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ORIGINAL PAPER

To the light side: molecular diversity and morphology of stomatopod larvae and juveniles (Crustacea: Malacostraca: Stomatopoda) from crustose coralline algal reefs in Taiwan

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Abstract

Biology of planktonic stomatopod larvae has long remained poorly understood and often considered "black boxes" in life history studies. From coralline crustose algal (CCA) reefs at Datan, Taoyuan, Taiwan, using light traps recently designed, we collected considerable number of stomatopod larvae and juveniles. Applying DNA barcoding techniques using mitochondrial cytochrome oxidase I (COI) and 16S ribosomal RNA (16S rRNA) gene sequences, 14 morphotypes were revealed to represent 12 distinct species, seven of which identified to species level by comparing against reference sequences available from online source (GenBank), whereas the other five do not cluster with any known sequences. All stomatopod larvae and juveniles were described and illustrated. We report *Manningia pilaensis* (De Man, 1888) and *Levisquilla jurichi* (Makarov, 1979) as new records of the stomatopod fauna of Taiwan and confirm the validity of *Lysiosquillina maculata* (Fabricius, 1793). Based on material we acquired from light traps, which include propelagic antizoea larvae (of *L. maculata*), and also postlarval and juvenile forms (of various squillid species), both positively phototactic, indicating the current understanding of negative-positive-negative phototactic tendency from early planktonic to postlarval stages through the development of stomatopod larvae, might not be as distinct as previously described.

Keywords Mantis shrimp larvae · Datan algal reef · Light trap · DNA barcoding · COI · 16S rRNA · New record

Introduction

Stomatopod larvae and juveniles are morphologically very distinct among zooplankton. Compared to larvae of other crustacean groups, little is known about biology of those of stomatopods, and the subject remains poorly understood in life history studies. Stomatopods experience a bipartite lifecycle through development, passing through multiple planktonic larval stages before maturing into juveniles and adults, eventually settling on benthic habitats. Upon hatching from egg masses brooded by the female parent, juveniles undergo a brief propelagic phase, taking shelter in mother's burrow, and then ascending into the water column to join with the zooplankton. The number of pelagic stages varies from one to nine depending on species (Ahyong et al. 2014; also see Greenwood and Williams 1984; Hamano and Matsuura 1987), after which individuals settle as postlarvae (form resembling adults). The morphology of planktonic larvae differs between superfamilies, with lysiosquillids (Lysiosquilloidea) first hatching into antizoea larvae, wanting of raptorial appendages, instead relying on yolk for nutrition. The gonodactyloids (Gonodactyloidea), parasquilloids (Parasquilloidea), and eurysquilloids (Eurysquilloidea) develop into erichthus larvae, with broad carapaces and abdomen (now pleon) (Provenzano and Manning 1978), whereas alima larvae are unique to squilloids (Squilloidea), having telson bearing more than four intermediate (IM) denticles (Morgan and Provenzano 1979; see synthesis by Ahyong et al. 2014). Some species have rather extreme or peculiar-looking larval forms (Haug et al. 2018). Larval behavior varies among stages: propelagic larvae are negatively phototactic, switching

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to positive phototaxis in the following planktonic stages, and again display positive thigmokinesis (preference towards the substrate) and negative phototaxis during later larval stages (Dingle 1969; Morgan and Goy 1987). Some stomatopod larvae possibly perform defensive behavior (Haug and Haug 2014). Anyhow, very little has been published on species diversity or taxonomy of stomatopod larvae in the western Pacific, particularly in East Asia.

Given nearly identical forms among closely related groups, and diagnostic features of adults not yet developed in earlier stages (not until later juvenile stages; see below), morphological identification of stomatopod larvae to species level has been notoriously difficult. Previous documentation of stomatopod larvae morphologies was performed by two major approaches, namely (1) sampling of planktonic forms, raising until reaching postlarval or juvenile stages, fostering reasonable identifications (listed by Provenzano and Manning 1978; see also e.g. Gurney 1946; Alikunhi 1952, 1967); or (2) recording stage-by-stage development of hatched individuals released from a positively identified ovigerous female (Provenzano and Manning 1978; Hamano and Matsuura 1987). Among the 70 stomatopod species (see below) so far recorded from Taiwan, only 23 had larval forms previously described in the literature (Table 1).

In recent years, DNA barcoding using mitochondrial cytochrome c oxidase subunit I (COI) (Hebert et al. 2003; also see Matzen da Silva et al. 2011) and 16S ribosomal RNA (16S rRNA) (Schubart et al. 1998, 2000), has been considered a faster and perhaps more accurate approach in assigning species in many animal groups, in comparison to traditional morphology-based identification techniques (e.g., Ward et al. 2005; Raupach and Radulovici 2015). This approach enables the assignment of unknown material (especially larvae or juveniles) by matching the sequences of identified adult voucher specimens (e.g., Webb et al. 2006; Bracken-Grissom et al. 2012; Chu et al. 2019; Li et al. 2019), and application of which in investigations on stomatopod fauna had been performed by Barber and Boyce (2006) from Red Sea, Tang et al. (2010) from shallow seas of Hong Kong, and Feller et al. (2013) and Palecanda et al. (2020) in Lizard Island, Australia. These studies revealed multiple unidentified larval forms from these regions, highlighting the still immense challenge that researchers face in recognizing and documenting biodiversity through alpha-taxonomy. Most of these molecular diversity approaches, however, do not contain morphological descriptions of identified larvae (except Feller et al. 2013).

Like various crustacean groups, stomatopods are common inhabitants of shallow reefs, dwelling within which, taking shelter, using the habitat as settlement sites and feeding and nursery grounds (Castro 1988; Steller et al. 2003; Glynn and Enochs 2011). Apart from extensive coral reefs common along tropical shores which structure formed by calcareous scleractinian corals, reefs of crustose coralline algal (CCA) are accumulations of non-geniculate coralline algae, which is a common phototrophic component of rocky shore and reef habitats. Performing similar ecological functions as coral reefs, CCA reefs are generally reported from temperate shores as extensive concretions, or reefs at shallow depths, limited by the availability of solar irradiance (see Ballesteros 2006). Along tropical and subtropical shores, on the other hand, CCA reefs are much more limited in distribution and are found only in sites of murky waters with lower light availability, while the structure is capable of resisting stronger wave actions (Bosence 1983; Adey 1998; Ballesteros 2006), growth of which reported to be very slow (Adey and Vassar 1975; also see Dethier and Steneck 2001). Between the tropics, these reefs are found at the Marshall Islands (Emery et al. 1954), Caribbean waters (Adey and Vassar 1975), and the Mediterranean (Ballesteros 2006). In this complex habitat, anyhow, in the course of assessing species diversity, detailed surveying of adult individuals of inhabiting organisms, often sampling done by scuba divers, can be excessively labor-intensive, and research efforts therefore are not as cost-effective (but see Bouchet et al. 2009), and our understanding on species diversity hence a gross underestimation (Plaistance et al. 2011). Alternatively as an innovative approach, by sampling zooplankton, planktonic young of these reef inhabitants, from the water column, likewise reflects species diversity. In the present study, a considerable number of stomatopods were collected by deploying light traps at a crustose coralline algal (CCA) reef in Taiwan. Adopting a synthetic approach, combining morphological examination (traditional taxonomy) and molecular barcoding techniques (COI and 16S rRNA sequences), we present species diversity of stomatopod larvae found in CCA reefs in northwestern Taiwan, attempting to contribute baseline information on stomatopod larval biology for the western Pacific region.

Materials and methods

Sites investigated

The only extensive CCA reef reported in the West Pacific situates in Taoyuan County, along the northwestern coast of the main island of Taiwan (Fig. 1). The CCA reefs in Datan, Taoyuan, are most extensive: measuring at least 27 km in length and a maximum width of 450 m, experiencing tidal inundation 4-m high (Dai et al. 2009; Liou et al. 2017; Fig. 1). The basal substratum of the Datan CCA reef is composed of sedimentary conglomerate with biogenic strata deposited during the Holocene (as recently as some 11,650 years ago), upon which the upper layers composed of scleractinian coral skeletons, overlain by masses of crustose coralline algae that are around 4500 years old (Wang et al. 2008; Dai et al. 2009). Dai et al. (2009) and Liou (2012) reported species diversity in

Table 1 Stomatopod species recorded from Taiwan with larval stages reported in the literature and GenBank accession numbers of matched reference sequences. Abbreviations: AL, alima larva; AZ, antizoea larva; EL, erichthus larva; J, juvenile; PL, postlarva; PZ, pseudolarva.

Superfamily	Family	Species	Sources	Matched reference sequences (GenBank acc. No.)	
				COI	16S rRNA
Gonodactyloidea	Gonodactylidae	*Gonodactylus chiragra* (Fabricius, 1781)	Shanbhogue (1975) (EL)		
		Gonodactylus smithii Pocock, 1893	This study (PL: Fig. 4)	See Remarks under *G. smithii.*	AF107615
	Pseudosquillidae	*Pseudosquilla ciliata* (Fabricius, 1787)	Townsley (1953) (EL, PL), Michel (1968) (EL), Shanbhogue (1975) (EL)		
Lysiosquilloidea	Lysiosquillidae	*Lysiosquilla sulcirostris* Kemp, 1913	Alikunhi (1952) (EL), Alikunhi (1967) (PL), Michel (1968) (EL)		
		Lysiosquillina maculata (Fabricius, 1793)	? Foxon (1939) (EL), Alikunhi and Aiyar (1943) (AL, PL), Alikunhi (1952) (EL), Townsley (1953) (PL), Alikunhi (1967) (PL), this study (AZ: Fig. 7)	KM982431 KM982432 KM982436	EU920935 HM138834 AF107618
	Nannosquillidae	*Acanthosquilla multifasciata* (Wood-Mason, 1895)	? Komai and Tung (1929) (PL),? Foxon (1939) (EL), Alikunhi and Aiyar (1943) (AL, PL), Alikunhi (1952) (EL), Alikunhi (1967) (PL), Shanbhogue (1975) (EL)		
Eurysquilloidea	Eurysquillidae	*Manningia pilaensis* (De Man, 1888)	This study (EL: Fig. 6)		KY236044
Squilloidea	Squillidae	*Alima hieroglyphica* (Kemp, 1911)	Alikunhi (1944) (AL), Alikunhi (1952) (AL), Alikunhi (1958) (AL), Alikunhi (1967) (PL), Shanbhogue (1975) (AL)		
		Alima orientalis Manning, 1978	Feller et al. (2013) (AL)		
		Anchisquilla fasciata (De Haan, 1844)	Alikunhi (1952) (AL), Alikunhi (1967) (PL)		
		Busquilla quadraticauda (Fukuda, 1911)	Alikunhi (1952) (AL), Alikunhi (1967) (PL)		
		Carinosquilla multicarinata (White, 1848)	This study (AL, J: Figs. 12, 13)	MH168265	MH168221
		Cloridopsis scorpio (Latreille, 1828)	Alikunhi (1952) (AL), Alikunhi (1967) (PL)		
		Erugosquilla woodmasoni (Kemp, 1911)	Alikunhi and Aiyar (1942) (AL, PL), Alikunhi and Aiyar (1943) (AL, PL), Alikunhi (1952) (AL), Alikunhi (1967) (PL), Michel (1968) (AL), Shanbhogue (1975) (AL)		
		Harpiosquilla harpax (De Haan, 1844)	Alikunhi (1958) (AL), Shanbhogue (1975) (AL)		
		Lenisquilla lata (Brooks, 1886)	Alikunhi (1952) (AL), Alikunhi (1967) (PL)		
		Levisquilla jurichi (Makarov, 1979)	This study (PL: Fig. 14)		MH168204
		Miyakella holoschista (Kemp, 1911)	Alikunhi and Aiyar (1942) (AL, PL), Alikunhi and Aiyar (1943) (AL, PL), Alikunhi (1952) (AL), Alikunhi (1958) (AL), Alikunhi (1967) (PL), Michel (1968) (AL)		
		Miyakella nepa (Latreille, 1828)	Alikunhi and Aiyar (1942) (AL, PL), Alikunhi and Aiyar (1943) (AL, PL), Alikunhi (1950) (AL), Alikunhi (1952) (AL), Alikunhi (1958) (AL), Alikunhi (1967) (PL), Shanbhogue (1975) (AL)		
		Oratosquilla oratoria (De Haan, 1844)	Komai and Tung (1929) (AL), Komai (1932) (AL), Hamano and Matsuura (1987) (PZ, AL, PL, J); this study (J: Fig. 17)	MH168274	MH168214
		Oratosquillina inornata (Tate, 1883)	Alikunhi (1958) (AL), this study (AL, J: Figs. 15, 16)	MH168266	MH168220
		Oratosquillina interrupta (Kemp, 1911)	Alikunhi (1952) (AL), Alikunhi (1958) (AL), Alikunhi (1967) (PL)		
		Quollastria gonypetes (Kemp, 1911)	Alikunhi (1952) (AL), Alikunhi (1967) (PL), Shanbhogue (1975) (AL)		

the Datan CCA reefs being immensely rich. Species composition of non-geniculate coralline algae was recently reported by Liu et al. (2018), who described one new genus and three new species, whereas Kuo et al. (2019) reported the discovery of an endangered scleractinian coral *Polycyanthus chiashanensis* Lin, Kitahara, Tachikawa, Keshavmurthy & Chen, 2012, which previously only known from Kaohsiung, southern Taiwan, its type locality. Crustacean fauna, however, as reported by Lin et al. (2013), is represented by 25 species, most of which (21) being decapods, mostly common to intertidal rocky reef habitats. Only one stomatopod, *Gonodactylus chiragra* (Fabricius, 1781), was recorded.

Specimen collection and morphological examination

Zooplankton was collected along the shores of the Datan CCA reef (25° 02′ 18.8″ N, 121° 02′ 55.4″ E; see Fig. 1a, b) from May to October, 2018 (May 16, June 26, July 13, October 26), using light traps placed along the lower intertidal zone, design of the device following Chan et al. (2016) (Fig. 1c–f). The traps were deployed at the subtidal level during low tides in the evening, left overnight, and collected in the morning to noon the next day. The collected zooplankton was sieved using a 300-μm mesh net and preserved in 95% ethanol.

