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A synopsis of *Macrobrachium* Spence Bate, 1868 (Decapoda: Caridea: Palaemonidae) from Hong Kong, with description of a new species

Lai Him Chow[1], Jeffery C.F. Chan[2,3] and Ling Ming Tsang[1,]

[1]Simon F.S. Li Marine Science Laboratory, School of Life Sciences, The Chinese University of Hong Kong, Shatin, Hong Kong SAR, China
[2]School of Biological Sciences, The University of Hong Kong, Pokfulam, Hong Kong SAR, China
[3]Science Unit, Lingnan University, Tuen Mun, Hong Kong SAR, China

Correspondence: L.M. Tsang; e-mail: lmtsang@cuhk.edu.hk

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ABSTRACT

Only four freshwater shrimp species from the genus *Macrobrachium* Spence Bate, 1868 are known previously from Hong Kong, namely *M. formosense* Spence Bate, 1868, *M. hainanense* (Parisi, 1919), *M. meridionale* Liang & Yan, 1983, and *M. nipponense* (De Haan, 1849). This is likely an underestimate as a result of insufficient sampling, given that recent efforts revealed several new records in their counterpart family Atyidae, and the presence of many more *Macrobrachium* species from the region (i.e., Guangdong Province, China). We report the occurrence of three more species in Hong Kong: *M. equidens* (Dana, 1852), *M. lar* (Fabricius, 1798), *M. venustum* (Parisi, 1919), and a new species being described, *M. lantau* **sp. nov.** The new species is erected from the highly variable *M. equidens* species complex, distinctive in live colouration and genetics. Decisive morphological differences from *M. equidens* sensu lato could not be confidently elucidated until the species complex is fully resolved. Molecular analysis shows that '*M. hainanense*' reported from Hong Kong actually refers to *M. laevis* Zheng, Chen & Guo, 2019. Morphological (and molecular) evidence suggest that *M. inflatum* Liang & Yan, 1985 and *M. superbum* (Heller, 1862) are possibly morphotypes and thus synonyms of *M. nipponense*. *Macrobrachium hainanense* and *M. heterorhynchos* Guo & He, 2008 are also likely synonyms of *M. formosense* and *M. equidens*, respectively. These species are, nevertheless, maintained as valid until examination of the type specimens concurs. The importance of an integrative approach and the associated matters needing attention in systematic studies of *Macrobrachium* are discussed.

KEY WORDS: biodiversity, Crustacea, freshwater shrimps, intra-specific variations, systematics, southern China, taxonomy

INTRODUCTION

Macrobrachium (family Palaemonidae), with > 260 species, is a numerically dominant genus of shrimps inhabiting freshwater and brackish environment with a few extending to offshore waters. They occur in all biogeographic regions except the Antarctic, with biodiversity concentrated in the Oriental region (De Grave *et al.*, 2008). Contrary to expectations, only three *Macrobrachium* species have long been known to occur in Hong Kong, namely *M. formosense* Spence Bate, 1868, *M. hainanense* (Parisi, 1919), and *M. nipponense* (De Haan, 1849) [De Haan, 1833–1850] (Dudgeon, 1985). An additional species, *M. meridionale* Liang & Yan, 1983, has also been reported being sourced from Hong Kong in a phylogenetic study (Wowor *et al.*, 2009). This low diversity of *Macrobrachium* species is likely an underestimate as a result of insufficient sampling, since considering their counterpart from the family Atyidae, recent efforts reveal several new records in Hong Kong (De Grave *et al.*, unpublished data). Since thirteen more *Macrobrachium* species have been reported from the region (i.e., Guangdong Province, China), including *M. asperulum* (von Martens, 1868), *M. dongaoensis* Chen, Chen & Guo, 2018, *M. equidens* (Dana, 1852), *M. fukienense* Liang & Yan, 1980, *M. heterorhynchos* Guo & He, 2008, *M. inflatum* Liang & Yan, 1985, *M. laevis* Zheng, Chen & Guo, 2019, *M. lar* (Fabricius, 1798), *M. maculatum* Liang & Yan, 1980, *M. pentazona* He, Gao & Guo, 2009, *M. superbum* (Heller, 1862), *M. venustum* (Parisi, 1919), and *M. vietnamiense* Đặng in Đặng & Nguyên, 1972 (Li

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et al., 2007; Guo & He, 2008; He *et al.*, 2009; Chen *et al.*, 2018; Zheng *et al.*, 2019; Huang & Mao, 2021), some are speculated to be distributed in Hong Kong.

As part of our efforts to scruntinise freshwater biodiversity in Hong Kong, field surveys have been undertaken since 2012. The present study serves to report the occurrence of *Macrobrachium* shrimps in Hong Kong and review their taxonomy based on these collections, with genetic analysis as a complement to assess species validity. A selective of synonymy is provided for each species, listing the original description, important synonyms, and references with taxonomically useful illustrations mainly sourcing from southern China.

MATERIALS AND METHODS

Sample collection

Samples were collected using hand nets, euthanised by freezing, and preserved in > 75% ethanol. Specimens examined are deposited in the Simon F.S. Li Marine Science Laboratory, The Chinese University of Hong Kong (CUHK-LMT). Comparative materials of *M. equidens* from Singapore were loaned from the Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum, National University of Singapore. The abbreviations 'pocl' and 'ov.' stand for post-orbital carapace length and ovigerous, respectively.

DNA extraction, PCR, and sequencing

Total genomic DNA was extracted from pleopods using the QIAamp DNA Micro Kit (QIAGEN, Hilden, Germany) following the manufacturer's instructions. Partial sequences of mitochondrial cytochrome c oxidase subunit I (COI) and 16S rRNA genes were amplified by PCR with primer pairs Trp F/dgH2198 (Folmer *et al.*, 1994; Chow *et al.*, 2021) and 16S-AR/16S-1472 (Palumbi *et al.*, 1991; Crandall & Fitzpatrick, 1996), respectively. PCR reactions were performed in a 25 μl volume containing 1.25–2 μl template DNA, 1X PCR reaction buffer, 200 μM dNTPs, 0.2 μM of each primer, 0.5 mM MgCl2 and 1.5U Taq polymerase (Takara, Kasatsu, Japan), with the following profile: initial denaturation at 95 °C for 3 min, followed by 35 cycles of 95 °C for 30 s, 50 °C for 40 s and 72 °C for 1 min, and a final extension at 72 °C for 3 min. The PCR products were purified by the sequencing company (BGI, Shenzhen, China). Sequences were generated using the forward primer on an Applied Biosystems (ABI) 3700 automated sequencer using the ABI Big-dye Ready-Reaction Mix Kit (Life Technologies, Carlsbad, CA, USA), following the standard cycle sequencing protocol.

Phylogenetic analyses

Specimens and GenBank accessions included in the phylogenetic analysis are listed in Tables 1 and 2. Sequences were aligned using MUSCLE (Edgar, 2004) with alignment of COI gene confirmed by translating sequences into amino acid sequences. Poorly aligned regions of the 16S rRNA gene were trimmed using trimAl v1.3 (Capella-Gutiérrez *et al.*, 2009) with a gap threshold of 80%. Sequences were then concatenated into a 1,042 bp-long alignment (COI: 611 bp; 16S: 431 bp). Partitions and best-fit substitution models were determined using PartitionFinder v2.1.1 (Lanfear *et al.*, 2017), according to the corrected Akaike information criterion (AICc). The substitution models used and partitioning for analysis of *Macrobrachium* species from Guangdong Province was as follows (partition 1: COI 1st codon position (TRN + I + G), partition 2: COI 2nd codon position (GTR + I), partition 3: COI 3rd codon position (TRN + G), partition 4: 16S (TVM + I + G)). Same partitioning was used for the analysis of the *M. equidens* species group but with different substitution models (COI 1st codon position (TIM + G), 2nd codon position (TVM), 3rd codon position (GTR + G), 16S (TVM + I + G). Maximum likelihood (ML) analysis was carried out using IQ-TREE v1.6.8 (Nguyen *et al.*, 2015) and branch support was assessed by ultrafast bootstrapping (Minh *et al.*, 2013) with 5,000 replicates. Bayesian inference (BI) analysis was carried out using MrBayes v3.2 (Ronquist *et al.*, 2012). Two independent Markov chain Monte Carlo (MCMC) runs of four chains were performed for two million generations, sampling every 2,000th generation. Convergence of chains was determined by having effective sample size (ESS) > 200 for all parameters. One-fourth of the trees were discarded as burn-in. All trees were rooted by three of the *Palaemon* species (family Palaemonidae) recorded from Hong Kong (*P. pacificus* (Stimpson, 1860), *P. serrifer* (Stimpson, 1860) and *P. tonkinensis* (Sollaud, 1914))

SYSTEMATICS

Family Palaemonidae Rafinesque, 1815

Genus *Macrobrachium* Spence Bate, 1868

Macrobrachium equidens (Dana, 1852)

(Figs. 1, 2A–C)

Palaemon equidens Dana, 1852: 26 [type locality: Singapore].

Macrobrachium equidens – Liu *et al.*, 1990: 110, fig. 8. — Short, 2004: 26, fig. 8.

Material examined: 4 males (pocl 9.9–15.8 mm), ov. female (pocl 17.0 mm), female (pocl 11.5 mm), Tai Tam Tuk, Hong Kong, leg. J.C.F. Chan, 28.VIII.2021, CUHK-LMT-CAR328; 2 males (pocl 13.1 and 13.4mm), female (pocl 12.2 mm), San Tau, Hong Kong, leg. J.C.F. Chan, 30.IX.2021, CUHK-LMT-CAR358; male (pocl 11.6 mm), Yi O, Hong Kong, leg. J.C.F. Chan, 03.II.2022, CUHK-LMT-CAR418; 2 females (pocl 13.7 and 16.9 mm), Pulau Ubin, Singapore, leg. P.K.L. Ng, VIII.1987, ZRC 1992.11050-11055.

Diagnosis: Rostrum straight, curved upwards distally, falling slightly short of to reaching slightly beyond end of scaphocerite, 0.9–1× pocl in males, 0.75–0.8× pocl in females; rostral formula 3–4 + 8–9/4–6, teeth above orbit usually more closely spaced except at tip. Carapace smooth. Fourth thoracic sternite armed with subacute process. First pereiopod fingers 0.8–1× as long as palm; carpus 1.8–2.25× as long as chela in males, 1.65–1.75× in females; merus 0.8–0.85× as long as carpus; ischium 0.65–0.7× as long as merus. Second pereiopods subequal, similar, covered with

Table 1. Details of specimens and GenBank accessions included in the phylogenetic analysis of *Macrobrachium* species from Guangdong Province, southern China. Newly generated sequences are highlighted in bold. –, missing data; † *Macrobrachium* species recorded in Hong Kong.

Species	**Voucher ID**	**Sampling locality**	**GenBank accession no.**		**Source**
			COI	**16S**	
Macrobrachium asperulum		Fujian Province, China	–	DQ194908	Liu *et al.* (2007)
		New Taipei City, Taiwan	AB250470	AB250418	Liu *et al.* (2011)
		Pingtung County, Taiwan	AB250530	AB250452	Liu *et al.* (2011)
Macrobrachium equidens†	CUHK-LMT-CAR328-1	Hong Kong SAR, China	**ON753698**	**ON754343**	Present study
	CUHK-LMT-CAR328-3	Hong Kong SAR, China	**ON753699**	**ON754344**	Present study
	ZRC 1992.11050-11055	Singapore	**ON753700**	**ON754345**	Present study
		Ilan County, Taiwan	–	DQ194918	Liu *et al.* (2007)
		Bohol, The Philippines	–	DQ194916	Liu *et al.* (2007)
		Kochi, India	–	KM593107	Jose *et al.* (2016)
		Queensland, Australia	–	AY282773	Murphy & Austin (2004)
Macrobrachium fukienense		Fujian Province, China	FM958065	FM986612	Wowor *et al.* (2009)
		Fujian Province, China	–	DQ194923	Liu *et al.* (2007)
Macrobrachium formosense†	CUHK-LMT-CAR301-1	Hong Kong SAR, China	**ON753701**	**ON754346**	Present study
	CUHK-LMT-CAR302-1	Hong Kong SAR, China	**ON753702**	**ON754347**	Present study
		Hong Kong SAR, China	MW817951	MN993990	Chow *et al.* (2020, 2021)
		Foshan, Guangdong, China	MK412780	–	Zheng *et al.* (2019)
		Hainan Province, China	–	DQ194921	Liu *et al.* (2007)
		Hualien County, Taiwan	–	DQ194919	Liu *et al.* (2007)
		Okinawa, Japan	–	DQ194922	Liu *et al.* (2007)
Macrobrachium hainanense		Hong Kong SAR, China	MH176973	–	Chow *et al.* (2018)
		Hong Kong SAR, China	MN018903	–	Wong *et al.* (2019)
		Hong Kong SAR, China	MW817952	MN993991	Chow *et al.* (2020, 2021)
		Hong Kong SAR, China	–	AY377841	Murphy & Austin (2005)
		Guangdong Province, China	–	DQ194927	Liu *et al.* (2007)
		Wuzhishan, Hainan, China	FM958068	FM986615	Wowor *et al.* (2009)
Macrobrachium inflatum		Anhui Province, China	–	DQ194931	Liu *et al.* (2007)
		Dongfang, Hainan, China	MK412787	–	Zheng *et al.* (2019)
Macrobrachium laevis†	CUHK-LMT-CAR290-1	Hong Kong SAR, China	**ON753703**	**ON754348**	Present study
	CUHK-LMT-CAR401-6	Hong Kong SAR, China	**ON753704**	**ON754349**	Present study

Table 1. Continued

Species	Voucher ID	Sampling locality	GenBank accession no.		Source
			COI	16S	
		Foshan, Guangdong, China	MK412774	–	Zheng *et al.* (2019)
		Jiangmen, Guangdong, China	MK412776	–	Zheng *et al.* (2019)
Macrobrachium lantau **sp. nov.**†	CUHK-LMT-CAR325-1	Hong Kong SAR, China	**ON753705**	**ON754350**	Present study
	CUHK-LMT-CAR325-2	Hong Kong SAR, China	**ON753706**	**ON754351**	Present study
Macrobrachium lar†	CUHK-LMT-CAR326	Hong Kong SAR, China	**ON753707**	**ON754352**	Present study
		Hualien County, Taiwan	–	DQ194939	Liu *et al.* (2007)
		Cebu, the Philippines	–	DQ194940	Liu *et al.* (2007)
		Iriomote Island, Japan	–	DQ194941	Liu *et al.* (2007)
		Manado, North Sulawesi, Indonesia	–	FM986621	Wowor *et al.* (2009)
		Queensland, Australia	–	AY282766	Murphy & Austin (2004)
		French Polynesia	–	EF588316	Page *et al.* (2008)
Macrobrachium maculatum		Anhui Province, China	–	DQ194910	Liu *et al.* (2007)
		Foshan, Guangdong, China	MK412770	–	Zheng *et al.* (2019)
		Foshan, Guangdong, China	MW069488	–	Zhou *et al.* (2021)
Macrobrachium meridionale†	CUHK-LMT-CAR183-1	Hong Kong SAR, China	**ON753708**	**ON754353**	Present study
	CUHK-LMT-CAR232-5	Hong Kong SAR, China	**ON753709**	**ON754354**	Present study
		Hong Kong SAR, China	–	FM986630	Wowor *et al.* (2009)
		Hainan Province, China	–	DQ194948	Liu *et al.* (2007)
		Tioman Island, Malaysia	–	DQ194949	Liu *et al.* (2007)
Macrobrachium nipponense†	CUHK-LMT-CAR235-1	Hong Kong SAR, China	**ON753710**	**ON754355**	Present study
		Foshan, Guangdong, China	MK412772	–	Zheng *et al.* (2019)
		Jiangsu Province, China	KY092232	KY084627	Chen *et al.* (2017)
		Guangxi Province, China	–	DQ194952	Liu *et al.* (2007)
		Yizhang, Hunan, China	FM958077	FM986632	Wowor *et al.* (2009)
		Kaohsiung, Taiwan	KU235942	KU235740	Chen *et al.* (2015)
		Ibaraki Prefecture, Japan	KY092207	KY084602	Chen *et al.* (2017)
		South Korea	KY092312	KY084707	Chen *et al.* (2017)
Macrobrachium nipponense† (‘inflatum’morph)	CUHK-LMT-CAR235-3	Hong Kong SAR, China	**ON753711**	**ON754356**	Present study
	CUHK-LMT-CAR276-1	Hong Kong SAR, China	**ON753712**	**ON754357**	Present study

Table 1. Continued

Species	Voucher ID	Sampling locality	GenBank accession no.		Source
			COI	16S	
Macrobrachium nipponense† (‘super-bum’morph)	CUHK-LMT-CAR305	Hong Kong SAR, China	**ON753713**	**ON754358**	Present study
	CUHK-LMT-CAR327	Hong Kong SAR, China	**ON753714**	**ON754359**	Present study
Macrobrachium pentazona		Huizhou, Guangdong, China	MN814449	–	Chen *et al.* (2021)
Macrobrachium superbum		Huizhou, Guangdong, China	MK994932	–	Zhu *et al.* (2020)
Macrobrachium venustum†	CUHK-LMT-CAR304-1	Hong Kong SAR, China	**ON753715**	**ON754360**	Present study
	CUHK-LMT-CAR347-1	Hong Kong SAR, China	**ON753716**	**ON754361**	Present study
		Phong Nha, Quang Binh, Vietnam	–	FM986644	Wowor *et al.* (2009)
Outgroup					
Palaemon pacificus	CUHK-LMT-CAR102	Dong’ao Island, Guangdong China	MW817957	MN993998	Chow *et al.* (2020, 2021)
Palaemon serrifer	CUHK-LMT-CAR136	Hong Kong SAR, China	**ON753717**	MN993996	Chow *et al.* (2020); Present study
Palaemon tonkinensis	CUHK-LMT-CAR231-2	Hong Kong SAR, China	**ON753718**	**ON754362**	Present study

Table 2. Additional GenBank accessions used in the phylogenetic analysis of *Macrobrachium equidens* species group.

