et al. 1999) and Japan (Sakai 1939) should be changed to *Thalamita pseudopoisonii* Stephenson & Rees, 1967 based on the morphological characters and geographical distributions (Stephenson and Rees 1967; Apel and Spiridonov 1998; Yang et al. 2012; Sasaki 2019). Later, Evans (2018) added *Caphyra bedoti* (Zehntner, 1894), *Cap. loevis* (A. Milne-Edwards, 1869) and *Cap. yookadai* Sakai, 1933 from Taiwan. Evans (2018) moved the genus *Coelocarcinus* Edmondson, 1930 into the family Carcinidae, so *Co. foliatus* Edmondson, 1930 is no longer a member of the Portunidae. In addition, *Ch. spiniferum* (Miers, 1884) was treated as a synonym of *Ch. hellerii* in Dessimoni et al. (2019). With regard to the genus *Vojmirophthalmus* Števčić, 2011, while some studies accepted it (Ng et al. 2017; Trivedi et al. 2018; Yosuva et al. 2020), others treated it as a synonym of *Podophthalmus* Lamarck, 1801 (Evans 2018; Sasaki 2019; Takeda et al. 2019). In our paper, we tentatively follow the latter decision and change *Vojmirophthalmus nacreus* in Ng et al. (2017) as *Podophthalmus nacreus*. This brings the total number of species in this family from Taiwan to 75.

Using mitochondrial cytochrome oxidase subunit I (*COI*) as the marker of DNA barcodes has helped reveal the diversity of animals (Hebert et al. 2003a b), including the crab families of Ocypodidae (Shih et al. 2010 2018 2019a; Shih and Poupin 2020), Sesarmidae (Shih et al. 2019b; Ng et al. 2020) and Varunidae (NK Ng et al. 2018; Shih et al. 2019c 2020a; Hsu and Shih 2020). With regard to the Portunidae, DNA barcodes have been used in the *Portunus pelagicus* complex (Lai et al. 2010), *Scylla* spp. (Ma et al. 2010; HY Ma et al. 2012), as well as to separate *Monomia gladiator* (Fabricius, 1798) and *M. haanii* (Stimpson, 1858) (Windsor et al. 2019).

In this study, the diversity of the swimming crabs from Taiwan was estimated using the *COI* marker. This method and morphological confirmation yielded 14 newly recorded species, bringing the current number of species in this family to 89 in Taiwan.

## MATERIALS AND METHODS

Specimens of the Portunidae collected from the Taiwan main island, as well as its adjacent and outlying islets, were examined and identified (Table 1; Fig. 1). They were preserved in 95% ethanol after collection and deposited into the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL). Other specimens were examined from the National Museum of Marine Biology and Aquarium, Taiwan (NMMB); the National Museum of Natural Science, Taichung, Taiwan (NMNS); and the National Taiwan Ocean University, Keelung Taiwan (NTOU). Morphological characters were illustrated with the aid of a drawing tube attached to a stereomicroscope. The terminology used primarily follows that in Davie et al. (2015). G1 refers to the male first gonopod. P2–P5 refers to pereiopods 2–5 (ambulatory legs 1–3 and natatory legs). Anterolateral tooth 1 is equal to the external orbital tooth.

Genomic DNA was isolated from muscle tissue using kits (see Shih et al. 2016 for details). A portion of the *COI* gene was amplified with PCR using the primers LCO1490, HCO2198 (Folmer et al. 1994) and COL14 (Roman and Palumbi 2004; Schubart 2009). The sequences were deposited into NCBI GenBank (accession numbers given in Table 1). We followed Hebert et al. (2003a) and Hebert and Gregory (2005) to generate a neighbor-joining (NJ) tree for *COI* sequences with the Kimura 2-parameter (K2P) model (Kimura 1980; also see Chu et al. 2015). The tree was constructed using the program MEGA (vers. 10.0.5, Kumar et al. 2018) with the pairwise deletion option and 1000 bootstrap reiterations. Other sequences from GenBank were included to further confirm the identifications (Table 1). Basepair (bp) differences and pairwise estimates of K2P distances for genetic diversities between species were also calculated with MEGA.

## RESULTS

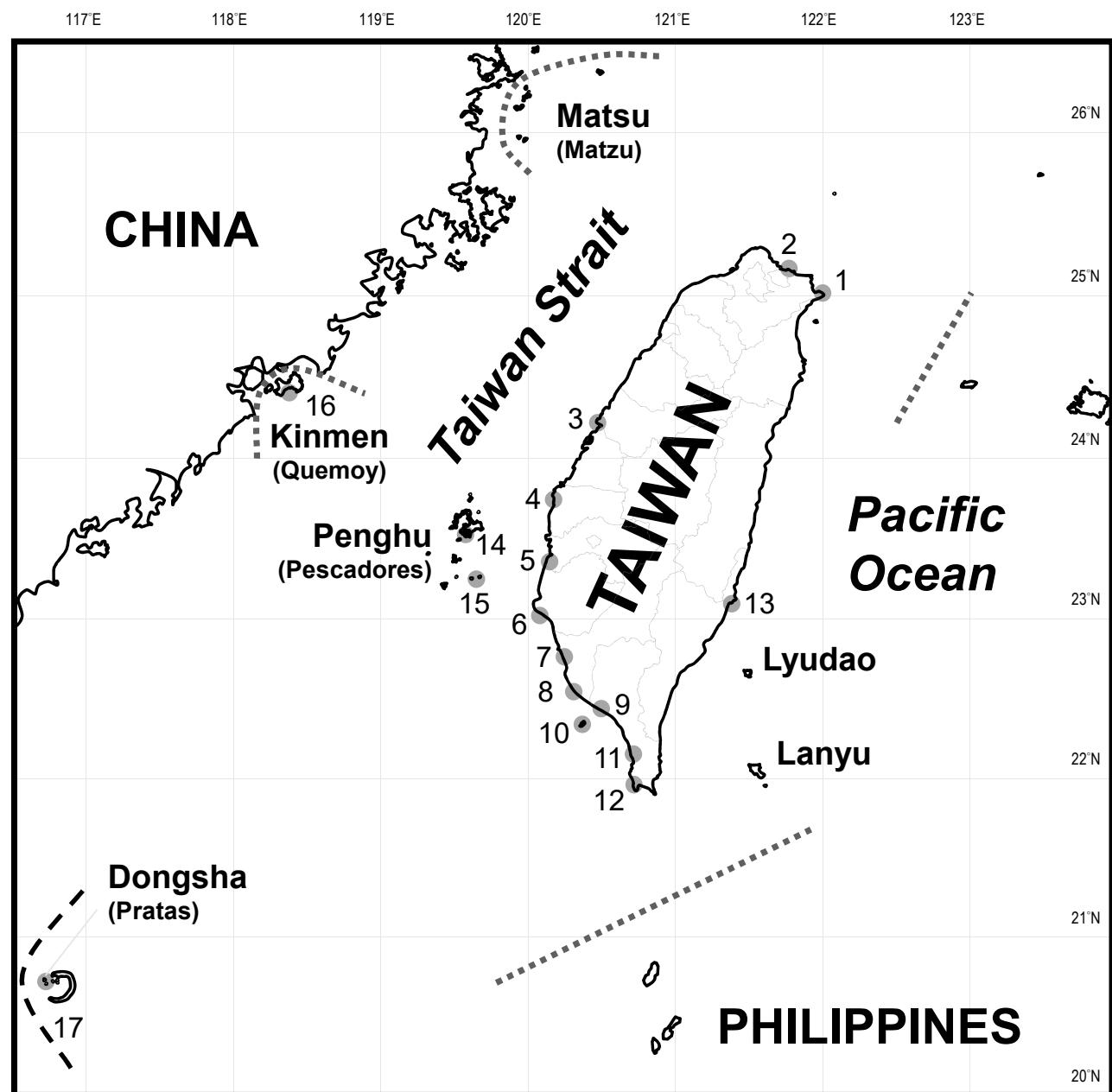
### Molecular analyses of *COI*

In total, 71 species identified from 89 specimens were used in our study, with an additional 52 sequences from 48 species from GenBank (Table 1; Fig. 2). The molecular results supported 12 newly recorded species with distinct characters (Table 1). Two additional new records, *Thalamita gatavakensis* Nobili, 1906 and *Thalamitoides quadridens* A. Milne-Edwards, 1869, are also reported here; however, despite great efforts, we were unable to generate molecular data for these

species. While most sequences from GenBank support the species identification in our study, the identification of some species from GenBank showed inconsistencies (see DISCUSSION), including *Charybdis hongkongensis* Shen, 1934, *Ch. variegata* (Fabricius, 1798), *Monomia argentata* (A. Milne-Edwards, 1861) and *Thalamita aff. admete* (Herbst, 1803) (Fig. 2). In addition, specimens of *Xiphonectes iranjae* identified by morphology in our study formed two sister clades on the phylogenetic tree (Fig. 2) tentatively named *X. nr. iranjae* 1 and *X. nr. iranjae* 2. We comment on this further in the

## DISCUSSION.

The minimum and mean pairwise nucleotide divergences of the K2P result of the 85 haplotypes for 71 species are shown in table S1. The lowest minimum interspecific divergence among the 71 species is 4.09%—between *Charybdis affinis* Dana, 1852 and *Ch. japonica* (A. Milne Edwards, 1861). However, two groups—*Ch. miles* (De Haan, 1835) and *Ch. sagamiensis* Parisi, 1916, as well as *Thranita pelsarti* (Montgomery, 1931) and *Thr. prymna* (Herbst, 1803)—were unresolved by the *COI* marker (see DISCUSSION).



**Fig. 1.** Taiwan main island and adjacent islets, with the collection localities shown in gray circles (see Table 1).

## Species diversity of portunids from Taiwan

Based on the specimens examined, 14 newly recorded species were confirmed from Taiwan (Table 1; Figs. 3, 4) and are described below. This means that

there are 89 recorded species of the family Portunidae from Taiwan; we list all 89 in table S2, with proposed Chinese names mainly following the etymology of the scientific names.

**Table 1.** The specimens and *COI* haplotypes of portunid species used in this study. The sequencing of *Thalamita gatavakensis* and *Thalamitoides quadridens* failed. For the museum abbreviations of the specimens used in this study, see MATERIALS AND METHODS, and the abbreviations for voucher specimens in GenBank are the Natural History Museum and Institute, Chiba, Japan (CBM); the Muséum National d'Histoire Naturelle, Paris, France (MNHN); the Nationaal Natuurhistorisch Museum Naturalis (formerly Rijksmuseum van Natuurlijke Historie), Leiden, Netherlands (RMNH); the Florida Museum of Natural History, University of Florida, Gainesville, USA (UF); the National Museum for Natural History, Smithsonian Institution, Washington DC, USA (USNM); the Zoological Museum of the Moscow University, Moscow, Russia (ZMMU); and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore, Singapore (ZRC). \*, newly recorded species to Taiwan; \*\*, conspecific specimens with the same haplotype; †, accession numbers from GenBank

Genus	Species (generic name abbreviated)	Locality [specimens used in this study with number of locality in Fig. 1]	Catalogue no. of NCHUZOOL (unless indicated)	Access. no.
Subfamily: Carupinae				
<i>Carupa</i>	<i>Car. ohashii</i> Takeda, 1993*	Taiwan: Dongsha I. [17]	16500	MZ393855
	<i>Car. tenuipes</i> Dana, 1852	Taiwan: Pingtung: Hengchun [12] French Polynesia	16463 UF 15565	MZ393856 KT365704†
Subfamily: Lupocyclinae				
<i>Lupocycloporus</i>	<i>Luo. gracilimanus</i> (Stimpson, 1858)	Taiwan: Penghu: Magong Fishing Port [14]	16469	MZ393857
	<i>Luo. minutus</i> (Shen, 1937)*	Vietnam: Nhatrang Bay	ZMMU Ma3381	JX398092†
<i>Lupocylclus</i>	<i>Luu. inaequalis</i> Semper, 1880*	Taiwan: Kaohsiung: Zuoying [7]	16534	MZ393858
	<i>Luu. philippinensis</i> Semper, 1880	Taiwan: Kaohsiung: Zuoying [7a]	16470	MZ393859
	<i>Luu. tugelae</i> Barnard, 1950*	Taiwan: Kaohsiung: Erzihliao Fishing Port [7b]	16551	MZ393860
		Taiwan: Pingtung: Donggang Fishing Port [9]	16468	MZ393861
		Taiwan: Kaohsiung: Erzihliao Fishing Port [7a, b]	16560 (2 ind.)	MZ393862, MZ393863
Subfamily: Necronectinae				
<i>Scylla</i>	<i>S. olivacea</i> (Herbst, 1794)	Taiwan: Taichung: Dadu R. estuary [3]	16576	MZ393864
		Taiwan: Pingtung: Donggang Fishing Port [9]	16547	MZ393865
	<i>S. paramamosain</i> Estampador, 1949	India	-	KC200563†
		Taiwan: Chiayi County: Budai [5]	16583	MZ393866
	<i>S. serrata</i> (Forskal, 1775)	China: Beibu Bay	-	MG197997†
		Taiwan: Taichung: Dadu R. estuary [3]	16574	MZ393867
		Taiwan: Pingtung: Donggang Fishing Port [9]	16582**	MZ393868
		Taiwan: Dongsha I. [17]	16461**	MZ393869
		Taiwan: Dongsha I. [17]	16575**	MZ393870
		India	-	KC200562†
	<i>S. tranquebarica</i> (Fabricius, 1798)	Taiwan: Pingtung: Donggang Fishing Port [9]	16581	MZ393871
		-	-	FJ827759†
Subfamily: Podophthalminae				
<i>Podophthalmus</i>	<i>Pod. minabensis</i> Sakai, 1961*	Taiwan: Kaohsiung: Siaogang [8]	16499	MZ393873
	<i>Pod. nacreus</i> (Alcock, 1899)	Taiwan: Kaohsiung: Zuoying [7]	16472	MZ393874
	<i>Pod. vigil</i> (Weber, 1795)	Vietnam: Nhatrang Bay	ZMMU Ma3440	JX398093†
		Taiwan: Tainan: Anping Fishing Port [6]	16471	MZ393872
		French Polynesia: Moorea Is.	UF 18116	KT365735†
Subfamily: Portuninae				
<i>Cycloachelous</i>	<i>Cy. granulatus</i> (H. Milne Edwards, 1834)	Taiwan: Pingtung: Siaoliouciou [10]	16464	MZ393875
		Taiwan: Penghu: Dongyupingu [15]	16541	MZ393876
		Taiwan: Dongsha I. [17]	16467	MZ393877
		Guam	UF 4169	KT365740†

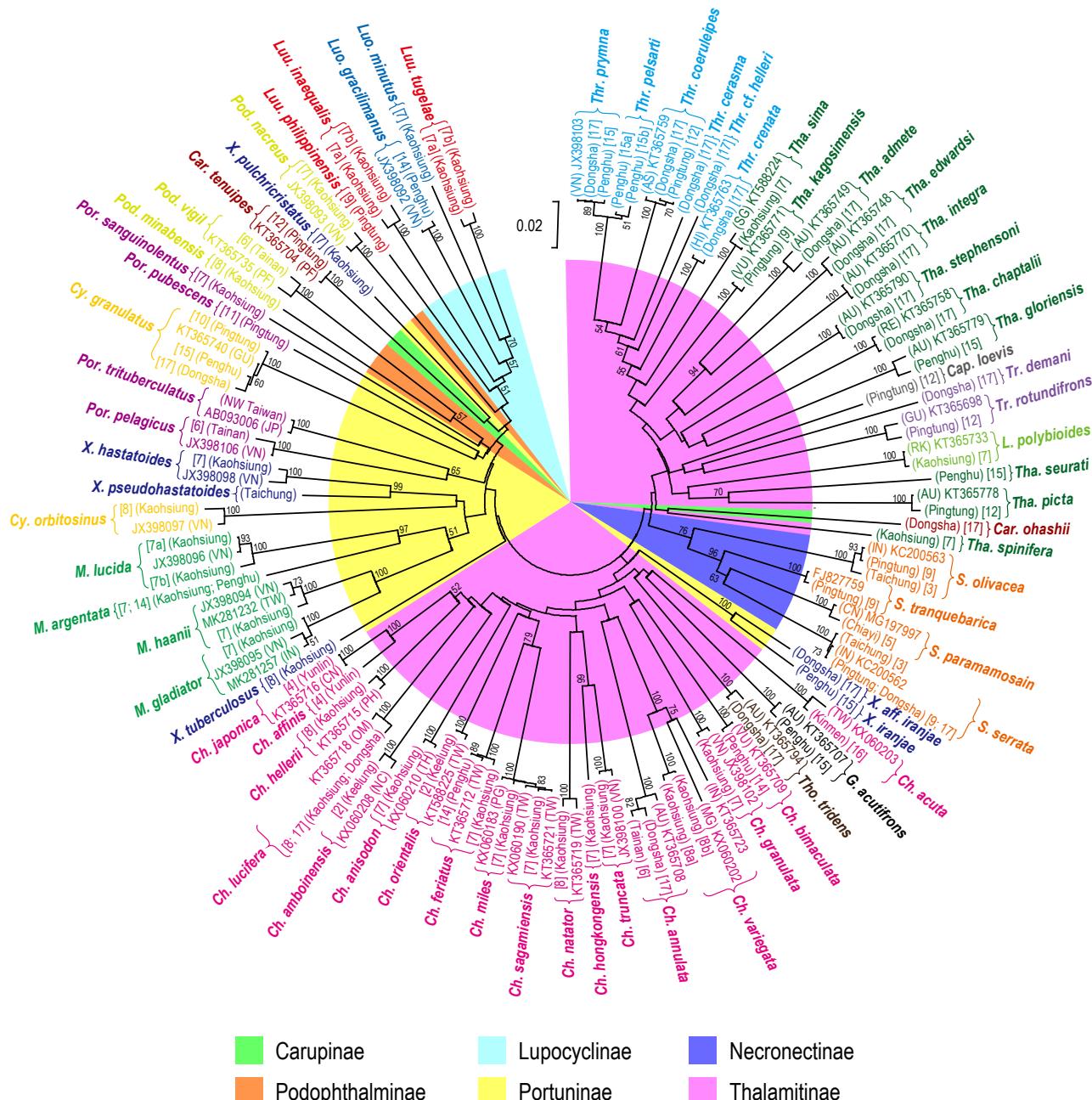
**Table 1.** (Continued)

Genus	Species (generic name abbreviated)	Locality [specimens used in this study with number of locality in Fig. 1]	Catalogue no. of NCHUZOOL (unless indicated)	Access. no.
	<i>Cy. orbitosinus</i> (Rathbun, 1911)	Taiwan: Kaohsiung: Siaogang [8] Vietnam: Nhatrang Bay	16580 ZMMU Ma3378	MZ393878 JX398097†
<i>Monomia</i>	<i>M. argentata</i> (A Milne-Edwards, 1861)	Taiwan: Kaohsiung: Zuoying [7] Taiwan: Penghu: Magong Fishing Port [14]	16543** 16544**	MZ393879 MZ393880
	<i>M. gladiator</i> (Fabricius, 1798)*	Taiwan: Kaohsiung: Erzihliao Fishing Port [7] India: Bay of Bengal: Pazhayar Fish Landing	16511 ZRC 2016.0145	MZ393881 MK281257†
	<i>M. haanii</i> (Stimpson, 1858)	Vietnam: Nhatrang Bay Taiwan: Kaohsiung: Erzihliao Fishing Port [7] Taiwan: Yilan: Daxi Fishing Port	ZMMU Ma3366 16508 USNM 1420828	JX398095† MZ393882 MK281232†
	<i>M. lucida</i> Koch & Ďuriš, 2018*	Vietnam: Nhatrang Taiwan: Kaohsiung: Zuoying [7a] Taiwan: Kaohsiung: Erzihliao Fishing Port [7b]	ZMMU Ma3368 16535 16536	JX398094† MZ393883 MZ393884
<i>Portunus</i>	<i>Por. pelagicus</i> (Linnaeus, 1758)	Vietnam: Nhatrang Bay Taiwan: Tainan: Yanshuei R. estuary [6]	ZMMU Ma3365 16545	JX398096† MZ393885
	<i>Por. pubescens</i> (Dana, 1852)	Taiwan: Pingtung: Checheng [11]	- 16579	JX398106† MZ393886
	<i>Por. sanguinolentus</i> (Herbst, 1783)	Taiwan: Kaohsiung: Erzihliao Fishing Port [7]	16577	MZ393887
	<i>Por. trituberculatus</i> (Miers, 1876)	Taiwan Strait near NW Taiwan	16546	MZ393888†
<i>Xiphonectes</i>	<i>X. hastatoides</i> (Fabricius, 1798)	Japan: Tokyo Taiwan: Kaohsiung: Zuoying [7] Vietnam: Nhatrang Bay	CBM ZC5916 16474 ZMMU Ma3392	AB093006† MZ393889 JX398098†
	<i>X. iranjae</i> (Crosnier, 1962)	Taiwan: Penghu: Dongyupingyu [15]	16542	MZ393890
	<i>X. aff. iranjae</i> (Crosnier, 1962)	Taiwan: Dongsha I. [17]	16473	MZ393891
	<i>X. pseudohastatoides</i> (Yang & Tang, 2006)	Taiwan Strait near Taichung	NMNS 004368-00042	MZ393892
	<i>X. pulchricristatus</i> (Gordon, 1931)	Taiwan: Kaohsiung: Erzihliao Fishing Port [7]	16475	MZ393893
	<i>X. tuberculatus</i> (A. Milne-Edwards, 1861)*	Taiwan: Kaohsiung: Siaogang [8]	16532	MZ393894
Subfamily: Thalamitinae				
<i>Caphyra</i>	<i>Cap. loewis</i> (A. Milne-Edwards, 1869)	Taiwan: Pingtung: Hengchun [12]	NMMB CD4090	MZ393895
<i>Charybdis</i>	<i>Ch. acuta</i> (A. Milne-Edwards, 1869)	Taiwan: Kinmen [16]	NTOU	MZ393896
	<i>Ch. affinis</i> Dana, 1852	Taiwan	UF 13466	KX060203†
	<i>Ch. amboinensis</i> Leene, 1938	Taiwan: Yunlin: Mailiao [4]	NTOU	MZ393897
	<i>Ch. anisodon</i> (De Haan 1835)	Taiwan: Keelung: Heping I. [2]	NTOU	MZ393898
	<i>Ch. annulata</i> (Fabricius, 1798)	New Caledonia	MNHN-IU-2014-10234	KX060208†
	<i>Ch. bimaculata</i> (Miers, 1886)	Taiwan: Kaohsiung: Erzihliao Fishing Port [7]	16491	MZ393899
	<i>Ch. feriatus</i> (Linnaeus, 1758)	Thailand	RMNH CRUST.D.42484	KX060210†
	<i>Ch. granulata</i> (De Haan, 1835)	Taiwan: Tainan: Zengwen R. estuary [6]	16548	MZ393900
	<i>Ch. hellerii</i> (A. Milne-Edwards, 1867)	Taiwan: Dongsha I. [17]	16490	MZ393901
	<i>Ch. hongkongensis</i> Shen, 1934	Australia: Ningaloo Reef	UF 22076	KT365708†
	<i>Ch. japonica</i> (A. Milne-Edwards, 1861)	Taiwan: Penghu: Magong Fishing Port [14]	16567	MZ393902
	<i>Ch. lucifera</i> (Fabricius, 1798)	Vanuatu: Aurora I.	ZRC 2017.0508	KT365709†
	<i>Ch. miles</i> (De Haan, 1835)	Taiwan: Kaohsiung: Erzihliao Fishing Port [7]	16492	MZ393903
	<i>Ch. natator</i> (Herbst, 1794)	Taiwan: Penghu: Magong Fishing Port [14]	16497	MZ393904
		Taiwan	UF 3739	KT365712†
		Taiwan: Kaohsiung: Erzihliao Fishing Port [7]	16494	MZ393905
		Vietnam: Nhatrang Bay	-	JX398102†
		Taiwan: Kaohsiung: Siaogang [8]	16549	MZ393906
		Philippines: Bohol I.	UF 11430	KT365715†
		Taiwan: Kaohsiung: Erzihliao Fishing Port [7]	16496	MZ393907
		Taiwan: Yunlin: Mailiao [4]	NTOU	MZ393908
		China	ZRC 2008.0567	KT365716†
		Taiwan: Kaohsiung: Siaogang [8]	16462**	MZ393909
		Taiwan: Dongsha I. [17]	16489**	MZ393910
		Oman	UF 7684	KT365718†
		Taiwan: Kaohsiung: Erzihliao Fishing Port [7]	16493	MZ393911
		Papua New Guinea	MNHN-IU-2013-633	KX060183†
		Taiwan: Kaohsiung: Siaogang [8]	16550	MZ393912

