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Gelasimus splendidus Stimpson, 1858 (Crustacea: Brachyura: Ocypodidae), a valid species of fiddler crab from the northern South China Sea and Taiwan Strait

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Abstract

The fiddler crab, *Uca splendida* (Stimpson, 1858) has been synonymized under *Uca crassipes* (White, 1847) since Crane (1975). Studies of specimens from the Hong Kong type locality and adjacent areas of China, Taiwan and Vietnam show that *U. splendida* is a valid species, with a characteristic suite of carapace and gonopod features as well as a distinct cytochrome oxidase I (COI) signature. Genetic work shows that *U. splendida* belongs to a well-supported clade and is the sister species of *U. crassipes*. The distribution of *U. splendida* is restricted to continental East and continental Southeast Asia, in contrast to the oceanic distribution of *U. crassipes*. Both species, however, are sympatric in Penghu Islands, western Taiwan and Dongsha Island (=Pratas Island).

Key words: *Uca splendida*, *U. crassipes*, *U. chlorophthalmus*, South China Sea, Taiwan Strait, cytochrome oxidase I, taxonomy

Introduction

Uca crassipes (White, 1847) is a common broad-fronted species of fiddler crab distributed widely in the western and central Pacific Ocean and the eastern margin of the Indian Ocean (Crane 1975). It was regarded as a subspecies of *U. chlorophthalmus* (H. Milne Edwards, 1837) by Crane (1975) but has been treated as a distinct species in recent years (Jones & Morton 1994; Rosenberg 2001; Beinlich & von Hagen 2006; Ng *et al*. 2008; Shih *et al*. 2010b). *Uca chlorophthalmus* and *U. crassipes* are very similar morphologically and can only be effectively separated by subtle differences in the structures of the major chela, ambulatory leg, first gonopod and female gonopore (Crane 1975). Together with *U. inversa* (Hoffmann, 1874) and *U. sindensis* (Alcock, 1900), they were placed in the subgenus *Paraleptuca* Bott, 1973 (= *Amphiuca* Crane, 1975) by von Hagen (1976) and Rosenberg (2001). Beinlich & von Hagen (2006) later synonymized the Indo-West Pacific members of *Celuca* Crane, 1975, with *Paraleptuca*, but considered *U. inversa* to belong to its own subgenus, *Cranuca* Beinlich & von Hagen, 2006. We keep with the original concept of *Paraleptuca* Bott, 1973, and retain *U. chlorophthalmus*, *U. crassipes* and *U. sindensis* in this subgenus, especially since Beinlich & von Hagen's (2006) definition of *Paraleptuca* seems to be paraphyletic (Naderloo *et al*. 2010).

There are several junior synonyms of *U. crassipes*: *Gelasimus gaimardi* H. Milne Edwards, 1852 (type locality: Tongatabou = Tongatabu, Tonga), *G. latreillei* H. Milne Edwards, 1852 (type locality: Bora Bora, French Polynesia), *G. splendidus* Stimpson, 1858 (type locality: Hong Kong), *G. pulchellus* Stimpson, 1858 (type locality: Tahiti, French Polynesia) and *Uca novaeguineae* Rathbun, 1913 (type locality: New Guinea) (cf. Crane 1975). Of these synonyms, *G. splendidus* is unique because its type locality, Hong Kong, is on continental Asia instead of being on oceanic islands like the others. In describing the species, Stimpson (1858, 1907) emphasized that *G. splendidus* is characterized by the coloration and morphology of the carapace. In fact, Crane (1975) had also noticed that there were

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some distinct features of the first gonopod and carapace in the Hong Kong specimens of *U. crassipes*. As smaller specimens did not show such characters, she felt that they did not need to be taxonomically separated.

Examination of a large series of specimens identified as *U. crassipes* from throughout its wide range have revealed that there are two distinct groups, distinguished by carapace form, color and genetics. Specimens from Penghu Is. (in the middle of Taiwan Strait), Hong Kong, Hainan and Vietnam can be confidently identified with *Gelasimus splendidus* Stimpson, 1858. We herein resurrect *Gelasimus splendidus* Stimpson, 1858, as a distinct species and assign a neotype collected from Hong Kong, its type locality.

Materials and methods

Specimens of *Uca crassipes s. l.* were collected from the Ryukyus, Taiwan (including Penghu Is.), Hong Kong, Hainan (China), Vietnam, Philippines, Guam, Indonesia, Cocos-Keeling Is., New Caledonia, Vanuatu, Wallis I., and Moorea, French Polynesia (see Table 1; material examined; Fig. 1). Specimens were preserved in 70–95% ethanol after collection and illustrated with the help of a drawing tube attached to a stereomicroscope. Material examined, including the specimens of the allied *U. chlorophthalmus*, are deposited in the following institutions: Museum National d'Histoire Naturelle, Paris, France (MNHN); Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL); Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung, Taiwan (NTOU); Queensland Museum, Brisbane, Australia (QM); National Taiwan Museum, Taipei, Taiwan (TMCD); and Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore (ZRC).

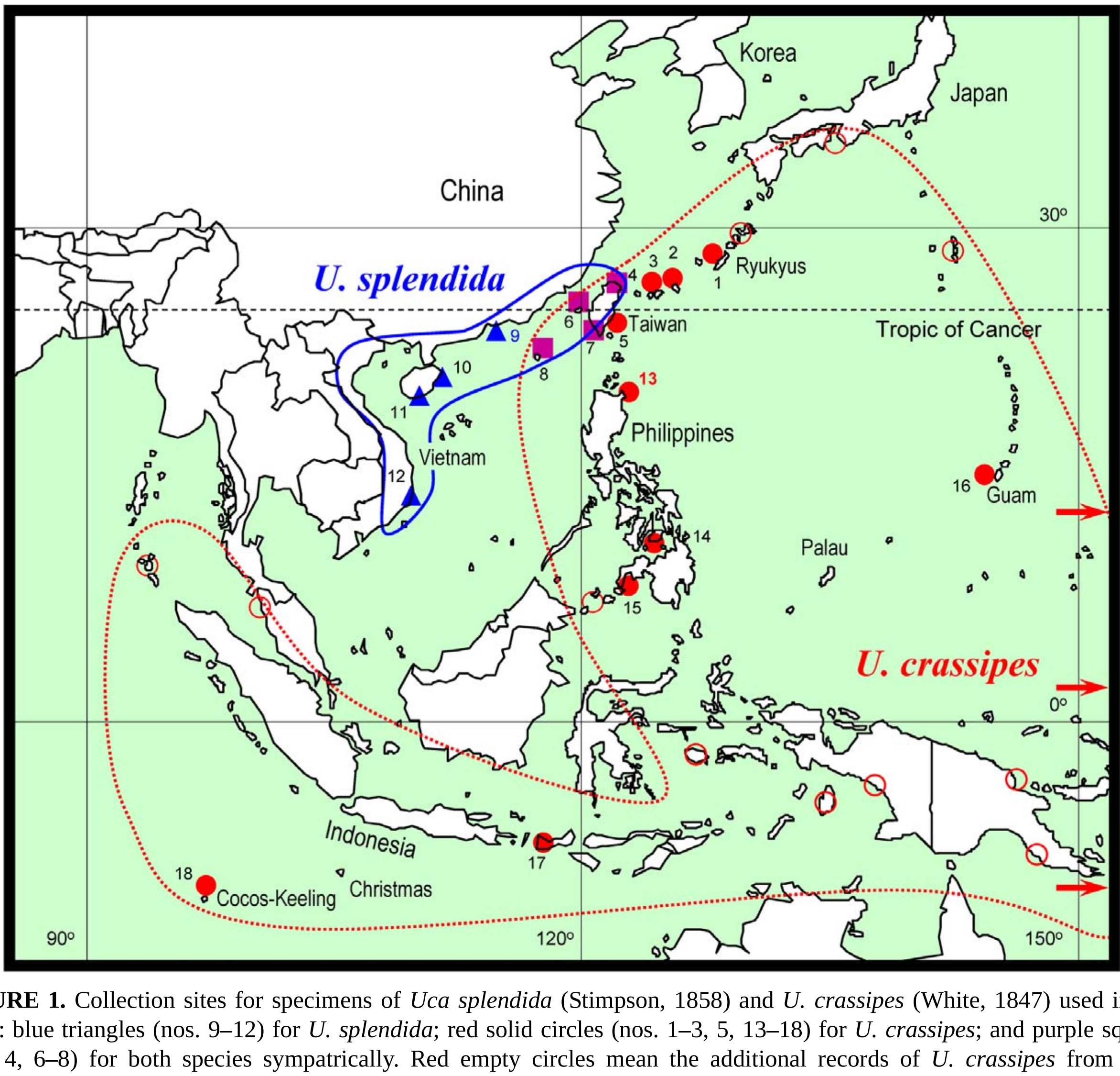

FIGURE 1. Collection sites for specimens of *Uca splendida* (Stimpson, 1858) and *U. crassipes* (White, 1847) used in this study: blue triangles (nos. 9–12) for *U. splendida*; red solid circles (nos. 1–3, 5, 13–18) for *U. crassipes*; and purple squares (nos. 4, 6–8) for both species sympatrically. Red empty circles mean the additional records of *U. crassipes* from other references (Sakai 1939; Crane 1975; Yoshigou 2001). Different lines indicate the updated ranges of the two species.

The abbreviation G1 is used for the male first gonopod. Measurements, in millimeters (mm), are of the carapace width and pollex length (PL) of the major cheliped. The terminology used essentially follows that of Crane (1975).

Genomic DNA was isolated from the muscle tissue of legs by 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 (5'-GGTCAACAAATCATAAAGATATTGG-3'), HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer *et al*. 1994), and COH6 (5'-TADACTTCDGGRTGDCCAAARAAYCA-3') (Schubart & Huber 2006). The PCR conditions for the above primers were denaturation for 50 s at 94°C, annealing for 70 s at 45–47°C, and extension for 60 s at 72°C (40 cycles), followed by extension for 10 min at 72°C. Sequences were obtained by automated sequencing (Applied Biosystems 3730) and were aligned manually, with the aid of ClustalW (vers. 1.4, Thompson *et al*. 1994), after verification with the complementary strand. Other Indo-West Pacific broad-fronted species, *U. lactea* (De Haan, 1835), *U. annulipes* (H. Milne Edwards, 1837), *U. perplexa* (H. Milne Edwards, 1837) and *U. triangularis* (A. Milne-Edwards, 1873), were used as outgroups. Sequences of different haplotypes have been deposited in the DNA Data Bank of Japan (DDBJ) (accession numbers AB734641–AB734656), with other sequences which published in earlier papers of the first author (Table 1).

TABLE 1. The haplotypes of COI gene of *U. splendida* (Stimpson, 1858) and *U. crassipes* (White, 1947) from the West Pacific, South Pacific and Indian Ocean, and the outgroups used in this study.