Species	Sampling locality	GenBank accession no.		Source
		COI	16S	
Macrobrachium bullatum	Northern Territory, Australia	KM978918	KM978918	Lee *et al.* (unpubl. data)
	Australia	–	JF310712	Page & Hughes (2011)
Macrobrachium idella	India	–	KP081666	Jose & Harikrishnan (2019)
Macrobrachium idae	Khanom, Thailand	–	DQ194930	Liu *et al.* (2007)
	Tioman Island, Malaysia	FM958070	FM986617	Wowor *et al.* (2009)
Macrobrachium mammillodactylus	Bohol Island, the Philippines	–	DQ194915	Liu *et al.* (2007)
	Samarinda, Indonesia	FM958075	FM986629	Wowor *et al.* (2009)
Macrobrachium novaehollandiae	Australia	–	JF310725	Page & Hughes (2011)
Macrobrachium rude	India	–	MG283139	John *et al.* (unpubl. data)
Macrobachium saigonense	Cambodia	FM958080	FM986638	Wowor *et al.* (2009)
Macrobrachium striatum	Kochi, India	–	KM610138	Jose *et al.* (2016)
Macrobrachium sp. 1	Papua New Guinea	–	JF310730	Page & Hughes (2011)
Macrobrachium sp. 2	Northern Territory, Australia	JF310734	JF310733	Page & Hughes (2011)

microspinules. Male second pereiopod fingers 0.75–0.9× as long as palm, with moderately dense setae on surface of fingers and along cutting edges which develop into velvety mat in large male (rarely in small males), dactylus with 2 teeth along proximal one-fifth to one-fourth, pollex with tooth at proximal one-seventh to one-fifth and a proximal low, ridged hump; palm 4–5.6× as long as wide, 0.65–0.7× as long as carpus, 0.85–1× as long as merus, 0.9–1.2× as long as ischium. Third pereiopod propodus 10.5–13× as long as wide, 3–3.5× as long as dactylus, 1.7–2× as long as carpus, 0.9–0.95× as long as merus, 1.7–1.95× as long as ischium; carpus 5–6× as long as wide; merus 9–11.5× as long as wide. Eggs small, 0.56–0.60 mm × 0.48–0.53 mm in diameter, numerous.

Ecology: Most commonly found amongst mangroves and under crevices in river mouths, occasionally observed further upstream or in marine waters. They have been observed preying

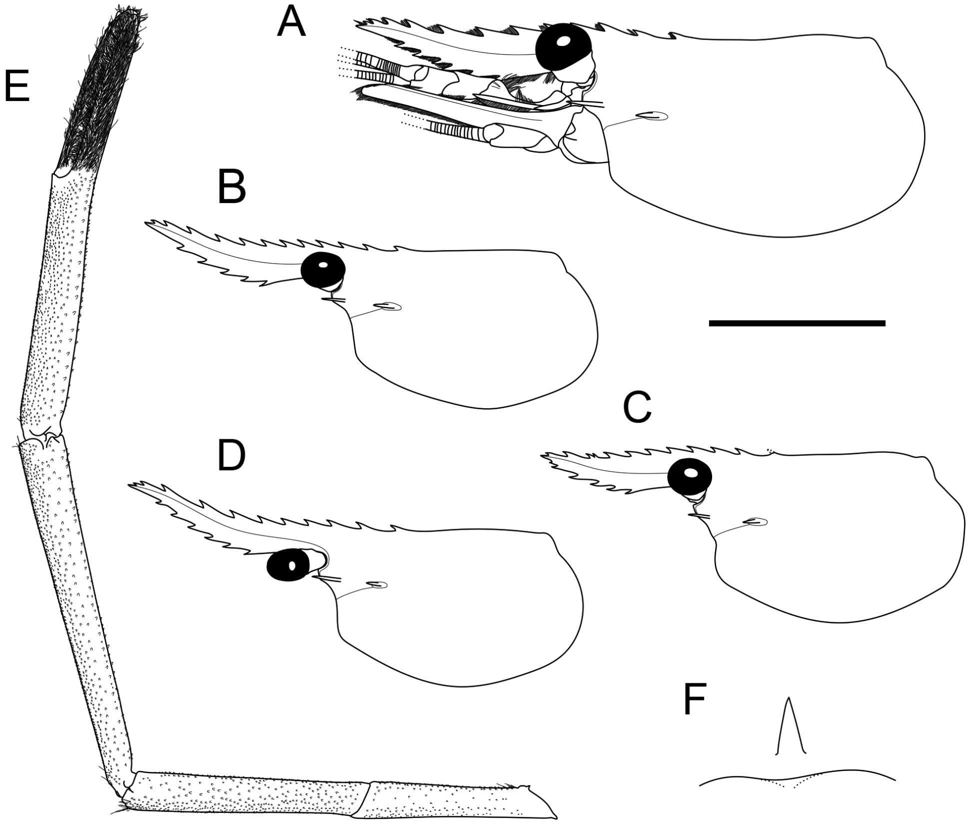

Figure 1. *Macrobrachium equidens*, male, pocl 15.8 mm (CUHK-LMT-CAR328-3) (**A**, **E**, **F**); male, pocl 13.4 mm (CUHK-LMT-CAR358-2) (**B**); ov. female, pocl 17.0 mm (CUHK-LMT-CAR328-1) (**C**); female, pocl 16.9 mm (ZRC 1992.11050-11055) (**D**). Cephalothorax, lateral view (**A**); carapace with eyes, lateral view, setae between rostral teeth omitted (**B**–**D**); left second pereiopod (**E**); process of fourth thoracic sternite (**F**). Scale bars = 13.5 mm (C, D), 11 mm (B), 10 mm (A, E), 2 mm (F).

on juveniles of the terapontid *Terapon jarbua* (Forsskål, 1775) in Hong Kong.

Distribution: Widespread throughout the Indo-West Pacific, from Madagascar to Solomon Islands (Chace & Bruce, 1993), introduced to West Africa and Brazil (Powell, 1986; Maciel *et al.*, 2011). Not previously recorded in Hong Kong; widespread locally but relatively low in abundance (Fig. 3B).

Remarks: *Macrobrachium equidens* is known to be a species complex (Liu *et al.*, 2007; Page & Hughes, 2011), and in Singapore, the type locality, at least two species exist under the same name. The first one corresponds to the present species with distinctive marbling on the second pereiopods (Fig. 2A–C), that still persists in one of the 35-year-old preserved specimens herein examined. The second species shows certain affinity to *Palaemon nasutus* sensu Nobili, 1903, which is currently treated as a junior synonym of *M. equidens*. A third species is possibly also present in Singapore based on photographic evidence, which is herein described as new, *M. lantau* **sp. nov.** Since the type specimens of *M. equidens* are no longer extant (Evans, 1967) and the original description was very brief, designation of a neotype is essential to stabilise its taxonomy but there is no clue about the identity of the real '*M. equidens.*' We herein propose the species being referred to here as *M. equidens* sensu stricto based on its long history of recognition and its acknowledgement in the scientific community. The 'typical' form of *M. equidens* mentioned in the earliest descriptions by De Man (1892, 1897, 1898) (as *Palaemon* (*Eupalaemon*) *sundaicus*) and Cowles (1914) (as *Palaemon sundaicus*), very likely referred to *M. equidens* sensu stricto. The 'typical' form of *M. equidens* previously reported and *M. equidens* sensu stricto share second pereiopods with a 'tortoise shell' pattern (and the presence of a cream-coloured transverse band on the tergum of the third abdominal somite), and similar second pereiopod article ratios across a size series. *Macrobrachium equidens* sensu stricto is also the most widely recognised species (as '*M. equidens*') in molecular studies (see Murphy & Austin, 2004; Liu *et al.*, 2007; Jose *et al.*, 2016; Jose & Harikrishnan, 2019; Mantelatto *et al.*, 2021), with > 70% of the 16S rRNA barcoding gene sequences of '*M. equidens*' from GenBank referring to it.

Guo & He (2008) described a morphologically very similar species, *M. heterorhynchos*, known only from the type material, from brackish water near Jiangmen, Guangdong Province, China, but did not compare it with *M. equidens* or any other closely related species. Based on the original description of its morphology and colour pattern, we argue that *M. heterorhynchos* is hardly separable from *M. equidens* sensu stricto, and thus may represent a junior synonym of the latter. There are three noteworthy differences from *M. equidens* sensu stricto, all of which could be attributed to intra-specific variation. 1) Sexual dimorphism in rostrum: 'rostrum of males very long, distal 1/3

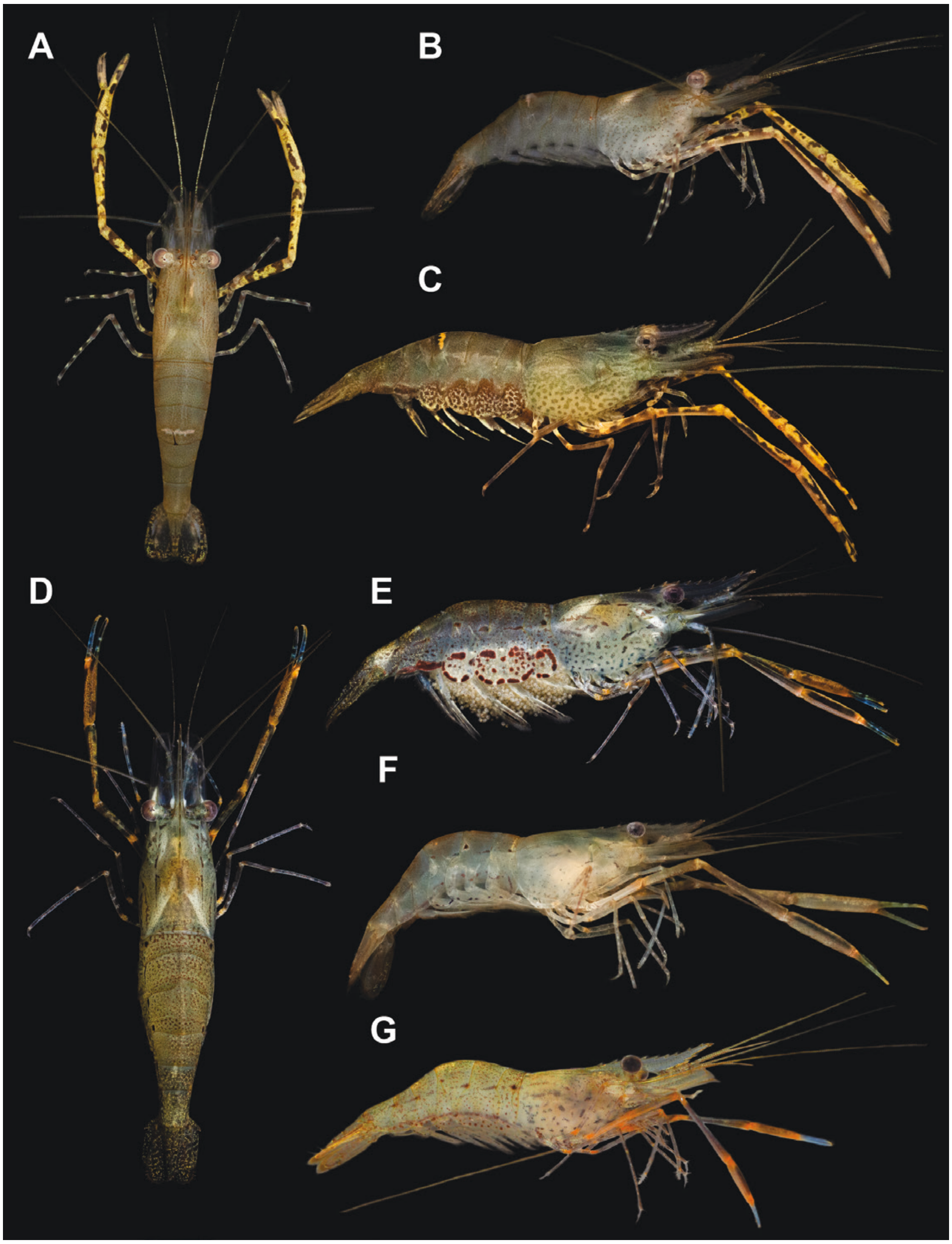

Figure 2. *Macrobrachium equidens* (**A**–**C**). Male, pocl 11.6 mm (CUHK-LMT-CAR418), dorsal view (**A**); same, habitus (**B**); ov. female, pocl 17.0 mm (CUHK-LMT-CAR328-1), habitus (**C**). *Macrobrachium lantau* **sp. nov.** (**D**–**G**). Paratype ov female, pocl 17.5 mm (CUHK-LMT-CAR357), dorsal view (**D**); same, habitus (**E**); paratype female, pocl 18.1 mm (CUHK-LMT-CAR419), habitus (**F**); holotype male, pocl 11.3 mm (CUHK-LMT-CAR325-2), post-mortem, habitus (**G**). Photographs by Zi Yi Kho (A–F) and Jeffery Chan (G).

extending beyond scaphocerite, tip strongly curved upwards, rl about as long as cl; … Females with rostrum just reaching end of scaphocerite, rl about 0.7 cl' (Guo & He, 2008: 12). In contradiction to this text, the rostrum of male *M. heterorhynchos* only slightly extends beyond scaphocerite (for about distal one-sixth) according to the illustration and specimen photo (Guo & He, 2008: figs. 1A, 7B), which is common in *M. equidens* sensu stricto. Cowles (1914) showed that rostrum length relative to scaphocerite, as well as the curvature of rostrum, are variable and not correlated with age or gender. The Hong Kong specimens do agree with *M. heterorhynchos* by males having a relatively longer rostrum than that of females and about as long as pocl (Fig. 1A–C), but females from Singapore have a relatively long rostrum typical of males from Hong Kong (Fig. 1D), supporting the variable nature of this character. 2) Sexual dimorphism in relative length of second pereiopod merus: 'merus of males slight longer than palm, 1.0–1.2 times as long as palm, in females merus shorter than palm, 0.8–0.9 times as long as palm' (Guo & He, 2008: 15). The relative length of the merus is another highly variable character in *M. equidens* sensu stricto, again not necessarily correlated with age or gender (Cowles, 1914). This sexual dimorphism observed in *M. heterorhychos* is likely an artefact attributed to small sample size. 3) Absence of pubescence on second pereiopod fingers. The largest male from the type

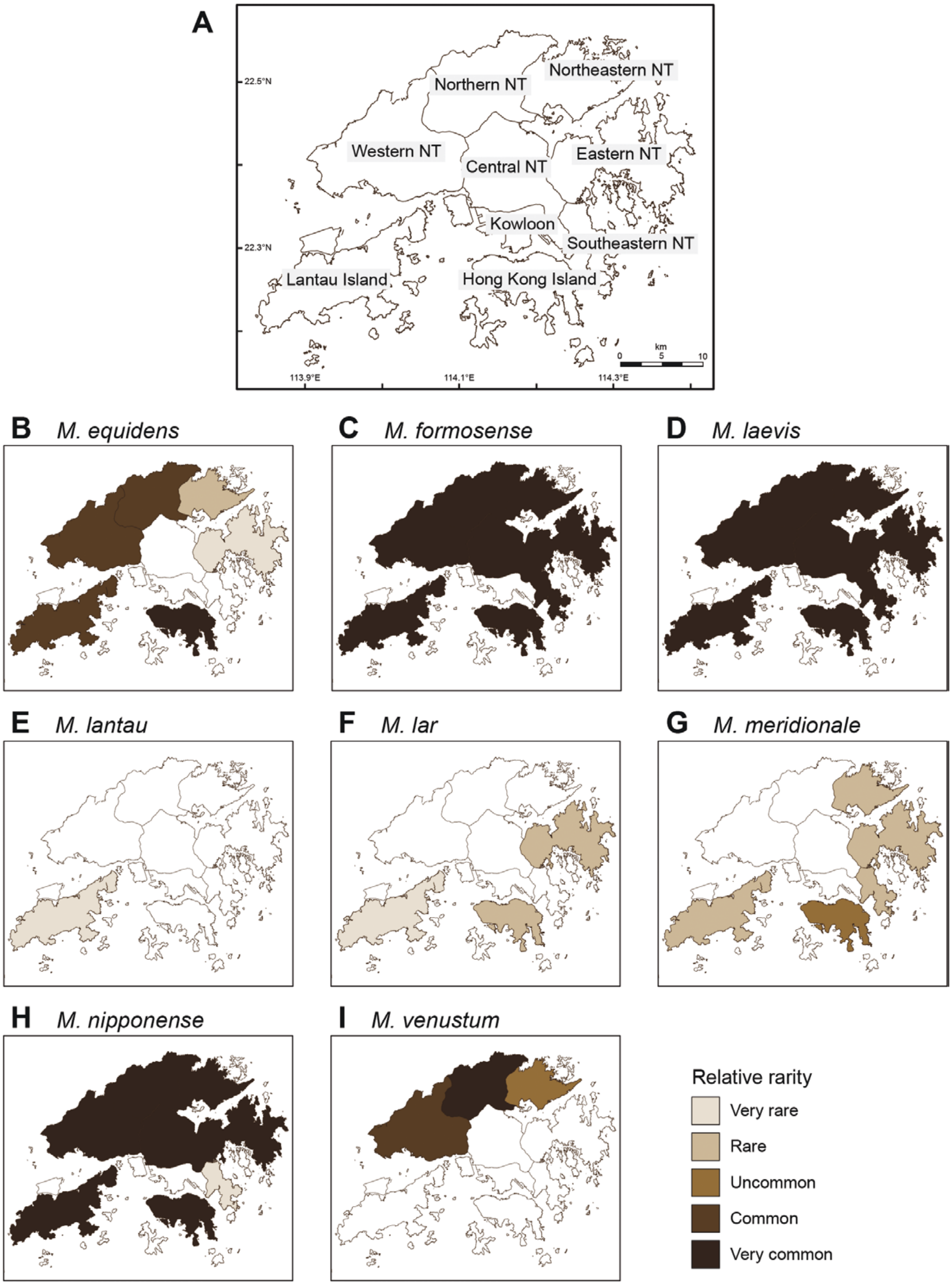

Figure 3. Map of Hong Kong with major regions delimited; NT, New Territories (**A**). Distribution of the eight *Macrobrachium* species in Hong Kong (**B**–**I**): *M. equidens* (**B**), *M. formosense* (**C**), *M. laevis* (**D**), *M. lantau* **sp. nov.** (**E**), *M. lar* (**F**), *M. meridionale* (**G**), *M. nipponense* (**H**), and *M. venustum* (**I**). Shaded regions indicate recorded presence with colour corresponding to relative rarity.

