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Diversity and Distribution of Fiddler Crabs (Crustacea: Brachyura: Ocypodidae) in Vietnam

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Based on recently collected material and records in the literature, 14 species of fiddler crabs (Crustacea: Ocypodidae: Gelasiminae) are reported from Vietnam. DNA barcoding analyses using the mitochondrial gene *COI* (cytochrome *c* oxidase subunit I) was performed to identify examined materials and their precise distributional range. Thirteen species-level taxa are identified and, with the exception of *Galsimus borealis* and *G. vocans*, have minimum interspcific divergences of at least 7.27%. The identified species include seven species of *Tubuca* Bott, 1973, three of *Austruca* Bott, 1973 and three of *Gelasimus* Latreille, 1817, and one *Paraleptuca* Bott, 1973. Two new records of Vietnam are herein reported: *Tubuca rhizophorae* and *T. dussumieri*. The southernmost distribution limits of East Asian *G. borealis*, *T. acuta* and *T. arcuata* are in northern Vietnam, *A. lactea* in central Vietnam, whereas northernmost limit of Southeast Asian *T. rhizophorae* and *T. forcipata* in southern Vietnam. A dichotomous key to identify the 14 Vietnamese species is provided.

Key words: Fiddler crabs, New records, *Austruca*, *Gelasimus*, *Paraleptuca*, *Tubuca*, Mitochondrial cytochrome *c* oxidase subunit I (*COI*), Barcodes.

BACKGROUND

Fiddler crabs (Ocypodidae) are a group of brachyurans dominant along intertidal zones of tropical and subtropical coasts (Crane 1975). Since the revision of the Ocypodidae by Shih et al. (2016b), several new species of fiddler crabs have been reported, and the group currently contains 11 genera with 107 species (Shih et al. 2018 2019; Shih and Poupin 2020). In the Indo-West Pacific region (IWP), 49 species have been reported. While the East Asian fiddler crab fauna has been relatively well studied in recent years (Shih et al. 2010b 2015 2016a), that in Southeast Asia has received relatively less attention.

Vietnam is located on the western shores of the South China Sea (SCS), between latitudes 8° and 21.5°N, and its coastline longitudinally spans across subtropical and tropical zones. The earliest record of the fiddler crab fauna of Vietnam can be traced back to a "*Uca latreillei*" (= *Paraleptuca splendida*) from "Phuc Son and Tourane, Annam" (the latter locality now Da Nang; Balss 1922). Serène (1937) reported *Uca arcuatus*

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from Tonkin, northern Vietnam. Dawydoff (1952) added *U. annulipes*, *U. arcuata* and *U. tetragonon* from French Indochina (including Vietnam and Cambodia), with "*U. manii*" (probably *Tubuca forcipata*) from Ca Mau (southernmost of Vietnam) and Cambodia, *U. lactea* from Ha Long Bay, northern Vietnam, and "*U. dubia*" (probably *Tubuca dussumieri* or *T. paradussumieri*) from the Paracels (= Xisha Islands or Hoang Sa Archipelago). Later, Crane (1975) only cited Serène's (1937) record of *Uca arcuatus*, missing Dawydoff's (1952) report.

In recent decades, Do (1996) listed "*Uca arcuata*", "*U. lactea*" and *Uca* sp. from Can Gio mangrove forest, southern Vietnam, but the identification was problematic. Kosuge et al. (1997) identified *U. acuta*, *U. arcuata*, *U. borealis*, *U. lactea* and *U. paradussumieri* from Hai Phong, northern Vietnam—results cited by Shih et al. (2010b) when revising Chinese records. Several species were listed in preliminary reports on the brachyuran fauna from northern Vietnam (Do and Hoang 2002 2004 2006; Hoang et al. 2010) and southern Vietnam (Do 2003; Hoang et al. 2012), yet the lack of illustrations or schematic descriptions make further verifications difficult. In resurrecting *Paraleptuca splendida* (then as *Uca* (*Paraleptuca*)), Shih et al. (2012) included specimens from Nha Trang, southern Vietnam. From the same area, detailed investigations by Chertoprud et al. (2012) revealed 10 fiddler species in vicinity of the Bay of Nha Trang, viz. *U. annulipes*, "*U. arcuata*" (probably *T. dussumieri* or *T. paradussumieri*), "*U. borealis*" (should be *G. vocans*), "*U. crassipes*" (= *P. splendida*), "*U. flammula*" (probably juveniles of *T. forcipata*), *U. forcipata*, *U. paradussumieri*, "*U. rosea*" (= *U. vocans*), *U. tetragonon*, and *U. vocans*. Kostina et al. (2016) identified four species from the Red River Delta, viz. *A. lactea*, *T. arcuata*, "*T. forcipata*" (probably *T. arcuata*) and "*T. dussumieri*" (probably *T. paradussumieri*); as well as three species from Nha Trang, viz. *A. annulipes*, *Gelasimus vocans* and "*T. urvillei*" (probably *T. paradussumieri*). As a summary of brachyuran material collected from Vietnam for over a decade, Wada (2019) listed *A. lactea*, *G. borealis*, *G. vocans*, *P. splendida*, *T. acuta*, *T. arcuata*, *T. paradussumieri* from northern Vietnam, and *A. perplexa* from southern Vietnam. In recent reports on brachyurans from southern Vietnam, Le et al. (2018) recorded *U. borealis*, *U. annulipes*, *U. crassipes*, *U. dussumieri*, *U. flammula*, *U. lactea* and *U. paradussumieri* from Tra Vinh Province; and Le et al. (2020) listed *Uca borealis*, *U. arcuata*, *U. dussumieri*, *U. flammula*, *U. urvillei*, *U. annulipes*, *U. crassipes* and *U. paradussumieri* from Soc Trang Province. No figures or diagnoses were appended in the latter report. From northern Vietnam, Do et al. (2021), Hoang et al. (2021) and Nguyen et al. (2022) identified *Uca arcuata*, *U. borealis*, *U. lactea* and *U. paradussumieri*.

We have reservations about some of the above listed records—several probably do not occur in northern nor southern Vietnam, or in various cases judged from attached illustrations, are nearly certainly misidentifications. Based on material amassed through years of surveys along the coasts of Vietnam, as well as examining past records in the literature, using an integrated approach of morphological analyses, and molecular evidence generated by DNA analyses on sequences from the mitochondrial gene *COI* (cytochrome oxidase subunit I), we revised records of fiddler crabs from Vietnam. Each species is illustrated and elaborated in detail. A key to the genus and species found is also provided.

MATERIALS AND METHODS

Material of fiddler crabs collected from the coastal regions in Vietnam (Table 1, Fig. 1) were preserved in 70% to 95% ethanol, and deposited into the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL); the Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore (ZRC); and the Zoology collection of the Biological Museum, VNU University of Science, Vietnam National University, Hanoi, Vietnam (ZVNU). The following abbreviations are used: CW = carapace width and G1 = male first gonopod. In the synonym list of each species, for simplicity, only the publications of original description of species, taxonomic revisions, and those including Vietnamese fauna are included. Dimensions of specimens are denoted by CW, in millimeters (mm).

Genomic DNA was isolated from muscle tissue using kits (see Shih et al. 2016b for details). A portion of the *COI* gene was amplified with a polymerase chain reaction (PCR) using the primers LCO1490, HCO2198 (Folmer et al. 1994), COL14 (Roman and Palumbi 2004), COL6, COH6 (Schubart 2009), ICOUB (Huang et al. 2021), and LCOB, HCOex, HCOex2 and HCOex3 (see Shih et al. 2022). PCR conditions for the above primers were 40 cycles of denaturation for 50 s at 94°C, annealing for 70 s at 45–47°C, and extension for 60 s at 72°C, followed by extension for 10 min at 72°C. Sequences were obtained by automated sequencing (Applied Biosystems 3730, USA). Sequences of the different haplotypes were deposited into GenBank (accession numbers given in Table 1).

A neighbor-joining (NJ) tree for *COI* sequences was established using the Kimura (1980) 2-parameter

(K2P) model with the complete deletion option using the program MEGA (vers. 11, Tamura et al. 2021). Basepair (bp) differences and pairwise estimates of K2P distances for genetic diversities between specimens were also calculated in MEGA.

RESULTS

Molecular analyses of *COI*

The *COI* sequences from 50 specimens of fiddler crabs collected from Vietnam (Table 1, Figs. 1, 7) correspond to 13 species with good support (Fig. 2). The mean pairwise nucleotide divergences of K2P distances and bp differences of haplotypes are shown in table 2. The intraspecific nucleotide divergences (and bp differences) are all ≤ 1.70% (≤ 11 bp), with *Paraleptuca splendida* and *Tubuca arcuata* possessing the highest intraspecific divergence. The interspecific divergences are ≥ 7.27% (45 bp) (except *Gelasimus borealis* and *G. vocans*), with the lowest interspecific divergence being between *T. arcuata* and *T. forcipata*.

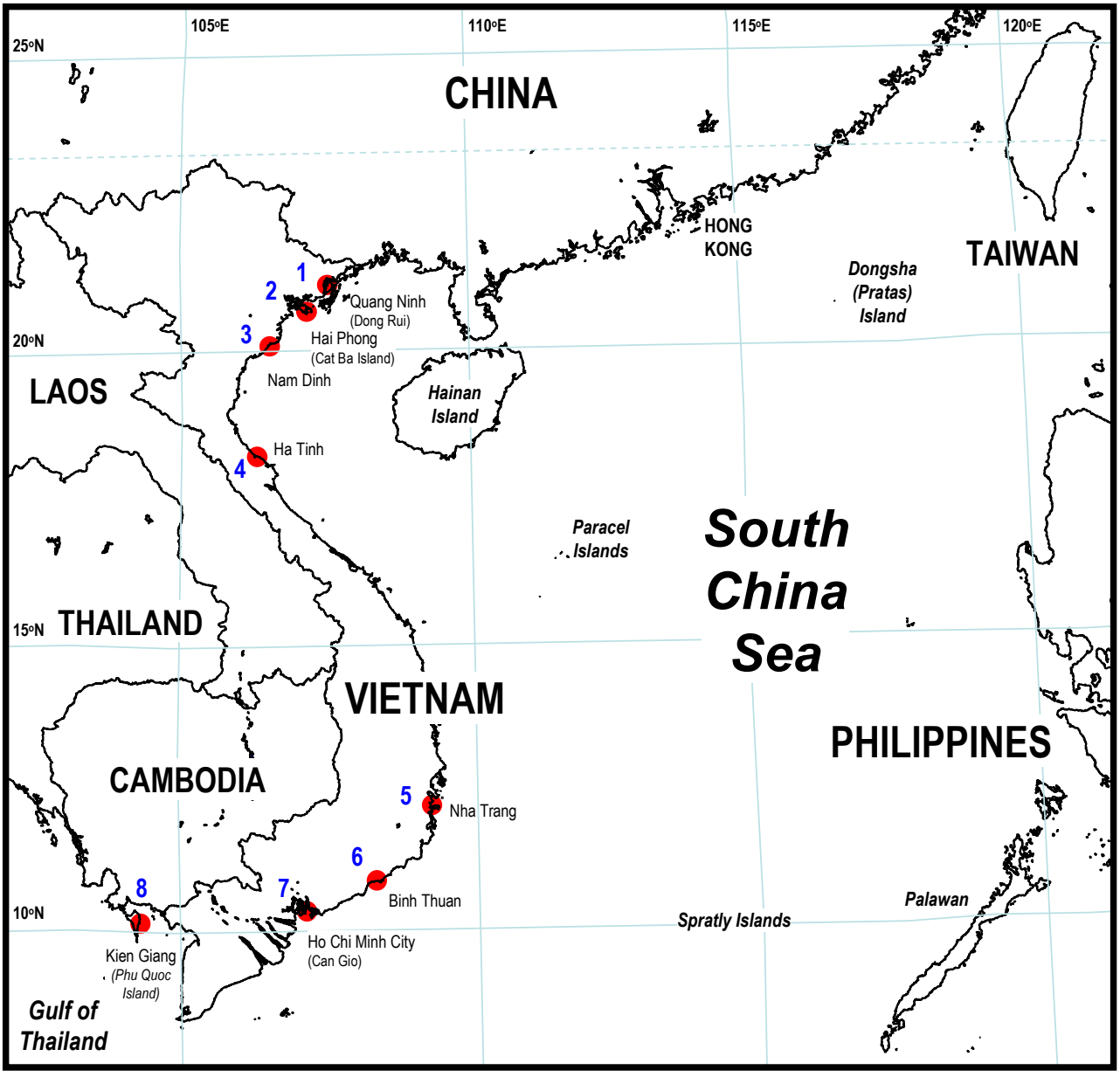

Fig. 1. Collection sites for specimens of fiddler crabs from Vietnam examined in this study (see Table 1).

