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***Uca (Xeruca)*, a new subgenus for the Taiwanese fiddler crab *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae), based on morphological and molecular evidence**

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Abstract

The fiddler crab *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae), restricted to the western part of Taiwan and the offshore Penghu (Pescadores) Islands in the Taiwan Strait, has been placed under the subgenus *Uca (Gelasimus)* Latreille, 1817 (= *Uca (Thalassuca)* Crane, 1975) based on only less than a dozen specimens, but later suggested under the subgenus *Tubuca* Bott, 1973 because the similarity of external morphology. A suite of characters of carapace, major cheliped, gastric mill, male first gonopod, and chela handedness, as well as the phylogenetic relationships (mitochondrial 16S rDNA and cytochrome oxidase subunit I, and nuclear 28S rDNA), nevertheless support this species belongs to its own subgenus. A new subgenus *Uca (Xeruca)* **subgen. nov.** is herein established for *U. formosensis*.

Key words: *Xeruca*, new subgenus, *Uca formosensis*, fiddler crab, Ocypodidae, taxonomy, Taiwan, 16S rDNA, cytochrome oxidase subunit I, 28S rDNA

Introduction

There are 102 extant species of fiddler crabs (Ocypodidae: genus *Uca*) in the world (Crane 1975; Rosenberg 2001; Beinlich & von Hagen 2006; Ng *et al.* 2008; Landstorfer & Schubart 2010; Naderloo *et al.* 2010; Shih *et al.* 2010, 2012, 2013a, b). The 44 Indo-West Pacific (IWP) species belong to six subgenera, including the narrow-fronted *Australuca* Crane, 1975, *Gelasimus* Latreille, 1817, and *Tubuca* Bott, 1973, and the broad-fronted *Austruca* Bott, 1973, *Cranuca* Beinlich & von Hagen, 2006, and *Paraleptuca* Bott, 1973 (see Crane 1975; Shih *et al.* 2013b). Among them, the subgenus *Tubuca*, composed of 14 species, is a group with the highest species diversity (see Ng *et al.* 2008).

Crane's (1975) monograph of *Uca* is a landmark publication for ocypodid researchers, with major updates by Rosenberg (2001) and Beinlich & von Hagen (2006). One taxon, which Crane regarded as "elusive" is *Uca formosensis* Rathbun, 1921, a species endemic to Taiwan, with only less than a dozen preserved specimens at the time of her study. She had tried to collect specimens in Danshuei (= Tamsui) in northwestern Taiwan during late April to May 1963 (Crane 1975; Sakai 1981), but was unsuccessful, probably because the habitat of this locality has substantially changed since the 1950s with a dense growth of mangroves now dominating (Shih 1997). She places *U. formosensis* in the subgenus *Thalassuca* Crane, 1975 (= *Gelasimus* Latreille, 1817), with other two species, *U. tetragonon* and *U. vocans* (with six subspecies). After examining more specimens from various localities in Taiwan, Shih *et al.* (1999) suggested the morphology of *U. formosensis* was closer to members of the subgenus *Tubuca* Bott, 1973 (= *Deltuca* Crane, 1975). The ecology and behavior of *U. formosensis* are nevertheless peculiar compared to other IWP narrow-fronted species. Its preferred habitat is in the high intertidal mudflat with clay sediment, and is only immersed by the high tide during spring tide; in addition, the male builds a tall chimney (mean height 9.2 cm) for underground mating during the neap tide (Shih *et al.* 2005). Other *Tubuca* species however generally inhabit in the wet areas between low and middle intertidal zones (Crane 1975). Although some species construct chimneys around burrow entrance, the builder is of either sex or at least the

female (reviewed by Shih *et al.* 2005). A morphological analysis by Rosenberg (2001) also showed that *U. formosensis* did not belong to *Tubuca*, *Gelasimus*, or *Australuca*.

In this study the morphology of *Uca formosensis* was re-examined and compared with other taxa. Its phylogenetic relationship using mitochondrial 16S rDNA and cytochrome oxidase subunit I (COI), and nuclear 28S rDNA was also reconstructed. All the results show this species has several unique characters and forms an independent clade. On the basis of this evidence, a new subgenus *Uca (Xeruca)* **subgen. nov.** is established for *U. formosensis* Rathbun, 1921.

Material and methods

Specimens of *Uca formosensis* from various localities in Taiwan and Penghu (Pescadores) Islands in the Taiwan Strait were collected and preserved in 75–95% ethanol (Fig. 1, Appendix 1, Table 1). Most specimens examined in Shih *et al.* (1999) are in the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL). The types are in the U.S. National Museum of Natural History, Smithsonian Institution, Washington DC, USA (USNM), and specimens deposited in the National Taiwan Museum, Taipei, Taiwan (TMCD) were also examined. Specimens of other related species, including the IWP narrow-fronted members of the subgenera *Gelasimus*, *Tubuca*, and *Australuca*; IWP broad-fronted taxa in the subgenera *Austruca*, *Cranuca*, and *Paraleptuca*; and the Atlantic-East Pacific members of the subgenera *Uca* Leach, 1814 and *Afruca* Crane, 1975, were compared for morphological and molecular studies. The material examined is deposited in NCHUZOOL; TMCD; National Museum of Natural Science, Taichung, Taiwan (NMNS); Museo Zoologico dell'Università di Firenze, Italy (MZUF); the Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung, Taiwan (NTOU); Queensland Museum, Brisbane, Australia (QM); Senckenberg Museum, Frankfurt am Main, Germany (SMF); and Zoological Reference Collection of the Lee Kong Chian Natural History Museum (formerly Raffles Museum of Biodiversity Research), National University of Singapore, Singapore (ZRC) (see Appendix 2, Table 1).

The carapace and male major cheliped were illustrated with the help of a drawing tube attached to a Carl Zeiss stereo-microscope. The scanning electron microscopy (SEM) of the right male first gonopod (G1) was made mainly following Shih *et al.* (1999). Measurements, in millimeters (mm), are of the carapace width (CW).

The gastric mill of *U. formosensis* and other related taxa were examined and compared. The stomach was removed with forceps inserted from the suture of posterior margin between carapace and abdomen. The gastric mill was examined and illustrated under the stereo-microscope and SEM. The description of the gastric mill mainly follows the terminology used by Yang (1986) and Allardyce & Linton (2010). The urocardiac ossicle can be divided roughly into three regions: anterior basal region, stem region, and posterior tooth plate. The median tooth is composed of several transverse tooth-like ridges or cusps, protruding from a longitudinal central ridge on the ventral side of the tooth plate as well as on the stem region for some species.

Sequences of 16S, COI and 28S were obtained following the method described by Shih *et al.* (2013b) and aligned with the aid of ClustalW (v. 1.4, Thompson *et al.* 1994), after verification with the complimentary strand. Sequences of the different haplotypes were deposited in the DNA Data Bank of Japan (DDBJ) (accession numbers in Table 1).

For a combined analysis of mitochondrial 16S, COI, and 28S markers, phylogenetic congruence among the three dataset partitions was tested under the maximum parsimony (MP) criterion using the incongruent length difference (ILD) test (Farris *et al.* 1994) implemented in the PAUP* program (v. 4.0b10, Swofford 2003) as the partition homogeneity test. The parameters included 1000 reiterations of a heuristic search with 100 randomly added sequence replications, TBR branch-swapping, using Steepest Descent, and the MULTREES option enabled. The topologies of the three data sets were congruent ($P = 0.535$) and as such, the sequences were combined.

For the combined dataset, the best-fitting models for sequence evolution of individual datasets were determined by MrModeltest (v. 2.2, Nylander 2005), selected by the Akaike information criterion (AIC). The obtained best models for the three individual dataset were all GTR + G + I, and were subsequently used for the partitioned Bayesian inference (BI) and maximum likelihood (ML) analyses. The Bayesian inference analysis was performed with MrBayes (v. 3.2.3, Ronquist *et al.* 2012). The search was run with 4 chains for 10 million generations and 4 independent runs, with trees sampled every 1000 generations. The convergence of chains was

determined by the effective sample size (ESS) (>200 as recommended) in Tracer (v. 1.5, Rambaut & Drummond 2009) and the first 1000 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). The maximum likelihood analysis was conducted in GARLI (v. 2.0, Zwickl 2006), with 10 replicate searches (searchreps = 10) and 100 bootstraps (bootstrapreps = 100). The consensus tree from GARLI output was computed using PAUP* program to assess node supports.