Species	Locality	no. on map	Catalogue no. of NCHUZOOL (unless indicated)	Sample size	Haplotype of COI	DDBJ Access. no.
U. splendida	Taiwan: Lanyang R., Ilan	4	13451	1	Usp1	AB734641
	Taiwan: Lanyang R., Ilan	4	13451	1	Usp2	AB734642
	Taiwan: Wazihwei, New Taipei City	4	13446	1	Usp1	AB734641
	Taiwan: Baoli R., Pingtung	7	13447	1	Usp3	AB734643
	Taiwan: Cingluo, Penghu	6	13256	1	Usp4	AB471918
	Taiwan: Cingluo, Penghu	6	13369	1	Usp5	AB734644
	Taiwan: Cingluo, Penghu	6	13457	1	Usp1	AB734641
	Taiwan: Citou, Penghu	6	13456	1	Usp6	AB734645
	Taiwan: Citou, Penghu	6	13450	1	Usp7	AB734646
	Taiwan: Citou, Penghu	6	13452	1	Usp8	AB734647
	Hong Kong (type locality)	9	13368	1	Usp9	AB734648
	Hong Kong (type locality)	9	ZRC 1998.0350	1	Usp10	AB734649
	Hong Kong (neotype)	9	ZRC 2012.0143	1	Usp11	AB734650
	China: Wenchang, Hainan	10	13369	1	Usp1	AB734641
	China: Wenchang, Hainan	10	13369	1	Usp12	AB734651
	China: Sanya, Hainan	11	13370	1	Usp13	AB734652
	China: Sanya, Hainan	11	13449	1	Usp14	AB734653
	Vietnam: Nha Trang	12	13448	1	Usp15	AB734654
	Vietnam: Nha Trang	12	13448	1	Usp7	AB734646
	Vietnam: Nha Trang	12	13459	1	Usp16	AB734655
U. crassipes	Ryukyus: Okinawa	1	13466	1	Ucr1	AB734656
	Ryukyus: Miyako	2	13469	1	Ucr1	AB734656
	Ryukyus: Iriomote	3	13465	1	Ucr1	AB734656
	Taiwan: Tainan	7	13470	1	Ucr1	AB734656

continued next page

TABLE 1. (continued)

Species	Locality	no. on map	Catalogue no. of NCHUZOOL (unless indicated)	Sample size	Haplotype of COI	DDBJ Access. no.
	Taiwan: Tainan	7	13472	1	Ucr1	AB734656
	Taiwan: Wanlitong, Kenting, Pingtung	7	13454	1	Ucr1	AB734656
	Taiwan: Wanlitong, Kenting, Pingtung	7	13454	1	Ucr1	AB734656
	Taiwan: Dulanwan, Taitung	5	NTOU	1	Ucr1	AB734656
	Taiwan: Citou, Penghu	6	13453	1	Ucr1	AB734656
	Taiwan: Shihcyuan, Penghu	6	13474	1	Ucr1	AB734656
	Taiwan: Dongsha I. (=Pratas I.), Kaohsiung	8	13455	1	Ucr1	AB734656
	Philippines: Luzon	13	ZRC JCEM 07-006	1	Ucr1	AB734656
	Philippines: Bohol	14	TMCD	1	Ucr1	AB734656
	Philippines: Siguijor (type locality)	14	ZRC	2	Ucr1	AB734656
	Philippines: Mindanao	15	13473	2	Ucr1	AB734656
	Guam	16	ZRC 2000.0637	1	Ucr1	AB734656
	Guam	16	ZRC 2000.0637	1	Ucr1	AB734656
	Indonesia: Lombok	17	ZRC 2009.0933	2	Ucr1	AB734656
	Cocos-Keeling Is.	18	ZRC	1	Ucr1	AB734656
	Cocos-Keeling Is.	18	ZRC	1	Ucr1	AB734656
	Cocos-Keeling Is.	18	ZRC	1	Ucr1	AB734656
	New Caledonia: Ouano Bay	19	13477	1	Ucr1	AB734656
	New Caledonia: Ouano Bay	19	13477	1	Ucr1	AB734656
	New Caledonia: Pointe de Pam	19	QM W24284	1	Ucr2	AB734656
	New Caledonia: Pont de Dumbea	19	QM W24285	1	Ucr1	AB734656
	New Caledonia: Ouano Bay	19	13476	1	Ucr1	AB734657
	New Caledonia: Ouano Bay	19	13563	1	Ucr1	AB734656
	Vanuatu: Santo	20	ZRC Santo 2006 VM19	1	Ucr1	AB734656
	Wallis I.: Halalo	21	MNHN	1	Ucr1	AB734656
	Wallis I.: Halalo	21	MNHN	1	Ucr3	AB734656
	Moorea, French Polynesia: Haapiti	22	13478	1	Ucr1	AB734656
Total				54		
Outgroups						
U. chlorophthalmus	Mayotte (Western Indian Ocean)		MNHN	1	Uch1	JX050999 (MDECA791-12)
	Mayotte (Western Indian Ocean)		MNHN	2	Uch2	JX050998 (MDECA792-12) JX050997 (MDECA793-12)
U. annulipes	China: Sanya, Hainan		13244			AB471907
U. lactea	Hong Kong		13250			AB471912
U. perplexa	Taiwan: Baoli Estuary, Pingtung		13251			AB471915
U. triangularis	Taiwan: Baoli Estuary, Pingtung		13254			AB471916

The best-fitting model for sequence evolution of the COI dataset was determined by jModelTest (v. 0.1.1, Posada 2008; Guindon & Gascuel 2003), selected by the Bayesian information criterion (BIC) and was subsequently applied for Bayesian inference (BI) analysis. The BI was performed with MrBayes (vers. 3.1.1, Ronquist & Huelsenbeck 2003) and the search was run with four chains for 10 million generations, with trees sampled every 1000 generations. The convergence of chains was determined by the effective sample size (ESS) (>200 as recommended) in Tracer (vers. 1.5, Rambaut & Drummond 2009) and the first 1100 trees were discarded as the burnin (determined by the average standard deviation of split frequency values below the recommended 0.01; Ronquist *et al.* 2005). Maximum likelihood (ML) analysis was conducted in RAxML (vers. 7.2.6, Stamatakis 2006). The model GTR + G (i.e. GTRGAMMA) was used with 100 runs, and found the best ML tree by comparing the likelihood scores. The robustness of the ML tree was evaluated by 1000 bootstrap pseudoreplicates under the model GTRGAMMA. A consensus MP tree was constructed using PAUP* program (vers. 4.0b10, Swofford 2003) with 2000 bootstrap reiterations of a simple heuristic search, tree bisection-reconnection (TBR) branch-swapping, and 100 randomly added sequence replications. All characters were equally weighted. Basepair (bp) difference and pairwise estimates of Kimura 2-parameter (K2P) distance (Kimura 1980) for inter- and intraspecific genetic diversities were also calculated by PAUP*.

Taxonomy

Family Ocypodidae Rafinesque, 1815

Genus *Uca* Leach, 1814

Subgenus *Paraleptuca* Bott, 1973

Uca (*Paraleptuca*) *splendida* (Stimpson, 1858)

(Figs. 2–4, 6, 7C)

Gelasimus splendidus Stimpson, 1858: 99–100.—Kingsley 1880: 149–150 [Hong Kong].—Stimpson 1907: 106–107, pl. 14: fig. 2 [Hong Kong].—Crane 1975: 98–99, 101–103, 599 [Hong Kong].

Gelasimus chlorophthalmus (not *Gelasimus chlorophthalmus* H. Milne Edwards, 1837) – Cano 1889: 92, 234 [Xiamen].

Uca splendida – Gee 1926: 165 [Hong Kong].

Uca gaimardi – Gordon 1931: 528 [list].—Shen 1936: 77 [Hainan].

Gelasimus gaimardi – Sakai 1939: 617–618, text-fig. 92, pl. 104(3) [Tainan, Taiwan] (part?).—Horikawa 1940: 28 [list].—Lin 1949: 26 [list].

Uca (*Amphiuca*) *chlorophthalmus crassipes* – Crane 1975: 101, pls. 15A–F, 46B, figs. 13A–I, 14, 26C, 37H, 39A, 56C, 60L, M, 68B, 81G, 82G, 83A [Hong Kong] (part).—Wang 1984: 42 [Kenting, Pingtung, Taiwan] (part?).—Dai *et al*. 1986: 428, pl. 59(5), fig. 238(1–2) [Guangdong].—Dai & Yang 1991: 468, pl. 59(5), fig. 238 [Guangdong]. Huang 1994: 595 [Guangdong].—Shih 1994: 60, 91–96, figs. 63–66 (part).—Ho 1996: 9–12, figs. 1–6 (part).

Uca crassipes – Huang *et al*. 1989: 193–194, fig. 2, pl. 1E–G [part].—Jones & Morton 1994: 26, pl. 3C, D, fig. 5 [Hong Kong].—Wang & Liu 1996a: 77, fig. 74–76.—Wang & Liu 1996b: 54–55, 2 unnumbered figs (part?).—Ho & Hung 1997: 65–66, 3 unnumbered figs (part).—Wang & Liu 1998a: 77–78, figs. 74–76.—Wang & Liu 1998b: 108, 3 unnumbered figs (part?).—Hung 2000: 140–141, figs. 424–425, 1 unnumbered fig (part).—Lee & Tung 2000: 41, 4 unnumbered figs. (part).—Lee 2001: 132, 3 unnumbered figs. (part).—Ng *et al*. 2001: 37 (part).—Chen 2002: 111, 2 unnumbered figs. (part).—Jeng 2003: 59, 1 unnumbered fig. (part) [Penghu].—Wang & Liu 2003: 77–78, figs. 74–76 (part?).—Chiou *et al*. 2004: 34, 2 unnumbered figs (part?).—Shen & Jeng 2005: 160–161, 3 unnumbered figs (part).—Kwok & Tang 2006: 4, figs. 8, 9 [Hong Kong].—Yang *et al*. 2008: 807 [Guangdong; Hainan].—Wang 2009: 103–105, 1 unnumbered fig. (part) [Tainan].—Liu & Wang 2010: 34–35, 4 unnumbered figs (part).—Shih *et al*. 2010b: 9 [Hong Kong].

Uca chlorophthalmus (not *Gelasimus chlorophthalmus* H. Milne Edwards, 1837)—Cai *et al*. 1998: 117 [Hong Kong].

Uca chlorophthalmus crassipes – Yu *et al*. 1996: 59, figs. 61–63 [Pingtung] (part).—Jeng 1997: 18 [Pingtung] (part).—Shen 1997: 45–47, fig. 18 [Penghu] (part).—Jeng 1998: 89–90, 3 unnumbered figs. (part) [Pingtung].—Shih 2000: 72, 1 unnumbered fig. (part).—Ye & Chen 2000: 17, 19–20, 23–25, 28, 37, 49–50, 60–61, figs. 9, 15, 33 [Penghu] (part).—Chen 2001: 206, 2 unnumbered figs. (part).—Tam & Wong 2000: 117, 1 unnumbered fig. [Hong Kong].—Huang 2008: 664 [Guangdong].

Uca (*Paraleptuca*) *crassipes*—Ng *et al*. 2008: 241 [list] (part).