TAXONOMY

Family Ocypodidae Rafinesque, 1815
Subfamily Gelasiminae Miers, 1886 (sensu Shih et al. 2016b)

Genus *Austruca* Bott, 1973

Austruca annulipes (H. Milne Edwards, 1837)
(Fig. 3A, B)

Cancer vocans minor Herbst, 1782: 81, pl. 1(10) [nomen oblitum]; Shih et al. 2021: 208, fig. 1A.
Gelasimus annulipes H. Milne Edwards, 1837: 55, pl. 18(10–13) (type locality: mer des Indes (= Indian Ocean)) [nomen protectum]; Kingsley 1880: 148, pl. 10(22) [part].
Gelasimus lacteus – Kingsley 1880: 149 [part].
Uca (*Celuca*) *lactea annulipes* – Crane 1975: 298, 611, figs. 18A–C, 19I–N, 20D–F, 24N, O, 27I–J, 29D, 32L, M, 41A, 54I, II, 69D, pls. 39A–D, 40C, D [part]; Dai et al. 1986: 426, pl. 59(3), fig. 236(2).
Uca (*Celuca*) *annulipes* – Dai and Yang 1991: 467, pl. 59(3), fig. 236(2).
? *Uca lactea* – Do 1996: 36.
Uca (*Paraleptuca*) *annulipes* – Ng et al. 2008: 241.
Uca lactea annulipes – Trivedi et al. 2018: 17, 20, fig. 3c.
Uca annulipes – Dawydoff 1952: 141; Yamaguchi 1994: 153, 183; S-L Yang et al. 2008: 807; Shih et al. 2009: 376; Shih et al. 2010b: 6; Chertoprud et al. 2012: 266, pl. 44C, D; Hoang et al. 2012: 75; Shih et al. 2013: 643; Saher et al. 2014: 67; Le et al. 2018: 41, fig. 5D; Le et al. 2020: 15.
Uca (*Austruca*) *annulipes* – Naderloo et al. 2010: 7, figs. 2a–h, 3a–e, 4b, 12a–c; Kostina et al. 2016: 196, 257.
Austruca annulipes – Shih et al. 2016b: 153, 168, fig. 8A; Sasaki 2019: 12424; Shih et al. 2021: 212, fig. 2.
Austruca (*Austruca*) *annulipes* – Rosenberg 2019: 734.

Material examined: Nha Trang: 4 ♂♂ (15.3–17.4 mm), 1 ♀ (13.3 mm) (NCHUZOOL 15111), mangrove I, coll. K. J. H. Wong and I-H. Chen, 24 Nov. 2010; 7 ♂♂ (13.2–21.7 mm), 3 ♀♀ (14.7–18.6 mm) (NCHUZOOL 15112), mangrove II, coll. I-H. Chen and K. J. H. Wong, 24 Nov. 2010. Binh Thuan: 20 ♂♂ (11.6–19.6 mm), 1 ♀ (14.0 mm) (NCHUZOOL 15110), Nguyen Thong, Phu Hai, Phan Thiet, coll. I-H. Chen et al., 26 Nov. 2010. Kien Giang: 2 ♂♂ (12.8, 13.4 mm)

Table 1. Specimens and *COI* haplotypes of the fiddler crabs from Vietnam and adjacent waters. The numbers within brackets following localities correspond to those in figure 1. See MATERIALS AND METHODS for abbreviations of museums and universities

Species	Locality in Vietnam (unless indicated)	Sample size	Catalogue no. of NCHUZOOL (unless indicated)	Haplotype	Access. no.
Austruca annulipes	Nha Trang [5]	2	15112	Aan1, Aan2	ON193445, ON193446
	Binh Thuan: Nguyen Thong, Phu Hai, Phan Thiet [6]	3	15110	Aan3, Aan4, Aan5	ON193447, ON193448, ON193449
	Kien Giang: Phu Quoc Island [8]	1	15113	Aan2	ON193450
	China: Sanya, Hainan	1	13244	Aan2	AB471907
	Malaysia: Tioman	1	13243	Aan2	AB471907
	Thailand: Phuket	1	13257	Aan3	AB491160
A. lactea	Hai Phong: Xuan Dam, Cat Ba Island [2]	3	15114	Ala1, Ala2, Ala3	ON193451, ON193452, ON193453
	Nam Dinh [3]	2	15115	Ala4, Ala5	ON193454, ON193455
	Taiwan: Siangshan, Hsinchu City	1	13249	Ala1	AB471912
	Hong Kong	1	13250	Ala1	ON193456
A. perplexa	Binh Thuan: Nguyen Thong, Phu Hai, Phan Thiet [6]	2	15116	Ape1	ON193457, ON193458
	Ho Chi Minh: Giong Ao, Can Thanh Town, Can Gio [7]	1	15117	Ape1	ON193459
	Kien Giang: Phu Quoc Island [8]	1	15119	Ape2	ON193460
	Malaysia: Jeram	1	15052	Ape1	ON193461
	Singapore	1	ZRC 2020.0288	Ape1	ON193462
Gelasimus borealis	Quang Ninh: Dong Rui [1]	2	15121, 15122	Gbo1, Gbo2	ON193463, ON193464
	Hai Phong: Cat Ba Island: Xuan Dam [2]	1	15120	Gbo3	ON193465

Table 1. (Continued)

Species	Locality in Vietnam (unless indicated)	Sample size	Catalogue no. of NCHUZOOL (unless indicated)	Haplotype	Access. no.
	Taiwan: Shengang, Changhua	1	13259	Gbo2	AB491163
	Hong Kong	1	13207	Gbo4	LC053376
G. tetragonon	Nha Trang: Luong Son, Vinh Luong [5]	2	15124	Gte	ON193466, ON193467
	Taiwan: Chitou, Penghu	1	13304	Gte	AB535431
	Egypt: Sinai: El Monqata	1	15096	Gte	AB535431
G. vocans	Nha Trang [5]	1	14913	Gvo1	ON193468
	Binh Thuan: Nguyen Thong, Phu Hai, Phan Thiet [6]	2	15125	Gvo2, Gvo3	ON193469, ON193470
	Singapore: Lim Chu Kang	1	13189	Gvo4	AB535425
	Philippines: Bohol	1	13205	Gvo5	AB813683
Paraleptuca splendida	Nha Trang [5]	1	15132	Psp1	ON193471
	Nha Trang [5]	2	13448	Psp2, Psp3	AB734654, ON193472
	Nha Trang: Luong Son, Vinh Luong [5]	1	13459	Psp4	AB734655
	Taiwan: Chitou, Penghu	1	13453	Psp5	AB734645
	Taiwan: Chitou, Penghu	1	13450	Psp3	AB734646
	Hong Kong: Tai Tam	1	13368	Psp6	AB734648
T. acuta	Haiphong: Cat Ba Island: Xuan Dam [2]	2	15134	Tac	ON193473, ON193474
	Nam Dinh: Xuan Thuy National Park [3]	2	15104, 15105	Tac	ON193475, ON193476
	Nam Dinh [3]	1	15133	Tac	ON193477
	Taiwan: Kinmen	1	13650	Tac	LC053369
	China: Hainan: Dongzhai	1	13351	Tac	LC150429
T. arcuata	Hai Phong: Cat Ba Island: Xuan Dam [2]	1	15140	Tar1	ON193478
	Nam Dinh: Xuan Thuy National Park [3]	1	15100	Tar1	ON193479
	Nam Dinh [3]	3	15144	Tar1	ON193480, ON193481, ON193482
	Ha Tinh: Cam Ha, Cam Xuyen District [4]	1	15141	Tar2	ON193483
	Japan: Kaeda River, Miyazaki	1	14610	Tar1	ON193484
	Taiwan: Cigu, Tainan	1	13260	Tar3	AB491165
T. forcipata	Ho Chi Minh: Giong Ao, Can Thanh Town, Can Gio [7]	1	15145	Tfo1	ON193485
	Ho Chi Minh: Giong Ao, Can Thanh Town, Can Gio [7]	2	15146	Tfo1, Tfo2	ON193486, ON193487
	Ho Chi Minh: Giong Ao, Can Thanh Town, Can Gio [7]	1	15147	Tfo1	ON193488
	Malaysia: Johor	1	NTOU	Tfo1	LC053372
T. paradussumieri	Quang Ninh: Dong Rui [1]	2	ZVNU.2019.010, ZVNU.2019.011	Tpa2	ON193489, ON193490
	Ho Chi Minh: Rung Sac, Long Hoa, Can Gio [7]	1	15157	Tpa1	ON193491
	South Vietnam	1	ZRC	Tpa1	ON193492
	China: Dongzhai, Hainan	1	13381	Tpa2	LC053373
	Malaysia: Kuching, Sarawak	1	ZRC 1965.12.8.72-81	Tpa2	ON193493
T. rhizophorae	Ho Chi Minh: Can Gio: Can Thanh Town: Giong Ao [7]	1	15148	Trh1	ON193494
	Ho Chi Minh: Rung Sac, Long Hoa, Can Gio [7]	1	15149	Trh2	ON193495
	Malaysia: Mersing	1	14923	Trh3	LC150442
	Malaysia: Kuching, Sarawak	1	14924	Trh4	LC150443
T. typhoni	Binh Thuan: Nguyen Thong, Phu Hai, Phan Thiet [6]	1	15150	Tty1	ON193496
	Ho Chi Minh: Rung Sac, Long Hoa, Can Gio [7]	1	15151	Tty2	ON193497
	China: Sanya, Hainan	1	13371	Tty3	LC150444
Total		76			

(NCHUZOOL 15113), Phu Quoc Island, coll. H.-T. Shih, 2 Dec. 2012.

Distribution: Pakistan, India, Myanmar, Thailand, Malay Peninsula, Singapore, Indonesia, Borneo, Vietnam, and South China (Hainan).

Remarks: *Austruca annulipes*, widely distributed in IWP, is a common species in Southeast Asia (Crane 1975; Shih et al. 2009 2022; Naderloo et al. 2010; Trivedi et al. 2018). In the region of the SCS, it has been reported from southern coast of Hainan Island (ca. 18°N; Figs. 1, 7), and northern part of the SCS (Dai et al. 1986; Dai and Yang 1991; Shih et al. 2010b), which is the northernmost distribution of this species in the West Pacific. However, the current records show it is only limited to the southern parts of Vietnam (ca. 12°N; Figs. 1, 7).

Fig. 2. A neighbor-joining (NJ) tree for species of the fiddler crabs from Vietnam based on the cytochrome *c* oxidase subunit I (*COI*) gene. Probability values at the nodes represent support values. Only values > 50% are shown. For haplotype names, see Table 1. NVN, northern Vietnam; SVN, southern Vietnam.

Table 2. Matrix of percentage pairwise nucleotide divergence with Kimura 2-parameter (K2P) distances (lower left) and mean numbers of differences (upper right) based on cytochrome *c* oxidase subunit I (*COI*) within and between species of fiddler crabs from Vietnam (see Table 1). Values of the range are shown in parentheses

	Intraspecific		Interspecific					
	Nucleotide divergence	mean nucleotide difference	*A. annulipes*	*A. lactea*	*A. perplexa*	*G. borealis*	*G. vocans*	*G. tetragonon*
Austruca annulipes	0.44 (0–1.08)	2.89 (0–7)		85.92 (82–89)	92.22 (90–95)	98.27 (94–103)	98.44 (94–102)	103.33 (102–105)
Austruca lactea	0.41 (0–0.92)	2.67 (0–6)	14.47 (13.7–15.06)		85.29 (84–88)	100.89 (98–104)	101.49 (98–103)	105.86 (104–108)
Austruca perplexa	0.1 (0–0.3)	0.67 (0–2)	15.67 (15.23–16.21)	14.38 (14.14–14.89)		94.53 (94–97)	94.53 (93–96)	106.67 (105–107)
Gelasimus borealis	0.37 (0–0.77)	2.4 (0–5)	16.8 (15.96–17.75)	17.26 (16.69–17.88)	16.1 (15.99–16.59)		3.24 (1–6)	68.2 (68–69)
Gelasimus vocans	0.37 (0.3–0.46)	2.4 (2–3)	16.84 (15.96–17.55)	17.38 (16.69–17.68)	16.1 (15.8–16.39)	0.5 (0.15–0.92)		67.4 (66–68)
Gelasimus tetragonon	0 (0–0)	0 (0–0)	17.85 (17.57–18.19)	18.23 (17.86–18.66)	18.45 (18.11–18.52)	11.3 (11.26–11.45)	11.15 (10.9–11.26)	
Paraleptuca splendida	0.79 (0–1.7)	5.14 (0–11)	15.67 (14.86–16.4)	15.78 (15.02–16.36)	17.98 (17.03–18.65)	15.8 (15.02–16.77)	15.88 (15.02–16.77)	14.72 (14.36–14.95)
Tubuca acuta	0 (0–0)	0 (0–0)	17.43 (17.32–17.72)	17.42 (16.93–17.53)	15.14 (14.98–15.17)	18.64 (17.28–18.98)	18.61 (18.36–18.77)	16.57 (16.57–16.57)
Tubuca arcuata	0.42 (0–1.7)	2.75 (0–11)	15.93 (15.58–16.55)	17.53 (17.11–18.11)	17.67 (16.98–17.81)	17.43 (17.26–17.9)	17.51 (17.26–17.9)	17.44 (17.39–17.59)
Tubuca forcipata	0.06 (0–0.15)	0.4 (0–1)	16.19 (15.53–16.7)	18.33 (17.88–18.49)	17.73 (17.56–17.76)	16.56 (16.4–17)	16.56 (16.4–16.8)	16.93 (16.77–16.97)
Tubuca paradussumieri	0.08 (0–0.15)	0.53 (0–1)	16.6 (16.36–16.96)	17.28 (16.68–17.67)	16.7 (16.31–16.9)	16.72 (16.41–17.21)	16.52 (16.21–16.81)	16.71 (16.64–16.84)
Tubuca rhizophorae	0.56 (0.3–0.92)	3.67 (2–6)	14.7 (14.25–15.18)	15.86 (15.19–16.17)	15.2 (15.02–15.6)	15.6 (15.25–16.06)	15.59 (15.05–15.86)	16.33 (16.23–16.43)
Tubuca typhoni	1.02 (0.77–1.39)	6.67 (5–9)	16.17 (15.58–16.76)	14.56 (13.68–15.01)	16.38 (16.15–16.94)	14.45 (13.76–15.51)	14.39 (13.57–15.31)	14.94 (14.1–15.65)