Sampled zooplankton was sorted and examined under stereomicroscopes (Olympus SZX7), and stomatopod larvae and juveniles were sorted based on morphology. The stomatopod material, consisting of antizoea (of lysiosquillids), erichthus and alima larvae, postlarvae and juveniles, was further identified as different morphotypes. Although postlarvae and juveniles share a body form similar to that of adults, postlarvae still retain their larval-type retina, although the structure is not as obvious in juveniles of squilloids (Ahyong et al. 2014). Representatives of each morphotype were examined and photographed, and key features (carapace, mouthparts, and telson) were illustrated with line drawings. The only antizoea morphotype collected was small in size, which was dehydrated using graded ethanol series, critical point-dried, coated with gold, and then observed and photographed under a scanning electron microscope (SEM; FEI Quanta 200, USA). Taxonomic schemes, measurements, and morphological terminology followed those presented by Ahyong (2001) and Ahyong et al. (2008). The abbreviations CL, TL, TS, AS, MD, SM, IM, and LT stand respectively for carapace length, total length, thoracic somites, abdominal somites, median, submedian, intermediate, and lateral. In planktonic larvae (antizoea, erichthus, and alima), given rostral and posterolateral spines often much elongated and easily broken off, CL is measured from the base of rostral spine, along midline to posterior margin, in addition of short postero-median spine, whereas TL is measured from the base of rostral spine, along midline to level of SM teeth of telson. Those of postlarva and juvenile individuals follow Manning (1998): CL from the base of rostral plate, along the midline to the posterior margin of carapace; TL from the anterior tip of rostral plate to the level of SM teeth of telson. The examined material was deposited into the collections of the Coastal Ecology Laboratory (CEL), Biodiversity Research Center, Academia Sinica, Taipei.

Molecular analysis

Total genomic DNA was extracted, either from entire antizoea individuals (given the small body size), or partially from larval and postlarval individuals of stomatopods ($n = 38$; from tissue of abdominal somites) using the DNeasy® Blood and Tissue Kit (Qiagen, California, USA) according to instructions provided by the manufacturer. Partial sequences of two mitochondrial DNA markers (COI and 16S rRNA) were amplified following the protocol from previous studies (Crandall and Fitzpatrick 1996; Folmer et al. 1994; Feller et al. 2013; Shih et al. 2019). Polymerase chain reactions (PCR) were conducted in DNA Engine Thermal Cycler (Bio-Rad, Richmond, California, USA), and the products were checked by electrophoresis on 1.5% agarose gel in 1 × TAE buffer. DNA purification and Sanger DNA sequencing were performed by Genomics BioSci & Tech Ltd. (New Taipei City, Taiwan). The sequences were assembled and edited in Geneious Prime 2020.1.1 (https://www.geneious.com).

The sequences were aligned with MUSCLE in Geneious Prime 2020.1.1 (https://www.geneious.com). Neighbor-joining (NJ) analysis with the Kimura 2-parameter (K2P) distance model and bootstrap values estimated from 1000 pseudoreplicates was conducted for COI and 16S rRNA, respectively, in MEGA X using referencing sequences downloaded from GenBank (Kumar et al. 2018; Table 2). K2P genetic distances were also calculated in MEGA X. Reference sequences downloaded from GenBank were involved in the previous molecular studies of stomatopods established in the past two decades (see Table 2).

Results

Species assignment by DNA barcoding

The neighbor-joining (NJ) phylogeny is shown in Fig. 2 (a, COI; b, 16S rRNA). Among the 38 larval and juvenile specimens examined, 25 clustered with available reference sequences with high bootstrap support (> 90%). These include *Carinosquilla multicarinata* (COI: MH168265; 16S rRNA: MH168221.1), *Gonodactylus smithii* (COI: DQ440603, MK397448, MT188302, AF205233, DQ440602, HM138788, MT188299 to MT188304; 16S rRNA: AF107615; but see below), *Lysiosquillina maculata* (COI: KM982431, KM982432, KM982436; 16S rRNA: AF107618, EU920935, HM138834), *Oratosquilla oratoria*

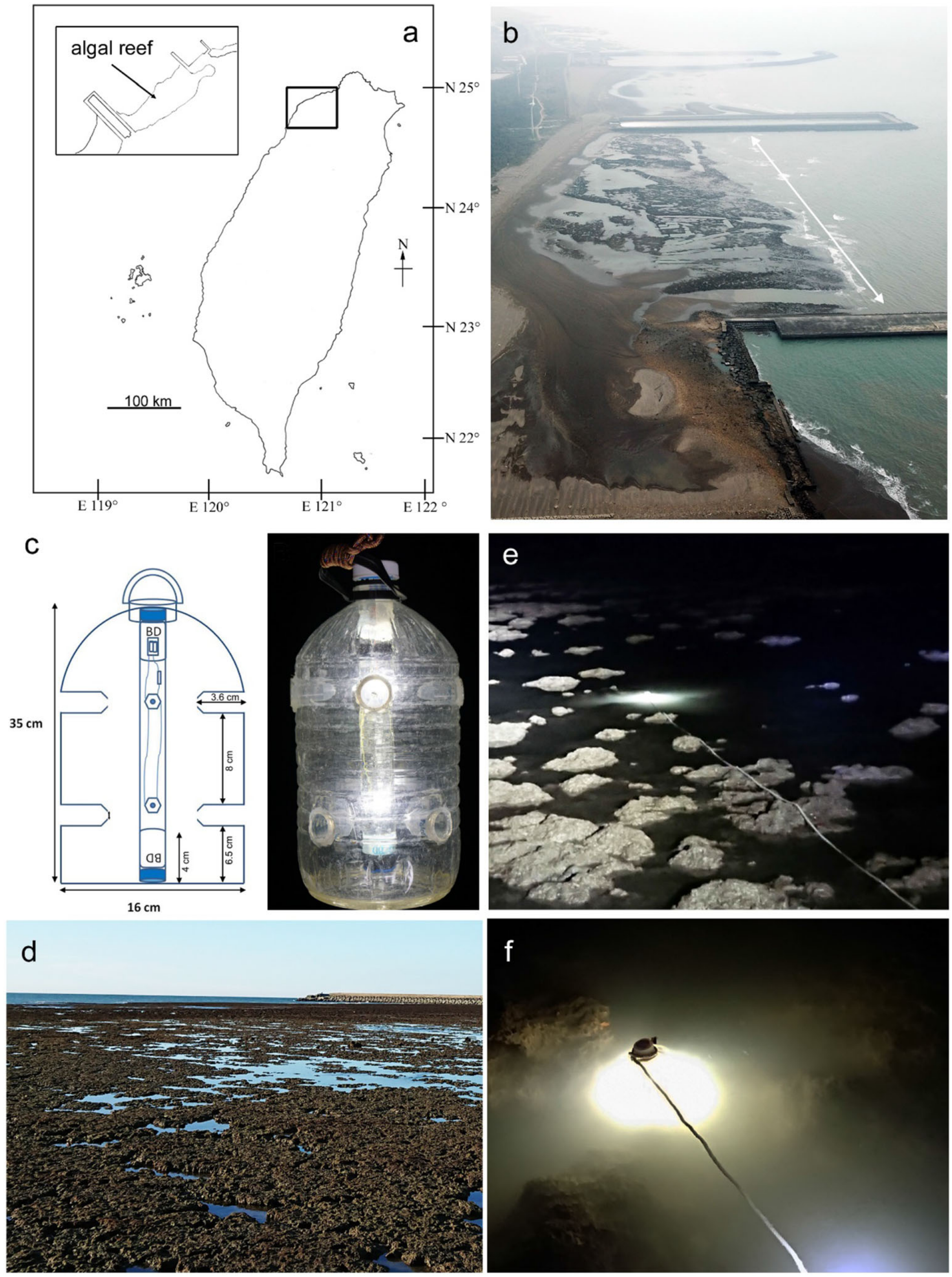

Fig. 1 **a** Map of collection site at Datan, Taoyuan; **b** aerial view of the CCA reef (indicated by the white double arrows) (photograph taken by Chu yu-wei, Juvenile Art Center); **c** light trap designed in Chan et al. (2016) for collecting stomatopod larvae; **d** the CCA reef exposed during low tides; **e**, **f** light traps deployed subtidal region in CCA reef at night

(COI: MH168274; 16S rRNA: MH168214), and *Oratosquillina inornata* (COI: MH168266; 16S rRNA: MH168220.1) (Fig. 2, Table 2). Five specimens (CEL-stom-046, 047, 053, 055, and 059) were clustered with 16S rRNA reference sequence of *Manningia pilaensis* (KY236044), likewise one specimen (CEL-stom-062) clustered with 16S rRNA reference sequence of *Levisquilla jurichi* (MH168204), in both cases, but no affiliated COI reference sequence was available (Fig. 2). Seven representative specimens comprised of five distinct species (one in Gonodactylidae, three in Nannosquillidae, and one in Squillidae), but did not cluster with any reference sequences, and were thus considered unknown species. These taxa were nevertheless identifiable to the family level using morphological evidence (see discussion below).

The frequency distributions of K2P genetic distances of COI and 16S rRNA sequences are shown in Fig. 3. For COI sequences, K2P genetic distances within species were below 2%, except for the specimens assigned as *G. smithii*, which showed distances above 4.5% (4.95 to 16.13%) to the reference sequences (Table S1; see below). Distances between species ranged from 6.97 to 30.74% (Table S1). As for 16S

Table 2 The specimens and DNA barcode reference data used in this study. # Species name of genbank sequences updated (S. T. Ahyong, pers. comm.). * Voucher specimen purchased from Donggang Fish Market, Pingtung

					Accession number		References	
Specimen number	Taxonomy (order; superfamily; family)	Species name	Morphotype shown in	Collection date	COI	16S rRNA	COI	16S rRNA
Query larval specimens								
CEL-stom-001	Stomatopoda; Squilloidea; Squillidae	*Carinosquilla multicarinata*	Fig. 13	2018.5.16	MT745839	MT753063	This study	This study
CEL-stom-007	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina maculata*	Fig. 7	2018.6.26	MT745840	MT753064	This study	This study
CEL-stom-010	Stomatopoda; Squilloidea; Squillidae	*Carinosquilla multicarinata*	Fig. 12	2018.5.16	MT745841	MT753065	This study	This study
CEL-stom-026	Stomatopoda; Gonodactyloidea; Gonodactylidae	Gonodactylidae sp.	Fig. 5	2018.5.16	MT745842	MT753066	This study	This study
CEL-stom-027	Stomatopoda; Gonodactyloidea; Gonodactylidae	Gonodactylidae sp.	Fig. 5	2018.5.16	MT745843	MT753067	This study	This study
CEL-stom-032	Stomatopoda; Squilloidea; Squillidae	*Carinosquilla multicarinata*	Fig. 12	2018.5.16	MT745844	MT753068	This study	This study
CEL-stom-034	Stomatopoda; Squilloidea; Squillidae	*Oratosquillina inornata*	Fig. 15	2018.6.26	–	MT753069	This study	This study
CEL-stom-035	Stomatopoda; Squilloidea; Squillidae	*Oratosquillina inornata*	Fig. 15	2018.5.16	–	MT753070	This study	This study
CEL-stom-041	Stomatopoda; Lysiosquilloidea; Nannosquillidae	Nannosquillidae sp. 3	Fig. 10	2018.5.16	MT745845	MT753071	This study	This study
CEL-stom-045	Stomatopoda; Lysiosquilloidea; Nannosquillidae	Nannosquillidae sp. 1	Fig. 8	2018.5.16	MT745846	MT753072	This study	This study
CEL-stom-046	Stomatopoda; Eurysquilloidea; Eurysquillidae	*Manningia pilaensis*	Fig. 6	2018.5.16	–	MT753073	This study	This study
CEL-stom-047	Stomatopoda; Eurysquilloidea; Eurysquillidae	*Manningia pilaensis*	Fig. 6	2018.5.16	MT745847	MT753074	This study	This study
CEL-stom-048	Stomatopoda; Squilloidea; Squillidae	*Oratosquillina inornata*	Fig. 10	2018.5.16	MT745848	MT753075	This study	This study
CEL-stom-050	Stomatopoda; Squilloidea; Squillidae	*Oratosquillina inornata*	Fig. 15	2018.5.16	MT745849	MT753076	This study	This study
CEL-stom-053	Stomatopoda; Eurysquilloidea; Eurysquillidae	*Manningia pilaensis*	Fig. 6	2018.5.16	MT745850	MT753077	This study	This study
CEL-stom-055	Stomatopoda; Eurysquilloidea; Eurysquillidae	*Manningia pilaensis*	Fig. 6	2018.5.16	MT745851	MT753078	This study	This study
CEL-stom-056	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*	Fig. 4	2018.5.16	MT745852	MT753079	This study	This study
CEL-stom-057	Stomatopoda; Squilloidea; Squillidae	*Oratosquillina inornata*	Fig. 12	2018.5.16	MT745853	MT753080	This study	This study
CEL-stom-058	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*	Fig. 4	2018.5.16	MT745854	MT753081	This study	This study
CEL-stom-059	Stomatopoda; Eurysquilloidea; Eurysquillidae	*Manningia pilaensis*	Fig. 6	2018.5.16	MT745855	MT753082	This study	This study
CEL-stom-061	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*	Fig. 4	2018.5.16	MT745856	MT753083	This study	This study
CEL-stom-062	Stomatopoda; Squilloidea; Squillidae	*Levisquilla jurichi*	Fig. 14	2018.5.16	MT745857	MT753084	This study	This study
CEL-stom-063	Stomatopoda; Lysiosquilloidea; Nannosquillidae	Nannosquillidae sp. 3	Fig. 10	2018.5.16	MT745858	MT753085	This study	This study
CEL-stom-064	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina maculata*	Fig. 7	2018.6.26	MT745859	MT753086	This study	This study
CEL-stom-067	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina maculata*	Fig. 7	2018.6.26	MT745860	MT753087	This study	This study
CEL-stom-069	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina maculata*	Fig. 7	2018.6.26	MT745861	MT753088	This study	This study

Table 2 (continued)