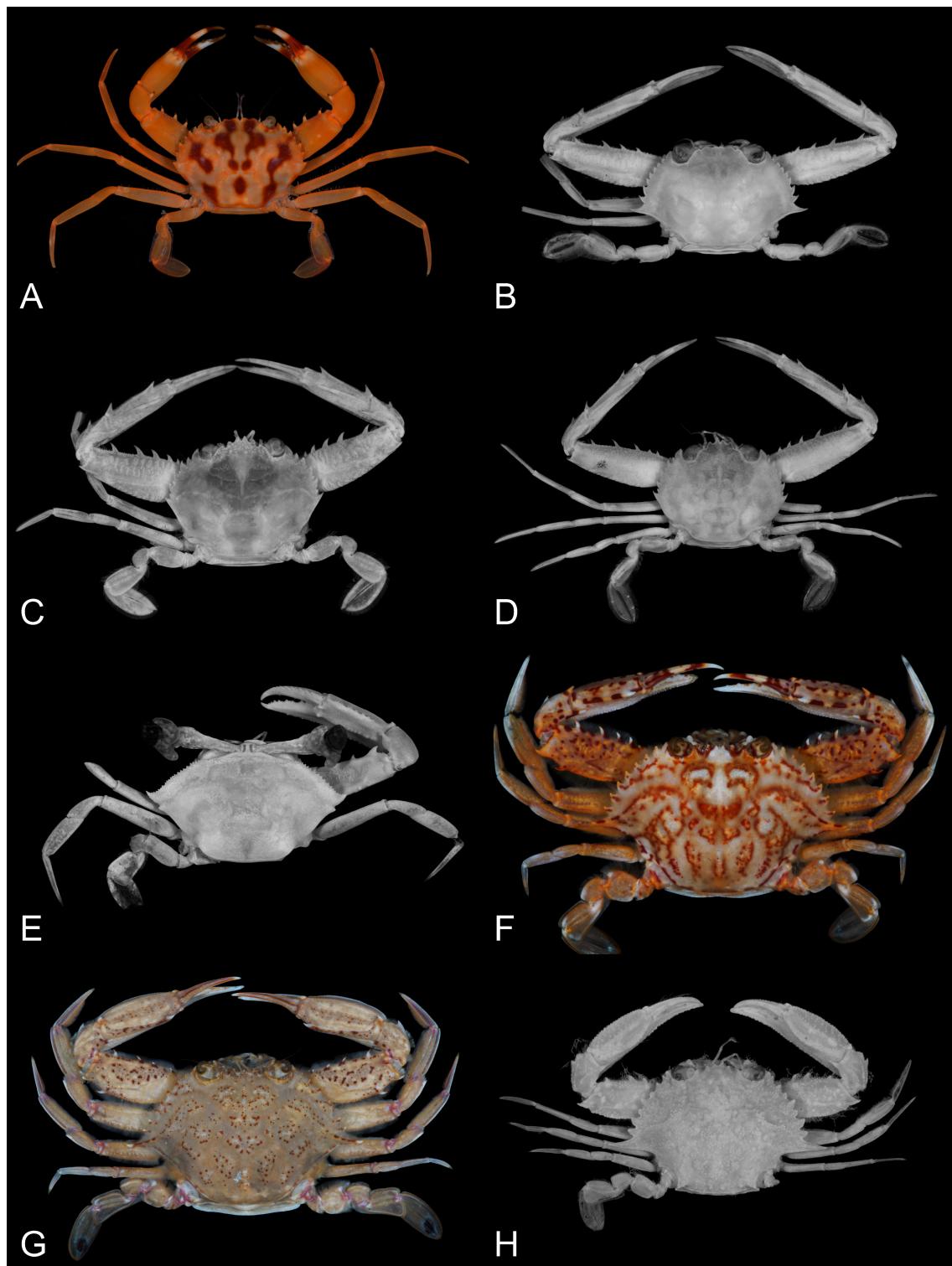
**Table 1.** (Continued)

Genus	Species (generic name abbreviated)	Locality [specimens used in this study with number of locality in Fig. 1]	Catalogue no. of NCHUZOOL (unless indicated)	Access. no.
	<i>Ch. orientalis</i> Dana, 1852	Taiwan Taiwan: Keelung: Badouzih [2]	UF 3707 NTOU	KT365719† MZ393913
	<i>Ch. sagamiensis</i> Parisi, 1916	Taiwan Taiwan: Kaohsiung: Erzihliao Fishing Port [7]	USNM 112062 16495	KT588225† MZ393914
	<i>Ch. truncata</i> (Fabricius, 1798)	Taiwan Taiwan: Kaohsiung: Erzihliao Fishing Port [7]	UF 29479 UF 29482	KT365721† KX060190†
	<i>Ch. variegata</i> (Fabricius, 1798)	Vietnam: Nhatrang Bay Taiwan: Kaohsiung: Siaogang [8a, b]	ZMMU Ma3363 16556 (2 ind.)	JX398100† MZ393916, MZ393917
<i>Goniosupradens</i>	<i>G. acutifrons</i> (De Man, 1879)	India Madagascar Taiwan: Penghu: Dongjiyu [15]	ZRC 2012.1115 MNHN-IU-2010-3154 16554	KT365723† KX060202† MZ393918
<i>Lissocarcinus</i>	<i>L. polybioides</i> Adams & White, 1849	Australia: Lizard I. Taiwan: Kaohsiung: Erzihliao Fishing Port [7]	UF 17047 16466	KT365707† MZ393919
<i>Thalamita</i>	<i>Tha. admete</i> (Herbst, 1803)	Japan: Okinawa Taiwan: Dongsha I. [17]	UF 35245 16480	KT365733† MZ393920
	<i>Tha. chaptalii</i> (Audouin, 1826)	Australia: Lizard I. Taiwan: Dongsha I. [17]	UF 16971 16477	KT365749† MZ393921
	<i>Tha. edwardsi</i> Borradaile, 1900	Reunion I. Taiwan: Dongsha I. [17]	UF 13103 16476**	KT365758† MZ393922
	<i>Tha. gatavakensis</i> Nobili, 1906*	Taiwan: Dongsha I. [17]	16478**	MZ393923
	<i>Tha. gloriensis</i> Crosnier, 1962	Australia: Queensland Taiwan: New Taipei City: Mao-ao [1]	UF 17745 NTOU	KT365748† -
	<i>Tha. integra</i> Dana, 1852	Taiwan: Penghu: Dongjiyu [15]	16540	MZ393924
	<i>Tha. kagoshimensis</i> Sakai, 1939	Australia, Heron I. Taiwan: Pingtung: Donggang Fishing Port [9]	UF 25902 16481	KT365779† MZ393926
	<i>Tha. picta</i> Stimpson, 1858	Vanuatu: Espiritu Santo Taiwan: Pingtung: Hengchun [12]	ZRC 2017.0514 16487	KT365771† MZ393927
	<i>Tha. seurati</i> Nobili, 1906	Australia: Heron I. Taiwan: Penghu: Dongjiyu [15]	UF 22085 16539	KT365770† MZ393928
	<i>Tha. sima</i> H. Milne Edwards, 1834	Taiwan: Kaohsiung: Erzihliao Fishing Port [7]	16488	MZ393929
	<i>Tha. spinifera</i> Borradaile, 1902*	Singapore Taiwan: Kaohsiung: Erzihliao Fishing Port [7]	UF 36191 16531	KT588224† MZ393930
	<i>Tha. stephensonii</i> Crosnier, 1962	Taiwan: Dongsha I. [17]	16484	MZ393931
<i>Thalamitoides</i>	<i>Tho. quadridens</i> A. Milne-Edwards, 1869*	Australia: Lizard I. Taiwan: Taitung: Sansiantai [13]	UF 17070 NTOU	KT365790† -
	<i>Tho. tridens</i> A. Milne-Edwards, 1869*	Taiwan: Dongsha I. [17]	16521	MZ393932
<i>Thranita</i>	<i>Thr. cerasma</i> (Wee & Ng, 1995)*	Australia: Lizard I. Taiwan: Dongsha I. [17]	UF 18231 16527	KT365794† MZ393933
	<i>Thr. coeruleipes</i> (Hombron & Jacquinot, 1846)*	Taiwan: Pingtung: Hengchun [12]	16507	MZ393934
	<i>Thr. crenata</i> (Rüppell, 1830)	Taiwan: Dongsha I. [17]	16516	MZ393935
	<i>Thr. cf. helleri</i> (Hoffmann, 1874)	American Samoa	UF 3232	KT365759†
	<i>Thr. pelsarti</i> (Montgomery, 1931)	Taiwan: Dongsha I. [17]	16485	MZ393936
	<i>Thr. prymna</i> (Herbst, 1803)	Hawaii Taiwan: Dongsha I. [17]	UF 8950 16483	KT365763† MZ393937
<i>Trierarchus</i>	<i>Tr. demani</i> (Nobili, 1905)	Taiwan: Penghu: Dongyupingyu [15a]	16552	MZ393938
	<i>Tr. rotundifrons</i> (A. Milne-Edwards, 1869)	Taiwan: Penghu: Dongyupingyu [15b]	16553	MZ393939
		Taiwan: Penghu: Dongyupingyu [15]	16589	MZ393940
		Taiwan: Dongsha I. [17]	16486	MZ393941
		Vietnam: Nhatrang Bay	ZMMU Ma3346	JX398103†
		Taiwan: Dongsha I. [17]	16498	MZ393942
		Taiwan: Pingtung: Hengchun [12]	NMMB CD5598	MZ393943
		Guam	UF 4079	KT365698†

## TAXONOMY

Superfamily Portunoidea Rafinesque, 1815  
Family Portunidae Rafinesque, 1815Subfamily Carupinae Paulson, 1875  
Genus *Carupa* Dana, 1851  
*Carupa ohashii* Takeda, 1993  
(Figs. 3A, 5)*Carupa ohashii* Takeda, 1993: 145, figs. 1–3 (type locality: Shimoji

**Fig. 2.** A neighbor-joining tree for the species of Portunidae from Taiwan based on the cytochrome c oxidase subunit I (COI) gene, with comparative sequences from GenBank. Probability values at the nodes represent support values. Only values > 50% are shown. Species of the same color are of the same genus, and those with the same background color are different subfamilies. Locality of specimens from Taiwan is shown in parentheses and its number from figure 1 and table 1 is in brackets. The countries or regions of sequences downloaded from GenBank are shown using the following abbreviations: AS = American Samoa; AU = Australia; CN = China; GU = Guam; HI = Hawaii; IN = India; JP = Japan; MG = Madagascar; NC = New Caledonia; OM = Oman; PF = French Polynesia; PG = Papua New Guinea; PH = Philippines; RE = Reunion; RK = Ryukyu; SG = Singapore; TH = Thailand; TW = Taiwan; VN = Vietnam; VU = Vanuatu.



**Fig. 3.** Species of the family Portunidae. A, *Carupa ohashii* Takeda, 1993, female ( $34.9 \times 23.1$  mm) (NCHUZOOI 16500), Dongsha I.; B, *Lupocycloporus minutus* (Shen, 1937), male ( $17.5 \times 9.7$  mm) (NCHUZOOI 16534), Zuoying, Kaohsiung; C, *Lupocyclus inaequalis* (Walker, 1887), male ( $21.6 \times 16.3$  mm) (NCHUZOOI 16551), Erzihliao Fishing Port, Kaohsiung; D, *Lupocyclus tugelae* Barnard, 1950, male ( $17.5 \times 13.1$  mm) (NCHUZOOI 16560), Erzihliao Fishing Port, Kaohsiung; E, *Podophthalmus minabensis* Sakai, 1961, male ( $25.2 \times 14.9$  mm) (NCHUZOOI 16499), Dalinpu, Siaogang, Kaohsiung; F, *Monomia gladiator* (Fabricius, 1798), male ( $53.0 \times 31.2$  mm) (NCHUZOOI 16506), Erzihliao Fishing Port, Kaohsiung; G, *Monomia lucida* Koch & Ďuriš, 2018, male ( $54.8 \times 30.7$  mm) (NCHUZOOI 16538), Erzihliao Fishing Port, Kaohsiung; H, *Xiphonectes tuberculatus* (A. Milne-Edwards, 1861), males ( $24.3 \times 14.3$  mm) (NCHUZOOI 16530), Zuoying, Kaohsiung.

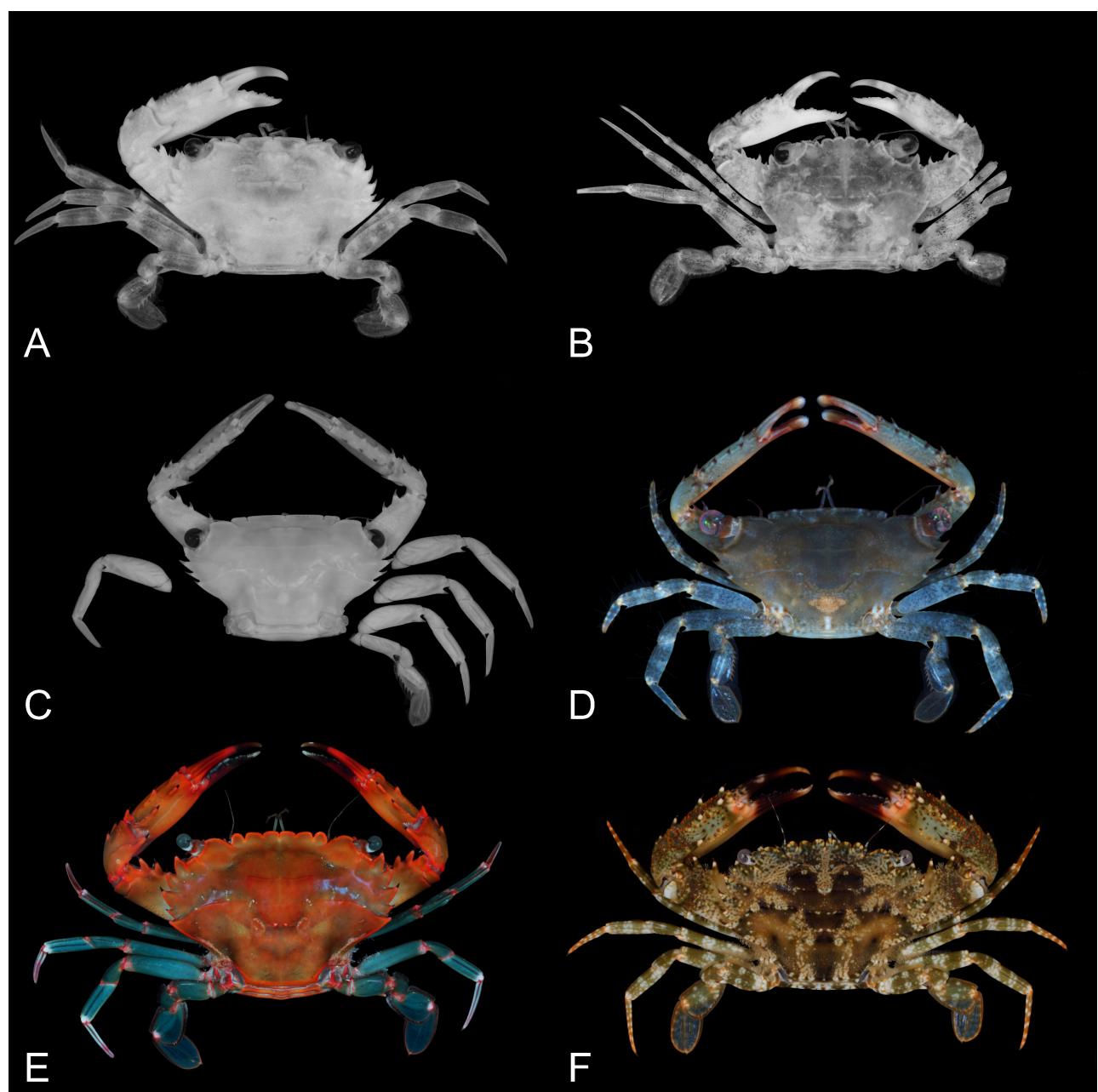
I., Japan; Japan: Ryukyus); Ng et al. 2008: 148 (list); Orchard 2012: 276, 1 unnumb. fig. (upper middle) (Christmas I.); Tan et al. 2014: 411 (Christmas I.); Sasaki 2019: 8893 (list).  
*Carupa* cf. *ohashii* – Shih et al. 2020b: 36 (Dongsha I.).

*Material examined:* Taiwan: 1 female (34.9 × 23.1 mm) (NCHUZOOL 16500), Dongsha I. (20°42'26.3"N 116°43'16.3"E), coll. YH Huang and CY

Chi, 2 Nov. 2019.

*Comparative material:* *Carupa tenuipes*: 1 female (17.0 × 11.0 mm) (NCHUZOOL 16463), Daguang, Kenting, Pingtung, Taiwan (21°56'01"N 120°44'48"E), coll. JH Lee, 13 Apr. 2012.

*Diagnosis:* Carapace subhexagonal, surface smooth, 1.5 times broader than long. All carapace ridges



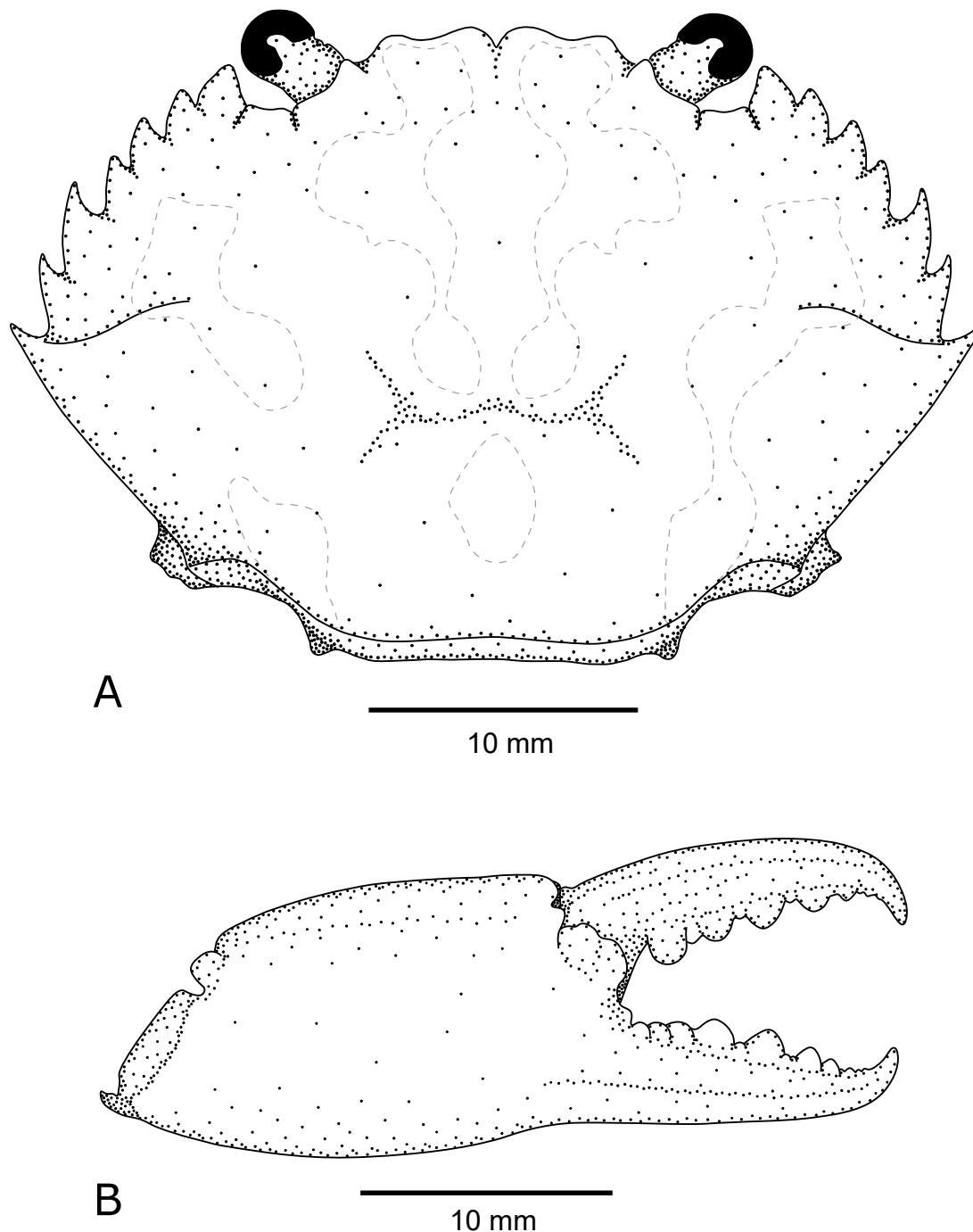
**Fig. 4.** Species of the family Portunidae. A, *Thalamita gatavakensis* Nobili, 1906, male (16.5 × 9.3 mm) (NTOU), Mao-ao, New Taipei City; B, *Thalamita spinifera* Borradaile, 1902, female (12.6 × 9.0 mm) (NCHUZOOL 16531), Erzihliao Fishing Port, Kaohsiung; C, *Thalamitoides quadridentis* A. Milne-Edwards, 1869, male (25.4 × 13.3 mm) (NTOU), Sansiantai, Taitung; D, *Thalamitoides tridens* A. Milne-Edwards, 1869, female (16.1 × 8.2 mm) (NCHUZOOL 16520), Dongsha I.; E, *Thranita cerasma* (Wee & Ng, 1995), female (66.4 × 42.6 mm) (NCHUZOOL 16537), Dongsha I.; F, *Thranita coeruleipes* (Hombron & Jacquinot, 1846), male (59.7 × 40.5 mm) (NCHUZOOL 16507), Wanlitong, Kenting, Pingtung.

absent, except epibranchial regions with a pair of ridges. Front with 2 lobes, each lobe slightly concave in median (Figs. 3A, 5A). Supraorbital margins with 2 notches, infraorbital margins with 3 teeth. Anterolateral margins with 7 teeth, tip of first 4 blunt, tip of last 3 sharp, tooth 5 largest (Figs. 3A, 5A). Chelipeds with merus having 3 sharp spines on inner margin; carpus with spine each on inner and outer margins; palm smooth without ridge

and spine (Figs. 3A, 5B). Surface of P5 smooth, inner margin of merus with small spine on distal end (Fig. 3A).

**Coloration:** Carapace bright orange with symmetrical dark orange stripes (Fig. 3A).

**Distribution:** Philippines (Mactan I.); Taiwan (Dongsha I.; Fig. 1: no. 17); Japan (Ryukyus); Christmas I. (Sasaki 2019; this study).



**Fig. 5.** *Carupa ohashii* Takeda, 1993, female ( $34.9 \times 23.1$  mm) (NCHUZOOL 16500). A, carapace; B, palm of right cheliped (outer view).

**Ecological notes:** A specimen was collected from Dongsha I. (Fig. 1: no. 17) from corals on seagrass bed.

**Remarks:** The genus *Carupa* Dana, 1851 currently contains 2 species, *Car. ohashii* Takeda, 1993 (West Pacific and Christmas I.) and *Car. tenuipes* Dana, 1852 (Indo-West Pacific) (Ng et al. 2008; Sasaki 2019). Our specimen agrees with the characters of *Car. ohashii*: (1) first 4 anterolateral teeth with blunt tips, last 3 sharp, tooth 5 largest in *Car. ohashii* (Fig. 5A; Takeda 1993: figs. 1, 3B, D) (vs. first 5 teeth small and blunt, last 2 sharp, tooth 6 largest in *Car. tenuipes*; Dana 1852: pl. 17(4a); Yang et al. 2012: fig. 25a, h); (2) carapace subhexagonal, anterolateral tooth 7 protruding laterally in *Car. ohashii* (Fig. 5A; Takeda 1993: figs. 1, 3B, D) (vs. carapace subelliptical, tooth 7 slightly protruding laterally in *Car. tenuipes*; Dana 1852: pl. 17(4a); Yang et al. 2012: fig. 25a, h); (3) chelipedal palm with surface smooth in *Car. ohashii* (Fig. 5B; Takeda 1993: figs. 1, 3A, C) (vs. chelipedal palm with 2 ridges and 1 spine on dorsal surface in *Car. tenuipes*; Yang et al. 2012: fig. 25a, b, i). Takeda (1993) suggested the brown symmetrical bands and the pattern of spots on the carapace in *Car. ohashii* (Fig. 3A; Takeda 1993: figs. 1, 3A, B, D) could be used as reliable characters to separate from the uniformly reddish carapace in *Car. tenuipes* (Sakai 1976: pl. 110(3); Takeda 1993).

### Subfamily Lupocyclinae Paulson, 1875

#### Genus *Lupocycloporus* Alcock, 1899

##### *Lupocycloporus minutus* (Shen, 1937)

(Figs. 3B, 6)

*Neptunus (Lupocycloporus) minutus* Shen, 1937: 115, fig. 10a–b (type locality: Siglap, Singapore).

*Portunus minutus* – Stephenson 1967: 16, pl. 2 (Indo-West Pacific); Stephenson 1975: 179 (Timor; Sumatra; Aceh); Cariaso and Garcia 1986: 213, fig. 26 (Philippines).

*Portunus (Lupocycloporus) minutus* – Serène 1968: 67 (list); Ng et al. 2008: 151 (list).

*Lupocycloporus minutus* – Sasaki 2019: 9038 (list).

**Material examined:** Taiwan: 3 males (17.0–17.6 × 9.7–10.1 mm) (NCHUZOOL 16534), Zuoying, Kaohsiung, Jun. 2001; 1 female (17.9 × 10.4 mm), 1 ovig. female (18.9 × 10.6 mm) (NCHUZOOL 16565), Dalinpu, Siaogang, Kaohsiung, Jun. 2001.