Material examined. Hong Kong; neotype for *Gelasimus splendidus*: 1 ♂ (16.1 mm) (ZRC 2012.0143), Tai Tam, south coast of Hong Kong I., coll. P.K.L. Ng & K.J.H. Wong, 25 Dec. 2011; 1 ♂ (13.5 mm) (ZRC 1998.0350), Tai Tam, coll. P.K.L. Ng & S.Y. Lee, 6 Jun. 1996; 1 ♂ (14.4 mm) (NZHUZOOL 13368), Tai Tam, coll. Y.-C. Fan, 27 Jul. 2006; 2 ♂♂ (13.8–15.5 mm), 1 ♀ (15.9 mm) (NZHUZOOL 13460), Tai Tam, coll. K.J.H. Wong, 21 Dec. 2011; 4 ♂♂ (13.9–17.0 mm), 1 ♀ (15.3 mm) (ZRC 2012.0036), same data as neotype; 1 ♂ (19.7 mm) (ZRC 2012.0046), aquarium dealer, Hong Kong, Dec. 2011. **Taiwan**: Penghu: 2 ♂♂ (18.6–19.7 mm) (NZHUZOOL 13490), Citou, coll. H.-T. Shih, 10 Jul. 1994; 5 ♂♂ (15.6–21.6 mm), 1 ♀ (15.8 mm) (NZHUZOOL 13452), Citou, coll. H.-T. Shih, 17 Aug. 1996; 4 ♂♂ (16.96–20.20) (NZHUZOOL 13486), Citou, coll. H.-T. Shih *et al*., 23 May 2008; 1 ♂ (22.9 mm) (NZHUZOOL 13450), Citou, coll. H.-T. Shih *et al*., 18 Aug. 2009; 1 ♂ (19.2 mm) (NZHUZOOL 13456); 3 ♀♀ (13.1–14.8 mm, incl. 1 ovig.) (NZHUZOOL 13484); 8 ♂♂ (11.8–16.3 mm), 5 ♀♀ (12.6–14.7 mm) (NZHUZOOL 13485), Citou, coll. H.-T. Shih *et al*., 19 Aug. 2009; 2 ♂♂ (19.2–21.4 mm) (NCHUZOOL 13458), Cingluo, coll. H.-T. Shih, 14 Aug. 1996; 4 ♂♂ (19.8–20.9 mm) (NCHUZOOL 13487), Cingluo, coll. H.-T. Shih, 15 Aug. 1996; 4 ♂♂ (20.4–23.5 mm), 2 ♀♀ (19.2–19.7 mm) (NCHUZOOL 13488), Cingluo, coll. H.-T. Shih *et al*., 27 Jun. 2006; 1 ♂ (17.2 mm) (NCHUZOOL 13457); 15 ♂♂ (12.2–20.6 mm) (NCHUZOOL 13481), Cingluo, coll. H.-T. Shih *et al*., 18 Aug. 2009; 1 ♂ (14.4 mm) (NZHUZOOL 13482), Shihcyuan, coll. H.-T. Shih *et al*., 27 Jun. 2006; 1 ovig. ♀ (17.4 mm) (NCHUZOOL 13483), Caiyuan, coll. H.-T. Shih *et al*., 18 Aug. 2009; Ilan: 1 ♂ (17.5 mm), 1 ♀ (13.1 mm) (NCHUZOOL 13451), Lanyang River estuary, coll. H.-C. Liu, 26 Jul. 2004; New Taipei City: 1 ♂ (13.0 mm) (NZHUZOOL 13446), Wazihwei, coll. H.-T. Shih, 6 Nov. 1995; Tainan: 1 ♀ (15.4 mm) (NCHUZOOL 13566), Yanshuei River estuary, coll. J.-H. Lee, 25 Apr. 2012; Kaohsiung: 3 ♂♂ (21.1–20.2 mm) (NCHUZOOL 13565), Yuanjhonggang, coll. J.-H. Lee, 22 Apr. 2012; Pingtung: 2 ♂♂ (15.9–17.0 mm) (NZHUZOOL 13447), Baoli River estuary, 20 Jul. 2011; Dongsha Island (=Pratas Island): 1 ♂ (19.9 mm) (NCHUZOOL 13568), coll. G.-C. Guo, 21 Jul. 2012. **China**: 12 ♂♂ (9.4–22.9 mm), 5 ♀♀ (12.4–17.8 mm, 1 damaged) (NCHUZOOL 13449), Yalongwan, Sanya, Hainan, coll. H.-T. Shih & J.-H. Lee, 28 Jun. 2004; 6 ♂♂ (12.5–17.7 mm) (NCHUZOOL 13369), Bamenwan, Wenchang, coll. K.J.H. Wong & S.-L Yang, 3 Dec. 2008. **Vietnam**: 4 ♂♂ (11.4–17.6 mm), 7 ♀♀ (12.9–14.5 mm) (NCHUZOOL 13459), Nha Trang, coll. P.-C. Tsai & I-H. Chen; 5 ♂♂ (15.5–19.6 mm) (NCHUZOOL 13448), Nha Trang, coll. I-H. Chen & K.J.H. Wong, 24 Nov. 2010; 1 ♂ (18.7 mm) (NCHUZOOL 13463), Miu Ne, coll. P.-C. Tsai & I-H. Chen, 26 Nov. 2010.

Comparative material. *Uca crassipes* (White, 1847). 1 ♂ (25 mm, cf. Forest & Guinot 1961: 141) (MNHN B3140, lectotype of *Gelasimus gaimardi* H. Milne Edwards, 1852), Tongatabou, coll. M.M. Quoy & Gaimard; 1 ♂ (23.0 mm, cf. Forest & Guinot 1961: 141) (MNHN B3147, identified as *Gelasimus latreillei* by A. Milne-Edwards), Viti, Fiji. **Ryukyus**: 1 ♀ (16.8 mm) (NCHUZOOL 13469), Miyako, coll. H.-T. Shih, 11 Apr. 2002; 1 ♂ (17.0 mm), 2 ♀♀ (18.4–18.5 mm) (NCHUZOOL 13465), Funaura Bay, Iriomote, coll. P.-C. Tsai, 8 Jul. 2011; 1 ♂ (10.7 mm), 1 ♀ (13.7 mm) (NCHUZOOL 13466), Manzamao, Okinawa, P.-C. Tsai, 7 Jul. 2009. **Taiwan**: Penghu: 1 ♂ (15.4 mm) (NCHUZOOL 13474), Shihcyuan, coll. H.-T. Shih *et al*., 27 Jun. 2006; 1 ♂ (14.8 mm) (NCHUZOOL 13453), Citou, coll. H.-T. Shih *et al*., 19 May 2007; Tainan: 1 ♂ (15.5 mm) (NCHUZOOL 13470), estuary of Yanshuei R., coll. J.-H. Lee, 27 May 2005; 6 ♂♂ (14.1–17.7 mm) (NCHUZOOL 13472), estuary of Yanshuei R., coll. J.-H. Lee *et al*., 4 Aug. 2009; 1 ovig. ♀ (16.6 mm) (NCHUZOOL 13475), estuary of Yanshuei R., coll. W.-C. Li, 12 Jul. 2010; 1 ♂ (17.9 mm), 4 ♀♀ (14.2–16.9 mm) (NCHUZOOL 13493); 1 ♂ (13.4 mm), 1 ♀ (14.1 mm) (NCHUZOOL 13567), estuary of Yanshuei R., coll. J.-H. Lee, 25 Apr. 2012; Kaohsiung: 3 ♂♂ (21.1–20.2 mm) (NCHUZOOL 13565), Yuanjhonggang, coll. J.-H. Lee, 22 Apr. 2012; Pingtung: 2 ♂♂ (16.3–16.9 mm) (NCHUZOOL 13454), Wanlitong, Kenting, coll. J.-H. Lee, 20 Aug. 2009; Taitung: 8 ♂♂ (7.4–18.1 mm), 6 ♀♀ (9.0–18.4 mm) (TMCD-2693), Beijyunjie, Donghe, coll. C.-H. Wang, 21 Sep. 1990; 3 ♂♂ (13.8–17.3 mm) (TMCD CHCD800), Beijyunjie, Donghe, coll. H.-C. Hung, 23 Apr. 1995; 2 ♂♂ (12.1–18.4 mm), 2 ♀♀ (12.7 mm, 1 damaged) (NTOU), Dulanwan, coll. P.-H. Ho, 7 Apr. 2001; Dongsha Island: 1 ♂ (23.1 mm) (NCHUZOOL 13464); 2 ♂♂ (21.3–22.3 mm) (NCHUZOOL 13491), coll. Y.-C. Yang, 15 Jun. 1997; 2 ♂♂ (17.3–18.6 mm), 1 ♀ (18.6 mm) (NCHUZOOL 13455), coll. J.-Y. Chong & Y.-H. Huang, 7 Jun. 2011; 1 ♂ (21.2 mm) (NCHUZOOL 13471), coll. H.-T. Shih *et al*., 21 Nov. 2011; 1 ♂ (17.5 mm) (NCHUZOOL 13500), coll. Z.-H. Ou, 26 Mar. 2012; 1 ♂ (19.1 mm) (NCHUZOOL 13569), coll. G.-C. Guo, 21 Jul. 2012. **Philippines**: 1 ♀ (13.0 mm) (ZRC JCEM 07-006), Municipality of Santa Ana, Cagayan Province, coll. T. Naruse & J.C.E. Mendoza, 23 Apr. 2007; 12 ♂♂ (10.7–16.6 mm), 8 ♀♀ (11.8–16.6 mm, 1 damaged) (ZRC), Dumanhog, Siguijor, coll. N.K. Ng *et al*., 26 Jan. 2005; 1 ♂ (14.3 mm), 1 ♀ (13.5 mm) (TMCD), Baclayon, Bohol, coll. H.-C. Hung, 10 May 1998; 5 ♂♂ (14.7–17.3 mm), 4 ♀♀ (9.8–15.8 mm) (ZRC), Panglao, 18 Jul. 2007; 5 ♂♂ (12.8–19.1 mm, 1 damaged) 2 ♀♀ (14.1–16.3 mm) (NCHUZOOL 13473), Zamboanga, Mindanao, coll. C.K. Rojo, 10 Jun. 2006. **Guam**: 4 ♂♂

(11.2–21.6 mm), 1 ♀ (19.1 mm) (ZRC 2000.0637), Apra Harbor, Sasa Bay, coll. P.K.L. Ng, 19 Apr. 2000. **Indonesia**: 2 ♂♂ (15.4–17.7 mm) (ZRC 2009.0933), Kuta, Lombok, coll. Z. Jaafar & A. Anker, 11 Feb. 2002. **Cocos-Keeling Is.**: 20 ♂♂ (9.4–20.0 mm), 7 ♀♀ (10.3–16.1 mm) (ZRC), coll. P.K.L. Ng, 20–24 Mar. 2011; **New Caledonia**: 1 ♂ (13.9 mm), 3 ♀♀ (11.7–14.8 mm) (NCHUZOOL 13479), Magenta, Ouémo, coll. P. Laboute, 29 Jul. 2003; 1 ♂ (11.0 mm) (MNHN IU-2011-5602); 1 ♂ (11.1 mm) (MNHN-IU-2011-5603), Ile des Pins, Baie de Gunta, 21 Dec. 1961; 1 ♂ (11.2 mm), 2 ♀♀ (9.8–12.3 mm) (QM W24285), Point de Dembea; 1 ♀ (11.2 mm) (QM W24284), Pointe de Pam, coll. J.L. Menou, 8 Feb. 1992; 6 ♂♂ (10.1–12.6 mm) (NCHUZOOL 13476); 1 ♂ (12.2 mm), 2 ♀♀ (12.5–14.4 mm) (NCHUZOOL 13477), western coast of Quano Bay, coll. B. Richer de Forge, 30 Nov. 2008; 1 ♂ (14.6 mm) (MNHN), Voh, Oundjo, coll. J. Poupin & M. Juncker, Mar. 2009. **Vanuatu**: 1 ♂ (12.0 mm) (ZRC Santo 2006 VM19), Santo, 2006. **Wallis I.**: 2 ♂♂ (13.0–19.8 mm) (MNHN), Halalo, coll. J. Poupin & M. Juncker, 23 Oct. 2007. **Moorea**: 3 ♂♂ (10.2–14.4 mm), 3 ♀♀ (13.2–15.2 mm) (MNHN) Haapiti, coll. J. Poupin, 11 Dec. 2006; 1 ♂ (14.8 mm) (NCHUZOOL 13478) Haapiti, coll. J. Poupin, Dec. 2006.

***Uca chlorophthalmus* (H. Milne Edwards, 1837). Kenya:** 1 ♂ (15.4 mm) (NCHUZOOL 13496); 1 ♂ (14.1 mm) (NCHUZOOL 13497); 1 ♂ (13.1 mm) (NCHUZOOL 13498), 1 ♂ (14.5 mm) (NCHUZOOL 13499), Gazi Bay, coll. M. Fusi, 10 Dec. 2011. **Tanzania:** 1 ♂ (18.9 mm) (NCHUZOOL 13561), Dar es Salaam, coll. S. Cannicci, 1 Sep. 2006; **Mayotte:** 1 ♂ (18.6 mm) (MNHN IU-2011-5599); 1 ♂ (19.2 mm) (MNHN-IU-2011-5600); 1 ♂ (16.2 mm) (MNHN IU-2011-5601), Malamani mangroves, 8 Oct. 2008.