	Interspecific						
	P. splendida	*T. acuta*	*T. arcuata*	*T. forcipata*	*T. paradussumieri*	*T. rhizophorae*	*T. typhoni*
Austruca annulipes	92.24 (88–96)	101.56 (101–103)	93.82 (92–97)	95.4 (92–98)	97.22 (96–99)	87.44 (85–90)	95 (92–98)
Austruca lactea	93 (89–96)	101.43 (99–102)	102.05 (100–105)	106.23 (104–107)	101.05 (98–103)	93 (89–95)	86.67 (82–89)
Austruca perplexa	103.67 (99–107)	89.83 (89–90)	102.33 (99–103)	102.83 (102–103)	98 (96–99)	89.92 (89–92)	96.17 (95–99)
Gelasimus borealis	93.03 (89–98)	108.2 (108–109)	100.73 (100–103)	96.8 (96–99)	97.53 (96–100)	91.75 (90–94)	85.53 (82–91)
Gelasimus vocans	93.43 (89–98)	107.2 (106–108)	101.13 (100–103)	96.8 (96–98)	96.53 (95–98)	91.75 (89–93)	85.27 (81–90)
Gelasimus tetragonon	86.86 (85–88)	97 (97–97)	101.25 (101–102)	98.8 (98–99)	97.33 (97–98)	95.5 (95–96)	88.33 (84–92)
Paraleptuca splendida		93.71 (92–95)	94.91 (92–97)	91.86 (90–95)	95.9 (94–98)	79.43 (76–82)	89.33 (87–95)
Tubuca acuta	16.02 (15.66–16.27)		86.13 (85–88)	83.8 (83–84)	75.33 (75–76)	71.25 (70–73)	82 (81–83)
Tubuca arcuata	16.27 (15.68–16.69)	14.64 (14.42–14.99)		47.08 (45–49)	71.71 (71–74)	77.63 (74–79)	71.92 (69–74)
Tubuca forcipata	15.62 (15.26–16.23)	14.2 (14.05–14.24)	7.64 (7.27–7.98)		74.13 (73–75)	77.45 (77–79)	69.13 (68–70)
Tubuca paradussumieri	16.47 (16.1–16.87)	12.62 (12.56–12.75)	11.88 (11.76–12.3)	12.3 (12.12–12.49)		76.58 (76–78)	65.67 (61–70)
Tubuca rhizophorae	13.29 (12.66–13.76)	11.95 (11.72–12.28)	13.09 (12.38–13.35)	13 (12.93–13.28)	12.89 (12.78–13.16)		73 (69–76)
Tubuca typhoni	15.23 (14.77–16.34)	13.9 (13.71–14.1)	11.99 (11.45–12.38)	11.44 (11.23–11.6)	10.84 (9.99–11.64)	12.27 (11.51–12.84)	

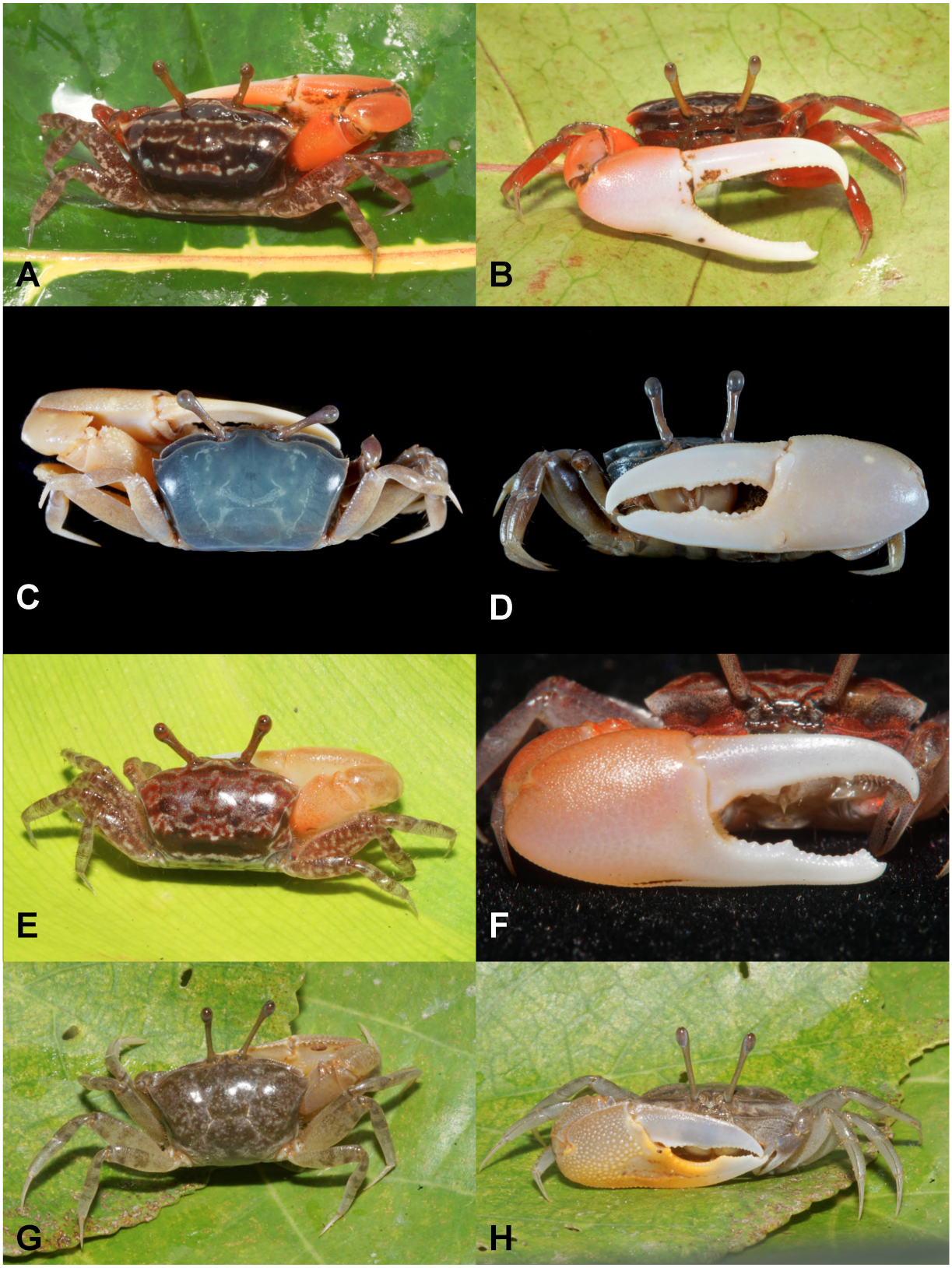

Fig. 3. Dorsal view of carapace and frontal view of major cheliped. *Austruca annulipes* (A, B, specimens not catalogued, Phu Quoc Island, Kien Giang); *A. lactea* (C, D, NCHUZOOL 15115, CW 13.1 mm, Nam Dinh); *A. perplexa* (E, F, NCHUZOOL 15117, CW 10.3 mm, Can Gio, Ho Chi Minh City); *Gelasimus borealis* (G, H, NCHUZOOL 15121, CW 21.1 mm, Dong Rui, Quang Ninh).

Austruca lactea **(De Haan, 1835)**
(Fig. 3C, D)

Ocypode (*Gelasimus*) *lactea* De Haan, 1835: 54, pl. 15(5) (type locality: Japan).
Gelasimus lacteus – Kingsley 1880: 149, pl. 10(28) [part].
Uca lactea – Dawydoff 1952: 141; Jones and Morton 1994: 28, fig. 6, pls. 2G, H, 3E, F; Yamaguchi 1994: 165; Kosuge et al. 1997: 182; Do and Hoang 2002: 128; Do and Hoang 2004: 15; Do and Hoang 2006: 36; S-L Yang et al. 2008: 807; Shih et al. 2009: 376; Shih et al. 2010b: 6, 10; Shih et al. 2013: 643; Le et al. 2018: 41; Do et al. 2021: 102.
Uca (*Celuca*) *lactea lactea* – Crane 1975: 298, 300, 612, figs. 19A, 54J–JJ, 69E, pl. 40A, B; Dai et al. 1986: 425, pl. 59(2), fig. 236(1).
Uca (*Celuca*) *lactea* – Dai and Yang 1991: 466, pl. 59(2), fig. 236(1).
? *Uca lacté* – Do 2003: 8.
Uca (*Paraleptuca*) *lactea* – Ng et al. 2008: 241.
Uca (*Austruca*) *lactea* – Naderloo et al. 2010: 19, figs. 10a–f, 11a–c, 14a, 15a, 18a, b; Kostina et al. 2016: 210, 211, 257; Shih et al. 2016a: 59, fig. 2A, B.
Austruca lactea – Shih et al. 2015: 182, figs. 146–151; Shih et al. 2016b: 153, 168, fig. 8D; Ng et al. 2017: 123; Sasaki 2019: 12430; Wada 2019: e142.
Austruca (*Austruca*) *lactea* – Rosenberg 2019: 734.

Material examined: Hai Phong: 4 ♂♂ (9.7–13.3 mm), 5 ♀♀ (9.8–12.3 mm) (NCHUZOOL 15114), Xuan Dam, Cat Ba Island, coll. B. K. K. Chan, 23 Nov. 2011. Nam Dinh: 3 ♂♂ (11.8–13.1 mm), 1 ♀ (11.2 mm) (NCHUZOOL 15115), coll. V. T. Do, Aug. 2013.

Distribution: Northern Vietnam, shores of China (including Hainan), Taiwan (including Penghu), Korea and main islands of Japan.

Remarks: *Austruca lactea* has been considered as a continental species (Shih 2012a), distributed from northern Vietnam, coasts of China, western Taiwan, to Korea and main islands of Japan (Crane 1975; Shih et al. 2010b 2015). The current southernmost records of this species in South China (the northern coast of Hainan Island) and Vietnam (Huong Phong, Thua Thien Province) are around the latitude of 20°N and 16°N, respectively (Figs. 1, 7; Shih et al. 2010b; Wada 2019).

Austruca perplexa **(H. Milne Edwards, 1852)**
(Fig. 3E, F)

Gelasimus perplexus H. Milne Edwards, 1852: 150, pl. 4(18) (type locality: Java).
Gelasimus annulipes – Kingsley 1880: 148 [part].
Gelasimus chlorophthalmus – Kingsley 1880: 151 [part].
Uca (*Celuca*) *lactea perplexa* – Crane 1975: 298, 300, 612, 613, figs. 18D–F, 19C–H, 26D, 31E, 54K, KK, 69C (part).
Uca perplexa – Yamaguchi 1994: 165; S-L Yang et al. 2008: 807; Shih et al. 2009: 376; Shih et al. 2013: 643.
Uca perplesca – Do 2003: 8.
Uca (*Paraleptuca*) *perplexa* – Ng et al. 2008: 241.
Uca (*Austruca*) *perplexa* – Naderloo et al. 2010: 24, figs. 16a–g, 17a, b, 18c–f; Shih et al. 2016a: 62, fig. 2C–E.
Austruca perplexa – Shih et al. 2015: 189, figs. 152–156; Shih et al. 2016b: 153, 168, fig. 8F; Ng et al. 2017: 123; Sasaki 2019: 12436; Wada 2019: e142.
Austruca (*Austruca*) *perplexa* – Rosenberg 2019: 734.

Material examined: Binh Thuan: 14 ♂♂ (8.2–17.4 mm), 3 ♀♀ (12.9–15.7 mm) (NCHUZOOL 15116), Nguyen Thong, Phu Hai, Phan Thiet, coll. I-H. Chen et al. 26 Nov. 2010. Ho Chi Minh: 6 ♂♂ (7.4–10.3 mm), 1 ♀ (7.0 mm) (NCHUZOOL 15117), 1 ♂ (9.8 mm), 1 ♀ (7.1 mm) (NCHUZOOL 15118), Giong Ao, Can Thanh Town, Can Gio, coll. H.-T. Shih and P.-Y. Hsu, 13 Oct. 2017. Kien Giang: 4 ♂♂ (11.1–12.4 mm), 1 ♀ (13.3 mm) (NCHUZOOL 15119), Phu Quoc Island, coll. H.-T. Shih, 2 Dec. 2012. Southern Vietnam: 2 ♂♂ (14.2, 18.7 mm) (ZRC), coll. V. T. Nguyen, 2010.

Distribution: Nicobar Islands, Indonesia, Australia, New Caledonia, New Guinea, Philippines, Borneo, Malay Peninsula, Thailand, Cambodia, Vietnam, Taiwan and Ryukyus.

Remarks: *Austruca perplexa* is widely distributed in the IWP, from the western part of the eastern Indian Ocean to the West Pacific, including the Ryukyus (and probably in main islands of Japan) and Taiwan (including Penghu and Dongsha Island) in the East Asia. Recently, Shih and Poupin (2020) recognized a new allied species, *A. citrus* Shih & Poupin, 2020, from Fiji and eastwards (see also Crane 1975; Shih et al. 2009; Naderloo et al. 2010; Trivedi et al. 2018; Shih and Poupin 2020). *Austruca perplexa* was often misidentified as *A. annulipes* and *A. lactea* (see Shih and Poupin 2020), but can be distinguished by the characters of the anterolateral angles, fingers in the male major cheliped and the G1 (see dichotomous key provided below in this study).