**Diagnosis:** Carapace transversely hexagonal, 1.7 times broader than long. Frontal ridge absent; protogastric, mesogastric, metagastric, cardiac regions each with a pair of faintly granulated ridges; epibranchial regions with a pair of granulated ridges; mesobranchial regions with 2 pairs of granulated ridges (Fig. 6A). Front granulated with 4 shallow lobes, lateral 2 broader than median. Supraorbital margins with 2 notches (Fig. 6A). Anterolateral margins with 9 teeth,

each tooth with posterior margin granulated, teeth 2–4 small and blunt, teeth 5–9 gradually increasing in size, tooth 9 largest (Fig. 6A). Chelipeds elongated with surface granulated, merus with 4 spines on inner margin, 2 spines on outer margin; carpus with 2 spines; palm slender with 3–4 spines on dorsal surface, outer surface with 1 granulated ridge. P5 with merus having spine on inner margin; propodus with inner margin smooth. Male pleon with pleomere 6 trapezoidal; telson longer than broad. G1 smooth, distal half slender, bent laterally (Fig. 6B, C).

**Distribution:** East Timor; Philippines; Taiwan; Japan (Ryukyu); Singapore (Siglap); Thailand (eastern side); India (Andaman and Nicobar Is.) (Sasaki 2019; this study).

**Ecological notes:** Specimens were collected by trawling at about 30 meters deep.

**Remarks:** *Lupocycloporus minutus* (Shen, 1937) is similar to *Luo. innominatus* (Rathbun, 1909), but both were described too briefly to distinguish them (Spiridonov 1999). Spiridonov (1999) found the specimens from Ambon agreed with the characters of “*Neptunus (Lupocycloporus) gracilimanus*” from Andamans (= *Luo. innominatus* (Rathbun, 1909)) in Alcock (1899: 45), with more prominent median front lobes and without protogastric ridges, differed from *Luo. minutus*, but it is also necessary to re-examine the type specimens of *Luo. minutus*. Our specimens agree with the characters of *Luo. minutus* in the shallow front lobes (Fig. 6A; Shen 1937: fig. 10a) and the G1 morphology (Fig. 6B, C; Cariaso and Garcia 1986: fig. 26c, d). This identification is also consistent with its distribution, because the type locality of *Luo. minutus* is Singapore (Shen 1937), which is closer to Taiwan, compared with Andamans of *Luo. innominatus* (Alcock 1899).

### Genus *Lupocycclus* Adams & White, 1849

#### *Lupocycclus inaequalis* (Walker, 1887)

(Figs. 3C, 7)

*Goniosoma inaequale* Walker, 1887: 116, pl. 8(4) (type locality: Singapore).

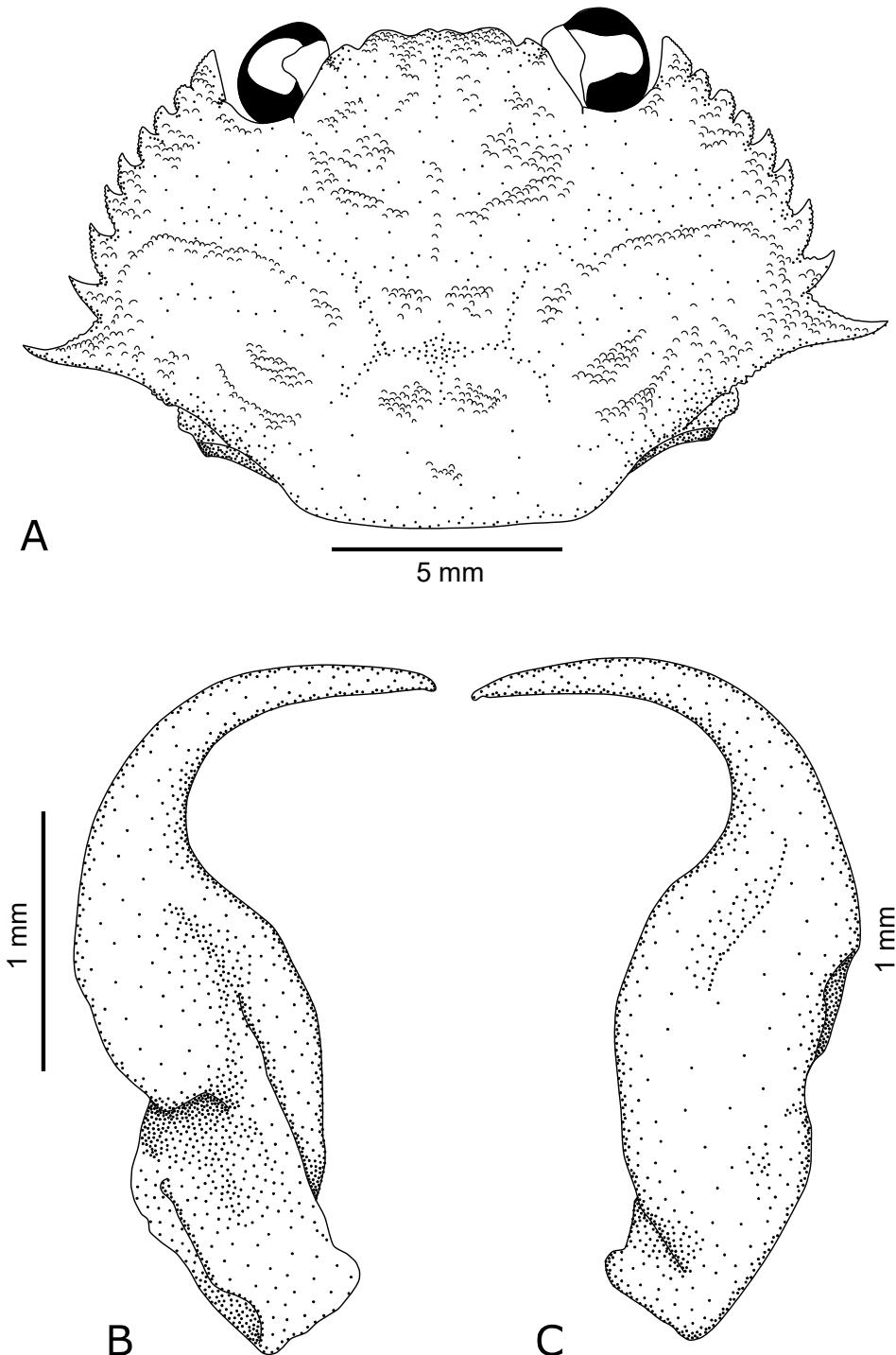
*Lupocycclus rotundatus* – Shen 1937: 98, fig. 1 (Singapore: Siglap); Huang and Yu 1997: 56, 1 unnumb. fig. (Taiwan: Yilan and Kaohsiung); Ng et al. 2017: 67 (list, part?), fig. 6h. (not *Lupocycclus rotundatus* Adams & White, 1849)

*Lupocycclus inaequalis* – Stephenson 1976: 15 (Philippines; Japan: Tosa Bay; Seychelles); Dai and Xu 1991: 20, fig. 16 (Nansha Is.); Fang 1991: 352 (Taiwan Strait); ZG Huang 1994: 585 (list; Nansha Is.); Ng et al. 2008: 151 (list); Yang et al. 2012: 108, fig. 39, pl. 8(5) (China; Nansha Is.); Sasaki 2019: 8917 (list).

**Material examined:** Taiwan: 1 female (17.2 × 13.3 mm) (NCHUZOOL 16470), Zuoying, Kaohsiung,

Jun. 2001; 1 male ( $21.6 \times 16.3$  mm) (NCHUZOOI 16551), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 30 Jul. 2018; 1 ovig. female ( $18.9 \times 14.9$  mm) (NCHUZOOI 16561), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 8 Jul. 2018; 1 ovig. female

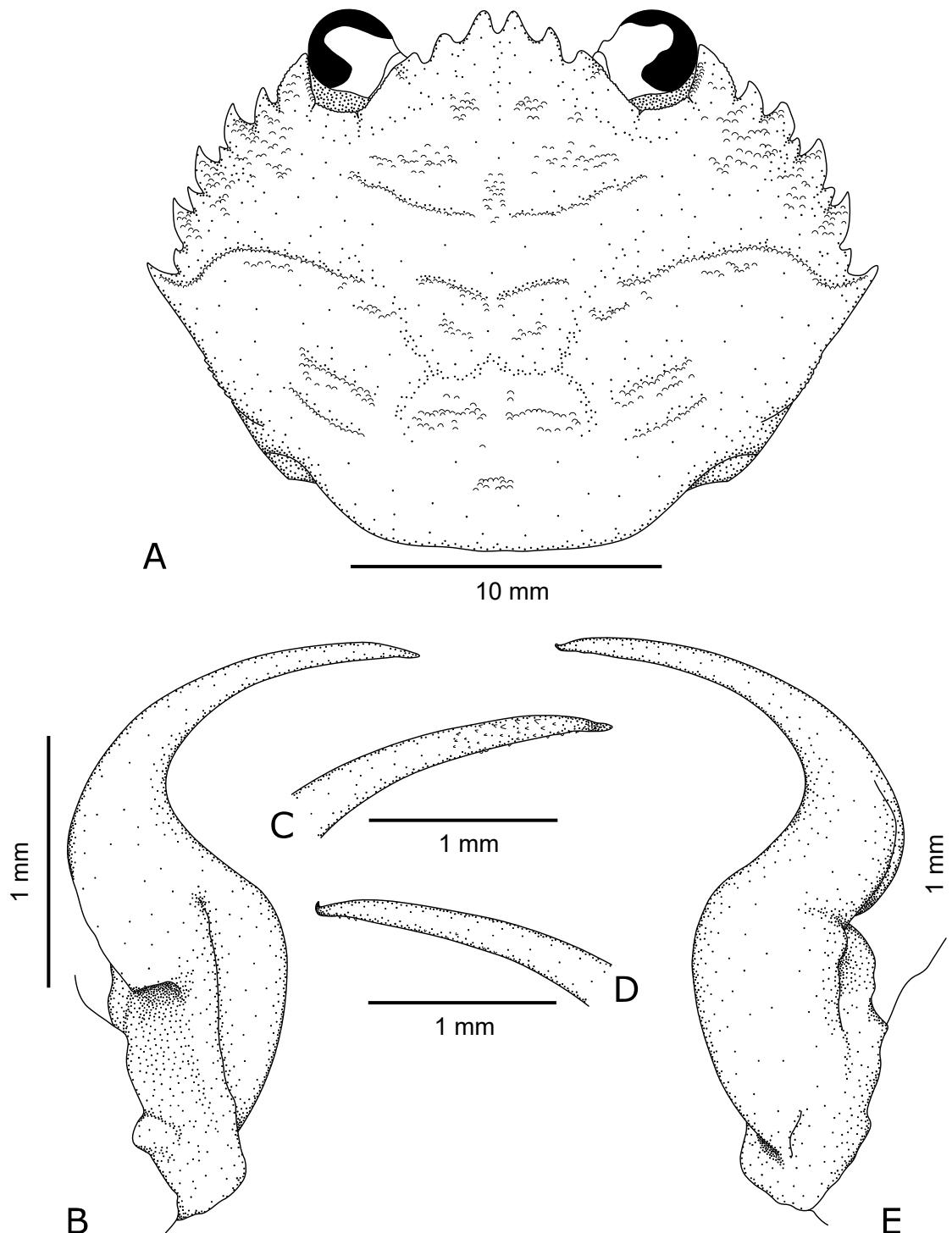
( $17.5 \times 13.6$  mm) (NCHUZOOI 16562), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 4 Apr. 2019; 1 female ( $17.3 \times 13.5$  mm) (NCHUZOOI 16563), Dalinpu, Siaogang, Kaohsiung, 3 Feb. 1997; 9 males ( $15.4\text{--}19.9 \times 12.0\text{--}14.8$  mm), 11 females ( $15.9\text{--}21.0$



**Fig. 6.** *Lupocycloporus minutus* (Shen, 1937), male ( $17.5 \times 9.7$  mm) (NCHUZOOI 16534). A, carapace; B, C, right G1; B, dorsal view; C, ventral view.

$\times 12.4\text{--}15.9\text{ mm}$ ) (NCHUZOOL 16564), Zuoying, Kaohsiung, 1 Feb. 1997; 1 male ( $24.4 \times 18.5\text{ mm}$ ), 1 ovig. female ( $23.5 \times 18.2\text{ mm}$ ) (NCHUZOOL 16570), Magong Fishing Port, Penghu, coll. YH Huang et al., 17 Jan. 2020.

*Diagnosis:* Carapace subhexagonal, slightly broader than long, surface pilose. Frontal and protogastric regions each with a pair of faintly granulated ridges; mesogastric, metagastric, epibranchial and cardiac regions each with a pair of granulated ridges;



**Fig. 7.** *Lupoclylus inaequalis* (Walker, 1887), male ( $21.6 \times 16.3\text{ mm}$ ) (NCHUZOOL 16551). A, carapace; B-E, right G1; B, C, dorsal view; D, E, ventral view.

mesobranchial regions with 2 pairs of granulated ridges (Fig. 7A). Front protruding with 4 teeth, median 2 more protruding than lateral. Supraorbital margins with 2 notches (Fig. 7A). Anterolateral margins with 9 teeth, surface granulated, teeth 2, 4, 6, 8 smaller than others (Fig. 7A). Chelipedal surface granulated and pilose; merus with 5 spines on inner margin, 2 spines on outer margin; carpus with spine each on inner and outer margins; palm with 3 spines on dorsal surface, inner and outer surfaces with granulated ridges. P5 with merus having spine on inner margin. Male pleon with pleomere 6 trapezoidal; telson longer than broad. G1 with distal half slender curved laterally, tip with spines on dorsal side (Fig. 7B–E).

**Distribution:** Hawaii; Australia (eastern); Indonesia (Amboina and Makassar); Borneo; Philippines; Nansha Is.; Taiwan; Japan (Tosa Bay); China (incl. Hainan I.); Singapore; India; Seychelles (Sasaki 2019; this study).

**Ecological notes:** Specimens were collected by trawling (this study). The habitats of this species include muddy-sand, broken shells or coral reefs at 23–85 meters deep (Yang et al. 2012).

**Remarks:** Dai and Xu (1991) and Yang et al. (2012) have pointed “*Lupocycrus rotundatus* Adams & White, 1849” in Shen (1937) was a misidentification of *Luu. inaequalis* (Walker, 1887) (see below). Similarly, based on the figures of Huang and Yu (1997) and Ng et al. (2017), the characters of their “*Luu. rotundatus*” agree well with *Luu. inaequalis* instead. Both species can be distinguished by (1) carapace subhexagonal, 1.3 times broader than long in *Luu. inaequalis* (vs. carapace subcircular, slightly broader than long in *Luu. rotundatus*; Yang et al. 2012); (2) gap between metagastric and epibranchial ridges narrower in *Luu. inaequalis* (vs. wider in *Luu. rotundatus*; Stephenson and Campbell 1960; Yang et al. 2012: figs. 39a, 41a); (3) G1 curved laterally in *Luu. inaequalis* (Fig. 7B–E; Yang et al. 2012: fig. 39e) (vs. slightly curved laterally in *Luu. rotundatus*; Stephenson and Campbell 1960: fig. 1K; Yang et al. 2012: fig. 41f). Fang (1991) has recorded *Luu. inaequalis* from the Taiwan Strait, however Ng et al. (2017) excluded this record from Taiwan because of the unclear locations. As a result, this is the first confirmed record of *Luu. inaequalis* from Taiwan.

### ***Lupocycrus tugelae* Barnard, 1950**

(Figs. 3D, 8)

*Lupocycrus rotundatus* – Sakai 1939: 382, pl. 80(5) (Japan: Shimada and Nagasaki). (not *Lupocycrus rotundatus* Adams & White, 1849)

*Lupocycrus tugelae* Barnard, 1950: 148, figs. 29e–h (type locality: Tugela River mouth, South Africa); Sakai 1976: 352, pl. 121(2) (Japan: Sagami Bay, Shimada, Tosa Bay and Nagasaki); Dai and Xu 1991: 18, fig. 14 (Nansha Is.); ZG Huang 1994: 585 (list;

Taiwan Strait; Nansha Is.); Ng et al. 2008: 151 (list); Yang et al. 2012: 117, fig. 43, pl. 8(6) (China; Nansha Is.); Sasaki 2019: 8923 (list).

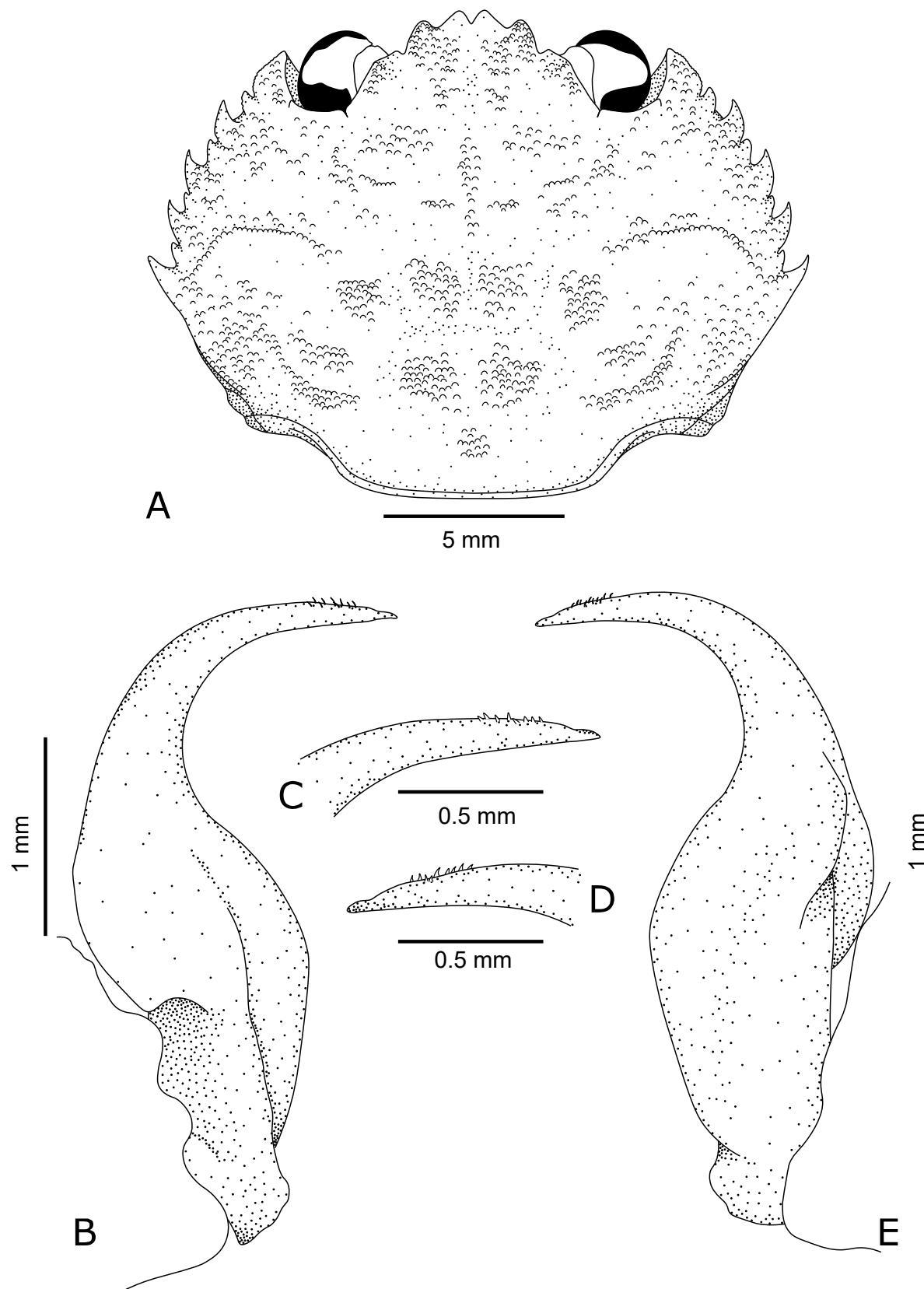
**Material examined:** Taiwan: 1 male (17.5 × 13.1 mm), 1 ovig. female (15.8 × 12.1 mm) (NCHUZOOL 16560), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 4 Apr. 2019; 1 female (14.1 × 10.7 mm) (NCHUZOOL 16593), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 9 Feb. 2019.

**Diagnosis:** Carapace subhexagonal, slightly broader than long, surface with granular patches and pilose. Frontal, metagastric and cardiac ridges absent; protogastric and mesogastric regions each with a pair of faintly granulated ridges; epibranchial regions with a pair of granulated ridges; mesobranchial regions with 2 pairs of faintly granulated ridges. Front protruding with 4 teeth, median 2 teeth more protruding than lateral (Fig. 8A). Orbit slightly as broad as front; supraorbital margins with 2 notches (Fig. 8A). Anterolateral margins with 9 teeth, surface granulated, teeth 2, 4, 6, 8 smaller than others, tooth 1 largest (Fig. 8A). Chelipeds slender with surface densely pilose; merus with surface squamous, 5 spines on inner margin, 2 on outer margin; carpus with 4 granulated ridges on dorsal surface, 1 spine each on inner and outer margins; palm with 2 granulated ridges and 3 spines on dorsal surface, 3 ridges on outer surface, 1 ridge on inner surface, ventral surface squamous. P5 with merus having a spine on inner margin; propodus slender, longer than broad. Male pleon with pleomere 6 trapezoidal, telson longer than broad. G1 with distal part curved laterally, tip slender with spines on mesial side (Fig. 8B–E).

**Distribution:** New Caledonia; Australia (western); Indonesia (Amboin; Talaud Archipelago; Makassar); Philippines; Nansha Is.; Taiwan (Erzihliao Fishing Port, Kaohsiung; Fig. 1: no. 7); Japan (Sagami Bay; Tosa Bay; Nagasaki); China (incl. Hainan I.); Red Sea; Kenya; Madagascar; South Africa (Tugela River mouth) (Sasaki 2019; this study).

**Ecological notes:** The habitats are composed of mud, muddy-sand or broken shells at 14–174 meters deep (Yang et al. 2012).

**Remarks:** *Lupocycrus tugelae* Barnard, 1950 can be distinguished from *Luu. inaequalis* by the following characters: (1) carapace with granular patches in *Luu. tugelae* (Fig. 8A) (vs. granulated ridges on mesogastric, metagastric, cardiac and mesobranchial regions in *Luu. inaequalis*; Fig. 7A); (2) G1 curved laterally at 1/3 from tip, tip with spines on mesial side in *Luu. tugelae* (Fig. 8B–E; Yang et al. 2012: fig. 43g) (vs. G1 curved at 1/2, tip with spines on dorsal side in *Luu. inaequalis*; Fig. 7B–E; Yang et al. 2012: fig. 39e). ZG Huang (1994) has included *Luu. tugelae* from the Taiwan Strait, however



**Fig. 8.** *Lupocylus tugelae* Barnard, 1950, male ( $17.5 \times 13.1$  mm) (NCHUZOOL 16560). A, carapace; B–E, right G1; B, C, dorsal view; D, E, ventral view.

Ng et al. (2017) excluded this record from Taiwan, because of the unclear locations. As a result, this is the first confirmed record of *Luu. tugelae* from Taiwan.

### **Subfamily Podophthalminae Dana, 1851**

#### **Genus *Podophthalmus* Lamarck, 1801**

#### ***Podophthalmus minabensis* Sakai, 1961**

(Figs. 3E, 9)

*Podophthalmus minabensis* Sakai, 1961: 144, fig. 2e, pl. 4(1) (type locality: Minabe, Japan); Sakai 1965b: 41, fig. 1 (Japan: Minabe); Bruce 1965: 287, fig. 1 (Malaysia: Sarawak); Sakai 1976: 384, fig. 207, pl. 135(1) (Japan: Minabe); Ng et al. 2008: 149 (list); Sasaki 2019: 9321 (list).

*Vojmirophthalmus minabensis* – Štević 2011: 138 (list); Yosuva et al. 2020: 535, figs. 1, 2 (India: Chennai).

**Material examined:** Taiwan: 1 male (25.2 × 14.9 mm) (NCHUZOOL 16499), Dalinpu, Siaogang, Kaohsiung, Jun. 2001.

**Diagnosis:** Carapace trapezoidal, 1.7 times broader than long. Frontal, protogastric and metagastric ridges absent; mesogastric, epibranchial and mesobranchial regions each with a pair of ridges; cardiac ridge unbroken (Fig. 9A). Front T-shaped, broader anteriorly, narrower between eyestalks (Fig. 9A). Supraorbital margins wide and denticulated (Fig. 9A). Eyestalks stout and long, with 2 plate-like expansions near cornea (Figs. 3E, 9A). Anterolateral margins with 2 teeth, first larger than second (Fig. 9A). Chelipedal merus with 2 spines on inner margin, 2 spines on outer margin; carpus with spine each on inner and outer margins; palm with tuberculous ridge on dorsal surface, outer surface with 3 ridges, inner surface with 1 ridge, ventral surface granulated; dactylus with outer margin denticulated. P5 with merus having a spine on inner margin; propodus with inner margin smooth. Male pleon with pleomere 6 trapezoidal, slightly longer than board. G1 with distal half slender, slightly bent laterally, tip with tubercles (Fig. 9B–E).

**Coloration in life.** Carapace and chelipeds yellowish brown with reddish-brown marking; P2–P5 pale yellowish brown, with propodus and dactylus bluish grey (Yosuva et al. 2020).

