

A review of the mud crab genus *Pseudohelice* Sakai, Türkay & Yang, 2006 (Crustacea: Brachyura: Varunidae), with redescription of *Cyclograpsus latreillii* H. Milne Edwards, 1837, from the western Indian Ocean

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Abstract. Members of the genus *Pseudohelice* Sakai, Türkay & Yang, 2006 (family Varunidae) inhabit estuaries and high intertidal zone with sediments composed of mud and sand in tropical to temperate regions. Previous studies showed only one species, *Pseudohelice subquadrata* (Dana, 1851) in this genus, with a wide distribution in the Indo-West Pacific. In the present study, the species from the western Indian Ocean is shown to be a valid species, *Pseudohelice latreillii* (H. Milne Edwards, 1837), based on morphological and molecular evidence. The latter species had previously been incorrectly synonymised with *Helice tridens* (De Haan, 1835). The two species are very similar to each other in morphology, but can be distinguished by a suite of characters, including the structures of the infraorbital ridges in both sexes, male gonopods 1 and female vulvae. Based on the molecular evidence from cytochrome oxidase subunit 1 (COI), *P. subquadrata* and *P. latreillii* form two well-supported clades, and the intraspecific and interspecific divergences of COI are 0–1.9% and 3.3%–5.1%, respectively. Geographically, *P. subquadrata* is distributed in the western Pacific while *P. latreillii* occurs in the western Indian Ocean.

Key words. taxonomy, *Pseudohelice*, *P. subquadrata*, *P. latreillii*, morphology, genetics, mitochondrial cytochrome c oxidase subunit I (COI)

INTRODUCTION

The varunid mud crabs of the *Helice/Chasmagnathus* complex (family Varunidae) consist of several genera that inhabit intertidal areas with sediment composed of mud and sand in tropical, subtropical, and temperate regions (Sakai et al., 2006). Among them, *Pseudohelice* Sakai, Türkay & Yang, 2006, a genus of relatively small varunids, was established by Sakai et al. (2006) (as a subgenus, with a second subgenus, *Parahelice* Sakai, Türkay & Yang, 2006). Sakai et al. (2006) distinguished the subgenera *Pseudohelice* and *Parahelice* by the characters of infraorbital ridges and male gonopods 1. Subsequently, Ng et al. (2008) recognised them as distinct genera. With regard to *Pseudohelice*, only one species, *P. subquadrata* (Dana, 1851), is known, with wide distribution in Indo-West Pacific (Sakai et al., 2006).

Sakai et al. (2006) argued that the type locality of *Chasmagnathus subquadratus* Dana, 1851 should be New South Wales, Australia (Sakai et al., 2006: 43), and as such, they designated a male specimen (QM W 2269) from Sydney as the neotype of the species. They considered *Helice leachii* Hess, 1865 (type locality in Sydney, Australia) to be a junior subjective synonym of *C. subquadratus*. In addition, Sakai et al. (2006) examined two supposed syntypes of *Cyclograpsus latreillii* (type locality, “Ile de France” = Mauritius) deposited in the Museum national d’Histoire naturelle, Paris (MNHN) and found that they belonged to different species. The male specimen (MNHN-B4647S) was identified as *Helice tridens* De Haan, 1835 and designated as the lectotype of *C. latreillii*; and the female paralectotype (MNHN-B 3468S) was referred to *P. subquadrata* (Sakai et al., 2006). As a result, *C. latreillii* became a junior synonym of *H. tridens*.

The character of the three anterolateral teeth is a major character that distinguishes *Pseudohelice* and *Parahelice* from *Helice* s. str., and both have been reported from the West Indian Ocean (WIO) (Sakai et al., 2006). After examining a series of specimens originally identified as “*P. subquadrata*” collected from Mauritius, Kenya, and the Red Sea, we found a suite of reliable characters, which separate them from material of *Pseudohelice subquadrata* s. str. from the West Pacific. The molecular evidence from mitochondrial cytochrome oxidase subunit I (COI) also supports both being distinct clades. To determine the name for the WIO population, we re-examined the various synonyms

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Table 1. Haplotypes of the cytochrome c oxidase subunit I (COI) gene of specimens of *Pseudohelice* from the Indo-West Pacific and the outgroups *Parahelice* species. The numbers within brackets after the localities correspond to those in Figure 4.

Species	Locality	Catalogue no.	Sample size	Haplotype	Access. no. of COI
<i>Pseudohelice subquadrata</i>	Japan: Miyako, Ryukyus [1]	NCHUZOO 13102	1	Ps1	AB334557
	Taiwan: Gangnan, Hsinchu City [2]	NCHUZOO 15724	1	Ps2	LC511075
	Taiwan: Sinfeng, Hsinchu County [2]	NCHUZOO 15723	1	Ps3	LC511076
	Taiwan: Dingtouer Shoal, Tainan [3]	NCHUZOO 15731	1	Ps4	LC511077
	Taiwan: Yanshuei R., Tainan [3]	NCHUZOO 15726	1	Ps5	LC511078
	Taiwan: Wanlitong, Pingtung [4]	NCHUZOO 15733	2	Ps6	LC511079
	Taiwan: Dongsha Island [5]	NCHUZOO 15725	1	Ps7	LC511080
	Guam [6]	ZRC 2013.1034	1	Ps8	LC511081
	Indonesia: Bali [7]	NCHUZOO 15722	1	Ps2	LC511082
	Indonesia: Bali [7]	NCHUZOO 15727	1	Ps9	LC511083
	Australia: SE Queensland [8]	QM W19922	1	Ps10	LC511084
Australia: SE Queensland [8]	QM W19922	1	Ps11	LC511085	
<i>Pseudohelice latreillii</i>	Egypt: Nabq-El Arwashie, Sinai [9]	MZUF 3790	1	PL1	MZ400781
	Kenya: Mida Creek [10]	MZUF 4985	1	PL2	MZ400782
	Kenya: Mida Creek [10]	MZUF 4993	1	PL2	MZ400783
	Kenya: Gazi [11]	MZUF 4987	1	PL3	MZ400784
	Kenya: Mida Creek [10]	NCHUZOO	1	PL4	MZ400785
	Seychelles: Mahé, Port Launay [12]	MZUF 2935	1	PL3	MZ400786
	Mauritius: Poste Lafayette [13]	MZUF 4994	2	PL2	MZ400787; MZ400788
	Mauritius: Melville [13]	MZUF 4997	1	PL2	MZ400789
	Mauritius: Rodrigues I. [14]	MZUF 4991	1	PL2	MZ400790
	Mauritius: Rodrigues I. [14]	MZUF 4999	1	PL2	MZ400791
Outgroups					
<i>Parahelice daviei</i>	Taiwan: Gangkou R., Pingtung	NCHUZOO 15717	1		LC511052
<i>Parahelice pilimana</i>	Taiwan: Baoli R., Pingtung	NCHUZOO 15681	1		LC511064
<i>Parahelice pilosa</i>	Taiwan: Gangkou R., Pingtung	NCHUZOO 15700	1		LC511071

that have been associated with species of *Helice*, *Helicana*, *Pseudohelice*, and *Parahelice*; and realised that the proposed synonymy of *Cyclograpsus latreillii* H. Milne Edwards, 1837 with *Helice tridens* De Haan, 1835 is incorrect, and that this name is actually applicable to our material.

In this study, *Cyclograpsus latreillii* H. Milne Edwards, 1837 is recognised as a valid taxon, with distribution in the WIO. We here redescribe *Pseudohelice latreillii* (H. Milne Edwards, 1837), discuss and resolve the nomenclatural

problems with this name, and provide molecular evidence of COI to support this species.

MATERIAL AND METHODS

Specimens of *Pseudohelice* collected from the West Pacific and those deposited in museums or institutes were examined (Table 1), including the Muséum national d'Histoire naturelle, Paris, France (MNHN); the Museo Zoologico

TAXONOMY

Superfamily Grapsoidea MacLeay, 1838

Family Varunidae H. Milne Edwards, 1853

Genus *Pseudohelice* K. Sakai, Turkey & Yang, 2006*Pseudohelice subquadrata* (Dana, 1851)

(Figs. 1, 2)

For other synonyms before 2006, see Sakai et al. (2006).