Specimen number	Taxonomy (order; superfamily; family)	Species name	Morphotype shown in	Collection date	Accession number COI	Accession number 16S rRNA	References COI	References 16S rRNA
CEL-stom-073	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina maculata*	Fig. 7	2018.6.26	MT745862	MT753089	This study	This study
CEL-stom-074	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina maculata*	Fig. 7	2018.6.26	MT745863	MT753090	This study	This study
CEL-stom-076	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina maculata*	Fig. 7	2018.6.26	MT745864	MT753091	This study	This study
CEL-stom-077	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina maculata*	Fig. 7	2018.6.26	MT745865	MT753092	This study	This study
CEL-stom-080	Stomatopoda; Squilloidea; Squillidae	*Oratosquilla oratoria*	Fig. 17	2018.7.13	MT745866	MT753093	This study	This study
CEL-stom-082	Stomatopoda; Squilloidea; Squillidae	Squillidae sp.	Fig. 11	2018.7.13	MT745867	MT753094	This study	This study
CEL-stom-083	Stomatopoda; Squilloidea; Squillidae	*Oratosquilla oratoria*	Fig. 17	2018.7.13	MT745868	MT753095	This study	This study
CEL-stom-084	Stomatopoda; Squilloidea; Squillidae	*Oratosquilla oratoria*	Fig. 17	2018.7.13	MT745869	MT753096	This study	This study
CEL-stom-085	Stomatopoda; Squilloidea; Squillidae	*Carinosquilla multicarinata*	Fig. 13	2018.7.13	MT745870	MT753097	This study	This study
CEL-stom-086	Stomatopoda; Lysiosquilloidea; Nannosquillidae	Nannosquillidae sp. 2	Fig. 9	2018.7.13	MT745871	MT753098	This study	This study
CEL-stom-088	Stomatopoda; Squilloidea; Squillidae	*Oratosquilla oratoria*	Fig. 17	2018.7.13	MT745872	MT753099	This study	This study
CEL-stom-091	Stomatopoda; Squilloidea; Squillidae	*Oratosquilla oratoria*	Fig. 17	2018.10.26	MT745873	MT753100	This study	This study
DNA barcode reference data								
from GenBank	Stomatopoda; Bathysquilloidea; Bathysquillidae	*Bathysquilla crassispinosa*			–	KY236045	–	Van Der Wal et al. 2017
from GenBank	Stomatopoda; Eurysquilloidea; Eurysquillidae	*Manningia pilaensis*			–	KY236044	–	Van Der Wal et al. 2017
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylaceus falcatus*			KM982433	HM138827	Feller and Cronin 2016	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylaceus glabrous*			AF205244	–	Barber and Erdmann 2000	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	# *Gonodactylaceus graphurus*	(as *Gonodactylus graphurus*)		–	AF133678	–	Elliott 2002
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylaceus ternatensis*			KT001540	KT001543	Bok et al. 2015	Bok et al. 2015
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylellus affinis*			KM982426	HM138823	Feller and Cronin 2016	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylellus annularis*			AF205226	HM138824	Barber and Erdmann 2000	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	# *Gonodactylellus barberi*	(as *G. hendersoni*)		AF205231	–	Barber and Erdmann 2000	–

Table 2 (continued)

Specimen number	Taxonomy (order; superfamily; family)	Species name	Morphotype shown in	Collection date	Accession number		References	
					COI	16S rRNA	COI	16S rRNA
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylellus caldwelli*			AF205256	–	Barber and Erdmann 2000	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylellus erdmanni*			DQ440593	–	Barber and Boyce 2006	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylellus espinosus*			GQ260976	HM138822	Plaisance et al. 2009	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylellus rubriguttatus*			AF205243	–	Barber and Erdmann 2000	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylellus viridis*			–	KT001545	–	Bok et al. 2015
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylopsis komodoensis*			AF205242	–	Barber and Erdmann 2000	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus childi*			AF205249	HM138825	Barber and Erdmann 2000	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus chiragra*			AF205250	AF107614	Barber and Erdmann 2000	Unpublished
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus platysoma*			AF205237	HM138828	Barber and Erdmann 2000	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*			AF205233	AF107615	Barber and Erdmann 2000	Unpublished
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*			DQ440602	HM138829	Barber and Boyce 2006	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*			DQ440603	–	Barber and Boyce 2006	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*			HM138788	–	Porter et al. 2010	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*			MK397448	–	Unpublished	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*			MT188299	–	Palecanda et al. 2020	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*			MT188300	–	Palecanda et al. 2020	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*			MT188301	–	Palecanda et al. 2020	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*			MT188302	–	Palecanda et al. 2020	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*			MT188303	–	Palecanda et al. 2020	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Gonodactylus smithii*			MT188304	–	Palecanda et al. 2020	–
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Neogonodactylus bahiahondensis*			HM138794	HM138836	Porter et al. 2010	Porter et al. 2010

Table 2 (continued)

					Accession number		References	
Specimen number	Taxonomy (order; superfamily; family)	Species name	Morphotype shown in	Collection date	COI	16S rRNA	COI	16S rRNA
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Neogonodactylus bredini*			KP254652	HM138837	Leray and Knowlton 2015	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Neogonodactylus oerstedii*			KP254195	AF107612	Leray and Knowlton 2015	Unpublished
from GenBank	Stomatopoda; Gonodactyloidea; Gonodactylidae	*Neogonodactylus wennerae*			KT001541	KT001544	Bok et al. 2015	Bok et al. 2015
from GenBank	Stomatopoda; Gonodactyloidea; Hemisquillidae	*Hemisquilla australiensis*			–	FJ871141	–	Ahyong and Jarman 2009
from GenBank	Stomatopoda; Gonodactyloidea; Hemisquillidae	*Hemisquilla californiensis*			HM138791	HM138832	Porter et al. 2010	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Odontodactylidae	*Odontodactylus cultrifer*			KM982427	HM138839	Feller and Cronin 2016	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Odontodactylidae	*Odontodactylus havanensis*			KT001542	HM138840	Bok et al. 2015	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Odontodactylidae	*Odontodactylus japonicus*			FJ229797	FJ224283	Tang et al. 2010	Tang et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Odontodactylidae	*Odontodactylus latirostris*			HM138797	HM138841	Porter et al. 2010	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Odontodactylidae	*Odontodactylus scyllarus*			AF205234	HM138842	Barber and Erdmann 2000	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Protosquillidae	# *Chorisquilla hystrix*	(as *C. spinosissima*)		AF205254	–	Barber and Erdmann 2000	–
from GenBank	Stomatopoda; Gonodactyloidea; Protosquillidae	*Haptosquilla glyptocercus*			AF205239	AF107610	Barber and Erdmann 2000	Unpublished
from GenBank	Stomatopoda; Gonodactyloidea; Protosquillidae	*Haptosquilla hamifera*			KM074037	KM074036	How et al. 2014	How et al. 2014
from GenBank	Stomatopoda; Gonodactyloidea; Protosquillidae	*Haptosquilla pulchella*			AF205238	–	Barber and Erdmann 2000	–
from GenBank	Stomatopoda; Gonodactyloidea; Protosquillidae	*Haptosquilla stoliura*			AF205241	–	Barber and Erdmann 2000	–
from GenBank	Stomatopoda; Gonodactyloidea; Protosquillidae	*Haptosquilla trispinosa*			AF205255	HM138831	Barber and Erdmann 2000	Porter et al. 2010
from GenBank	Stomatopoda; Gonodactyloidea; Protosquillidae	*Hoplosquilla said*			AF205248	–	Barber and Erdmann 2000	–
CEL-stom-093*	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquilla tredecimdentata*		2016.12.2	MT745874	MT753101	This study	This study
from GenBank	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina maculata*			KM982436	AF107618	Feller and Cronin 2016	Unpublished
from GenBank	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina maculata*			KM982432	HM138834	Feller and Cronin 2016	Porter et al. 2010
from GenBank	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina maculata*			KM982431	EU920935	Feller and Cronin 2016	Toon et al. 2009
from GenBank	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina maculata*			–	AF107618	–	Unpublished

Table 2 (continued)

Specimen number	Taxonomy (order; superfamily; family)	Species name	Morphotype shown in	Collection date	Accession number COI	Accession number 16S rRNA	References COI	References 16S rRNA
from GenBank	Stomatopoda; Lysiosquilloidea; Lysiosquillidae	*Lysiosquillina sulcata*			–	HM138835	–	Porter et al. 2010
from GenBank	Stomatopoda; Lysiosquilloidea; Nannosquillidae	*Alachosquilla vicina*			KM982440	AF107608	Unpublished	Unpublished
from GenBank	Stomatopoda; Lysiosquilloidea; Nannosquillidae	*Austrosquilla tsangi*			–	FJ871139	–	Ahyong and Jarman 2009
from GenBank	Stomatopoda; Lysiosquilloidea; Nannosquillidae	*Platysquilla eusebia*			–	MF346763	–	Ďuriš 2018
from GenBank	Stomatopoda; Lysiosquilloidea; Nannosquillidae	*Pullosquilla thomassini*			KJ828806	AF107611	Feller and Cronin 2014	Unpublished
from GenBank	Stomatopoda; Lysiosquilloidea; Tetrasquillidae	*Heterosquilla tricarinata*			AF048823	FJ871140	Unpublished	Ahyong and Jarman 2009
from GenBank	Stomatopoda; Parasquilloidea; Parasquillidae	*Faughnia profunda*			MH168240	KY236046	Van Der Wal et al. 2019	Van Der Wal et al. 2017
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Alima maxima*			–	MH168208	–	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Alima orientalis*			KF214292	MH168229	Feller et al. 2013	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Alima orientalis*			KF205337	HM138813	Feller et al. 2013	Porter et al. 2010
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Alima orientalis*			MT179626	–	Palecanda et al. 2020	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Alima pacifica*			KF205336	HM138814	Feller et al. 2013	Porter et al. 2010
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Alima pacifica*			KM982424	–	Feller and Cronin 2016	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Alima pacifica*			KM982434	–	Feller and Cronin 2016	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Alima pacifica*			HM138774	–	Porter et al. 2010	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Anchisquilla fasciata*			MH168243	MH168211	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Anchisquilloides mcneilli*			MH168242	–	Van Der Wal et al. 2019	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Busquilla plantei*			HM138775	–	Porter et al. 2010	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Busquilla quadraticauda*			–	MH168223	–	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Carinosquilla multicarinata*			MH168265	MH168221	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Clorida decorata*			MH168256	MH168200	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Cloridina moluccensis*			MH168255	–	Van Der Wal et al. 2019	–

Table 2 (continued)

Specimen number	Taxonomy (order; superfamily; family)	Species name	Morphotype shown in	Collection date	Accession number COI	Accession number 16S rRNA	References COI	References 16S rRNA
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Cloridopsis scorpio*			MH168247	MH168234	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Dictyosquilla foveolata*			MH168249	MH168236	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Erugosquilla grahami*>			–	MH168226	–	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Erugosquilla massavensis*			MH447073	–	Unpublished	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Erugosquilla woodmasoni*			MH168262	MH168225	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Fallosquilla fallax*			HM138781	HM138821	Porter et al. 2010	Porter et al. 2010
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Harpiosquilla annandalei*			MH168264	MH168202	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Harpiosquilla harpax*			MH168261	MH168203	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Harpiosquilla japonica*			MH168259	–	Van Der Wal et al. 2019	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Harpiosquilla melanoura*			MH168260	MH168201	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Harpiosquilla raphidea*			KJ004663	–	Unpublished	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Kempella stridulans*			MH168263	MH168213	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Lenisquilla lata*			–	MH168235	–	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Levisquilla jurichi*			–	MH168204	–	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Lophosquilla costata*			–	MH168237	–	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Meiosquilla dawsoni*			MH168245	MH168206	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Meiosquilla swetti*			–	MH168210	–	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Miyakella holoschista*			MH168248	MH168230	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Miyakella nepa*			MH168269	MH168205	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Oratosquilla fabricii*			MH168267	MH168227	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Oratosquilla oratoria*			MH168274	MH168214	Van Der Wal et al. 2019	Van Der Wal et al. 2019

Table 2 (continued)

Specimen number	Taxonomy (order; superfamily; family)	Species name	Morphotype shown in	Collection date	Accession number COI	Accession number 16S rRNA	References COI	References 16S rRNA
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Oratosquillina anomala*			MH168270	MH168217	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Oratosquillina asiatica*			MH168268	MH168238	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Oratosquillina inornata*			MH168266	MH168220	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Oratosquillina interrupta*			MH168251	MH168219	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Oratosquillina nordica*			MH168275	–	Van Der Wal et al. 2019	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Oratosquillina perpensa*			MH168278	MH168218	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Pterygosquilla schizodontia*			MH168254	MH168216	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Quollastria gonypetes*			MH168277	–	Van Der Wal et al. 2019	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Quollastria imperialis*			MH168279	MH168207	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Rissoides barnardi*			MH168250	MH168228	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Rissoides desmaresti*			KT208805	–	Raupach et al. 2015	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Squilla chydaea*			MH168257	–	Van Der Wal et al. 2019	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Squilla edentata*			MH168258	–	Van Der Wal et al. 2019	–
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Squilla empusa*			NC_007444	NC_007444	Unpublished	Unpublished
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Squilla mantis*			NC_006081	NC_006081	Cook et al. 2005	Cook et al. 2005
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Squilla rugosa*			HM138810	HM138854	Porter et al. 2010	Porter et al. 2010
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Squilloides leptosquilla*			MH168252	MH168224	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Taku spinosocarinatus*			MH137219	AF107613	Ahyong et al. 2018	Unpublished
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Triasquilla profunda*			MH168253	MH168215	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Stomatopoda; Squilloidea; Squillidae	*Vossquilla kempi*			MH168276	MH168212	Van Der Wal et al. 2019	Van Der Wal et al. 2019
from GenBank	Anaspidacea; Anaspididae	*Anaspides tasmaniae*			DQ889076	AF133694	Costa et al. 2011	Elliott 2002

Table 2 (continued)

Specimen number	Taxonomy (order; superfamily; family)	Species name	Morphotype shown in	Collection date	Accession number		References	
					COI	16S rRNA	COI	16S rRNA
from GenBank	Decapoda; Nephropoidea; Nephropidae	*Homarus gammarus*			EU186145	NC_020020	Chan et al. 2009	Shen et al. 2013
from GenBank	Euphausiacea; Euphausiidae	*Meganyctiphanes norvegica*			MG935405	MG677875	Unpublished	Vereshchaka et al. 2018
from GenBank	Mysida; Mysinae; Mysidae	*Neomysis americana*			FJ581789	HM179997	Radulovici et al. 2009	Porter et al. 2010

rRNA sequences, K2P genetic distances within species were below 0.91%, except for the specimens assigned as *G. smithii*, which showed distances ranged from 0 to 2.77% to the reference sequence, and between two reference sequences of *Alima orientalis* (3.47%). The distance between species ranges from 1.13 to 25.85% (Table S2). Specimens assigned as *Carinosquilla multicarina* and *Oratosquillina inornata* were represented by both alima larvae and juveniles in our material. Fourteen morphotypes, assigned as 12 distinct species, were verified by molecular approaches and are enumerated and illustrated below.

Systematic account

Superfamily Gonodactyloidea Giesbrecht, 1910.
Family Gonodactylidae Giesbrecht, 1910.