**Distribution:** Taiwan (Siaogang, Kaohsiung; Fig. 1: no. 8); Japan (incl. Ryukyus); Malaysia (Borneo: Sarawak); India (Chennai) (Sasaki 2019; Yosuva et al. 2020; this study).

**Ecological notes:** A specimen was collected by trawling at around 30 meters deep (this study).

**Remarks:** The specimen from Taiwan is consistent with *Podophthalmus minabensis* by the following characters: (1) carapace trapezoidal (Fig. 9A; Sakai 1961: pl. 4(1)); (2) eyestalks with 2 plate-like expansions near cornea (Fig. 9A; Sakai 1961: pl.

4(1); Sakai 1965b: fig. 1a); (3) chelipeds with dactylus denticulated on outer margin (Fig. 3E; Sakai 1965b: fig. 1b).

### **Subfamily Portuninae Rafinesque, 1815**

#### **Genus *Monomia* Gistel, 1848**

#### ***Monomia gladiator* (Fabricius, 1798)**

(Figs. 3F, 10)

*Portunus gladiator* – Fabricius, 1798: 368 (type locality: Tranquebar, India); Stephenson 1972: 135 (Japan: Sagami Bay; Singapore; Sunda Strait; Thailand); Yang et al. 2008: 788 (list; China); Yang et al. 2012: 134 (part), fig. 49a–e, h–i (China, incl. Hainan I.; Nansha Is.).

*Portunus haanii* – Stephenson and Cook 1973: 429 (part), figs. 6A–E, 7A–E, 8A–E, 9A, 10A, C, G (W Malay Peninsula; Madagascar); Yang and Dai 1994: 139, fig. 14, pl. 1(7) (Nansha Is.). (not *Amphitrite haanii* Stimpson, 1858).

*Portunus (Monomia) gladiator* – Ng et al. 2008: 151 (list).

*Monomia haanii* – Chertoprud et al. 2012: 314, pl. 51G (Vietnam: Nhatrang Bay). (not *Amphitrite haanii* Stimpson, 1858).

*Monomia gladiator* – Trivedi et al. 2018: 66 (list; India); Windsor et al. 2019: 21, figs. 1A–D, 3A–C, 4A–D (lectotype; W Australia; Malay Peninsula; Singapore; Thailand; Myanmar; India); Sasaki 2019: 9044 (list).

?*Neptunus (Amphitrite) gladiator* – Shen 1937: 101, fig. 2 (Singapore: Siglap); Shen 1940: 220 (Hong Kong).

not *Cancer gladiator* – Fabricius 1793: 449. (= *Cancer sanguinolentus* Herbst, 1783).

not *Portunus (Amphitrite) gladiator* – De Haan 1833: 39, pl. 1(5). (= *Amphitrite haanii* Stimpson, 1858).

not *Portunus (Amphitrite) gladiator* – De Haan 1833: 65, pl. 18(1). (= *Portunus orbitosinus* Rathbun, 1911).

not *Neptunus gladiator* – Sato 1936a: 1954 (Taiwan: Tainan); Sato 1936b: 142 (Taiwan: Tainan). (= *Amphitrite haanii* Stimpson, 1858).

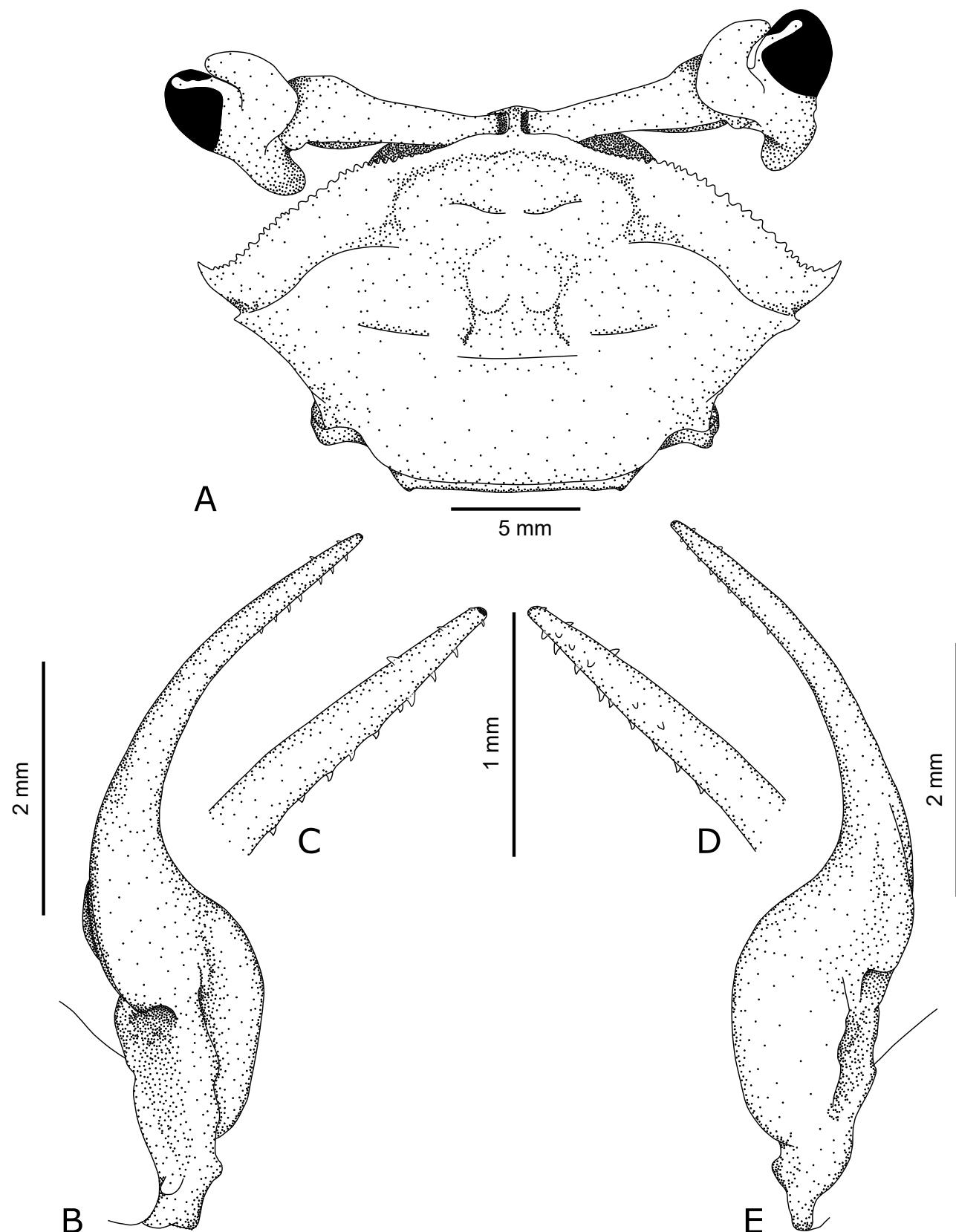
not *Neptunus (Amphitrite) gladiator* – Sakai 1939: 390, fig. 5a, pl. 47(3) (Japan); Kamita 1941: 96, fig. 47 (Korea); Lin 1949: 19 (Taiwan: Kaohsiung); Chang 1963: 97 (Taiwan: Penghu); Shen and Dai 1964: 49, 1 unnumb. fig. (upper) (China). (= *Amphitrite haanii* Stimpson, 1858).

not *Portunus gladiator* – Sakai 1965a: 118, pl. 57(1) (Japan); Yu 1979: 54, fig. 9 (Taiwan: Yilan, Penghu); Yang et al. 2012: 134 (part), fig. 49f–g, pl. 1(5); Wang et al. 2013: 513 (Taiwan: Yilan); Wang et al. 2014: 2453 (Taiwan: Yilan), fig. 2K. (= *Amphitrite haanii* Stimpson, 1858).

not *Portunus (Monomia) gladiator* – Kim 1973: 624 (Korea); Sakai 1976, 341, fig. 180a, pl. 120(1) (Japan); Wang and Chen 1981: 153 (Taiwan: Tainan); Yang and Chang 1996: 41, 1 unnumb. fig. (Taiwan); Wang et al. 2017: in appendix (Taiwan: Yilan and Pingtung). (= *Amphitrite haanii* Stimpson, 1858).

**Material examined:** Taiwan: 1 male (53.0 × 31.2 mm) (NCHUZOOL 16506), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 8 Jul. 2018; 1 female (44.4 × 26.0 mm) (NCHUZOOL 16511), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 8 Jul. 2018; 1 female (57.8 × 33.7 mm) (NCHUZOOL 16571), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 8 Jul. 2018.

**Comparative material:** *Monomia haanii*: 1 male (86.2 × 46.5 mm), 1 female (67.4 × 37.6 mm)



**Fig. 9.** *Podophthalmus minabensis* Sakai, 1961, male ( $25.2 \times 14.9$  mm) (NCHUZOOL 16499). A, carapace; B–E, right G1; B, C, dorsal view; D, E, ventral view.

(NCHUZOOOL 16508), Erzihliao Fishing Port, Kaohsiung, Taiwan, coll. YH Huang, 8 Jul. 2018.

**Diagnosis:** Carapace transversely hexagonal, 1.7 times broader than long, surface densely pilose, with granular patches. All carapace ridges absent, except epibranchial regions with a pair of granulated ridges (Fig. 10A). Front with 4 rounded teeth, median 2 smaller than lateral, sulcus between median teeth continuing ventrally to triangular projection. Epistome with median tooth projecting beyond front. Supraorbital margins with 2 notches, lateral notch with tooth-like elevation before anterolateral tooth 1. Inner supraorbital angles tooth-like, with ventromesial ledge. Infraorbital margins with deep lateral notch. Anterolateral margins with 9 teeth, tooth 9 largest and projecting laterally (Fig. 10A). Basal antennal segment with lateral blunt lobe entering orbital cavity. Chelipedal merus with 4 spines on inner margin, 2 on outer margin; carpus with spine each on inner and outer margins; palm with 2 spines on dorsal surface. P5 with merus granulated on distal inner and outer margins. Maxillipeds 3 with merus longer than broad, anteroexternal angle strongly expanding to a prominent auriculiform structure. Male pleon with pleomere 6 longer than broad, lateral margins slightly convex. G1 with distal half slender and bent laterally, tip with spines (Fig. 10B–E).

**Coloration:** Carapace and chelipeds white with orange stripes, P5 with white band on propodus (Fig. 3F).

**Distribution:** New Caledonia; Australia; New Guinea; Taiwan (Erzihliao Fishing Port, Kaohsiung; Fig. 1: no. 7); China (incl. Hong Kong; Hainan I.); Vietnam; Malaysia (Malay Peninsula); Singapore; Thailand; Myanmar; India (Tranquebar); Sri Lanka; Madagascar; Mauritius; South Africa (Sasaki 2019; this study).

**Ecological notes:** The habitats are 30–100 meters deep, with bottoms composed of sand, broken shells or pebbles (Sakai 1976).

**Remarks:** *Monomia gladiator* (Fabricius, 1798) is similar to *M. haanii* (Stimpson, 1858), but can be distinguished by a suit of characters (Windsor et al. 2019). Our specimens agree with *M. gladiator* by the following characters: (1) carapace with granular patches prominently and protruding in *M. gladiator* (Fig. 3F; Windsor et al. 2019: fig. 1C, D) (vs. smaller and less protruding in *M. haanii*; Windsor et al. 2019: fig. 1F); (2) carapace with bright orange and white stripes in *M. gladiator* (Fig. 3F; Windsor et al. 2019: fig. 1C, D) (vs. uniformly tannish and reddish granules in *M. haanii*; Windsor et al. 2019: fig. 1F); (3) distal propodus and dactylus of P5 without purple spot and area in *M. gladiator* (Fig. 3F; Windsor et al. 2019: fig. 1C, D) (vs. distal propodus with large purple spot and distal dactylus with purple area in *M. haanii* (Windsor et al.

2019: fig. 1E, F); (4) The anterolateral margins of male pleomere 6 slightly convex in *M. gladiator* (Windsor et al. 2019: fig. 3A–C) (vs. margins subparallel and converging anteriorly in *M. haanii*; Windsor et al. 2019: figs. 2B, 3D–F); (5) G1 with distal half bent laterally, with angle below 90° in *M. gladiator* (Fig. 10B–E; Windsor et al. 2019: fig. 4A–D) (vs. angle bent almost at 90° in *M. haanii*; Windsor et al. 2019: figs. 2C, 4E–H). With regard to the earlier records of “*M. gladiator*” from Taiwan, Ng et al. (2001 2017) considered they should be confused with *M. haanii*. As a result, this is the first confirmed record of *M. gladiator* from Taiwan.

### ***Monomia lucida* Koch & Ďuriš, 2018**

(Figs. 3G, 11)

*Portunus argentatus* – Stephenson and Rees 1967: 16 (part), fig. 2a, b (Philippines); Cariaso and Garcia 1986: 209, fig. 23 (Philippines). (not *Neptunus argentata* A. Milne-Edwards, 1861).

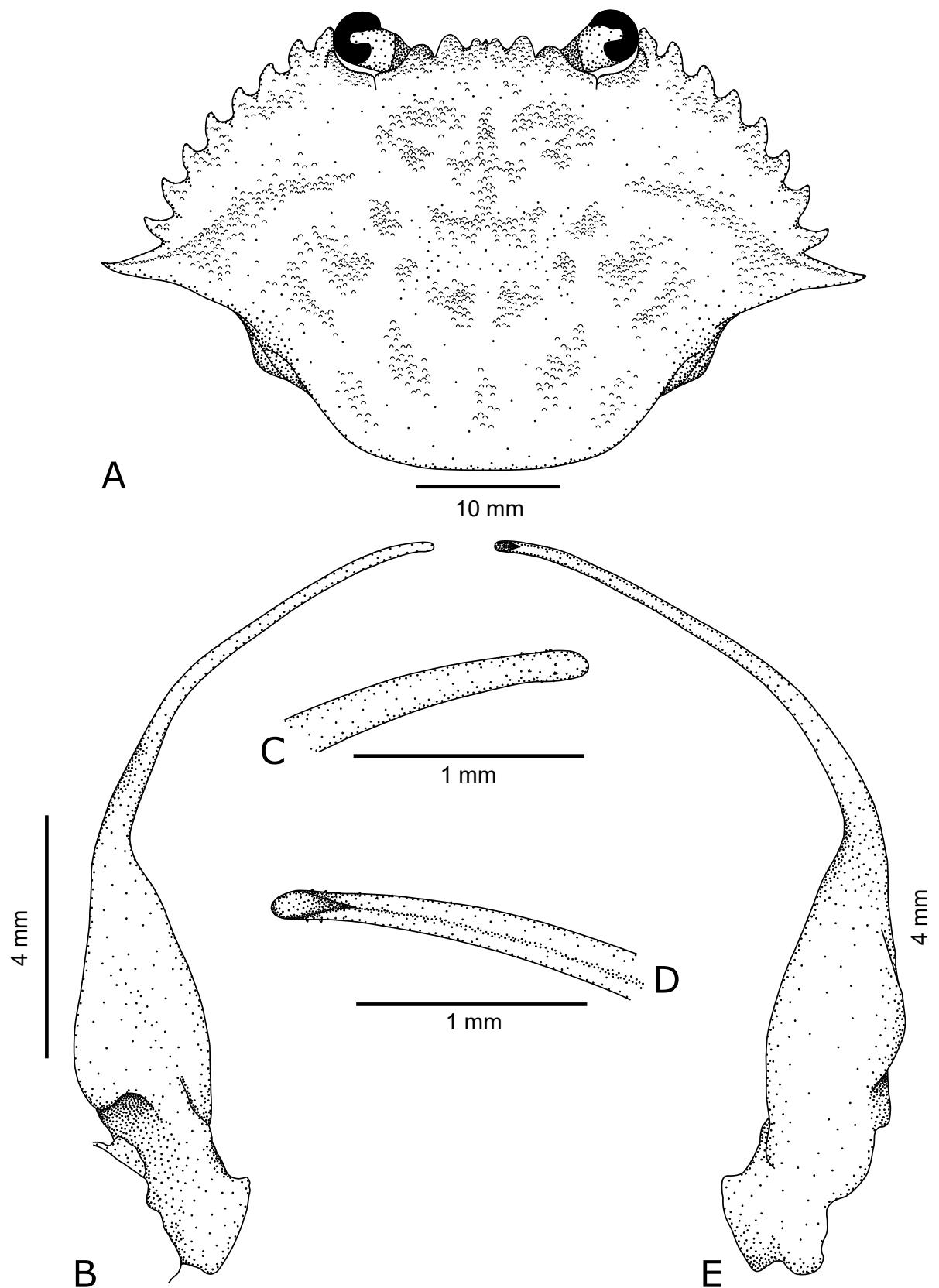
*Monomia argentata* – Chertoprud et al. 2012: 313 (part), pl. 51F (Vietnam). (not *Neptunus argentata* A. Milne-Edwards, 1861).

*Monomia lucida* Koch & Ďuriš, 2018: 569, figs. 1–3 (type locality: Nhatrang, Vietnam); Sasaki 2019: 9052 (list).

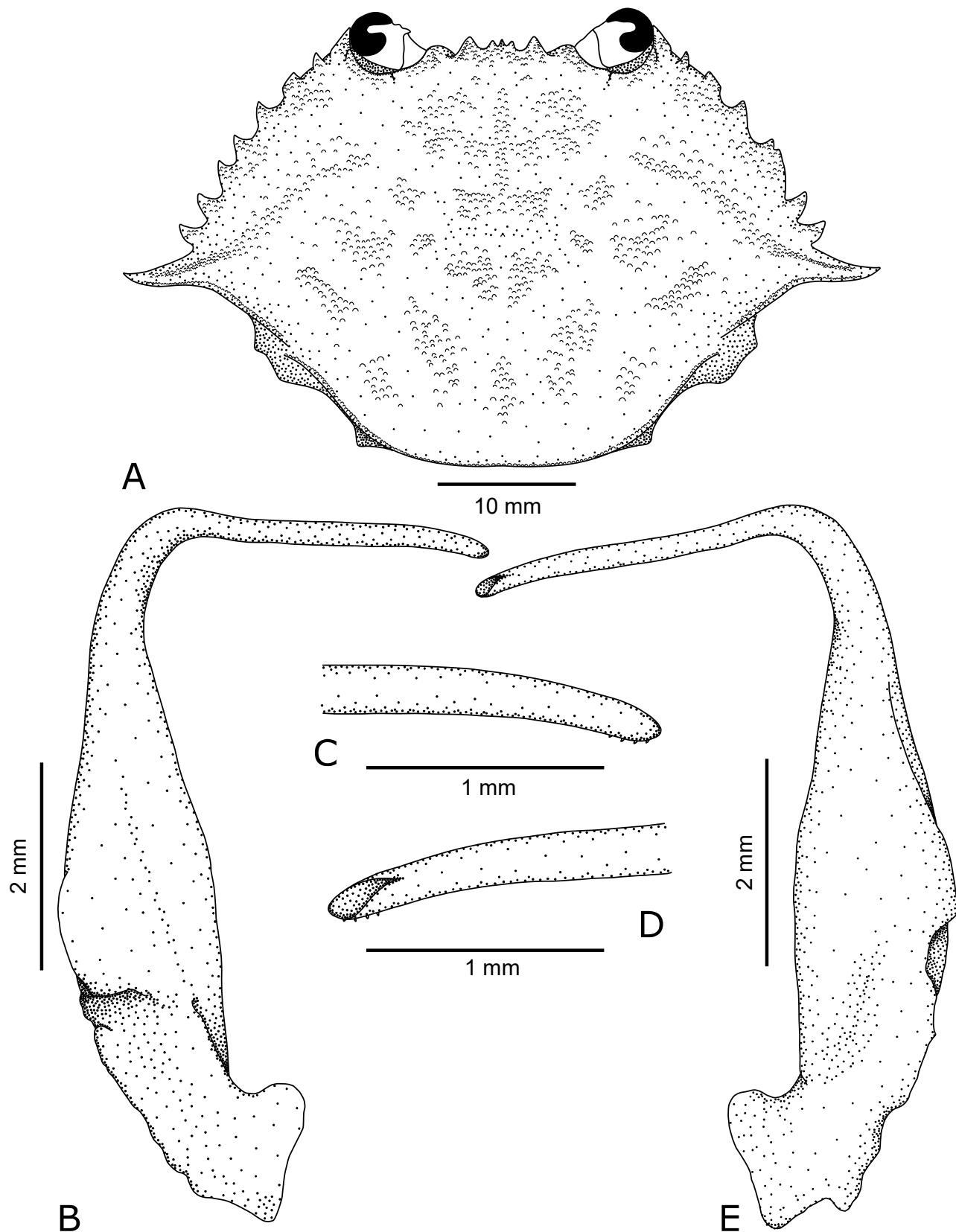
**Material examined:** Taiwan: 3 males (47.1–51.1 × 27.4–30.6 mm), 3 ovig. females (46.8–49.7 × 26.4–28.7 mm) (NCHUZOOOL 16510), Dalinpu, Siaogang, Kaohsiung, Aug. 2001; 4 males (30.8–53.5 × 17.3–30.2 mm) (NCHUZOOOL 16533), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 21 Jan. 2020; 2 males (21.6–34.6 × 11.9–19.3 mm), 1 female (32.0 × 17.1 mm) (NCHUZOOOL 16535), Zuoying, Kaohsiung, 2 Oct. 2001; 1 male (59.9 × 33.7 mm), 1 ovig. female (48.3 × 27.3 mm) (NCHUZOOOL 16536), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 20 May 2016; 1 male (54.8 × 30.7 mm) (NCHUZOOOL 16538), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 8 Jul. 2018.

**Comparative material:** *Monomia argentata*: 1 male (20.7 × 11.0 mm) (NCHUZOOOL 16543), Zuoying, Kaohsiung, Taiwan, Jun. 2001; 4 males (31.2–37.7 × 16.1–21.3 mm) (NCHUZOOOL 16544), Magong Fishing Port, Penghu, Taiwan, coll. YH Huang et al., 17 Jan. 2020.

**Diagnosis:** Carapace transversely hexagonal, 1.7–1.8 times broader than long, surface densely pilose, with granular patches. All carapace ridges absent, except epibranchial regions with a pair of faintly granulated ridges (Fig. 11A). Front with 4 rounded teeth, median 2 smaller than lateral, sulcus between median teeth continuing ventrally to triangular projection. Epistome with median tooth projecting beyond front. Supraorbital margins with 2 notches, lateral notch with tooth-like elevation before anterolateral tooth 1. Inner supraorbital angle tooth-like, with ventromesial ledge. Infraorbital



**Fig. 10.** *Monomia gladiator* (Fabricius, 1798), male ( $53.0 \times 31.2$  mm) (NCHUZOOL 16506). A, carapace; B–E, right G1; B, C, dorsal view; D, E, ventral view.



**Fig. 11.** *Monomia lucida* Koch & Ďuriš, 2018. A, carapace, male ( $54.8 \times 30.7$  mm) (NCHUZOOl 16538); B–E, male ( $41.4 \times 22.6$  mm) (NCHUZOOl 16533), right G1; B, C, dorsal view; D, E, ventral view.

margins with deep lateral notch. Anterolateral margins with 9 teeth, tooth 9 largest and projecting laterally, teeth 2–4 smallest (Fig. 11A). Basal antennal segment with lateral blunt lobe entering orbital cavity. Chelipedal merus with 4 spines on inner margin, 2 on outer margin; carpus with spine each on inner and outer margins; palm with 2 spines on dorsal surface. P5 with merus granulated on inner margin distal part. Maxillipeds 3 with merus longer than broad, anteroexternal angle strongly expanding to a prominent auriculiform structure. Male pleon with pleomere 6 longer than broad, lateral margins subparallel and slightly converging anteriorly. G1 with distal half slender and bent laterally about 90°, tip with spines (Fig. 11B–E).

**Coloration:** Carapace and chelipeds tannish with patches of white and brown granules. P5 with a large black spot on dactylus (Fig. 3G).

**Distribution:** Philippines; Taiwan; Vietnam (Nhatrang Bay); India (northwestern) (Cariaso and Garcia 1986; Koch and Ďuriš 2018; this study).

**Ecological notes:** Specimens were caught by trawling and collected from a fishing port.

**Remarks:** *Monomia lucida* Koch & Ďuriš, 2018 is similar to *M. argentata* (A. Milne-Edwards, 1861) in coloration and morphology (Fig. 3G; Koch et al. 2017: fig. 5; Koch and Ďuriš 2018: fig. 1). Biogeographically *M. lucida* was only distributed from Vietnam and northwestern India (Koch and Ďuriš 2018), and *M. argentata* is distributed widely in the Indo-West Pacific (Sasaki 2019). The specimens from Taiwan is consistent with *M. lucida* by the following characters: (1) lateral margins of male pleomere 6 subparallel in *M. lucida* (Koch and Ďuriš 2018: fig. 2B) (vs. median part convex in *M. argentata*; Koch et al. 2017: figs. 7B, 8A–D); (2) G1 with distal part slender, tip subtriangular in *M. lucida* (Fig. 11B–E; Koch and Ďuriš 2018: fig. 3A, B) (vs. distal part stout, tip blunt in *M. argentata*; Koch et al. 2017: fig. 4); (3) female with long transverse ridges on both pleomeres 4 and 5 in *M. lucida* (Koch and Ďuriš 2018: fig. 3C) (vs. with medium and short ridges on pleomeres 4 and 5 respectively in *M. argentata* (Koch et al. 2017: fig. 8E)).