Chasmagnathus subquadratus Dana, 1851: 251 (type locality: possibly New South Wales, Australia).*Helice leachii*—Sakai, 1939: 698, text-fig. 126; Takeda, 1982: 223, fig. 662; Dai et al., 1986: 505, fig. 286(5–6), pl. 72(1).*Helice leachi*—Miyake, 1983: 241 (list); Sakai, 1976: 672, text-figs. 370a, b, pl. 228(2).*Helice (Helice) leachii*—Dai & Yang, 1991: 553, fig. 286(5–6), pl. 72(1).*Pseudohelice (Pseudohelice) subquadrata*—Sakai et al., 2006: 37, figs. 53–59 (part).*Pseudohelice subquadrata*—Shih, 2007: 22, figs. 45–48; Sun et al., 2009: 325 (China: Hainan); Liu & Wang, 2010: 69, 2 unnumb. figs. (Taiwan); Nishigaki et al., 2011: 87, fig. 1E–H (Ryukyus); Komatsu, 2011: 277 (list) (Japan: Ogasawara Is.); Japanese Association of Benthology, 2012: 203, 1 unnumb. fig.; Shih, 2012: 94, figs. 133–135 (Taiwan: Dongsha I.); Ko & Lee, 2012: 40 (Korea); Li & Chiu, 2013: 61 (part), 1 unnumb. fig. (upper left only) (Taiwan); Lee et al., 2013: 106, 2 unnumb. figs. (Taiwan); Pratiwi & Rahmat, 2015: 198 (Indonesia: Jakarta); Ng et al., 2017: 110 (list); Li & Chiu, 2019: 94, 3 unnumb. figs. (Taiwan); Toyota et al., 2019: 280, 5 unnumb. figs. (Japan: Ryukyus); Kim et al., 2020: fig. 1B (Korea); Shih, 2020: 126, figs. 153–155 (Taiwan: Dongsha I.); Shih et al., 2020: 251, tab. 1; Itoh, 2020: 49, fig. 2 (Japan: Izu Peninsula); Inui et al., 2021: 138, fig. 2D (Japan: Sagami Bay).*Pseudohelice quadrata* [sic]—Ng et al., 2008: 227 (list).not *Pseudohelice subquadrata*—Bouchard, 2009: 6, 28 (Mayotte) (= *Parahelice balssi* (Sakai, Turkey & Yang, 2006)); Bouchard et al., 2009: 23, 45 (list) (Mayotte) (= *Parahelice balssi* (Sakai, Turkey & Yang, 2006)); Li & Chiu, 2013: 61 (part): 2 unnumb. fig. (upper right = *Parahelice daviei* (Sakai, Turkey & Yang, 2006)); lower = *Parahelice pilosa* (Sakai, Turkey & Yang, 2006)); Bouchard et al., 2013: 29, fig. 24 (Mayotte) (= *Parahelice balssi*); Poupin et al., 2018: 73 (Mayotte) (= *Parahelice balssi* (Sakai, Turkey & Yang, 2006)).**Material examined.** Australia: 1 male (19.2 × 17.1 mm), 1 female (20.9 × 18.3 mm) (QM W19922), Elimbah Creek, Toorbul, SE Queensland, coll. P. Davie, 5 July 1994; 2 males (16.4 × 8.8, 20.0 × 17.4 mm), 1 female (14.7 × 12.0 mm) (MNHN-IU-2013-14771 = MNHN-B20874), South West Rocks, Trial Bay, New South Wales, coll. 1920 (identified by M. Turkey in 1983 as *Helice leachii* Hess, 1865). New Caledonia: 2 males (18.8 × 11.9, 23.8 × 20.6 mm), 1 female (25.5 × 21.7 mm) (MNHN-IU-2013-8633), Nouméa, coll. R. Serène, 10 August 1971 (identified by S.-L. Yang in 1993 as *Pseudohelice subquadrata* (Dana, 1851)). Japan: 1 male (11.3 × 9.7 mm), 1 female (12.8 × 11.2 mm) (NCHUZOO 16696), Hiyagon Swamp, Okinawa I., Ryukyus, 20 June 2005; 1 male (16.2 × 13.8 mm) (NCHUZOO 16705),

dell'Università di Firenze, Italy (MZUF); the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOO); the Queensland Museum, Brisbane, Australia (QM); and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore (ZRC).

Morphological characters were illustrated with the aid of the drawing tube attached to a stereomicroscope. The morphological characters and terminology used follow those of Sakai et al. (2006), Guinot et al. (2013), and Davie et al. (2015). The abbreviation G1 is used for the male first gonopod. Measurements of the maximum carapace width (CW) and carapace length (CL) are all in millimetres (mm).

Genomic DNA was isolated from the muscle tissue of legs or chelipeds using the GeneMark tissue and cell genomic DNA purification kit (Taichung, Taiwan). A portion of the COI gene was amplified with PCR using the primers LCO1490, HCO2198, and COH6 (Folmer et al., 1994; Schubart & Huber, 2006). The PCR conditions for the above primers were denaturation for 50 seconds at 94°C, annealing for 70 seconds at 45–47°C, and extension for 60 seconds at 72°C (40 cycles), followed by another extension for 10 minutes at 72°C. Sequences were obtained by automated sequencing (Applied Biosystems 3730) after verification with the complementary strand. Sequences of different haplotypes have been deposited into GenBank, with other sequences published in Shih & Suzuki (2008) and Shih et al. (2020) (accession numbers given in Table 1). Outgroups were selected based on the phylogeny in Shih et al. (2020: fig. 8), viz. *Parahelice daviei* (Sakai, Turkey & Yang, 2006), *Par. pilimana* (A. Milne-Edwards, 1873) and *Par. pilosa* (Sakai, Turkey & Yang, 2006).

The best-fitting model for sequence evolution was determined by PartitionFinder (ver. 2.1.1, Lanfear et al., 2017) and was selected by the Bayesian information criterion (BIC). The obtained best model (GTR+G) was subsequently used for a Bayesian inference (BI) analysis. The BI analysis was performed with MrBayes (ver. 3.2.3, Ronquist et al., 2012). Phylogenetic analyses were run with four chains for 10 million generations and four independent runs, with trees sampled every 1,000 generations. The convergence of chains was determined by the average standard deviation of split frequency values below the recommended 0.01 (Ronquist et al., 2005), and the first 700 trees were accordingly discarded as burnin. A maximum likelihood (ML) analysis was conducted in RAxML (ver. 7.2.6, Stamatakis, 2006). The GTR+G model (i.e., GTRGAMMA) was used with 100 runs, and the best ML tree was determined by comparing likelihood scores. The robustness of the ML tree was evaluated by 1,000 bootstrap pseudoreplicates under the GTRGAMMA model. Basepair (bp) differences and pairwise estimates of Kimura 2-parameter (K2P) distances (Kimura, 1980) for genetic diversities between specimens were calculated with MEGA (ver. 10.0.5, Kumar et al., 2018).

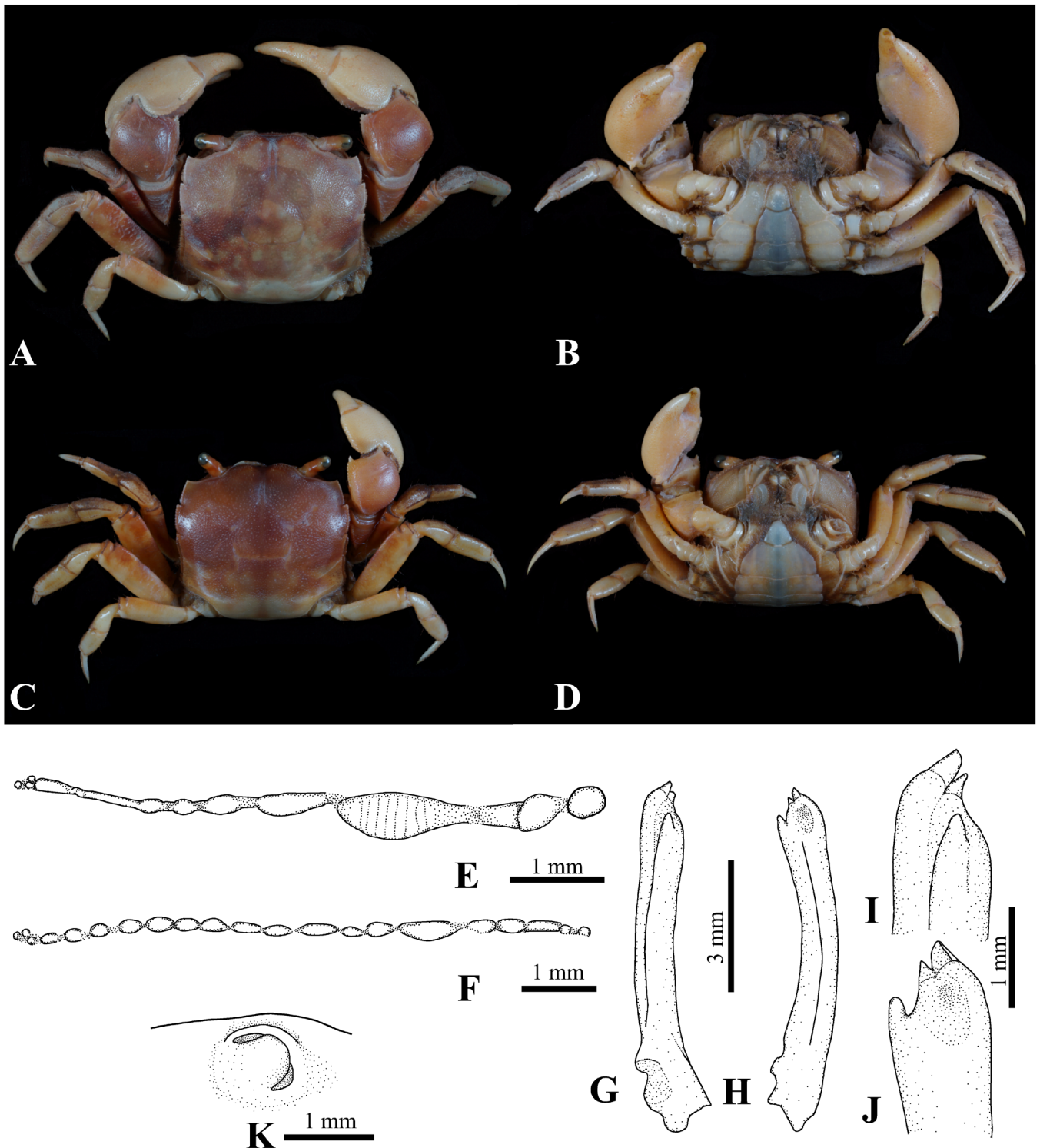


Fig. 1. *Pseudohelice subquadrata* (Dana, 1851). A, B, E, G–J, male (19.2 × 17.1 mm, QM W19922); C, D, F, K, female (20.9 × 18.3 mm, QM W19922); A–D in preservative. A, dorsal view of male; B, ventral view of male; C, dorsal view of female; D, ventral view of female; E, left male infraorbital ridge; F, left female infraorbital ridge; G, I, dorsal view of left G1 (horizontally flipped); H, J, ventral view of left G1 (horizontally flipped for comparison with the right G1s of other specimens); K, right vulva.