series of *M. heterorhynchos* was only 71 mm in total length (tl) (pocl 16.9 mm), which is the marginal size where *M. equidens* starts developing such pubescence according to Cowles (1914). Moreover, pubescence development is also strongly influenced by intra-specific variation in the rate of cheliped development. The finger-to-palm ratio in males generally decreases with body size from 1 to as low as 0.5 (see Cowles, 1914), which is also quite a consistent ontogenetic trend among *Macrobrachium* species. In the present study, the two specimens with well-developed pubescence both have the same and the lowest ratio of 0.75, despite that they differ substantially in body size (pocl 15.8 and 11.6 mm). Males of *M. heterorhynchos* were remarked as having fingers about as long as palm in the original description by Guo & He, (2008), potentially suggesting an underdeveloped nature, so the absence of pubescence is insufficient to justify its validity. As the type specimens of *M. heterorhynchos* were not examined, it is herein still considered as a valid species likely representing a non-fully developed adult of *M. equidens* sensu stricto.

***Macrobrachium lantau* sp. nov.**

(Figs. 2D–G, 4, 5)

Macrobrachium equidens – Holthuis, 1950: 162, fig. 36 (in part). — Yoshigou, 2002: 4, fig. 3, pl. 1B.
(?) *Palaemon sundaicus* – Kubo, 1941: 313, fig. 7 (in part).

Type material: holotype: male (pocl 11.3 mm), San Tau, Hong Kong, leg. J.C.F. Chan, 13.VIII.2021, CUHK-LMT-CAR325-2; paratypes male (pocl 13.4 mm), same collection data as holotype, CUHK-LMT-CAR325-1; ov. female (pocl 17.5 mm), San Tau, Hong Kong, leg. J.C.F. Chan, 30.IX.2021, CUHK-LMT-CAR357; female (pocl 18.1 mm), Yi O, Hong Kong, leg. J.C.F. Chan, 03.II.2022, CUHK-LMT-CAR419.

Diagnosis: Rostrum straight to sinuous, curved upwards distally, slightly overreaching scaphocerite, subequal to pocl in male, 0.75–0.85× pocl in female; rostral formula 2–3 + 7–8/5–6, teeth above orbit more closely spaced except at tip. Carapace smooth. Fourth thoracic sternite armed with subacute process. First pereiopod fingers 0.9–1× as long as palm; carpus 1.95–2× as long as chela; merus ~0.8× as long as carpus; ischium 0.6–0.7× as long as merus. Second pereiopods subequal, similar, covered with microspinules. Male second pereiopod fingers ~0.7× as long as palm, dactylus with 2 teeth along proximal one-fourth, pollex with tooth at proximal one-fifth and proximal low, ridged hump; palm 4.6–4.8× as long as wide, ~0.65× as long as carpus, 0.95–1× as long as merus, ~1.05× as long as ischium. Third pereiopod propodus 10.5–14× as long as wide, 3–3.5× as long as dactylus, 1.75–2× as long as carpus, 0.9–0.95× as long as merus, 1.65–1.8× as long as ischium; carpus 5–6× as long as wide; merus 8–11.5× as long as wide. Eggs small, 0.68–0.84 mm × 0.44–0.59 mm in diameter, numerous.

Description: Rostrum (Fig. 4A–C) straight to sinuous, very slightly convex above orbit, distally upturned, tip maybe horizontal; slightly overreaching scaphocerite, subequal to pocl in male, 0.75–0.85× pocl in female; shallow, 5.8–7.3× as long as maximum depth, slightly less than dorsoventral diameter of eye; lateral carina well developed. Rostral formula 2–3 + 7–8/5–6, dorsal teeth above orbit and near tip more closely spaced, gapping between second and/or third anteriormost tooth and next posterior tooth unless there is only one subapical tooth, ventral teeth slightly more closely spaced on posterior region; row of setae present between teeth.

Carapace smooth. Ocular cornea well developed. Inferior orbital margin moderately produced, angular, post-antennular carapace margin broadly rounded or straight. Antennal spine sharp, slender, continuing posteriorly as ridge, situated below inferior orbital angle; hepatic spine smaller, situated at same level as or slightly below antennal spine. Branchiostegal suture running from hepatic spine to carapace margin. Pterygostomial margin rounded, not produced. Stylocerite sharp, reaching 0.3–0.4 of article length, distolateral tooth of first antennular article reaching to about mid-length of second article. Scaphocerite (Fig. 4D) broad, 0.7–0.75× pocl, ~3× as long as wide, lateral margin almost straight, distal margin rounded, slightly produced at inner angle, lamina not overreached by anteriolateral tooth. Carpocerite reaching to about one-third of scaphocerite length. Fourth thoracic sternite (Fig. 4E) armed with subacute process.

Abdomen smooth, first to third pleurites broadly rounded, fourth and fifth pleurites feebly produced posteriorly, sub-rectangular, sixth abdominal somite ~1.5× as long as fifth, with posteroventral angle feebly produced, subacute. Telson (Fig. 4F) relatively slender, 3.5–4× as long as median wide, ~1.5× as long as sixth abdominal segment, lateral margin straight, convergent, with 2 pairs of dorsal spines at ~0.5 and 0.7–0.75 of telson length, ending in a median projection; lateral spines smaller than dorsal spines, intermediate spines well developed, with long plumose setae in between.

Epistome completely divided into 2 rounded lobes. Mouthparts not dissected, typical for the genus in external view. Third maxillipeds with robust endopod, distal half of ultimate article reaching beyond antennal peduncle; ultimate article ~0.8× as long as penultimate article; ischiomerus slightly bow-shaped; exopod reaching to or slightly overreaching distal end of ischiomerus; coxa with oval lateral plate.

First pereiopods (Fig. 5A) slender, reaching beyond scaphocerite by entire chela; fingers 0.9–1× as long as palm; carpus 1.95–2× as long as chela; merus ~0.8× as long as carpus; ischium 0.6–0.7× as long as merus; with few scattered stiff setae especially on fingers and ischium, and carpal-propodial brush. Second pereiopods (Fig. 5B) slender, subequal, similar, 0.6–0.85× tl, reaching beyond scaphocerite by proximal one-fourth to one-half of carpus, all articles covered with anteriorly directed, feebly hooked microspinules and few scattered stiff setae, microspinules sparse on ischium; male fingers ~0.7× as long as palm, dactylus with 2 subacute teeth of similar sizes along proximal one-fourth, pollex with similar tooth (but sometimes abraded) at proximal one-fifth and proximal low, ridged hump, distal cutting edge laminar, entire, non-gapping, tip uncinated (Fig. 5C); palm subcylindrical, not inflated, 4.6–4.8× as long as wide; carpus club-shaped, tapered posteriorly, ~1.5× as long as palm; merus feebly dilated anteriorly, 1–1.05× as long as palm; ischium ~0.95× as long as palm. Female second pereiopod fingers 0.7–0.8× as long as palm, armature on cutting edge as in male; palm 4.4–4.9× as long as wide; carpus 1.2–1.3× as long as palm; merus 0.8-0.95× as long as palm; ischium 0.7–0.9× as long as palm.

Third pereiopods (Fig. 5D) slender, smooth, reaching to about end of scaphocerite, scattered with few stiff setae, denser at distal propodus and along dorsal margin of dactylus; dactylus moderately slender, terminating in unguis; propodus 10.5–14× as long as distal wide, 3–3.5× as long as dactylus, with 6–9 ventral and pair of distoventral spines; carpus 5–6× as long as wide, 0.5–0.6× as long as propodus; merus 8–11.5× as long as wide, 1.05–1.15× as long as propodus; ischium 0.55–0.6× as long as propodus. Fourth pereiopods reaching to about end of antennular peduncle, slightly longer than third pereiopods, similar in form. Fifth pereiopods (Fig. 5E) longest, reaching to about end of scaphocerite, grooming setae well-developed; propodus 13–17× as long as wide, ~4× as long as dactylus, with 10–13 ventral spines and distoventral spine; carpus 6.5–7.5× as long as wide, 0.55–0.65× as long as propodus; merus 10–12× as long as wide, 0.9–1.1× as long as propodus; ischium 0.45–0.6× as long as propodus.

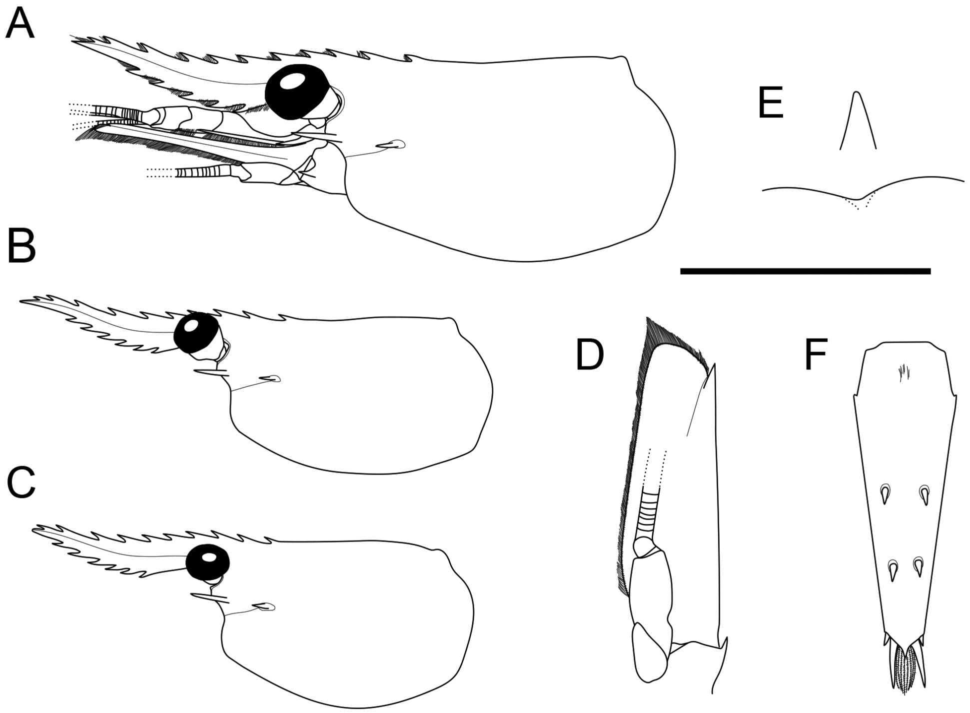

Figure 4. *Macrobrachium lantau* **sp. nov.**, holotype male, pocl 11.3 mm (CUHK-LMT-CAR325-2) (**A**, **D**–**F**); paratype male, pocl 13.4 mm (CUHK-LMT-CAR325-1) (**B**); paratype ov. female, pocl 17.5 mm (CUHK-LMT-CAR357) (**C**). Cephalothorax, lateral view (**A**); carapace with eyes, lateral view, setae between rostral teeth omitted (**B**–**C**); scaphocerite, ventral view (**D**); process of fourth thoracic sternite (**E**); telson (**F**). Scale bars = 19 mm (C), 15 mm (B), 10 mm (A), 7.5 mm (D), 5.5 mm (F) or 2 mm (E).

Uropodal diaeresis with acute, movable spine, longer than or subequal to outer angle.

Eggs small, 0.68–0.84 mm × 0.44–0.59 mm in diameter, numerous.

Etymology: After its type locality in Lantau Island, Hong Kong. Used as a noun in apposition.

Ecology: Occasionally found co-existing with *M. equidens* and *M. formosense* in Hong Kong, and seemingly favours the sections of the river mouth with mangroves, plentiful leaf litter and silty substrate.

Distribution: Likely has a wide Indo-West Pacific distribution, including Hong Kong and Japan (Satsunan Islands, Ryukyu Islands) (Yoshigou, 2002). This species possibly also occurs in Bangladesh (Kuakata) based on DNA barcodes retrieved from GenBank; Taiwan based on photographs in guidebooks (Lee *et al.*, 2013); and Singapore (Saint John Islands) and the Philippines (La Union) based on photographs uploaded to the citizen science website, iNaturalist (https://www.inaturalist.org/) under the name '*M. equidens*'. In Hong Kong, the species is rare and currently known only from Lantau Island (Fig. 3E).

Remarks: The new species belongs to the Indo-West Pacific *M. equidens* species group (*sensu* Johnson, 1973). On account of the symmetrical and rough second pereiopods with chela longer than carpus, as well as the occurrence in estuaries and the very small egg size, it shows certain affinity to *M. equidens*, *M. mammillodactylus* (Thallwitz, 1891), *M. novaehollandiae* (De Man, 1908), *M. rude* (Heller, 1862), *M. saigonense* Nguyên, 2006, and *M. striatum* Pillai, 1991. The presence and distribution of various ornamentations on the second pereiopods of large males, including pubescence and tubercles along cutting edges, are one of the major characters separating species of the group. The lack of large male specimens of the new species hinders convenient comparison with closely related species, but nevertheless, some other details, including rostral shape, rostral formula, relative length among second pereiopod articles of comparably sized specimens, and colouration, are shown to be sufficient for differentiating the species from all of the others in the group.