Gonodactylus smithii (Pocock, 1893)

Fig. 4

Description (based on individual CEL-stom-056). Postlarva, CL 1.8 mm, TL 8.5 mm. Specimen overall subcylindrical in cross-section, devoid of conspicuous pigment. Eyestalk inflated, cornea spheroidal. Rostral plate as long as broad, triangular, anteriorly produced as an acute spine, lateral margins markedly concave. Carapace glabrous, gastric grooves extending 1/4 of length from bases of rostral plate (Fig. 4a). All maxillipeds epipod-bearing; raptorial appendage robust, propodus and dactylus unarmed along occlusal margin, dactylus mildly inflated proximally on flexor margin (Fig. 4g). TS5–8, to AS5 glabrous, devoid of longitudinal ridges. AS6 posteriorly armed with small but distinct SM, IM and LT spines (Fig. 4k). Telson longer than broad, markedly sculptured, MD carina stout; SM carina pronounced, each terminating with an elongated movable spine, between which armed with 11 to 12 SM denticles on each side; pronounced tooth situated between SM and IM tooth, each notch bearing a small denticle; LT tooth defined by a notch along the lateral margin. Uropod robust, penultimate segment of exopod bearing 7 stout LT spines and 1 distal spine (Fig. 4k).

Type locality. Arafura Sea.

Remarks. Molecular analyses showed that the COI sequences of several postlarval individuals from Taiwan (CEL-stom-056, 058, 061) are indeed conspecific (K2P distance 0.46 to 0.61%), while marginally matching with those identified as *Gonodactylus smithii* on GenBank (accession nos. DQ440603, MK397446, AF205223, DQ440602, HM138788, MT188299 to MT188304), with nucleotide (K2P) distances of 4.95 to 16.13%. Distances between sequences below 3% considered conspecific, those exceeding 5% being interspecific variation (Hebert et al. 2003). As addressed by Palecanda et al. (2020), in the case of *G. smithii*,

Fig. 2 Neighbor-joining (NJ) tree of **a** COI and **b** 16S rRNA sequences. Branch length represents Kimura 2-parameter (K2P) distances, and the bootstrap values are showed on the nodes only when > 90. "*" indicated those specimens that are not clustered to any reference sequence with COI but do cluster to reference sequence with 16S rRNA. Details of specimens from the present study (in bold, starting with CEL-stom) and those from reference sequences derived from GenBank are listed in Table 2

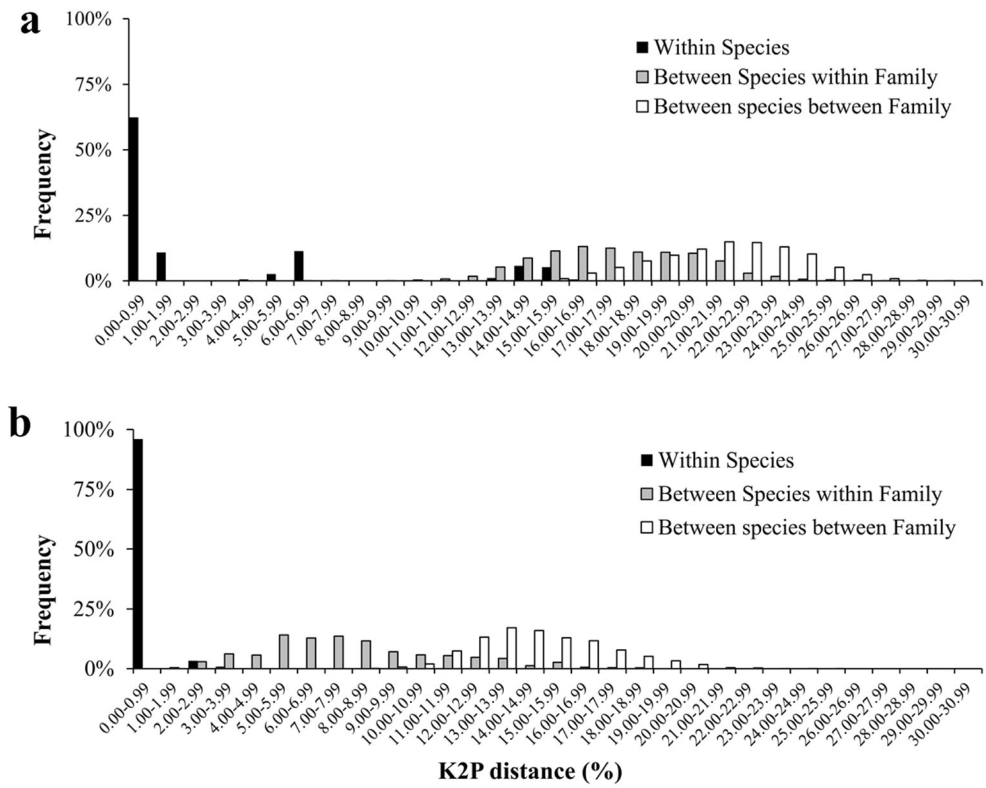

Fig. 3 Frequency distributions of genetic K2P distances of stomatopod larvae and juveniles representing 12 distinct species: **a** COI sequences for 134 individuals; **b** 16S rRNA sequences for 117 individuals

based on reference published on GenBank and ones newly acquired, genetic divergence of COI sequences among their three putative species can vary by as much as 20%. Our material from Taiwan comprises of the fourth clade, sister to their "*G. smithii* species 1" (K2P distance 4.95 to 6.98%; Fig. 2a; Table S2), adding to the heterogeneity of the "*G. smithii* species complex." This discrepancy might be result of genetic distance not as effective in species delineation and identification (see e.g., Meier et al. 2006), or alternatively, misidentification of relevant material.

Previous taxonomic studies based largely on morphological approaches gave the distribution range of *G. smithii* from the western Indian Ocean to the Red Sea, towards Vietnam, Australia, and New Caledonia (Serène 1947; Holthuis 1967; Manning 1968; Manning and Lewinsohn 1986; Manning 1995; Ahyong 2001). Hwang and Yu (1980) recorded the species based on material from Lanyu, Taiwan, under the name *Pseudosquilla ornata* (Ahyong et al. 2008). Taxonomic works already indicated marked variations particularly the form of the rostral plate, and the following extremely similar species are involved: *G. acutirostris* De Man, 1898 (type locality: Mergui) (considered synonymous with *G. smithii* by Serène (1954) and Holthuis (1967), but Manning and Lewinsohn (1986) and Manning (1995) kept both species distinct), *G. chiragra* var. *anancyrus* Borradaile, 1900 (type locality: New Britain, Papua New Guinea, and Loyalty Islands), *G. minikoiensis* Ghosh, 1990 (type locality: Minikoi, Lakshadweep), and *G. arabica* Ghosh, 1990 (type locality: Kavaratti, Lakshadweep). The above three species were placed under a synonymy of *G. smithii* by Manning (1995) and Ahyong (2001). Ahyong (2005) examined material from Sodwana Bay, South Africa, and remarked that the species *G. smithii*, as previously understood, was probably heterogeneous (also see Ahyong et al. 2008).

Gonodactylidae species

Fig. 5

Description (based on individual CEL-stom-027, and telson based on CEL-stom-026). Erichthus larva, CL 2.0 mm, TL 4.5 mm (CEL-stom-026). Carapace elongated, elevated along midline, extending towards posterior margin of AS2 (Fig. 5a), length excluding rostral and posterolateral spines approximate that of AS1 to telson; rostrum awl-shaped, ventrally armed with 4 oblique slender spines, anterolateral angle as a mere conical tubercle; posterior spine short, not extending beyond posterior margin, posterolateral spine prominent. Antennule triramous, flagella yet differentiated. Eyestalks inflated, cornea spheroidal. Only first two maxillipeds developed, both epipod-bearing, which small but discernable; raptorial claw propodus serrated along occlusal margin (Fig. 5g); dactylus not inflated, unarmed. AS6-telson yet differentiated despite faintly discernable margins, longer than broad, medially bearing 2 small posterior-oriented spines on proximal 1/5, laterally armed with 2 minute spines before

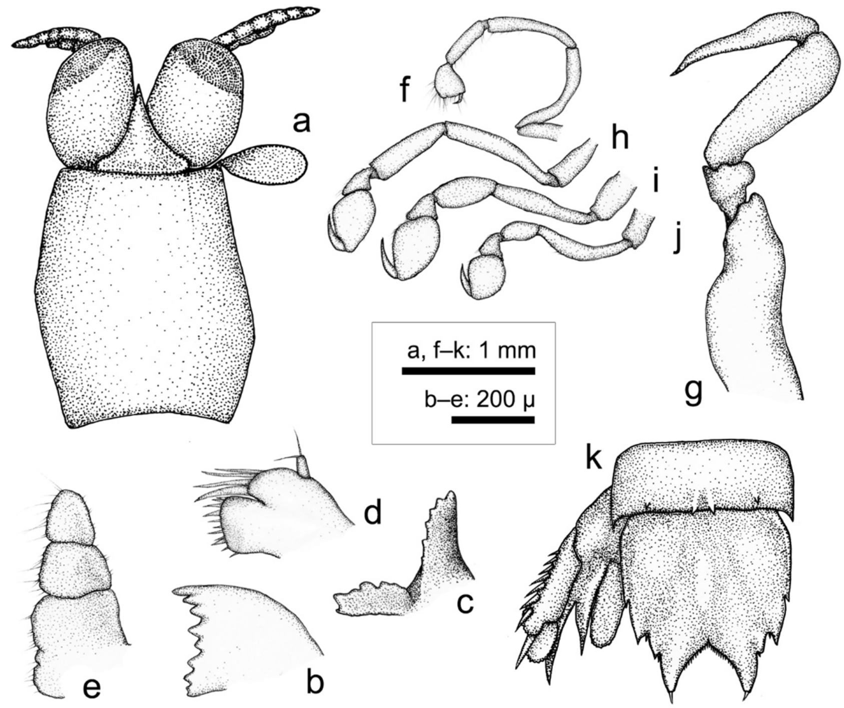

Fig. 4 *Gonodactylus smithii* Pocock, 1893 (postlarva: CEL-stom-056): **a** carapace; **b** left mandible, posterior view; **c** left mandible, mesial view; **d** left maxillule; **e** left maxilla; **f** left maxilliped 1; **g** right maxilliped 2; **h**–**j** left maxillipeds 3 to 5; **k** telson and left uropod

posterolateral angle, posterior margin armed with approximately 24 minute spinules (Fig. 5h).

Remarks. Molecular evidence based on COI and 16S rRNA mitochondrial sequences place the present form, represented by two specimens (CEL-stom-026 and 027), among the Gonodactylidae, yet precise identities remain uncertain. Given the specimen CEL-stom-026 with telson and preceding somites damaged, telson of this form is illustrated based on another individual, CEL-stom-027.

Superfamily Eurysquilloidea Manning, 1977.
Family Eurysquillidae Manning, 1977.

Manningia pilaensis (De Man, 1888)

Fig. 6

Description (based on individual CEL-stom-046). Erichthus larva, CL 2.5 mm, TL 7.2 mm. Carapace elongated, extending along midline to TS7, length excluding rostral and posterolateral spines less than that of AS1 to 4; rostrum compressed, blade-like, ventrally armed with at least 6 slender, oblique spines; anterolateral spine acute, not reaching bases of cornea; posterior spine strong but short, merely producing beyond outline of carapace, dorsal of which armed with another shorter accessory spine; posterolateral spine prominent, reaching posterior margin of AS2, ventrally armed with a short accessory spine (Fig. 5a). Antennules of three-segmented stalk, distally reaching to the tip of rostrum anteriorly. Eyestalks inflated, cornea spheroidal (Figs. 6a, b). All maxillipeds epipod-bearing, of which rounded; raptorial appendages propodus pectinated with minute spines along occlusal margin, proximally bearing 1 slender movable spine; dactylus slender, teeth along flexor margin barely discernable (Figs. 6a, b). AS6 posteriorly armed with small but distinct SM spines. Telson longer than broad, medially elevated, SM teeth pronounced, apexes fixed, breadth between exceeding half of telson width, medially divided by a shallow V-shaped notch, along the margin lined with 14 SM denticles on each side; IM and LT teeth prominent, apexes fixed, each with a small denticle. Uropod developed, distal segment of exopod armed with 2 LT spines.

Type locality. Elphinstone Island, Mergui Archipelago, Myanmar.

Remarks. Molecular analyses showed that the 16S rRNA mitochondrial sequences of several erichthus larvae (individuals CEL-stom-046, 047, 053, 055, 059) matched those of *Manningia pilaensis* (GenBank accession no. KY236044; K2P distance: $< 0.64\%$). Distribution of this cryptic reef species ranges from the eastern Indian Ocean (Mergui Archipelago, Myanmar) to Vietnam and South China (Amoy = Xiamen) (see Manning 1967, 1995; also as *M. serenei*), and the herein report from Taiwan is not unexpected. The genus *Manningia* Serène, 1962, now includes 11 species (Ahyong 2001; see also Manning 1995), which largely found in the Indo-West Pacific, except for *M. posteli* Manning, 1977, which was recorded from Congo to Guinea, West Africa. The genus was described in a generic revision of *Pseudosquilla* Dana, 1852, by Serène (1962), raised to familial status by Manning (1977) under Gonodactyloidea (see Manning 1995), and later

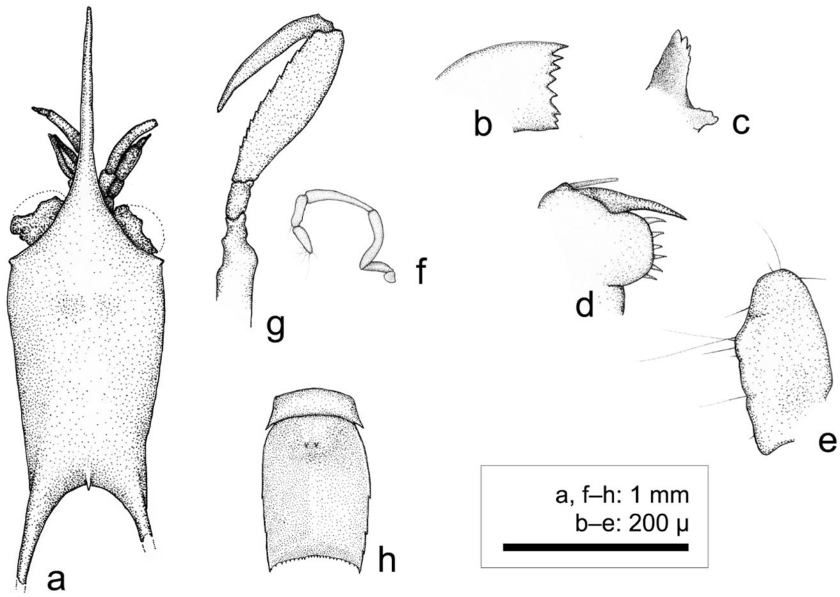

Fig. 5 Gonodactylidae species (erichthus larva): **a** carapace; **b** right mandible, posterior view; **c** right mandible, mesial view; **d** right maxillule; **e** left maxilla; **f** left maxilliped 1; **g** right maxilliped 2; **h** telson. **a**–**d**, **g**: CEL-stom-027; **e**, **f**, **h**: CEL-stom-026

identified as a distinct superfamily by Ahyong (2001). Despite the lack of adult material from Taiwan, the current report nevertheless represents the first record of the Eurysquillidae and Eurysquilloidea from Taiwan (see Ahyong et al. 2008).