Miyara R., Ishigaki I., Ryukyus, 2 August 2005. Taiwan: 1 male (13.2 × 11.0 mm) (NCHUZOO 13218), Wazihwei, New Taipei City, 17 November 1995; 1 male (9.5 × 7.9 mm) (NCHUZOO 16697), Tiaoshih coast, New Taipei City, 25 July 2002; 2 females (14.8 × 12.4, 16.8 × 14.3 mm) (NCHUZOO 16177), Jhuwei, New Taipei City, 1 June 2007; 2 males (14.4 × 12.1, 15.9 × 13.5 mm), 2 females (14.7 × 12.2, 17.7 × 15.1 mm) (NCHUZOO 16178),

Jhuwei, New Taipei City, 30 June 2006; 2 females (13.6 × 11.5, 16.0 × 13.5 mm) (NCHUZOO 16181), Houhu R., Taoyuan City, coll. P.-Y. Hsu & Y.-H. Huang, 2 September 2011; 1 female (13.4 × 11.2 mm) (NCHUZOO 15724), Gangnan, Hsinchu City, 19 July 2012; 3 males (19.3 × 16.5, 20.4 × 17.6, 20.9 × 18.2 mm) (NCHUZOO 15723), Sinfeng, Hsinchu County, 31 August 2012; 1 male (12.3 × 10.7 mm) (NCHUZOO 16698), Zhonggang R. estuary,



Fig. 2. *Pseudohelice subquadrata* (Dana, 1851), colour in life. A, dorsal view, male (15.6 × 13.1 mm, NCHUZOOL 16176, Dongsha I.); B, ventral view, male (15.6 × 13.1 mm, NCHUZOOL 16176, Dongsha I.); C, male (NCHUZOOL 16704, Dongsha I.); D, male (NCHUZOOL 16720, Dongsha I.); E, female (17.4 × 15.2 mm, NCHUZOOL 15727, Bali); F, male (18.0 × 14.7 mm, NCHUZOOL 16704, Dongsha I.); G, burrows of *P. subquadrata* (Hsinchu County: Sinfeng); H, habitat of *P. subquadrata* (Hsinchu County: Sinfeng).

Table 2. Comparison of characters of males and females between two species of *Pseudohelice*.

Characters	<i>P. subquadrata</i>	<i>P. latreillii</i>
Males		
infraorbital ridge	mesial part with several small tubercles, followed by several large, elongated and less convex tubercles; lateral part with 1 significantly largest, very convex and elliptical tubercle, and 2–5 large convex tubercles (Fig. 1E)	mesial part with several small, rounded tubercles, followed by several large, elongated and less convex tubercles; lateral part with 1 largest, very convex and rounded tubercle, and 2 larger rounded and convex tubercles (Fig. 3E)
G1s	stouter and blunter, upper part slightly flatter; chitinous structure at top relatively smaller and thinner, tip pointed (Fig. 1G–J)	more slender, upper part tubular; chitinous structure at top relatively wider, shorter and thicker, tip blunter (Fig. 3H–K)
Females		
infraorbital ridge	mesial part with several dense, small tubercles, followed by several closely spaced, larger tubercles, lateral part with 1 largest elongated tubercle and 2–5 larger convex tubercles (Fig. 1F)	form I: mesial part with several tubercles, followed by several well-spaced, isomorphically rounded tubercles in lateral part (Fig. 3F) form II: mesial part with several well-spaced and larger tubercles, followed by several well-spaced, small tubercles, lateral part with 1 largest and 2–5 larger convex tubercles (Fig. 3G)
vulva	longer semicircular sternal vulvar cover (Fig. 1K)	shorter semicircular sternal vulvar cover (Fig. 3L, M)
distribution	from eastern Indian Ocean to West Pacific (Fig. 4)	WIO, including Red Sea, eastern Africa, Mauritius, and Rodrigues I. (Fig. 4)

Houlong, Miaoli, 30 May 2014; 2 males (12.8 × 10.9, 13.0 × 11.2 mm) (NCHUZOOOL 16699), Jhonggang R. estuary, Houlong, Miaoli, 30 May 2014; 1 male (12.8 × 10.9 mm) (NCHUZOOOL 16180), Dingtouer Shoal, Cigu, Tainan, coll. J.-H. Lee & W.-C. Wang, 23 February 2010; 1 female (15.3 × 13.0 mm) (NCHUZOOOL 15731), Dingtouer Shoal, Cigu, Tainan, coll. J.-H. Lee & W.-C. Wang, 23 February 2010; 1 male (14.9 × 13.0 mm), 2 females (16.2 × 13.5, 17.2 × 14.9 mm) (NCHUZOOOL 16718), Dingtouer Shoal, Cigu, Tainan, coll. J.-H. Lee & W.-C. Wang, 23 February 2010; 7 males (13.6 × 11.8–17.6 × 15.1 mm), 7 females (14.6 × 12.2–18.0 × 15.1 mm) (NCHUZOOOL 16719), Dingtouer Shoal, Cigu, Tainan, coll. J.-H. Lee & W.-C. Wang, 23 February 2010; 1 male (16.6 × 14.8 mm), 2 females (17.3 × 14.5, 18.8 × 16.0 mm) (NCHUZOOOL 15726), Yanshuei R., Tainan, coll. J.-H. Lee & W.-C. Wang, 9 November 2009; 2 males (8.0 × 6.7, 8.1 × 6.9 mm) (NCHUZOOOL 16183), Baoli R. estuary, Checheng, Pingtung, 3 September 2011; 1 female (12.1 × 10.3 mm) (NCHUZOOOL 16184), Baoli R. estuary, Checheng, Pingtung, coll. J.-H. Lee & W.-C. Wang, 1 March 2010; 1 male (8.3 × 7.0 mm) (NCHUZOOOL 16182), Wanlitong, Pingtung, 20 December 2011; 1 male (12.7 × 10.7 mm), 2 females (11.6 × 9.9, 14.5 × 12.4 mm) (NCHUZOOOL 15733), Wanlitong, Pingtung, coll. J.-H. Lee, 20 August 2012; 3 males (7.8 × 6.6, 10.3 × 8.8, 13.0 × 11.2 mm), 2 females (9.9 × 8.3, 12.1 × 10.3 mm) (NCHUZOOOL 16185), Gangkou R. estuary, Hengchun, Pingtung, coll. P.-Y. Hsu et al., 7 November 2018; 1 female (16.1 × 13.4 mm) (NCHUZOOOL 16706), Dulanwan, Donghe, Taitung, 9 August 2017; 1 male (13.7 × 11.8 mm) (NCHUZOOOL 15725), Dongsha I., 2 September 2011; 2 males (14.7 × 12.5, 15.6 × 13.1 mm), 2 females (16.6 × 14.0, 16.8 × 14.3 mm) (NCHUZOOOL

16176), Dongsha I., 2 September 2011; 1 female (18.2 × 15.4 mm) (NCHUZOOOL 16179), Dongsha I., 6 September 2011; 1 male (17.8 × 14.7 mm), 1 female (13.9 × 11.5 mm) (NCHUZOOOL 16700), Dongsha I., 22 March 2012; 1 male (11.9 × 10.3 mm), 1 female (15.9 × 12.9 mm) (NCHUZOOOL 16701), Dongsha I., 25 May 2012; 2 males (12.6 × 10.9, 15.5 × 13.5 mm) (NCHUZOOOL 16702), Dongsha I., 29 May 2012; 1 male (12.6 × 10.8 mm) (NCHUZOOOL 16703), Dongsha I., 3 September 2011; 1 male (18.0 × 14.7 mm) (NCHUZOOOL 16704), Dongsha I., 5 September 2011; 1 female (17.0 × 14.5 mm) (NCHUZOOOL 16716), Dongsha I., 2 September 2011; 1 male (17.2 × 15.1 mm), 1 female (15.3 × 12.7 mm) (NCHUZOOOL 16717), Dongsha I., 24 March 2012; 1 male (12.5 × 10.5 mm) (NCHUZOOOL 16720), Dongsha I., 3 September 2011; 1 male (15.1 × 12.6 mm), 1 female (14.7 × 12.4 mm) (NCHUZOOOL 16721), Dongsha I., 2 September 2011; 1 male (16.0 × 14.1 mm), 1 female (18.1 × 15.1 mm) (NCHUZOOOL 16722), Dongsha I., 17 November 2012; 1 male (16.3 × 13.1 mm) (NCHUZOOOL 16723), Dongsha I., 22 July 2012. Indonesia: 1 female (5.9 × 5.2 mm) (NCHUZOOOL 15722), Gadon Beach, Tabanan, Bali, 22 July 2014; 5 females (15.5 × 13.2, 16.4 × 14.0, 16.7 × 14.5, 17.4 × 15.2, 17.5 × 15 mm) (NCHUZOOOL 15727); Gadon Beach, Tabanan, Bali, 22 July 2014.

Diagnosis. Carapace (Fig. 1A, C) quadrate, slightly broader than long, 1.18 times as broad as long; surface convex, weakly punctate, granulated, with noticeable groove between epigastric regions. Frontal margin slightly concave. Anterolateral margins with 3 teeth including orbital tooth; last tooth weak, sometimes indistinct. Infraorbital ridge (Fig. 1E, F) in both sexes heteromorphic; in male, mesial part

with several small rounded or elongated tubercles, followed by well-spaced several large, heteromorphic, elongated and less convex tubercles, lateral part with 1 significantly largest, elliptical and very convex tubercle, and 2–5 large convex tubercles (Fig. 1E); in female, mesial part with several dense small rounded tubercles, followed by closely spaced several larger, elongated and less convex tubercles, lateral part with 1 largest and 2–5 larger convex tubercles (Fig. 1F); tubercles in lateral part more convex in male, less convex in female. Cheliped palm bulky, almost glabrous; usually unequal in adult male, equal in adult female. Ambulatory legs (Fig. 1A–D) slender, anterior margins of merus, carpus, and propodus covered with dense short setae. Male G1 (Fig. 1G–J) stout, blunter, distal part relatively flat with small chitinous beak-like structure distally; female vulvae (Fig. 1K) with an elongated semi-circular sternal vulvar cover; sunken on inner part.

Colour in life. Varied, from yellowish-brown, orange, olive green, dark green, dark purple to dark grey, with several irregular light brown or white patches on carapace in some individuals. Colour of chelipeds usually lighter (except dorsal margins of palms), often light brown or off-white (Fig. 2).