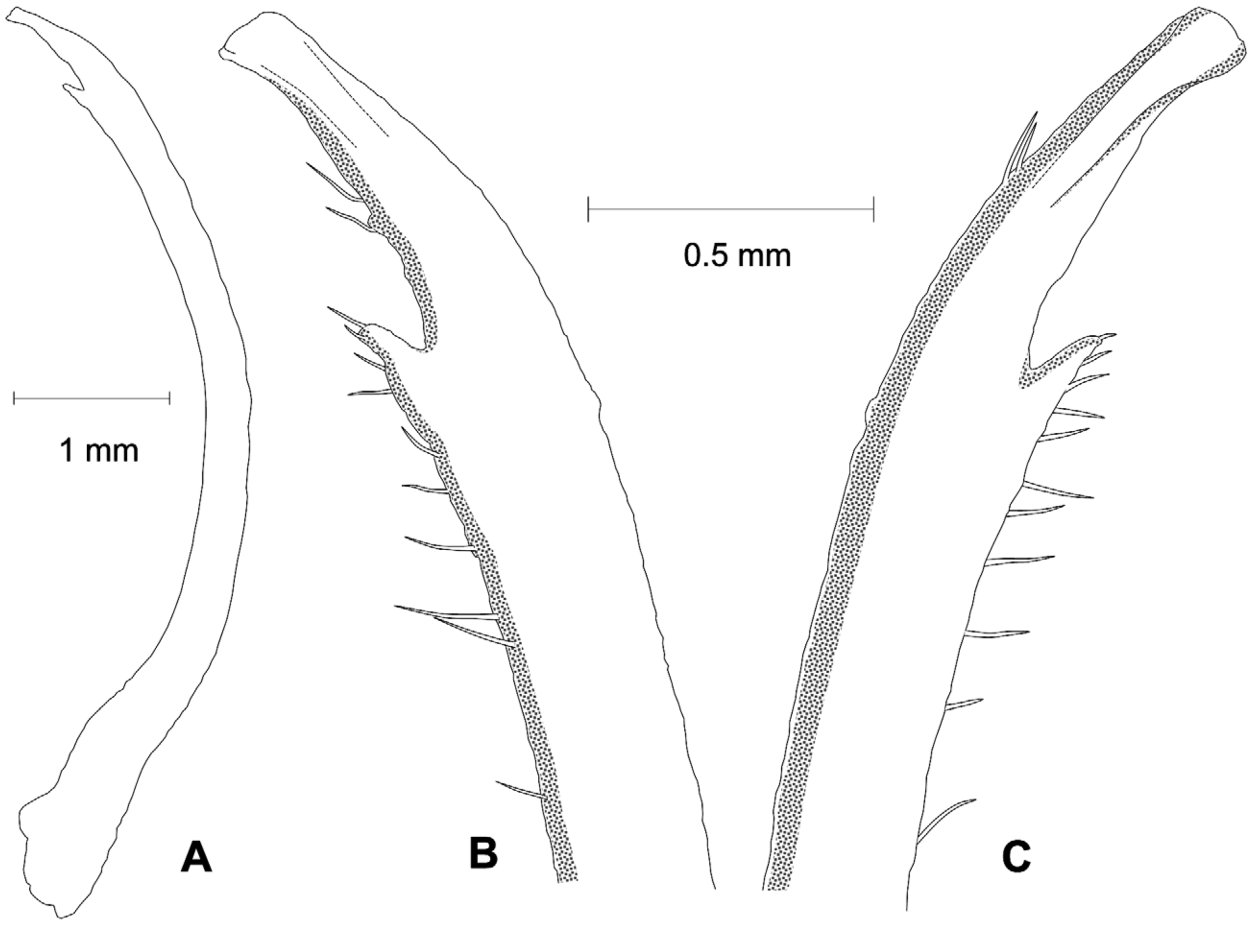

FIGURE 2. *Uca splendida* (Stimpson, 1858). G1 of neotype (ZRC 2012.0143); A, right G1, lateral view; B, distal part of right G1, lateral view; C, distal part of right G1, mesial view.

Diagnosis. Front wide; narrowest below eyestalk bases. Orbits slightly oblique (Fig. 3C). Anterolateral angles moderately acute, produced anteriorly. Anterolateral margins relatively long, distinct, almost straight; turning at an angle into well-marked dorsolateral margins (Figs. 3A, 4A, C, F, 6); one posterolateral stria. Shallow, triangular depression outside pollex base (Figs. 3B, 4B). Tip of pollex with small subdistal tooth, sometimes irregularly bifid. Palm finely granular. Ambulatory meri moderately broad. G1 tip without flanges, tubular; thumb short (Figs. 2, 7C).

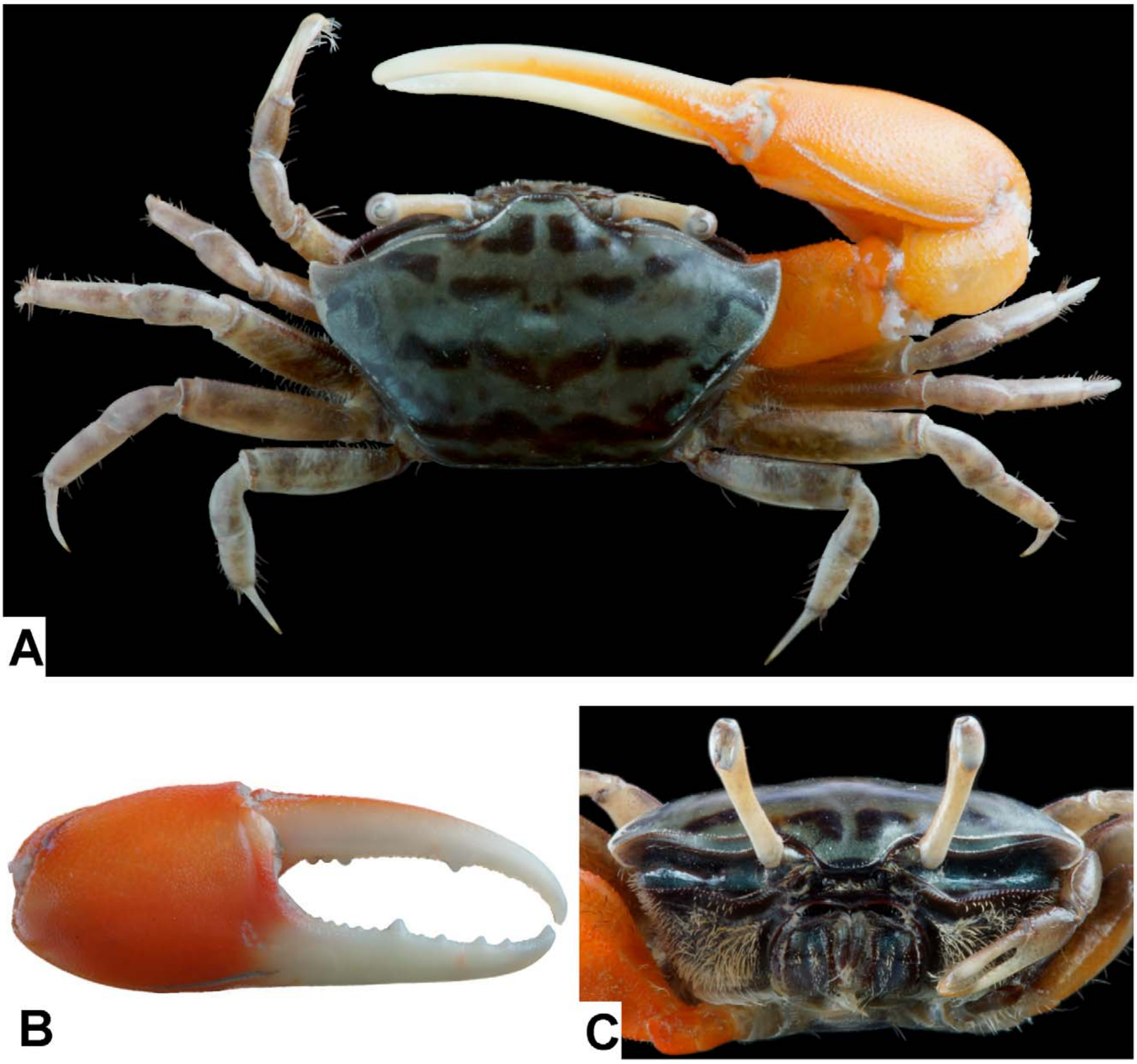

FIGURE 3. *Uca splendida* (Stimpson, 1858). A–C, neotype (ZRC 2012.0143). A, habitus, dorsal view; B, right major chela; C, frontal view.

Size. Largest male 23.5 mm, PL 39.1 mm (Fig. 6E: bottom) and largest female 19.7 mm (Cingluo, Penghu, Taiwan; NCHUZOOL 13488).

Coloration. Carapace dark blue, pale blue to grayish white, with similar transverse black bands (Figs. 3A, 4A, B, E). Some females with anterior carapace orange-red (Fig. 4C, D). Carapace of juveniles cream-yellow or pale green with mottled brown (Fig. 4F). Major chelipeds scarlet red to orange, pollex and dactyl pink-white to white (Fig. 4A, B). Legs orange to red, or mottled dark brown (Fig. 4A–F). Eyestalks pale red to orange-red (Fig. A–F, H).

Distribution. Taiwan (including Penghu), China (Fujian?, Guangdong, Hong Kong, Hainan) and Vietnam (Fig. 1).

Ecology. Sandy mudflats, salt marshes and mangroves. In Tai Tam, Hong Kong, *U. splendida* is found on the supralittoral region of mangroves where the substratum is composed of rock fragments and course sand and covered by coastal vegetation. Burrows have openings of 1–2 cm in diameter, with these not deeper than 20 cm, often limited by rock fragments beneath. *Uca splendida* is locally sympatric with *Parasesarma affine* (De