Superfamily Lysiosquilloidea Giesbrecht, 1910
Family Lysiosquillidae Giesbrecht, 1910

Lysiosquillina maculata (Fabricius, 1793)

Fig. 7

Description (based on individual in SEM images). Antizoea larva, CL 1.2 mm, TL 1.9 mm. Carapace elongated, cylindrical, rostral spine slender, approximately 1/3 of CL, slightly curved upwards distally, entire dorsally and ventrally; posterior spine slender, short; posterolateral spine slender, approximately 1/5 of CL; corneal spheroidal, sessile, still undifferentiated from carapace (Fig. 7a, b). Antennule uniramous. Maxillipeds 1 to 5 biramous. Pleopods and uropods not yet developed (Fig. 7a). Telson depressed, unornamented, laterally armed with acute MG, LT, IM and SM teeth, posteriorly lined with 12 minute SM denticles (Fig. 7c).

Type locality. Manado, Indonesia (neotype; Ahyong 2001).

Remarks. Many small antizoea individuals were captured during our study, and COI and 16S rRNA mitochondrial gene sequences were amplified from eight representative individuals (CEL-stom-007, 064, 067, 069, 073, 074, 076, 077). Given unsatisfactory condition of the small and fragile antizoea specimens, sequencing from most individuals failed (over 70 individuals sequenced). Anyhow, COI sequences from all eight individuals cluster with *Lysiosquillina maculata* (GenBank accession nos. KM982431, KM982432, KM982436: from Lizard Island, Australia), with intraspecific genetic K2P distance ranging from 0 to 0.92% (Fig. 2a, Table S2). Phylogeny derived from 16S rRNA sequences also indicates our material being conspecific with *Lysiosquillina maculata* (GenBank accession nos. HM138834, AF107618, EU920935), with K2P distance less than 0.91% (Fig. 2a, Table S2). From morphological examinations, we interpret very subtle morphological variations among samples as intraspecific. We have no evidence suggesting multiple lysiosquilloid species being represented in this bulk antizoea lot. As such, we confirm the presence of *L. maculata* in Taiwan.

Records of *Lysiosquillina maculata* (previously *Lysiosquilla*) had been recorded in Taiwan starting from the early twentieth century (Fukuda 1913; Komai 1927; Lee and Wu 1966). However, Ahyong et al. (2008) considered the specimen represented by this name by Lee and Wu (1966) to be *Lysiosquilla tredecimdentata* instead. The same study only verified *L. tredecimdentata* and *L. sulcirostris* Kemp, 1913, as records of Lysiosquillidae from Taiwan. However, *Lysiosquillina maculata* sensu stricto was confirmed in Japan by Hamano (1989: material from Ryukyus), and its presence in Taiwan is not unexpected. While other large lysiosquillids often found in deeper waters of muddy substrates and captured by trawls, *Lysiosquillina maculata* prefers shallow subtidal sandflats in vicinity of coral reefs (S. T. Ahyong, pers. comm). This possibly accounts for the absence of *L. maculata* sensu stricto in past Taiwanese records (see "Discussion" section below).

In attempt to resolve records of Lysiosquillidae in Taiwan, we sequenced one large adult male individual from our laboratory collections identified as *Lysiosquilla tredecimdentata*

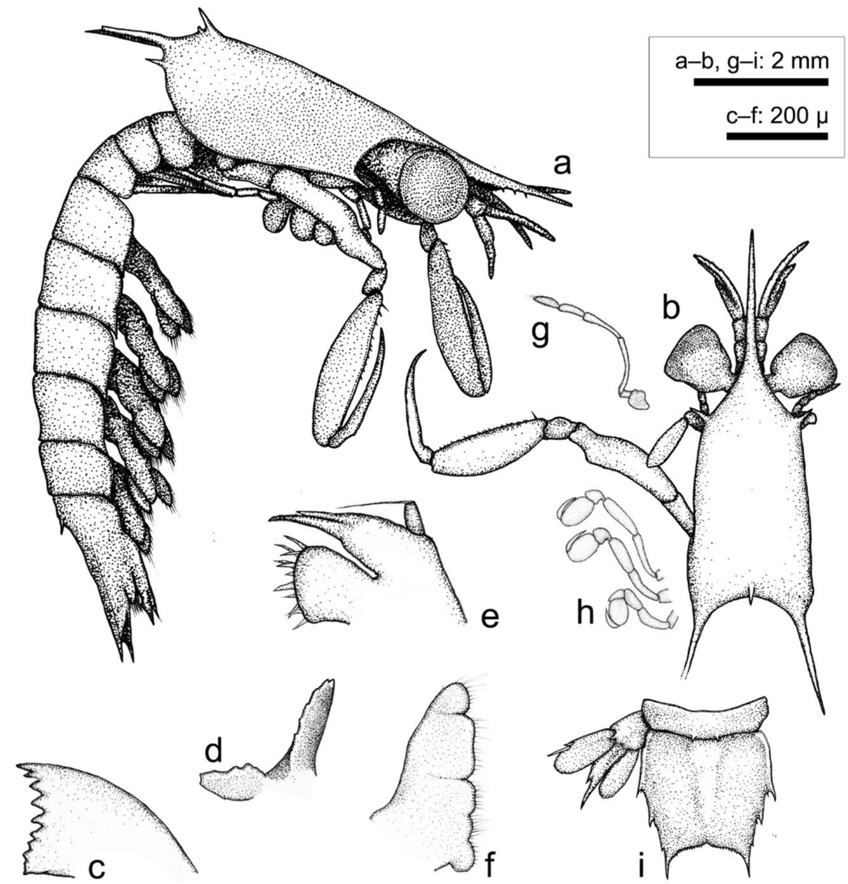

Fig. 6 *Manningia pilaensis* (De Man, 1888) (erichthus larva: CEL-stom-046): **a** overall habitus, lateral view; **b** carapace and left maxilliped 2, dorsal view; **c** left mandible, posterior view; **d** mandible, mesial view; **e** left maxillule; **f** right maxilla; **g** left maxilliped 1; **h** left maxillipeds 3 to 5; **i** telson and left uropod

Holthuis, 1941 (based on Ahyong et al. 2008), purchased from the Donggang fish market, Pingtung, Taiwan (CL: 27.3 mm, TL: 134.1 mm; as CEL-stom-093). Based on COI and 16S rRNA sequences, this specimen is shown to be distinct from antizoea individuals herein identified as *L. maculata* (genetic K2P distance: 14.94 to 15.14% for COI, 8.63% for 16S rRNA).

Family Nannosquillidae Manning, 1980

Nannosquillidae species 1

Fig. 8

Description (based on individual CEL-stom-045). Postlarva, CL 2.1 mm, TL 10.1 mm. Specimen overall dorsoventrally depressed, devoid of conspicuous pigment. Eyestalk stout, cornea slightly inflated. Rostral plate rounded triangular, slightly broader than long, distally rounded, laterally nearly straight; carapace depressed, glabrous, devoid of marked longitudinal grooves (Fig. 8a). All maxillipeds epipod-bearing, those of maxillipeds 1 and 2 more pronounced, transversely auricular, of maxillipeds 3 and 4 smaller, rounded; raptorial appendages robust; propodus broad, subovate, along occlusal margin pectinated, proximally bearing 2 elongated movable spines; dactylus armed with 6 teeth, along extensor margin bearing 2 low proximal lobes (Fig. 8a); propodus of maxilliped 4 distinctly subquadrate. Telson approximately 1.5 times broader than long, subquadrate; MD carina stout, posteriorly terminating as an acute spine; SM teeth fixed, prominent, breadth between occupying more than 1/3 of telson width, between which armed with 12 denticles on each side; IM and LT teeth prominent, lined with several small IM and 1 LT denticles (Fig. 8j). Uropod robust, protopod strongly bifurcate; endopod ovate, bearing marked proximal fold; penultimate segment of exopod laterally armed with 3 acute spines, distal segment subovate, mesial margin sinuous (Fig. 8j).

Remarks. Molecular evidence based on COI and 16S rRNA mitochondrial sequences showed that three forms—herein indicated as Nannosquillidae species 1 to 3—at species level not matching any of the available reference sequences. Based on COI sequences, the three nannosquillid species are shown to be distinct, while all showing some affinity to *Alachosquilla vicina* (Nobili, 1904) (GenBank accession no. KM982440 and AF107608) with high bootstrap values (Fig. 2), a nannosquillid having broad range of distribution across the Indo-West Pacific (Ahyong 2001). The three distinct species were each represented by limited number of postlarval individuals (sp. 1: 1 specimen; sp. 2: 1 specimen; sp. 3: 2 specimens), all bearing a marked proximal fold on the uropodal endopod (Figs. 8j, 9j, 10k), a diagnostic feature in adults of the family

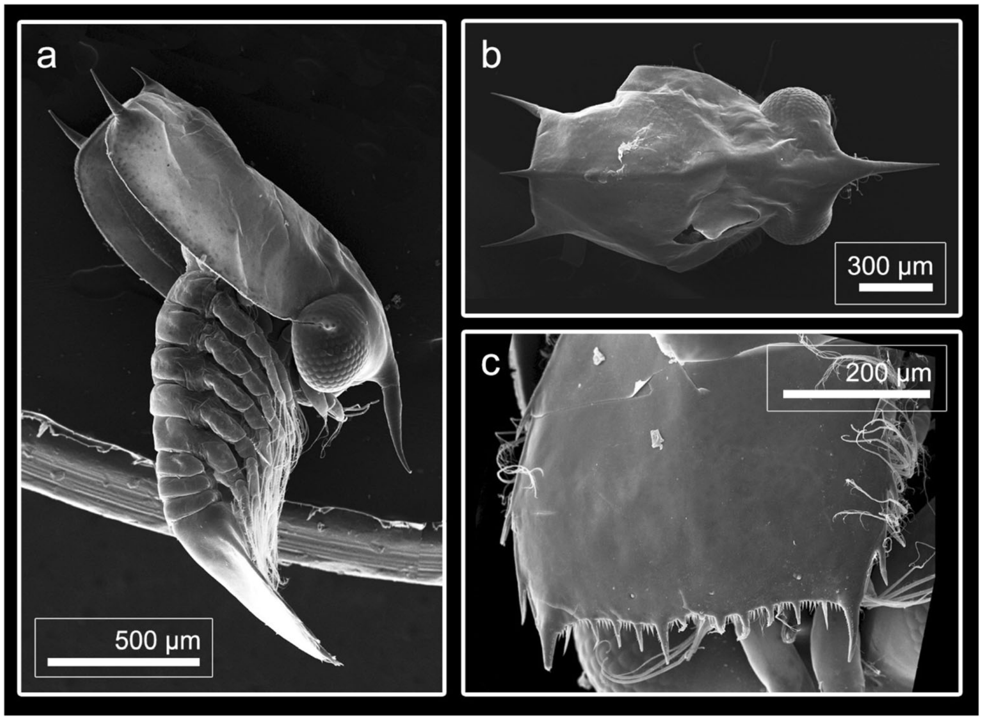

Fig. 7 *Lysiosquillina maculata* (Fabricius, 1793) (antizoea larva): **a** overall habitus, lateral view; **b** carapace, dorsal view; **c** telson, dorsal view

(see Manning 1995; Ahyong 2001; Ahyong et al. 2008), already well developed in earlier postlarval stages. Other diagnostic features allowing identification to generic level, such as form of rostral plate, are still wanting in our material, and not developed until early juvenile stages, whereas this Nannosquillidae species 1 probably belongs to the "*Acanthosquilla*" group (S. T. Ahyong, pers. comm.).

So far seven nannosquillid species have been recorded from Taiwan: *Acanthosquilla derijardi* Manning, 1970, *A. manningi* Makarov, 1978, *A. multifasciata* (Wood-Mason, 1895), *Bigelowina phalangium* (Fabricius, 1798), *Pullosquilla litoralis* (Michel & Manning, 1971), *P. pardus* (Moosa, 1991), and *P. thomassini* Manning, 1978 (Ahyong et al. 2008; Wang and Chiou 2017). Further molecular analyses may reveal the identities of the three postlarval forms reported herein.

Nannosquillidae species 2

Fig. 9

Description (based on individual CEL-stom-086). Postlarva, CL 2.1 mm, TL 10.8 mm. Specimen dorsoventrally depressed, devoid of conspicuous pigment. Eyestalks stout, cornea spheroidal. Rostral plate triangular, slightly broader than long, laterally mildly concave; carapace depressed, glabrous, longitudinal grooves nearly wanting (Fig. 9a). All maxillipeds epipod-bearing, those of maxillipeds 1 to 3 more pronounced, somewhat cordiform; raptorial appendage robust, propodus markedly broad, ovate, occlusal margin pectinated, proximally of 1 elongated movable spine, dactylus armed with 6 teeth, along extensor margin bearing 2 low proximal teeth (Fig. 9f); propodi of maxillipeds 3 and 4 distinctly subquadrate. Telson approximately 1.5 times broader than long, subquadrate, median carina stout, posteriorly of an acute spine; SM teeth fixed, prominent, breadth between occupying more than half of telson, each side armed with about 18 SM denticles, medial cleft wanting; IM and LT teeth prominent, each accompanied by small denticle (Fig. 9j). Uropod robust, protopod strongly bifurcated, endopod ovate, proximally folded; penultimate segment of exopod laterally armed with 3 small but distinct acute spines, distal segment ovate, lined with 1 longitudinal crest (Fig. 9j).