Genus *Gelasimus* Latreille, 1817

Gelasimus borealis **(Crane, 1975)**
(Fig. 3G, H)

Uca (*Thalassuca*) *vocans borealis* Crane, 1975: 89, 597, fig. 64A (type locality: Hong Kong); Dai et al. 1986: 424, pl. 58(8).
Uca (*Thalassuca*) *borealis* – Dai and Yang 1991: 464, pl. 58(8).
Uca borealis – Jones and Morton 1994: 22, fig. 4, pls. 2E, F, 3A, B; Kosuge et al. 1997: 182; Do and Hoang 2002: 128; Do and Hoang 2004: 15; Do and Hoang 2006: 37; Hoang et al. 2010: 156; S-L Yang et al. 2008: 807; Shih et al. 2010b: 6, 8; Do et al. 2021: 102, fig. 4(3); Hoang et al. 2021: 116.
Uca vocans – Do and Hoang 2002: 128; Do and Hoang 2004: 15; Do and Hoang 2006: 36.
Uca (*Gelasimus*) *borealis* – Ng et al. 2008: 240; Shih et al. 2016a: 63, fig. 3A–D; Le et al. 2018: 41.
Gelasimus borealis – Shih et al. 2015: 200, figs. 162–167; Shih et al. 2016b: 151, 169, fig. 7A; Ng et al. 2017: 125; Sasaki 2019: 12445; Wada 2019: e142; Nguyen et al. 2022: 39.

Gelasimus (*Gelasimus*) *borealis* – Rosenberg 2019: 734.

Material examined: Quang Ninh: 1 ♂ (21.1 mm) (NCHUZOOL 15121), 1 ♀ (14.4 mm) (NCHUZOOL 15122), 7 ♂♂ (11.5–18.3 mm), 2 ♀♀ (13.6, 13.8 mm) (NCHUZOOL 15123), Dong Rui, coll. H.-T. Shih and P.-Y. Hsu, 9 Oct. 2017. Hai Phong: 1 ♀ (16.1 mm) (NCHUZOOL 15120), Xuan Dam, Cat Ba Island, coll. B. K. K. Chan, 23 Nov. 2011.

Distribution: Northern Vietnam, South China (including Hainan), Taiwan (including Penghu) and main islands of Japan.

Remarks: *Gelasimus borealis* is distributed in East Asia, showing a continental distribution (Shih 2012a), from northern Vietnam, South China, western Taiwan to main island of Japan (Shih et al. 2010b). This species shares a similar distribution pattern with *Austruca lactea* and *Tubuca arcuata*, but remains absent in Korea and the Ryukyus (Shih 2012a; Shih et al. 2016a). Genetic evidence derived from *COI* sequences do not support differentiation of several species under the *Gelasimus vocans* species complex (*G. borealis*, *G. dampieri* (Crane, 1975), *G. vocans* and *G. vomeris* (McNeill, 1920)), but they are nevertheless morphologically distinct in terms of form of male major chelae and G1s, as well as female vulvae (Shih et al. 2010a). The external morphologies of females, however, are not useful in species identification (Crane 1975; Shih et al. 2015).

Gelasimus tetragonon **(Herbst, 1790)**
(Fig. 4A, B)

Cancer tetragonon Herbst 1790: 257, pl. 20(110) (type locality: unknown).
Gelasimus tetragonon – Kingsley 1880: 143, pl. 9(11); Shih et al. 2015: 213, figs. 174–181; Shih et al. 2016b: 151, 169, fig. 7F; Ng et al. 2017: 125; Sasaki 2019: 12450.
Uca tetragonon – Dawydoff 1952: 141; Yamaguchi 1994: 177, 184; S-L Yang et al. 2008: 807; Shih et al. 2010b: 11, fig. 3E, F; Chertoprud et al. 2012: 270, pl. 46C, D.
Uca (*Thalassuca*) *tetragonon* – Crane 1975: 77, 596, figs. 37D, 63A, B, 81F, 82E, pl. 13; K Sakai 1999: 38, pl. 20D (holotype).
Uca (*Gelasimus*) *tetragonon* – Ng et al. 2008: 240; Shih et al. 2016a: 66, fig. 4A, B.
Gelasimus (*Mesuca*) *tetragonon* – Rosenberg 2019: 734.

Material examined: Nha Trang: 2 ♂♂ (21.7, 23.4 mm), 3 ♀♀ (17.4–24.0 mm) (NCHUZOOL 15124), Luong Son, Vinh Luong, coll. K. J. H. Wong and I-H. Chen, 23 Nov. 2010.

Distribution: Western Indian Ocean, India, eastern Indian Ocean and West Pacific Ocean (with eastern end of Gambier Islands, French Polynesia).

Remarks: *Gelasimus tetragonon* is probably one of the most widely distributed fiddler crab species, covering the entire range of IWP, from eastern Africa and the Red Sea, to Gambier Islands, French Polynesia (Crane 1975). Along shores of western South China Sea, this species can only be found in southern Vietnam (Nha Trang) and southern Hainan (Sanya) (Shih et al. 2010b). Type locality of *Cancer tetragonon* was indicated as unknown in the original description (Herbst 1790). In an attempt to locate type material of this species, Crane (1975: 80) noted which "apparently not extant" in the Herbst collection at the Zoological Museum of Berlin, subsequently designated a neotype selected among material examined by A. Milne-Edwards collected from Egypt. The neotype locality was indicated as Egypt by several later authors (*e.g.*, Davie 2002; Shih et al. 2010a 2015). However, the holotype of *C. tetragonon* was eventually reported by K Sakai (1999). According to the International Code of Zoological Nomenclature (ICZN 1999: Article 75.8), which states "If, after the designation of a neotype, the name-bearing type (holotype, syntypes, lectotype or previous neotype) of the nominal species-group taxon that was (were) presumed lost is (are) found still to exist, on publication of that discovery the rediscovered material again becomes the name-bearing type and the neotype is set aside", the name-bearing status of the male holotype at Berlin, as reported by K Sakai (1999), must be preserved, and the corresponding type locality should be indicated as "unknown".

Gelasimus vocans **(Linnaeus, 1758)**
(Fig. 4C, D)

Cancer vocans Linnaeus, 1758: 626 (type locality: East Indies, probably Amboina (Crane 1975)).
Gelasimus cultrimanus – Kingsley 1880: 140, pl. 9(7) [?part].
Gelasimus marionis – Kingsley 1880: 141, pl. 9(8) [part].
Uca (*Thalassuca*) *vocans vocans* – Crane 1975: 85, 92, 598, figs. 38I, L, 56B, 60C–E, 64F, FF, pl. 14E–H; Dai et al. 1986: 423, pl. 58(7), fig. 234(1, 2).
Uca (*Thalassuca*) *vocans* – Dai and Yang 1991: 463, pl. 58(7), fig. 234.
Uca vocans – Yamaguchi 1994: 180 [part]; S-L Yang et al. 2008: 807; Shih et al. 2010b: 16; Chertoprud et al. 2012: 271, pl. 46E–G.
Uca (*Gelasimus*) *vocans* – Ng et al. 2008: 240; Kostina et al. 2016: 206, 257; Shih et al. 2016a: 66, fig. 3G, H.
? *Uca borealis* – Do 2003: 8.
Uca vocans – Do 2003: 8.
Uca borealis – Chertoprud et al. 2012: 270, pl. 46A, B.
Uca rosea – Chertoprud et al. 2012: 269, pl. 45G, H.
Gelasimus vocans – Shih et al. 2015: 221, figs. 182–188; Shih et al. 2016b: 151, 169, fig. 7G; Ng et al. 2017: 125; Sasaki 2019: 12453; Wada 2019: e142.
Gelasimus (*Gelasimus*) *vocans* – Rosenberg 2019: 734.
? *Uca* (*Gelasimus*) *borealis* – Le et al. 2020: 15.

Material examined: Nha Trang: 1 ♂ (12.1 mm) (NCHUZOOL 15126), 17 ♂♂ (6.8–19.8 mm), 9 ♀♀

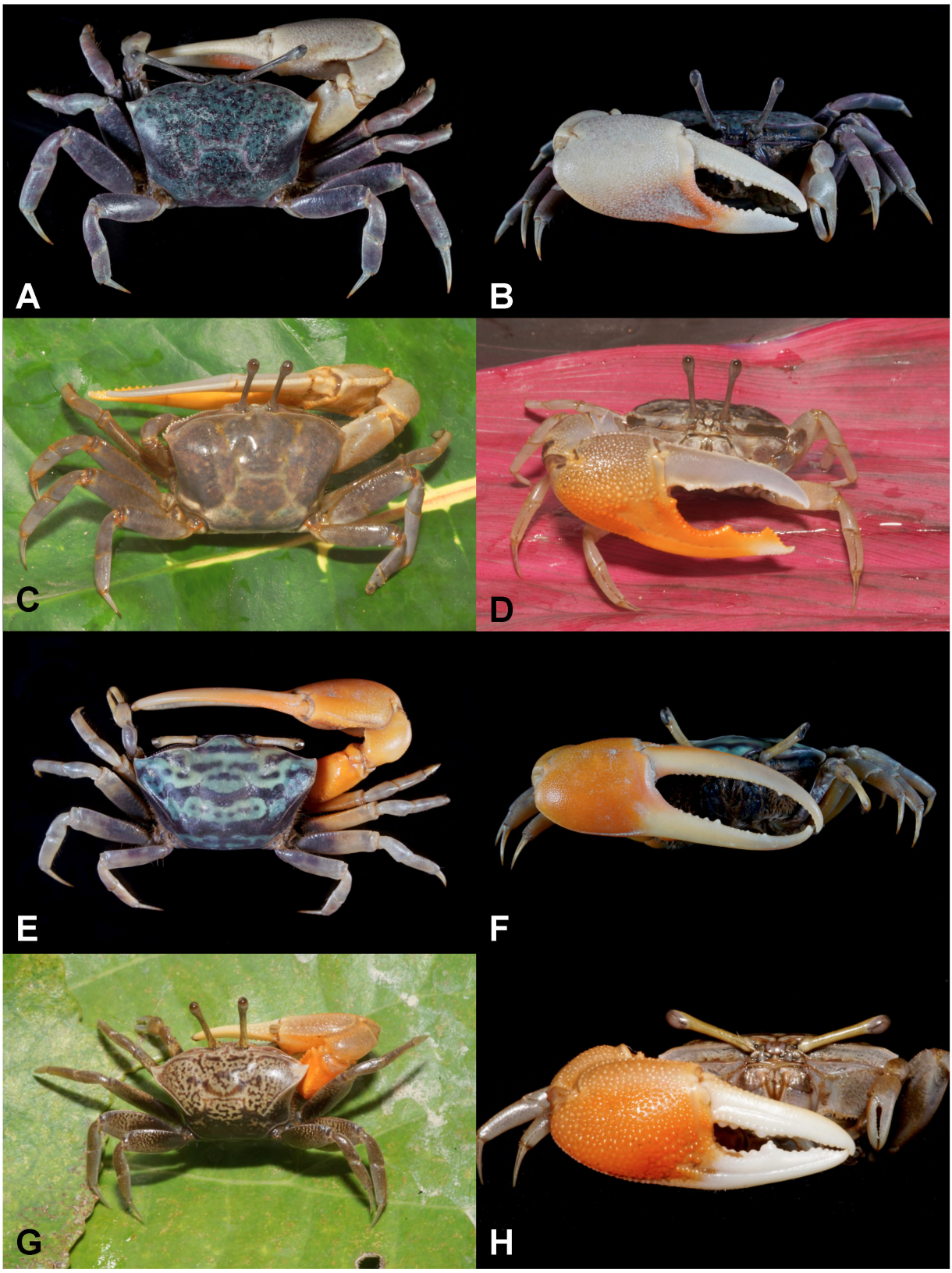

Fig. 4. Dorsal view of carapace and frontal view of major cheliped. *G. tetragonon* (A, B, NCHUZOOL 15124, CW 23.4 mm, Vinh Luong, Nha Trang, Khanh Hoa); *Gelasimus vocans* (C, D, specimens not catalogued, Phu Quoc Island, Kien Giang); *Paraleptuca splendida* (E, F, NCHUZOOL 13448, CW 19.5 mm, Vinh Luong, Nha Trang); *Tubuca acuta* (G, H, NCHUZOOL 15138, CW 15.9 mm, Dong Rui, Quang Ninh).

(8.9–16.6 mm) (NCHUZOOL 15136), mangrove I, coll. I-H. Chan and K. J. H. Wong, 24 Nov. 2010; 12 ♂♂ (12.2–23.8 mm), 1 ♀ (13.3 mm) (NCHUZOOL 15127), 1 ♂ (16.1 mm) (NCHUZOOL 14913), 3 ♂♂ (20.0–22.2 mm) (NCHUZOOL 15135), mangrove II, coll. I.-H. Chan and K. J. H. Wong, 24 Nov. 2010; 30 ♂♂ (10.9–27.2 mm) (NCHUZOOL 15128), 14 ♀♀ (12.5–22.2 mm), 1 ovig. ♀ (21.0 mm) (NCHUZOOL 15129), Luong Son, Vinh Luong, coll. I-H. Chen et al., 23 Nov. 2010. Binh Thuan: 13 ♂♂ (10.6–21.2 mm), 6 ♀♀ (9.3–20.5 mm) (NCHUZOOL 15125), Nguyen Thong, Phu Hai, Phan Thiet, coll. I-H. Chen et al., 26 Nov. 2010. Kien Giang: 2 ♀♀ (14.9, 17.0 mm) (NCHUZOOL 15130), Phu Quoc Island, coll. B. K. K. Chan, 2 Dec. 2012; 12 ♂♂ (9.9–18.6 mm), 3 ♀♀ (10.5–14.6 mm), 4 ovig. ♀♀ (12.6–16.9 mm) (NCHUZOOL 15131), 2 ♂♂ (6.9, 17.5 mm), 3 ♀♀ (16.6–18.2 mm) (NCHUZOOL 15137), Phu Quoc Island, coll. H.-T. Shih, 2 Dec. 2012.