Ecology. The habitats include mudflats, mangroves, and marginal areas of coastal forest. It is sympatric with some species of *Parahelice* in Taiwan (Shih et al., 2020).

Distribution. French Polynesia, Samoa, Fiji, New Caledonia, E. Australia, Caroline Is., Guam, Japan (including Ryukyus and Ogasawara Is.), Korea (Jejudo), Taiwan, China (Hainan), Philippines, Indonesia (Sulawesi, Bali, and Lombok) and western Thailand (Surin I., Phang Nga) (Sakai et al., 2006; this study) (Fig. 4).

Size. The largest male specimen examined is CW 20.9 mm (NCHUZOO 15723), and female is CW 20.9 mm (QM W19922).

Remarks. Sakai et al. (2006) selected a male specimen (QM W2269) from Sydney as the neotype of *P. subquadrata* (Sakai et al., 2006: figs. 53–59). In our study, the specimens collected from SE Queensland (QM W19922) agree with the description in Sakai et al. (2006). This species is similar to *P. latreillii* but can be distinguished by the structures of the infraorbital ridges, G1s, and vulvae (see Remarks under *P. latreillii*; Table 2).

***Pseudohelice latreillii* (H. Milne Edwards, 1837)**

(Fig. 3)

Cyclograpsus latreillii H. Milne Edwards, 1837: 80 (Mauritius).
Helice latreilli—H. Milne Edwards, 1853: 190 (part) (Mauritius).
Pseudohelice subquadrata—Sakai et al., 2006: 37 (part) (Egypt, Kenya, Mauritius, Seychelles; “paralectotype” of *C. latreillii*); Naderloo, 2017: 360, fig. 32.4 (Socotra).
 ? *Pseudohelice subquadrata*—Hywel-Davies, 1994 (Oman); Naderloo et al., 2015: 408 (list) (Oman).

Material examined. Neotype male (16.6 × 14.0 mm) (MZUF 4991), Petit Gravier, Rodrigues I., Mauritius, coll.

M. Vannini, 9 July 1989; leg. M. Vannini. Egypt: 1 female (14.8 × 12.3 mm) (MZUF 3790), Nabq-El Arwashie, Sinai, coll. S. Barbaresi, A. Conti, S. Fratini & G. Innocenti, 15 October 2004. Kenya: 1 female (17.5 × 14.8 mm) (MZUF 4985), Mida Creek, coll. M. Vannini, March 1999; 1 female (17.8 × 15.1 mm) (MZUF 4993), Mida Creek, coll. M. Vannini, September 1998; 1 female (17.4 × 14.8 mm) (MZUF 4987), Gazi, coll. S. Cannicci, August 1998. Seychelles: 2 females (13.9 × 11.8, 14.6 × 12.2 mm) (MZUF 2935), Mahé, Port Launay, coll. S. Fratini, December 2005; 2 males (15.8 × 13.6, 18.7 × 16.3 mm) (MZUF 4989), Ile Moustiques, Aldabra, coll. M. Vannini, March 1979. Mauritius: 1 female (21.5 × 16.1 mm) (MNHN-IU-2000-3468 = MNHN-B3468); 1 female (17.5 × 14.5 mm) (MNHN-IU-2013-14768 = MNHN-B3468); 6 males (15.3 × 13.0, 18.4 × 16.6, 18.7 × 15.4, 19.1 × 16.6, 19.4 × 16.5, 19.8 × 16.9 mm), 2 females (16.3 × 14.0, 19.5 × 16.4 mm) (MNHN-IU-2013-14769 = MNHN-B12096), 4 males (14.0 × 12.2, 15.5 × 13.3, 16.5 × 14.4, 18.4 × 16.0 mm), 7 females (14.2 × 12.4, 15.9 × 13.4, 16.8 × 14.2, 16.9 × 13.7, 18.0 × 15.5, 19.3 × 15.9, 19.3 × 16.0 mm) (MNHN-IU-2013-14770 = MNHN-B12095), coll. M. Carié, 1913 (identified by M. Türkay in 1983 as *Helice leachii* Hess, 1865); 1 male (15.9 × 13.4 mm) (MZUF 4991), Petit Gravier, Rodrigues I., coll. M. Vannini, 9 July 1989; 1 male (18.5 × 16.0 mm) (MZUF 4999), Baie Aux Huitres, Rodrigues I., coll. M. Vannini, 8 July 1989; 4 males (14.8 × 12.3, 16.5 × 14.0, 17.0 × 14.7, 17.1 × 14.2 mm), 3 females (11.1 × 9.5, 14.2 × 12.2, 16.5 × 14.0 mm) (MZUF 4994), Poste Lafayette, coll. M. Vannini, 4 July 1989; 3 females (7.7 × 6.6, 9.8 × 8.2, 17.3 × 14.2 mm) (MZUF 4997), Melville, coll. M. Vannini, 1 July 1989.

Description. Carapace (Fig. 3A, C) quadrate, slightly broader than long, 1.18 times as broad as long; surface convex, weakly punctate, granulated, with noticeable groove between epigastric regions. Frontal margin slightly concave. Anterolateral margins with 3 teeth including orbital tooth; last tooth weak, sometimes indistinct. Posterolateral margins almost parallel, not divergent posteriorly, moderately sloping outwards; lateral and posterolateral margins regularly furnished with short, soft setae.

Infraorbital ridge (Fig. 3E) in male heteromorphic, mesial part with several small rounded tubercles, followed by several large, elongated and less convex tubercles, lateral part with 1 largest and very convex rounded tubercle, and 2 large rounded and convex tubercles; 2 forms in female, form I: mesial part with several small rounded tubercles, followed by well-spaced several small, isomorphically rounded tubercles in lateral part (Fig. 3F); form II: mesial part with several larger rounded tubercles, followed by well-spaced several small, heteromorphic, elongated and less convex tubercles, lateral part with 1 largest and 2–5 larger convex tubercles (Fig. 3G). Chelipeds (Fig. 3D) with palm bulky, almost glabrous; usually unequal in adult male and equal in adult female. Ambulatory legs (Fig. 3A, B) slender, anterior margins of merus, carpus, and propodus covered with dense short setae; posterior margins with sparse short setae. Male G1 (Fig. 3H–K) slender, weakly tapering, slightly curved towards lateral end, with a pointed tip, distal

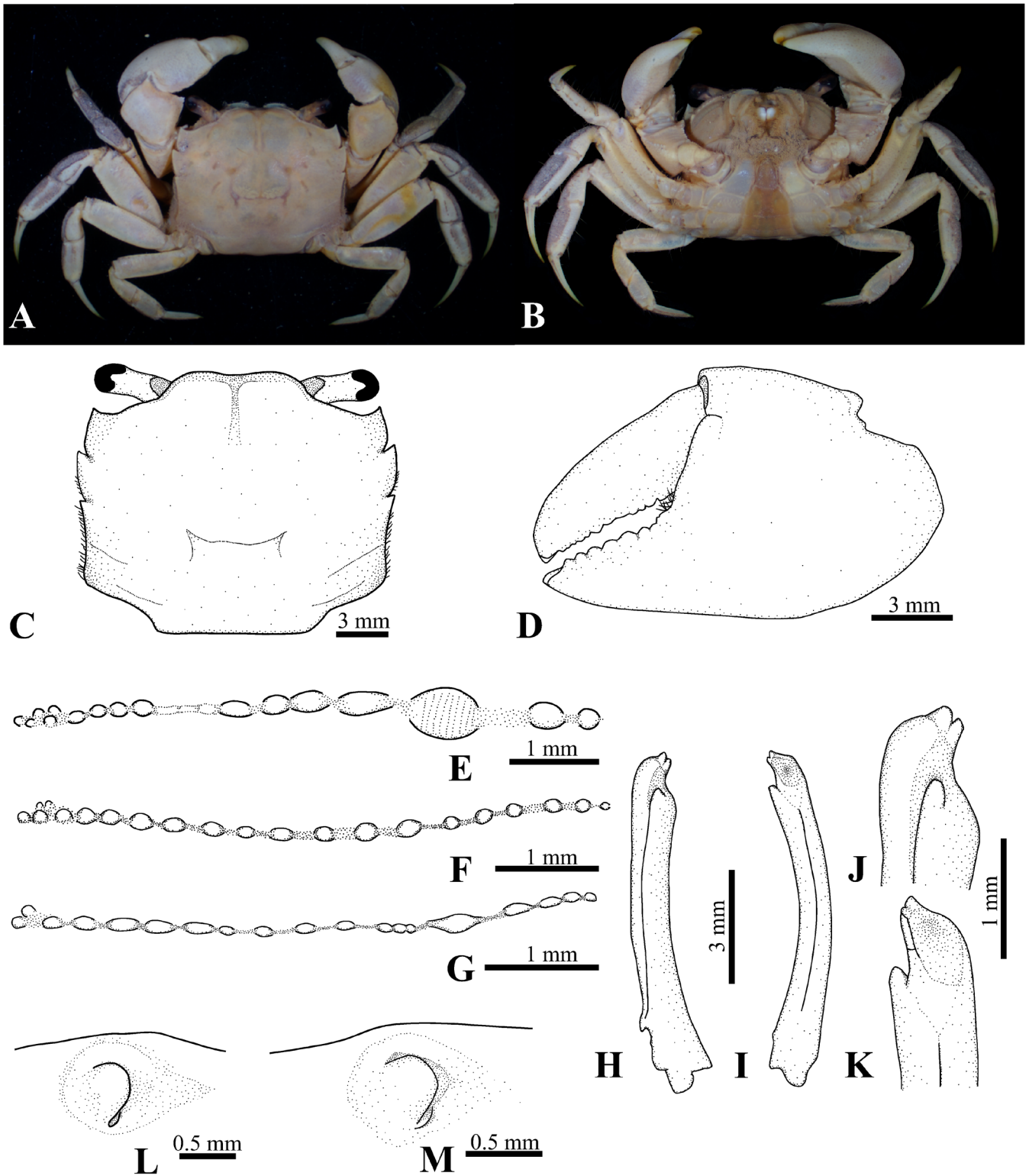


Fig. 3. *Pseudohelice latreillii* (H. Milne Edwards, 1837). A–D, H–K, male (16.6 × 14.0 mm, neotype, MZUF 4991); F, L, female (17.3 × 14.2 mm, MZUF 4997); G, M, female (14.6 × 12.2 mm, MZUF 2935). A, dorsal view of male; B, ventral view of male; C, carapace; D, outer view of male left cheliped; E, left male infraorbital ridge; F, G, left female infraorbital ridge (F, form I; G, form II); H, J, dorsal view of right G1; I, K, ventral view of right G1; L, M, right vulva.

part slightly V-shaped, bilobed; female vulvae (Fig. 3L–M) with an elongated semi-circular sternal vulvar cover; sunken on inner part.