Macrobrachium lantau **sp. nov**. can be separated from *M. novaehollandiae* by the shallow (i.e., maximum depth less than dorsoventral diameter of eye), distally upturned rostrum (deep, straight rostrum in *M. novaehollandiae*), proportionally shorter palm with article ratios, from dactylus to ischium, of 0.7–0.8: 1: 1.2–1.5: 0.8–1.05: 0.7–1 (0.35–0.5: 1: 1.25: 0.75–0.8: 0.4–0.7 from specimens between 12.5–29.6 mm in pocl in *M. novaehollandiae*; see Short, 2004), and the lack of stripes on the lateral carapace. Similarly, the shallow rostrum and the lack of stripes separates the new species from *M. mammillodactylus*. It also bears fewer dorsal but more ventral rostral teeth than *M. mammillodactylus* (10 or 11 dorsal, 5 or 6 ventral teeth; 11–13 dorsal, 3 or 4 ventral teeth in *M. mammillodactylus*). The new species is readily differentiated from *M. striatum* by colouration, where the latter bears distinctive longitudinally stripped body, and by the slightly shorter second pereiopod palm (article ratios 0.7–0.8: 1: 1.2–1.5: 0.8–1.05: 0.7–1, 0.55–0.6: 1: 1.1–1.2: 0.65–0.75: 0.5–0.6 from specimens between 68–82 mm in tl in *M. striatum*:

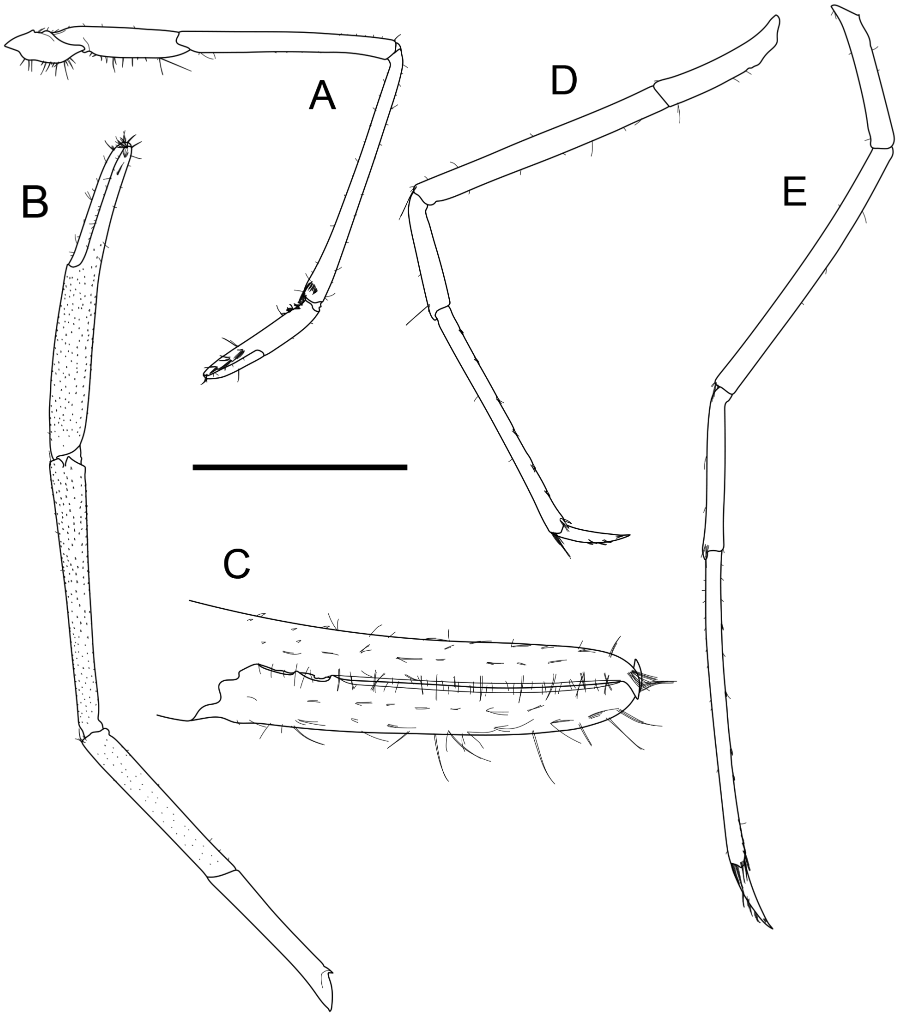

Figure 5. *Macrobrachium lantau* **sp. nov**., holotype male, pocl 11.3 mm (CUHK-LMT-CAR325-2). Left first pereiopod (**A**); left second pereiopod (**B**); same, cutting edge, mesial view (**C**); left third pereiopod (**D**); left fifth pereiopod (**E**). Scale bars = 7 mm (B), 5 mm (A, D, E) or 3.5 mm (C).

see Pillai, 1991). It would not be mistaken as *M. rude* due to the rostral shape (tip situated higher than basal convexity, lower in *M. rude*) and the spinular second pereiopod (*versus* granular), as well as having distinct distribution (western Pacific Ocean to eastern Indian Ocean *versus* western Indian Ocean from South Africa to east coast of India). It differs from *M. saigonense* by the same rationale on rostral shape, as well as having slightly different rostral formula (10 or 11 dorsal, 5 or 6 ventral teeth; 12 or 13, rarely 11 or 14 dorsal, 4 or 5, rarely 3 or 6 ventral teeth in *M. saigonense*). It also has proportionally longer second pereiopod carpus (1.2–1.5× as long as palm, 1.35–1.5× as long as merus; 1.1–1.3× and 1.15–1.5×, respectively, from specimens between 55–88 mm in tl in *M. saigonense*; see Nguyên, 2006). Molecular data also support that *M. lantau* **sp. nov.** represents a valid species, genetically distinct from the above mentioned closely related species of the *M. equidens* species group (Fig. 6B).

Among the species from the *M. equidens* species group, *M. lantau* **sp. nov.** is morphologically the most similar to *M. equidens* sensu lato. Holthuis (1950) mentioned that some of his specimens of *M. equidens* had bluish second pereiopod fingers, which is distinctive for the new species, suggesting that his collection probably was a mix of the two species. Likewise, based on a colour photograph, the large male '*M. equidens*' reported by Yoshigou (2002: pl. 1B) from Japan also likely refers to the new species (see below for comparison of colour pattern). The confusion between the two species was attributed to the presence of pubescence on the second pereiopod fingers in both species (as reported in Yoshigou, 2002 for *M. lantau* **sp. nov.**), a character commonly observed in *M. equidens* sensu lato. The Japanese specimen also had similar second pereiopod article ratios to those reported previously for large males of *M. equidens* sensu lato (Nobili, 1899; Cowles, 1914; De Man, 1915). A question then arose is whether the proposed new species could be one of the seven synonymised varieties of *M. equidens* sensu lato (except the 'typical' form which is proposed to be *M. equidens* sensu stricto), namely var. *bataviana* sensu De Man, 1897, var. *brachydactyla* sensu Nobili, 1899, var. *demani* sensu Nobili, 1899, var. *acanthosoma* sensu Nobili, 1899, var. *baramensis* sensu De Man, 1902, var. *nasutus* sensu Nobili, 1903 and another unnamed variety by Nobili (1903). Holthuis (1950) synonymised all the varieties on the basis of the high variability of rostrum and relative length of second pereiopod articles. When

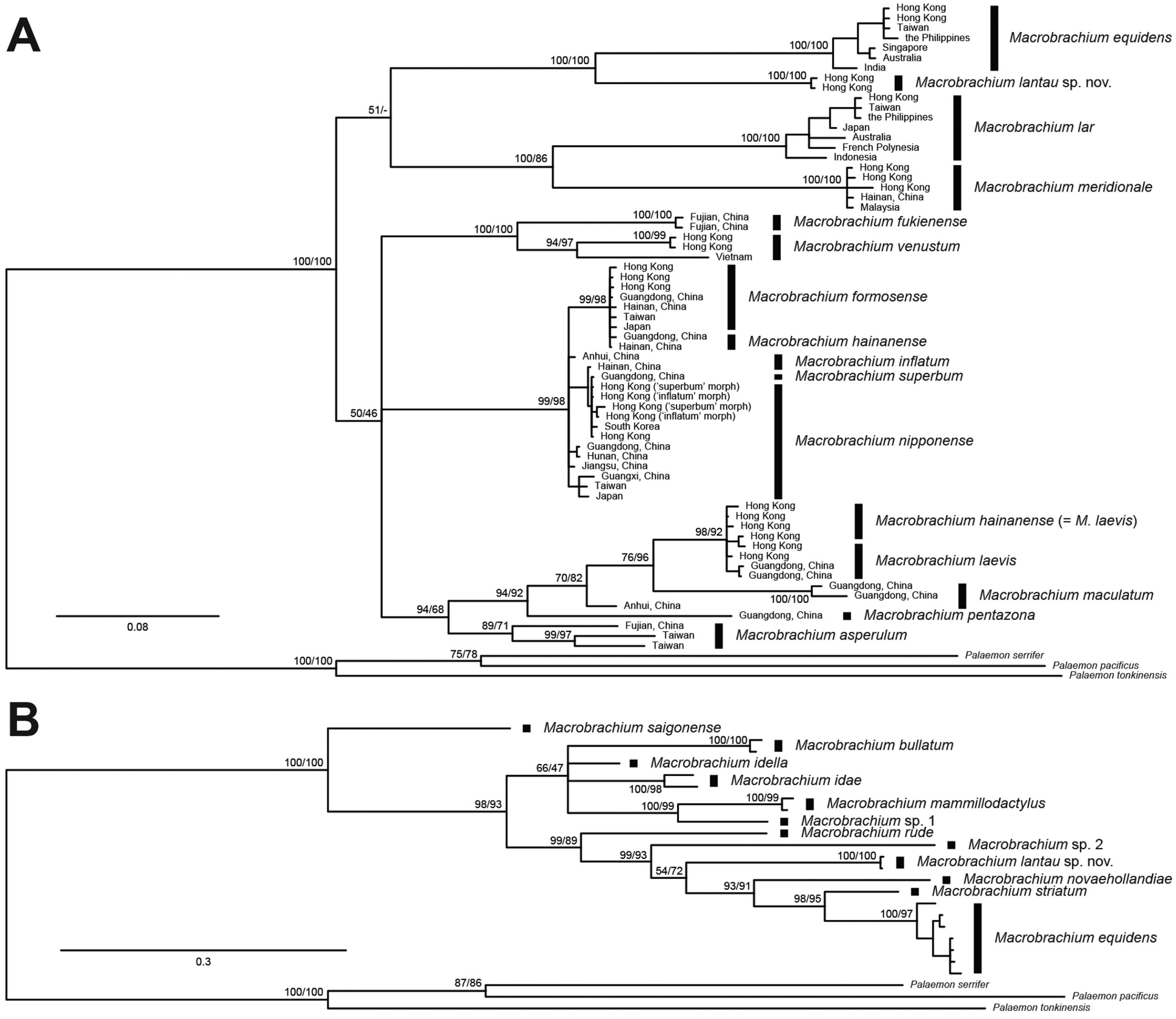

Figure 6. Bayesian phylogenetic trees of *Macrobrachium* species reported from Guangdong Province, southern China (**A**) and selected species of the *M. equidens* species group (**B**), constructed using mitochondrial 16S rRNA and COI markers. Branch support values (PP/BP) are indicated as percentages and not shown for most of the nodes under species level.

specimens of the same gender and comparable sizes are compared, however, the range of variability among varieties overlaps less with the 'typical' form or not at all, suggesting that some of the varieties might actually be cryptic species. The new species, however, is closest to the 'typical' form and there is no evidence suggesting it to be the other varieties. Two possible exceptions are var. *acanthosoma* and var. *brachydactyla*, both were only represented by large male specimens that largely conformed to the 'typical' form. Their true identities, however, would likely remain elusive as the limited type specimens could not document sufficient variations required for accurate identification in view of the extensive degree of variation observed.

Our examination of specimens shows that males of *M. lantau* **sp. nov.** appear to have slightly shorter second pereiopod fingers, compared with *M. equidens* sensu stricto of comparable sizes examined (0.7× as long as palm, 0.75–0.90× from specimens of *M. equidens* between 10.5–13.4 mm in pocl). The male specimens of similar sizes examined by Cowles (1914) (tl between 59.5–66.5 mm) also exhibited similarly longer fingers viz. 0.85–1× as long as palm. The new species also has slightly slenderer rostrum than in specimens of *M. equidens* sensu stricto from Hong Kong (5.8–7.3× as long as maximum depth, 5–6.3× in *M. equidens* sensu stricto), but the measurement overlaps more extensively if Singapore specimens of the latter are also included. The new species appears to have a more northern distribution in the western Pacific, extending to the Satsunan Islands, Japan. *Macrobrachium equidens*, however, has a northern limit in Taiwan but can be found as far south as in Queensland, Australia. The occurrence of *M. equidens* in the Ryukyu Islands, Japan, has been reported by Kubo (1941), but the identification was considered doubtful by Holthuis (1950) and followed by subsequent literatures (see Johnson, 1973; Short, 2004). According to Japanese reports and guidebooks (Yoshigou, 2002; Toyoda, 2019), *M. lantau* **sp. nov.** is likely a common species recognised as '*M. equidens*' in Japan, with no evidence suggesting the occurrence of *M. equidens* sensu stricto in Japan to date. It is therefore possible that the Japanese specimens listed by Kubo (1941) refer to the new species. Nevertheless, in view of the varied rostral shapes figured where the aberrant forms were not typical for *M. equidens* or *M. lantau* **sp. nov.**, his collection might comprise more than one species.

Live colouration appears to be the most obvious and consistent character separating *M. lantau* **sp. nov.** from sympatric *M. equidens* sensu stricto *in situ* (Fig. 2). Similar to *M. equidens* sensu stricto, it also has marbled second pereiopods. The dark patches are nevertheless more regular and continuous, forming bands along dorsal and ventral borders of the palm and carpus, and on the merus and ischium, so that the limbs appear darker and duller. Moreover, fingers of the new species (except the tips) are distinctively bluish but homogenous with the other articles in *M. equidens* sensu stricto. The ventrolateral carapace of the new species is generally less crowded with spots. Distinct spots are present on the lateral midline of the pleurite near the condyles in the new species, one each on the first, second, fifth and sixth, and two on the third somite. The spots on the second, fifth, and sixth somites are extended posteriorly into a short streak. These spots are not present in *M. equidens* sensu stricto, but a transverse scar or band cream to orange in colour is often seen on the dorsoposterior margin of third pleurite except for small individuals. The cloud-shaped pattern on the condyles of the first three pleurites in ovigerous female of the new species are in the form of dark red broken patches rimming a central space with sparse spots of the same colour (Fig. 2E). The developing pattern is more bluish in colour in pre-ovigerous females (Fig. 2F). The pattern is rimmed only dorsally by a continuous brown band with dense brown spots or mottles at the central space in ovigerous females of *M. equidens* sensu stricto (Fig. 2C).

Macrobrachium formosense Spence Bate, 1868

(Figs. 7, 8A–C)

Macrobrachium formosense Spence Bate, 1868: 364, pl. 31, fig. 1 [type locality: Tansui, Taiwan].

Macrobrachium formosense – Guo & He, 2008: 16, figs. 3, 7C.

Material examined: 3 males (pocl 9.4–17.0 mm), ov. female (pocl 10.7 mm), Pak Mong, Hong Kong, leg. L.M. Tsang, 09.V.2012, CUHK-LMT-CAR294; male (pocl 20.9 mm), female (pocl 26.1 mm), Deep Water Bay, Hong Kong, leg. L.M. Tsang, 12.V.2012, CUHK-LMT-CAR234; 5 males (pocl 4.8–26.0 mm), ov. female (pocl 19.8 mm), 5 females (pocl 4.4–16.7 mm), Deep Water Bay, Hong Kong, leg. L.H. Chow, 25.VI.2021, CUHK-LMT-CAR301; male (pocl 11.4 mm), 2 females (pocl 8.1 and 8.7 mm), Tai Tam Tuk, Hong Kong, leg. L.H. Chow, 25.VI.2021, CUHK-LMT-CAR302.

Diagnosis: Rostrum feebly arched, reaching between end of antennular peduncle and end of scaphocerite, 0.6–1× pocl; rostral formula 3–4 + 8–10/3–4, posteriormost dorsal teeth well separated from the second. Carapace covered with microspinules in large adults. Fourth thoracic sternite armed with rounded process. First pereiopod fingers 0.7–0.85× as long as palm; carpus 1.6–2× as long as chela; merus 0.8–0.9× as long as carpus; ischium 0.6–0.7× as long as merus. Second pereiopods subequal, similar, covered with microspinules. Male second pereiopod fingers 0.5–0.85× as long as palm, strongly gapping in large individuals, dactylus with 2 teeth along proximal two-fifth to one-fourth, pollex with tooth at proximal one-third to one-fifth and series of 2–4 denticles more proximally; palm 4–7× as long as wide, 0.8–1.05× as long as carpus, 0.9–1.5× as long as merus, 1–2.5× as long as ischium. Ambulatory pereiopods covered with microspinules in large adults. Third pereiopod propodus 8–12× as long as distal wide, 3–3.5× as long as dactylus, 1.5–2× as long as carpus, 0.85–0.95× as long as merus, 1.55–1.95× as long as ischium; carpus 4–5.5× as long as wide; merus 6–9.5× as long as wide. Eggs small, 0.46–0.57 mm × 0.41–0.46 mm in diameter, numerous.

Ecology: Found from estuaries to hill streams that are connected to the sea, fairly persistent even in fragmented habitats. Compared with some of the other amphidromous *Macrobrachium* species in Hong Kong (*M. lar* and *M. meridionale*), *M. formosense* penetrates much further upstream, and are more capable of scaling waterfalls and man-made obstructions such as dams and concretised canals. They are voracious predators and have been observed hunting for fishes (e.g., the cyprinid *Barbodes semifasciolatus* (Günther, 1868)) and cannibalising on smaller individuals.

Distribution: Southern and eastern China (Fujian, Guangdong, and Zhejiang provinces), Taiwan, southern Japan, and possibly Indonesia (Java) (as *M. hainanense*, Chace & Bruce, 1993). Widely distributed and in high densities in Hong Kong (Fig. 3C).