### Genus *Xiphonectes* A. Milne-Edwards, 1873

#### *Xiphonectes tuberculatus* (A. Milne-Edwards, 1861)

(Figs. 3H, 12)

*Neptunus tuberculatus* A. Milne-Edwards, 1861: 333, pl. 31(5) (type locality: Hawaii).

*Neptunus (Hellenus) tuberculatus* – Shen 1940: 220 (Hong Kong).

*Portunus tuberculatus* – Stephenson and Rees 1967: 52, fig. 18, pl. 6B (Palau; Philippines; China); Moosa 1981: 147 (Philippines); Dai et al. 1986: 199, fig. 116(3), pl. 26(6) (China, incl. Hainan I.); Dai and Yang 1991: 218, fig. 116(3), pl. 26(6) (China, incl.

Hainan I.); Dai and Xu 1991: 23, fig. 18 (Nansha Is.); Yang et al. 2008: 788 (list).

*Portunus (Xiphonectes) tuberculatus* – Ng et al. 2008: 153 (list).

*Xiphonectes tuberculatus* – Sasaki 2019: 9130 (list).

not *Portunus tuberculatus* – Chou et al. 1999: 30 (Taiwan: Kaohsiung). (= *Neptunus trituberculatus* Miers, 1876).

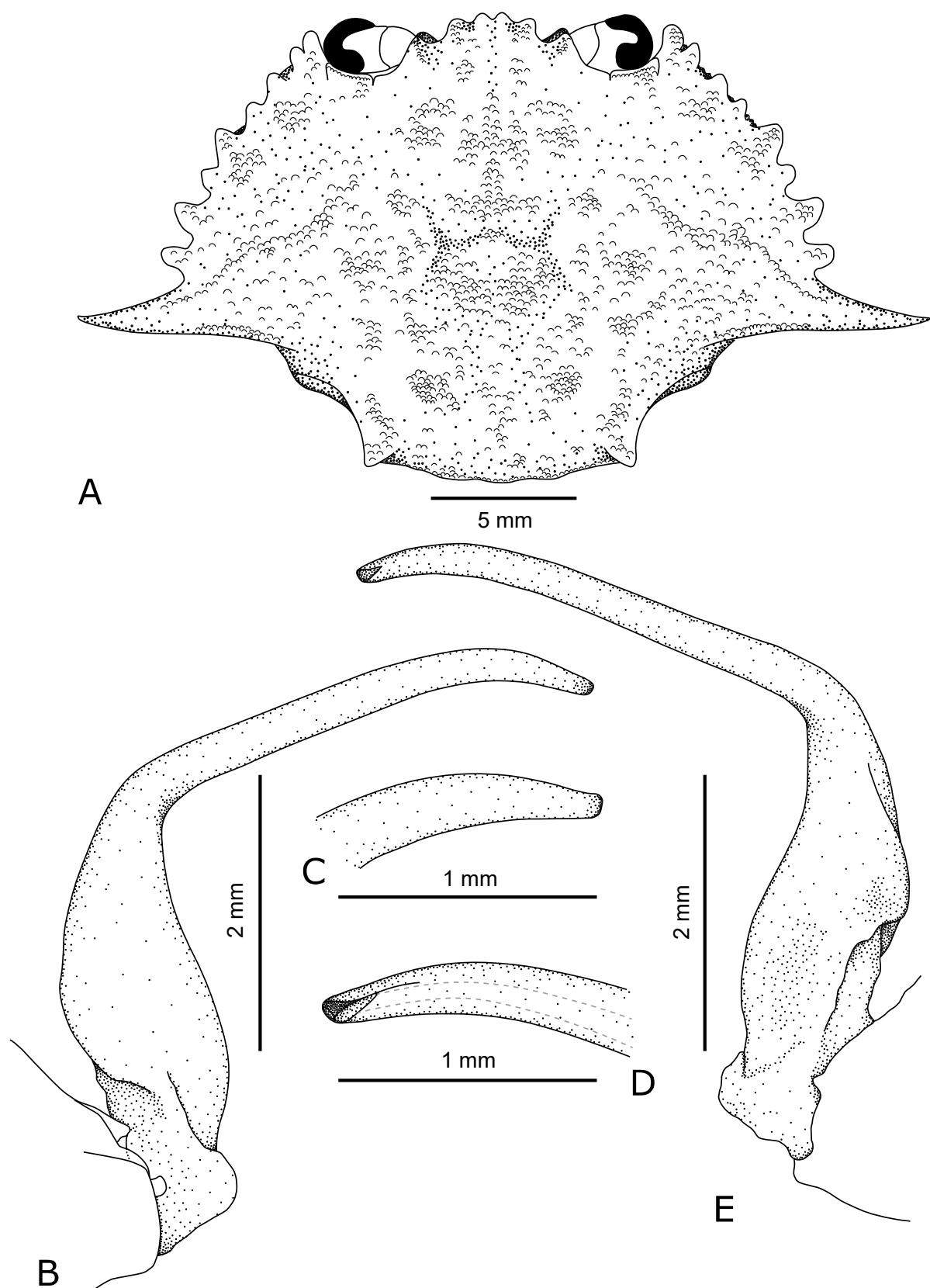
**Material examined:** Taiwan: 3 males (20.3–26.9 × 12.0–15.8 mm), 2 females (23.2–23.5 × 13.2–13.7 mm) (NCHUZOOOL 16530), Zuoying, Kaohsiung, Jun. 2001; 1 male (26.4 × 16.4 mm) (NCHUZOOOL 16532), Dalinpu, Siaogang, Kaohsiung, 12 May 1997; 1 female (20.7 × 11.9 mm) (NCHUZOOOL 16559), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 8 Jul. 2018; 1 male (25.1 × 14.7 mm), 1 ovig. female (26.8 × 15.9 mm) (NCHUZOOOL 16594), Dalinpu, Siaogang, Kaohsiung, Jun. 2001.

**Diagnosis:** Carapace transversely hexagonal, 1.7 times broader than long, surface densely pilose, with granular patches. All carapace ridges absent, except epibranchial regions with a pair of granulated ridges (Fig. 12A). Front with 4 rounded teeth, median 2 smaller and more protruding than lateral (Fig. 12A). Supraorbital margins with 2 notches, inner supraorbital angle tooth-like, with ventromesial ledge. Anterolateral margins with 9 teeth, tooth 9 largest (Fig. 12A). Junction between posterolateral and posterior margins tooth-like (Fig. 12A). Basal antennal segment with a lateral blunt lobe entering orbital cavity. Chelipeds granulated and pilose, merus with 3 blunt spines on inner margin, outer margin with 1 spine; carpus with spine each on inner and outer margins; palm with 2 granulated ridges and 1 spine on dorsal surface, outer surface with 3 ridges. P5 with merus granulated on inner margin. Maxillipeds 3 with merus longer than broad, anteroexternal angle strongly expanding to a prominent auriculiform structure. Male pleon with pleomere 6 trapezoidal, longer than broad. G1 smooth, distal half slender and bent laterally (Fig. 12B–E).

**Distribution:** Hawaii; Australia; Indonesia (Makassar); Guam; Palau; Philippines; Nansha Is.; Taiwan; Japan (incl. Ryukyus); China (incl. Hong Kong; Hainan I.); Vietnam; Thailand; India; Sri Lanka; Maldives; Gulf of Aden; Gulf of Oman; Seychelles; Tanzania; Madagascar (Sasaki 2019; this study).

**Ecological notes:** Specimens were collected by trawling at about 30 meters deep (this study).

**Remarks:** Chou et al. (1999) recorded the name “*Portunus tuberculatus*” from Taiwan, but Ng et al. (2001 2017) considered it should be a typographical mistake of *Portunus trituberculatus*. As a result, *Xiphonectes tuberculatus* is the first confirmed record from Taiwan in our study.



**Fig. 12.** *Xiphonectes tuberculatus* (A. Milne-Edwards, 1861). A, carapace, male ( $26.9 \times 15.8$  mm); B-E, male ( $24.3 \times 14.3$  mm) (NCHUZOOI 16530), right G1; B, C, dorsal view; D, E, ventral view.

**Subfamily Thalamitinae Paulson, 1875**  
**Genus *Thalamita* Latreille, 1829**  
***Thalamita gatavakensis* Nobili, 1906**  
(Figs. 4A, 13)

*Thalamita pilumnoides* var. *gatavakensis* Nobili, 1906: 262 (type locality: Gatavaké, Tuamotus Is., French Polynesia).

*Thalamita pilumnoides* ssp. *gatavakensis* – Forest and Guinot 1961: 34, figs. 23–25 (lectotype) (French Polynesia: Gambier Is.: Mangareva).

*Thalamita granosimana* – Stephenson 1961: 119, figs. 2E, 4A, pls. 3(4), 4J, 5G (Western Australia). (not *Thalamita* var. *D. granosimana* Borradaile, 1902)

*Thalamita gatavakensis* – Crosnier 1962: 106, figs. 156 bis. a–c, e (syntype), 177 bis. (Madagascar: Nosy Be); Stephenson and Rees 1967: 75 (French Polynesia: Tuamotus Is. and Society Is.; Philippines); Stephenson 1972: 149 (Indonesia: Bali; Philippines); Wee and Ng 1995: 82, fig. 43; Ng et al. 2008: 154 (list); Sasaki 2019: 9236 (list).

**Material examined:** Taiwan: 1 male (16.5 × 9.3 mm) (NTOU), Mao-ao, New Taipei City, coll. CH Yang, 16 Aug. 2006.

**Comparative material:** *Thalamita gloriensis*: 2 males (15.7–18.1 × 8.6–10.0 mm) (NCHUZOOOL 16540), Waiping, Dongjiyu, Penghu, Taiwan, coll. YH Huang et al., 14 May 2020.

**Diagnosis:** Carapace transversely hexagonal, 1.8 times broader than long, surface pilose. All anterior carapace ridges and mesobranchial ridges paired, except metagastric and cardiac ridges unbroken (Fig. 13A). Front with 2 lobes. Supraorbital margins with 2 notches. Anterolateral margins with 5 teeth, first 3 subequal, tooth 4 smallest, tooth 5 largest (Fig. 13A). Basal antennal segment granulated. Chelipeds with surface granulated, merus with 3 spines on inner margin, inner margin with distal end granulated; carpus with 1 spine on inner margin, 3 smaller spines on outer margin; palm with 4 spines on dorsal surface, outer surface with 3 granulated ridges, inner and lower surfaces smooth. P5 with merus having spine on inner margin, distal end of inner margin with small spine; propodus with a row of granules, inner margin with 7–8 spines; dactylus with spinules on distal margins. Pleomere 6 of male pleon with lateral margins subparallel and slightly converging anteriorly. G1 with distal part slender, tip spoon-shaped with bristles (Fig. 13B–E).

**Distribution:** French Polynesia; Australia (western); Indonesia (Bali); Philippines; Taiwan (Mao-ao, New Taipei City; Fig. 1: no. 1); Japan (incl. Ogasawara Is.; Ryukyus); China (Hainan I.); Vietnam; Malaysia; Thailand (western); Kenya; Tanzania; Mayotte I.; Madagascar (Nosy Be) (Sasaki 2019; this study).

**Ecological notes:** The habitat is the intertidal zone with a bottom composed of coral sand (Crosnier 1962).

**Remarks:** *Thalamita gatavakensis* Nobili, 1906 is similar to *Tha. pilumnoides* Borradaile, 1902 and both are widely distributed in the Indo-West Pacific (Sasaki 2019). The specimen from Taiwan is consistent with *Tha. gatavakensis* by the following characters: (1) G1 with distal part curved in *Tha. pilumnoides* (Crosnier 1962: fig. 256; Stephenson and Rees 1967: fig. 32a; Yang et al. 2012: fig. 118f) (vs. not curved in *Tha. gatavakensis*; Fig. 13B–E; Crosnier 1962: figs. 177 bis. c, d); (2) male pleon with pleomere 6 broader than long in *Tha. pilumnoides* (Borradaile 1902: 207; Crosnier 1962: fig. 255; Stephenson and Rees 1967: fig. 32b; Yang et al. 2012: fig. 118e) (vs. nearly as broad as long in *Tha. gatavakensis*; Crosnier 1962: fig. 177 bis. b).

*Thalamita gatavakensis* is also similar to *Tha. gloriensis* Crosnier, 1962, with the latter distributed widely in the Indo-West Pacific as well (Sasaki 2019). The specimen from Taiwan is consistent with *Tha. gatavakensis* by the following characters: (1) inner supraorbital lobes slightly arched in *Tha. gatavakensis* (Fig. 13A; Crosnier 1962: fig. 156 bis. a–c, e) (vs. inner supraorbital lobe subparallel to front in *Tha. gloriensis*; Crosnier 1962: fig. 156 bis. d); (2) male pleon with pleomere 6 straight on posterior margin in *Tha. gatavakensis* (Crosnier 1962: fig. 177 bis. b) (vs. posterior margin convex in *Tha. gloriensis*; Crosnier 1962: fig. 169); (3) G1 with distal part slender, lateral and mesial sides with bristles in *Tha. gatavakensis* (Fig. 13B–E; Crosnier 1962: fig. 177 bis. c, d) (vs. G1 with distal part stout, mesial side with bristles in *Tha. gloriensis*; Crosnier 1962: figs. 159, 160).

***Thalamita spinifera* Borradaile, 1902**

(Figs. 4B, 14)

*Thalamita exetastica* var. *spinifera* Borradaile, 1902: 203 (type locality: Maldives).

*Thalamita exetastica* – Sakai 1935: 76, figs. 9, 10a, c (Japan: Sagami Bay); Sakai 1939: 417, fig. 12 (Japan: Sagami Bay); Sakai 1965a: 126, pl. 64(3) (Japan: Sagami Bay); Stephenson 1976: 20 (Japan). (not *Thalamita exetastica* Alcock, 1899)

*Thalamita spinifera* – Stephenson and Rees 1967: 93, fig. 34 (Philippines); Sakai 1976: 371, pl. 133(2) (Japan: Sagami Bay); Stephenson 1976: 24 (Japan: Sagami Bay); Moosa 1981: 148 (Philippines); Cariaso and Garcia 1986: 235, fig. 41 (Philippines); Dai and Xu 1991: 33, fig. 25 (Nansha Is.); Wee and Ng 1995: 116, fig. 65; Ng et al. 2008: 155 (list); Yang et al. 2008: 790 (list; Nansha Is.); Yang et al. 2012: 328, fig. 128, pl. 14(2) (China; Nansha Is.); Sasaki 2019: 9271 (list).

**Material examined:** Taiwan: 1 ovig. female (12.6 × 9.0 mm) (NCHUZOOOL 16531), Erzihliao Fishing Port, Kaohsiung, coll. YH Huang, 8 Jul. 2018.

**Diagnosis:** Carapace subhexagonal, 1.4 times broader than long, surface densely pilose, posterior margin slightly broader than frontal (Fig. 14A). All

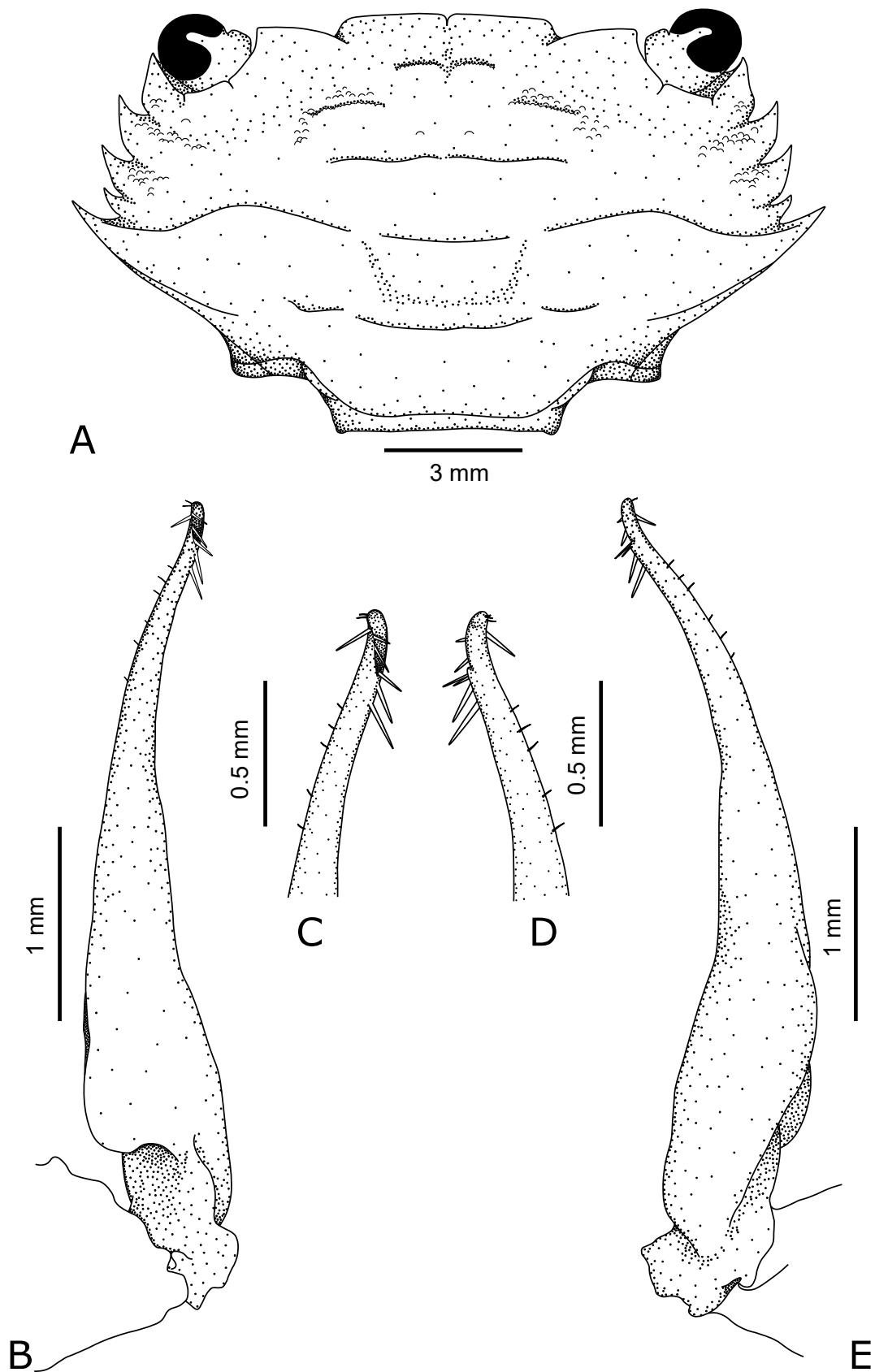
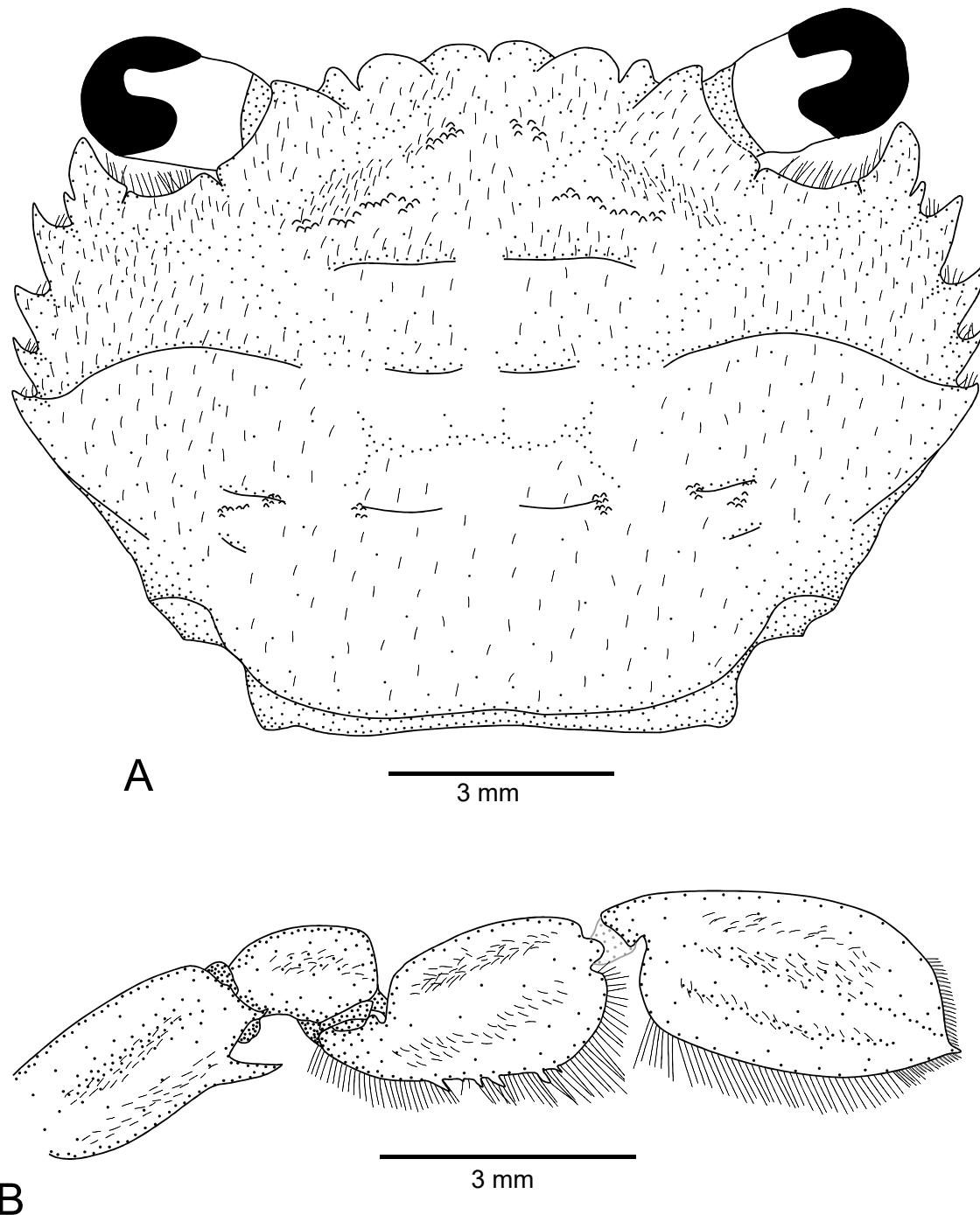


Fig. 13. *Thalamita gatavakensis* Nobili, 1906, male ( $16.5 \times 9.3$  mm) (NTOU). A, carapace; B–E, right G1; B, C, dorsal view; D, E, ventral view.

anterior carapace ridges and cardiac ridges paired, mesobranchial regions with 2 pairs of ridges (Fig. 14A). Front with 6 lobes, median 2 lobes lower than submedian, lateral lobes smallest and tooth-like. Supraorbital margins broad with 2 notches. Anterolateral margins with 5 teeth, tooth 1 with small subsidiary basal tooth (Fig. 14A). Basal antennal segment granulated.

Chelipeds with surface granulated; merus with 3 spines on inner margin; carpus with spine on inner margin, 3 smaller spines on outer margin; palm with 5 spines on dorsal surface, outer distal spine small or reduced to a tubercle, outer surface with 3 granulated ridges. Propodus of P5 with spines on inner margin (Fig. 14B).

*Coloration in life:* Carapace, chelipeds and P2–P5



**Fig. 14.** *Thalamita spinifera* Borradaile, 1902, female (12.6 × 9.0 mm) (NCHUZOOL 16531). A, carapace; B, right P5 (dorsal view).

gray.

**Distribution:** Hawaii; French Polynesia; New Caledonia; Australia (western); Indonesia (Banda); Guam; Philippines; Nansha Is.; Taiwan (Erzihliao Fishing Port, Kaohsiung; Fig. 1: no. 7); Japan (incl. Ogasawara Is.; Ryukyus); China (incl. Hainan I.); Malaysia (Malay Peninsula); Thailand; India; Maldives; Red Sea; Seychelles; Mayotte I.; Madagascar (Sasaki 2019; this study).

**Ecological notes:** Specimens were caught by trawling and collected from fishing port (this study). The habitats are 30–80 meters deep, with muddy, sandy or pebbly bottoms (Sakai 1976).

**Remarks:** *Thalamita spinifera* Borradaile, 1902 is similar to *Tha. exetastica* Alcock, 1899, with *Tha. spinifera* distributed widely in the Indo-West Pacific and *Tha. exetastica* distributed in the Indian Ocean and the South China Sea (Sasaki 2019). The female specimen from Taiwan is consistent with *Tha. spinifera* by the spines on the inner margin of propodus of P5 (Fig. 14B; Yang et al. 2012: fig. 128e, pl. 14(2)) (vs. smooth in *Tha. exetastica*; Alcock and McArdle 1900: pl. 47(2); Yang et al. 2012: fig. 104e, pl. 12(4)).

#### Genus *Thalamitoides* A. Milne-Edwards, 1869

##### *Thalamitoides quadridentis* A. Milne-Edwards, 1869

(Figs. 4C, 15)

*Thalamitoides quadridentis* A. Milne-Edwards, 1869: 147, pl. 6(8–15) (type locality: Madagascar); Stephenson and Rees 1967: 101, fig. 37 (Hawaii; Samoa; Philippines); Sakai 1976: 381, pl. 134(3) (Japan: Ryukyus); Cariaso and Garcia 1986: 237, fig. 43 (Philippines); Dai and Xu 1991: 35, fig. 26 (Nansha Is.); Ng et al. 2008: 155 (list); Yang et al. 2008: 791 (list) (Nansha Is.); Yang et al. 2012: 342, fig. 135, pl. 14(7) (Nansha Is.); Sasaki 2019: 9276 (list).