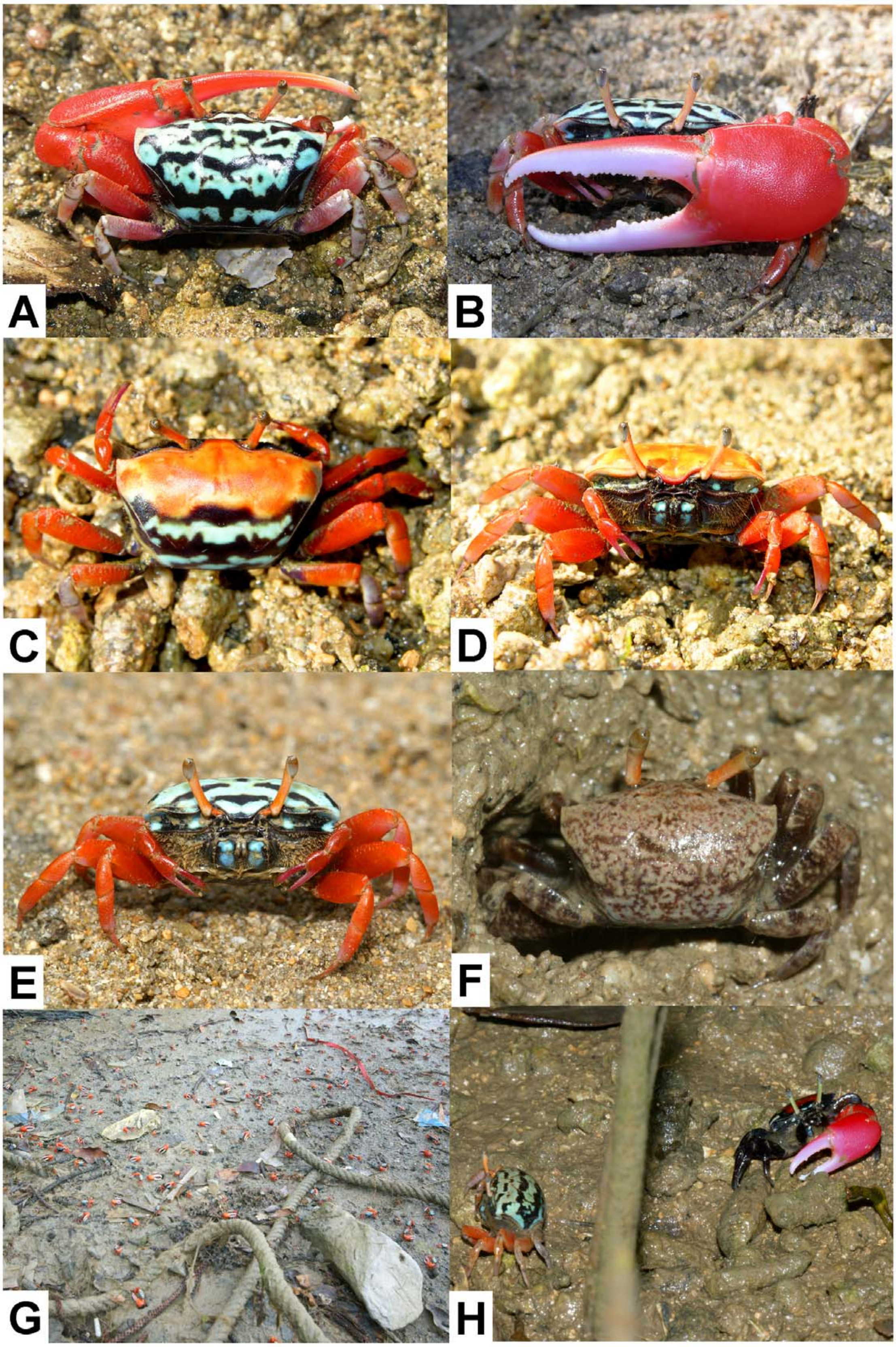

FIGURE 4. *Uca splendida* (Stimpson, 1858). Live coloration of adults (A–E) and juvenile (F); C and D, the same female with different views; G, a population with high density near the bank; H, a female *U. splendida* (left) and a male *U. crassipes* (White, 1947) (right) sympatric in one locality, with reddish eyestalks for the former and greenish eyestalks for the latter. Photos taken from Cingluo (A–E, H) and Citou (F, G), Penghu, Taiwan.

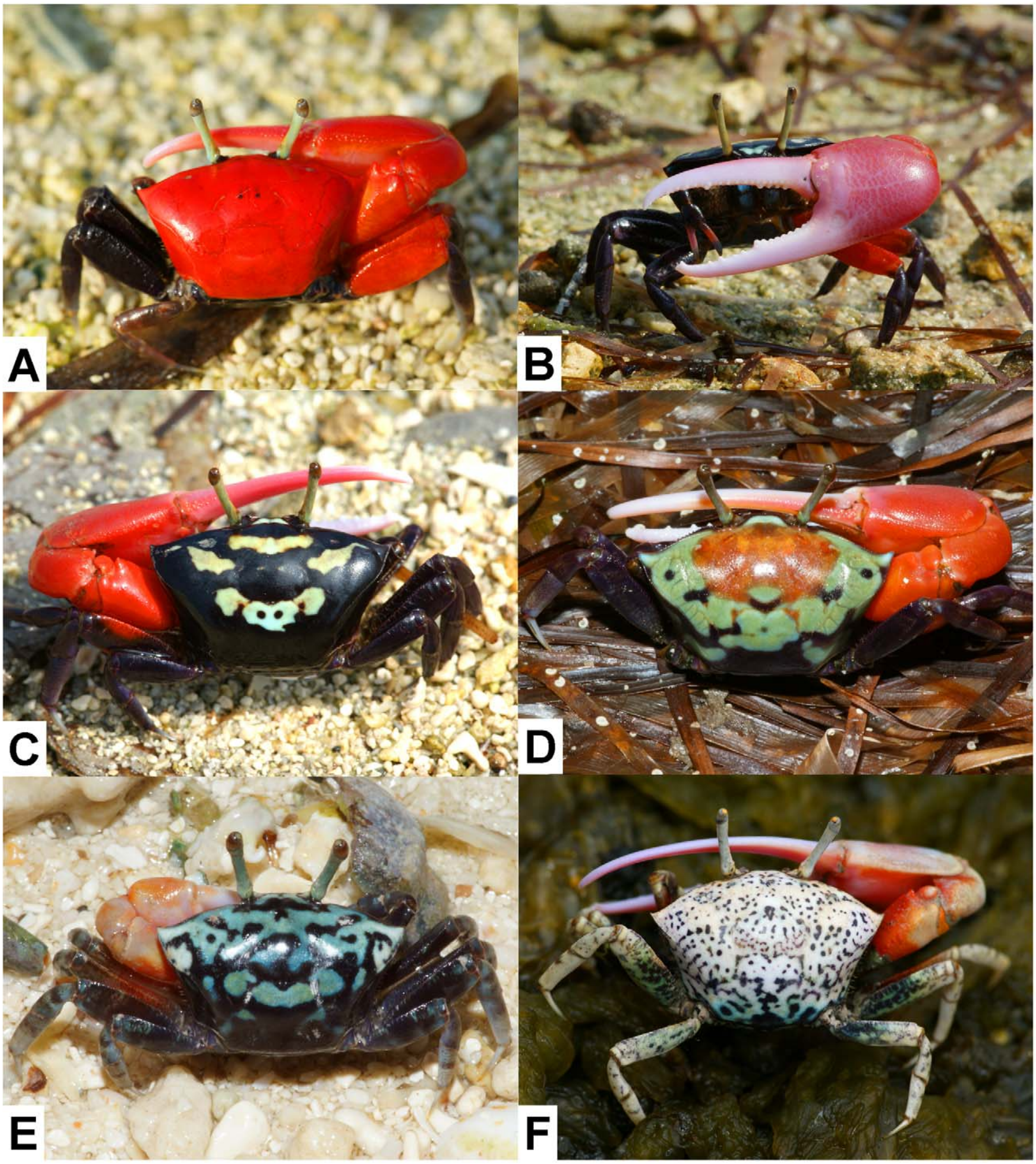

FIGURE 5. *Uca crassipes* (White, 1847). Live coloration of adults (A–D, F) and juvenile (E). Photos taken from Dongsha Island, Taiwan (A–E) and Cocos-Keeling, Australia (F).

Haan, 1837), and *Pseudohelice* sp., but less commonly with other *Uca* species. *Uca splendida* also occurs along landward fringes of sandy beaches, or on compact mud banks in Hong Kong. It is often found sympatrically with *U. dussumieri* (H. Milne Edwards, 1852), *U. crassipes*, *U. jocelynae* Shih, Naruse & Ng, 2010, *U. borealis* Crane, 1975, *U. tetragonon* (Herbst, 1790) and *U. lactea* in Penghu. Shih (1997, 2008) showed that *U. crassipes s. l.* is the dominant species in number among the intertidal crabs of Cingluo, Penghu. Although *U. splendida* and *U. crassipes* are sometimes sympatric, the former appears to be the dominant species in Penghu (see below). In Nha Trang, Vietnam, *U. splendida* is similarly found in supratidal salt marshes on sandy substratum, while being sympatric with the more common *U. lactea* complex and *U. borealis*.

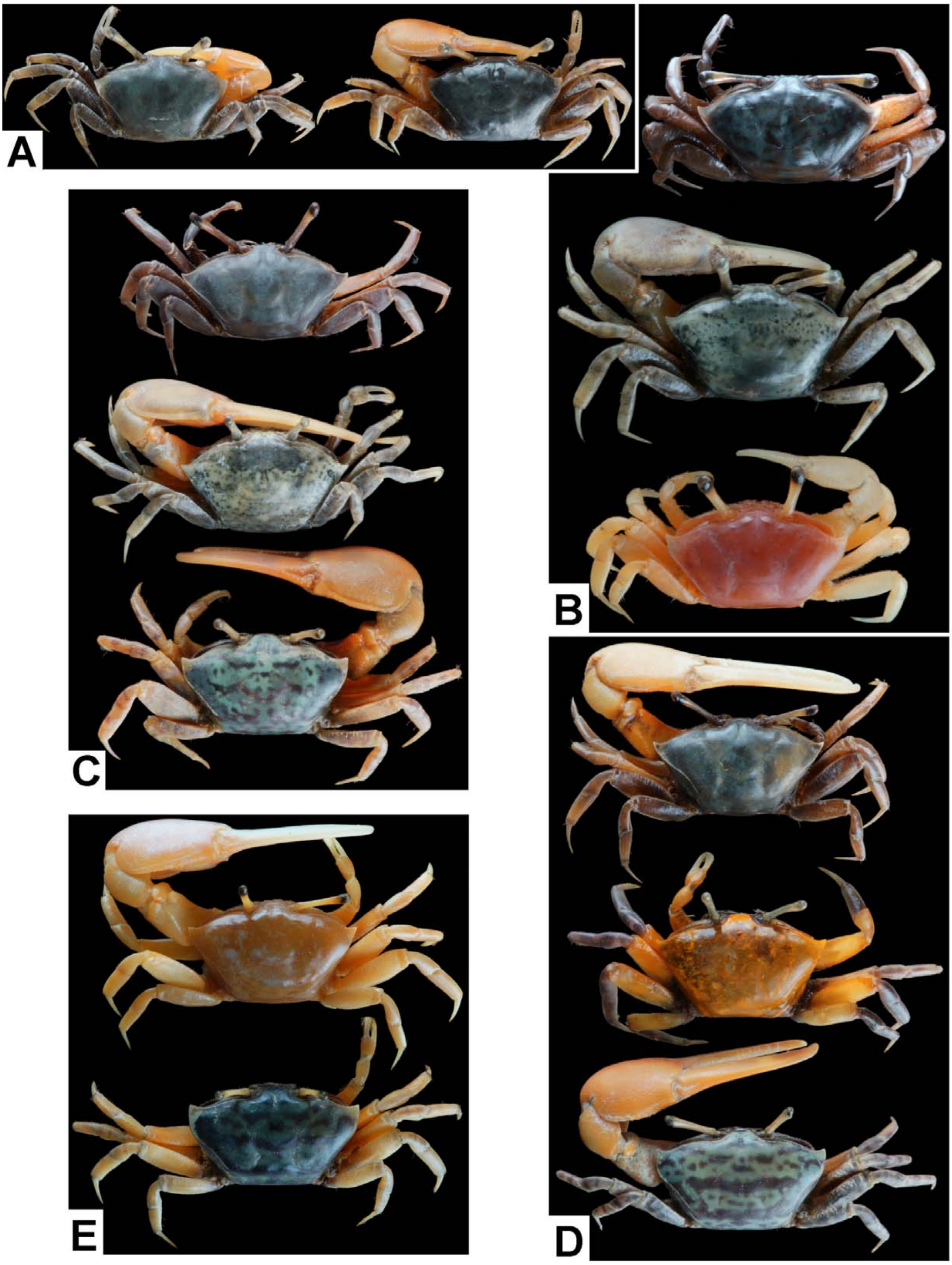

FIGURE 6. Morphology of different sizes of *Uca chlorophthalmus* (H. Milne Edwards, 1837), *U. crassipes* (White, 1847) and *U. splendida* (Stimpson, 1858) males (top, middle and bottom in B–D). A, left: *U. crassipes*, 11.2 mm (Guam; ZRC 2000.0637) and right: *U. splendida*, 11.3 mm (Hainan, China; NCHUZOOL 13449). B, 13.1 mm (Kenya; NCHUZOOL 13498), 13.1 mm (Cocos-Keeling; ZRC) and 13.0 mm (New Taipei, Taiwan; NCHUZOOL 13446), respectively. C, 16.2 mm (Mayotte; MNHN-IU-2011-5601), 16.3 (Cocos-Keeling; ZRC) and 16.2 mm (Penghu, Taiwan; NCHUZOOL 13481), respectively. D, 19.2 mm (Mayotte; MNHN-IU-2011-5600), 19.1 mm (Philippines; NCHUZOOL 13473), 19.2 mm (Penghu, Taiwan; NCHUZOOL 13456), respectively. E, top: *U. crassipes*, 23.1 mm (Dongsha, Taiwan; NCHUZOOL 13464) and bottom: *U. splendida*, 23.5 mm (Penghu, Taiwan; NCHUZOOL 13488). Some males' chelae are separated from the body.