Remarks: There has been a history of confusion over the identity of *M. formosense* and *M. hainanense*. Holthuis (1950) considered both species valid, but suggested a possible conspecific status. He nevertheless regarded a current junior synonym of *M. formosense*, *Palaemon similis* Yu, 1931, as a synonym of *M. hainanense*. He separated the two species by the number of rostral teeth, the slenderness of the second pereiopod palm and carpus and the length of second pereiopod fingers relative to palm. Huang & Yu (1982) studied *M. formosense* from Taiwan and showed that these characters overlap between the two species, and suggested a synonymisation. Li *et al.* (2007) continued to treat the two species as valid, and separated them by their relative lengths of the second pereiopod carpus (subequal or longer than palm in *M. formosense*, subequal or shorter in *M. hainanense*). This character was actually invalid, since the holotype of *M. hainanense* has slightly longer carpus (carpus-to-palm ratio = 1.03) whereas *M. formosense* reported by Yu (1931) (as *P. similis*) has ratios varying 0.95–1.00. The overlap of carpus-to-palm ratio in *M. hainanense* and *M. formosense* was also remarked in Holthuis (1950), and thus this character was not considered by Holthuis (1950) for differentiating the two species. One of our adult male specimens also possesses shorter carpus than the other specimens examined (carpus-to-palm ratio = 0.97, 1.01–1.1 in the other specimens), supporting the observation by Yu (1931). Guo & He (2008) further separated the species by the number of denticles at the proximal cutting edge of the second pereiopod pollex (2 or 3 denticles in *M. formosense*, 4 or 5, rarely 3 in *M. hainanense*). The present specimens, however, bear 2–4 denticles, and Parisi (1919) also reported 3 or 4 denticles (as *P. longipes* De Haan, 1849 [De Haan,

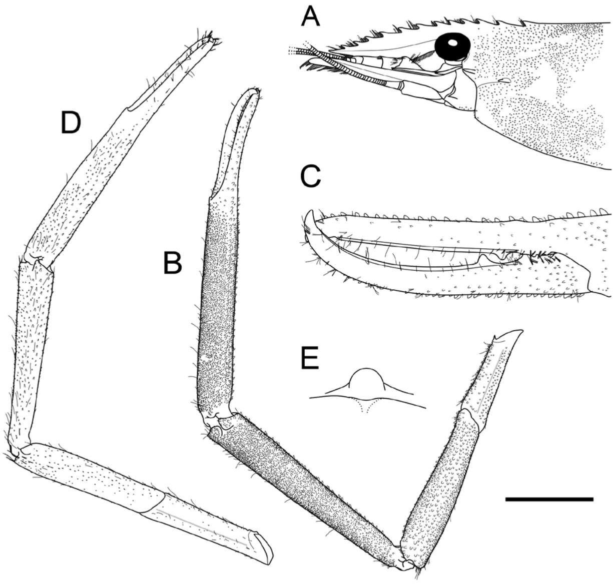

Figure 7. *Macrobrachium formosense*, male, pocl 26.0 mm (CUHK-LMT-CAR301-1) (**A**–**C**, **E**); male, pocl 17.0 mm (CUHK-LMT-CAR294-4) (**D**). Frontal region, lateral view (**A**); left second pereiopod (**B**); same, cutting edge, lateral view (**C**); left second pereiopod (**D**); process of fourth thoracic sternite (**E**). Scale bars = 12 mm (B), 10 mm (A), 5 mm (C, D) or 1.5 mm (E).

1833–1850]). On the other hand, Holthuis (1950) reported the presence of 2 or 3 denticles in *M. hainanense*. Taken together, there are no apparent morphological differences between *M. formosense* and *M. hainanense*. Phylogenetic analyses by Liu *et al.* (2007) and Wowor *et al.* (2009) showed that *M. hainanense* (including materials from the type locality, Hainan Province), did not deviate from *M. formosense* genetically (Fig. 6A). As such, *M. hainanense* is highly possible to be a junior synonym of *M. formosense* as suggested by Holthuis (1950) and Huang & Yu (1982).

Regarding ratios among second pereiopod articles, *M. formosense* exhibits allometric growth with the palm, followed by the carpus, being the slowest growing articles. Article ratios from dactylus to ischium are 0.5–0.6: 1: 0.95–1.1: 0.65–0.75: 0.4–0.5 in large males (pocl > 19 mm) (Fig. 7B), 0.7: 1: 1–1.1: 0.9: 0.8 in intermediate males (pocl 10–19 mm) (Fig. 7D), and 0.85: 1: 1.25: 1.1: 1 in small males (pocl < 10 mm). Large females and one of the intermediate females have ratios comparable to intermediate males, whereas the remaining females are similar to small males or somewhat in between. The denticles on the proximal cutting edge of the pollex in large males are distinctively larger than those in smaller males and females.

Macrobrachium laevis Zheng, Chen & Guo, 2019

(Figs. 8D–F, 9)

Macrobrachium laevis Zheng *et al.*, 2019: 70, pl. 3, figs. 2, 3 [type locality: Zhaomu Mountain Forest Park, Foshan, Guangdong, China].

Material examined: 2 males (pocl 17.6 and 19.5 mm), Wu Kau Tang, Hong Kong, leg. L.M. Tsang, 26.V.2011, CUHK-LMT-CAR352; male (pocl 19.8 mm), Tai Mo Shan, Hong Kong, leg. L.M. Tsang, 10.VII.2012, CUHK-LMT-CAR400; 2 females (pocl 10.7–14.0 mm), Wu Kau Tang, Hong Kong, leg. L.M. Tsang, 02.X.2012, CUHK-LMT-CAR291; 5 males (pocl 14.1–21.6 mm), female (pocl 14.4 mm), Tsing Fai Tong, Hong Kong, leg. L.M. Tsang, 15.XI.2012, CUHK-LMT-CAR401; 2 males (pocl 15.5 and 20.3 mm), female (pocl 14.1 mm), Ta Tit Yan, Hong Kong, leg. L.M. Tsang, 17.XII.2012, CUHK-LMT-CAR233; 2 males (pocl 18.3 and 20.2 mm), Ta Tit Yan, Hong Kong, leg. N.W.Y. Wong, 03.VI.2015, CUHK-LMT-CAR402; male (pocl 17.2 mm), ov. female (pocl 13.3 mm), Ng Tung Chai, Hong Kong, leg. N.W.Y. Wong, 03.VI.2015, CUHK-LMT-CAR403; male (pocl 19.2 mm), 2 ov. females (pocl 11.3 and 13.0 mm), A Kung Kok Shan, Hong Kong, leg. N.W.Y. Wong, 03.VII.2015, CUHK-LMT-CAR399; 3 males (pocl 7.9–10.3 mm), Shing Mun, Hong Kong, leg. L.M. Tsang, 26.VI.2020, CUHK-LMT-CAR290; male (pocl 14.6 mm), Ho Pui, Hong Kong, leg. Z.Y. Kho, 24.III.2021, CUHK-LMT-CAR275; male (pocl 18.4 mm), Shing Mun, Hong Kong, leg. J.C.F. Chan, 21.X.2021, CUHK-LMT-CAR420.

Diagnosis: Rostrum feebly arched, reaching between end of antennular peduncle and end of scaphocerite, 0.55–0.7× pocl; rostral formula 2–4 + 5–8/2–4, teeth above orbit more closely spaced. Carapace rough, covered with microspinules in large individuals, smooth in small individuals. Fourth thoracic sternite armed with blunt, triangular process. First pereiopod fingers 0.75–0.95× as long as palm; carpus 1.6–1.8× as long as chela; merus 0.8–0.85× as long as carpus; ischium 0.65–0.75× as long as merus. Second pereiopods subequal, similar, covered with microspinules. Male second pereiopod fingers 0.6–0.85× as long as palm, sometimes gapping in large individuals, dactylus with 2 teeth along proximal one-fifth to one-fourth, pollex with 2 teeth along proximal one-sixth to one-fifth, basal tooth formed by 1, 2, or 3 denticles, often as low hump in small individuals, rest of both cutting edges entire, with row of as many as > 25 tubercles or papillae on the mesial side and > 12 on the lateral side of each cutting edge in large individuals, none in small individuals; palm 4–6.7× as long as wide, 1–1.45× as long as carpus, 1.15–1.55× as long as merus, 1.15–2.05× as long as ischium. Ambulatory pereiopods covered with microspinules. Third pereiopod propodus 7–10× as long as distal wide, 2.7–3.7× as long as dactylus, 1.4–1.65× as long as carpus, 0.8–0.95× as long as merus, 1.3–2× as long as ischium; carpus 3.5–5× as long as wide; merus 5–7.5× as long as wide. Eggs large, 1.47–1.97 mm × 1.03–1.53 mm in diameter, few.

Ecology: Inhabits mostly upland streams but can also be found in lowland streams with a preference for good water quality and waterflow. Populations in Hong Kong occur in a wide range of altitude, generally between 30 m to > 700 m above sea level. They are one of the major predators in local hill streams, vital in controlling community of sedentary macroinvertebrates (Mantel & Dudgeon, 2004).

Distribution: Known only from Guangdong Province, southern China (Hong Kong, Foshan, Jiangmen, Shenzhen). Very widespread and common in Hong Kong (Fig. 3D).

Remarks: Several infra-specific variations not documented in the original description, some attributed to allometric growth,

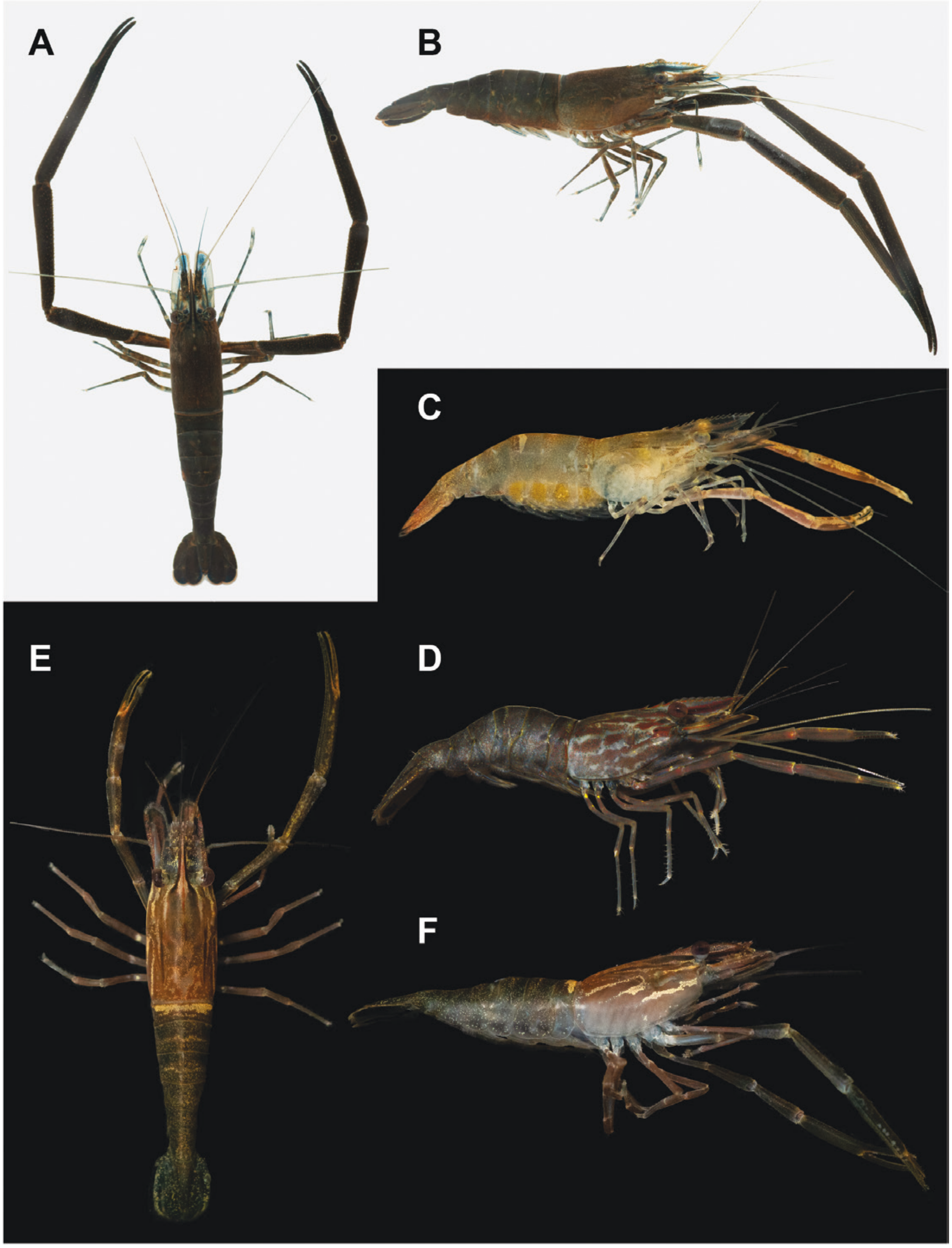

Figure 8. *Macrobrachium formosense* (**A**–**C**). Male, pocl 25.2 mm (CUHK-LMT-CAR301-7), dorsal view (**A**); same, habitus (**B**); ov. female, pocl 19.8 mm (CUHK-LMT-CAR301-2), habitus (**C**). *Macrobrachium laevis* (**D**–**F**). Male, pocl 14.6 mm (CUHK-LMT-CAR275-1), habitus (**D**); male, pocl 18.4 mm (CUHK-LMT-CAR420), left second pereiopod regenerating, dorsal view (**E**); same, habitus (**F**). Photographs by Zi Yi Kho (A–C, E, F) and Lai Him Chow (D).

have been identified following the collection of both large and small specimens. Compared with the type material, the present specimens have 1) carapace covered with microspinules in large individuals (pocl > 17 mm) (always smooth in the type specimens); 2) dorsal rostral teeth above orbit more closely spaced (*versus* evenly spaced) (Fig. 9A); 3) slenderer scaphocerite (2.8–3.2× as long as wide *versus* 2.4–2.6×); 4) second pereiopod extending beyond scaphocerite by distal one-third of merus to entire carpus in some large individuals (pocl > 17 mm), by proximal one-fourth to half of carpus in the others (*versus* by half of carpus); 5) all articles of the second pereiopod covered with microspinules, those on palm surface, especially on lateral side, often abraded, merus and ischium largely smooth in small individuals (*versus* largely smooth with only small amount of microspinules along palm margins) (Fig. 9B, E); 6) proportionally shorter second pereiopod carpus (1.05–1.25× as long as merus *versus* 1.2–1.4×); 7) second pereiopod dactylus and pollex each armed with two proximal teeth, rest of both cutting edges with papillae on the mesial (and lateral) side(s) in large individuals (pocl > 17 mm), none in small individuals (*versus* two teeth on dactylus, one on pollex, no papillae) (Fig. 9F, G); 8) more strongly armed ventral margin of ambulatory pereiopod propodi (13–21 *versus* 5–7 spines) (Fig. 9C, D); 9) spine on uropodal diaeresis longer than, rarely subequal to lateral

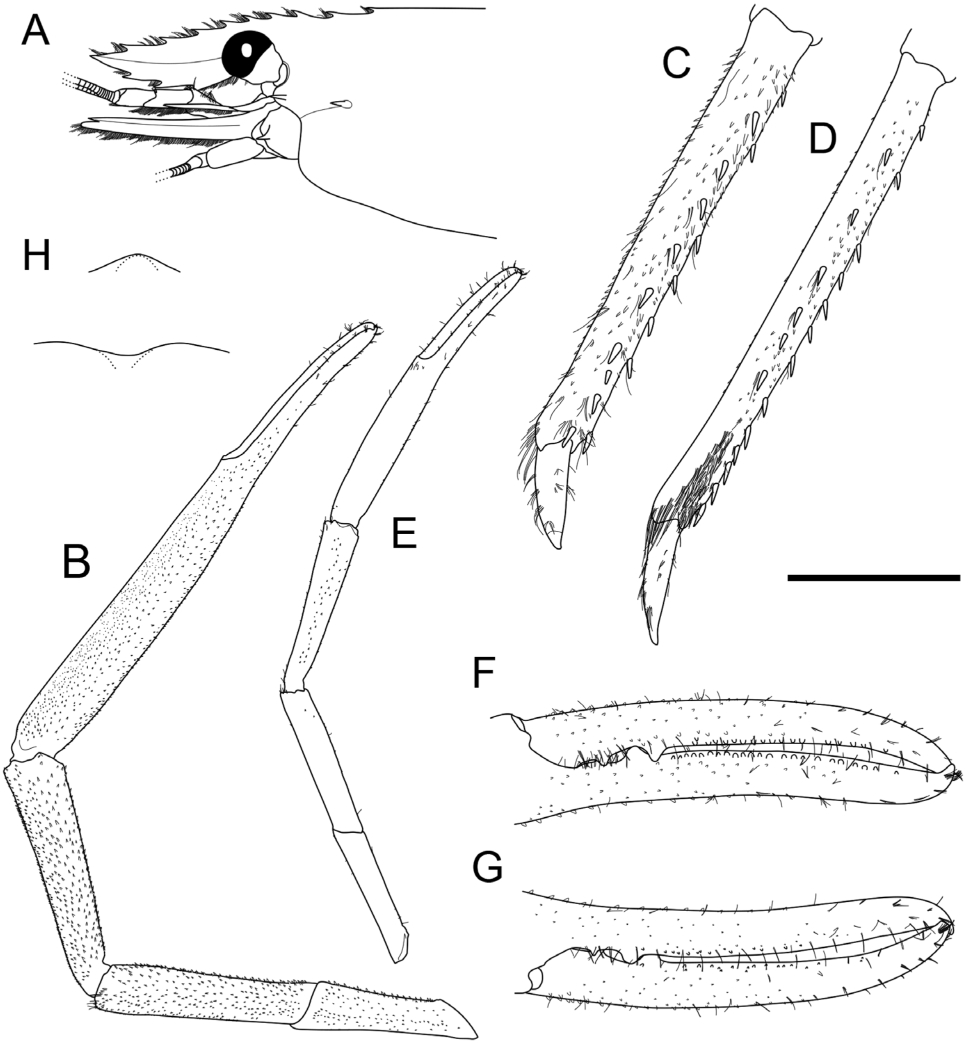

Figure 9. *Macrobrachium laevis*, male pocl 20.3 mm (CUHK-LMT-CAR233-1) (**A**–**D**); male, pocl 15.5 mm (CUHK-LMT-CAR275) (**E**); male, pocl 17.6 mm (CUHK-LMT-CAR352-1) (**F**–**H**). Frontal region, lateral view, microspinules omitted (**A**); left second pereiopod (**B**); left third pereiopod, propodus and dactylus (**C**); left fifth pereiopod, propodus and dactylus (**D**); left second pereiopod (**E**); right second pereiopod, cutting edge, mesial view (**F**); same, lateral view (**G**); process of fourth thoracic sternite (**H**). Scale bars = 10 mm (A, B, E), 5mm (F, G), 3 mm (C, D) or 1 mm (H).

angle (*versus* shorter). In general, larger males (pocl > 17 mm) have proportionally longer and slenderer second pereiopod palm (5.1–6.7× as long as wide) with ratios among articles from dactylus to ischium being 0.6–0.7: 1: 0.7–0.85: 0.65–0.75: 0.5–0.6, whereas smaller males have a ratio of 0.7–0.85: 1: 0.85–1: 0.75–0.9: 0.65–0.85 with the palm being 3.9–4.5× as long as wide (Fig. 9B, E).