**Material examined:** Taiwan: 1 male (25.4 × 13.3 mm) (NTOU), Sansiantai, Taitung, 1 Jul. 1987.

**Diagnosis:** Carapace with surface smooth, slightly convex, 1.9 times broader than long, broadest between anterolateral tooth 2. Frontal and mesogastric ridges unbroken; epibranchial regions with a pair of ridges; protogastric, metagastric, mesobranchial and cardiac ridges absent (Fig. 15A). Front with 4 lobes, median 2 lobes 2.5 times broader than lateral. Supraorbital margins with 2 notches, inner lobe slightly arched (Fig. 15A). Anterolateral margins with 4 teeth, decreasing in size posteriorly, tooth 1 with posterior margin serrated (Fig. 15A). Basal antennal segment with a row of granules. Chelipedal merus with 4 spines on inner margin, distal end of ventral surface with a spinule near articulation of carpus; carpus with 5–6 sharp spines; palm with 2 rows of spines on dorsal surface, inner row

with 4 spines, outer with 5 spines; finger tips spoon-shaped (Fig. 15C). P5 with merus having strong spine on inner margin, distal end with small spine; propodus with 8 sharp spines on inner margin, dactylus with spinules on distal margins (Fig. 15B). Male pleon with pleomere 6 trapezoidal. G1 stout, distal part with bristles on lateral side (Fig. 15D–G).

**Distribution:** Hawaii; French Polynesia; Samoa; Fiji; New Caledonia; Australia (western); Indonesia (Banda); East Timor; Guam; Philippines; Nansha Is.; Taiwan (Sansiantai, Taitung; Fig. 1: no. 13); Japan (Ryukyus); Thailand; Red Sea; Somalia; Tanzania; Mayotte I.; Madagascar (Sasaki 2019; this study).

**Ecological notes:** The habitats include coral reefs and shallow waters (Sakai 1976).

**Remarks:** The genus *Thalamitoides* A. Milne-Edwards, 1869 currently contains 3 species, viz. *Tho. quadridens* A. Milne-Edwards, 1869, *Tho. spinigera* Nobili, 1905 and *Tho. tridens* A. Milne-Edwards, 1869 (Ng et al. 2008). Geographically, *Tho. quadridens* and *Tho. tridens* are distributed in the Indo-West Pacific; and *Tho. spinigera* is in the northwestern Indian Ocean (Sasaki 2019). The specimen from Taiwan is consistent with *Tho. quadridens* by the character of 4 anterolateral teeth (Fig. 15A; A. Milne-Edwards 1869: pl. 6 (8, 15)) (vs. 3 teeth in *Tho. spinigera* and *Tho. tridens* (Fig. 16A; A. Milne-Edwards 1869: pl. 6(1); Spiridonov and Neumann 2008: fig. 2A)).

#### *Thalamitoides tridens* A. Milne-Edwards, 1869

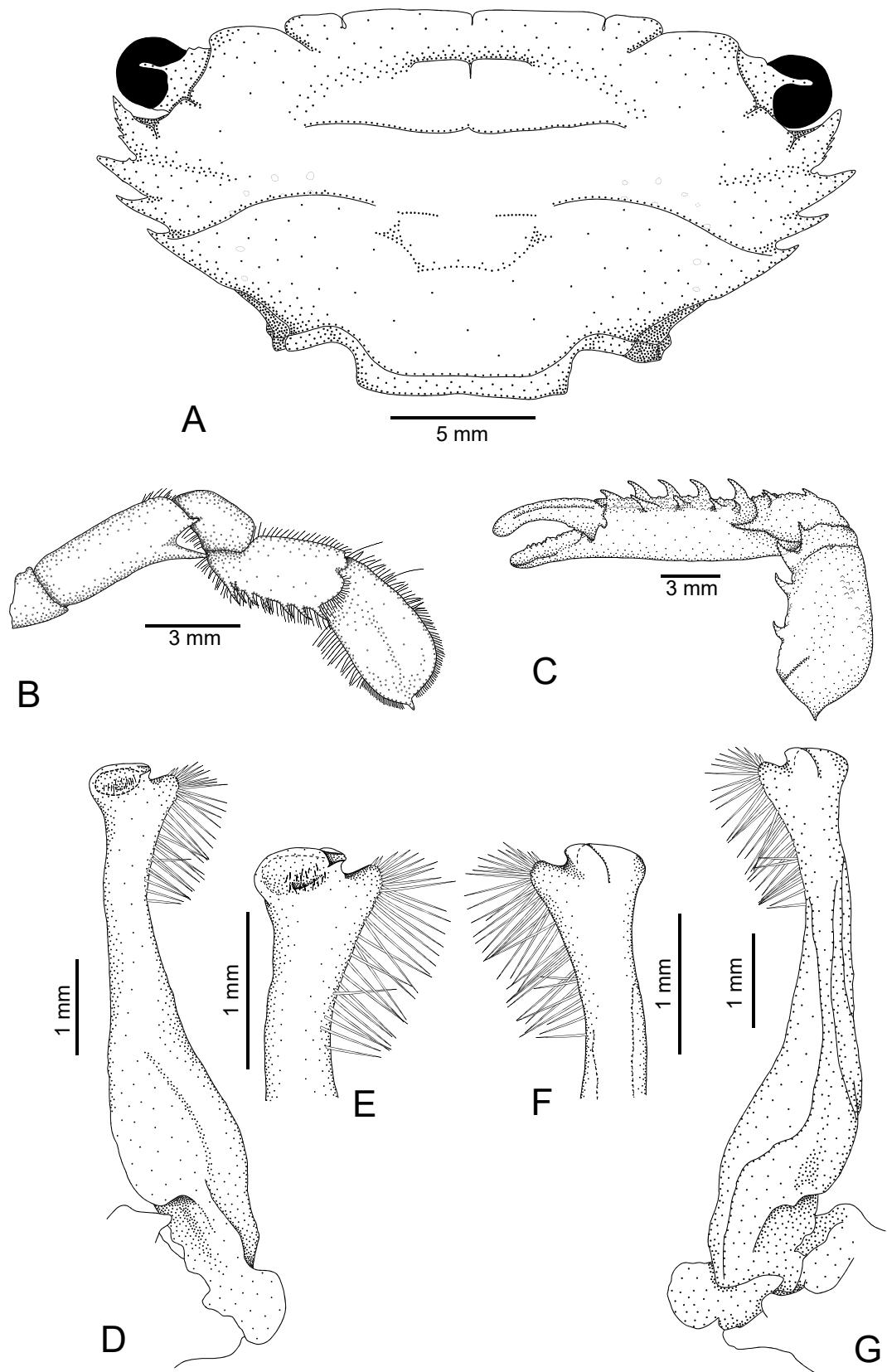
(Figs. 4D, 16)

*Thalamitoides tridens* A. Milne-Edwards, 1869: 149, pl. 6(1–7) (type locality: Tulear, Madagascar); Stephenson and Rees 1967: 102, fig. 38 (Samoa; Palau; Philippines); Sakai 1976: 382, pl. 134(2) (Japan: Ryukyus); Chen 1980: 134, fig. 17, pl. 3(5) (Xisha Is.); Dai et al. 1986: 239, fig. 140B (Xisha Is.); Dai and Yang 1991: 259, fig. 140B (Xisha Is.); Yang et al. 2008: 791 (list; Xisha Is.); Yang et al. 2012: 343, fig. 136 (Xisha Is.); Sasaki 2019: 9278 (list).

*Thalamitoides tridens* – Ng et al. 2008: 155 (list).

*Thalamitoides cf. tridens* – Shih et al. 2020b: 36 (Dongsha I.).

**Material examined:** Taiwan: 1 male (14.9 × 7.4 mm), 2 females (16.1 × 8.2 mm, 1 soft shell) (NCHUZOOL 16520), Dongsha I. (20°42'3.1"N 116°43'4.4"E), coll. YH Huang and CY Chi, 16 Aug. 2019; 4 males (9.1–11.6 × 5.0–6.1 mm), 3 females (9.0–10.9 × 4.7–5.7 mm) (NCHUZOOL 16521), Dongsha I. (20°42'18.6"N 116°43'43.5"E), coll. YH Huang and CY Chi, 18 Jun. 2019; 1 female (15.8 × 7.5 mm) (NCHUZOOL 16522), Dongsha I. (20°42'3.1"N 116°43'4.4"E), coll. YH Huang and CY Chi, 23 Sep. 2019; 1 male (11.2 × 5.9 mm), 3 females (7.9–11.8 × 4.2–6.2 mm) (NCHUZOOL 16523), Dongsha I.



**Fig. 15.** *Thalamitoides quadridens* A. Milne-Edwards, 1869, male ( $25.4 \times 13.3$  mm) (NTOU). A, carapace; B, right P5 (dorsal view); C, right cheliped (dorsal view); D–G, right G1; D, E, dorsal view; F, G, ventral view.

( $20^{\circ}42'18.6''N$   $116^{\circ}43'43.5''E$ ), coll. YH Huang et al., 15 Jun. 2019; 3 males ( $8.6-10.6 \times 4.5-5.4$  mm), 1 female ( $7.5 \times 3.9$  mm) (NCHUZOOL 16595), Dongsha I. ( $20^{\circ}42'18.6''N$   $116^{\circ}43'43.5''E$ ), coll. YH Huang, 17 Jun. 2019.

**Diagnosis:** Carapace with surface smooth slightly convex, 1.9 times broader than long, broadest between anterolateral tooth 1. Frontal and mesogastric ridges unbroken; epibranchial regions with a pair of ridges; protogastric, metagastric, mesobranchial and cardiac ridges absent (Fig. 16A). Front with 4 lobes, median 2 lobes 2.5 times broader than lateral. Supraorbital margins with 2 notches, inner lobe slightly arched (Fig. 16A). Anterolateral margins with 3 teeth, decreasing in size posteriorly (Fig. 16A). Basal antennal segment with a row of granules (Fig. 16B). Chelipeds with surface smooth, merus with 4 spines on inner margin, distal end of ventral surface with a spinule near articulation of carpus; carpus with 5 sharp spines, palm with 2 rows of spines on dorsal surface, inner row with 4 spines, outer with 3 spines; finger tips spoon-shaped (Fig. 16C). P5 with merus having strong spine on inner margin, distal end with small spine; carpus with 1 spine on outer margin; inner margin of propodus with 8–10 spines; dactylus with spinules on distal margins. Male pleon with pleomere 6 trapezoidal. G1 stout, distal part with bristles on lateral side (Fig. 16D–E).

**Coloration in life:** Carapace, chelipeds and legs dark green (Fig. 4D).

**Distribution:** Hawaii; Samoa; Fiji; New Caledonia; Australia (eastern); Indonesia; Guam; Palau; Philippines; Taiwan (Dongsha I.; Fig. 1: no. 17); Japan (Ryukyus); Xisha Is.; Gulf of Aden; Red Sea; Madagascar (Tuléar); Mauritius (Sasaki 2019; this study).

**Ecological notes:** This species can be found from the intertidal and shallow subtidal zones in rocky shore and coral reefs. The juveniles were found from the seagrass beds or under stones on intertidal flats with coral sand.

**Remarks:** *Thalamitoides tridens* A. Milne-Edwards, 1869 is similar to *Tho. spinigera* Nobili, 1905 in the character of 3 anterolateral teeth. The specimens from Taiwan agree with *Tho. tridens* in the following characters: (1) basal antennal segment with granules in *Tho. tridens* (Fig. 16B; A. Milne-Edwards 1869: pl. 6(2)) (3–4 spines in *Tho. spinigera*; Nobili 1905: 403; Spiridonov and Neumann 2008: fig. 2B); (2) *Tho. spinigera* with lateral front lobes rounder than *Tho. tridens* (Fig. 16A; A. Milne-Edwards 1869: pl. 6(1); Spiridonov and Neumann 2008: fig. 2A); (3) G1 tip enlarged in *Tho. tridens* (Fig. 16D–E; Yang et al. 2012: fig. 136d, e) (vs. not enlarged in *Tho. spinigera*; Spiridonov and Neumann 2008: fig. 2D, E).

## Genus *Thranita* Evans, 2018

### *Thranita cerasma* (Wee & Ng, 1995)

(Figs. 4E, 17)

*Thalamita cerasma* Wee & Ng, 1995: 62, figs. 30–32 (type locality: Singapore); Ng et al. 2008: 154 (list).

*Thalamita cerasma rectifrons* – Crosnier and Moosa 2002: 395, figs. 6, 7A, C–F, H–J (French Polynesia: Austral Is. and Society Is.).

*Thalamita cerasma cerasma* – Naruse and Shokita 2003: 43, figs. 2, 3 (Japan: Ryukyus).

*Thranita cerasma* – Evans 2018: 43 (list); Sasaki 2019: 9281 (list).

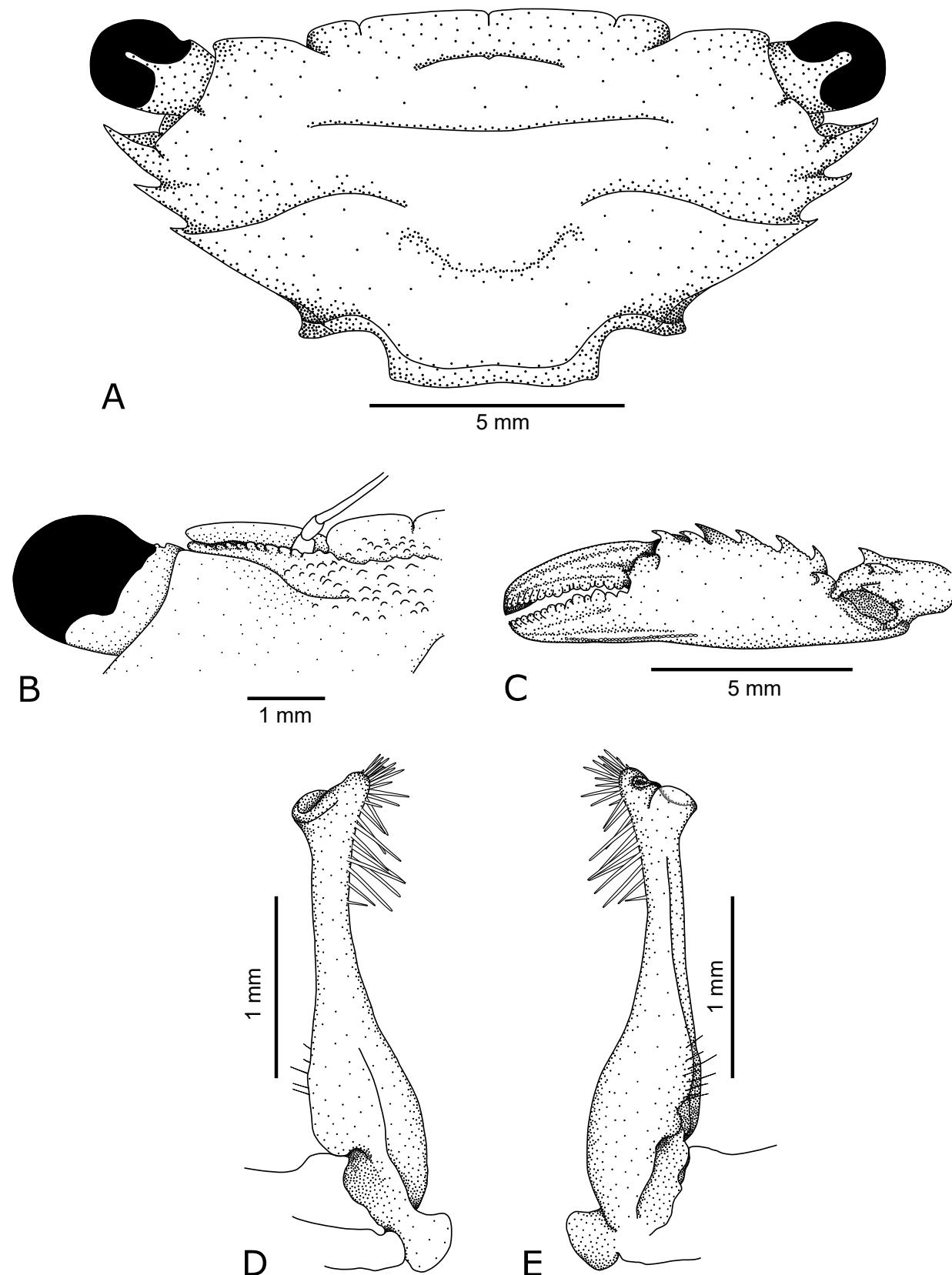
*Thranita cf. cerasma* – Shih et al. 2020b: 36 (Dongsha I.).

? *Thalamita cerasma* – Takeda and Marumura 1997: 16, fig. 1C, D (Japan: Kii Peninsula: Shirahama: Tanabe Bay).

**Material examined:** Taiwan: 1 male ( $44.5 \times 28.9$  mm), 1 female ( $59.7 \times 38.8$  mm) (NCHUZOOL 16509), Dongsha I. ( $20^{\circ}42'26.3''N$   $116^{\circ}43'16.3''E$ ), coll. YH Huang and CY Chi, 2 Nov. 2019; 1 female ( $35.1 \times 24.8$  mm) (NCHUZOOL 16526), Dongsha I. ( $20^{\circ}42'26.3''N$   $116^{\circ}43'16.3''E$ ), coll. YH Huang and CY Chi, 23 Sep. 2019; 1 male ( $16.3 \times 11.0$  mm) (NCHUZOOL 16527), Dongsha I. ( $20^{\circ}42'3.1''N$   $116^{\circ}43'4.4''E$ ), coll. YH Huang and CY Chi, 16 Aug. 2019; 1 male ( $20.1 \times 13.5$  mm) (NCHUZOOL 16528), Dongsha I. ( $20^{\circ}42'23.1''N$   $116^{\circ}43'37.7''E$ ), coll. YH Huang and K Chang, 5 Nov. 2019; 1 male ( $38.5 \times 23.7$  mm), 1 female ( $26.8 \times 17.5$  mm) (NCHUZOOL 16529), Dongsha I. ( $20^{\circ}42'26.3''N$   $116^{\circ}43'16.3''E$ ), coll. YH Huang and CY Chi, 3 Nov. 2019; 3 females ( $22.2-66.4 \times 14.4-42.6$  mm) (NCHUZOOL 16537), Dongsha I. ( $20^{\circ}42'26.3''N$   $116^{\circ}43'16.3''E$ ), coll. YH Huang and CY Chi, 25 Sep. 2019.

**Diagnosis:** Carapace subhexagonal, 1.5–1.6 times broader than long, with broadest between anterolateral tooth 3, surface smooth. Frontal, protogastric and epibranchial regions each with a pair of ridges; mesogastric and metagastric ridges unbroken; mesobranchial and cardiac ridges absent (Fig. 17A). Front with 6 lobes. Supraorbital margins with 2 notches, inner lobe arched (Fig. 17A). Inner infraorbital lobes ending at acute angle. Anterolateral margins with 5 teeth, first 3 teeth large, tooth 4 smaller than 5 (Fig. 17A). Basal antennal segment with 2–3 sharp spines. Chelipeds slightly unequal; merus with 3 sharp spines on inner margin, a spinule each on distal end of dorsal and ventral surfaces near articulation of carpus; carpus with granules on dorsal surface, 1 strong spine on inner margin, 3 smaller spines on outer margin; palm with 5 sharp spines on dorsal surface, outer surface with 1 ridge, inner surface smooth. P5 with merus having strong spine on inner margin, distal end with small spine; propodus with inner margin serrated. G1 stout, with distal part gradually curved (Fig. 17B–E).

**Coloration in life:** Carapace and chelipeds bright orange; P2–P4 green, joints orange, dactylus white with



**Fig. 16.** *Thalamitoides tridens* A. Milne-Edwards, 1869, male ( $14.9 \times 7.4$  mm). A, carapace; B, basal antennal segment; C, palm of left cheliped (outer view); D–E, right G1; D, dorsal view; E, ventral view.

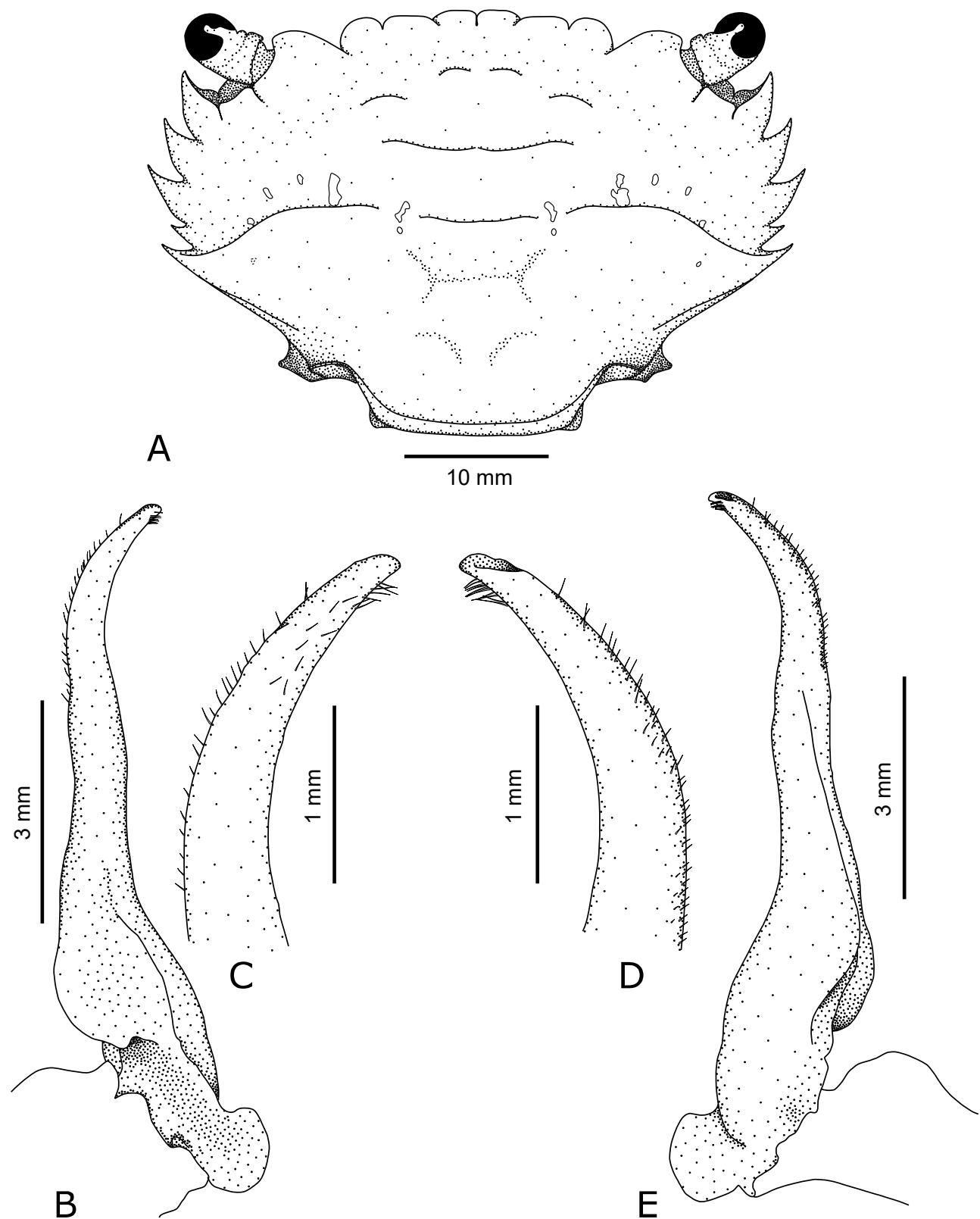


Fig. 17. *Thranita cerasma* (Wee & Ng, 1995), male ( $44.5 \times 28.9$  mm). A, carapace; B–E, right G1; B, C, dorsal view; D, E, ventral view.

pink stripes; P5 with dactylus green, border orange (Fig. 4E).

**Distribution:** French Polynesia; Taiwan (Dongsha I.; Fig. 1: no. 17); Japan (Ryukyu); Malaysia; Singapore (Sasaki 2019; this study).

**Ecological notes:** The habitat is the shallow subtidal zone of coral reefs and seagrass beds. Adult specimens were collected from around the corals (*Porites*) in the shallow subtidal zone, and the juveniles were found on the seagrass beds.

**Remarks:** *Thranita cerasma* (Wee & Ng, 1995) is similar to *Thr. rubridens* (Apel & Spiridonov, 1998), with *Thr. cerasma* distributed in the Pacific Ocean (Sasaki 2019) and *Thr. rubridens* restricted in the Arabian Gulf (Apel and Spiridonov 1998). The specimens from Taiwan agree with *Thr. cerasma* by the following characters: (1) P2–P4 green with joints orange in *Thr. cerasma* (Fig. 4E; Naruse and Shokita 2003: fig. 2a) (vs. P2–P4 uniformly orange with joints pink in *Thr. rubridens*; Apel and Spiridonov 1998: pl. 9); (2) G1 with distal part stout, tip with setae on lateral and mesial sides in *Thr. cerasma* (Fig. 17B–E; Wee and Ng 1995: fig. 32C–E) (vs. distal part slender, tip with setae on lateral side in *Thr. rubridens*; Apel and Spiridonov 1998: figs. 79a–c, 80, 81); (3) basal antennal segment with elongated spines (Wee and Ng 1995: fig. 32F) (vs. with short spines in *Thr. rubridens*; Apel and Spiridonov 1998: fig. 78a). With regard to the specimens identified as *Thr. cerasma* in Takeda and Marumura (1997: fig. 1C, D) with whole body orange and joints pink, which is similar to *Thr. rubridens* (Apel and Spiridonov 1998: pl. 9) and may not belong to *Thr. cerasma*.