Distribution: Myanmar, Thailand, Malay Peninsula, Indonesia, Borneo, Philippines, South China (Hainan), Taiwan and the Ryukyus.

Remarks: *Gelasimus vocans* shows a broad distribution from the eastern Indian Ocean to West Pacific, including southern Hainan, China, Taiwan (including Penghu) and the Ryukyus (and probably in main islands of Japan) in East Asia (Crane 1975; Shih et al. 2010b 2015 2016a). In Vietnam, *G. vocans* only occurs in the south, clearly separated from *G. borealis* in the northern regions (see DISCUSSION below). However, various members of the *G. vocans* species complex are reported to be sympatric in Taiwan: *G. borealis* and *G. jocelynae* in northeastern and southwestern Taiwan (Yilan and Tainan); *G. vocans* and *G. jocelynae* in southern and eastern Taiwan (Hengchun Peninsula, Pingtung and Taitung); and the three species in southern Taiwan (Dapengwan, Pingtung) and Penghu (Shih et al. 2015 2016a).

Genus *Paraleptuca* Bott, 1973

Paraleptuca splendida (Stimpson, 1858)

(Fig. 4E, F)

Gelasimus splendidus Stimpson, 1858: 99 (type locality: Hong Kong); Kingsley 1880: 149; Stimpson 1907: 106, pl. 14(2); Crane 1975: 98, 101, 599.

Uca latreillei – Balss 1922: 142.

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 (part); Dai et al. 1986: 428, pl. 59(5), fig. 238(1–2); Dai and Yang 1991: 468, pl. 59(5), fig. 238.

Uca crassipes – Jones and Morton 1994: 26, fig. 5, pl. 3C, D; Do and Hoang 2006: 36; S-L Yang et al. 2008: 807; Shih et al. 2010b: 6, 9; Chertoprud et al. 2012: 268, pl. 44E–G; Aoki and Wada 2013: 790; Le et al. 2018: 41; Le et al. 2020: 15.

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

Uca chlorophthalmus – Hoang et al. 2012: 75.

Uca (*Paraleptuca*) *splendida* – Shih et al. 2012: 30, figs. 2–4, 6, 7C; Shih et al. 2016a: 69, fig. 4E, F.

Uca splendida – Shih et al. 2013: 643.

Paraleptuca splendida – Shih et al. 2015: 236, figs. 195–200; Shih et al. 2016b: 156, 173, fig. 10E; Rosenberg 2019: 734; Sasaki 2019: 12504; Wada 2019: e142, fig. 1H.

Paraleptuca splendidus – Ng et al. 2017: 126, fig. 15c.

Material examined: Nha Trang: 1 ♂ (12.5 mm) (NCHUZOOL 15132), mangrove I, coll. I-H. Chen, 24 Nov. 2010; 5 ♂♂ (15.4–19.5 mm), mangrove II, coll. I-H. Chen and K. J. H. Wong, 24 Nov. 2010; 4 ♂♂ (11.3–14.8 mm), 7 ♀♀ (12.9–14.5 mm) (NCHUZOOL 13459), Luong Son, Vinh Luong, coll. P.-C. Tsai and I-H. Chen, 23 Nov. 2010. Binh Thuan: 1 ♂ (18.7 mm) (NCHUZOOL 13463), Nguyen Thong, Phu Hai, Phan Thiet, coll. P.-C. Tsai and I-H. Chen, 26 Nov. 2010.

Distribution: Vietnam, South China (including Hainan), Taiwan and the Ryukyus (Iriomote).

Remarks: *Paraleptuca splendida* was recently shown as valid species, distinct from its long-synonymized congener, *P. crassipes* (Shih et al. 2012). This species shows a narrower range of distribution, from south of Vietnam, Dongsha Island, South China, western Taiwan (including Penghu) and southern Ryukyus, in comparison with *P. crassipes* with a much wider West-Pacific distribution (Balss 1922; Chertoprud 2012; Shih 2012b 2020; Shih et al. 2010b 2012 2015 2016a). Considering the geographical range of *P. splendida*, in addition to a typical pattern shown by continental species (East Asia and northern Vietnam), this species has also been found in northern Vietnam (Da Nang = "Tourane, Annam" in Balss 1922; Fig. 7), southern Vietnam, southern Hainan, Dongsha Island and southern Ryukyus (Shih 2012a). The current southernmost records of this species in Vietnam (Binh Thuan) are around the latitude of 11°N (Figs. 1, 7; this study).

Genus *Tubuca* Bott, 1973

Tubuca acuta (Stimpson, 1858)

(Fig. 4G, H)

Gelasimus acutus Stimpson, 1858: 99 (type locality: Macao); Kingsley 1880: 144; Stimpson 1907: 105, pl. 14(3).

Uca (*Deltuca*) *acuta acuta* – Crane 1975: 25, 592, fig. 61B, pl. 1E–H.

Uca acuta acuta – Yamaguchi 1994: 183.

Uca acuta – Jones and Morton 1994: 12, fig. 1, pls. 1A, B, 2A, B; Kosuge et al. 1997: 182; Do and Hoang 2006: 36; S-L Yang et al. 2008: 807; Shih et al. 2010b: 3, fig. 2A–D.

Uca (*Tubuca*) *acuta* – Ng et al. 2008: 241; Shih et al. 2016a: 69, figs. 4G, H, 5, 6A, B.

Tubuca acuta – Shih et al. 2015: 244, figs. 201–205; Shih et al. 2016b: 159, 173; Ng et al. 2017: 126, fig. 15d; Sasaki 2019: 12506;

Wada 2019: e142, fig. 1I.
Tubuca (*Angustuca*) *acuta* – Rosenberg 2019: 735.

Material examined: Quang Ninh: 1 ♂ (15.9 mm) (NCHUZOOL 15138), 5 ♂♂ (14.5–17.8 mm) (NCHUZOOL 15139), Dong Rui, coll. H.-T. Shih and P.-Y. Hsu, 9 Oct. 2017. Hai Phong: 9 ♂♂ (7.8–19.7 mm), 5 ♀♀ (13.3–16.9 mm) (NCHUZOOL 15134), Xuan Dam, Cat Ba Island, coll. B. K. K. Chan, 23 Nov. 2011. Nam Dinh: 1 ♂ (23.2 mm), 1 ♀ (12.0 mm) (NCHUZOOL 15133), coll. V. T. Do, Aug. 2013; 7 ♂♂ (18.0–21.0 mm) (NCHUZOOL 15102), 2 ♂♂ (18.2, 19.6 mm) (NCHUZOOL 15103), 1 ♂ (20.9 mm) (NCHUZOOL 15104, 1 ♂ (18.6 mm) (NCHUZOOL 15105), Xuan Thuy National Park, coll. V. T. Do, Dec. 2014.

Distribution: Vietnam, South China (including Hainan) and Taiwan.

Remarks: *Tubuca acuta* is not uncommon along the coasts of South China and northern Vietnam, although it is less reported in the literature (*e.g.*, not included in Dawydoff 1952; Dai et al. 1986; Dai and Yang 1991), probably a result of its marked resemblance in coloration and morphology hence misidentification with *Tubuca arcuata* (Crane 1975; Jones and Morton 1994). This species was described based on material from Macao, South China (Stimpson 1858), but erroneously recorded in Chinese records under different names (see Crane 1975; Shih et al. 2010b). The identity of *T. acuta* (then as *Uca* (*Deltuca*) *acuta*) was eventually revised and confirmed by Crane (1975), an understanding since followed by subsequent authors (*e.g.*, Jones and Morton 1994; Kosuge et al. 1997; S-L Yang et al. 2008). *Tubuca acuta* and *T. rhizophorae* were considered as subspecies of *U.* (*Deltuca*) *acuta* by Crane (1975) due to their morphological similarities. They are, however, clearly distinct, the molecular evidence being diagnostic (Shih et al. 2016b), and are respectively found in northern and southern Vietnam (see DISCUSSION below).

Tubuca arcuata **(De Haan, 1835)**
(Fig. 5A, B)

Ocypode (*Gelasimus*) *arcuata* De Haan, 1835: 53, pl. 7(2) (type locality: Japan).
Gelasimus arcuatus – Kingsley 1880: 143, pl. 9(10).
Uca arcuatus – Serène 1937: 76.
Uca arcuata – Dawydoff 1952: 141; Jones and Morton 1994: 13, fig. 2, pls. 1C, D, 2C, D; Yamaguchi 1994: 154, fig. 1; Kosuge et al. 1997: 182; Do and Hoang 2002: 127; Do and Hoang 2004: 15; Do and Hoang 2006: 36; S-L Yang et al. 2008: 807; Hoang et al. 2010: 154; Shih et al. 2010b: 6, fig. 2E, F; Do et al. 2021: 102, fig. 4(2); Hoang et al. 2021: 116.
Uca (*Deltuca*) *arcuata* – Crane 1975: 44, 594, figs. 8C, 9C, 61J, pls. 5A–F; Dai et al. 1986: 420, pl. 58(5), fig. 232; Dai and Yang 1991: 460, pl. 58(5), fig. 232.
Uca (*Tubuca*) *arcuata* – Ng et al. 2008: 241; Kostina et al. 2016: 210, 211, 257; Shih et al. 2016a: 71, fig. 6C–E.
Tubuca arcuata – Shih et al. 2015: 249, figs. 206–214; Shih et al. 2016b: 159, 173, fig. 10G; Ng et al. 2017: 126, fig. 15e; Sasaki 2019: 12507; Wada 2019: e142; Nguyen et al. 2022: 39, fig. 2E.
? *Uca* (*Tubuca*) *forcipata* - Kostina et al. 2016: 210, 211, 257.
Tubuca (*Tubuca*) *arcuata* – Rosenberg 2019: 735.

Material examined: Quang Ninh: 1 ♀ (27.1 mm) (NCHUZOOL 15106), 4 ♂♂ (32.4–39.3 mm), 1 ♀ (15.8 mm) (NCHUZOOL 15107), Dong Rui, coll. H.-T. Shih and P.-Y. Hsu, 9 Oct. 2017; 1 ♂ (30.1 mm) (NCHUZOOL 15142), 1 ♂ (25.7 mm) (NCHUZOOL 15143), Mui Chua, Tien Lang, Tien Yen, coll. H.-T. Shih and P.-Y. Hsu, 8 Oct. 2017. Hai Phong: 1 ♀ (20.5 mm) (NCHUZOOL 15140), Xuan Dam, Cat Ba Island, coll. B. K. K. Chan, 23 Nov. 2011. Nam Dinh: 10 ♂♂ (13.6–31.9 mm), 5 ♀♀ (19.2–25.2 mm) (NCHUZOOL 15144), coll. V. T. Do, Aug. 2013; 4 ♂♂ (25.3–33.3 mm) (NCHUZOOL 15100), 5 ♂♂ (23.5–30.8 mm) (NCHUZOOL 15101), Xuan Thuy National Park, coll. V. T. Do, Dec. 2014. Ha Tinh: 1 ♂ (31.9 mm) (NCHUZOOL 15141), Cam Ha, Cam Xuyen District, coll. V. T. Do, 2 Oct. 2014.

Distribution: Vietnam, South China (including Hainan), Taiwan, Japan (including Ryukyus) and Korea.

Remarks: *Tubuca arcuata* is common and widely distributed in the East Asia (Crane 1975; Dai et al. 1986; Dai and Yang 1991; Kosuge et al. 1997; Shih et al. 2010b 2015 2016a), range of which conforming to continental group of fiddler crabs (Shih 2012a). Interestingly, *T. arcuata* and *T. forcipata* have been shown to be sister species based on genetic evidence (Shih et al. 2016b), and show allopatric distributions in northern and southern Vietnam, respectively (see DISCUSSION below).

Tubuca dussumieri **(H. Milne Edwards, 1852)**

Gelasimus dussumieri H. Milne Edwards, 1852: 148, pl. 4(12) (type locality: Java).
Uca dubia – T Sakai 1936: 170; Miyake 1936: 511; Miyake 1938: 109; Miyake 1939: 222.
? *Uca dubia* – Dawydoff 1952: 141.
Uca (*Deltuca*) *dussumieri dussumieri* – Crane 1975: 37, pls. 2E, F, 3A–D, figs. 5, 8A, 9A, 34A, 36A, 61F; Dai et al. 1986: 421, fig. 233(1–4).
Uca (*Deltuca*) *dussumieri* – Dai and Yang 1991: 461, fig. 233(1–4).
Uca (*Tubuca*) *dussumieri* – Ng et al. 2008: 242; Shih et al. 2016a: 73, fig. 7A–C.
Uca dussumieri – Shih et al. 2010b: 9; Le et al. 2018: 41.
? *Uca arcuata* – Chertoprud et al. 2012: 267, pl. 45A, B.
Tubuca dussumieri – Shih et al. 2015: 265, figs. 221–225; Shih et al. 2016b: 159, fig. 11B; Sasaki 2019: 12514.
Tubuca (*Tubuca*) *dussumieri* – Rosenberg 2019: 735.

Material examined: none.