With the extension of intra-specific variations, *M. laevis* is more morphologically similar to several related species than originally expected (i.e., *M. asperulum*, *M. bilineare* Chen, Chen, Hu, Ma & Guo, 2021, *M. maculatum*, *M. vietnamiense*). Morphological separation among these species is deemed to be difficult, since some details were not mentioned in the original descriptions, and ratios among their second pereiopod articles largely overlaps with allometric variations further complicating identification. *Macrobrachium maculatum* can be separated from *M. laevis* by having slightly more rostral teeth (3–5 + 6–9/3–5, 2–4 + 5–8/2–4 in *M. laevis*) and slenderer scaphocerite (3.5× as long as wide *versus* 2.8–3.2×). The male second pereiopods of *M. maculatum* also seemingly grow at a faster rate, growing longer than tl as early as reaching 69 mm long in tl (Li *et al.*, 2007), whereas *M. laevis* rarely have second pereiopods longer than tl. *Macrobrachium bilineare* differs from *M. laevis* by the slenderer scaphocerite (3.8–4× as long as wide, 2.8–3.2× in *M. laevis*) and the absence of tubercles or papillae along the second pereiopod cutting edges, even in male as large as 21.9 mm long in pocl (*versus* presence in male > 17 mm in pocl). *Macrobrachium asperulum* differs from *M. laevis* by the shorter adult male second pereiopod fingers (0.5–0.6× as long as palm, 0.6–0.7× as long as carpus; 0.6–0.7× and 0.7–0.95×, respectively, in *M. laevis*) and carpus (~1.3× as long as merus *versus* 1.05–1.2×) and the teeth on the second pereiopod cutting edges are restricted to the proximal two-fifth (*versus* one-fourth). *Macrobrachium vietnamiense* has second pereiopod article ratios very similar to *M. asperulum*, and Li *et al.* (2007) suggested colouration as a critical character to differentiate the two species. *Macrobrachium asperulum* was mentioned to be greenish brown with a creamy longitudinal stripe on the dorsum, whereas *M. vietnamiense* is dark with golden stripes on carapace and a golden band on the anterior margin of first pleurite which surprisingly matches that of *M. laevis* (Fig. 5D–F). The holotype of *M. vietnamiense* was 24 mm long in pocl and *M. laevis* of this size has never been seen during our years of surveying. The difference in the second pereiopod article ratios between the two species may, therefore, be attributed to allometric variation. Nevertheless, we recommend to treat the two species as distinct, until genetic analysis on topotypic specimens of *M. vietnamiense* and/or morphological examination of larger specimens of *M. laevis* suggest otherwise. According to Li *et al.* (2007), adult *M. asperulum*, *M. maculatum*, and *M. vietnamiense* can also be separated by the number of papillae or tubercles on the second pereiopod cutting edges: 10 mesial and 3–4 lateral papillae in *M. asperulum*, 20–30 mesial and > 10 lateral papillae in *M. maculatum*, and 7–12 mesial and no lateral papillae in *M. vietnamiense*. This diagnostic feature is of uncertain validity, however, since no size series of specimens were examined by Li *et al.* (2007) and age (and cheliped growth) is known to affect its manifestation as shown in *M. laevis*.

Our phylogenetic analysis shows that the '*M. hainanense*' from Hong Kong in several previous studies align with *M. laevis* (Fig. 6A). Previous ecological studies also mentioned that '*M. hainanense*' from Hong Kong produces small broods of large eggs with abbreviated larval development (Wong, 1989; Mantel & Dudgeon, 2005), but *M. hainanense* is typically amphidromous, producing numerous small eggs. Morphologically, *M. laevis* can be differentiated from *M. hainanense* by having fewer dorsal rostral teeth (8–12, 11–14 in *M. hainanense*), and shorter adult male second pereiopod carpus (0.7–0.95× as long as palm *versus* 0.95–1.00×).

Macrobrachium lar (Fabricius, 1798)

(Figs. 10, 11A, B)

Palaemon lar Fabricius, 1798: 402 [type locality: India].

Macrobrachium lar – Liu *et al.*, 1990: 104, fig. 21. — Short, 2004: 75, fig. 29, 36K.

Material examined: male (pocl 41.5 mm), Deep Water Bay, Hong Kong, leg. J.C.F. Chan, 20.VIII.2021, CUHK-LMT-CAR326.

Diagnosis: Rostrum sinuous, curved upwards distally, reaching to end of antennular peduncle, ~0.5× pocl; rostral formula 2 + 6/3, posteriormost dorsal teeth well separated from the second, subterminal tooth smallest. Carapace smooth. Fourth thoracic sternite armed with blunt, triangular process. First pereiopods with microspinules on merus and ischium; fingers ~0.85× as long as palm; carpus ~2.6× as long as chela; merus ~0.8× as long as carpus; ischium ~0.5× as long as merus. Second pereiopods subequal, similar, covered with microspinules. Male second pereiopod fingers ~0.75× as long as palm, strongly gapping, dactylus with conspicuously large, triangular tooth at around half-length and two broad, low humps at proximal one-fifth and one-tenth, respectively, pollex with slightly smaller, triangular tooth and much smaller tooth with proximal row of 3 denticles, opposing the 2 humps on dactylus, respectively; palm ~6.2× as long as wide, ~1.65× as long as carpus, ~1.45× as long as merus, ~2.9× as long as ischium. Ambulatory pereiopods covered with microspinules. Third pereiopod propodus ~9.5× as long as distal wide, ~3.5× as long as dactylus, ~1.65× as long as carpus, ~0.9× as long as merus, ~2.2× as long as ischium; carpus ~4.3× as long as wide; merus ~6.3× as long as wide. Pre-anal carina well developed.

Ecology: An elusive species inhabiting pool sections of upland streams, often found in small, steep coastal streams rather than large perennial streams.

Distribution: Widespread throughout the Indo-West Pacific, from East Africa to the Marquesas Islands, and to southern Japan to the north (Short, 2004). Introduced to the Hawaiian Islands (Atkinson, 1977). Not previously recorded from Hong Kong, scarcely distributed in the eastern New Territories, Hong Kong Island and Lantau Island in low abundance (Fig. 3F).

Remarks: The present specimen largely matches previous description of large adult male (Short, 2004), except with the second pereiopods subequal in length.

Macrobrachium meridionale Liang & Yan, 1983

(Figs. 11C, D, 12)

Macrobrachium meridionalis Liang & Yan, 1983: 213, fig. 2 [type locality: Jingjiang River, Cengmai, Hainan, China].

Macrobrachium meridionalis – Liu *et al.*, 1990: 115, fig. 13. — Yeo *et al.*, 1999: 227, figs. 15, 16. — Guo & He, 2008: 18, figs. 4–6.

Material examined: male (pocl 16.1 mm), ov. female (pocl 12.1 mm), Tong Fuk, Hong Kong, leg. L.M. Tsang, 07.V.2012, CUHK-LMT-CAR232; 2 males (pocl 19.7 and 20.5 mm), ov. female (pocl 17.0 mm), Tung Chung, Hong Kong, leg. L.M. Tsang, 09.V.2012, CUHK-LMT-CAR183; male (pocl 9.9 mm), Pak Mong, Hong Kong, leg. L.M. Tsang, 09.V.2012, CUHK-LMT-CAR293; 2 males (pocl 21.8 and 26.3 mm), Deep Water Bay, Hong Kong, leg. J.C.F. Chan, 18.VII.2021, CUHK-LMT-CAR308.

Diagnosis: Rostrum feebly arched, nearly reaching to end of antennular peduncle, 0.45–0.6× pocl; rostral formula 5–7 + 6–8/3–4, postorbital teeth more distantly spaced. Carapace smooth. Fourth thoracic sternite armed with blunt, triangular process. First pereiopods with appressed scales on merus and ischium in adults; fingers 0.7–0.8× as long as palm; carpus 1.6–1.75× as long as chela; merus ~0.9× as long as carpus; ischium 0.5–0.6× as long as merus. Second pereiopods in both sexes unequal, slightly dissimilar, covered with appressed scales. Adult male major second pereiopod fingers 0.45–0.55× as long as palm, strongly gapping in large individuals, dactylus with 3 or 4 teeth along proximal half to three-fifth, pollex with 1 or 2 teeth along proximal one-third to one-half and series of 6–9 denticles more proximally, anteriormost denticles may be enlarged into bifid or trifid teeth in large individuals; palm 3.3–4.6× as long as wide, 1.3–1.6× as long as carpus, 1.5–1.8× as long as merus, 2.2–2.5× as long as ischium. Adult male minor second pereiopod fingers 0.55–0.7× as long as palm, strongly gapping in large individuals, dactylus with 3 or 4 teeth along proximal one-third to one-half, pollex with tooth along proximal one-third to two-fifth and series of 8–11 denticles more proximally, anteriormost denticles may be enlarged into 1 or 2 simple or bifid

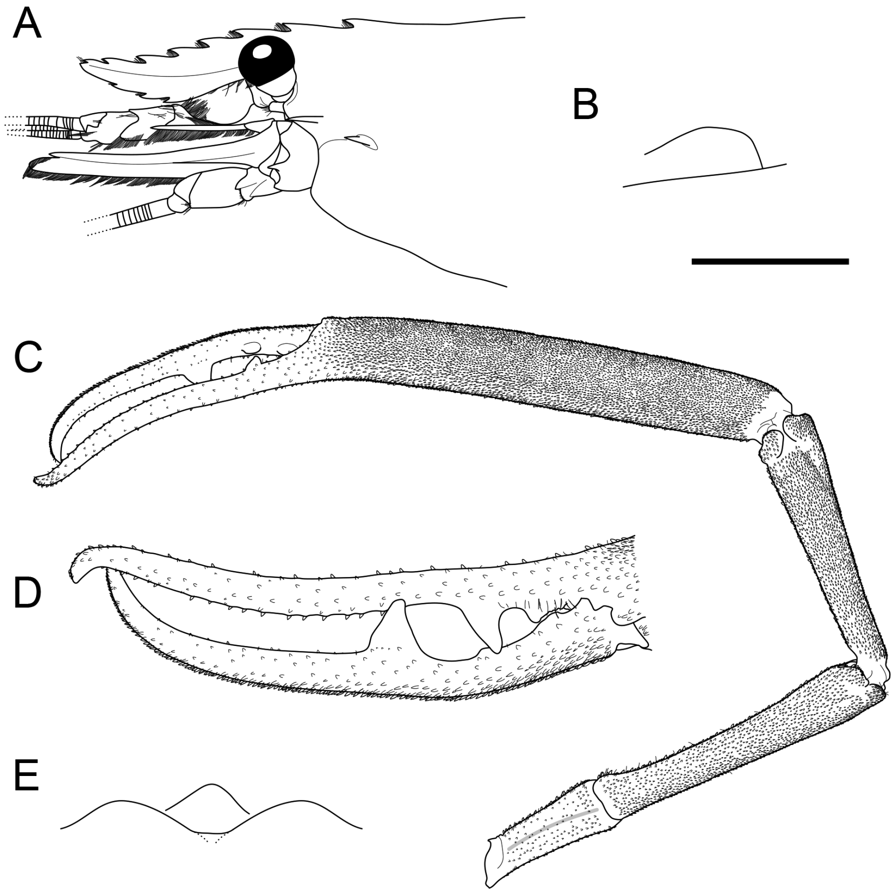

Figure 10. *Macrobrachium lar*, male, pocl 41.5 mm (CUHK-LMT-CAR326). Frontal region, lateral view (**A**); pre-anal carina, lateral view, telson on the right (**B**); right second pereiopod (**C**); same, cutting edge, mesial view (**D**); process of fourth thoracic sternite (**E**). Scale bars = 20 mm (C), 16mm (A), 12 mm (D), 3 mm (E) or 2 mm (B).

teeth in large individuals; palm 3.1–3.8× as long as wide, 1.2–1.3× as long as carpus, 1.2–1.4× as long as merus, 1.6–1.9× as long as ischium. Ambulatory pereiopods covered with appressed scales in adults. Third pereiopod propodus 6–8× as long as wide, ~3× as long as dactylus, 1.3–1.5× as long as carpus, 0.75–0.85× as long as merus, 1.6–1.7× as long as ischium; carpus 3–4× as long as wide; merus 4–5× as long as wide. Pre-anal carina well-developed. Eggs small, 0.44–0.58 mm × 0.35–0.50 mm in diameter, numerous.

Ecology: Most often found in riffles of hill streams that are connected to the sea. Typically not found beyond dams or waterfalls, but individuals have been observed in a stream within an impounded reservoir. Locally co-occur with *M. formosense* and *M. lar* (with partition of microhabitats with *M. lar* (i.e., riffles *versus* pools)).

Distribution: Southern China (Fujian, Guangdong, Hainan, Zhejiang provinces) and Malaysia (Tioman Island) (Yeo *et al.*, 1999; Li *et al.*, 2007). Relatively rare in Hong Kong, with distribution largely confined to the northeastern, eastern, and southeastern New Territories, and Lantau and Hong Kong islands (Fig. 3G).

Remarks: All present specimens have a well-developed pre-anal carina, quarter-circular to triangular shaped in lateral view with the curved side directed anteriorly (Fig. 12B). Corroborating the observation by Yeo *et al.* (1999) and Guo & He (2008), both the major and minor second pereiopods in large adult males (pocl > 19 mm) are provided with a groove on the surface (Fig. 12C, D). The groove is only obvious on the major pereiopod and ischium of the minor pereiopod in small adult males and females. The groove in juvenile males (pocl < 10 mm) is only discernible on the ischium of both pereiopods. Ratios among second pereiopod articles of females and juvenile males, from dactylus to ischium, are 0.6–0.7: 1: 0.85: 0.75–0.85: 0.7–0.8 and 0.7–0.8: 1: 0.95–1: 0.9–1: 0.9 for major and minor pereiopods, respectively.

Compared with the Malaysian specimens reported by Yeo *et al.* (1999), some of the present specimens have relatively more robust ambulatory pereiopods (third pereiopod propodus ~6× as long as wide, 7.8× in Malaysian specimens) (Fig. 12E), showing a slight affinity with *M. horstii* (De Man, 1892) known from Taiwan, Indonesia, and the Philippines. The present specimens can, however, still be distinguished from *M. horstii* by several characters, which are discussed in Yeo *et al.* (1999) and Wowor *et al.* (2004). Some of the most obvious differences include the presence of appressed scales on first pereiopod merus and ischium (absent in *M. horstii*), the proportionally shorter male major second pereiopod carpus (0.65–0.75× as long as palm, 0.75–0.95× in *M. horstii*) and more denticles on proximal cutting edges of the male major second pereiopod (> 9 *versus* < 9 denticles). These features, however, are only applicable to adult *M. meridionale*.

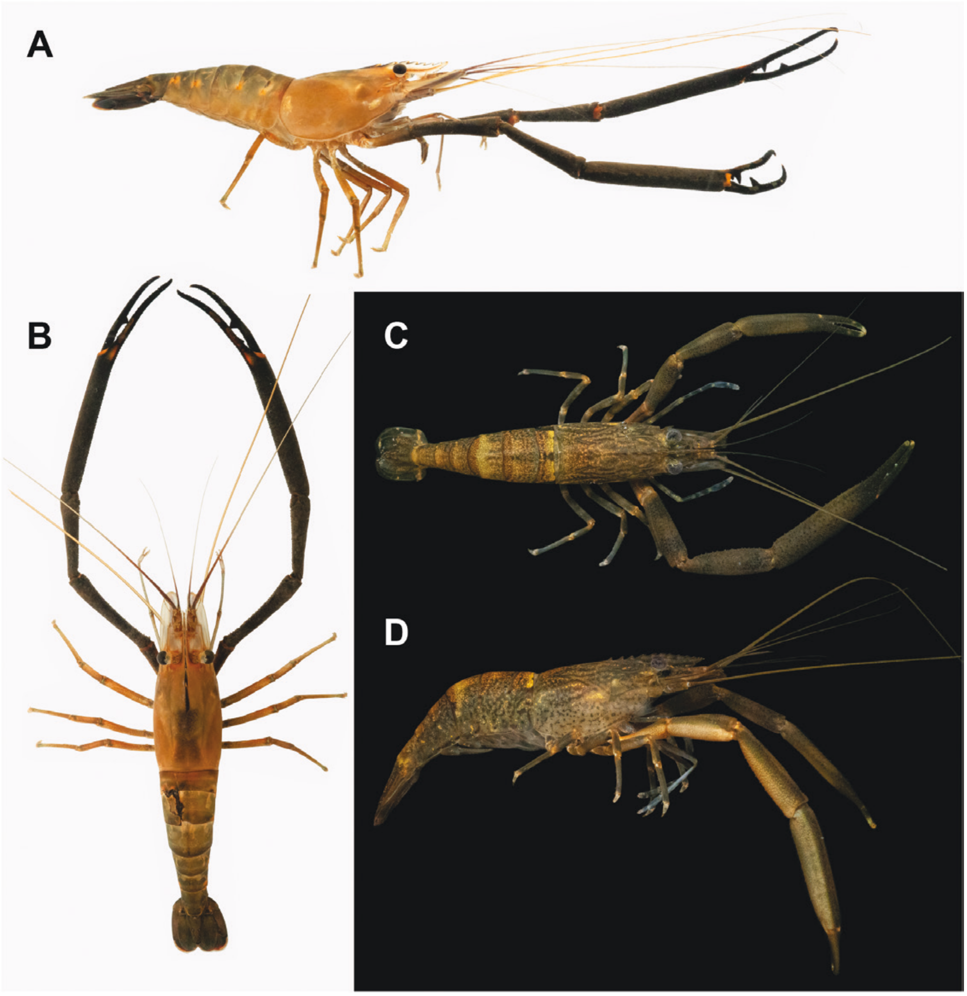

Figure 11. *Macrobrachium lar* (**A**, **B**). Male, pocl 41.5 mm (CUHK-LMT-CAR326), habitus (**A**); same, dorsal view (**B**). *Macrobrachium meridionale* (**C**, **D**). Male, pocl 21.8 mm (CUHK-LMT-CAR308-1), dorsal view (**C**); same, habitus (**D**). Photographs by Zi Yi Kho.