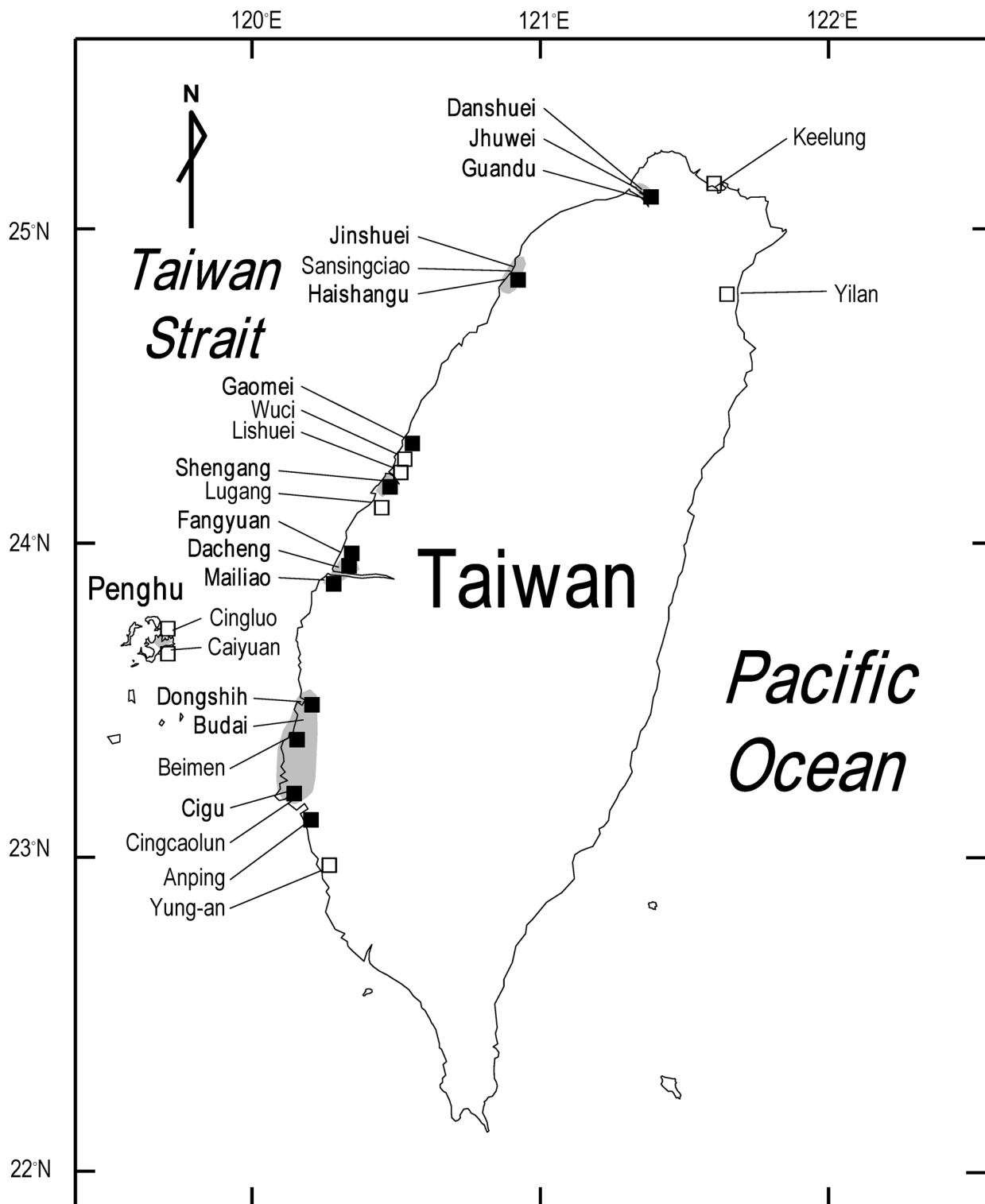


FIGURE 1. Updated distributional records of *Uca formosensis* of Shih *et al.* (1999). Black squares (■) (and gray area) and place names in boldface represent habitats with substantial number of individuals; empty squares (□) and place names in normal font represent habitats with none or few individuals, although the species was formerly recorded from these locations.

Systematic account

Family Ocypodidae Rafinesque, 1815

Subfamily Ocypodinae Rafinesque, 1815

Genus *Uca* Leach, 1814

Uca (*Xeruca*) subgen. nov.

Uca (*Thalassuca*) Crane, 1975: 75 (part); Rosenberg 2001: 840, 848, 851 (part).

Tubuca Bott, 1973: 322 (part).

Uca (*Tubuca*)—Beinlich & von Hagen 2006: 10, 14, 15, 25 (part); Ng *et al.* 2008: 241 (part).

Type species. *Uca formosensis* Rathbun, 1921, by present designation.

Etymology. From the Greek *xeros* for “dry,” for the high intertidal habitat of the type species, in arbitrary combination with the genus name *Uca*. Gender feminine.

Diagnosis. Carapace highly arched, branchial chambers strongly tumid; front narrow; anterolateral angles acute, produced forwards (Figs. 2A, C, 3A, 4A). Male with anterolateral margins long, strongly developed, almost straight; turning at an angle to join convergent, distinct, dorsolateral margins (Figs. 2A, C, 3A, 4A); female with anterolateral, dorsolateral margins strongly beaded, with definite boss or tuberculate swelling on carapace behind dorsolateral margin (Fig. 2E).

Suborbital crenellations rolled out in male, becoming minute or absent along outer angle; suborbital crenellations erect in female, becoming strong, truncate, separated, larger towards antero-external angle (Fig. 2B; Shih *et al.* 1999: fig. 1E, F). Orbital floor with mound, pile in female, none in male; suborbital region, upper pterygostomial regions naked in male, setose in female (Shih *et al.* 1999: fig. 1E, F). Male without pleonal clasping apparatus in sterno-abdominal cavity.

Major cheliped with fingers laterally flattened, smooth; lower margin of pollex, upper margin of dactylus almost straight, not arched; cutting margins with distal half almost straight, without depression or enlarged teeth; proximal half with shallow elliptical space; furrows on external surface of fingers very faint or absent; outer surface of manus with low, well-separated tubercles (Figs. 2A, D, 3B, 5A). Male handedness 1:1. Minor cheliped with fingers longer than manus, gape narrow, female with enlarged teeth in middle of gape (Fig. 2F), male without teeth in gape (Fig. 2G). Meri of second, third ambulatory legs moderately wide, dorsal margin of first, fourth meri almost straight in male (Figs. 2A, C, 3A); dorsal margin of meri of ambulatory legs slightly convex in female (Shih *et al.* 1999: fig. 1B–D).

G1 with pore moderately large; anterior flange very narrow, distal tip tapering, beyond the tip of inner process; posterior flange broad, slightly curved, much wider than pore; inner process long, broad, thick, bent forwards at right angles; thumb moderate length, not reaching base of flange (Fig. 6). Female gonopore in shallow sternal depression, rimmed along postero-external quarter but not tuberculate (Shih *et al.* 1999: fig. 3E, F).

Urocardiac ossicles of gastric mill simple, median tooth with 2 pairs of similar transverse ridges, separated by gaps reached deeply near central ridge, on posterior tooth plate. 2 to 3 lower, weak pairs of cusps on stem region; stem region with widen middle part (Fig. 7).

Remarks. The carapace of *Xeruca* subgen. nov. (Fig. 4A) features a highly arched and quadrate shape, with long and straight anterolateral margins and well-marked dorsolateral margins. Its carapace is similar to that of *Australuca* species (Fig. 4B–D), especially *U. (Australuca) seismella* Crane, 1975 (Fig. 4C), but the dorsolateral margins of *Australuca* are proportionately shorter. Adult *Australuca* species are smaller in size, with the largest-size species is *U. (Australuca) elegans* George & Jones, 1982 with CW 26.6 mm (cf. George & Jones 1982: 25) while in *U. (Xeruca) formosensis*, the largest CW is 34.9 mm (cf. Shih *et al.* 1999: 170). *Tubuca* species are different on account of their triangular carapaces (Fig. 4E, F), with shorter and convergent anterolateral margins, although *U. (Tubuca) arcuata* (De Haan, 1835) (Fig. 4E) has long and straight anterolateral margins. The carapaces of *Gelasimus* species are also different, with oblique orbital margins in *U. (Gelasimus) tetragonon* (Herbst, 1790) (Fig. 4G), and the anterolateral margins are very short with weak dorsolateral margins in the *U. (Gelasimus) vocans* species complex (e.g. *U. (Gelasimus) jocelynae* Shih, Naruse & Ng, 2010 in Fig. 4H).