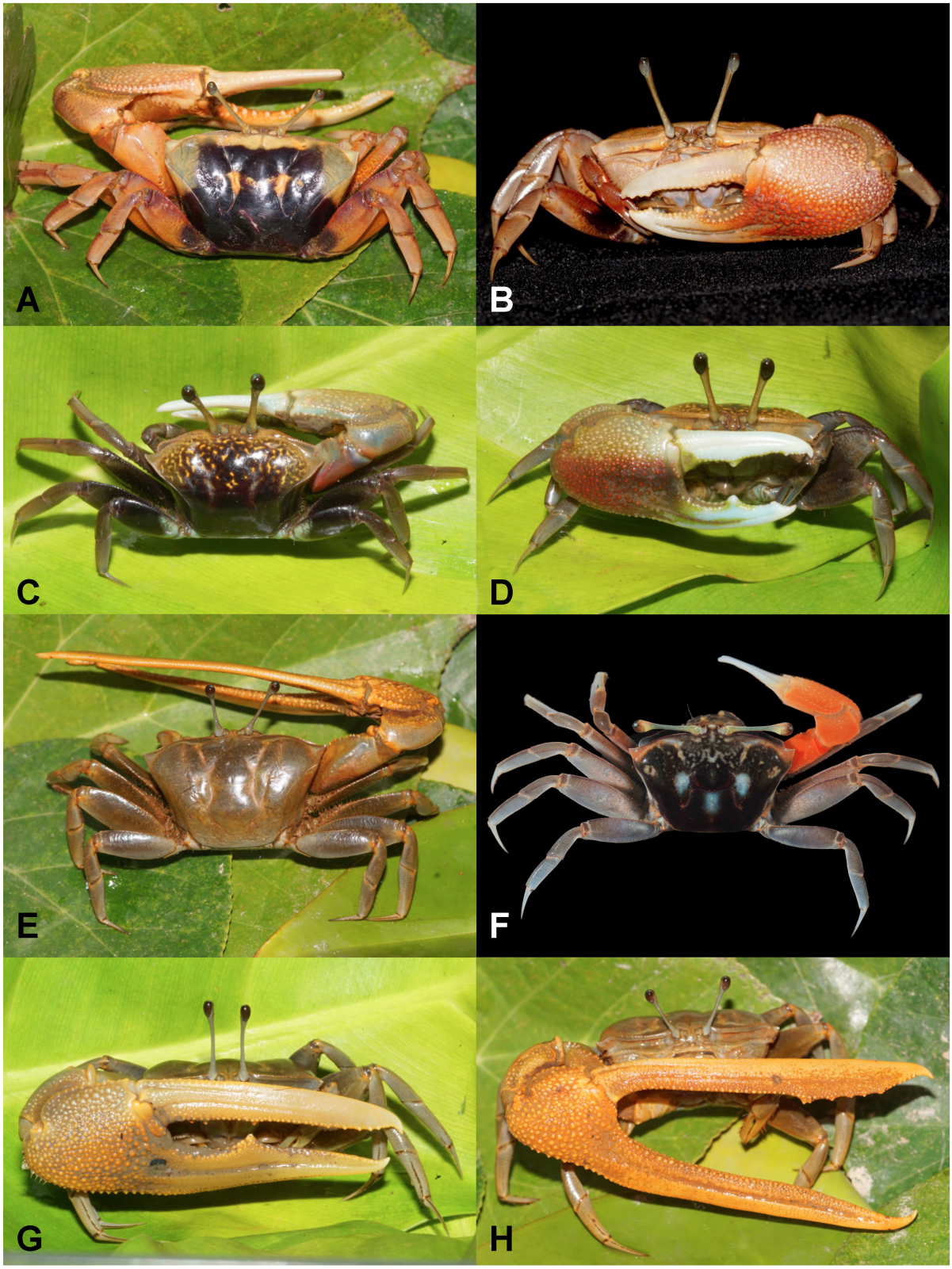

Fig. 5. Dorsal view of carapace and frontal view of major cheliped. *Tubuca arcuata* (A, NCHUZOOL 15107 CW 39.3 mm, Dong Rui, Quang Ninh; B, NCHUZOOL 15142, CW 30.1 mm, Tien Lang, Tien Yen, Quang Ninh); *T. forcipata* (C, D, NCHUZOOL 15145, CW 22.0 mm, Can Gio, Ho Chi Minh City); *T. paradussumieri* (E, H, NCHUZOOL 15155, CW 35.0, Dong Rui, Quang Ninh; F, ZVNU.2019.011, CW 18.3 mm, Dong Rui, Quang Ninh; G, NCHUZOOL 15158, CW 32.3 mm, Can Gio, Ho Chi Minh City).

Distribution: West Thailand (Koh Surin Island), Malay Peninsula (Tioman), Indonesia (including Sumatra), New Guinea, Philippines, Taiwan and Ryukyus.

Remarks: The image of "*Uca arcuata*" (pl. 45A, B) from Hon Tre Island, Nha Trang provided by Chertoprud et al. (2012) shows an individual of *T. dussumieri*. The distribution of *T. dussumieri* spans the tropical West Pacific, and its presence in Vietnam is not unexpected. This report contributes to a new record for Vietnam. See DISCUSSION below for its record in Vietnam.

Tubuca forcipata **(Adams & White, 1849)**

(Fig. 5C, D)

Gelasimus forcipatus Adams & White, 1849: 50 (type locality: Borneo); Kingsley 1880: 142, pl. 9(9).
? *Uca manii* – Dawydoff 1952: 141.
Uca (*Deltuca*) *forcipata* – Crane 1975: 48, 595, fig. 26B, 38A–D, 61K, pls. 5G, H, 6A–D, 46A.
Uca forcipata – Yamaguchi 1994: 163, 184; Chertoprud et al. 2012: 269, pl. 45E, F.
? *Uca arcuata* – Do 1996: 36.
Uca (*Tubuca*) *forcipata* – Ng et al. 2008: 242.
? *Uca flammula* – Chertoprud et al. 2012: 269; Le et al. 2018: 41; Le et al. 2020: 15.
? *Uca arcuata* – Hoang et al. 2012: 75.
Tubuca forcipata – Shih et al. 2016b: 159, 174, fig. 11D; Sasaki 2019: 12519.
Tubuca (*Tubuca*) *forcipata* – Rosenberg 2019: 735.
? *Uca* (*Tubuca*) *arcuata* – Le et al. 2020: 15.
? *Uca urvillei* – Le et al. 2020: 15.

Material examined: Ho Chi Minh: 1 ♂ (22.0 mm) (NCHUZOOL 15145), 2 ♂♂ (9.5, 10.6 mm) (NCHUZOOL 15146), 1 ♂ (10.4 mm) (NCHUZOOL 15147), Giong Ao, Can Thanh Town, Can Gio, coll. H.-T. Shih and P.-Y. Hsu, coll. 13 Oct. 2017; 8 ♂♂ (5.8–18.6 mm) (NCHUZOOL 15109), 2 ♂♂ (18.6, 19.8 mm), 2 ♀♀ (7.4, 7.6 mm) (NCHUZOOL 15108), Rung Sac, Long Hoa, Can Gio, coll. H.-T. Shih and P.-Y. Hsu, coll. 12 Oct. 2017.

Distribution: Eastern Thailand, Malay Peninsula, Singapore, Borneo, Indonesia and Philippines.

Remarks: *Tubuca forcipata* is a common species in Southeast Asia (Crane 1975). As this species can be found in eastern Thailand and Borneo, its presence at the Mekong Delta, southern Vietnam is not unexpected.

Tubuca paradussumieri **(Bott, 1973)**

(Fig. 5E–H)

Gelasimus caerulens Adams, 1847: 437 (type locality: Kuching, Malaysia) [nomen oblitum]; Shih et al. 2021: 214.
? *Uca dubia* – Dawydoff 1952: 141.
Mesuca (*Latuca*) *paradussumieri* Bott, 1973: 317, fig. 10 (type locality: Bengal, India) [nomen protectum].
Uca (*Deltuca*) *dussumieri spinata* Crane, 1975: 36, 592, figs. 27A–C, 35C, D, 37A, 38E–H, 45A–DD, 46B, 54B, 56A, 60A, B, 61G, 72A–CC, 81C, pl. 3 E–H (type locality: Singapore); Dai et al. 1986: 423, pl. 58(6), fig. 233(5, 6); Yamaguchi 1994: 162, fig. 6.
Uca dussumieri spinata – Yamaguchi 1994: 184.
Uca (*Deltuca*) *paradussumieri* – Dai and Yang 1991: 463, pl. 58(6), fig. 233(5, 6).
Uca paradussumieri – Jones and Morton 1994: 18, fig. 3, pl. 1E, F; Kosuge et al. 1997: 182; Do and Hoang 2004: 15; S-L Yang et al. 2008: 807; Shih et al. 2010b: 6, 10, fig. 3A–D; Chertoprud et al. 2012: 269, pl. 45G, H; Hoang et al. 2012: 75; Le et al. 2018: 41, fig. 5C; Le et al. 2020: 15; Hoang et al. 2021: 116.
? *Uca dussumieri* – Do and Hoang 2002: 127; Hoang et al. 2012: 75; Le et al. 2020: 15.
Uca (*Tubuca*) *paradussumieri* – Ng et al. 2008: 242; Shih et al. 2016a: 74, fig. 7D, E.
? *Uca arcuata* – Chertoprud et al. 2012: 267, pl. 45A, B.
? *Uca urvillei* – Hoang et al. 2012: 75.
Tubuca paradussumieri – Shih et al. 2015: 270, figs. 226–230; Shih et al. 2016b: 159, 174; Ng et al. 2017: 127; Sasaki 2019: 12521; Wada 2019: e142; Shih et al. 2021: 215, figs. 3, 4; Nguyen et al. 2022: 39, fig. 2F, G, H.
? *Uca* (*Tubuca*) *dussumieri* – Kostina et al. 2016: 210, 214, 257.
? *Uca* (*Tubuca*) *urvillei* – Kostina et al. 2016: 186, 257.
Tubuca (*Tubuca*) *paradussumieri* – Rosenberg 2019: 735.
Uca dussumieri – Do et al. 2021: 102, fig. 4(1).

Material examined: Quang Ninh: 1 ♂ (35.0 mm), 1 ♀ (32.9 mm) (NCHUZOOL 15155), 12 ♂♂ (16.9–33.4 mm) (NCHUZOOL 15156), Dong Rui, coll. H.-T. Shih and P.-Y. Hsu, 9 Oct. 2017; 1 ♂ (23.4 mm) (NCHUZOOL 15154), Mui Chua, Tien Lang, coll. H.-T. Shih and P.-Y. Hsu, 9 Oct. 2017; 1 ♂ (15.0 mm) (ZVNU.2019.010), 1 ♂ (18.3 mm) (ZVNU.2019.011), Dong Rui, coll. S. T. Nguyen and S. D. Do, 12 Sep. 2019. Nam Dinh: 7 ♂♂ (28.4–36.9 mm), 1 ♀ (31.7 mm) (NCHUZOOL 15152), 11 ♂♂ (21.7–32.2 mm) (NCHUZOOL 15153), Xuan Thuy National Park, coll. V. T. Do, Dec. 2014. Ho Chi Minh: 1 ♂ (32.3 mm), 1 ovig. ♀ (37.1 mm) (NCHUZOOL 15158), 8 ♂♂ (9.8–13.4 mm), 1 ♀ (29.9 mm) (NCHUZOOL 15159), Giong Ao, Can Thanh Town, Can Gio, coll. H.-T. Shih and P.-Y. Hsu, 13 Oct. 2017; 1 ♂ (20.2 mm) (NCHUZOOL 15157), Rung Sac, Long Hoa, Can Gio, coll. H.-T. Shih and P.-Y. Hsu, 12 Oct. 2017. Southern Vietnam: 1 ♂ (26.5 mm) (ZRC), 2010.

Distribution: Bengal, Myanmar, Thailand, Malay Peninsula, Singapore, Indonesia (Sumatra), Borneo, Vietnam, China (including Hainan), Taiwan.

Remarks: The distribution of *T. paradussumieri* spans the eastern Indian Ocean and West Pacific, with preferred habitats along the continental coasts and Borneo (Crane 1975; Jones and Morton 1994; Kwok and Tang 2006; Shih et al. 2015 2021), and is found along the shores of northern and southern Vietnam (see DISCUSSION below).

Tubuca rhizophorae **(Tweedie, 1950)**
(Fig. 6A, B)

Uca rhizophorae Tweedie, 1950: 357, fig. 7a–c (type locality: Kuching, Malaysia).
Uca (*Deltuca*) *acuta rhizophorae* – Crane 1975: 27, 592, figs. 61A, 90A, B, pl. 1A–D.
Uca acuta rhizophorae – Yamaguchi 1994: 153, 183.
Uca (*Tubuca*) *rhizophorae* – Ng et al. 2008: 242.
Tubuca rhizophorae – Shih et al. 2016b: 159, 174, fig. 11F; Sasaki 2019: 12523.
Tubuca (*Angustuca*) *rhizophorae* – Rosenberg 2019: 735.

Material examined: Ho Chi Minh: 1 ♂ (11.8 mm), 1 ♀ (12.2 mm), 1 ovig. ♀ (13.2 mm) (NCHUZOOL 15149), Rung Sac, Long Hoa, Can Gio, coll. H.-T. Shih and P.-Y. Hsu, 12 Oct. 2017; 1 ♂ (15.4 mm) (NCHUZOOL 15148), Giong Ao, Can Thanh Town, Can Gio, coll. H.-T. Shih and P.-Y. Hsu, 13 Oct. 2017.

Distribution: Borneo, Malay Peninsula and southern Vietnam.

Remarks: *Tubuca rhizophorae* is a less-known species, with a limited distribution in eastern Malay Peninsula and northwestern Borneo (Crane 1975). In our study, this species is confirmed from the Mekong Delta, southern Vietnam, which is a new record to Vietnam and Indochina.