Macrobrachium nipponense (De Haan, 1849) [De Haan, 1833–1850]

(Figs. 13, 14A–C)

Palaemon nipponense De Haan, 1849 [De Haan, 1833–1850]: 171 [type locality: Japan].

Macrobrachium nipponense – Liu *et al.*, 1990: 111, fig. 9.

Material examined: 18 males (pocl 12.0–18.6 mm), female (pocl 10.0 mm), Mai Po, Hong Kong, leg. K.Y. Ma, 16.XII.2016, CUHK-LMT-CAR235; female (pocl 6.5 mm), Tai Tam, Hong Kong, leg. L.M. Tsang, 30.X.2020, CUHK-LMT-CAR256; male (pocl 10.3 mm), 3 females (pocl 7.4–9.7 mm), Ho Pui, Hong Kong, leg. Z.Y. Kho, 24.III.2021, CUHK-LMT-CAR276; male (pocl 10.2 mm), Lau Shui Heung, Hong Kong, leg. L.H. Chow, 14.VII.2021, CUHK-LMT-CAR305; male (pocl 5.6 mm), Ha Wo Hang Tsuen, Hong Kong, leg. L.H. Chow, 25.VIII.2021, CUHK-LMT-CAR327; male (pocl 15.5 mm), ov. female (pocl 12.7 mm), female (pocl 16.3 mm), Mai Po, Hong Kong, leg. K.Y. Ma, 15.IX.2021, CUHK-LMT-CAR349; male (pocl 9.6 mm), female (pocl 9.0 mm), same collection data, CUHK-LMT-CAR350.

Diagnosis: Rostrum horizontal, can be slightly inclined upwards, almost straight, falling short of to slightly overreaching end of scaphocerite, 0.7–1× pocl; rostral formula 2–4 + 8–11/3–4, posteriormost dorsal teeth well separated from the second. Carapace smooth. Fourth thoracic sternite armed with conical process. First pereiopod fingers 0.75–0.95× as long as palm; carpus 1.8–2.3× as long as chela; merus 0.75–0.9× as long as carpus; ischium 0.55–0.7× as long as merus. Second pereiopods subequal, similar, covered with microspinules in large individuals. Male second pereiopod fingers 0.75–1.5× as long as palm, densely setose along cutting edges in large individuals, dactylus unarmed or with 2 teeth along proximal one-seventh to one-fourth, pollex unarmed or with tooth at proximal one-ninth to one-fifth and a low hump with 2–4 denticles more proximally that are often abraded; palm 3–5.2× as long as wide, 0.5–0.85× as long as carpus, 0.6–1.15× as long as merus, 0.65–1.3× as long as ischium. Third pereiopod propodus 10–16× as long as distal wide, 2–3× as long as dactylus, 1.8–2.2× as long as carpus, 0.85–0.95× as long as merus, 1.8–2.2× as long as ischium; carpus 4.5–7.5× as long as wide; merus 7.5–13× as long as wide. Eggs small, 0.40–0.48 mm × 0.33–0.43 mm in diameter, numerous.

Ecology: Found in streams, ponds, reservoirs, estuaries, and salt marshes, with both land-locked and amphidromous populations occurring in Hong Kong. Some populations, especially those

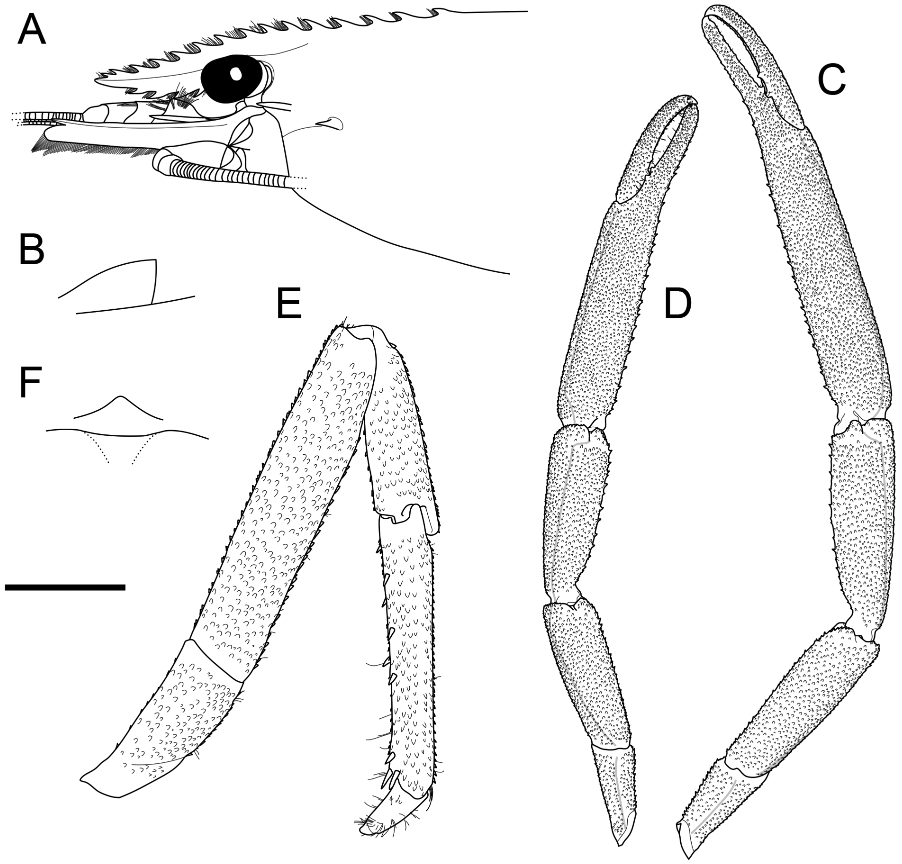

Figure 12. *Macrobrachium meridionale*, male, pocl 20.5 mm (CUHK-LMT-CAR183-3) (**A**, **C**–**F**); ov. female, pocl 17.0 mm (CUHK-LMT-CAR183-2) (**B**). Frontal region, lateral view (**A**); pre-anal carina, lateral view, telson on the right (**B**); right major second pereiopod (**C**); left minor second pereiopod (**D**); right third pereiopod (**E**); process of fourth thoracic sternite (**F**). Scale bars = 10 mm (**C**, **D**), 6 mm (**A**), 3 mm (**E**) or 1 mm (**B**, **F**).

in reservoirs and streams adjacent to fishponds, may have been released as fish feed and fishpond escapees, respectively.

Distribution: Native to East and Southeast Asia (China, Japan, Korea, Myanmar, Taiwan, Vietnam) (Yu & Miyake, 1972; Cai & Ng, 2002). Introduced to other places in Southeast Asia (Laos, Malaysia, Singapore, the Philippines), Central, South and West Asia (Bangladesh, Iran, Iraq, Kazakhstan, Uzbekistan), and Eastern Europe (European Russia, Belarus, Moldova, Ukraine) (Chong *et al.*, 1987; Cai & Shokita, 2006; De Grave & Ghane, 2006; Salman *et al.*, 2006; Hanamura *et al.*, 2011; Son *et al.*, 2020; Ahmed *et al.*, 2021). Generally widespread and abundant in Hong Kong (Fig. 3H).

Remarks: Allometric morphological variations in *M. nipponense* have been partly discussed in Ortmann (1891) and Suzuki & Kusamura (1997). The present specimens also show extensive variations but do not necessarily correlate with age. Large adult males (not herein collected) typically have rough carapace, abdomen, uropods, and telson covered with microspinules, and second pereiopods longer than tl with dense setation along cutting edges (Li *et al.*, 2007). Ratios among second pereiopod articles, from dactylus to ischium, are 0.6–0.7: 1: 1.1–1.3: 0.7–0.75: 0.5–0.6. The most common morph in the present material represents allometric variations of this typical large adult morph. Two of the males, including the largest collected (pocl 15.5 and 18.6 mm), have largely smooth body and second pereiopods slightly longer than tl (only in the larger male) but dense setation along cutting edges is present (Fig. 13C). They have proportionally shorter palm with article ratios being 0.9: 1: 1.45–1.55: 1: 0.8–0.85 (Fig. 13B). The other males (pocl 12.0–17.8 mm) have less well developed microspinules on the second pereiopods, often restricted to the dorsal and ventral margins (also seen in the small male aforementioned), and sparse setation along the cutting edges. Their second pereiopod fingers, carpus, and merus are proportionally shorter but the ischium is proportionally longer, with article ratios being 0.75–0.9: 1: 1.15–1.45: 0.85–1: 0.8–0.95. Their palm is also slightly stouter, 4.3–4.7× as long as wide (4.9–5.2× in the more developed males).

About one-third of the male specimens, ranging from pocl 10.3–16.6 mm in size, are distinctive in the inflated second pereiopod palm (3.3–3.9× as long as wide, 4.3–5.2× in the typical morph) (Fig. 13E). This second morph had also been observed by Yu (1931) among individuals of the typical morph. Their ratios among second pereiopod articles are largely similar to typical specimens of comparable sizes, except the fingers are slightly longer, being 0.9–1× as long as the palm. They also have slightly longer rostrum of 0.75–0.9× length pocl (0.7–0.8× in the typical morph). On account of these two features, they highly resemble *M. inflatum*, and can only be separated by minor details, including proportionally longer second pereiopod merus (0.75–0.8× as long as carpus, 0.65–0.7× in *M. inflatum*) and shorter ischium (0.9–1× as long as merus *versus* 1.1×). The present specimens also differ from the original description of *M. inflatum* by Liang & Yan (1985), but agree with Cai & Dai (1999), by the broader scaphocerite (2.8–3× as long as wide, 3.4× in the original description) and non-gapping second pereiopod (*versus* distally gapping). Abrasion of the lamella on the entire cutting edges is not uncommon in *Macrobrachium* species, and this may explain the presence of an obvious gap in the original description. *Macrobrachium nipponense* and *M. inflatum* are often reported being found together (Cai & Dai, 1999; Guo & He, 2008) and our phylogenetic analysis shows that some specimens identified as *M. inflatum* by previous studies nested within *M. nipponense* (Fig. 6A). Given the minor morphological differences and the molecular evidence, *M. inflatum* likely represents a subadult to small adult form and thus a synonym of *M. nipponense*, which has also been noted by Short (2004) as potentially being described from an undeveloped male.

A third morph was observed in a few small specimens (pocl 5.6–10.2 mm), characterised by having second pereiopod fingers unarmed or bearing a scarcely visible tooth (distinctively armed in the other two morphs) and longer than palm (1.1–1.5× as long as palm *versus* 0.75–1×), resembling *M. superbum* (Fig. 13G). They also share other features not observed in the other morph(s), including a relatively longer rostrum (~0.9–1× pocl, 0.7–0.8× in the typical morph), longer second pereiopod carpus, merus, and ischium (article ratios 1.1–1.5: 1: 1.8–2: 1.35–1.65: 1.4–1.6, 0.75–1: 1: 1.15–1.7: 0.9–1.45: 0.8–1.4 in the other two morphs, inclusive of females) (Fig. 13F), slenderer ambulatory pereiopods (third pereiopod propodus 12.5–16× as long as wide, carpus 5.2–7.5× as long as wide, merus 12.5–13× as long as wide; 10–12×, 4.5–5.5×, and 8–11.5×, respectively, in the other two morphs). The larger specimen collected, with abnormally asymmetric second pereiopods, is indeed intermediate between *M. superbum* and *M. nipponense*. While its shorter cheliped conforms to that of *M. superbum*, its longer cheliped is more similar to that of *M. nipponense*, with fingers shorter than the palm (~0.9× as long) and barely visible teeth at cutting edges appeared as low humps. Although the longer cheliped has a relatively longer carpus of ~1.7× palm length, this is common in *M. nipponense* females collected, and possibly in undeveloped

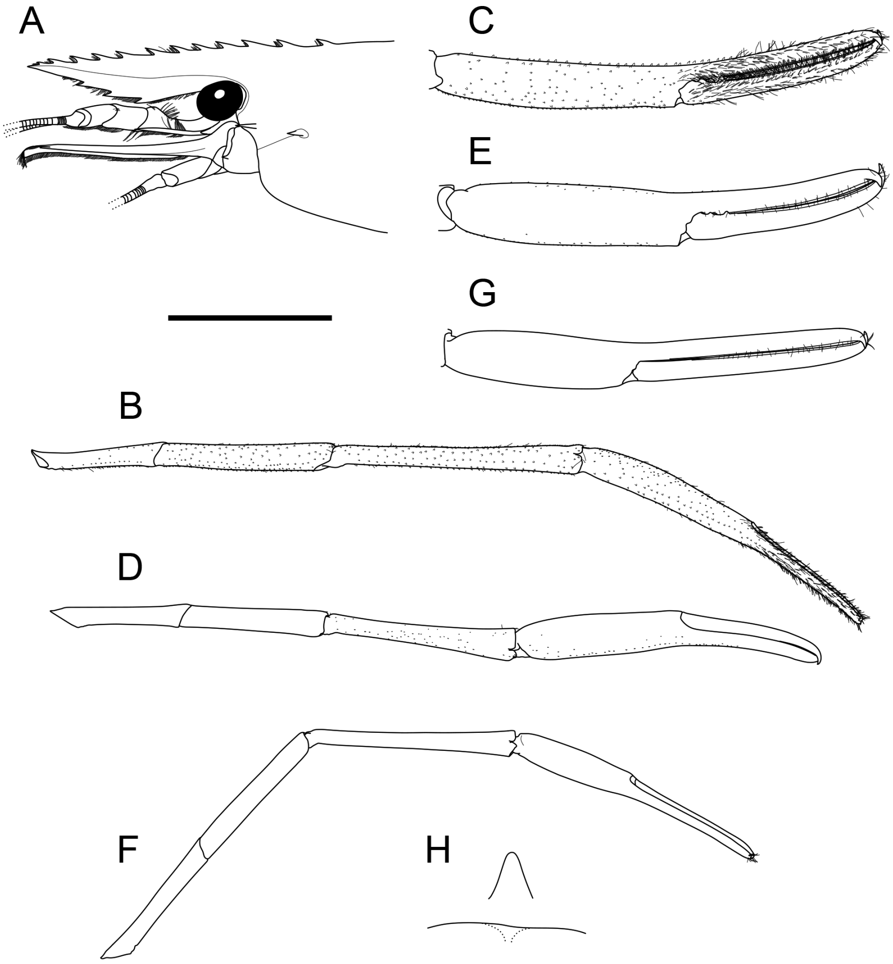

Figure 13. *Macrobrachium nipponense*, male, pocl 18.6 mm (CUHK-LMT-CAR235-1) (**A**–**C**, **H**); male, pocl 16.6 mm (CUHK-LMT-CAR235-7) (**D**–**E**); male, pocl 9.6 mm (CUHK-LMT-CAR350-2) (**F**–**G**). Frontal region, lateral view (**A**); left second pereiopod (**B**); same, chela, mesial view (**C**); left second pereiopod (**D**); same, chela, mesial view (**E**); left second pereiopod (**F**); same, chela, mesial view (**G**); process of fourth thoracic sternite (**H**). Scale bars = 14 mm (B), 10 mm (A, C, D), 7 mm (E), 5.5 mm (F), 3.5 mm (G) or 1 mm (H).

males as well. *Macrobrachium superbum* is typically small, not known to exceed 13.5 mm in pocl (Yu, 1931), and probably also represents an undeveloped form as suggested for *M. inflatum* (Short, 2004). Similar to *M. inflatum*, some specimens identified as *M. superbum* in previous studies also nested within *M. nipponense* in the phylogeny (Fig. 6A). As *M. superbum* often co-occurs with *M. nipponense* (Liu *et al.*, 1990; Cai & Dai, 1999; Hanamura *et al.*, 2011), it is suspected to be juveniles or subadults, and thus synonym of *M. nipponense*.

Macrobrachium venustum (Parisi, 1919)

(Figs. 14D–F, 15)

Palaemon (Eupalaemon) venustus Parisi, 1919: 82, pl. 4 fig. 1, pl. 6 figs. 5–13 [type locality: Hainan, China].