### ***Thranita coeruleipes* (Hombron & Jacquinot, 1846)**

(Figs. 4F, 18)

*Thalamita coeruleipes* Hombron & Jacquinot, 1846: 53, pl. 5(6–10) (type locality: Mangareva I., French Polynesia); Forest and Guinot 1961: 32 (French Polynesia: Tahiti; Mangareva I. (lectotype)); Shen and Dai 1964: 61, 1 unnumb. fig. (upper) (Xisha Is.); Stephenson and Rees 1967: 64 (French Polynesia; Samoa; E Australia; Mariana Is.; Philippines); Minei 1971: 64, pl. 3C (Japan: Ryukyu); Sakai 1976: 371, pl. 132(2) (Japan: Ryukyu); Cariaso and Garcia 1986: 219, fig. 30 (Philippines); Dai et al. 1986: 227, fig. 135(1), pl. 30(6) (Xisha Is.); Dai and Yang 1991: 247, fig. 135(1), pl. 30(5) (Xisha Is.); Ng et al. 2008: 154 (list); Yang et al. 2008: 790 (list; Nansha Is.; Xisha Is.); Yang et al. 2012: 265, fig. 98, pl. 11(5) (Nansha Is.; Xisha Is.).

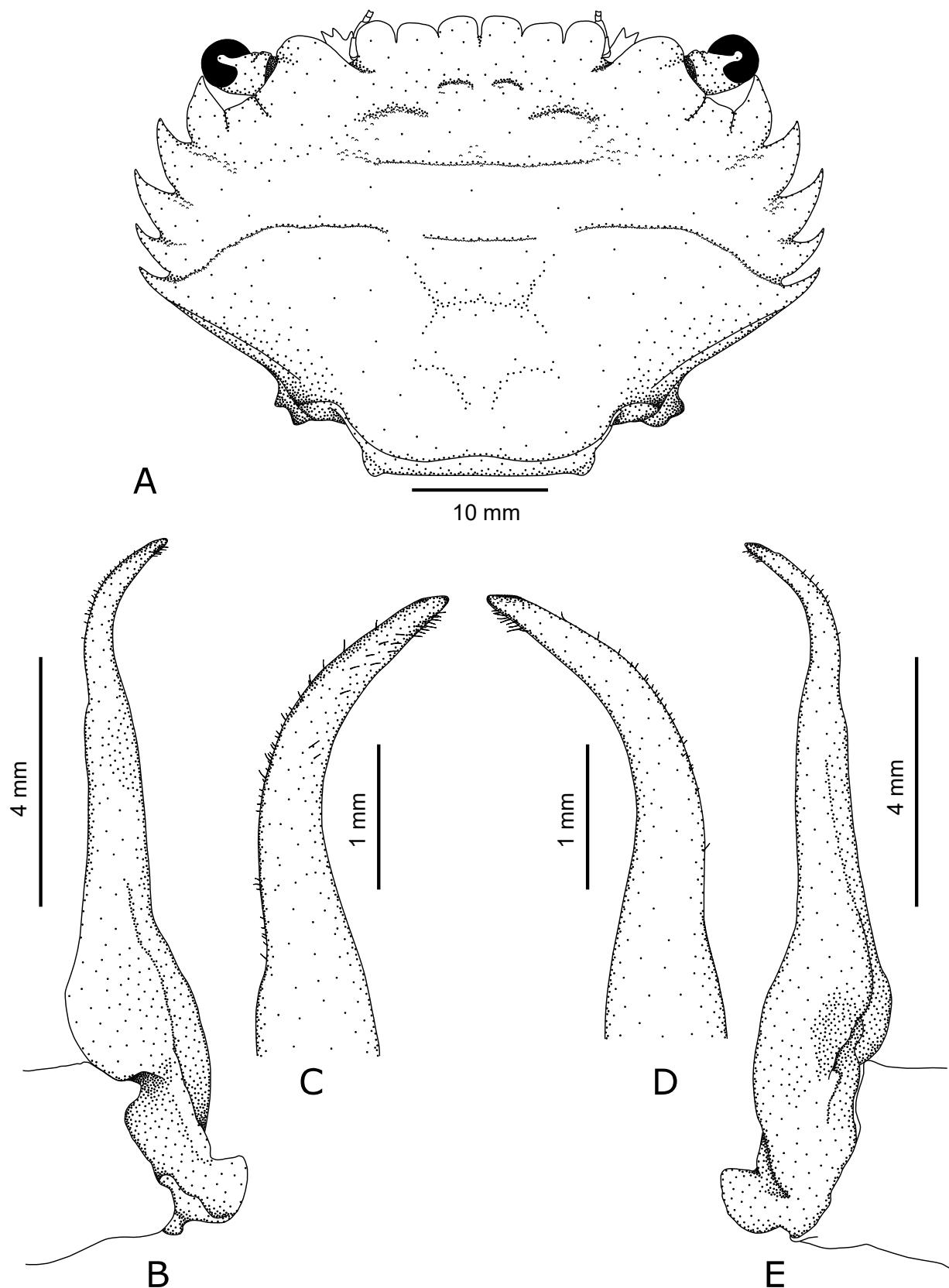
*Thalamita spinimana* – Huang and Yu 1997: 148, 1 unnumb. fig. (Taiwan: Keelung; Heping I.; Pingtung: Siaoliouciou and Wanlitong); Chen and Lo 2014: 85, 3 unnumb. figs. (Taiwan: Pingtung: Siaoliouciou). (not *Thalamita spinimana* Dana, 1852).

*Thranita coeruleipes* – Evans 2018: 4, fig. 2I (Samoa); Sasaki 2019: 9282 (list).

*Thranita cf. coeruleipes* – Shih et al. 2020b: 36 (Taiwan: Dongsha I.).

**Material examined:** Taiwan: 1 male (59.7 × 40.5 mm) (NCHUZOOL 16507), Wanlitong, Kenting, Pingtung (21°59'43.0"N 120°42'19.4"E), coll. YH Huang et al., 10 Apr. 2020; 1 male (48.5 × 33.4 mm) (NCHUZOOL 16512), shallow subtidal zone in Bitou Fishing Port, Kenting, Pingtung (21°54'17.4"N 120°50'55.5"E), coll. YH Huang et al., 8 Apr. 2020; 1 ovig. female (57.3 × 38.9 mm) (NCHUZOOL 16513), Cichihmen, Dongyupingyu, Penghu (23°15'21.1"N 119°30'47.2"E), coll. YH Huang et al., 9 May 2020; 1 female (35.8 × 25.0 mm) (NCHUZOOL 16514), Cichihmen, Dongyupingyu, Penghu (23°15'20.3"N 119°30'51.9"E), coll. YH Huang et al., 10 May 2020; 1 male (26.0 × 18.3 mm), 1 female (28.9 × 19.9 mm) (NCHUZOOL 16515), Sihzihjiao, Dongyupingyu, Penghu (23°15'19.3"N 119°30'38.3"E), coll. YH Huang et al., 11 May 2020; 1 male (40.4 × 27.4 mm) (NCHUZOOL 16516), Dongsha I. (20°42'4.5"N 116°43'5.9"E), 20 Jul. 2012; 1 male (41.4 × 28.0 mm) (NCHUZOOL 16517), Dongyupingyu, Penghu (23°15'22.2"N 119°30'40.8"E), coll. YH Huang et al., 10 May 2020; 2 males (36.7–37.2 × 25.2–25.3 mm) (NCHUZOOL 16518), Dongyupingyu, Penghu (23°15'27.0"N 119°30'46.2"E), coll. YH Huang et al., 1 Aug. 2020; 1 male (38.4 × 26.4 mm) (NCHUZOOL 16519), Dongjiyu, Penghu (23°15'12.2"N 119°40'3.7"E), coll. YH Huang et al., 2 Aug. 2020; 1 male (46.1 × 31.8 mm) (NCHUZOOL 16524), Wanlitong, Kenting, Pingtung, coll. HT Hung, 13 Feb. 2003; 1 male (46.5 × 31.2 mm), 1 ovig. female (40.0 × 28.3 mm) (NCHUZOOL 16525), Dongsha I. (20°41'53.6"N 116°43'29.8"E), coll. YH Huang and K Chang, 6 Nov. 2019; 1 male (11.9 × 8.4 mm) (NCHUZOOL 16592), Dongsha I. (20°42'21.6"N 116°42'39.0"E), coll. YH Huang and K Chang, 5 Nov. 2019.

**Diagnosis:** Carapace subhexagonal, 1.4–1.5 times broader than long, with broadest between anterolateral tooth 3, surface densely pilose. Frontal, protogastric and epibranchial regions each with a pair of ridges; mesogastric and metagastric ridges unbroken; mesobranchial and cardiac ridges absent (Fig. 18A). Front with 6 lobes. Supraorbital margins with 2 notches, inner lobe arched (Fig. 18A). Inner infraorbital lobes ending in spine. Anterolateral margins with 5 teeth, last 2 subequal, smaller than first 3 teeth (Fig. 18A). Basal antennal segment with 2–3 sharp spines. Chelipeds slightly unequal, with surface granulated, merus with 3 sharp spines on inner margin, a spinule each on distal end of dorsal and ventral surfaces near articulation of carpus; carpus with 1 strong spine on inner margin, 3 spines on outer margin; palm with 5 sharp spines on dorsal surface, outer surface with 3 granulated ridges, inner surface with 1 ridge. P5 with merus having strong



**Fig. 18.** *Thranita coeruleipes* (Hombron & Jacquinot, 1846), male ( $46.5 \times 31.2$  mm) (NCHUZOOL 16525). A, carapace; B–E, right G1; B, C, dorsal view; D, E, ventral view.

spine on inner margin, distal end with small spine; propodus with inner margin serrated. G1 stout, with distal part gradually curved (Fig. 18B–E).

**Coloration:** Carapace with brown and white stripes; chelipeds with orange and yellow granules; ambulatory legs brownish green with white stripes, dactylus orange with white stripes (Fig. 4F).

**Distribution:** Hawaii (suspect, see Castro 2011); French Polynesia; Samoa; Fiji; Australia; New Guinea; Indonesia; Guam; Palau; Philippines; Nansha Is.; Taiwan (incl. Dongsha I.; Fig. 1: no. 17); Japan (Ryukyus); Xisha Is.; India; Madagascar; Mauritius (Huang and Yu 1997; Chen and Lo 2014; Sasaki 2019; this study).

**Ecological notes:** This species inhabits the shallow subtidal zones in coral reefs and seagrass beds. Juveniles were often found on seagrass beds.

**Remarks:** In the genus *Thranita* Evans, 2018, there are six species having spines on basal antennal segment, viz. *Thr. cerasma* (Wee & Ng, 1995), *Thr. coeruleipes* (Hombron & Jacquinot, 1846), *Thr. pelsarti* (Montgomery, 1931), *Thr. pseudopelsarti* (Crosnier, 2002), *Thr. rubridens* (Apel & Spiridonov, 1998) and *Thr. spinimana* (Dana, 1852) (Hombron and Jacquinot 1846; Wee and Ng 1995; Apel and Spiridonov 1998; Crosnier 2002). Among them, *Thr. spinimana* and *Thr. pelsarti* were reported previously from Taiwan (Ng et al. 2017); and *Thr. cerasma* and *Thr. coeruleipes* are added in this study.

*Thranita coeruleipes* has been sometimes misidentified under the name “*Thr. spinimana*” in Taiwan (e.g., Huang and Yu 1997; Chen and Lo 2014). They can be distinguished by the following characters: (1) chelipedal carpus with granules on dorsal surface in *Thr. coeruleipes* (Fig. 4F; Hombron and Jacquinot 1846: pl. 5(6)) (vs. armed with 2–3 spines in *Thr. spinimana*; Wee and Ng 1995: fig. 67D; Yang et al. 2012: fig. 129b); (2) palm with 5 spines on dorsal surface in *Thr. coeruleipes* (Hombron and Jacquinot 1846: pl. 5(6); Yang et al. 2012: fig. 98d) (vs. 7–9 spines in *Thr. spinimana*; Dana 1852: pl. 17(8b); Wee and Ng 1995: fig. 67D; Yang et al. 2012: fig. 129b); (3) G1 stout, distal part bent laterally in *Thr. coeruleipes* (Fig. 18B–E; Dai et al. 1986: fig. 135(1); Yang et al. 2012: fig. 98g) (vs. slender, slightly bent laterally in *Thr. spinimana*; Dai et al. 1986: fig. 135(2); Wee and Ng 1995: fig. 67K–M; Yang et al. 2012: fig. 129f).

*Thranita coeruleipes* can be distinguished from *Thr. pelsarti* by the following characters: (1) anterolateral teeth 4 and 5 subequal in *Thr. coeruleipes* (Fig. 18A; Hombron and Jacquinot 1846: pl. 5(6)) (vs. tooth 4 smaller than tooth 5 in *Thr. pelsarti* (Fig. 22A; Montgomery 1931: pl. 28(3)); (2) front lobes blunt in *Thr. coeruleipes* (Fig. 18A; Hombron and Jacquinot

1846: pl. 5(6)) (vs. straight in *Thr. pelsarti*; Fig. 22C; Montgomery 1931: pl. 28(3)).

## DISCUSSION

### Species identification

Some sequences from GenBank were included in the NJ tree of the *COI* marker (Fig. 1) to help identify specimens from Taiwan. However, several species identified are inconsistent, and these are discussed here. (1) The accession number “JX398100”, identified as “*Charybdis hongkongensis*” in Spiridonov et al. (2014), is clustered with the specimens of *Ch. truncata* from Taiwan, but not with the specimens of *Ch. hongkongensis* from Taiwan. After confirming our specimens of *Ch. hongkongensis* with the G1 morphology in Shen (1934: fig. 12b), we conclude that the specimen of “*Ch. hongkongensis*” in Spiridonov et al. (2014) is actually *Ch. truncata*. (2) “JX398096”, identified as “*Monomia argentata*” in Spiridonov et al. (2014), and is clustered with specimens of *M. lucida* from Taiwan. *Monomia lucida* was described as a new species from the *M. argentata* complex by Koch and Ďuriš (2018), so the specimen used in Spiridonov et al. (2014) is actually *M. lucida* (Windsor et al. 2019). (3) “KT365748” was identified as “*Thalamita* aff. *admete*” in Evans (2018) and is discussed in the next section.

The sequences “KT365723” and “KX060202” of *Charybdis variegata* (type locality: Indian Ocean) (Negri and Mantelatto 2017; Evans 2018) are clustered with the sequences of this species in our study, resulting in a large intraspecific genetic divergence, which implies that additional cryptic species existed within the species complex of *Ch. variegata*. Similarly, there is a large divergence (6.25%) between specimens identified as “*Xiphonectes iranjae*” from Penghu (Dongyupingu; Fig. 1: no. 15) and Dongsha I. (Fig. 1: no. 17) (Fig. 2; Table S1). The specimens from Dongyupingu (Fig. 1: no. 15) are more similar to the holotype (type locality: Nosy Iranja, Madagascar; Crosnier 2002: fig. 4), and are thus referred to as *X. iranjae*, and specimens from Dongsha I. (Fig. 1: no. 17) are tentatively named *X. aff. iranjae*. Further studies are necessary to clarify these species complexes.

*Thalamita wakensis* Edmondson, 1925 was considered to be valid in Ng et al. (2001 2017) and Yang et al. (2012), but Crosnier (2002) treated it as a junior synonym of *Thalamita seurati* Nobili, 1906, as did Ng et al. (2008), Takeda et al. (2019) and Sasaki (2019). As a result, the previous record of *Tha. wakensis* in Taiwan was changed to *Tha. seurati* in this study.

With regard to *Thranita helleri* (Hoffmann, 1874)

and *Thr. foresti* (Crosnier, 1962), Apel and Spiridonov (1998: 241) suggested that they might be the same species and that *Thr. helleri* is the senior synonym, which was followed by Poupin et al. (2018: 32) for the species in Mayotte and Sasaki (2019) for the list of world species. In our study, we collected a juvenile male that was preliminarily identified as *Thr. cf. helleri* based on the basal antennal segment. More adult specimens in the future will help confirm the identity.

## Molecular analyses

Excluding the two unresolved groups (*Charybdis miles* and *Ch. sagamiensis*; *Thranita pelsarti* and *Thr. prymna*), the minimum K2P interspecific divergences of *COI* among 67 other species are at least 4.09% (between *Ch. affinis* and *Ch. japonica*, Table S1), which can be considered as not high compared with the subtidal and shallow-water crabs in Chu et al. (2015). For example, the minimum interspecific divergences of other portunids are 5.2% between *Ch. affinis* and *Ch. japonica* (Chu et al. 1999) and 8.1% between *Scylla paramamosain* and *S. tranquebarica* (Ma et al. 2010); the mean interspecific divergence of *Monomia gladiator* and *M. haanii* is 7.74% (Windsor et al. 2019). However, the minimum interspecific divergences in our study appear to be high compared with other semi-terrestrial and terrestrial crabs, e.g., 1.49% between *Leptarma liho* (Koller, Liu & Schubart, 2010) and *L. paucitorum* (Rahayu & Ng, 2009) (Sesarmidae) (Shih et al. 2019b); 3.2% between *Sesarmops imperator* Ng, Li & Shih, 2020 and *S. impressus* (H. Milne Edwards, 1837) (Sesarmidae) (Ng et al. 2020); 3.78% between *Tubuca urvillei* (H. Milne Edwards, 1852) and *T. alcocki* Shih, Chan & Ng, 2018 (Ocypodidae) (Shih et al. 2018); and 4.59% between *Austruca citrus* Shih & Poupin, 2020 and *A. perplexa* (H. Milne Edwards, 1852) (Ocypodidae) (Shih and Poupin 2020).

## Species complexes revealed by interspecific nucleotide divergences

While there are more and more studies being done on the cryptic or pseudocryptic species (Knowlton 1993 2000; Bickford et al. 2007) of crabs (e.g., Daniels et al. 2003; Ragionieri et al. 2009 2012; Jesse et al. 2010; Shih et al. 2013 2018; Ng and Shih 2014; Lai et al. 2017; Innocenti et al. 2020), crabs with distinct morphological characters, but small interspecific nucleotide divergence, are not uncommon, and could be considered “anti-cryptic” species (Bickford et al. 2007; Chapple et al. 2011). For example, *Helice formosensis*, *H. latimera* and *H. tientsinensis* (Varunidae) form an unresolved clade based on their mitochondrial 12S, 16S

and *COI* and nuclear ITS-2 sequences (Shih and Suzuki 2008; Yin et al. 2009; NK Ng et al. 2018); *Plagusia squamosa* and *P. immaculata* (Plagiisiidae) cannot be separated by mitochondrial 16S and nuclear histone 3 (Schubart and Cuesta 2010); *Gelasimus borealis*, *G. dampieri*, *G. vocans* and *G. vomeris* of the *Gelasimus vocans* complex (Ocypodidae) share similar haplotypes of 16S and *COI* (Shih et al. 2010). However, the intermediate morphological form of *H. latimera* and *H. tientsinensis* has been found (Xu et al. 2010) and the morphological differences were suggested to be intraspecific variations (NK Ng et al. 2018). In contrast, using nuclear ITS-1 sequences, at least some species in the *Gelasimus vocans* complex can be separated successfully (Chu et al. 2015; HT Shih unpublished). Further studies using higher resolution marker or nuclear markers, and studies addressing ecology and behavior may elucidate the taxonomic issues (Shih et al. 2010; Chu et al. 2015).

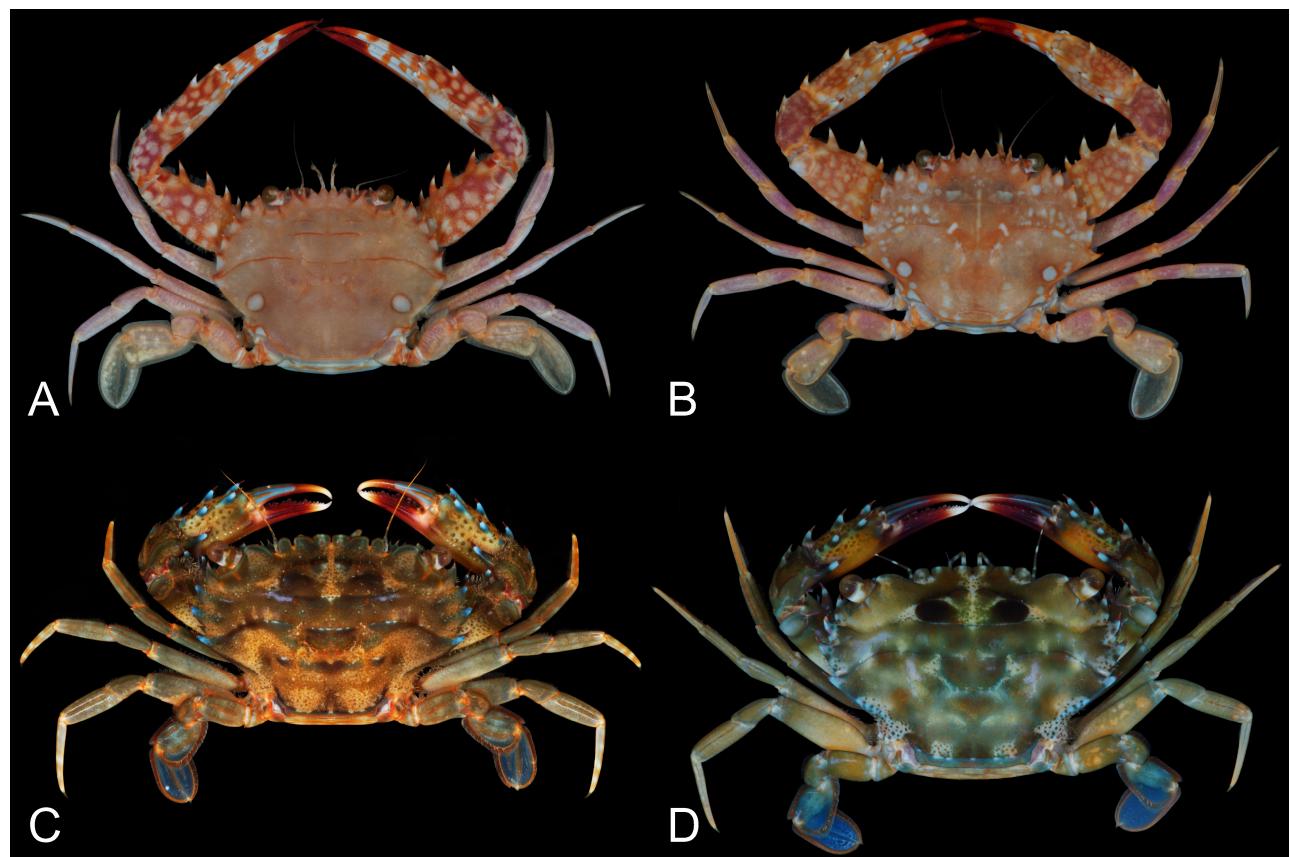
In our study, specimens identified as *Charybdis miles* and *Ch. sagamiensis* were based on the characters suggested by Spiridonov and Türkay (2001): (1) carapace with surface pilose in *Ch. miles* (vs. surface smooth in *Ch. sagamiensis*); (2) carapace with prominent ridges in *Ch. miles* (vs. weak ridges in *Ch. sagamiensis*); (3) carapace of *Ch. miles* narrower than *Ch. sagamiensis*, carapace width/length ratio being 1.4 in *Ch. miles* (vs. 1.5 in *Ch. sagamiensis*); (4) chelipedal palm with squamiform markings in *Ch. miles* (vs. without markings in *Ch. sagamiensis*). Based on our study, the color in life of these two species is also different (Figs. 19A–B, 20, 21). Both species inhabit a depth of 40–50 meters (Spiridonov and Türkay 2001). However, specimens of the two species from Taiwan and Papua New Guinea cannot be separated on the phylogenetic tree (Fig. 2). Similarly, the 16S and *COI* haplotypes from *Ch. miles*, *Ch. crosnieri*, *Ch. sagamiensis*, *Ch. riversandersoni* and *Ch. Rufodactylus*—all in the *Ch. miles* species group (Spiridonov and Türkay 2001)—also form an unresolved clade, without further subdivision (Negri and Mantelatto 2017: fig. 1).