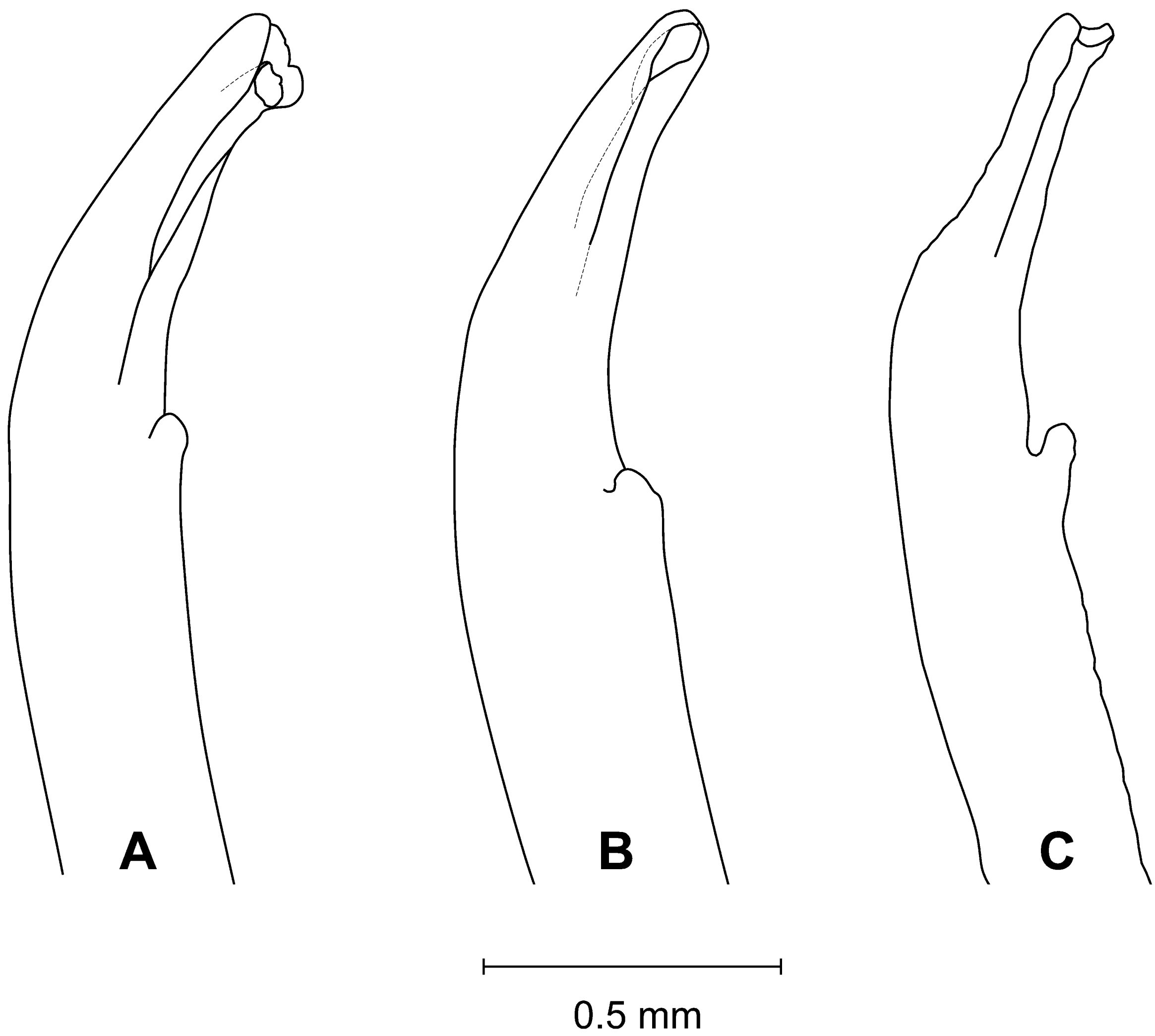

FIGURE 7. The distal part of right G1 (in mesial view) of *Uca chlorophthalmus* (H. Milne Edwards, 1837) (A), *U. crassipes* (White, 1947) (B) and *U. splendida* (Stimpson, 1858) (C), with similar carapace widths around 19.1 mm. Specimens used are the same in (D) of Fig. 6.

Remarks. *Uca splendida* (Stimpson, 1858), is morphologically similar to *U. crassipes* (White, 1847) (type locality: Siquejor, Philippines, lectotype male figured by Crane 1975: pl. 15E, F) and *U. chlorophthalmus* (H. Milne Edwards, 1837) (type locality Mauritius, possible holotype, in fragments, see Crane 1975: 101). It can be separated from these two species by the shapes of the carapace, the morphology of the G1 and live coloration. The anterolateral angles are moderately acute and produced anteriorly in *U. splendida*, but are strongly acute and produced anterolaterally in the other two species (Fig. 6). The anterolateral margins are relatively longer and almost straight in *U. splendida*, but are proportionately shorter or absent in other species (Fig. 6). The tube of the G1 is relatively more slender in *U. splendida*, but proportionately broader in the other two species, with the flanges vestigial in *U. chlorophthalmus*, but absent in *U. crassipes* and *U. splendida* (Fig. 7).

The live coloration of the carapace is a reliable character to separate *U. splendida* and *U. crassipes* in the field, especially when they are sympatric (Fig. 4H), although their chelae are identical (Figs. 3B, 4B, 5B). The carapace of most adult *U. splendida* has similar transverse black bands on the bluish carapace and in some females, the anterior part of the carapace is orange-red (Fig. 4A–E). The carapace coloration of *U. crassipes* varies in color, including being entirely scarlet red (Fig. 5A); with different degrees of red on a black, blue or green background; blue or green bands on a dark background (Fig. 5B–E); and mottled dark spots on a white background (Fig. 5F). Whereas the eyestalks of *U. splendida* are invariably red (Fig. 4A–F, H), *U. crassipes* tends to have green or white eyestalks (Figs. 4H, 5A–F), although a few specimens sometimes possess red eyestalks. Some specimens of *U. crassipes* may have a carapace that has a mixture of blue and black patterns (Fig. 5C, E), similar to that of *U.*

splendida, but the dark part is invariably more irregular and the transverse bands not as prominent as the latter. In addition, the blue coloration is always relatively darker in *U. crassipes* (Fig. 5E).

DNA analysis. A 658-bp segment of COI from 20 specimens of *U. splendida* and 34 specimens of *U. crassipes* was amplified, resulting in 19 different haplotypes (Table 1). The studied segment of the COI sequences was AT rich (61.7%) (T, 32.1%; A, 29.6%; G, 16.8%; C, 21.6%). In this gene fragment, 46 positions were variable and 21 were parsimoniously informative. The best model selected was TPM1uf+I model (proportion of invariable sites = 0.685). The phylogram of BI analysis, with the posterior probability and bootstrap values from the ML and MP analyses, is shown in Figure 8. Only values > 50% are shown. For the MP analysis, a single tree was recovered with a tree length of 336 steps, a consistency index of 0.72, and a retention index of 0.71.

According to the phylogenetic tree (Fig. 8), *U. chlorophthalmus*, *U. crassipes* and *U. splendida* form a monophyletic clade, with the latter two as sister species. The pairwise nucleotide divergences for COI with K2P distance (and differences in the total bp numbers) are shown in Table 2. The mean interspecific K2P distance of *U. splendida* is 2.79% (17.84 bp) with the closest *U. crassipes*, which is 3.4 (3.4) times greater than the mean intraspecific distance of *U. splendida*, 0.82% (5.32 bp) (Table 2). In addition, the lowest interspecific K2P distance of *U. splendida* is 2.49% with *U. crassipes,* which is 1.3 times greater than the largest intraspecific distance of *U. splendida*, 1.86%.

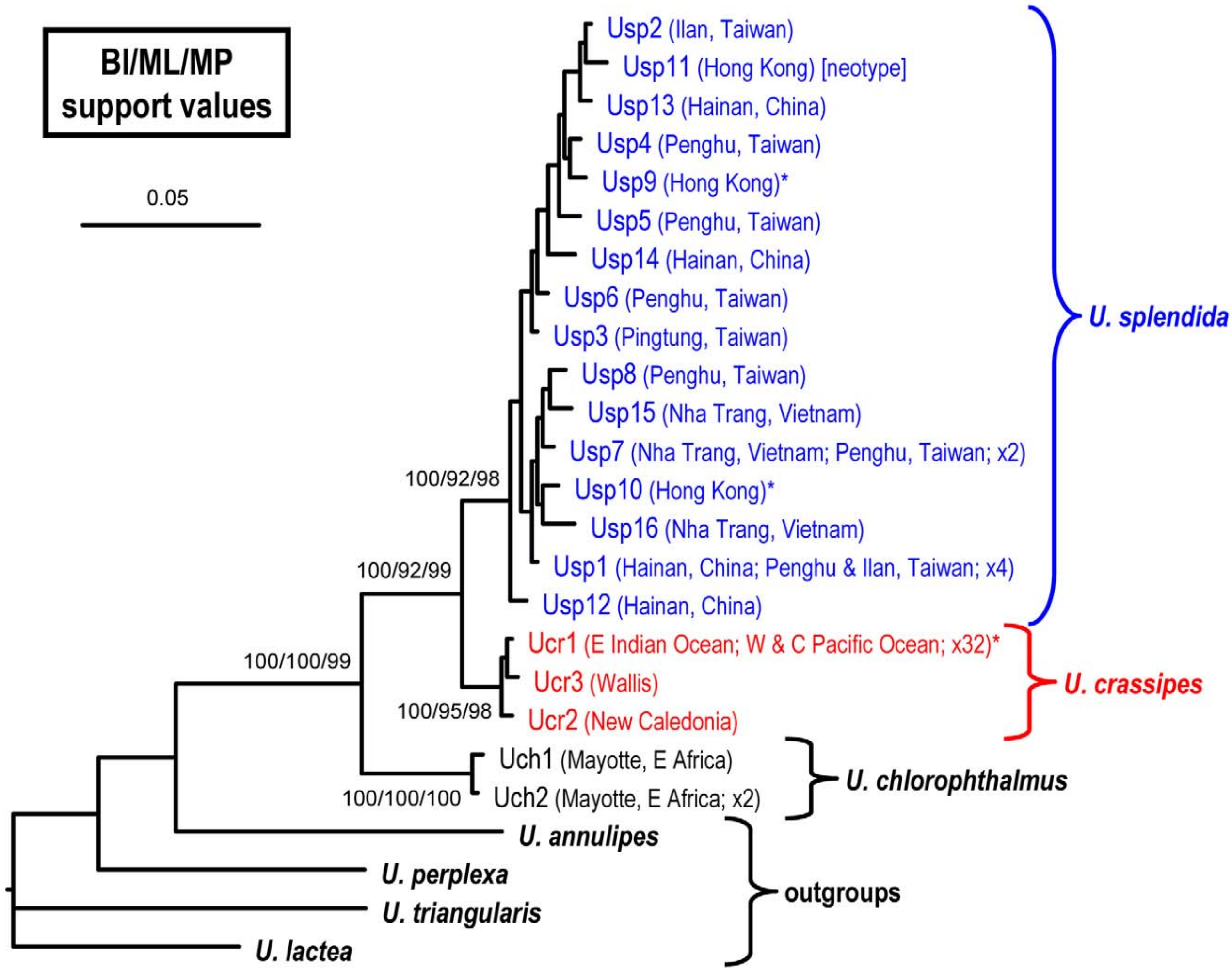

FIGURE 8. A Bayesian inference (BI) tree for *Uca chlorophthalmus* (H. Milne Edwards, 1837), *U. crassipes* (White, 1947) and *U. splendida* (Stimpson, 1858) from the Indo-West Pacific and outgroups, based on COI gene. Probability values at the nodes represent support values for BI, maximum likelihood (MI) and maximum parsimony (MP). "*" indicates specimens from the type locality of *U. splendida* or *U. crassipes*. For haplotype names, see Table 1.