Size. Largest male CW 18.7 mm (MZUF 4989), largest female CW 17.5 mm (MZUF 4985).

Distribution. Oman (?), Yemen (Socotra I.), Egypt (Red Sea), Kenya, Seychelles, Mauritius, and Rodrigues I. (Sakai et al., 2006; Naderloo et al., 2015; this study; Fig. 4).

Remarks. After examining a series of specimens, identified as “*P. subquadrata*”, collected from Mauritius, Kenya, and the Red Sea, we found they have a suite of reliable characters

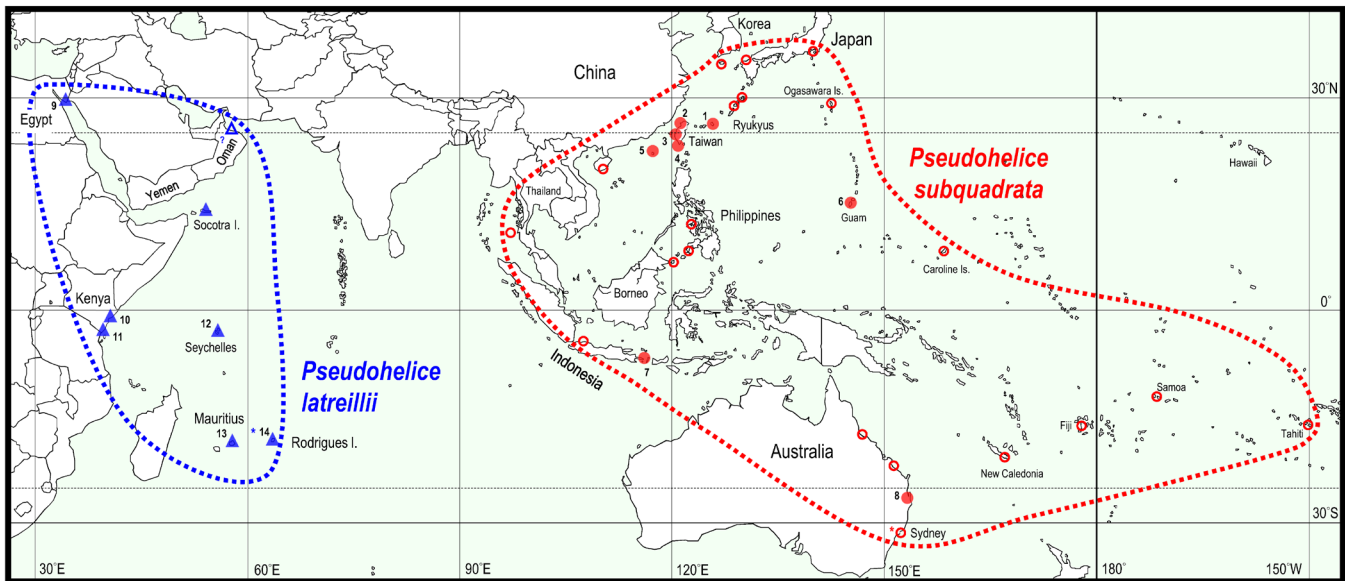


Fig. 4. The geographical distribution of *Pseudohelice subquadrata* (red dotted line) and *P. latreillii* (blue dotted line). The red solid circles are collection sites of specimens used in this study. The range was established by the additional records from references (see synonym lists for each species). The numbers correspond to the locality of specimens in Table 1. Empty triangles and circles mean the additional records from other references (see list of synonymies). “*” indicates the type locality.

different from those of *Pseudohelice subquadrata* from the West Pacific. The challenge was to decide which name should be applied to this second *Pseudohelice* species, or if it should be described as new. We here argue that the name *Cyclograpsus latreillii* H. Milne Edwards, 1837 should be applied to it.

In the collection of MNHN, three of H. Milne Edwards’ specimens of *Cyclograpsus latreillii* (2 dry and 1 regenerated in alcohol) from “Ile de France” (= Mauritius) have been found. The dry male specimen (MNHN-IU-2000-4647 = MNHN-B4647), with CW and CL of 33.7×27.2 mm is the lectotype of *C. latreillii* selected and identified as *Helice tridens* by Sakai et al. (2006: fig. 34). Sakai et al. (2006: 24) cited the measurements of the lectotype as 35.0×27.0 mm but in their caption for the photograph of the specimen, it was stated to be 35.0×28.0 mm (Sakai et al., 2006: 25); nevertheless, these are close enough to the present measurements. Sakai et al. (2006) commented that since *Helice tridens* is only known from East Asia, their lectotype of *Cyclograpsus latreillii* must have been incorrectly labelled as being from Mauritius. Another dry female (MNHN-IU-2000-3468 = MNHN-B3468) (21.5×16.1 mm) is the paralectotype of *C. latreillii* selected by Sakai et al. (2006) and was referred to *Pseudohelice subquadrata* by Sakai et al. (2006). A third female specimen (MNHN-IU-2013-14768 = MNHN-B3468) (ca. 17.5×14.5 mm), regenerated in alcohol and labelled as a syntype, was not examined by Sakai et al. (2006), but was identified as “*Pseudohelice leachi*” by M. Türkay in 1983 (not published); this taxon is now regarded as a junior synonym of *Pseudohelice subquadrata*. Photographs of both female specimens were examined, and the structure of their infraorbital ridges agree with the material from eastern Africa, i.e., the second species of *Pseudohelice*. The dry specimen (MNHN-IU-2000-3468) has the “form II” type of infraorbital ridge while the wet-preserved female (MNHN-IU-2013-14768) has “form I” type (see later).

Although these three MNHN specimens are labelled as syntypes, and Sakai et al. (2006) accepted their authenticity, selecting a lectotype in the process, we do not believe they are actually types. There are serious discrepancies in the description and measurements provided by H. Milne Edwards (1837) when compared to the three specimens. In his brief description of *C. latreillii*, H. Milne Edwards (1837: 80) wrote “Carapace presque quadrilatère, très-élevée et armée de trois dents de chaque côté.” [Carapace almost quadrilateral, very high, and armed with three teeth on each side]. Of the three supposed syntypes, only the two females of *Parahelice subquadrata* (MNHN-IU-2000-3468, 21.5×16.1 mm; MNHN-IU-2013-14768, ca. 17.5×14.5 mm), have three anterolateral teeth. The dry male of *Helice tridens* (MNHN-IU-2000-4647, 33.7×27.2 mm) has four anterolateral teeth and even though the last one is small, it is still visible and H. Milne Edwards is unlikely to have missed this tooth in his account. Henri Milne Edwards (1837: 80) also clearly stated that the CL of the species was “4 lignes” (ca. 9 mm). This size is substantially smaller than any of the three supposed syntypes. While H. Milne Edwards (1837) did not state how many specimens he had on hand, and it is possible that the 9 mm CL specimen H. Milne Edwards listed is now lost, it is still most unlikely that he would cite the smallest specimen he had in the publication and not measure the largest one! While *Pseudohelice subquadrata* has three anterolateral teeth, both the supposed syntypes are much larger than 9 mm CL; and the even larger supposed lectotype has four anterolateral teeth instead. Many years later, H. Milne Edwards (1853: 190) redescribed the taxon (as *Helice latreilli*), stating that it was a large species with four anterolateral teeth, the last being rudimentary; but he did not state how many specimens he had or provide sizes. The available evidence thus indicates that the three supposed specimens of *Cyclograpsus latreillii* now in MNHN are not syntypes, having been mislabelled in the past, and that the 9 mm CL specimen listed by H. Milne Edwards is now lost.

Table 3. Matrix of percentage pairwise nucleotide divergences with K2P distance and number of bp differences based on COI within and between the species *Pseudohelice subquadrata* (Dana, 1851) and *Pseudohelice latreillii* (H. Milne Edwards, 1837). In the right half, lower-left values are K2P distance and upper-right ones are bp differences. Range of values are given in parentheses.

	Intraspecific		Interspecific	
	Nucleotide divergence	bp difference	<i>P. subquadrata</i>	<i>P. latreillii</i>
<i>P. subquadrata</i>	0.8 (0–1.4)	5.05 (0–9)		25.1 (21–32)
<i>P. latreillii</i>	0.4 (0–1.9)	2.51 (0–12)	4.0 (3.3–5.1)	

Between 1837 when he named the species, and 1853 when he redescribed it, H. Milne Edwards probably obtained more specimens of this species, but these cannot be treated as types. This additional non-type material probably included the large male selected as the lectotype by Sakai et al. (2006), and someone incorrectly labelled the specimens as types.