Tubuca typhoni **(Crane, 1975)**
(Fig. 6C, D)

Uca (*Deltuca*) *demani typhoni* Crane, 1975: 41, 593, fig. 61C, pl. 4E–H (type locality: Manila, Luzon).
Uca typhoni – Do 2003: 8; Shih et al. 2010b: 13, figs. 4A, B, 5A, C.
Uca (*Tubuca*) *typhoni* – Ng et al. 2008: 242.
Tubuca typhoni – Shih et al. 2016b: 159, 174; Sasaki 2019: 12525.
Tubuca (*Tubuca*) *typhoni* – Rosenberg 2019: 735.

Material examined: Binh Thuan: 1 ♂ (23.0 mm) (NCHUZOOL 15150), Nguyen Thong, Phu Hai, Phan Thiet, coll. I-H. Chen et al. 26 Nov. 2010. Ho Chi Minh: 1 ♂ (17.5 mm) (NCHUZOOL 15151), Rung Sac, Long Hoa, Can Gio, coll. H.-T. Shih and P.-Y. Hsu, 12 Oct. 2017.

Distribution: Northern Philippines, South China (Hainan) and southern Vietnam.

Remarks: *Tubuca typhoni* is distributed sporadically in northern Philippines, southern Hainan in China and the Mekong Delta in southern Vietnam (Crane 1975; Shih et al. 2010b; this study). This species has

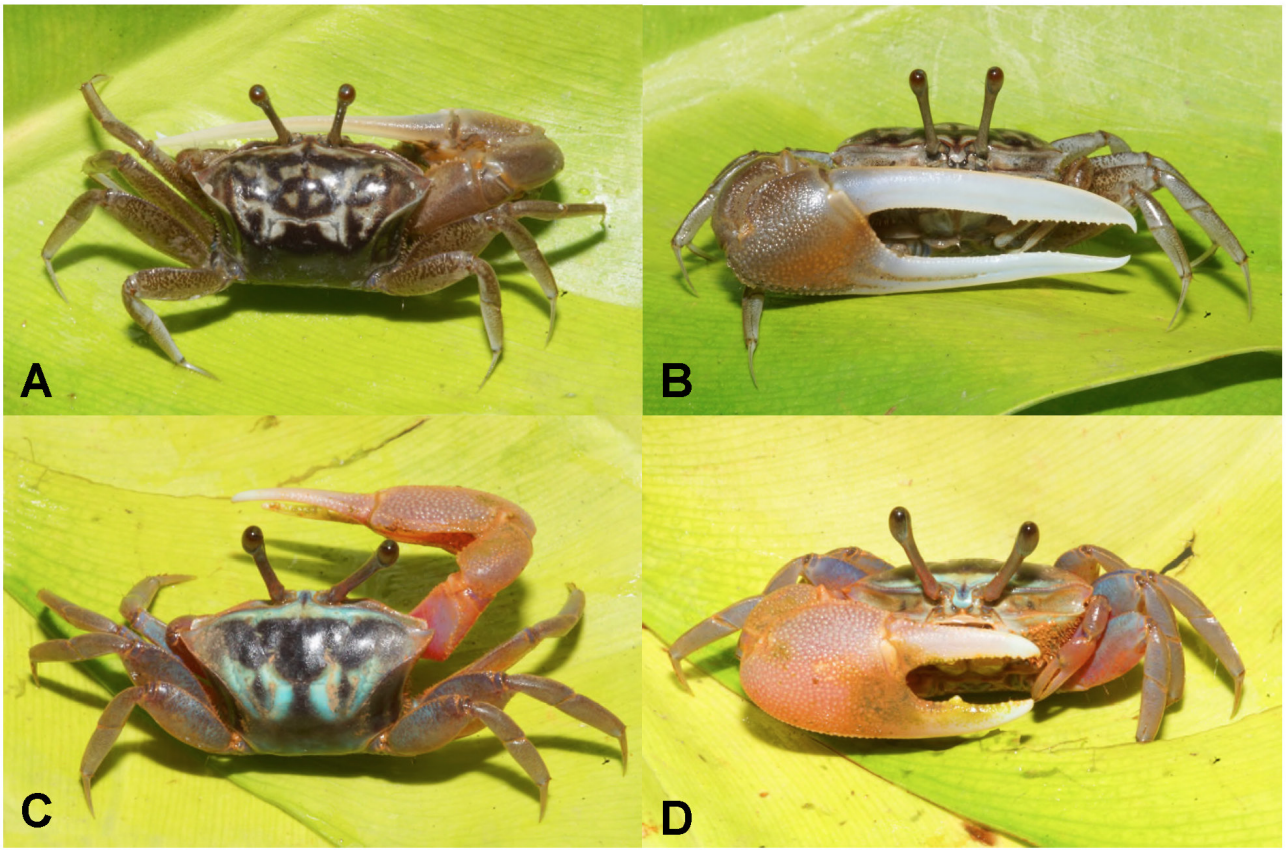

Fig. 6. Dorsal view of carapace and frontal view of major cheliped. *Tubuca rhizophorae* (A, B, NCHUZOOL 15148, CW 15.4 mm, Can Gio, Ho Chi Minh City); *T. typhoni* (C, D, NCHUZOOL 15151, CW 17.5 mm, Can Gio, Ho Chi Minh City).

been included in the list of brachyuran fauna collected from southern Vietnam, albeit the lack of illustrations (Do 2003). With both morphological and molecular evidence, our report confirms the presence of this species from southern Vietnam.

A key to the genera and species of fiddler crabs in Vietnam

1. Front narrow; outer major manus tubercular 2
- Front wide; outer major manus smooth 11
2. Outer major dactylus without groove; major carpus without delimited anterodorsal area flattened; more than 90% of males with major chela on the right; orbital floor without any elevations ..... 3 (*Gelasimus*)
- Outer major dactylus with 1 to 2 grooves; major carpus with delimited anterodorsal area flattened; roughly 50% of males with major chela on either side; orbital floor often with tubercles, ridge or mound ..... 5 (*Tubuca*)
3. Outer major manus with small tubercles; fingers narrow and thick; outer pollex without groove; female with pile posteriorly on carapace sides ..... *G. tetragonon*
- Outer surface of major manus with large tubercles; fingers broad and flat; outer pollex with one groove; female without pile posteriorly on carapace sides 4
4. Major pollex with shallow or without distal depression in gape, dactyl deeper than pollex only in young; oblique ridge of inner major manus low ..... *G. borealis*
- Major pollex with both deep proximal and distal depressions in gape, dactyl not deeper than pollex; oblique ridge of inner major manus high ..... *G. vocans*
5. Meri of first 3 ambulatory legs broad 6
- Meri of first 3 ambulatory legs slender 10
6. Floor of orbit with a row of tubercles; anterolateral margin shorter ..... *T. typhoni*
- Floor of orbit without a row of tubercles; anterolateral margin longer 7
7. Carapace strongly arched; large size (up to CW ~37 mm); major manus with large tubercles, fingers with a series of slightly enlarged predistal teeth (< 1/4 length of inner margins of fingers) in pollex and dactyl, or absent; young male with short fingers .. 8
- Carapace not strongly arched; small size (up to CW ~20 mm); major manus with small tubercles, fingers slender, with a series of slightly enlarged predistal teeth (near 1/2 length of inner margins of fingers) in pollex and dactyl 9
8. Ambulatory legs broader; major manus with large tubercles covering entire surface; G1 with relatively narrower genital opening and broad posterior flanges ..... *T. arcuata*
- Ambulatory legs narrower; major manus with large tubercles covering upper surface; G1 with relatively wider genital opening and vestigial flanges ..... *T. forcipata*
9. Groove of front broader, with sides not convergent distally; suborbital granules detectable; tubercles on outer manus larger ... . *T. acuta*
- Groove of front narrower, with sides convergent distally; suborbital granules absent; tubercles on outer manus smaller .... *T. rhizophorae*
10. Front with distinct narrow median groove; G1 with distal tuberculate chitinous process; female without large tooth on either finger in gape; large size (up to CW ~38 mm) .... *T. paradussumieri*
- Front almost without discernible median groove, but clearly separated; G1 with distal blunt chitinous process; female always with a large tooth on both fingers in gape; medium size (up to CW ~27 mm) ..... *T. dussumieri*
11. A shallow, triangular depression outside major pollex base; fourth ambulatory merus broad, its dorsal margin convex .... *Paraleptuca* (*P. splendida*)
- No triangular depression outside major pollex base; fourth ambulatory merus slender, its dorsal margin straight .... 12 (*Austruca*)
12. Anterolateral angles triangular; major pollex without or with small predistal triangular tooth in gape; major dactyl arched throughout; G1 with thumb long, reaching well beyond flange base, flange wider than long ..... *A. lactea*
- Anterolateral angles moderately acute; major pollex with moderate to large predistal triangular tooth in gape; major dactyl arched only distally; G1 with thumb moderately long, reaching flange base, flange wider than long ..... *A. perplexa*
- Anterolateral angles strongly acute; major pollex with small to moderate predistal triangular tooth in gape; major dactyl arched throughout; G1 with thumb short, not reaching flange base, flange remarkably long ..... *A. annulipes*

DISCUSSION

Molecular analyses

Of the 14 species reported in this study, DNA analyses on mtDNA *COI* sequences support recognition of 13 species-level taxa, with the exception of two members of the *Gelasimus vocans* species complex. Among the taxa recognized by the molecular data, the minimum interspecific divergence is observed between *Tubuca arcuata* and *T. forcipata* at 7.27% (Table 2). This interspecific distinction is substantial in considering values from published studies of various closely related allopatric species pairs of fiddler crabs, including: *Austruca citrus* Shih & Poupin, 2020 and *A. perplexa* (H. Milne Edwards, 1852) (≥ 1.29%, Shih and Poupin 2020); *Gelasimus excisus* (Nobili, 1906) (= *G. neocultrimanus* (Bott, 1973)) and *G. jocelynae* Shih, Naruse & Ng, 2010 (≥ 4.77%, recalculated from Shih et al. 2010a); *Minuca rapax* (Smith, 1870) and *M. virens* (Salmon & Atsaides, 1968) (≥ 3.29%, Thurman et al. 2018); *Paraleptuca splendida* (Stimpson, 1858) and *P. crassipes* (White, 1847) (≥ 2.49%, Shih et al. 2012); and *Tubuca alcocki* Shih, Chan & Ng, 2018 and *T. urvillei* (H. Milne Edwards, 1852) (3.78%, Shih et al. 2018). On the other hand, despite well-defined morphological differences among members of the *Gelasimus vocans* species complex, the minimum interspecific divergence between *G. borealis* and *G. vocans* is substantially lower at 0.15% (Table 2), agreeing with results published in the literature (Shih et al. 2010a; Chu et al. 2015). In any case, the considerable interspecific divergences among most of the species reported in this study (Table 2) indicate these species are genetically well differentiated in Vietnam.

With regard to the intraspecific divergences, the highest values are observed among *Paraleptuca splendida* and *Tubuca arcuata* at 1.70%. Some species, however, show low values of intraspecific variation. For example, no divergence was found in *Gelasimus tetragonon* and *Tubuca acuta*; and 0.15% in *Tubuca forcipata* and *T. paradussumieri* (Table 2). This low haplotype and nucleotide diversity has been reported in *Austruca occidentalis* (Naderloo, Schubart & Shih, 2016) from eastern Africa, implying involved species might have experienced strong bottlenecks due to founder effects, low lineage-specific mutations rates or natural selection (García-Merchán et al. 2012; Fratini et al. 2016).

Comparison of fiddler crab faunae within Vietnam and adjacent regions

While the fiddler crab faunae between northern and southern Vietnam are quite distinct, *Paraleptuca splendida* and *Tubuca paradussumieri* occur in both regions (Table 3). For the remaining species, a north-south pattern of segregation is apparent: *A. lactea*, *G. borealis*, *T. acuta* and *T. arcuata* are only distributed in northern Vietnam, whereas *A. annulipes*, *A. perplexa*, *G. tetragonon*, *G. vocans*, *T. dussumieri*, *T. forcipata*, *T. rhizophorae* and *T. typhoni* are only found in the south. This segregation is particularly interesting as pairs of sister species (or members of species complex) (Shih et al. 2016b) are involved, showing allopatric distributions, namely *A. lactea* vs. *A. perplexa*, *G. borealis* vs. *G. vocans*, *T. acuta* vs. *T. rhizophorae* and *T. arcuata* vs. *T. forcipata*, respectively from northern and southern Vietnam. The different faunae in northern and southern Vietnam are assumed to be caused by (1) variation along the temperature (and climatic) gradient in the two regions (Jian et al. 2006); (2) the lack of vast intertidal zones with soft sediment in central Vietnam, which has been described as having "no mangroves along the entire seashore" only "[narrow] strips of brackish water mangroves... along river banks" (Phan and Hoang 1993), and as a region in which mangroves "are limited to a narrow strip within estuaries" for current condition (Veettil et al. 2019); (3) the southward and northward ocean currents along Vietnamese coasts merged to form an eastward current at around 12°N (southeastern Vietnam) in summer (Quan et al. 2016), the reproduction season, which probably serves as a strong north-south barrier, preventing the planktonic larvae of most fiddler species in either region from dispersing further. The two species which occur in both northern and southern Vietnam, *P. splendida* and *T. paradussumieri*, have a broader of distribution in comparison with other species – for *P. splendida* spanning from coasts of Vietnam, southern Hainan, Dongsha Island and southern Ryukyus, and for the

Table 3. Distribution of fiddler crabs in northern Vietnam and southern Vietnam (including the Gulf of Thailand ecoregion in Fig. 7), and adjacent areas of China, Malay Peninsula and Borneo