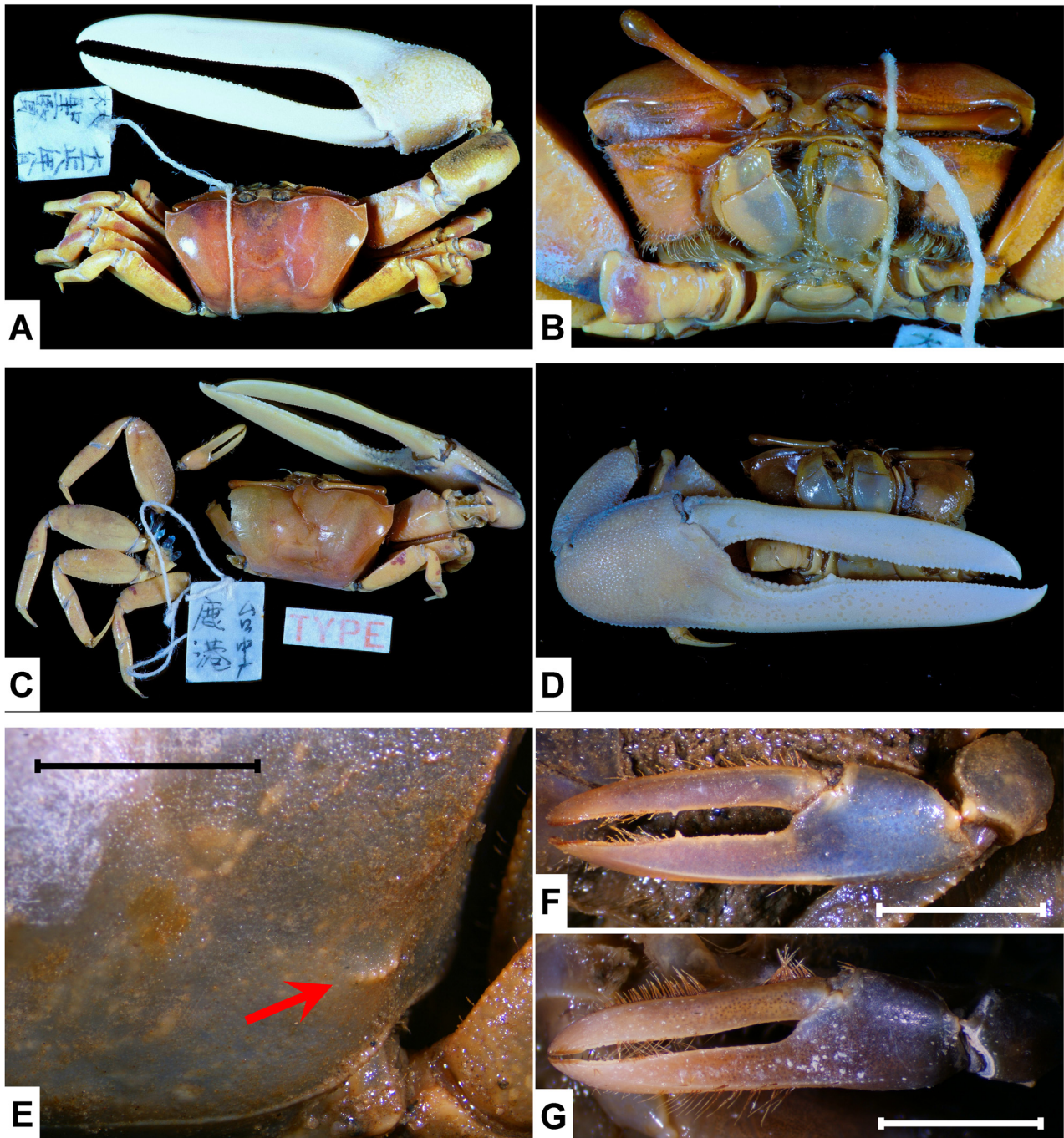


FIGURE 2. *Uca formosensis*. A, B, holotype (USNM 54472, CW 28.8 mm) recognized by Crane (1975); C, D, a paratype specimen (USNM 54472, CW 27.6 mm); E, F, ♀ from Haishangu, Hsinchu (NCHUZOO 13849, CW 32.2 mm), showing the tuberculate swelling on carapace behind right dorsolateral margin (arrowed) (E) and left minor chela (F); G, ♂ from Cigu, Tainan (NCHUZOO 13907, CW 31.8 mm) showing the left minor chela. E, F, G, scale = 5 mm.

Another character of *Xeruca* is having a major cheliped with straight cutting margins (i.e. the pollex's lower and dactylus's upper margins) more than half the length of the fingers, and the gape less than half the length of the fingers (Fig. 5A). This character is different from most other species with "forceps-like" fingers (cf. Crane 1975: figs. 38–41). Some subgenera however have such "scissor-like" fingers, but the distal cutting margins of the fingers are less than half the length of the fingers, and are slightly curved in most species, e.g. *U. (Australuca) longidigitum* (Kingsley, 1880) (Fig. 5B), *U. (Australuca) bellator* (White, 1847) (Fig. 5C), *U. (Uca) princeps* (Smith, 1870) (Fig. 5D), and *U. (Afruca) tangeri* (Eydoux, 1835) (Crane 1975: fig. 45, pl. 18).



FIGURE 3. *Uca formosensis*, ♂ from Haishangu, Hsinchu, Taiwan (NCHUZOO 13673, CW 27.9 mm), A, dorsal view; B, frontal view showing the right major chela.

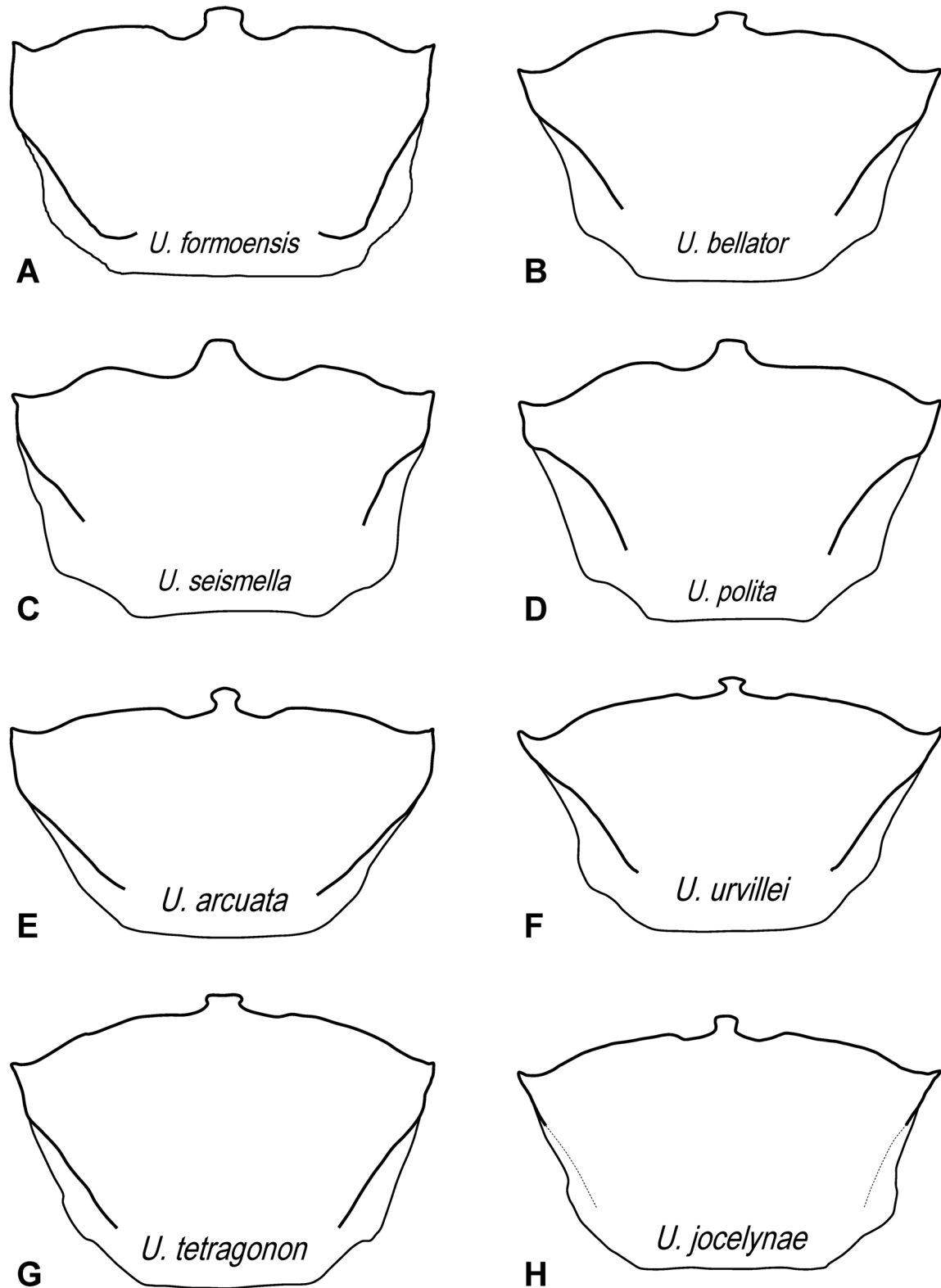


FIGURE 4. Carapaces of *Uca formosensis* and other species with similar morphology. A, *U. formosensis* (NCHUZOO 13672, CW 29.6 mm, left-handed; modified from Shih *et al.* 1999); B, *U. bellator* (NCHUZOO 13653, CW 18.7 mm, left-handed); C, *U. seismella* (USNM 137666, holotype, CW 13.0 mm, right-handed; modified from Crane 1975); D, *U. polita* (USNM 137667, holotype, CW 22.5 mm, right-handed; modified from Crane 1975); E, *U. arcuata* (NCHUZOO 13660, CW 38.2 mm, left-handed); F, *U. urvillei* (NCHUZOO 13661, CW 30.1 mm, left-handed); G, *U. tetragonon* (NCHUZOO 13664, CW 18.3 mm, right-handed); H, *U. jocelynae* (NMNS 6177-001, holotype, CW 21.7 mm, right-handed).