As a result, the designation of lectotype and paralectotype by Sakai et al. (2006) is suggested to be invalid (Article 74.2, ICZN, 1999). The original description by H. Milne Edwards (1837) unfortunately is too brief and does not allow us to determine if the species is *Pseudohelice* or *Parahelice* as both genera occur in eastern Africa (Sakai et al., 2006). Sakai et al. (2006) reports “*Pseudohelice subquadrata*” from eastern Africa (which includes our present material) and described *Parahelice balssi* (Sakai, Türkay & Yang, 2006) from South Africa. *Cyclograpsus latreillii* can be either or neither taxon, and since the type(s) is here regarded as lost, the only objective way to resolve its identity is to select a neotype for the species. The two old non-type MNHN specimens (MNHN-IU-2000-3468, MNHN-IU-2013-14768) listed above are *Pseudohelice latreillii* as discussed, but both are not in good condition, and a male specimen is preferable as a neotype having more characters. In addition, considering the wrong provenance of the third specimen (the incorrectly designated lectotype male), we are not sure if they originated from Mauritius. Since *Parahelice balssi* is already described in detail and from South Africa (not yet known from Mauritius), for the purpose of nomenclatural stability, it is prudent to select a male specimen of the second species of *Pseudohelice* from eastern Africa (which is known from Mauritius) to be the neotype. Among material from the WIO, small specimens with ca. 9 mm CL (MZUF 4994 and MZUF 4997) also agree with the description of H. Milne Edwards (1837) in the shape of the carapace and the number of anterolateral margin teeth. We here select a male (16.6 × 14.0 mm) (MZUF 4991) collected from Rodrigues I., Mauritius as the neotype of *Cyclograpsus latreillii* H. Milne Edwards, 1837.

Morphologically, *Pseudohelice latreillii* is similar to *P. subquadrata* and the two can be easily confused. In both sexes of adults, no obvious difference was found in the characters of dorsal carapace, chelae, and ambulatory legs, but they can be distinguished by the forms of their infraorbital ridges, G1s, and vulvae (Table 2). For the males of *Pseudohelice latreillii*, the largest tubercle of the lateral part of the infraorbital ridges is rounded (Fig. 3E)

(vs. elliptical in *P. subquadrata*; Fig. 1E; Sakai et al., 2006: fig. 57); and the G1 is slenderer, the distal part is tubular, the chitinous structure at the top is relatively wider, shorter and thicker, and the tip is blunter (Fig. 3H–K) (vs. the G1 is stouter and blunter, the distal part is slightly flatter; the chitinous structure at the top is relatively smaller and thinner, and the tip is pointed in *P. subquadrata*; Fig. 1G–J; Sakai et al., 2006: fig. 53).

Two forms of infraorbital ridges have been observed in female *P. latreillii*. As both forms can be found in our specimens with similar sizes and/or from the same region, for now we treat them as intraspecific variations. Form I in *P. latreillii* is distinct from that in *P. subquadrata*, but the form II of *P. latreillii* is more similar to that in *P. subquadrata* (Table 2). Among the specimens of *P. latreillii*, form I (Fig. 3F) is more common, with the infraorbital ridge consisting of several small rounded tubercles in mesial part, and well-spaced several small isomorphically rounded tubercles in lateral part. Form II (Fig. 3G) is less common, the infraorbital ridge consisting of several well-spaced and larger rounded tubercles in the mesial part, followed by well-spaced several small heteromorphic elongated and less convex tubercles, the lateral part with 1 largest and 2–5 larger convex tubercles (vs. several dense small tubercles in the mesial part, followed by closely spaced several larger and less convex tubercles, the lateral part with 1 largest and 2–5 larger convex tubercles in *P. subquadrata*; Fig. 1F; Sakai et al., 2006: fig. 58). In addition, the sternal vulvar cover is relatively but consistently shorter in *P. latreillii* (Fig. 3L–M) (vs. longer in *P. subquadrata*; Fig. 1K).

An additional note on *Pseudohelice subquadrata* s. str. is necessary. Sakai et al. (2006) showed that *Helice leachii* Hess, 1865 is a junior synonym of *Pseudohelice subquadrata* s. str. but noted that Hess’ specimens could not be found. Hess (1865: 153) stated that his material was from “Sydney” but it is well known that they could also have come from anywhere else in the South Pacific. Ng (2012) and Ng et al. (2020) discussed the problem at length and searched for Hess’ material in Germany and Sweden. We are now confident that the types of *Helice leachii* are no longer extant. Although we are here describing a second species of *Pseudohelice* from some distance away in the WIO, it is in the interests of stability that the identity of *Helice leachii* Hess, 1865 must be fixed through the appropriate designation of a neotype that will keep it as a synonym of *Pseudohelice subquadrata* (Dana, 1851) s. str., and not potentially cause problems with

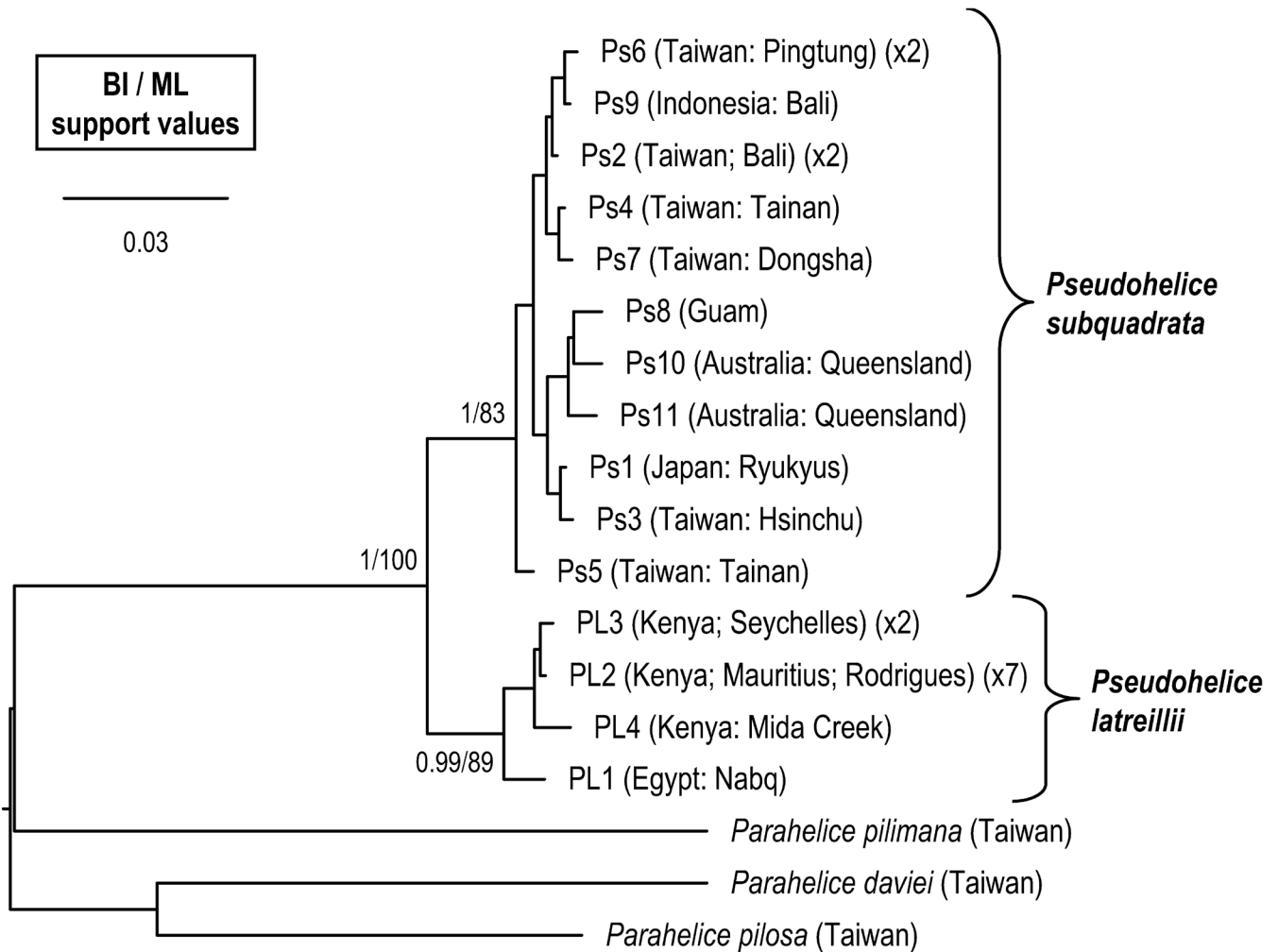


Fig. 5. Bayesian inference (BI) tree for *Pseudohelice subquadrata* and *P. latreillii*, and the outgroups, based on the cytochrome c oxidase subunit I (COI) gene. Probability values at the nodes represent support values for BI and maximum likelihood (ML). For haplotype names, see Table 1.

other taxa. As such, we here select the specimen designated as the neotype of *Chasmagnathus subquadratus* Dana, 1851 (a male, 18.2 × 16.0 mm) from Salilor’s Bay, Sydney, New South Wales, Australia (Queensland Museum catalogue number QM W 2269) to be the simultaneous neotype of *Helice leachii* Hess, 1865. As a result, both names now become objective synonyms.

Molecular analyses. The COI sequences analysed include 13 specimens of *Pseudohelice subquadrata* from Taiwan, Guam, Indonesia (Bali), and eastern Australia, and 11 specimens of *P. latreillii* from eastern Africa (Table 1). The pairwise nucleotide divergences of K2P distances and bp differences among haplotypes of the two species are shown in Table 3. The intraspecific nucleotide divergences (and bp differences) of *P. subquadrata* and *P. latreillii* are ≤ 1.4% (≤ 9 bp) and ≤ 1.9% (≤ 12 bp), respectively. The interspecific divergences are 3.3%–5.1% (21–32 bp).

The phylogenetic tree (Fig. 5) based on COI shows that the specimens from the western Pacific form a distinct clade, sister to another clade with the specimens from eastern Africa. The nucleotide divergences and the phylogeny both support the recognition of two distinct species.