Remarks. The three forms of Nannosquillidae species which have high bootstrap value in their COI and 16S rRNA phylogenies, share a proximally folded uropodal endopod, a diagnostic feature of the family. The three forms are nevertheless distinct and identifiable by (1) carapace of species 3 bearing marked longitudinal (gastric) grooves, which is vaguely defined or absent in species 1 and 2; (2) raptorial appendage dactylus of species 1 and 2 armed with 6 spines, whereas that of species 3 has 8; (3) form of telson, especially marginal armature, and relative width between both submedian spines; (4) uropodal endopod of species 2 and 3 sub- to rounded triangular, while that of species 1 ovate; and (5) penultimate segment of uropodal exopod laterally of 2 to 3 spines in species 1, 4 to 5 spines in species 2 and 6 acute spines in species 3. It remains nearly impossible to make solid identifications based solely on morphological characters of adults given in

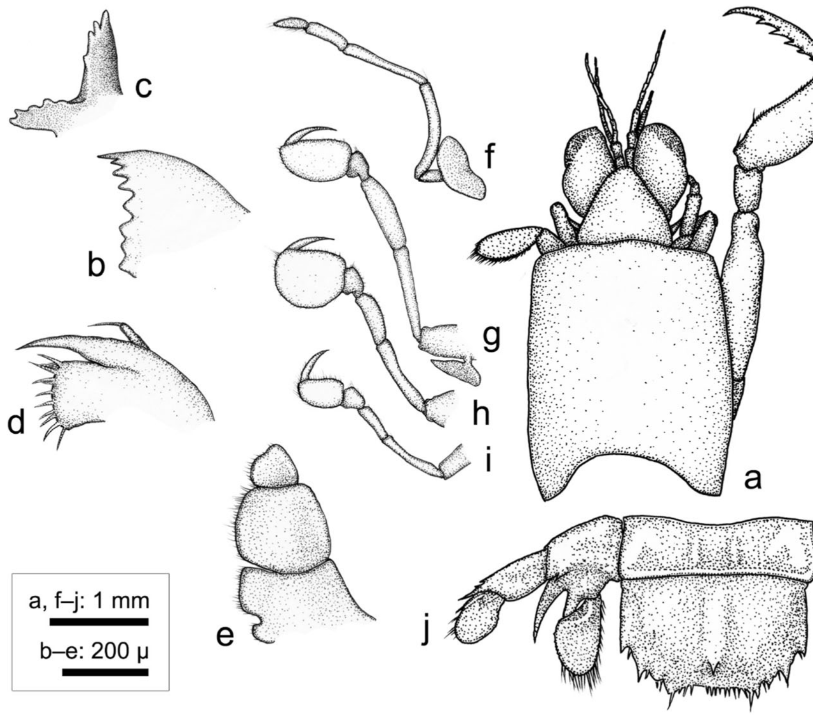

Fig. 8 Nannosquillidae species 1 (postlarva: CEL-stom-045): **a** carapace and right maxilliped 2; **b** left mandible, posterior view; **c** left mandible, mesial view; **d** left maxillule; **e** left maxilla; **f** left maxilliped 1; **g–i** left maxillipeds 3 to 5; **j**, telson and left uropod

past taxonomic works. See also Remarks for Nannosquillidae species 1 above.

Nannosquillidae species 3

Fig. 10

Description (based on individual CEL-stom-063). Postlarva, CL 2.0 mm, TL 9.5 mm. Specimen dorsoventrally depressed, devoid of conspicuous pigment. Eyestalks stout, cornea spheroidal. Rostral plate rounded triangular, broader than long, distally rounded, lateral margins concave; carapace depressed, glabrous, longitudinal groove marked (Fig. 10a). All maxillipeds epipod-bearing, those of anterior 4 more pronounced; raptorial appendages robust; propodus occlusal margin pectinated, proximally bearing 2 elongated movable spines, dactylus armed with 8 teeth, along extensor margin bearing 2 low proximal lobes (Fig. 10g); propodi of maxillipeds 3 and 4 well developed, that of 3 rounded triangular, that of 4 distinctly subquadrate. Telson approximately 1.3 times broader than long, median carina stout, posteriorly terminating in an acute spine; SM teeth fixed, prominent, breadth between occupying more roughly half of telson width, medially separated by a shallow V-shaped cleft, on each side armed with 8 to 9 SM denticles; laterally armed with prominent IM and LT teeth, each armed with 1 small denticle (Fig. 10k). Uropod robust, protopod strongly bifurcate; endopod subtriangular, bearing marked proximal fold; exopod penultimate segment laterally armed with 6 acute spines, distal segment ovate (Fig. 10k).

Remarks. See Remarks for both Nannosquillidae species above.

Superfamily Squilloidea Latreille, 1802.
Family Squillidae Latreille, 1802.

Squillidae species

Fig. 11

Description (based on individual CEL-stom-082). Postlarva, CL 3.7 mm, TL 16.5 mm. Specimen squilloid-type, overall with dark spots arranged into short longitudinal markings symmetrical along midline. Eyestalks stout, cornea inflated, bilobed. Rostral plate slightly longer than broad, triangular, medial ridge conspicuous (Fig. 11a). Carapace overall glabrous, along midline furnished with dorsal pit, and a slightly elongated depression behind base of rostral plate; gastric groove apparent, extending 2/3 of carapace length; IM and LT carinae marked (Fig. 11a). Anterior 4 maxillipeds epipod-bearing, those of maxillipeds 3 and 4 small, rounded; raptorial appendage robust, propodus proximally armed with two slender movable spines, occlusal margin pectinated; dactylus armed with 5 spines (Fig. 11g). TS5 to 8 bearing marked submedian and lateral carinae, TS5 laterally bilobed, anterior one acute, curved, lower than the posterior lobe; TS6 single-lobed, anterior margin sinuous (Fig. 11k). AS armed with pronounced SM, IM and LT carinae; SM carinae of AS5 and 6 produced posteriorly (Fig. 11l). Telson longer than broad, median carina well-defined, prominent; submedian teeth fixed, separated medially by broad V-shaped notch, on

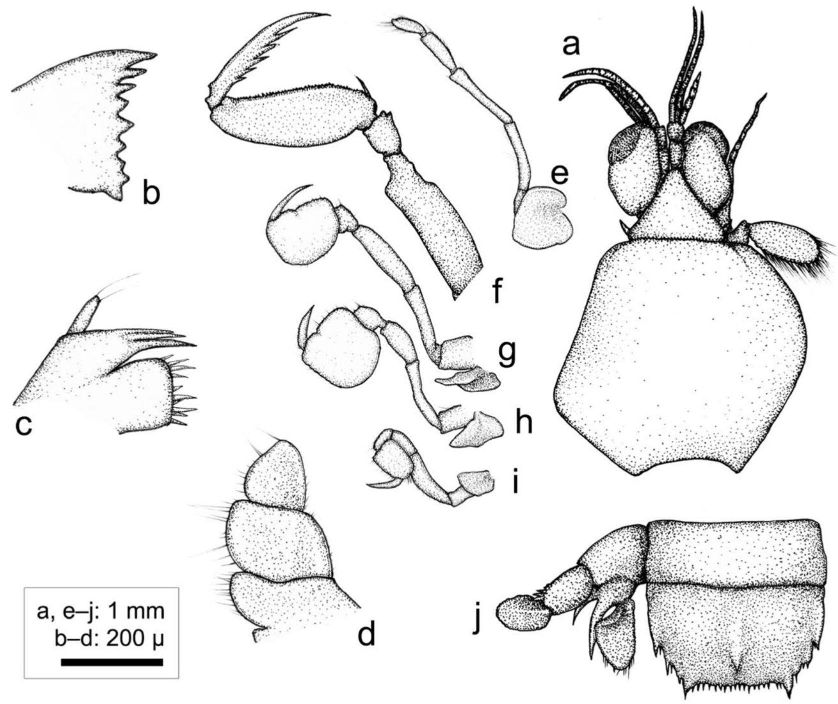

Fig. 9 Nannosquillidae species 2 (postlarva: CEL-stom-086): **a** carapace; **b** right mandible, posterior view; **c** right maxillule; **d** left maxilla; **e**–**i** left maxillipeds 1 to 5; **j** telson and left uropod

each side armed with 5 to 7 SM denticles, IM (10 to 11 IM denticles) and LT carinae prominent (Fig. 11l). Uropod robust, protopod bifurcated, mesial tooth bearing a pronounced rounded lobe on outer margin; exopod penultimate segment laterally armed with eight stout spines laterally (Fig. 11l).

Remarks. Considering morphology of the single specimen examined (CEL-stom-082), the placement into *Alima* Leach, 1817, appears to be appropriate, given (1) lateral process of TS5 bilobed and TS6 and 7 single-lobed and (2) raptorial claw merus distally unarmed along outer inferodistal margin. Two species of *Alima* have been recorded from Taiwan, namely *A. orientalis* Manning, 1978, and *A. hieroglyphica* (Kemp, 1911) (Ahyong et al. 2008). Comparison of COI reference sequences of *Alima* species acquired from GenBank (voucher specimens from Lizard Island, Australia; Feller et al. 2013), our material match neither *A. orientalis* (KF205337, KF214292, MT179626; K2P distance 18.01 to 18.63%), *A. pacifica* (HM138774, KM982423, KM982434; 20.57 to 21.25%), nor a phylogenetically close squilloid *Busquilla plantei* Manning, 1978 (HM138775; 22.09%). Results derived from 16S rRNA sequences are likewise inconclusive: showing affinity with *Alima orientalis* Manning, 1978 (HM138814; 7.64%), but with low bootstrap support. As such, we remain to report the present form as Squillidae species.

Carinosquilla multicarinata (White, 1848)

Figs. 12–13

Description: alima larva (based on individual CEL-stom-010). CL 6.0 mm, TL 14.4 mm. Carapace elevated along midline, elongated, posterior margin reaching TS7, posterolateral spine reaching AS1; rostral spine slender, elongated, about 1/3 length of carapace (spines exclusive); posterior spine short; lateral margin towards posterolateral spine armed with about 8 small denticles, separately dispersed along the ventral-internal margin (Fig. 12a, b). Antennules of three-segmented stalk, reaching to the tip of rostrum anteriorly, distally bearing triramous segmented flagella. Eyestalks inflated, cornea spheroidal (Fig. 12a). Maxillipeds well developed; anterior 2 maxillipeds epipod-bearing, of which rounded; raptorial claw propodus minutely pectinated along occlusal margin, proximally armed with 2 acute fixed spines, dactylus unarmed (Fig. 12c). Pereiopods well developed. AS6 and telson yet articulating despite faint suture discernable; AS6 armed posteriorly with SM spines (Fig. 12j). Telson markedly longer than broad, SM teeth pronounced (4 SM denticles on each side); IM (9 IM denticles) and LT teeth pronounced, the latter confluent with lateral margin (Fig. 12j). Uropod developed, penultimate segment of exopod laterally armed with 5 acute spines (Fig. 12j).

Description: juvenile (based on individual CEL-stom-085). CL 3.1 mm, TL 14.8 mm. Specimen squilloid-type, overall with dark streaks arranged into short longitudinal markings symmetrical along midline, including some along LT carinae on AS. Eyestalks stout, cornea inflated as adult individuals. Rostral plate triangular, median carina distinct (Fig. 13a). Carapace bearing faint but discernible median carina, anteriorly bifurcated, almost continuous; IM, LT, and reflected MG carinae marked (Fig. 13a). Mandibular palp absent. Anterior 4 maxillipeds epipod-

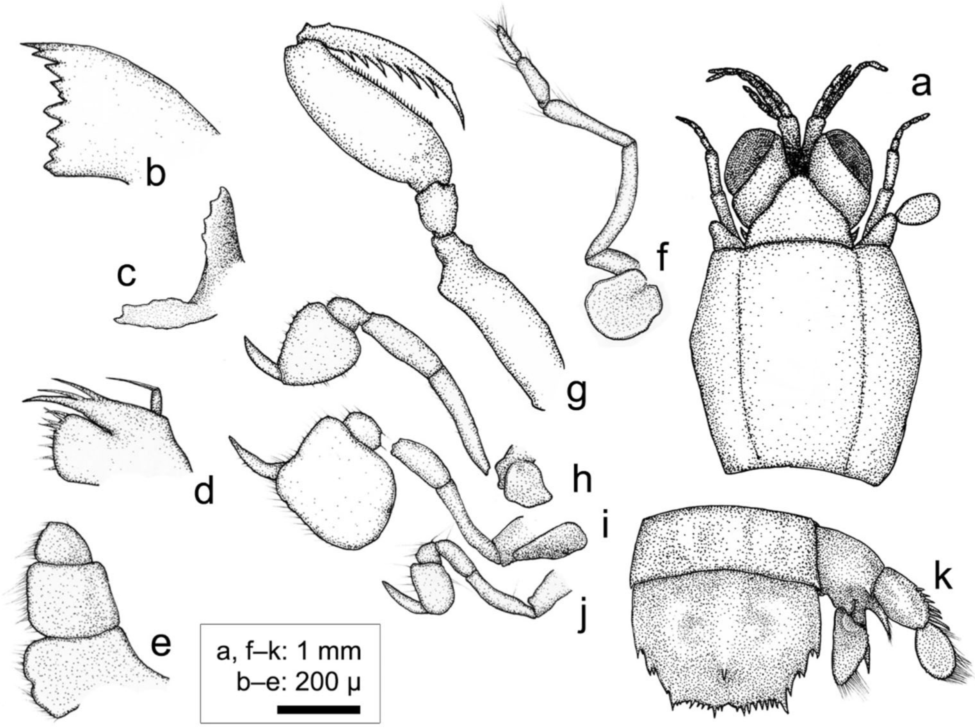

Fig. 10 Nannosquillidae species 3 (juvenile: CEL-stom-063): **a** carapace; **b** left mandible, posterior view; **c** left mandible, mesial view; **d** left maxillule; **e** left maxilla; **f**–**j** left maxillipeds 1 to 5; **k** telson and right uropod

bearing, those of maxillipeds 1 and 2 more pronounced, of 3 and 4 small, rounded; raptorial appendage robust, propodus proximally armed with 3 slender movable spines, occlusal margin pectinated; dactylus armed with 5 spines (Fig. 13a). TS6 to 8 with marked SM and LT carinae, TS6 markedly bilobed, TS7 concave on anterior margin (Fig. 13a). AS1 to 6 armed with conspicuous SM and IM, LT and MG carinae; SM carina of AS6 posteriorly armed. Telson longer than broad, MD carina well-defined, prominent, posteriorly terminating in distinct spine; SM teeth fixed, separated medially by narrow V-shaped notch (5 SM denticles on each side), IM (7 to 9 IM denticles)

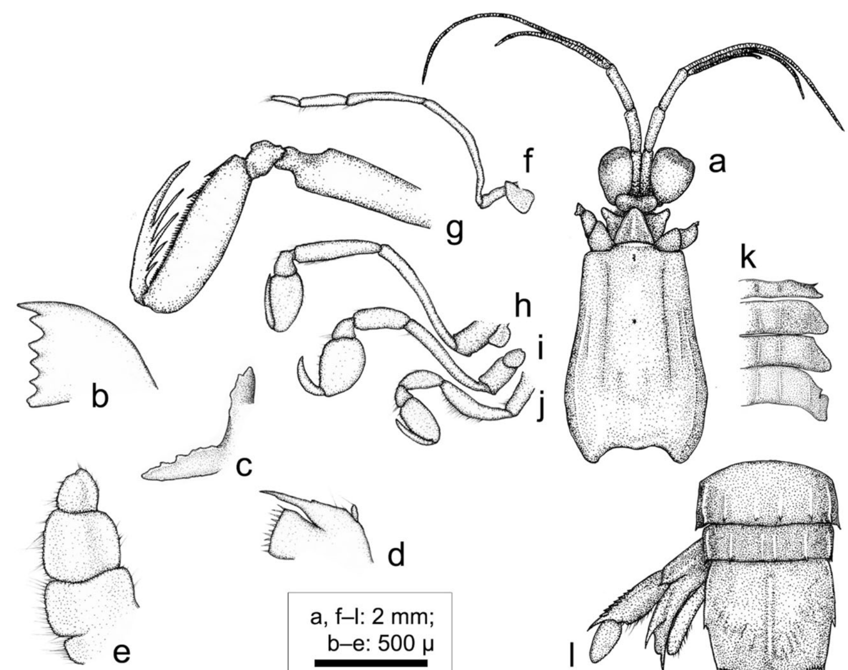

Fig. 11 Squillidae species (postlarva: CEL-stom-082): **a** carapace; **b** left mandible, posterior view; **c** left mandible, mesial view; **d** left maxillule; **e** left maxilla; **f**–**j** left maxillipeds 1 to 5; **k** thoracic somites 6 to 8; **l** telson and left uropod

and LT carinae prominent (Fig. 13h). Uropod robust, protopod bifurcated, mesial margin serrated, mesial spine bearing a pronounced rounded lobe in outer margin; exopod penultimate segment armed with 8 stout LT spines (Fig. 13h).