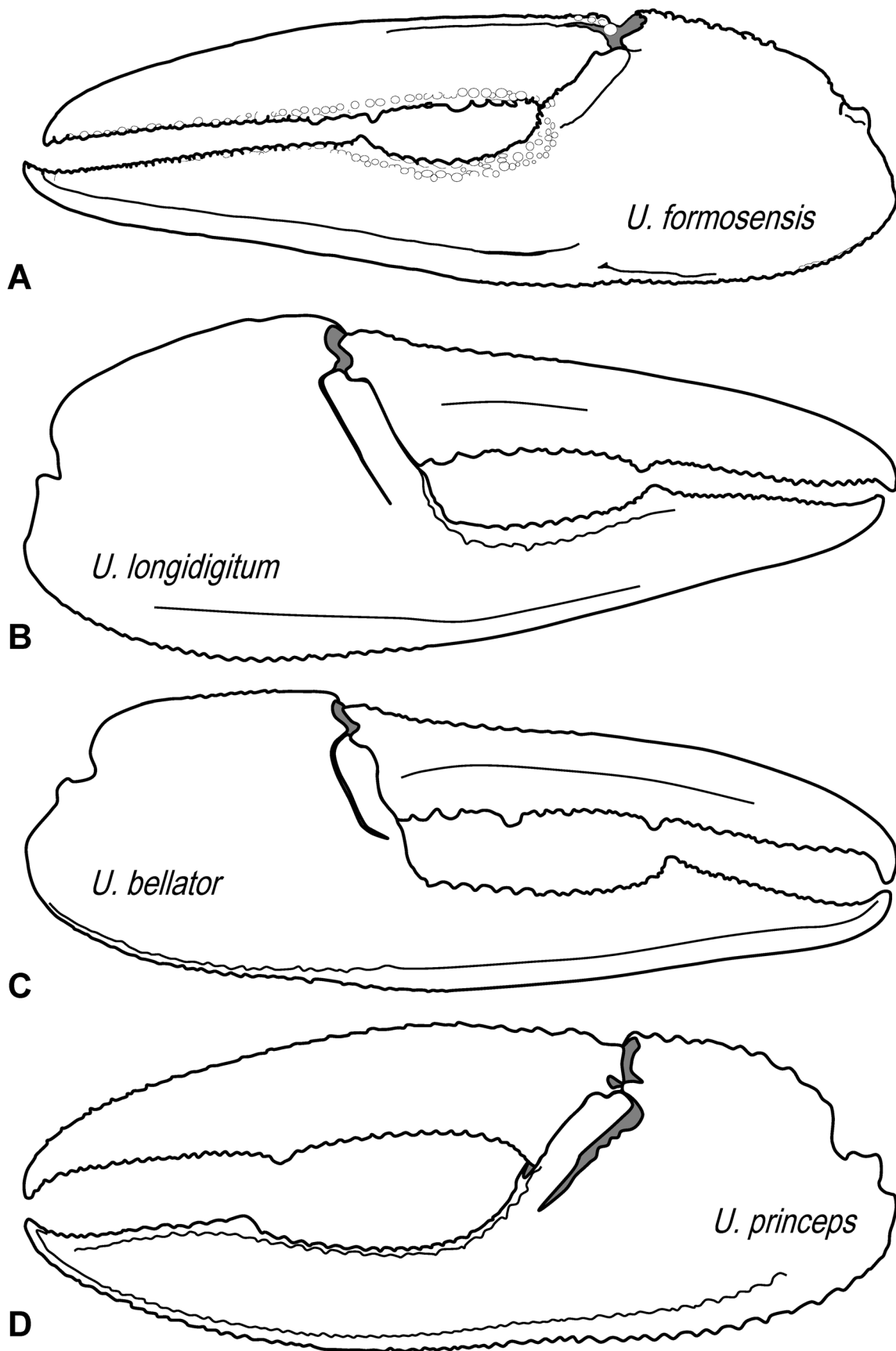


FIGURE 5. Major chelipeds of *Uca formosensis* and other species with similar morphology. A, *U. formosensis* (NCHUZ00L 13672, CW 29.6 mm; modified from Shih *et al.* 1999); B, *U. longidigitum* (NCHUZ00L 13656, CW 16.7 mm); C, *U. bellator* (NCHUZ00L 13653, CW 18.7 mm); D, *U. princeps* (SMF 13164, CW 36.5 mm).

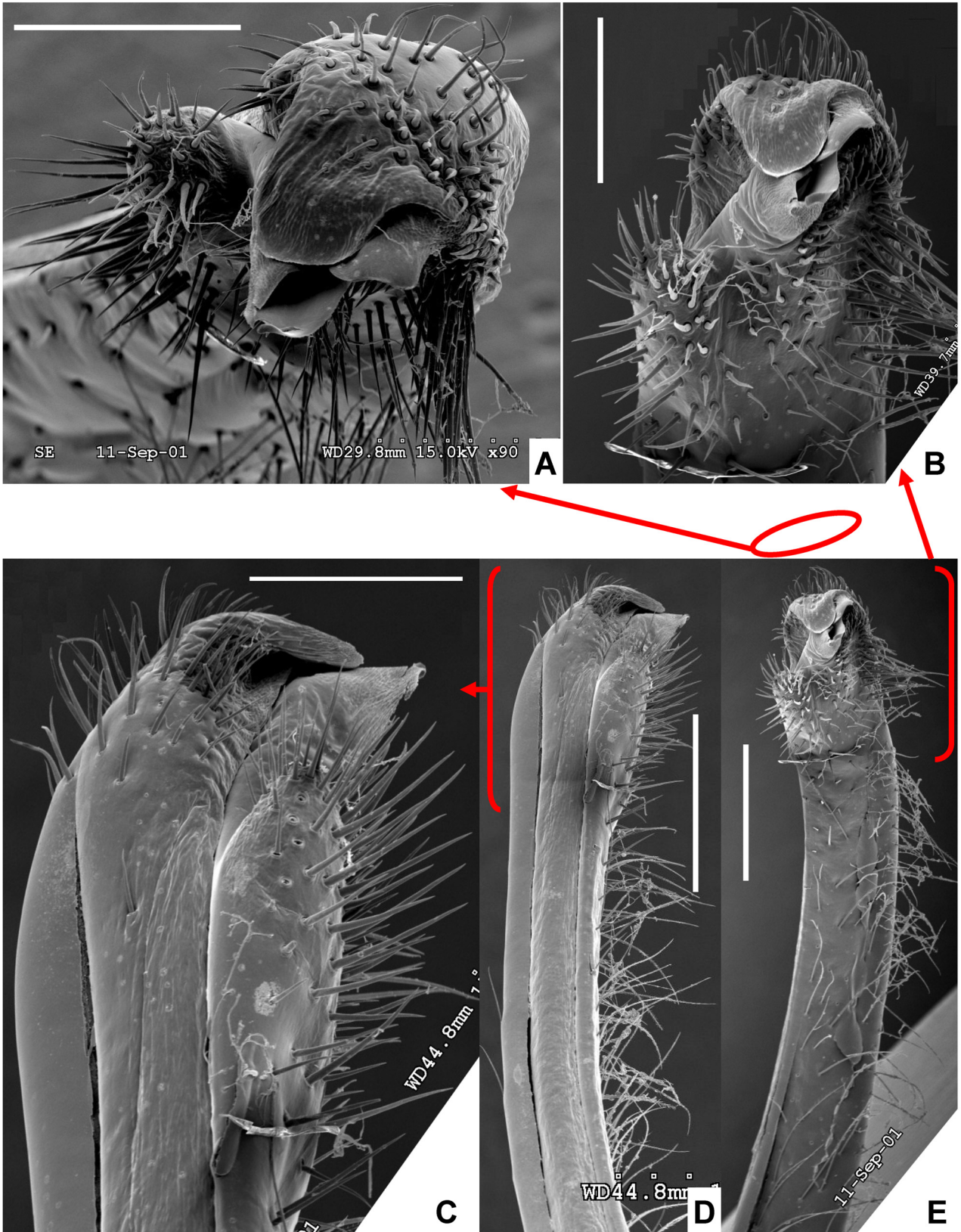


FIGURE 6. *Uca formosensis*, male right first gonopod (G1) (NCHUZ00L 13671, CW 33.0 mm). A, B, C, scale = 500 μ m; D, E, scale = 1 mm.