DISCUSSION

Records of *Pseudohelice* from the WIO. There are several records of “*Pseudohelice subquadrata*” from eastern Africa (Sakai et al., 2006; Bouchard, 2009; Bouchard et al., 2009, 2013; Naderloo, 2017; Poupin et al., 2018; Fig. 4). While some can be clearly identified as *P. latreillii*, others are likely the misidentification of *Parahelice* spp. instead. Sakai et al. (2006) identified the Indo-West Pacific specimens as *Pseudohelice subquadrata*, but those from eastern Africa (including Kenya, Mauritius, and Seychelles) should be *P. latreillii*. The records of “*Pseudohelice subquadrata*” from Mayotte (Bouchard, 2009; Bouchard et al., 2009, 2013), however, are likely to be *Parahelice balssi* (Sakai, Turkey & Yang, 2006), based on the description (the infraorbital ridge comprised of a row of long tubercles) and figures (cheliped palm with dense short setae at base of fingers) (Bouchard et al., 2013: fig. 24). The record in Poupin et al. (2018) should also be *Parahelice balssi* because the same specimens (MNHN B32363, 2 males and 1 female) were examined by these authors. With regard to the records of “*Pseudohelice subquadrata*” from Oman (Naderloo et al., 2015; Naderloo, 2017), it is not possible to identify the species with insufficient figures or detailed morphological

description available (except a picture of a female specimen from Socotra (SMF 48471) shown in dorsal view; Naderloo, 2017: fig. 32.4). Because of the photograph and geography, we provisionally identify their Socotra specimen (SMF 48471) as *Pseudohelice latreillii*.

Molecular analyses. Based on the molecular evidence, *Pseudohelice latreillii* and its sister species, *P. subquadrata* form two reciprocally well-supported clades (Fig. 5) with enough interspecific genetic distance (Table 3). The interspecific divergence (K2P) of COI between the two species is 3.3%–5.1% (Table 3), which is large enough compared with other members of this family. For example, the minimum interspecific divergences of the family Varunidae are 2.97% between *Helice latimera* complex and *H. epicure* N. K. Ng, Naruse & Shih, 2018 (N. K. Ng et al., 2018); 3.80% between *Hemigrapsus penicillatus* (De Haan, 1835) and *H. takanoi* Asakura & Watanabe, 2005 (Markert et al., 2014); 15.87% between *Metaplax longipes* Stimpson, 1858 and *M. tredecim* Tweedie, 1950 (Shih et al., 2019); 13.13% between *Parahelice daviei* (Sakai, Türkay & Yang, 2006) and *P. pilosa* (Sakai, Türkay & Yang, 2006) (Shih et al., 2020); 12.20% between *Ptychognathus hachijoensis* Sakai, 1955 and *P. takahasii* Sakai, 1939 (Hsu & Shih, 2020); and 12.29% between *P. sakaii* Hsu, Shih & Li, 2022 and *P. stimpsoni* Hsu & Shih, 2020 (Hsu et al., 2022).

With regard to other intertidal and terrestrial crabs, the minimum interspecific distances are 2.96% between *Sesarmops imperator* Ng, Li & Shih, 2020 and *S. impressus* (H. Milne Edwards, 1837) (Sesarmidae) (Ng et al., 2020); 2.49% between *Paraleptuca crassipes* (White, 1847) and *P. splendida* (Stimpson, 1858) (Shih et al., 2012) (Ocypodidae); 3.78% between *Tubuca alcocki* Shih, Chan & Ng, 2018 and *T. urvillei* (H. Milne Edwards, 1852) (Ocypodidae) (Shih et al., 2018); 3.78% between *Austruca citrus* Shih & Poupin, 2020 and *A. perplexa* (H. Milne Edwards, 1852) (Ocypodidae) (Shih & Poupin, 2020); and 3.62% between *Mictyris brevidactylus* Stimpson, 1858 and *M. guinotae* Davie, Shih & Chan, 2010 (Mictyridae) (Davie et al., 2010).

Geographical distribution. The geographical distributions of the two species of *Pseudohelice* (Fig. 4) are different and without any overlapping region. The distribution of *P. latreillii* is the WIO, including the Red Sea, eastern Africa, and islands near the centre of southern WIO (Mauritius and Rodrigues I.) (Sakai et al., 2006; Naderloo et al., 2015; this study), except the record from Oman which needs further confirmation. *Pseudohelice subquadrata* is distributed from the eastern Indian Ocean to the West Pacific, including Koh Surin in western Thailand, main islands of Japan, northern and eastern Australia, and French Polynesia (Sakai et al., 2006; this study).

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LITERATURE CITED

- Asakura A & Watanabe S (2005) *Hemigrapsus takanoi*, new species, a sibling species of the common Japanese intertidal crab *H. penicillatus* (Decapoda: Brachyura: Grapsoidea). *Journal of Crustacean Biology*, 25(2): 279–292.
- Bouchard JM (2009) Crabes de Mangrove. Étude systématique réalisée sur le site de Malamani (Mayotte). Résultats préliminaires de la mission d'inventaire des Crustacés Décapodes de Mayotte. Rapport K UW/DAF réalisé dans le cadre du projet "Mangrove et bioremédiation. Un projet-pilote à Mayotte pour le traitement d'eaux usées domestiques". 31 pp.
- Bouchard JM, Poupin J, Cléva R, Dumas J & Dinhut V (2009) Rapport de mission du 2 au 22 novembre. Mission Crustacés Mayotte 2009. Rapport Kraken Underwater Works, KUW, Mamoudzou, Mayotte, 151 pp.
- Bouchard JM, Poupin J, Cléva R, Dumas J & Dinhut V (2013) Land, mangrove and freshwater decapod crustaceans of Mayotte region (Crustacea Decapoda). *Atoll Research Bulletin*, 592: 1–60.
- Dai AY & Yang SL (1991) Crabs of the China Seas. China Ocean Press, Beijing, 21 + 608 pp., 74 pls.
- Dai AY, Yang SL, Song YZ & Chen GX (1986) Crabs of the China Seas. China Ocean Press, Beijing, 17 + 568 pp., 74 pls. [In Chinese]
- Dana JD (1851) *Conspectus Crustaceorum quae in Orbis Terrarum circumnavigatione, Carolo Wilkes e classe Reipublicae Foeratae Duce, lexit et descripsit*. Proceedings of the Academy of Natural Sciences of Philadelphia, 5: 247–254.
- Davie PJF, Guinot D & Ng PKL (2015) Anatomy and functional morphology of Brachyura. In: Castro P, Davie PJF, Guinot D, Schram FR & Von Vaupel Klein JC (eds.) *Decapoda: Brachyura, Treatise on Zoology – Anatomy, Taxonomy, Biology*. Volume 9C-1. Brill, Leiden/Boston, pp. 11–163.
- Davie PJF, Shih HT & Chan BKK (2010) A new species of *Mictyris* (Decapoda, Brachyura, Mictyridae) from the Ryukyu Islands, Japan. *Crustaceana Monographs*, 11: 83–105.
- De Haan W (1833–1849) *Crustacea*. In: Siebold PF von (ed.) *Fauna Japonica sive Descriptio Animalium, Quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Noitis, Observationibus et Adumbrationibus Illustravit*. Amstelodami apud J. Müller et Co., Lugduni-Bavorum (=Leiden), pp. i–xvii, i–xxxii, ix–xvi + 1–243, pls. 1–55, A–Q, (2).
- Folmer O, Black M, Hoeh W, Lutz R & Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3: 294–299.