Type locality. The Philippines, precise locality unspecified.

Remarks. COI and 16S rRNA mitochondrial sequences from alima larval and juvenile individuals match those of *Carinosquilla multicarina* (GenBank accession no. MH168265 and MH186221.1; genetic K2P distances: 0.47 to 0.62% for COI, 0.00% for 16S rRNA). It appears the diagnostic multiple longitudinal carinae on the adult carapace, a diagnostic feature of the genus, had not yet emerged in the earlier stages of the juvenile, as shown above.

Levisquilla jurichi (Makarov, 1979)

Fig. 14

Description (based on individual CEL-stom-062). Postlarva, CL 1.8 mm, TL 7.5 mm. Specimen dorsal ventrally depressed, devoid of conspicuous pigment. Eyestalks stout, cornea slightly inflated. Rostral plate triangular, slightly longer than broad, medial ridge faint, yet completely separated from carapace (Fig. 14a). Carapace depressed, glabrous, gastric groove marked, extending to posterior margin; posterior spine as faint, rounded tooth (Fig. 14a). At least anterior 2 maxillipeds epipod-bearing; raptorial appendage robust, propodus along occlusal margin pectinated, dactylus armed with 6 teeth (Fig. 14e). TS5 to 8 laterally single-lobed (Fig. 14i). AS1 to 5 glabrous; AS6 posteriorly armed with small but distinct SM and LT spines (Fig. 14i). Telson slightly broader than long, MD carina stout, SM tooth terminating as movable spine, distance between more than half of telson width (lined with approximately 14 SM denticles); IM (5 to 6 IM denticles) and LT teeth prominent (Fig. 14j). Uropod robust, protopod bifurcated, mesial margin serrated, mesial spine bearing large rounded lobe along outer margin; endopod elongated, margins serrated; exopod penultimate segment laterally armed with 4 spines (Fig. 14j).

Type locality. Kavieng, Papua New Guinea.

Remarks. Molecular analyses based on 16S rRNA sequences show the present specimen to be phylogenetically closest to *Levisquilla jurichi* (Makarov, 1979) (GenBank accession no. MH168204; K2P distance 1.60%), a species found from the Indo-West Pacific to the Andaman Sea, Vietnam, New Caledonia, and Australia (Manning 1995; Ahyong 2001). The only postlarval individual at hand (CEL-stom-062) was soft, probably freshly molted, was in poor condition; we hence failed to retrieve either mandible. Other morphological features, nevertheless, share in common with adults of *Levisquilla*: (1) single-lobed lateral extensions of thoracic somites 5 to 8; (2) SM carina of telson bearing articulated apexes; and (3) mesial margin of uropodal protopod serrated. Given minimal K2P distance in comparison with *L. jurichi*, and morphological features agreeing with the genus, we identify the present specimen as *L. jurichi*, representing a new record for the stomatopod fauna of Taiwan. Previously, the only species in this genus recorded from Taiwan is *L. inermis* (Manning, 1965) (Ahyong et al. 2008).

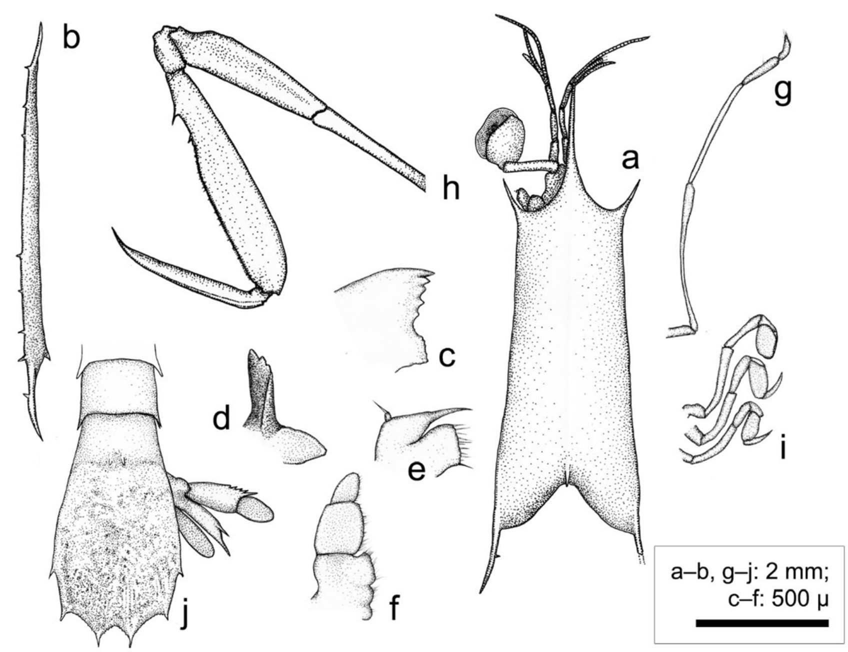

Fig. 12 *Carinosquilla multicarina* (White, 1848) (alima larva: CEL-stom-010): **a** carapace, dorsal view; **b** carapace, lateral view; **c** left mandible, posterior view; **d** left mandible, mesial view; **e** left maxillule; **f** left maxilla; **g** right maxilliped 1; **h** left maxilliped 2; **i** right maxillipeds 3 to 5; **j** telson and right uropod

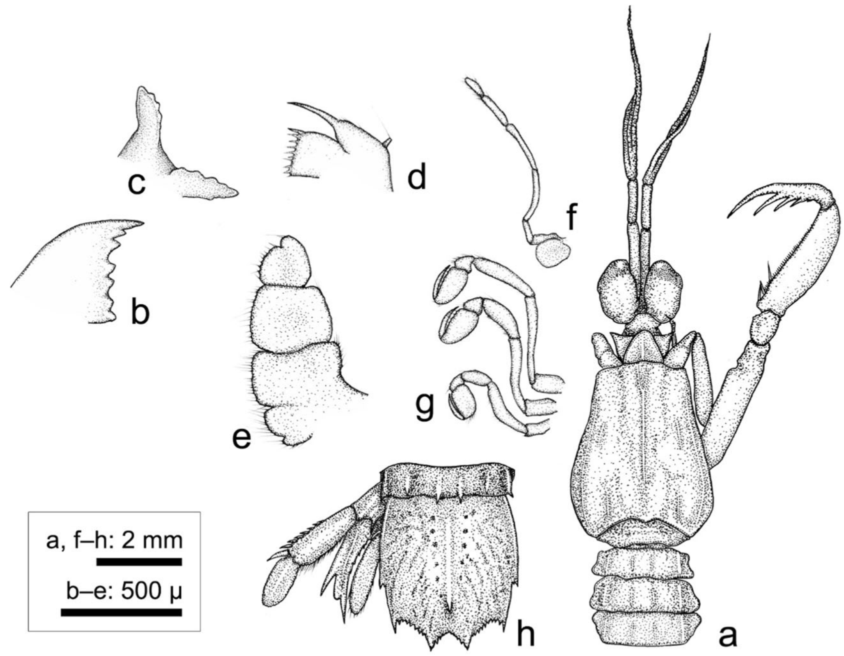

Fig. 13 *Carinosquilla multicarina* (White, 1848) (juvenile: CEL-stom-085): **a** carapace and right maxilliped 2; **b** right mandible, posterior view; **c** right mandible, mesial view; **d** left maxillule; **e** left maxilla; **f** left maxilliped 1; **g** left maxillipeds 3 to 5; **h** telson and left uropod

Oratosquillina inornata **(Tate, 1883)**

Figs. 15–16

Description: alima larva (based on individual CEL-stom-050). CL 6.4 mm, TL 16.5 mm. Carapace elevated along midline, elongated, posteriorly reaching TS6; rostral spine slender, elongated, slightly less than half of carapace length; anterolateral spine prominent, reaching base of eyestalk; posterolateral spine reaching AS1; posterior spine prominent, short; lateral margin towards posterolateral spine ventrally armed with about 9 small denticles, the 4 near the posterior margin more pronounced, separately dispersed along the ventral-internal margin (Fig. 15a, b). Antennules of three-segmented stalk, reaching to the tip of rostrum anteriorly, distally triflagellate. Eyestalks inflated, cornea spheroidal (Fig. 15a). Maxillipeds well developed, anterior 2 epipod-

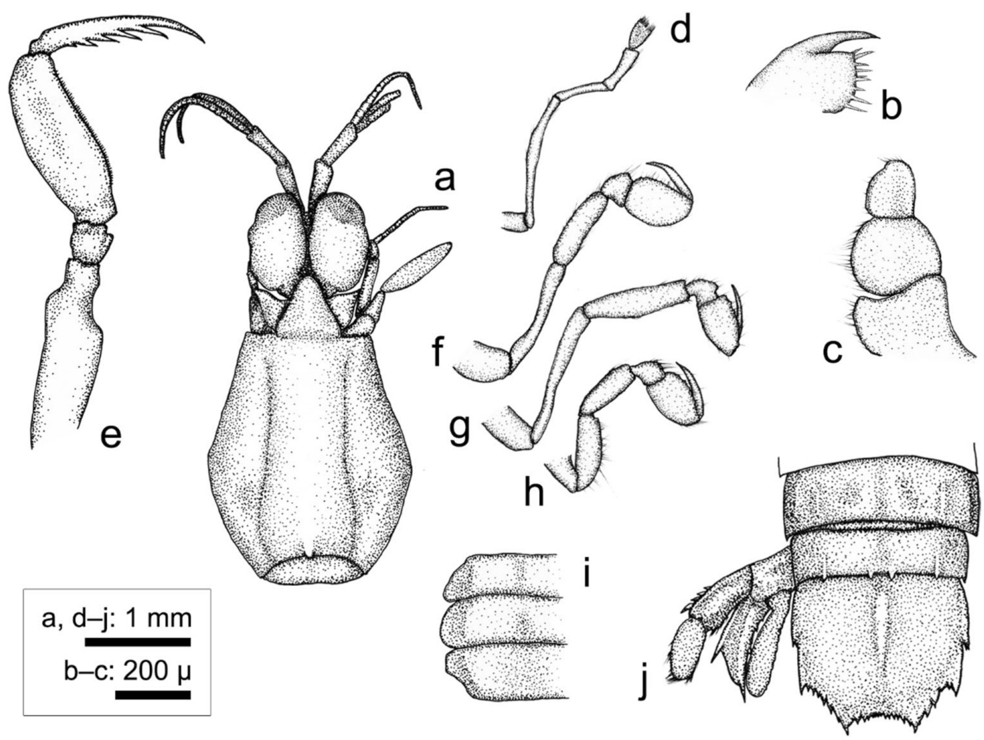

Fig. 14 *Levisquilla jurichi* (Makarov, 1979) (postlarva: CEL-stom-062): **a** carapace; **b** right maxillule; **c** left maxilla; **d** right maxilliped 1; **e** left maxilliped 2; **f–h** right maxillipeds 3 to 5; **i** thoracic somites 6 to 8; **j** telson and left uropod

bearing, of which rounded; raptorial claw propodus minutely pectinated along occlusal margin, proximally armed with 2 acute fixed spines, dactylus slender, unarmed (Fig. 15a). Pereiopods well developed. AS6 and telson yet articulating despite faint suture discernable; AS6 armed posteriorly with SM spines (Fig. 15i). Telson markedly longer than broad, SM teeth separated by broad V-shaped notch (13 to 15 SM denticles on each side); IM (9 IM denticles) and LT teeth pronounced, confluent with lateral margin (Fig. 15i). Uropod developed, penultimate segment of exopod laterally armed with about 3 small but acute spines (Fig. 15i).

Description: juvenile (based on individual CEL-stom-048). CL 3.1 mm, TL 15.2 mm. Specimen squilloid-type, overall with dark spots arranged into longitudinal lines symmetrical along midline, more pronounced along posterior margins of exposed TS and AS. Eyestalks stout, cornea inflated as adult individuals. Rostral plate rounded triangular, median carina distinct, yet completely separated from carapace (Fig. 16a). Carapace bearing faint but discernable median carina, dorsal pit marked; IM and LT carinae conspicuous (Fig. 16a). Mandibular palp absent. Anterior 4 maxillipeds epipod-bearing, those of anterior 2 more pronounced, the other 2 smaller, rounded; raptorial appendage robust, propodus proximally armed with 1 slender movable spine, occlusal margin pectinated; dactylus armed with 6 robust spines (Fig. 16g). TS6 to 8 with marked SM and LT carinae, TS5 to 7 laterally bilobed (Fig. 16i). AS1 to 6 armed with conspicuous SM and IM carinae. Telson longer than broad, MD carina well-defined, prominent, interrupted on proximal 1/5, posteriorly terminating with a distinct spine; SM teeth fixed, separated medially by narrow V-shaped notch (4 SM denticles on each side), IM (8 IM denticles) and LT carinae prominent (Fig. 16j). Uropod robust, protopod bifurcated, mesial margin serrated, mesial tooth bearing a pronounced rounded lobe in outer margin; exopod penultimate segment laterally armed with 9 stout lateral spines (Fig. 16j).