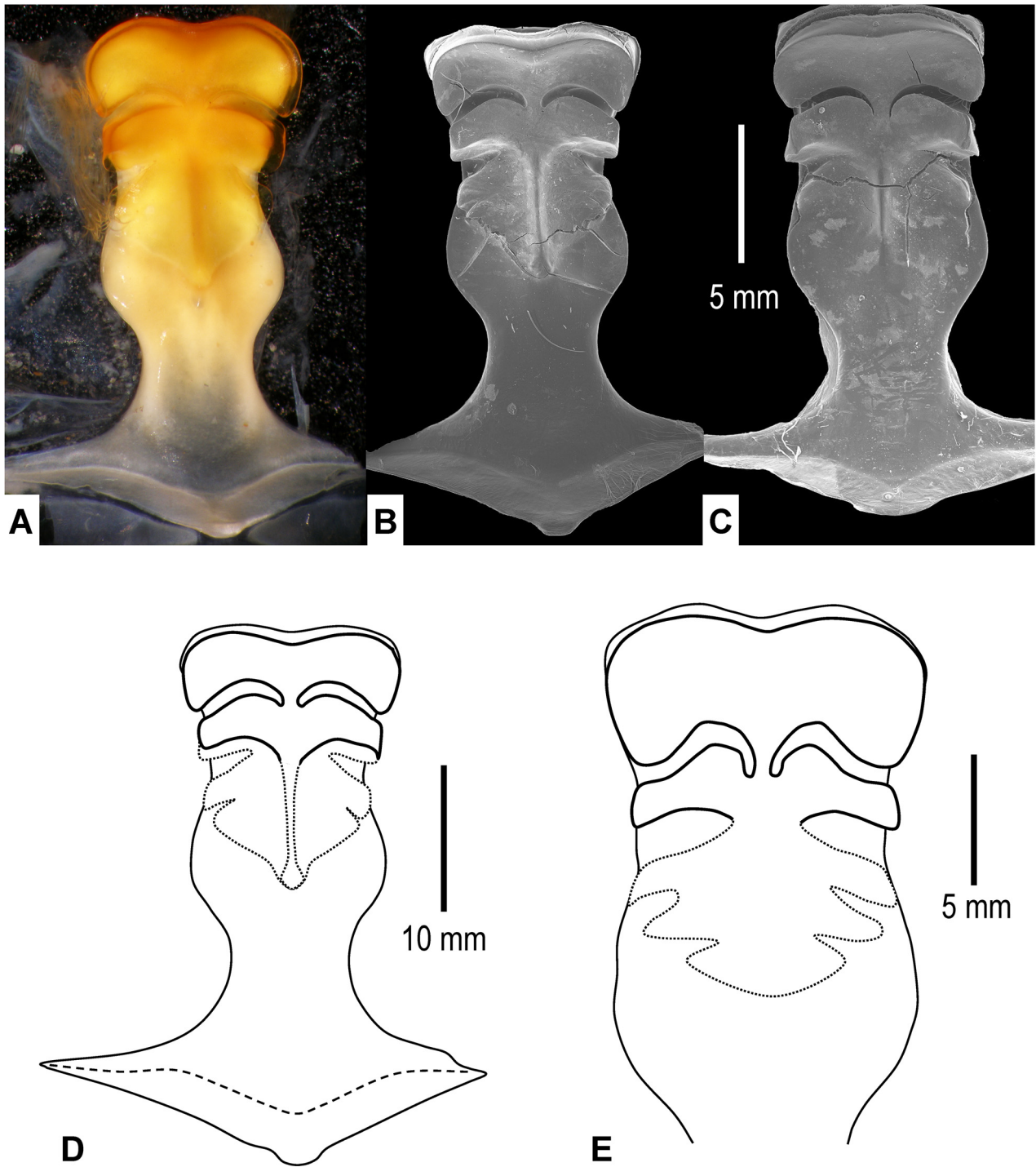


FIGURE 7. Urocardiac ossicle of *Uca formosensis*. A, B, D, NCHUZOO 13668 (CW 33.1 mm, ♂); C, NCHUZOO 13669 (CW 14.2 mm, ♀); E, NCHUZOO 13670 (CW 26.2 mm, ♀).

Some species of the subgenus *Uca* have conspicuous depth of the dactylus and pollex of the major cheliped, with longer and straight distal cutting margins in some individuals, e.g. *U. (Uca) insignis* (Milne-Edwards, 1852) (Bott 1954: pl. 14(1)), *U. (Uca) maracoani* (Crane 1975: pl. 21A–D), *U. (Uca) monilifera* (Crane 1975: pl. 18E–H), and *U. (Uca) ornata* (Crane 1975: pl. 21E–H). However, because the character of the deep fingers is peculiar, they can be easily separated from *Xeruca* and other species of fiddler crabs.

The handedness of *Xeruca* is close to a 1:1 ratio (Shih *et al.* 1999), which is consistent with the ratio of most species, but different from the mostly right-handed *Gelasimus* (Barnwell 1982; Yamaguchi 1994).

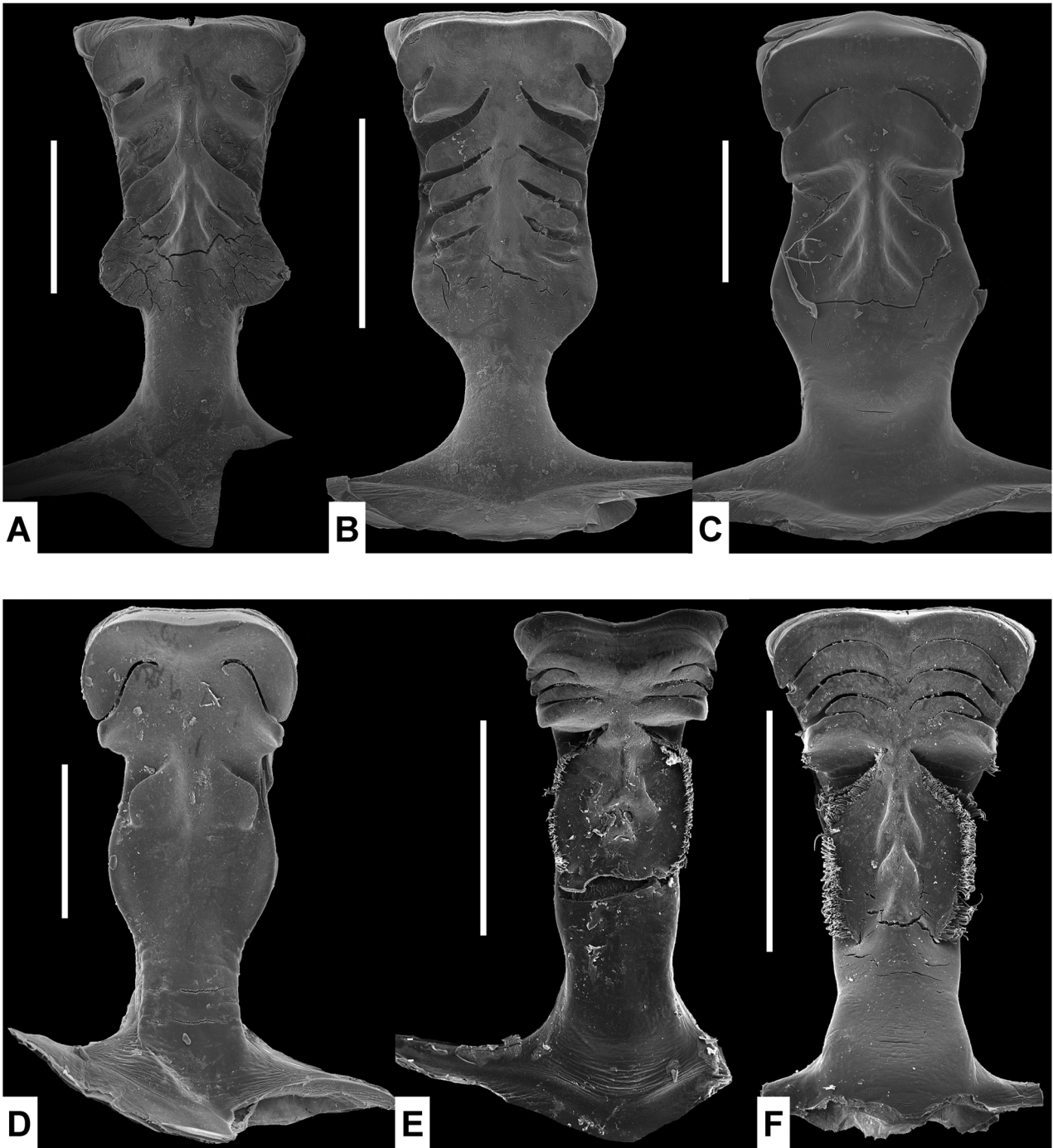


FIGURE 8. Urocardiac ossicles of *Uca tangeri* (A, NCHUZOOOL 13655, CW 26.9 mm, ♂), *U. stylifera* (B, NCHUZOOOL 13578, CW 21.9 mm, ♂), *U. acuta* (C, NCHUZOOOL 13665, CW 19.0 mm, ♂), *U. lactea* (D, NCHUZOOOL 13213, CW 15.4 mm, ♂), *U. tetragonon* (E, NCHUZOOOL 13666, CW 17.0 mm, ♀), and *U. vocans* (F, NCHUZOOOL 13667, CW 20.2 mm, ♂). A, B, E, F, scale = 10 mm; C, D, scale = 5 mm.