Members of the species complex composed of *Thranita pelsarti* and *Thr. prymna* were identified based on the following characters (Wee and Ng 1995). (1) All surfaces of palm pilose and granulated, immovable finger with deep groove on ventral surface in *Thr. pelsarti* (Wee and Ng 1995: fig. 48) (vs. inner and ventral surface smooth, immovable finger without groove in *Thr. prymna*; Wee and Ng 1995: figs. 51C, 52C, 53C, 54C–D). (2) Palm with 5–7 spines on dorsal surface in *Thr. pelsarti* (Wee and Ng 1995: fig. 48A–B) (vs. 5 spines in *Thr. prymna*; Wee and Ng 1995: fig. 54A–B). (3) Inner supraorbital lobes in *Thr. prymna*

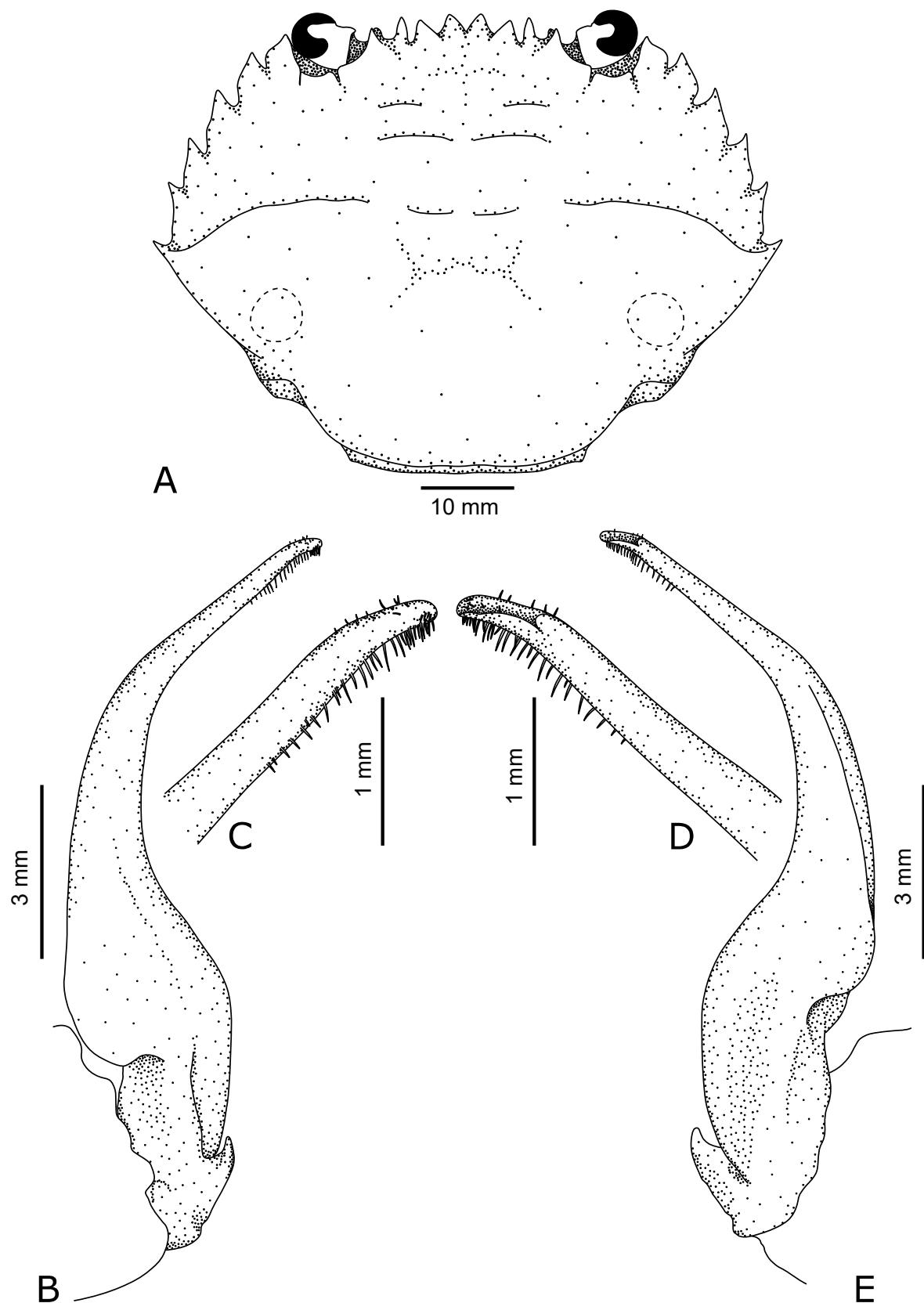
broader than *Thr. pelsarti* (Figs. 22A, 23A; Wee and Ng 1995: figs. 46A, 51A). (4) Inner infraorbital lobes ending in spine in *Thr. pelsarti* (Fig. 22B; Wee and Ng 1995: fig. 47A) (vs. rounded in *Thr. prymna*; Fig. 23B; Wee and Ng 1995: fig. 53A). (5) Meri of P2–P5 grooved in *Thr. pelsarti*, with surface pilose (Wee and Ng 1995: fig. 47B) (vs. not grooved and surface smooth in *Thr. prymna*; Wee and Ng 1995: fig. 53B). (6) Basal antennal segment with 3–5 spines in *Thr. pelsarti* (Fig. 22B; Wee and Ng 1995: figs. 47A, 49I) (vs. 1–2 fused spines in *Thr. prymna*; Fig. 23B; Wee and Ng 1995: figs. 53A, 57G). The color in life of the two species is different as well (Fig. 19C–D). Both species could be found from the same habitats in Dongyupingyu and Dongjiyu, Penghu (Fig. 1: no. 15). However, specimens of the two species from Taiwan are not significantly divergent on the phylogenetic tree (Fig. 2). Tweedie (1950) listed two morphological forms of *Thr. prymna*, and Stephenson and Hudson (1957) further synonymized *Thr. pelsarti* to *Thr. prymna* because the key difference in hairiness and granulations on the chelipeds could be influenced

by the degrees of wear and tear on different individuals, but Wee and Ng (1995) still treated the two species as different.

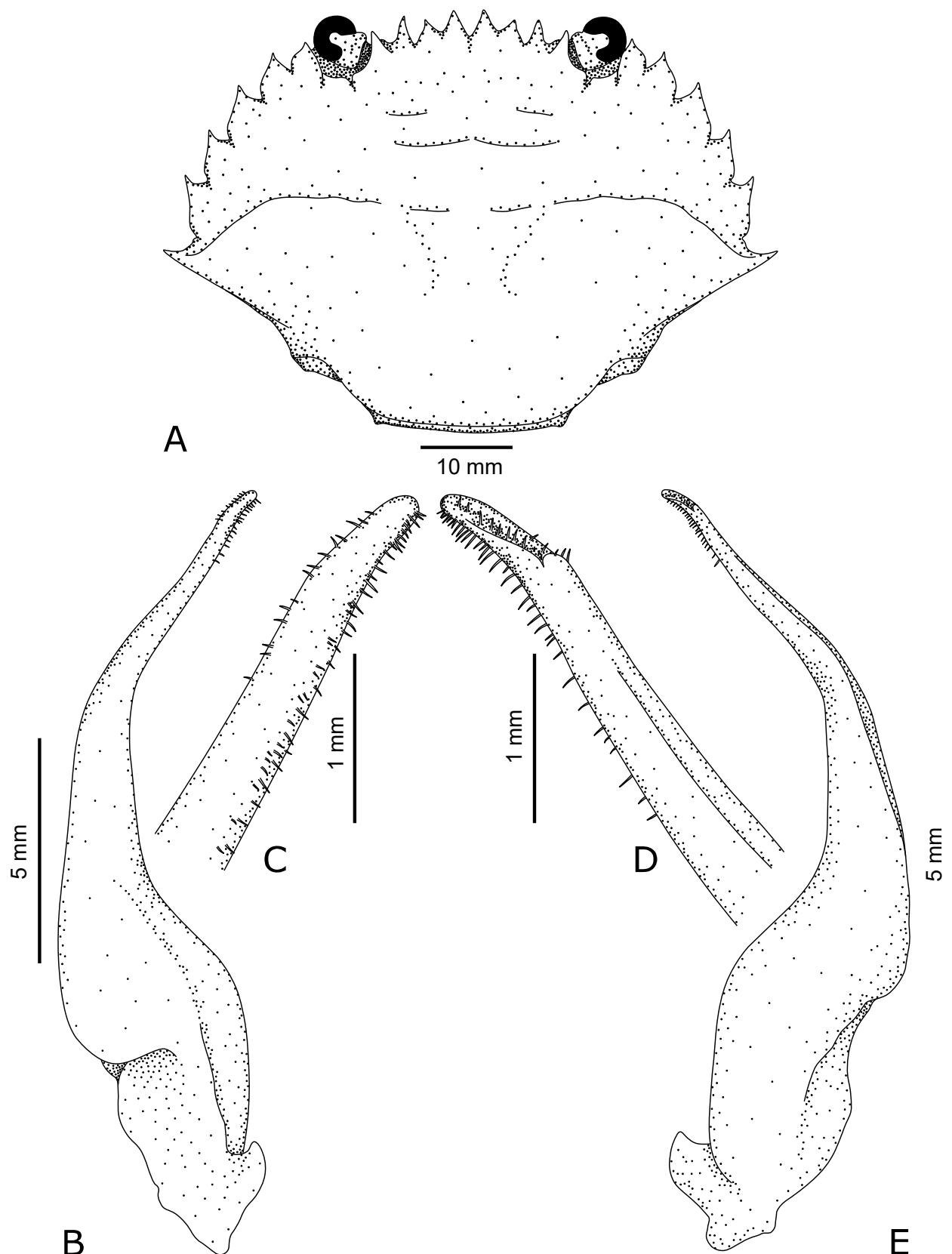
Our genetic findings (Fig. 2) using *COI* may support the decision of Stephenson and Hudson (1957) that *Thr. pelsarti* and *Thr. prymna* are the same species with large intraspecific morphological variation (e.g., Schubart et al. 2001; Chen and Ng 2004). However, while our findings are consistent with the unpublished work conducted by N. Evans (pers. comm.)—who, using *COI* and other markers, recovered *Thr. pelsarti*, *Thr. prymna*, and *Thr. tenuipes* (Borradaile, 1902) as forming a species complex with very little genetic divergence—there are still clear morphological distinctions among them (results forthcoming in a revision of the Thalamitinae study by N. Evans). To solve the issues of species complexes with contrasting morphologies and genetics, we suggest that future studies use molecular markers with a higher resolution (e.g., control region, ITS-1 and ITS-2), examine specimens with an intermediate form if available, and



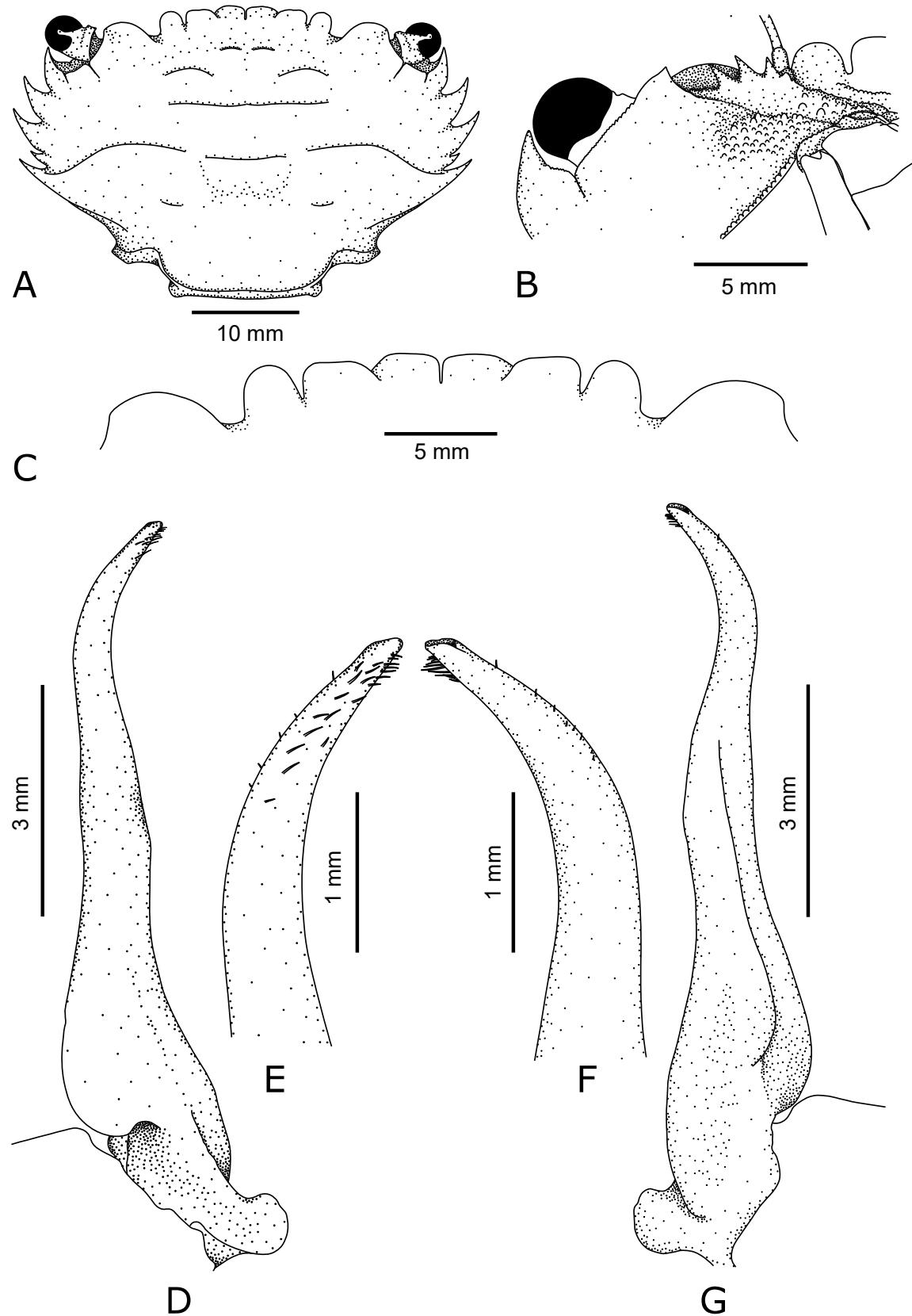
**Fig. 19.** Species of the family Portunidae. A, *Charybdis miles* (De Haan, 1835), female ( $67.4 \times 49.6$  mm) (NCHUZOOL 16493), Erzihliao Fishing Port, Kaohsiung; B, *Charybdis sagamiensis* Parisi, 1916, male ( $66.9 \times 47.1$  mm) (NCHUZOOL 16495), Erzihliao Fishing Port, Kaohsiung; C, *Thraniita pelsarti* (Montgomery, 1931), male ( $43.6 \times 27.5$  mm) (NCHUZOOL 16568), Dongyupingyu, Penghu; D, *Thraniita prymna* (Herbst, 1803), female ( $38.8 \times 25.1$  mm) (NCHUZOOL 16569), Daguang, Kenting, Pingtung.



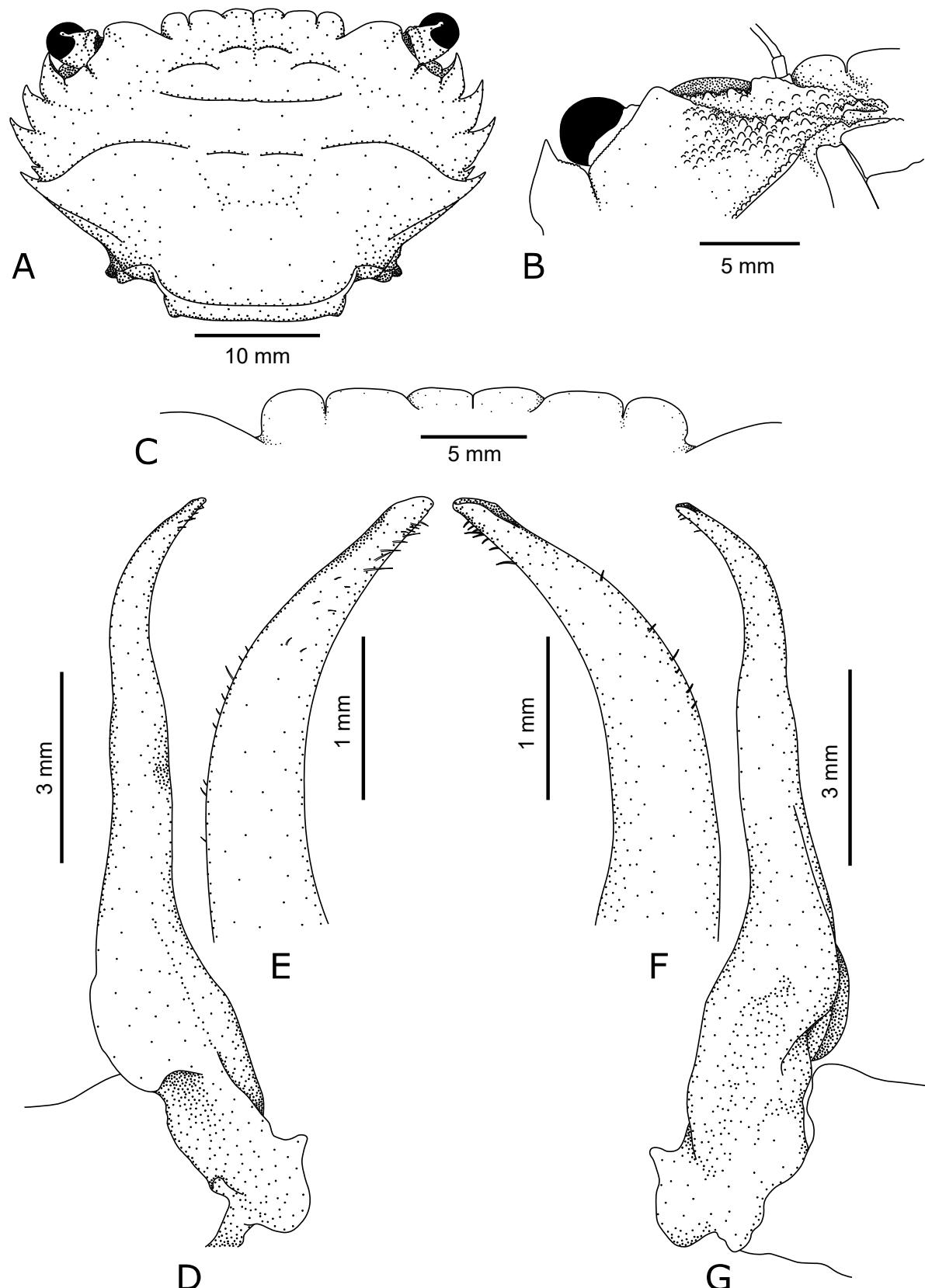
**Fig. 20.** *Charybdis miles* (De Haan, 1835). A, carapace: female ( $67.4 \times 49.6$  mm) (NCHUZOOOL 16493). B–E, male ( $49.6 \times 36.1$  mm) (NCHUZOOOL 16572), right G1; B, C, dorsal view; D, E, ventral view.



**Fig. 21.** *Charybdis sagamiensis* Parisi, 1916, male ( $66.9 \times 47.1$  mm) (NCHUZOOL 16495). A, carapace; B–E, right G1; B, C, dorsal view; D, E, ventral view.



**Fig. 22.** *Thranita pelsarti* (Montgomery, 1931), male ( $43.6 \times 27.5$  mm) (NCHUZOOL 16568). A, carapace; B, basal antennal segment; C, frontal lobes; D–G, right G1; D, E, dorsal view; F, G, ventral view.



**Fig. 23.** *Thranita prymna* (Herbst, 1803). A, carapace, female ( $38.8 \times 25.1$  mm) (NCHUZOOI 16569). B–G, male ( $49.4 \times 31.9$  mm) (NCHUZOOI 16573); B, basal antennal segment; C, frontal lobes; D–G, right G1; D, E, dorsal view; F, G, ventral view.

observe the morphological changes before and after molts.

In contrast, the molecular results of our study (Fig. 2; Table S1) suggested that two similar species, *Thalamita edwardsi* Borradaile, 1900 and *Tha. admete* (Herbst, 1803), are typical cases of pseudocryptic species. They can be distinguished by the following characters: (1) mesobranchial regions of carapace without distinct ridge in *Tha. edwardsi* (Yang et al. 2012: fig. 103a) (vs. with distinct ridges in *Tha. admete*; Yang et al. 2012: fig. 95a); (2) outer surface of chelipedal palms with faint ridges in *Tha. edwardsi* (Yang et al. 2012: fig. 103e) (vs. with granulated ridges in *Tha. admete*; Yang et al. 2012: fig. 95c); (3) tip of G1 divided into 2 lobes, with lateral lobe larger than mesial lobe in *Tha. edwardsi* (Yang et al. 2012: fig. 103h) (vs. 2 lobes subequal in *Tha. admete*; Yang et al. 2012: fig. 95g). The specimens of “KT365748”, identified as “*Thalamita* aff. *admete*” in Evans (2018), are likely *Tha. edwardsi* because it is clustered with the specimens of *Tha. edwardsi* from Taiwan (Fig. 2).

Two similar species, *Xiphonectes hastatoides* (Fabricius, 1798) (type locality: Indian Ocean) and *X. pseudohastatoides* (Yang & Tang, 2006) (type locality: Longmen, Guangxi, China), can be distinguished by several characters (Yang and Tang 2006; Wong et al. 2010; Yang et al. 2012), including (1) front with median teeth shorter than lateral teeth (Yang and Tang 2006: fig. 3B; Wong et al. 2010: fig. 1B) (vs. median teeth more protruding or subequal to lateral teeth; Yang and Tang 2006: fig. 1B; Wong et al. 2010: fig. 1K); (2) tip of G1 with truncated opening and microscopic spines (Wong et al. 2010: fig. 2A, B) (vs. tip of G1 with spoon-shaped opening and obvious spines; Yang and Tang 2006: fig. 2C; Wong et al. 2010: fig. 2E, F). *Xiphonectes hastatoides* is widely distributed across the Indo-West Pacific (Wong et al. 2010), whereas *X. pseudohastatoides* is limited in the West Pacific currently (Sasaki 2019). Our molecular results supported the two species are different (Fig. 2), although Wong et al. (2010) suggested the presence of additional cryptic species in the complex.

## Diversity and biogeography of portunid crabs from Taiwan

The present study confirmed 14 newly recorded species of portunids belonging to nine genera (Table 1), bringing the total number of species and genera in Taiwan to 89 and 20, respectively. Among the 89 species from Taiwan proper, *Carupa ohashii*, *Thranita cerasma* and *Thalamitoides tridens* are only distributed in Dongsha I. in the northeastern South China Sea's (Table 1). The other 86 species can be found from

Taiwan's main island, Penghu Is., and adjacent islets (Table 1), with a species number comparable to the portunid diversity in adjacent regions, e.g., 80 in the main islands of Japan, 83 in the Ryukyus (Sasaki 2019), 78 species in China (incl. Hainan I.; Yang et al. 2012), and 77 in the South China Sea (including Dongsha I.; Yang et al. 2012; Shih et al. 2020b).

As Taiwan proper is located within the distributional ranges of most of these new recorded portunids, it is not surprising to find them in Taiwan. For example, according to the marine ecoregions defined by Spalding et al. (2007), *Lupocycclus inaequalis*, *Thalamita gatavakensis*, *Tha. spinifera*, *Thalamitoides quadridens*, *Tho. tridens*, *Thranita coeruleipes* and *Xiphonectes tuberculatus* are widely distributed throughout the whole Indo-West Pacific (= IWP) realm; *Lupocycloporus minutus*, *Luu. tugelae*, *Monomia gladiator* and *Podophthalmus mindabensis* are widely distributed in the Western IWP and Central IWP subrealms; *Carupa ohashii* is distributed in the Central IWP subrealm; and *Thranita cerasma* is widely distributed in the Central IWP and Eastern IWP subrealms (Sasaki 2019). However, as other new records are expected to be found in Taiwan, only the record of *M. lucida* extended its northmost range to the subtidal soft bottom in southwestern Taiwan, with previous distribution in India, Vietnam and the Philippines (Koch and Ďuriš 2018; Sasaki 2019).

## CONCLUSIONS

In our study, the mitochondrial *COI* marker successfully distinguished most portunids species from Taiwan, with at least 4.09% of the minimum interspecific divergences. However, two groups, *Charybdis miles* and *Ch. sagamiensis*, as well as *Thranita pelsarti* and *Thr. prymna*, cannot be resolved based on *COI* evidence, which may be the result of their recent speciation or large intraspecific variation in morphology. Fourteen new records were described, raising the total number of Portunidae species from Taiwan to 89. Among them, *Monomia lucida* recorded from southwestern Taiwan is the northmost distribution of this species to date.

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**Authors' contributions:** YHH performed the morphological description and part of the molecular analysis, and drafted the manuscript. HTS performed the molecular analysis, participated in the discussion and drafted the manuscript. Both authors read and approved the final manuscript.

**Competing interests:** YHH and HTS declare that they have no conflict of interest.

**Availability of data and materials:** Sequences generated in the study were deposited into the GenBank database (accession numbers in Table 1).

**Consent for publication:** Not applicable.

**Ethics approval consent to participate:** Not applicable.

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## Supplementary materials

**Table S1.** Matrix of percentage pairwise nucleotide divergence with Kimura 2-parameter (K2P) distances (minimum: lower left; mean: upper right) based on cytochrome *c* oxidase subunit I (*COI*) among 71 species of the Portunoidea from Taiwan (see Table 1). (download)

**Table S2.** List and proposed Chinese names of the 89 species in the family Portunidae recorded from Taiwan. (download)