TABLE 2. Matrix of percentage pairwise nucleotide divergences with K2P distance (lower left) and mean number of differences (upper right) based on 658 bp of COI within and between species of *Uca splendida* (Stimpson, 1858), *U. crassipes* (White, 1947) and *U. chlorophthalmus* (H. Milne Edwards, 1837). Values of range are shown in parentheses.

	Intraspecific		Interspecific		
	Nucleotide divergence	Mean nucleotide difference	*U. splendida*	*U. crassipes*	*U. chlorophthalmus*
U. splendida	0.82 (0–1.86)	5.32 (0–12)	—	17.84 (16–22)	44.47 (43–48)
U. crassipes	0.02 (0–0.3)	0.11 (0–2)	2.79 (2.49–3.46)	—	40.22 (40–42)
U. chlorophthalmus	0.05 (0–0.15)	0.33 (0–1)	7.23 (6.97–7.85)	6.49 (6.45–6.8)	—

Discussion

Gelasimus splendidus Stimpson, 1858, was described as a new species by virtue of the shape of carapace as well as its distinct coloration (Stimpson 1858, 1907). Crane (1975) considered that the Hong Kong material could be a subspecies of *Uca chlorophthalmus* because of the slightly longer first gonopod tip and carapace morphology. However, because Crane (1975: 99) had observed variation in smaller specimens from Hong Kong and Cocos-Keeling Is., she dismissed these differences and treated *G. splendidus* as a junior synonym of *U. crassipes* (White, 1847).

Based on the evidence of morphology, coloration (see Remarks) and genetics (Fig. 8), *Uca splendida* (Stimpson, 1858), is clearly a valid species and not a synonym of *U. crassipes* (White, 1847). In the field, especially where they are sympatric, the coloration and/or the form of the anterior carapace margin easily separate the two species, even among young and female individuals. The juveniles of the two species (Fig. 6A), however, share a similar longer anterior carapace margin, although their different color patterns (e.g., even on the eyestalks in preserved specimens) are still apparent.

The observed coloration of *U. splendida* agrees well with the description and photographs of specimens from Hong Kong (Stimpson 1858, 1907; Jones & Morton 1994; Kwok & Tang 2006). We nevertheless have yet to find individuals with the entirely scarlet-red carapaces and major chelipeds that Crane (1975: 99) reported in Hong Kong individuals, although some females in Penghu might look entirely scarlet in frontal view (Fig. 4D) with only half of the carapace is actually red (Fig. 4C).

The distribution of the East Asian fiddler crabs can be divided into a continental group of species (*U. acuta* (Stimpson, 1858), *U. arcuata* (De Haan, 1835), *U. borealis*, *U. lactea*, *U. paradussumieri* (Bott, 1973)) and an oceanic group (*U. annulipes*, *U. coarctata* (H. Milne Edwards, 1852), *U. dussumieri*, *U. jocelynae*, *U. perplexa*, *U. tetragonon*, *U. typhoni* Crane, 1975, *U. vocans* (Linnaeus, 1758)) (cf. Shih *et al*. 2010b). The two species in the present study also show such a biogeographic pattern. From the available data, *Uca splendida* has a more continental distribution, with the northernmost record being Ilan, Taiwan, and Nha Trang, Vietnam as the southernmost (Fig. 1; Table 1). *Uca crassipes* on the other hand, is widely distributed in the eastern Indian Ocean, West Pacific (main islands of Japan, the Ryukyus, Taiwan, Philippines, New Guinea), Central and South Pacific (Fig. 1; Sakai 1939; Crane 1975; Yoshigou 2001). Although there is a record of *Gelasimus chlorophthalmus* from Xiamen, Fujian, China (Cano 1889), this is probably *U. splendida* instead, at least according to the known distribution, assuming that the locality is accurate. There are, however, no recent records of *Uca splendida* from this area (Xiamen and Kinmen) (Wang & Liu 1996c; Ng *et al*. 2001; Shih *et al*. 2010b).

Uca splendida and *U. crassipes* can be found sympatrically in Penghu. Other sympatric areas include southwestern Taiwan (Yanshuei R., Tainan; Yuanjhonggang, Kaohsiung; Baoli R., Pingtung), northeastern Taiwan (Hemei, New Taipei City; Dezihkuo R. and Lanyang R., Ilan) and Dongsha Island (Table 1; material examined; Ho 1995, 1996; unpublished data). The other areas where *U. splendida* has been recorded are Danshuei (= Tamsui) River (New Taipei City), Sinfeng (Hsinchu County) and Jhunan (Miaoli County), northwestern Taiwan (Table 1; material examined; G. Guo, pers. comm.). *Uca crassipes* has also been found in Taitung (eastern Taiwan) and Kenting, Pingtung (southern Taiwan) (Table 1; Tzeng & Chen 1992; Ho *et al*. 1993; Jeng 1998).

Uca splendida is found in the high intertidal in Hong Kong, typically in salt marshes composed of *Zoysia sinica* (Poaceae) (Morton & Morton 1983, as *U. crassipes*), with relatively finer sediment and lower organic content (mostly from leaf-derived humus) (Jones & Morton 1994). The substrate invariably contains large pieces of rock and substantial organic debris. The ecological study of "*U. crassipes*" in Penghu by Shih (2008) actually also included material of *U. splendida* as the latter was still regarded as its junior synonym. However, observations suggest that the microhabitats of the two species appear to be different, with *U. crassipes* preferring more muddy areas (unpublished data). We have not observed any behavioral interactions between the two species (Fig. 4H; unpublished data).

The minimum interspecific divergence (K2P) of COI between *U. splendida* and *U. crassipes* (mean is 2.79% and lowest distance is 2.49%; Table 2) is relatively small when compared with other intertidal crabs: 3.62 % for *Mictyris guinotae* vs. *M. brevidactylus* (Davie *et al*. 2010); 4.43 % for *Scopimera ryukyuensis* vs. *S. globosa* (Wong *et al*. 2010); 4.74% for *Helice tridens* vs. *H. latimera* clade (Shih & Suzuki 2008); and 4.77% for *Uca jocelynae* vs. *U. neocultrimana* (Shih *et al*. 2010a). As the two species form two well-supported reciprocally monophyletic clades (Fig. 8), have consistent morphological differences and are sympatric in Penghu and western Taiwan, they should be recognized as separate species, not subspecies as suggested by Crane (1975: 99). The small divergence suggests both species speciated very recently. If the substitution rate of COI, at 1.66%/10^6 yr for marine sesarmids (Schubart *et al*. 1998) is applied, the two species separated about 1.7 million years ago (with the p-distance 2.83%). This suggests that this was the result of isolation by early Pleistocene glaciation events (Haq *et al*. 1987; Woodruff 2003) around the Taiwan Strait and northern part of the South China Sea.

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References

Beinlich, B. & Hagen, H.O.von (2006) Materials for a more stable subdivision of the genus *Uca* Leach. *Zoologische Mededelingen*, 80, 9–32.

Bott, R. (1973) Die verwandtschaftlichen Beziehungen der *Uca* Arten. *Senckenbergiana biologica*, 54, 315–325.

Cai, L.-Z., Tam, N.F.Y. & Wong, Y.S. (1998) Characteristics of quantitative distribution and species composition of macrozoobenthos in mangrove stands in eastern Hong Kong. *Journal of Xiamen University* (*Natural Science*), 37, 115–121. [In Chinese]

Cano, G. (1889) Crostacei brachiuri ed anomuri raccolti nel viaggio della "Vettor Pisani" intorno al globo. *Bollettino della Societa di Naturalisti in Napoli*, 3, 79–106, 169–268.

Chen, Y.-H. (2001) *Seashore Life (2): 700 Intertidal Species in Taiwan*. Recreation Press, Taipei, 279 pp. [In Chinese]

Chen, Y.-H. (2002) *Seashore Life in Kenting National Park*. Kenting National Park, Pingtung, Taiwan, 168 pp.

Chiou, Y.-C., Chen, J.-C. & Lue, Z.-M. (2004) *The Resource of the Crabs in Kaoh Ping Stream*. Chung Yun Elementary School, Kaohsiung, Taiwan, 59 pp. [In Chinese]

Crane, J. (1975) *Fiddler Crabs of the World (Ocypodidae: Genus* Uca*)*. Princeton University Press, Princeton, New Jersey, xxiii + 736 pp.

Dai, A.-Y. & Yang, S.-L. (1991) *Crabs of the China Seas*. China Ocean Press, Beijing, 682 pp.

Dai, A.-Y., Yang, S.-L., Song, Y.-Z. & Chen, G.-X. (1986) *Crabs of the China Seas*. China Ocean Press, Beijing, 642 pp. [In Chinese]

Davie, P.J.F., Shih, H.-T. & Chan, B.K.K. (2010) A new species of *Mictyris* (Decapoda, Brachyura, Mictyridae) from the Ryukyu Islands, Japan. *Crustaceana Monographs*, 11, 83–105.

Duncan, F.M. (1937) On the dates of publication of the Society's 'Proceedings,' 1859–1926. With an appendix containing the dates of publication of ‘Proceedings,’ 1830–1858, compiled by the late F.H. Waterhouse, and of the ‘Transactions,’ 1833–1869, by the late Henry Peavot, originally published in P. Z. S. 1893, 1913. *Proceedings of the Zoological Society of London*, series A (General and Experimental), 1937(1), 71–84.

Evenhuis, N.L. (2003) Publication and dating of the journals forming the *Annals and Magazine of Natural History* and the *Journal of Natural History*. *Zootaxa*, 385, 1–68. [Additional unnumbered page of errata is available at the *Zootaxa* website: http://www.mapress.com/zootaxa/corrigenda/zt385correction.pdf]

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.

Forest, J. & Guinot, D. (1961) *Crustacés Décapodes Brachyoures de Tahiti et des Tuamotu*. Expédition Française sur les Récifs Coralliens de la Nouvelle Calédonie, Paris, xi + 195 pp.

Gee, N.G. (1926) Tentative list of Chinese decapod Crustacea. *Lingnaan Agricultural Review*, 3(2), 156–166. [Imprint is 1925]

Gordon, I. (1931) Brachyura from the coasts of China. *Journal of the Linnean Society (Zoology)*, 38, 525–558.

Guindon, S. & Gascuel, O. (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology*, 52, 696–704.

Hagen, H.O.von (1976) Review of Jocelyn Crane: Fiddler Crabs of the World. Ocypodidae: Genus *Uca*. *Crustaceana*, 31, 221–224.

Haq, B.U., Hardenbol, J., Vail, P.R. (1987) Chronology of fluctuating sea levels since the Triassic. *Science*, 235, 1156–1167.

Ho, P.-H. (1995) Fiddler crabs (1). *Fisheries Extension*, Taipei, 110, 9–12. [In Chinese]

Ho, P.-H. (1996) Fiddler crabs (12): *Uca chlorophthalmus crassipes*. *Fisheries Extension*, Taipei, 121, 9–12. [In Chinese]

Ho, P.-H. & Hung, M.-S. (1997) *Seashore Crabs of Hsin Chu City*. Hsinchu City Government, Hsinchu City, Taiwan, 122 pp. [In Chinese]

Ho, P.-H., Wang, C.-H., Lin, J.-T. & Yu, H.-P. (1993) First record of the fiddler crab *Uca tetragonon* (Herbst, 1790) (Crustacea: Decapoda: Ocypodidae) from Taiwan, with notes on its handedness. *Journal of Taiwan Museum*, 46, 17–25.

Horikawa, Y. (1940) A list of Formosan crabs. *Scientific Taiwan* 8, 21–31. [In Japanese]

Huang, J.-F., Yu, H.-P. & Takeda, M. (1989) Fiddler crabs (Crustacea: Decapoda: Ocypodidae) of Taiwan. *Bulletin of the Institute of Zoology, Academia Sinica*, 28, 191–209.