The gastric mill (especially the urocardiac ossicles) had recently become an important character in crab systematics, from familial to specific levels (Yang 1986; Beinlich & von Hagen 2006; Sakai *et al.* 2006; Allardyce & Linton 2010; Naderloo *et al.* 2010). The urocardiac ossicles of *Xeruca* are of the simple form, i.e. fewer transverse ridges of median teeth, especially those on the posterior tooth plate (Fig. 7). There are two transverse ridges of median teeth on the tooth plate, with additional weak and lower 2 to 3 cusps on the stem region, although this is not discernible on smaller individuals (e.g. CW 14.6 mm; Fig. 7C). Both subgenera *Afruca* and *Uca* are also characterized by possessing two transverse ridges of median teeth on the tooth plate (Fig. 8A, B; Franklin

Barnwell, personal communication). The number of transverse ridges on the tooth plate is variable for other subgenera (Naderloo *et al.* 2010; unpublished data), but some species that also have similar simple forms, e.g., *U. (Tubuca) acuta* (Stimpson, 1858) (Fig. 8C) and *U. (Australuca) lactea* (De Haan, 1835) (Fig. 8D). However, *Xeruca* can be distinguished from others by different shapes of ridges and the gaps not reaching to the central ridge, as well as variable numbers and shapes of cusps or transverse ridges on the stem region.

Although Crane (1975) placed *U. formosensis* under the same subgenus together with *U. tetragonon* and the *U. vocans* species complex, their urocardiac ossicles are totally different. Species of the subgenus *Gelasimus* have a unique setal structure on the lateral margins of the posterior stem region, with 4 to 5 transverse ridges on the tooth plate (e.g., *U. (Gelasimus) tetragonon*, Fig. 4E; *U. (G.) vocans* (Linnaeus, 1758), Fig. 4F; unpublished data), which are not seen in *Xeruca* (Fig. 7).

The G1 of *Xeruca* (Fig. 6) is similar to that of *U. (Gelasimus) tetragonon* and some members of *Tubuca* (e.g. *U. (Tubuca) arcuata* and the *U. (Tubuca) dussumieri* species complex) (Crane 1975: figs. 61, 63A, B), but can be separated by the broad and thickened inner process, bent obliquely forward at right angles in *Xeruca* (Fig. 6; Crane 1975: fig. 63C).

Uca (Xeruca) formosensis Rathbun, 1921

(Figs. 2–8)

Uca formosensis Rathbun, 1921: 155; Maki & Tsuchiya 1923: 205, pl. 23(4); Barnwell 1982: 79; Shih 1988: 105, fig. 9, pls. 11, 12; 1997: 68, figs. 5, 17, 41; 2000: 74, 4 unnumbered figs; Fukui *et al.* 1989: 227, fig. 3; Huang *et al.* 1989: 199, fig. 8, pl. 4D–F; Wang & Liu 1996a: 50, 1 unnumbered fig.; 1996b: 73, figs. 66–70; 1998: 73, figs. 66–70; 2003: 73, figs. 66–70; Ho & Hung 1997: 54; Shih *et al.* 1999: 164, figs. 1–4; Hung 2000: 140, fig. 440; Lee & Tung 2000: 34, 38, 7 unnumbered figs; Chen 2001: 202, fig. 637a, b; Lee 2001: 102, 3 unnumbered figs; Ng *et al.* 2001: 37; Rosenberg 2001: 848, 851, 860, 866; Shen & Jeng 2005: 164, 2 unnumbered figs; Beinlich & von Hagen 2006: 25; Wang 2009: 107–109, 2 unnumbered figs; Liu & Wang 2010: 37, 5 unnumbered figs; Lee *et al.* 2013: 68, 2 unnumbered figs.

Gelasimus formosensis—Sakai 1939: 620, text-fig. 94b, pl. 105(1); Horikawa 1940: 28; Lin 1949: 26.

Uca (Thalassuca) formosensis—Crane 1975: 83, fig. 63C, pl. 14A–D; Sakai 1976: 604, text-fig. 331; Su & Lue 1984: 64, fig. 5; Dai *et al.* 1986: 425, fig. 235, pl. 59(1); Dai & Yang 1991: 465, fig. 235, pl. 59(1); Shih 1994: 82, figs. 15, 16, 56–59; Ho 1996: 9, figs. 1–7.

Uca (Tubuca) formosensis—Ng *et al.* 2008: 242.

Material examined: holotype ♂ (28.8 mm), paratype ♂ (27.6 mm), USNM 54472, Rokko (= Lugang), Changhua, Taiwan, coll. Taihoku Normal School, Aug. 1919. **Others:** see Appendix 1. **Comparative material:** see Appendix 2.

DNA analyses and discussion. A 578 bp segment of the 16S, 658 bp segment of COI and 633 bp segment of 28S from 26 species of fiddler crabs were amplified and aligned (Table 1). The phylogenetic tree of the combined markers was reconstructed from Bayesian inference analysis, with the support values from the maximum likelihood analysis (Fig. 9). It is clear that most subgenera (including *Xeruca* **subgen. nov.**) are highly supported by both methods. *Xeruca* is sister to *Tubuca* and *Australuca*. While *Australuca* is monophyletic, *Tubuca* becomes paraphyletic. The “*Tubuca* + *Australuca*” clade, however, has high support. *Gelasimus* is sister to *Cranuca*, at least highly supported by Bayesian inference method. The clade of *Australuca* is monophyletic, has a high support value by Bayesian inference, with medium support by maximum likelihood. The American subgenus *Uca* is closely related to *Afruca* from eastern Atlantic.

After Crane (1975), the systematics of fiddler crabs has been revised by Rosenberg (2001) and Beinlich & von Hagen (2006), with the IWP broad-fronted groups studied by Shih *et al.* (2009a, 2013b) and Naderloo *et al.* (2010). *Uca formosensis* was established by Rathbun (1921), but only less than a dozen museum specimens could be examined until the 1980s (Crane 1975: 83; Barnwell 1982) and Crane mentioned it as an “elusive species.” Shih *et al.* (1999) revised and updated the taxonomy and morphology of the species, as well as adding ecological information after finding its preferred habitat, and examined more than 400 specimens. They suggested this species is closer to *Uca (Tubuca)*, instead of the original designation under *Uca (Thalassuca)* Crane, 1975 (= *Uca (Gelasimus)* Bott, 1973), but notes the need for more evidence to confirm the status. Rosenberg’s (2001) detailed morphological analyses on fiddler crabs also found that *U. formosensis* does not clearly belong to any of the known subgenera, although closer to *Tubuca* and *Australuca*.

TABLE 1. Haplotypes of 16S rDNA, COI and 28S rDNA for the subgenus *Xeruca subgen. nov.* and other related subgenera used in this study. See Material and methods for abbreviations of institutions.

Subgenus	Species	Locality	NCHUZOO catalog no. (unless indicated)	DDBJ Access. no. of 16S	DDBJ Access. no. COI	DDBJ Access. no. of 28S
<i>Xeruca subgen. nov.</i>	<i>U. formosensis</i>	Taiwan: Budai, estuary of Baijiang R., Chiayi	13742	LC053346	LC053363	LC053381
		Taiwan: Cingluo, Penghu	13770	LC053347	LC053364	LC053382
	<i>U. bellator</i>	Malaysia: Labuan, Sabah	13649	LC053348	LC053365	LC053383
	<i>U. elegans</i>	Australia: Lacrose I., West Australia	QM W21038	LC053349	LC053366	LC053384
	<i>U. longidigitum</i>	Australia: Hervey Bay, Queensland	QM W19274	LC053350	LC053367	LC053385
	<i>U. seismella</i>	Indonesia: West Papua	ZRC 2000.2059	AB813668	AB813685	AB813714
	<i>U. signata</i>	Australia: Hucks Landing, Queensland	QM W19211	LC053351	LC053368	LC053386
	<i>U. acuta</i>	Taiwan: estuary of Wujiang R., Kinmen	13650	LC053352	LC053369	LC053387
	<i>U. arcuata</i>	China: Dongzhai, Hainan	13363	AB813667	AB813684	AB813713
		South Korea: Ganghwa I., Incheon	13651	LC053353	LC053370	LC053388
<i>Gelasimus</i>	<i>U. coarctata</i>	Taiwan: Citou, Penghu	13231	LC053354	LC053371	LC053389
	<i>U. forcipata</i>	Malaysia: Johor	NTOU	LC053355	LC053372	LC053390
	<i>U. paradassumieri</i>	China: Dongzhai, Hainan	13381	LC053356	LC053373	LC053391
	<i>U. rosea</i>	Malaysia: Johor	NTOU	LC053357	LC053374	LC053392
	<i>U. urvillei</i>	Mayotte: Poroani	ZRC 1999.1107	LC053358	LC053375	LC053393
	<i>U. borealis</i>	Hong Kong	13207	LC053359	LC053376	LC053394
	<i>U. joceylinae</i>	Taiwan: Dulanwan, Taitung	NTOU	AB535392	AB535392	LC054955
	<i>U. vocans</i>	Philippines: Bohol	13205	AB535399	AB813683	AB813712
	<i>U. tetragonon</i>	Taiwan: Kenting, Pingtung	TMCD CHCD 526	AB535405	AB535431	LC053395
		Madagascar: Sarodrano	ZRC THH04-17	AB535405	LC053377	LC053396
<i>Cranuca</i>	<i>U. inversa</i>	Kenya: Gazi	MZUF 1024	AB813658	AB813674	AB813703
		Tanzania: Dar es Salaam	13255	AB471904	AB471917	AB813703
<i>Paraleptuca</i>	<i>U. crassipes</i>	Japan: Okinawa, Ryukyus	13467	AB813656	AB734656	AB813700
	<i>U. amulipes</i>	Thailand: Phuket	13258	AB471894	AB491161	AB813686
<i>Austruca</i>	<i>U. bengali</i>	Malaysia: Selangor	13575	AB813651	AB813672	AB813695
	<i>U. lactea</i>	Hong Kong	13250	AB471898	AB471912	AB813693
<i>Uca</i>	<i>U. triangularis</i>	Philippines: Cebu	13574	AB813650	AB813671	AB813694
	<i>U. major</i>	Bahamas: Pigeon Creek	13652	LC053360	LC053378	LC053397
<i>Afruca</i>	<i>U. stylifera</i>	Panama: Rodman	13578	LC053361	LC053379	LC053398
	<i>U. tangeri</i>	Spain: Puerto de Santa Maria, Cádiz	13585	AB813666	AB813682	AB813711
		Ghana: Elmina	13654	LC053362	LC053380	LC053399