- Guinot D, Tavares M & Castro P (2013) Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa. *Zootaxa*, 3665: 1–414.
- Hess W (1865) Beiträge zur Kenntniss der Decapoden-Krebse Ost-Australiens. *Archiv für Naturgeschichte*, Berlin, 31: 127–173.
- Hsu JW & Shih HT (2020) Diversity of Taiwanese brackish crabs genus *Ptychognathus* Stimpson, 1858 (Crustacea: Brachyura: Varunidae) based on DNA barcodes, with descriptions of two new species. *Zoological Studies*, 59: 59.
- Hsu JW, Shih HT & Li JJ (2022) Description of a new species of brackish-water crab of the genus *Ptychognathus* Stimpson, 1858 (Crustacea: Brachyura: Varunidae) from southern Taiwan. *Nauplius*, 30: e2022002.
- Hywel-Davies A (1994) A quantitative analysis of the horizontal and vertical zonation of Brachyura and Mollusca associated with the Qurm mangal, Muscat, Sultanate of Oman. Unpublished Master's Thesis. School of Ocean Sciences, University of Wales, Bangor, U.K., 68 pp. [Not seen]
- ICZN (International Commission on Zoological Nomenclature) (1999) International Code of Zoological Nomenclature (4th edition). The International Trust for Zoological Nomenclature, London, xxix + 306 pp.
- Inui N, Yamakawa U, Aoki T & Koreeda R (2021) Seven noteworthy records of crab species (Crustacea: Decapoda) from Sagami Bay and adjacent waters collected after September 2019. *Natural History Report of Kanagawa*, 2021(42): 135–141.
- Itoh T (2020) Record of rare crab, *Pseudohelice subquadrata* (Dana, 1851) from southeast area of Izu Peninsula, central Japan. *Cancer*, 29: 49–52. [In Japanese]
- Japanese Association of Benthology (2012) Threatened Animals of Japanese Tidal Flats: Red Data Book of Seashore Benthos. Tokai University Press, Hatano, Japan, xvii + 285 pp. [In Japanese]
- Kim JM, Kim JG, Kim SY, Choi WY, Kim HS & Kim MS (2020) DNA barcoding of the marine protected species *Pseudohelice subquadrata* (Decapoda, Varunidae, *Pseudohelice*) from the Korean waters. *Animal Systematics, Evolution and Diversity*, 36: 228–231.
- Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16: 111–120.
- Ko HS & Lee SH (2012) Crabs and zoeas 1: Arthropoda, Crustacea, Decapoda, Brachyura, Thoracotremata: Grapsoidea, Ocypodoidea. *Invertebrate Fauna of Korea*, 21(15): 1–83.
- Komatsu H (2011) Crabs dredged off the Ogasawara Islands (Crustacea, Decapoda, Brachyura). *Memoirs of the National Museum of Nature and Science*, Tokyo, 47: 219–277.
- Kumar S, Stecher G, Li M, Knyaz C & Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution*, 35: 1547–1549.
- Lanfear R, Frandsen PB, Wright AM, Senfeld T & Calcott B (2017) PartitionFinder 2: new methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, 34: 772–773.
- Lee JH, Chiu YW, Wu ZZ, Wu TT, Tseng LK & Huang YC (2013) A Field Guide to the Shrimps, Crabs and Shells of Taijiang National Park. Taijiang National Park, Tainan City, Taiwan, 240 pp. [In Chinese]
- Li JJ & Chiu YW (2013) Land Crabs of Hengchun Peninsula. National Museum of Marine Biology & Aquarium, Pingtung, 91 pp. [In Chinese]
- Li JJ & Chiu YW (2019) An Atlas of Land Crabs of Hengchun Peninsula 2.0. National Museum of Marine Biology & Aquarium, Pingtung, 136 pp. [In Chinese]
- Liu HC & Wang CH (2010) Taiwan Coastal Wetland Crabs. *Wild Bird Society of Taipei*, Taipei, 79 pp. [In Chinese]
- MacLeay WS (1838) On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. In: Smith A (ed.) *Illustrations of the Annulosa of South Africa; being a portion of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835. and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa"*. Smith, Elder, and Co., London, pp. 63–72, pl. 3.
- Markert A, Raupach MJ, Segelken-Voigt A & Wehrmann A (2014) Molecular identification and morphological characteristics of native and invasive Asian brush-clawed crabs (Crustacea: Brachyura) from Japanese and German coasts: *Hemigrapsus penicillatus* (De Haan, 1835) versus *Hemigrapsus takanoi* Asakura & Watanabe 2005. *Organisms Diversity Evolution*, 14: 369–382.
- Milne Edwards H (1837) *Histoire naturelle des Crustacés comprenant l'anatomie, la physiologie et la classification de ces animaux*. Librairie Encyclopedique de Roret, Paris, 531 pp. (Volume 2) + 32 pp. (separate atlas to Volume 2).
- Milne Edwards H (1852) Observations sur les affinités zoologiques et la classification naturelle des Crustacés. *Annales des Sciences Naturelles, Zoology*, 3(18): 109–166, pls. 3, 4.
- Milne Edwards H (1853) Mémoire sur la famille des Ocypodiens. Suite (1). Deuxième Tribu Principale. *Annales des Sciences Naturelles, Zoology*, 20: 163–228, pls. 6–11.
- Milne-Edwards A (1873) Recherches sur la faune carcinologique de la Nouvelle-Calédonie, Deuxième Partie. *Nouvelles Archives du Muséum d'Histoire naturelle*, Paris, 9: 155–332, pls. 4–18.
- Miyake S (1983) Japanese Crustacean Decapods and Stomatopods in Color. Volume 2. Brachyura (Crabs). Hoikusha Publishing Co., Osaka, 8 + 277 pp., 64 pls. [In Japanese]
- Naderloo R (2017) *Atlas of Crabs of the Persian Gulf*. Springer, Cham, Switzerland, 444 pp.
- Naderloo R, Ebrahimnejad S & Sari A (2015) Annotated checklist of the decapod crustaceans of the Gulf of Oman, northwestern Indian Ocean. *Zootaxa*, 4028: 397–412.
- Ng NK, Naruse T & Shih HT (2018) *Helice epicure*, a new species of varunid mud crab (Brachyura, Decapoda, Grapsoidea) from the Ryukyus, Japan. *Zoological Studies*, 57: 15.
- Ng PKL (2012) The identity of *Sesarma rotundata* Hess, 1865, and description of a new species of arboreal crab of the genus *Labuanium* Serène & Soh, 1970, from Guam, western Pacific (Crustacea: Decapoda: Brachyura: Sesarmidae). *Raffles Bulletin of Zoology, Supplement 25*: 265–277.
- Ng PKL, Guinot D & Davie PJF (2008) *Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world*. *Raffles Bulletin of Zoology, Supplement 17*: 1–296.
- Ng PKL, Li JJ & Shih HT (2020) What is *Sesarmops impressus* (H. Milne Edwards, 1837) (Crustacea: Brachyura: Sesarmidae)? *Zoological Studies*, 59: 27.
- Ng PKL, Shih HT, Ho PH & Wang CH (2017) An updated annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *Journal of the National Taiwan Museum*, 70(3/4): 1–208.
- Nishigaki K, Saeki T & Naruse T (2011) New records of *Parahelice daviei* (K. Sakai, Türkay and Yang, 2006) and *Parahelice pilimana* (A. Milne-Edwards, 1873) (Crustacea: Decapoda: Brachyura: Varunidae) from Ishigakijima Island, Ryukyu Archipelago, Japan. *Biological Magazine of Okinawa*, 49: 85–93. [In Japanese]
- Poupin J, Cleva R, Bouchard JM, Dinhut V & Dumas J (2018) The crabs from Mayotte Island (Crustacea, Decapoda, Brachyura). *Atoll Research Bulletin*, 617: 1–109.
- Pratiwi R & Rahmat (2015) The mangrove crabs (Crustacea: Decapoda) recorded in reference collection of Research Centre for Oceanografi-Indonesian Institute of Sciences 1960–1970. *Berita Biologi*, 14: 195–202. [In Indonesian]

- Ronquist F, Huelsenbeck JP, Teslenko M, Zhang C & Nylander JAA (2020) MrBayes version 3.2 Manual. <https://nbsiwebden.github.io/MrBayes/manual.html> (Accessed 15 March 2022).
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA & Huelsenbeck JP (2012) MRBAYES 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61: 539–542.
- Sakai K, Türkay M & Yang SL (2006) Revision of the *Helice/Chasmagnathus* complex (Crustacea: Decapoda: Brachyura). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 565: 1–76.
- Sakai T (1939) Studies on the Crabs of Japan. IV. Brachygnatha, Brachyrhyncha. Tokyo Bunrika Daigaku, Tokyo, pp. 365–741, pls. 42–111.
- Sakai T (1955) On some rare species of crabs from Japan. *Bulletin of the Biogeographical Society of Japan*, 16–19: 106–113.
- Sakai T (1976) Crabs of Japan and the Adjacent Seas. Kodansha Ltd., Tokyo, 773 pp., 251 pls.
- Schubart CD & Huber MGJ (2006) Genetic comparisons of German populations of the stone crayfish, *Austropotamobius torrentium* (Crustacea: Astacidae). *Bulletin Français de la Pêche et de la Pisciculture*, 380–381: 1019–1028.
- Shih HT (2007) Natural history of the helioid crabs (Crustacea: Varunidae). *Wetlands Taiwan*, 64: 6–27. [In Chinese]
- Shih HT (2012) Warrior — the Seashore Crabs of Dongsha Island. Marine National Park Headquarters, Kaohsiung, Taiwan, 159 pp. [In Chinese]
- Shih HT (2020) Crescent Swordsmen—the Seashore Crabs of Dongsha Island. Marine National Park Headquarters, Kaohsiung, Taiwan, 207 pp. [In Chinese]
- Shih HT, Chan BKK & Ng PKL (2018) *Tubuca alcocki*, a new pseudocryptic species of fiddler crab from the Indian Ocean, sister to the southeastern African *T. urvillei* (H. Milne Edwards, 1852) (Crustacea, Decapoda, Brachyura, Ocypodidae). *ZooKeys*, 747: 41–62.
- Shih HT, Hsu JW, Li JJ, Ng NK & Lee JH (2020) The identities of three species of *Parahelice* Sakai, Türkay & Yang, 2006 (Crustacea: Brachyura: Varunidae) from the western Pacific, based on morphological and molecular evidence. *Zootaxa*, 4728: 249–265.
- Shih HT, Hsu JW, Wong KJH & Ng NK (2019) Review of the mudflat varunid crab genus *Metaplex* (Crustacea, Brachyura, Varunidae) from East Asia and northern Vietnam. *ZooKeys*, 877: 1–29.
- Shih HT, Ng PKL, Wong KJH & Chan BKK (2012) *Gelasimus splendidus* Stimpson, 1858 (Crustacea: Brachyura: Ocypodidae), a valid species of fiddler crab from the northern South China Sea and Taiwan Strait. *Zootaxa*, 3490: 30–47.
- Shih HT & Poupin J (2020) A new fiddler crab of *Austruca* Bott, 1973, closely related to *A. perplexa* (H. Milne Edwards, 1852) (Crustacea: Brachyura: Ocypodidae), from the South Pacific Islands. *Zoological Studies*, 59: 26.
- Shih HT & Suzuki H (2008) Taxonomy, phylogeny, and biogeography of the endemic mudflat crab *Helice/Chasmagnathus* complex (Crustacea: Brachyura: Varunidae) from East Asia. *Zoological Studies*, 47: 114–125.
- Stamatakis A (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, 22: 2688–2690.
- Stimpson W (1858) *Prodromus descriptionis animalium evertibratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars V. Crustacea Ocypodoidea*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 10: 93–110.
- Sun H, Jin Y, Zhang D, Yang S, Li Q, Song D & Zhou K (2009) Mitochondrial sequence data reveals the phylogeny of the Asian *Helice* group of crabs (Decapoda: Brachyura: Varunidae). *Journal of Zoological Systematics and Evolutionary Research*, 47: 322–327.
- Takeda M (1982) *Keys to the Japanese and Foreign Crustaceans Fully Illustrated in Colors*. Hokuryukan Ltd., Tokyo, 58 + 284 pp. [In Japanese]
- Toyota K, Seki S & Komai T (2019) *Fresh and Brackish Water Shrimps and Crabs of Japan*. Midori Shobo, Tokyo, 339 pp. [In Japanese]
- Tweedie MWF (1950) Grapsoid crabs from Labuan and Sarawak. *Sarawak Museum Journal*, 5: 338–369.
- White A (1847) Short descriptions of some new species of Crustacea in the collection of the British Museum. *Proceedings of the Zoological Society of London*, 1847(15): 84–86.