Huang, Z.-G. (1994) *Marine Species and Their Distributions in China’s Seas*. China Ocean Press, Beijing, 764 + 134 pp. [In Chinese]

Huang, Z.-G. (2008) *Marine Species and Their Distributions in China*. China Ocean Press, Beijing, 1191 pp. [In Chinese]

Hung, K.-H. (2000) *Common Marine Biology in Penghu*. Bureau of Culture, Penghu County, Penghu, Taiwan, 218 pp. [In Chinese]

Jeng, M.-S. (1997) *Studies on the Land and Aquatic Decapod Crustacean Fauna of the Kenting National Park* (*II*)—*Communities of Decapod Crustaceans around the Sea*. Ministry of the Interior, R.O.C., Taipei, 66 pp. [In Chinese]

Jeng, M.-S. (1998) *The Prawns and Crabs of Kenting National Park*. Kenting National Park, Pingtung, Taiwan, 133 pp. [In Chinese]

Jeng, M.-S. (2003) *A Guide to the Intertidal Zone Life of Penghu*. Second edition. Penghu National Scenic Area Administration, Tourism Bureau Ministry of Transportation and Communications, Penghu, Taiwan, 124 pp. [In Chinese]

Jones, D.S. & Morton, B. (1994) The fiddler crabs (Ocypodidae: *Uca*) of Hong Kong. *Asian Marine Biology*, 11, 9–40.

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.

Kingsley, J.S. (1880) Carcinological notes, no. II.—Revision of the Gelasimi. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1880, 135–155.

Kwok, W.P.W. & Tang, W.S. (2006) Fiddler crabs in Hong Kong—an overview. *Hong Kong Biodiversity*, 12, 1–7.

Lee, J.-H. (2001) *A Field Guide to Crabs in Taiwan*. Bigtrees Co., Taipei, 174 pp. [In Chinese]

Lee, J.-H. & Tung, S.-C. (2000) *Crabs of Tainan County Coast*. Tainan County Government and Kung San Institute of Technology, Tainan, Taiwan, 72 pp. [In Chinese]

Lin, C.-C. (1949) A catalogue of brachyurous Crustacea of Taiwan. *Quarterly Journal of the Taiwan Museum*, 2, 10–33.

Liu, H.-C. & Wang, C.-H. (2010) *Taiwan Coastal Wetland Crabs*. Wild Bird Society of Taipei, Taipei, 79 pp. [In Chinese]

Milne Edwards, H. (1837) *Histoire Naturelle des Crustacés Comprenant l’Anatomie, la Physiologie et la Classification de ces Animaux*. Librairie Encyclopedique de Roret, Paris, vol. 2, 531 pp.; vol. 2 (Atlas), 32 pp.

Milne Edwards, H. (1852) Observations sur les affinités zoologiques et la classification naturelle des Crustacés. *Annales des Sciences Naturelles, Zoology*, 3(18), 109–166.

Morton, B. & Morton, J. (1983) *The Sea Shore Ecology of Hong Kong*. Hong Kong University Press, Hong Kong, 350 pp.

Naderloo, R., Türkay, M. & Chen, H.-L. (2010) Taxonomic revision of the wide front fiddler crabs of the *Uca lactea* group (Crustacea: Decapoda: Brachyura: Ocypodidae) in the Indo West-Pacific. *Zootaxa*, 2500, 1–38.

Ng, P.K.L., Guinot, D. & Davie, P.J.F. (2008) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology, Supplement*, 17, 1–296.

Ng, P.K.L., Wang, C.-H., Ho, P.-H. & Shih, H.-T. (2001) An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *National Taiwan Museum Special Publication Series*, 11, 1–86.

Posada, D. (2008) jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution*, 25, 1253–1256.

Rambaut, A. & Drummond, A.J. (2009) *Tracer v1.5. [http://beast.bio.ed.ac.uk/Tracer]*.

Rathbun, M.J. (1913) Descriptions of new species of crabs of the family Ocypodidae. *Proceedings of the United States National Museum*, 44, 615–620.
Ronquist, F. & Huelsenbeck, J.P. (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.
Ronquist, F., Huelsenbeck, J.P. & Mark, P. van der (2005) *MrBayes 3.1 Manual*. [http://mrbayes.csit.fsu.edu/manual.php].
Rosenberg, M.S. (2001) The systematics and taxonomy of fiddler crabs: a phylogeny of the genus *Uca*. *Journal of Crustacean Biology*, 21, 839–869.
Sakai, T. (1939) *Studies on the Crabs of Japan. IV. Brachygnatha, Brachyrhyncha.* Yokendo, Tokyo, pp. 365–741.
Schubart, C.D., Diesel, R. & Hedges, S.B. (1998) Rapid evolution to terrestrial life in Jamaican crabs. *Nature*, 393, 363–365.
Schubart, C.D. & Huber, M.G.J. (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.
Shen, C.-J. (1936) On a collection of brachyuran Decapoda from Hainan Island with descriptions of three new species. *Chinese Journal of Zoology*, 2, 63–80.
Shen, Y.-L. (1997) Dancers in mud—Jauchau crab: an ecological introduction of Jauchau crab and an investigation of Jauchau crab in marsh around Penghu Island coast. *Bureau of Culture Quarterly of Penghu*, 8, 37–48. [In Chinese]
Shen, Y.-L. & Jeng, M.-S. (2005) *Crabs of Penghu*. Fisheries Research Institute, COA, Keelung, Taiwan, vi + 239 pp. [In Chinese]
Shih, H.-T. (1994) *Fiddler Crabs*. National Museum of Marine Biology/Aquarium, Pingtung, Taiwan, xiv + 190 pp. [In Chinese]
Shih, H.-T. (1997) The fiddler crabs, *Uca formosensis*, belongs to Formosa. Where should they go?—the present condition of an endemic fiddler crab of Taiwan. *Taiwan Natural Science*, 16(2), 68–80. [In Chinese]
Shih, H.-T. (2000) The wetland violinist—the fiddler crabs. *In*: Lai, Y.-M. (Ed), *Vanishing Dancers*. Council of Agriculture, Executive Yuan, R.O.C., Taipei, pp. 70–75. [In Chinese]
Shih, H.-T. (2008) A preliminary study on the diversity and community structure of the fiddler crabs in Penghu. *Notes and Newsletter of Wildlifers*, 12(4), 17–21. [In Chinese]
Shih, H.-T., Naruse, T. & Ng, P.K.L. (2010a) *Uca jocelynae* sp. nov., a new species of fiddler crab (Crustacea: Brachyura: Ocypodidae) from the Western Pacific. *Zootaxa*, 2337, 47–62.
Shih, H.-T., Ng, P.K.L., Fang, S.-H., Chan, B.K.K. & Wong, K.J.H. (2010b) Diversity and distribution of fiddler crabs (Brachyura: Ocypodidae: *Uca*) from China, with new records from Hainan Island in the South China Sea. *Zootaxa*, 2640, 1–19.
Shih, H.-T. & 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) Crustacea Ocypodoidea. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers ducibus, observavit et descripsit, Pars V. *Proceedings of the Academy of Natural Science, Philadelphia*, 10, 93–110.
Stimpson, W. (1907) Report on the Crustacea (Brachyura and Anomura) collected by the North Pacific Exploring Expedition, 1853–1856. *Smithsonian Miscellaneous Collections*, 49(1717), 1–240.
Swofford, D.L. (2003) *PAUP*: Phylogenetic Analysis Using Parsimony* (**and Other Methods*), *version 4*. Sinauer Associates, Sunderland, Massachusetts.
Tam, N.F.Y. & Wong, Y.S. (2000) *Hong Kong Mangroves*. City University of Hong Kong Press, Hong Kong, 158 pp.
Thompson, J.D., Higgins, D.G. & Gibson, T.J. (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalties and weight matrix choice. *Nucleic Acid Research*, 22, 4673–4680.
Tzeng, C.-S. & Chen, Y.-S. (1992) *Guide to the Seashore Life in the East Coast National Scenic Area of Taiwan*. East Coast National Scenic Area Administration, Tourism Bureau Ministry of Transportation and Communications, Taitung, Taiwan, 221 pp. [In Chinese]
Wang, C.-H. (1984) Primary studies on the crabs in Kenting National Park in Taiwan. *Annual of Taiwan Museum*, 27, 39–44. [In Chinese]
Wang, C.-H. & Liu, H.-C. (1996a) *Common Seashore Crabs of Taiwan*. Taiwan Museum, Taipei, 136 pp. [In Chinese]
Wang, C.-H. & Liu, H.-C. (1996b) *Estuarine Crabs of Taiwan*. Wild Bird Society of Kaohsiung, Kaohsiung, Taiwan, 113 pp. [In Chinese]
Wang, C.-H. & Liu, H.-C. (1996c) Preliminary investigations of the crab diversity of Wu-Jiang estuary mangrove area in Kinmen. *In*: *Proceedings of a Conference on Mangrove Ecology*, Taiwan Endemic Species Research Institute, Nantou, Taiwan, pp. 223–229. [In Chinese]
Wang, C.-H. & Liu, H.-C. (1998a) *Common Seashore Crabs of Taiwan*, 2nd edition. Taiwan Museum, Taipei, 136 pp. [In Chinese]
Wang, C.-H. & Liu, H.-C. (1998b) Mangrove crabs of Taiwan. *In*: Huang, S., Shih, J.-T. & Hsueh, M.-L. (Eds.), *Mangroves of Taiwan*. Taiwan Endemic Species Research Institute, Nantou, Taiwan, pp. 94–150. [In Chinese]
Wang, C.-H. & Liu, H.-C. (2003) *Common Seashore Crabs of Taiwan*, 3rd edition. Taiwan Museum, Taipei, 136 pp. [In

Chinese]
Wang, Y.-T. (2009) *Intertidal Biota of Tainan*. Tainan County Government, Tainan, Taiwan, 303 pp. [In Chinese]
White, A. (1847a) 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. [Published 20 July 1847, see Duncan (1937: 80); reprinted as White (1847b)]
White, A. (1847b) Short descriptions of some new species of Crustacea in the collection of the British Museum. *In*: Proceedings of Learned Societies. Zoological Society. May 25, 1847.—Harpur Gamble, Esq., M.D., in the Chair. *Annals and Magazine of Natural History*, ser. 1, 20(132), 205–207. [Published 1 September 1847, see Evenhuis (2003: 15); reprint of White (1847b)]
Wong, K.J.H., Chan, B.K.K. & Shih, H.-T. (2010) Taxonomy of the sand bubbler crabs *Scopimera globosa* De Haan, 1835, and *S. tuberculata* Stimpson, 1858 (Crustacea: Decapoda: Dotillidae) in East Asia, with description of a new species from the Ryukyus, Japan. *Zootaxa*, 2345, 43–59.
Woodruff, D.S. (2003) Neogene marine transgressions, palaeogeography and biogeographic transitions on the Thai Malay Peninsula. *Journal of Biogeography*, 30, 551–567.
Yang, S.-L., Chen, H.-L. & Jiang, W. (2008) Brachyura. *In*: Liu, R.-Y. (Ed), *Checklist of Marine Biota of China Seas*. Science Press, Beijing, pp. 761–810. [In Chinese]
Ye, J.-Y. & Chen, H.-S. (2000) *Study on the Ecological Environment of the Fiddler Crabs from Siyu Island, Penghu*. Chi Ma Elementary School, Penghu, Taiwan, vi + 62 pp. [In Chinese]
Yoshigou, H. (2001) Japanese species of genus *Uca* (Crustacea: Decapoda: Ocypodidae) and distribution of *U. lactea* in Hiroshima Prefecture, Japan. *Hibakagaku*, 200, 1–12. [In Japanese]
Yu, H.-P., Jeng, M.-S., Chan, T.-Y., Ho, P.-H. & Shy, J.-Y. (1996) *Studies on the Land and Aquatic Decapod Crustacean Fauna of the Kenting National Park*. Ministry of the Interior, R.O.C., Taipei, 79 pp. [In Chinese]