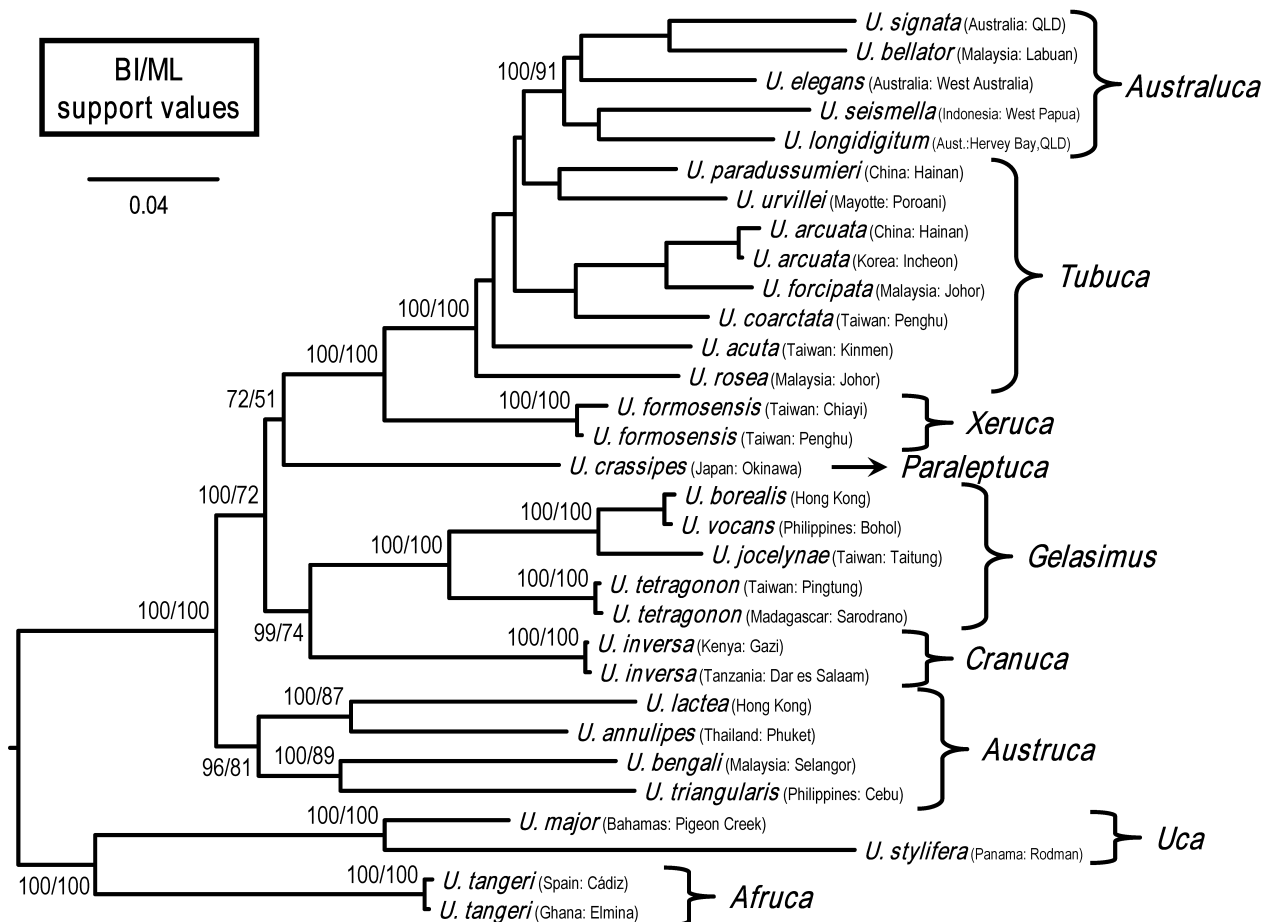


FIGURE 9. A Bayesian inference (BI) tree of *Xeruca* subgen. nov. and other related subgenera, based on the combined 16S rDNA, cytochrome oxidase subunit I genes (COI) and 28S rDNA. See Table 1 for details of the specimens. Probability values at the nodes represent support values for BI and maximum likelihood (ML).

The new subgenus of *Xeruca* is established herein for *Uca formosensis* based on a suite of morphological characters, including carapace, major chela, handedness, G1 and gastric mill, which are supported by the phylogenetic analyses using mitochondrial and nuclear markers. Previous studies on the morphology showed that *U. formosensis* is closer to *Tubuca* and *Australuca* (Shih *et al.* 1999; Rosenberg 2001), which is also revealed by the molecular evidence (Fig. 9). *Xeruca* can be easily separated from *Tubuca* by the carapace shape (Fig. 4) and the fingers of the chela (Fig. 5). Although *Xeruca* is more similar to *Australuca*, the latter can be distinguished by its smaller adult size, relatively shorter dorsolateral margins, and the possession of a longer gap between the closed fingers of the adult major chela (Figs. 4, 5).

The molecular evidence (Fig. 9) shows that the subgenera *Tubuca* and *Australuca* form an unresolved clade in conflict with the present taxonomy based on morphological characters (Crane 1975; Rosenberg 2001), although the *Australuca* species belong to their own clade. It is likely that *Australuca* Crane, 1975, is a synonym of *Tubuca* Bott, 1973. Further studies that include more species into the analysis may clarify the problem.

The morphology of gastric mills is related to different functions of feeding and seems unsuitable for phylogenetic study. This may be true for the lateral gastric teeth, but not for the foregut ossicles (Brösing & Türkay 2011), which has been reflected by other studies: e.g. Yang (1986) on various crabs, especially Macrophthamidae; Sakai *et al.* (2006) on the species of the *Helice* and *Chasmagnathus* complex; Brösing (2010) on several brachyuran families; and Naderloo *et al.* (2010) on the *Uca lactea* species complex. Based on the systematic study of the morphology of the gastric mills of IWP *Uca* species (in preparation), some groups have unique characters and could be used for the systematics of fiddler crabs. As mentioned above, there are several consistent characters for each of the following subgenera: *Gelasimus*, *Uca*, and *Afruca* (Fig. 8).

Uca formosensis was published in 1921, however, its systematic position was uncertain, either in *Uca*

(*Gelasimus*) (Crane 1975) or *Uca* (*Tubuca*) (Shih *et al.* 1999). The morphological analyses by Rosenberg (2001) have shown this species is substantially different from other species and should be placed in its own subgenus. According to the evidence of morphology and DNA sequences of this study, as well as the peculiar ecology and reproduction behavior (Shih *et al.* 2005), the establishment of a new subgenus *Xeruca* is appropriate to solve the uncertain position of this species.

The monotypic *Xeruca* becomes a subgenus with the narrowest distribution among the known subgenera of fiddler crabs. Its distribution restricted to Taiwan and the offshore Penghu Islands also implies the cladogenesis of this subgenus is related with the geological history of Taiwan Island during early Pliocene (reviewed by Shih *et al.* 2006, 2009b, 2011) and more studies are necessary to clarify it. Shih *et al.* (1999) have suggested this species to be included in the list of protected species of the Wildlife Conservation Law, R.O.C., because several habitats have been destroyed by industrial development, illegal fishing ponds, and mangrove overgrowth (Fig. 1; Shih *et al.* 1999). However, this species has not been considered as a protected species yet, although some populations of *U. formosensis* have been under different pressures, e. g. the Penghu population has become extinct in 2008 after the inappropriate replanting of introduced mangroves for about 15 years; and an unthoughtful ecological engineering on the habitat of Shengang, Changhua in 2006 nearly exterminated the local population (Shih 2008a, b). The conservation policy and management for *U. formosensis* have to be reconsidered by government of Taiwan, because it is not only an endemic species to Taiwan, but also an endemic subgenus of fiddler crabs.