Type locality. Gulf St. Vincent, South Australia.

Remarks. COI and 16S rRNA sequences from individuals of this species suggest that they are *Oratosquillina inornata*, a common shallow-sea species in Taiwan (GenBank accession no. MH168266 and MH168220; genetic K2P distances: COI: < 0.47%; 16S rRNA: < 0.23%). Like *C. multicarinata* above, there are several crucial morphological features in adults but not juveniles: the anterior part of the carapace and a bracket-shaped pair of ridges separated from the median ridge behind in adults (Fig. 16a).

Oratosquilla oratoria (De Haan, 1844)

Fig. 17

Description (based on individual CEL-stom-080). Juvenile, CL 4.2 mm, TL 20.0 mm. Specimen squilloid-type, overall with dark spots arranged into short longitudinal lines symmetrical along midline. Eyestalks stout, cornea inflated as adult individuals. Rostral plate triangular, median carina distinct (Fig. 17a). Carapace overall glabrous, along midline bearing faint but discernable carina, anteriorly bifurcated, almost continuous, followed by dorsal pit; gastric groove marked, extending from anterior margin to 9/10 carapace length; IM and LT carinae marked (Fig. 17a). Mandibular

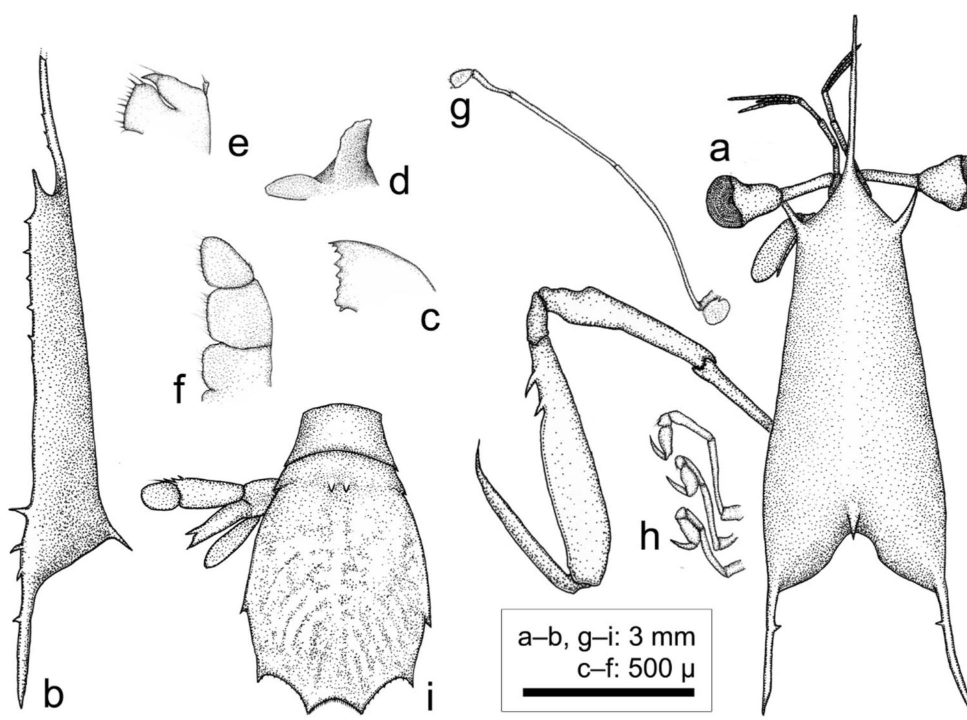

Fig. 15 *Oratosquillina inornata* (Tate, 1883) (alima larva: CEL-stom-050): **a** carapace and left maxilliped 2, dorsal view; **b** carapace, lateral view; **c** left mandible, posterior view; **d** left mandible, mesial view; **e** left maxillule; **f** left maxilla; **g** left maxilliped 1; **h** left maxillipeds 3 to 5; **i** telson and left uropod

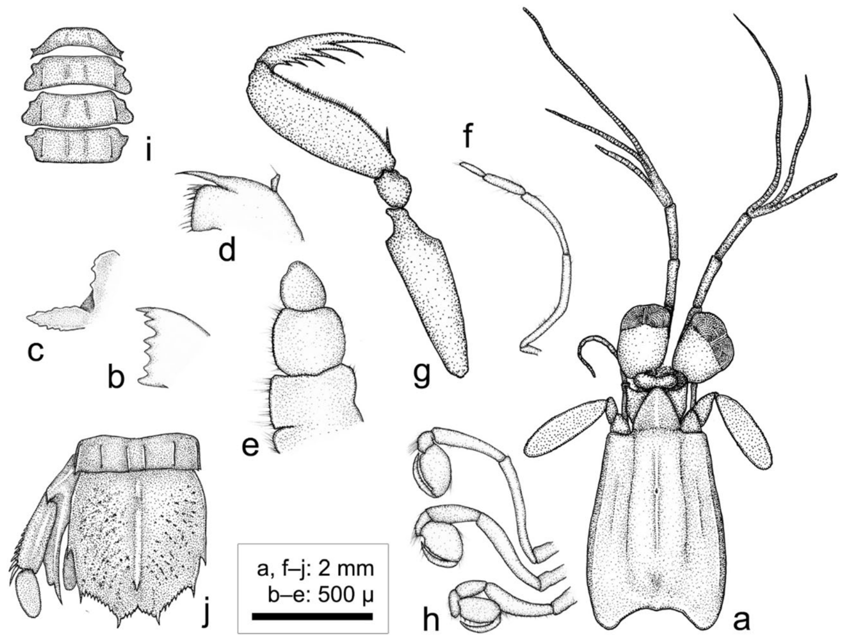

Fig. 16 *Oratosquillina inornata* (Tate, 1883) (juvenile: CEL-stom-048): **a** carapace; **b** left mandible, posterior view; **c** left mandible, mesial view; **d** left maxillule; **e** left maxilla; **f**–**h** left maxillipeds 1 to 5; **i** thoracic somites 5 to 8; **j** telson and left uropod

palp absent. Anterior 4 maxillipeds epipod-bearing, which of anterior 2 more pronounced, those of 3 and 4 smaller, rounded; raptorial appendage robust, propodus proximally armed with 2 slender movable spines, occlusal margin pectinated; dactylus armed with 6 spines (Fig. 17g). TS5 to 8 bearing distinct SM and LT carinae, TS5 to 7 laterally bilobed (Fig. 17k). AS1 to 6 each armed with pronounced SM, IM and LT carinae, SM carinae of AS6 produced posteriorly. Telson longer than broad, MD carina well-defined, prominent, posteriorly terminating with a distinct spine; SM teeth fixed, separated medially by narrow V-shaped notch, on each side armed with 5 SM denticles; IM (IMD 8) and LT carinae prominent (Fig. 17l). Uropod robust, protopod bifurcated, mesial tooth bearing a pronounced rounded lobe in outer margin; exopod penultimate segment laterally armed with 7 stout LT spines (Fig. 17l).

Type locality. Japan, precise locality unspecified.

Remarks. Morphological features of juveniles of this form match well with those of *O. oratoria*, including bilobed lateral processes of TS5 to 7 (Fig. 17k) and anteriorly bifurcated median carina on carapace (Fig. 17a). Juveniles examined, however, appear to differ from typical adult forms by a weakly indicated anterolateral spine, and telson with prelateral lobe nearly undefined (Fig. 17l). Molecular analyses show that the COI and 16S rRNA sequences of the material examined match well with those of *O. oratoria* (GenBank accession no. MH168274 and MH 168214; genetic K2P distances: 0.31 to 0.78% for COI and < 0.45% for 16S rRNA).

Discussion

Although taxonomic accuracy of metazoan mitochondrial gene sequences in GenBank is generally considered reliable (Leray et al. 2019; Meiklejohn et al. 2019), caution should be maintained on credibility of individual sequences. In the present study, we have used two marker genes and the results were largely consistent. Furthermore, some of the sequences cluster with reference sequences with high support value (such as *Lysiosquillina maculata* clade in 16S rRNA NJ tree: Fig. 2b). As such, we are confident that the taxonomic assignments made in the present study being reliable. In this study, based on COI and 16S rRNA gene sequences, 14 morphotypes of stomatopods larvae/juveniles are revealed, representing 12 distinct species, five of which could not be assigned with certainty to species level based on comparisons to sequences currently in GenBank. We herein report erichthus larva assigned to *Manningia pilaensis* (De Man, 1888) and a postlarva of *Levisquilla jurichi* (Makarov, 1979), as new records of Taiwan.

The planktonic stomatopod larvae collected using light traps comprised of several postlarval and juvenile forms, among which squilloid species (Squillidae) were especially prominent. This shows that the transition of phototactic behavior from planktonic to postlarval (settlement) stages may not be as distinct as previously assumed (see Dingle 1969; Morgan and Goy 1987). Additionally, large quantities of antizoea larvae of *Lysiosquillina maculata* (more than 70 individuals, represented by eight sequenced samples above) were captured, and these “premature” juveniles, not yet equipped with thoracic appendages, a feature that is unique to the lysiosquilloids, are at least positively phototactic at some point during this phase.

Two recorded species belong to the Gonodactylidae, a group of stomatopods which found to be species-rich in reef-associated habitats were recorded. One species was assigned as *Gonodactylus smithii* (which is involved in a

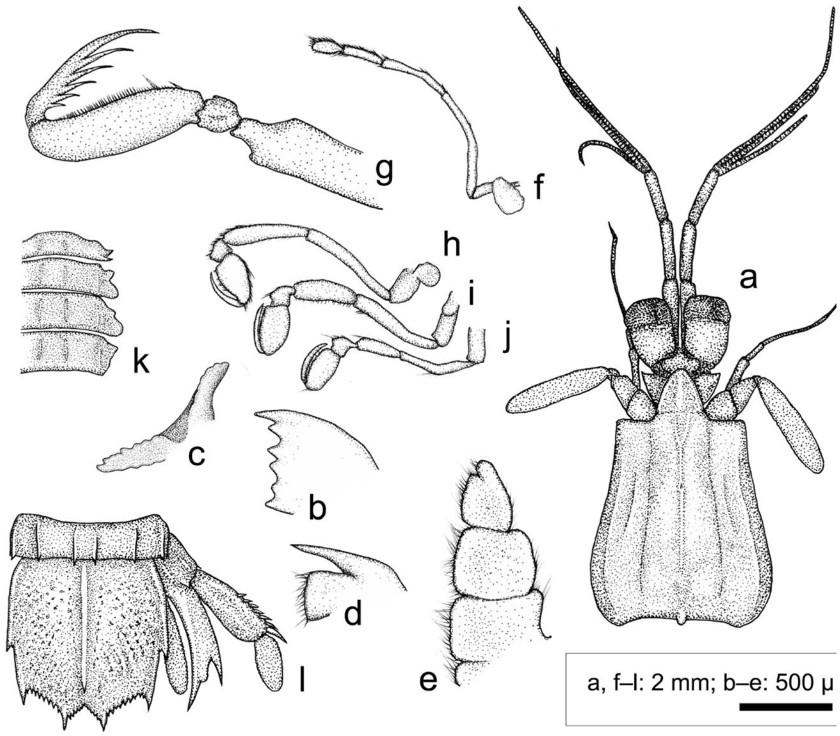

Fig. 17 *Oratosquilla oratoria* (De Haan, 1844) (juvenile: CEL-stom-080): **a** carapace; **b** left mandible, posterior view; **c** left mandible, mesial view; **d** left maxillule; **e** left maxilla; **f–j** left maxillipeds 1 to 5; **k** thoracic somites 5 to 8; **l** telson and uropod

yet-deciphered species complex, see above), reported by Ahyong et al. (2008) as a coral reef species from various sites in Taiwan. Among those sites was Danshuei, Taipei, which a pronouncedly estuarine locality, indicating substantial plasticity in habitat preference, and the present record from CCA reefs in Taoyuan is not surprising. The remaining eight species, three of the Nannosquillidae and five of Squillidae, generally prefer habitats with soft substrates (see also discussions on the ecology of *Pullosquilla* by Wang and Chiou (2017)). It appears the planktonic larvae and juveniles of these species also utilize and take advantage of the more complex structure of algae reefs in these shallow, murky waters, emphasizing the ecological value of this precious habitat.

The stomatopod fauna of Taiwan has been relatively well documented in the past decades, and was synthesized and illustrated in considerable detail by Ahyong et al. (2008). Post-2008 additions to the Taiwanese fauna include papers by Yeh and Hsueh (2010) and Wang and Chiou (2017), adding *Taku spinosocarinatus* (Fukuda, 1909), and three species of *Pullosquilla* (*P. litoralis* (Michel & Manning, 1971), *P. thomassini* (Manning, 1978), and *P. pardus* (Moosa, 1991)), respectively, making the total number of species 67. The present work, adopting molecular barcoding approaches on taxonomic assignment, added new records of *Manningia pilaensis* and *Levisquilla jurichi*, also confirming the validity of *Lysiosquillina maculata*, bringing the total number of stomatopod species in Taiwan to 70, which is comparable to the number of stomatopod species elsewhere in East Asia: 104 species in Chinese and adjacent seas (15 Taiwan-exclusive records included; Wang and Liu 2008), 68 from Japanese seas (Ahyong 2012), and 120 from the vicinity of the South China Sea (Moosa 2000). However, as Ahyong et al. (2008) argued, a considerable portion of the Taiwanese records was obtained from commercial trawlers, therefore heavily biased towards estuarine seas, and shallow to deeper depths on sandy-muddy substrates. The bias is reflected by the dominating richness of the Squilloidea (two-thirds of the Taiwanese fauna), a group common as burrowers in these habitats. Structures such as rocky and coral reefs, based on reported species counts of associated gonodactylids, were apparently poorly surveyed. The above findings show, despite decades of research, sampled by traditional surveying methods, fauna inhabiting structurally complex habitats such as reefs, are not as adequate in documenting stomatopod fauna of Taiwan. There is, nevertheless, high potential for an innovative approach that synergizes morphology-based taxonomy, molecular barcoding techniques, and online database resources.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This article does not contain any studies with animals performed by any of the authors.

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Data availability statement Authors deposited sequences of the specimens in NCBI GenBank (https://www.ncbi.nlm.nih.gov/genbank/).

Author contribution statement BKKC and RJM designed the study. PCT, BKKC, RJM, WPH, and HRL conducted field samplings and laboratory sorting. WPH conducted the SEM observations. YFT and HRL conducted molecular analysis. KW prepared line drawings. KW, BKKC, and YFT wrote the MS.

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