Species	Continental China (incl. N Hainan)	N Vietnam	S Vietnam	S Hainan	E Malay Peninsula (incl. Singapore)	Malaysian Borneo
Austruca annulipes			*	*	*	*
Austruca lactea	*	*				
Austruca perplexa			*		*	*
Austruca triangularis						*
Gelasimus borealis	*	*				
Gelasimus hesperiae					*	
Gelasimus tetragonon			*	*	*	
Gelasimus vocans	*?[a]		*	*	*	*
Paraleptuca splendida	*	*	*	*		
Tubuca acuta	*	*				
Tubuca arcuata	*	*				
Tubuca bellator						*
Tubuca dussumieri	*?[a]		*		*	
Tubuca forcipata			*		*	*
Tubuca paradussumieri	*	*	*		*	*
Tubuca rhizophorae			*		*	*
Tubuca typhoni			*	*		
species number	8 (6)	6	10	5	9	8

[a] see Shih et al. 2010b.

latter, an extensive distribution from the Bay of Bengal, Malay Peninsula, Borneo to South China (Crane 1975; Shih 2012b 2020; Shih et al. 2010b 2012 2015 2016a). The broad distributional range of both species implies stronger dispersal abilities of their larvae against eastward currents around southeast Vietnam, as well as their broader ecological tolerances. Comparing fiddler crab faunae with the adjacent areas (Table 3), the species composition of northern Vietnam bears a similarity with that of continental China (including northern Hainan) and other East Asian regions (Shih et al. 2010b 2015 2016a), with overlapping species including *A. lactea*, *G. borealis*, *P. splendida*, *T. acuta*, *T. arcuata* and *T. paradussumieri*. That of southern Vietnam is more similar with eastern Malay Peninsula and northern Borneo (Crane 1975; Tan and Ng 1994), sharing the below species: *A. annulipes*, *A. perplexa*, *G. tetragonon*, *G. vocans*, *T. forcipata*, *T. paradussumieri* and *T. rhizophorae*. However, three species from eastern Malay Peninsula and northern Borneo, viz. *A. triangularis* (A. Milne-Edwards, 1873), *G. hesperiae* (Crane, 1975) and *T. bellator* (White, 1847), have not been recorded from Vietnam so far. Based on the current data, the shore of Vietnam is biogeographically significant, where the northern part is located as the southernmost limit of *G. borealis*, *T. acuta* and *T. arcuata*; and *A. lactea* is extended to the central part (cf. Wada 2019); and the southern part is the northernmost limit of *T. rhizophorae* and *T. forcipata* (at least in continental eastern Asia).

On records of *Tubuca dussumieri* from Vietnam and the continental coasts of the SCS

Sister species *Tubuca dussumieri* and *T. paradussumieri* share a marked morphological resemblance and are discernible only by minor differences (Crane 1975; Shih et al. 2016b). Geographically, their distributions are more or less separated, with *T. paradussumieri* appearing to be limited to vicinity of the SCS and the Andaman Sea (*i.e.*, continental coasts from eastern Indian Ocean, via Peninsular Malaysia and Borneo, to East Asia), and *T. dussumieri* appearing to be more widely distributed in oceanic islands (Crane 1975: map 18). This segregation is also reflected in their required habitat, with *T. paradussumieri* present on intertidal mudflats composed of finer sediments, and *T. dussumieri* preferring intertidal mudflats with coarser sediments (Jones and Morton 1994; Kwok and Tang 2006; Shih et al. 2015 2021). Even so, there were still reports of *T. dussumieri* from the SCS and adjacent regions from localities such as Guangdong in South China (Dai et al. 1986; Dai and Yang 1991; S-L Yang et al. 2008), Gulf of Thailand and southwestern Borneo (Crane 1975: map 18), Koh Surin Island in western Thailand (Frith and Frith 1977 1978), and Singapore (Tan and Ng 1994). However, the following records require verification: the Paracels in western SCS (as "*U. dubia*" in Dawydoff 1952) and southern Vietnam (as "*U. arcuata*" in Chertoprud et al. 2012). Reports of *T. dussumieri* from Tioman Island (southeastern Peninsular Malaysia) and Pawai Island (Singapore), both oceanic islands with coarse sediments, have been confirmed by morphological and molecular evidence (HT Shih unpublished). Because *T. dussumieri* generally inhabits oceanic islands, the record presented by Chertoprud et al. (2012) from the oceanic Hon Tre Island in Nha Trang Bay (as "*Uca arcuata*") is reliable.

Biogeography of fiddler crabs in Vietnam in relation to ecoregions and oceanographic currents

In the present study, the distribution of the 14 species of fiddler crabs in Vietnam follows the ecoregions (Fig. 7) as defined in Spalding et al. (2007). The coastline of Vietnam is divided into three ecoregions: the Gulf of Tonkin ecoregion (GTo), which includes the northern coastline; the Southern Vietnam ecoregion (SV), which includes the southern coastline (Spalding et al. 2007); and the Gulf of Thailand ecoregion, which includes the Gulf of Thailand and is separated from the SV by a boundary at the region around Nha Trang. The division of these three regions is supported by the oceanographic currents around the Vietnam coastline. Climatic conditions of Vietnam are heavily influenced by the East Asian Monsoon, characterized by seasonally opposite patterns in atmospheric and oceanic circulations (see Lau et al. 1998). The northern Vietnam coastline is affected by several currents. The Gulf of Tonkin Surface Current flows southward along the coastline of northern Vietnam (Liu et al. 2016; Fig. 7). The northern coastline is also affected by a buoyancy-driven river plume originating from the runoff of the Red River (Hong River) in the north, flowing southeastwards towards the central reaches of the shore. There is an intrusion of the South China Sea Branch of Kuroshio Current, which enters from the Luzon Strait and hits the middle region of Vietnam from May to September, close to Nha Trang (Xue et al. 2004; J Yang et al. 2008; Fig. 7).

The southern part of the Vietnam coastline is affected by the Southeast Vietnam Offshore Current flowing northward and mixing with the South China Sea Branch of Kuroshio Current (J Yang et al. 2008; Tsang et al. 2012; Quan et al. 2016; Fig. 7). There is a runoff from the Mekong River along the southern coastline towards the northeast (Chen et al. 2012). The

mixing of different currents at around latitude 11–12°N, immediately south of Nha Trang, forms an upwelling zone with sea surface temperatures of approximately 24 to 25°C, some 3 to 5°C lower than surrounding seas, accompanied with enhanced chlorophyll concentration ("cold filament"; Xie et al. 2003; Doan et al. 2010). This upwelling shows inter-annual variations, contributing to a differing extent of cooling of sea surface temperatures

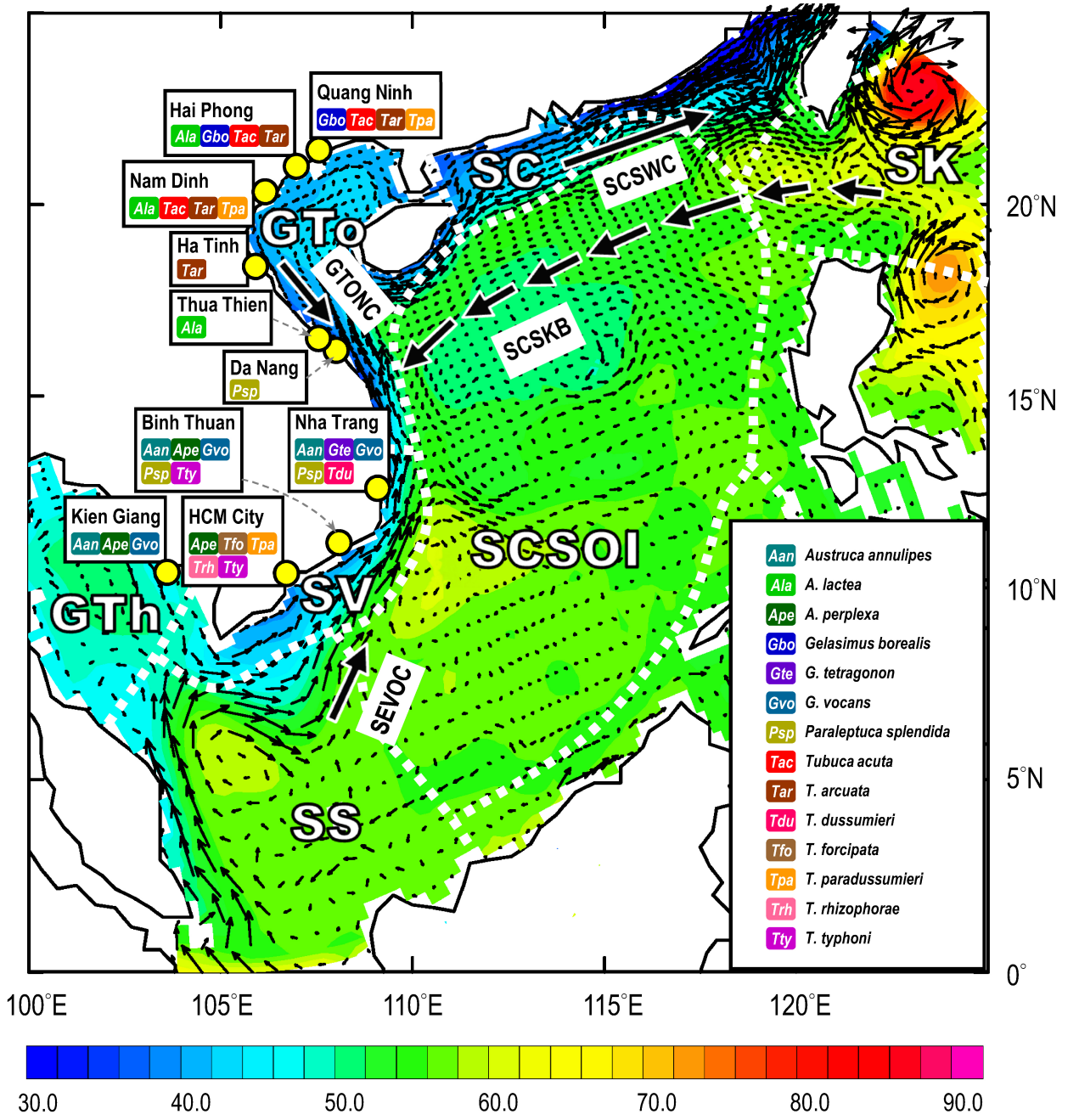

Fig. 7. Oceanographic currents (summer) around Vietnamese waters and the distribution of fiddler crabs. Oceanographic current map is adopted from figure 5D in Xue et al. (2004) (Lincence number: 5380661146310, offered by JOHN WILEY AND SONS LICENSE). Marine ecoregions are indicated by bold dashed lines. Abbreviations: Ocean currents: GTONC – Gulf of Tonkin Current, SCSWC – South China Sea Warm Current, SCSKB – South China Sea Branch of Kuroshio, SEVOC – Southeast Vietnam Offshore Current; marine ecoregions (with numbers as listed in Spalding et al. 2007): GTo – Gulf of Tonkin (112), SC – Southern China (113), SCSOI - South China Sea Oceanic Islands (114), GTh – Gulf of Thailand (115), SV – Southern Vietnam (116), SS – Sunda Shelf (117), SK – South Kuroshio (121). Colorations depicted on marine areas represent sea surface elevation in centimeters. The record of *Paraleptuca splendida* in Da Nang was reported in Balss (1922) and *Austruca lactea* in Huong Phong, Thua Thien was recorded by Wada (2019).

(Xie et al. 2003). The Gulf of Thailand is affected by the monsoonal currents with anticyclonic gyre in summer (March to August) and cyclonic in winter (September to November) (Liu et al. 2016). The two sets of currents probably help explain the northern and southern Vietnamese species assemblages of fiddler crabs. The northern Vietnamese assemblage (Table 3, Fig. 7) found in the Bay of Tonkin ecoregion includes *Austruca lactea*, *Gelasimus borealis*, *Paraleptuca splendida*, *Tubuca acuta*, *T arcuata* and *T. paradussumieri*. The southern Vietnamese species assemblage (Table 3, Fig. 7) distributed in the Southern Vietnam ecoregion includes *A. annulipes*, *A. perplexa*, *G. tetragonon*, *G. vocans*, *P. splendida*, *T. dussumieri*, *T. forcipata*, *T. paradussumieri*, *T. rhizophorae* and *T typhoni*; and the Gulf of Thailand assemblage is so far composed of *A. annulipes*, *A. perplexa* and *G. vocans*. The distinct distributions of fiddler crab assemblages between northern Vietnam and southern Vietnam (and Gulf of Thailand) correspond well with the oceanographic currents (Fig. 7) suggesting the larval pools of these assemblages are separated by the current patterns.

CONCLUSIONS

14 species of fiddler crabs were reported from Vietnam, including the newly recorded *Tubuca rhizophorae* and *T. dussumieri*. Based on DNA barcoding analyses, we show the mitochondrial *COI* marker can successfully distinguish most species-level taxa (13; with the exception of *G. borealis* and *G. vocans*), with the minimum interspecific divergences at least 7.27%. Species compositions of fiddler crabs in northern and southern Vietnam are different, with only *Paraleptuca splendida* and *Tubuca paradussumieri* being common in both regions. The fauna of northern Vietnam bears a similarity with China and other East Asian regions, whereas that of southern Vietnam is closer to that of the Malay Peninsula and Borneo.

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Authors' contributions: HTS conceived this study, performed the molecular analysis, and drafted the manuscript. KJHW, BKKC, TSN, VTD, XQN and PYH collected and processed the samples, participated in the discussion and drafted the manuscript. All authors read and approved the final manuscript.

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