Macrobrachium venustum – Liu *et al.*, 1990: 12, fig. 17.

Material examined: 2 males (pocl 7.0 and 9.4 mm), 2 ov. females (pocl 8.7 and 9.1 mm), Lau Shui Heung, Hong Kong, leg. L.H. Chow, 14.VII.2021, CUHK-LMT-CAR304; 2 males (pocl 10.3 and 14.3 mm), ov. female (pocl 8.7 mm), Tai Lam, Hong Kong, leg. J.C.F. Chan, 18.IX.2021, CUHK-LMT-CAR347; 2 males (pocl 14.3 and 16.8 mm), 2 females (pocl 11.0 and 11.4 mm), Lau Shui Heung, Hong Kong, leg. J.C.F. Chan, 23.IX.2021, CUHK-LMT-CAR348; 2 males (pocl 13.1 and 15.1 mm), Sheung Wo Hang Tsuen, Hong Kong, leg. J.C.F. Chan, 13.XI.2021, CUHK-LMT-CAR369.

Diagnosis: Rostrum slightly arched or directed downwards, reaching beyond end of antennular peduncle, 0.6–0.8× pocl; rostral formula 2–4 + 5–7/2–3. Carapace slightly rough, sparsely covered with microspinules in large individuals. Fourth thoracic sternite armed with small, triangular process. First pereiopod fingers 0.8–0.9× as long as palm; carpus 1.65–2.1× as long as

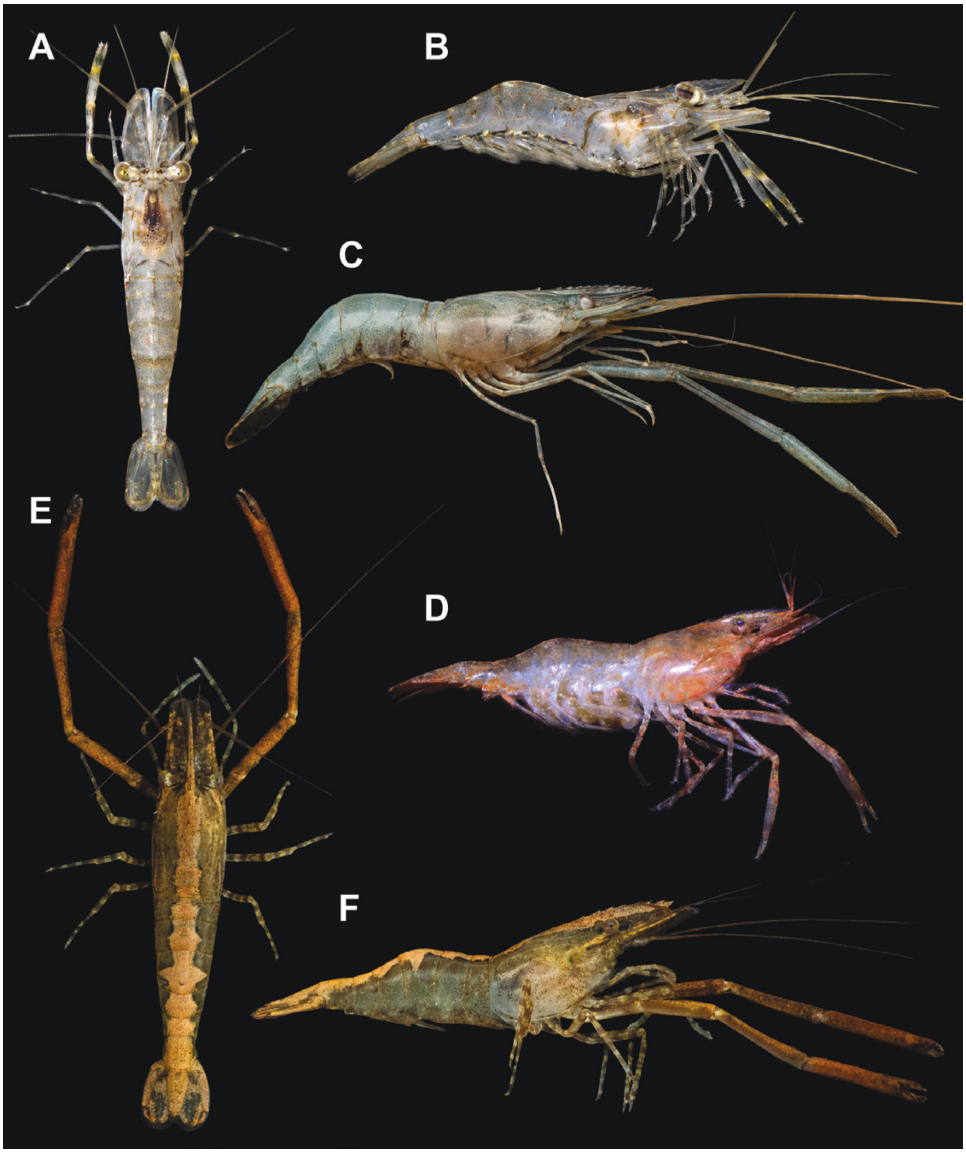

Figure 14. *Macrobrachium nipponense* (**A**–**C**). Female, pocl 8.3 mm (CUHK-LMT-CAR276-2), dorsal view (**A**); same, habitus (**B**); male, pocl 15.5 mm (CUHK-LMT-CAR349-1), habitus (**C**). *Macrobrachium venustum* (**D**–**F**). Ov. female, pocl 8.7 mm (CUHK-LMT-CAR347-1), habitus (**D**); male, pocl 16.8 mm (CUHK-LMT-CAR348-1), dorsal view (**E**); same, habitus (**F**). Photographs by Lai Him Chow (A, B, D) and Zi Yi Kho (C, E, F).

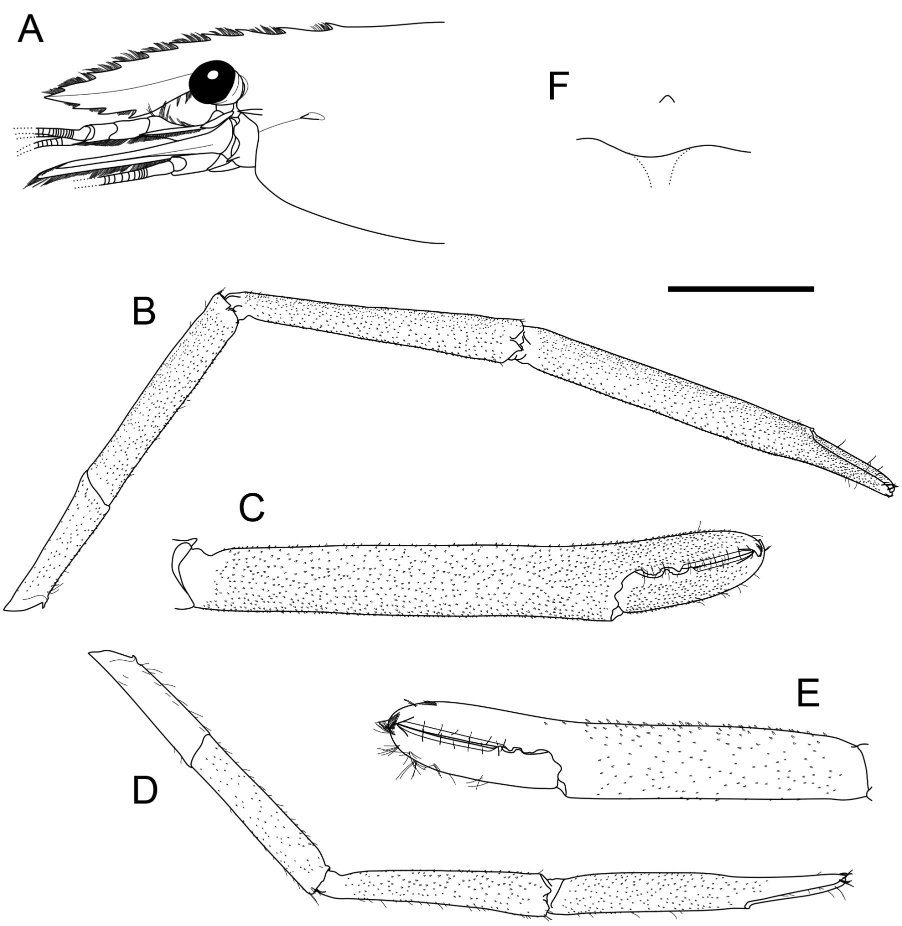

Figure 15. *Macrobrachium venustum*, male, pocl 14.3 mm (CUHK-LMT-CAR348-2) (**A**–**C**, **F**); male, pocl 9.4 mm (CUHK-LMT-CAR304-1) (**D**, **E**). Frontal region, lateral view (**A**); left second pereiopod (**B**); same, chela, mesial view (**C**); right second pereiopod (**D**); same, chela, mesial view (**E**); process of fourth thoracic sternite (**F**). Scale bars = 7 mm (A, B), 5 mm (C), 4 mm (D), 2.5 mm (E) or 0.7 mm (F).

chela; merus 0.75–0.85× as long as carpus; ischium 0.65–0.8× as long as merus. Second pereiopods subequal, similar, covered with microspinules except in very small individuals. Male second pereiopod fingers 0.4–0.8× as long as palm, dactylus with 2 teeth along proximal one-fourth to one-half, pollex with 2 teeth along proximal one-fifth to two-fifth, basal tooth bifid or trifid, manifested as small hump in smaller individuals; palm 4–5.5× as long as central wide, 0.6–1× as long as carpus, 0.8–1.25× as long as merus, 0.95–1.7× as long as ischium. Third pereiopod propodus 7.5–10× as long as wide, 2.5–3.5× as long as dactylus, 1.45–1.7× as long as carpus, 0.9–1× as long as merus, 1.6–1.9× as long as ischium; carpus 4–5.5× as long as wide; merus 6–8× as long as wide. Eggs large, 1.96–2.26 mm × 1.40–1.56 mm in diameter, few.

Ecology: Inhabits both upland and lowland streams. Frequently found in relatively slow-flowing tannic water with macrophytes.

Distribution: Southern China (Guangdong, Hainan provinces) and Vietnam (Quang Binh Province) (Li *et al.*, 2007; Wowor *et al.*, 2009). Not previously recorded in Hong Kong and representing the second record in Guangdong Province, China. Occurs in the western, northern and northeastern New Territories in Hong Kong, and not considered rare but much less abundant than the also land-locked *M. laevis* (Fig. 3I).

Remarks: The present specimens largely match the original description by Parisi (1919). They differ from the type series as follows: 1) rostrum arched or inclined downwards (almost straight in the type series) (Fig. 15A); 2) proportionally longer first pereiopod fingers (0.8–0.9× as long as palm *versus* 0.65×); 3) slightly longer second pereiopod merus (0.8–0.85× as long as palm *versus* 0.75–0.8×) and ischium (0.55–0.6× as long as palm *versus* ~0.4×) in large males (Fig. 15B); 4) shorter second pereiopods of comparably sized large males (at most subequal to tl *versus* 1.45× longer). Parisi (1919) mentioned a peculiar male of similar size having second pereiopods only 0.8× tl, and suspected the limbs to be regenerating since the fingers were proportionally longer than the others. The large males herein examined show typical article ratios but still possess much shorter second pereiopods than the type specimens. Molecular analysis shows that specimens from Hong Kong and Vietnam have an ~4% 16S rRNA divergence (Fig. 6A), which exceeds the typical species delimitation threshold for land-locked shrimps, suggesting that *M. venustum* may represent a species complex yet to be resolved.

The examination of small specimens reveals strong allometric variation in this species. Concerning ratios among the articles of the second pereiopod, relatively large males (pocl 13.1–16.8 mm) typically have ratios of 0.4–0.45: 1: 1–1.05: 0.8–0.85: 0.55–0.6 (Fig. 15B), whereas smaller males (pocl 9.4–10.3 mm) have proportionally shorter and stouter palm (~4× as long as central wide, 5–6× in larger males) with ratios of 0.6: 1: 1–1.2: 0.85–1: 0.7–0.8 (Fig. 15D). In the smallest male collected (pocl 7 mm), the palm is much shorter with ratios of 0.8: 1: 1.6: 1.3: 1.05 and the entire limb is devoid of microspinules. Moreover, the second pereiopod palm in large males is more strongly dilated at the distal end (Fig. 15C, E). Their fingers are also stouter (4.5× as long as wide, 5–7× in smaller males), with teeth placed more distally (along one one-half and two-fifth, respectively on dactylus and pollex *versus* one-fourth to two fourth and one-fifth to two-seventh, respectively). Ratios among articles of the second pereiopod of all females (pocl 8.7–11.4 mm) are within the variations observed in small males.

DISCUSSION

The present study confirms the presence of eight *Macrobrachium* species in Hong Kong, including the four previously recorded species, *M. formosense*, *M. laevis* (long misidentified as *M. hainanense*), *M. nipponense*, and *M. meridionale*; three new records, *M. equidens*, *M. lar*, and *M. venustum*; and one new to science, *M. lantau* **sp. nov.** Hong Kong now contains nearly half of the *Macrobrachium* species diversity in the region, close to doubling of that previously known. This figure might be an underestimate as some species in the region not found in Hong Kong are possibly junior synonyms of other species, including *M. hainanense*, *M. heterorhynchos*, *M. inflatum*, and *M. superbum*. The distribution of the two land-locked *Macrobrachium* species in Hong Kong (i.e., *M. laevis* and *M. venustum*) suggests that the local freshwater caridean shrimp diversity was possibly derived from paleo-drainage connection in the northern South China Sea shelf (i.e., Pearl River Mouth, Qiongdongnan, Beibu, and Yinggehai basins) during past sea-level regression events. This is supported by the similar distribution pattern in all six land-locked species of *Caridina* H. Milne Edwards, 1837 [H. Milne Edwards, 1834–1840] (family Atyidae) non-endemic to Hong Kong (De Grave *et al*., unpubl. data).

The taxonomy of *Macrobrachium* has long been challenging due to the extensive intra-specific variations mostly as a result of allometric growth and sexual dimorphism (Holthuis, 1950). While description of new *Macrobrachium* species conventionally relies on sexually mature 'adult' males, there is arbitrariness to what shall be considered 'adult.' Short (2004) defined males of *Macrobrachium* into four developmental stages: 1) undeveloped, sexually immature; 2) undeveloped, sexually mature; 3) developing, sexually mature; and 4) fully developed, sexually mature. With a limited collection, however, one would never be certain whether specimen of a putatively new species has reached its full development, especially when some currently known species are relatively small in size. Such 'new' species may therefore represent an allometric variant of existing species, differing in characters well-known to be age-dependent such as presence/absence, distribution or density of various ornamentation on the carapace and second pereiopods (e.g., microspinules, pubescence, papillae), length-width ratio of articles of appendages, and relatively length of rostrum and second pereiopods (see Holthuis, 1950). To add to the confusion, potentially hierarchical morphotypes that are not strictly age-related may exist, as confirmed herein in *M. nipponense* and some other *Macrobrachium* species (Kuris *et al*., 1987; Moraes-Riodades & Valenti, 2004; Wortham & Van Maurik, 2012).

The extensive morphological variability in *Macrobrachium* exerts a huge gap for the morphological delimitation species, where the extent of intraspecific variation in some species may exceed that between closely related species. An integrative approach incorporating DNA barcoding is undoubtedly necessary to validate the status of morphologically distinct entities (Page & Hughes, 2011). It would not be surprising that, within the current *Macrobrachium* diversity, a number of synonyms will eventually be revealed using such approach (e.g., Pileggi & Mantelatto, 2012; García-Velazco *et al*., 2017), despite the possible presence of even more cryptic species (e.g., Castelin *et al*., 2017; Siriwut *et al*., 2020). Since many of the freshwater obligates are highly allopatric and restricted in distribution, local research efforts from both taxonomy and molecular biology fields are critical in jointly establishing a genetic database for *Macrobrachium*. Misidentification among closely related species is not uncommon in taxonomic studies, nevertheless, researchers should take personal responsibility in verifying the new DNA sequences, re-examining the vouchered specimens, and making a corrigendum when necessary and feasible. As we were gathering published sequences deposited in GenBank for phylogenetic analysis, several aberrant sequences were noticed. One of the instances concern *M. dongaoensis*, not known elsewhere from Dong'ao Island, Zhuhai, Guangdong Province, China. The only COI sequence available (accession no. MK412789), which was probably derived from the type material, shows clear affinity to *Caridina* species, matching exactly sequences of *C. zhongshanica* Liang, 2004 in particular (accession nos. MN701597–MN701598). Since the sequences of both species were processed by the same group of researchers, it is tempting to conclude that cross-contamination had occurred. Despite the fact that this error is easily recognisable, the erroneous sequence of *M. dongaoensis* is still being used in subsequent studies, as one of the genetic references justifying the erection of a new species, where a sister position with outgroup *Palaemon* species was inappropriately imposed in the phylogeny (see Zheng *et al*., 2019; Chen *et al*., 2021). These incautious instances potentially impede the progression of alpha taxonomy in groups where consistent differences in multiple characters (e.g., morphological and molecular) are routinely required for validation, such as *Macrobrachium*. It is when the alpha taxonomy of *Macrobrachium* is robustly delimited that the systematics and biogeographic pattern of this widespread and diverse genus (which is known to be non-monophyletic; see Chow *et al*., 2021; Mantelatto *et al*., 2021) could be truly resolved.

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