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APPENDIX 1. Other specimens of *Uca formosensis* examined

New Taipei City: Jhuwei. 5 ♂♂ (22.5–27.5 mm), NCHUZOO 13755, coll. H.-T. Shih, 17 May 1996; 4 ♂♂ (25.6–27.6 mm), NCHUZOO 13753, 13754, 13759, 13760, 2 ♀♀ (19.3–23.1 mm), NCHUZOO 13757, 13758, 1 ovig. ♀ (25.9 mm), NCHUZOO 13756, coll. H.-T. Shih, 20 Aug. 1996. **Hsinchu City: Jinshuei.** 3 ♂♂ (26.9–29.6 mm), NCHUZOO 13707, coll. H.-T. Shih, 4 Nov. 1995. **Haishangu.** 7 ♂♂ (10.2–34.4 mm), 3 ♀♀ (19.2–28.7 mm), NCHUZOO 13708, coll. H.-T. Shih, 5 Jan. 1996; 1 ovig. ♀ (27.9 mm), NCHUZOO 13909, coll. H.-T. Shih, 8 Apr. 1996; 1 ♂ (26.5 mm), 1 ovig. ♀ (28.5 mm), NCHUZOO 13709, 1 ♂ (31.1 mm), 1 ♀ (20.9 mm), NCHUZOO 13710, coll. H.-T. Shih, 20 June 1996; 10 ♂♂ (19.6–

31.5 mm), NCHUZOO 13711, 13712, 13718, 13720, 13722, 13728, 13731, 13734, 13736, 13739, 1 ♀ (27.7 mm), NCHUZOO 13721, 9 ♀♀ (19.4–31.4 mm), NCHUZOO 13713, 13716, 13717, 13719, 13724, 13732, 13733, 13735, 13740, coll. H.-T. Shih, 19 Aug. 1996; 3 ♂♂ (27.6–28.7 mm), NCHUZOO 13714, 13715, 13730, coll. H.-T. Shih, 20 Aug. 1996; 3 ♂♂ (21.5–30.8 mm), 2 ♀♀ (13.8–15.8 mm), NCHUZOO 13726, coll. H.-T. Shih, 28 Oct. 1996; 2 ♂♂ (23.4–25.3 mm), NCHUZOO 13725, coll. H.-T. Shih, 1 Jan. 1997; 1 ♂ (25.9 mm), 1 ♀ (28.1 mm), NCHUZOO 13729, 1 ♀ (25.1 mm), NCHUZOO 13727, coll. H.-T. Shih, 1 Mar. 1997; 2 ♂♂ (29.7–31.2 mm), NCHUZOO 13861, 13867, 1 ♀ (31.9 mm), NCHUZOO 13868, coll. by students*, 29 Oct. 2004; 1 ♀ (19.5 mm), NCHUZOO 13723, coll. by students, 10 Aug. 2005; 3 ♂♂ (21.3–28.8 mm), 2 ♀♀ (19.6–26.0 mm), NCHUZOO 13853, coll. by students, 15 Mar. 2006; 6 ♂♂ (9.5–30.9 mm), NCHUZOO 13862, coll. by students, 17 Mar. 2006; 2 ♂♂ (30.8–31.7 mm), 2 ♀♀ (26.3–27.1 mm), NCHUZOO 13851, coll. by students, 30 Mar. 2006; 2 ♂♂ (27.1–27.9 mm), NCHUZOO 13673, 2 ♂♂ (26.1–27.3 mm), 1 ♀ (18.6 mm), NCHUZOO 13864, 3 ♂♂ (27.2–29.0 mm), NCHUZOO 13911, coll. by students, 31 Mar. 2006; 7 ♂♂ (11.4–30.7 mm, 2 damaged), NCHUZOO 13854, 1 ♂ (24.6 mm), 1 ♀ (20.7 mm), NCHUZOO 13892, coll. by students, 15 May 2006; 6 ♂♂ (25.5–29.9 mm), NCHUZOO 13859, coll. by students, 12 June 2006; 3 ♂♂ (28.1–30.3 mm), 1 ♀ (25.0 mm), NCHUZOO 13847, coll. by students, 27 July 2006; 2 ♂♂ (26.5–30.3 mm), NCHUZOO 13874, coll. by students, 8 Aug. 2006; 3 ♂♂ (26.2–29.4 mm), NCHUZOO 13848, coll. by students, 25 Aug. 2006; 4 ♂♂ (22.2–26.8 mm), 1 ♀ (20.4 mm), NCHUZOO 13855, coll. by students, 25 Sep. 2006; 3 ♂♂ (22.3–32.0 mm), NCHUZOO 13860, coll. by students, 23 Oct. 2006; 2 ♂♂ (22.9–26.7 mm), NCHUZOO 13902, coll. by students, 5 Nov. 2006; 1 ♂ (30.9 mm), NCHUZOO 13901, coll. by students, 15 Mar. 2007; 1 ♂ (30.7 mm), NCHUZOO 13908, coll. by students, 6 May 2007; 1 ♂ (22.0 mm), 1 ♀ (28.3 mm), NCHUZOO 13896, coll. by students, 14 July 2007; 3 ♂♂ (21.1–22.0 mm, 1 damaged), NCHUZOO 13865, coll. by students, 13 Aug. 2007; 4 ♂♂ (10.9–28.4 mm), 2 ♀♀ (14.1–25.7 mm), NCHUZOO 13852, coll. by students, 14 Aug. 2007; 2 ♂♂ (25.1–31.0 mm), 1 ♀ (32.2 mm), NCHUZOO 13849, coll. by students, 11 Sep. 2007; 2 ♂♂ (21.9–29.8 mm), NCHUZOO 13876, coll. by students, 13 Sep. 2007; 6 ♂♂ (20.5–32.8 mm, 2 damaged), 4 ♀♀ (18.9–31.8 mm), NCHUZOO 13856, 1 ♂ (30.8 mm), NCHUZOO 13737, coll. by students, 11 Oct. 2007; 1 ♂ (29.8 mm), 2 ♀♀ (28.6 mm, 1 damaged), NCHUZOO 13877, coll. by students, 13 Oct. 2007; 1 ♂ (23.2 mm), NCHUZOO 13738, coll. by students, 24 Oct. 2007; 2 ♂♂ (27.4–27.7 mm), NCHUZOO 13850, coll. by students, 10 Dec. 2007; 1 ♀ (27.7 mm), NCHUZOO 13870, coll. by students, 22 Feb. 2008. **Taichung City: Gaomei.** 1 ♂ (23.1 mm), NCHUZOO 13880, coll. by students, 27 Aug. 2007; 1 ♂ (21.2 mm), NCHUZOO 13748, coll. by students, 16 Feb. 2011. **Changhua County: Shengang.** 1 ♂ (19.7 mm), NCHUZOO 13845, coll. H.-T. Shih, 22 Dec. 1995; 1 ♂ (21.4 mm), NCHUZOO 13830, coll. H.-T. Shih, 28 Dec. 1995; 1 ♂ (29.6 mm), 1 ♀ (23.8 mm), NCHUZOO 13672, coll. H.-T. Shih, 22 June 1996; 1 ♂ (29.2 mm), 1 ♀ (21.6 mm), NCHUZOO 13806, 1 ♂ (27.1 mm), NCHUZOO 13808, 1 ♂ (28.0 mm), NCHUZOO 13809, 1 ♀ (23.5 mm), NCHUZOO 13819, 1 ♂ (27.5 mm), 1 ♀ (22.2 mm), NCHUZOO 13820, 1 ♂ (26.8 mm), 1 ♀ (24.5 mm), NCHUZOO 13821, 1 ♂ (29.0 mm), 1 ♀ (21.2 mm), NCHUZOO 13846, coll. H.-T. Shih, 9 July 1996; 1 ♂ (33.1 mm), NCHUZOO 13668, 1 ♂ (33.0 mm), 1 ♀ (22.9 mm), NCHUZOO 13671, 1 ♂ (31.0 mm), 1 ♀ (22.4 mm), NCHUZOO 13829, 1 ♂ (32.2 mm), 1 ♀ (22.4 mm), NCHUZOO 13832, coll. H.-T. Shih, 10 July 1996; 1 ♂ (28.3 mm), 2 ♀♀ (14.2–15.8 mm), NCHUZOO 13669, coll. H.-T. Shih, 11 July 1996; 3 ♂♂ (27.1–32.5 mm), 1 ♀ (30.7 mm), NCHUZOO 13807, 13816, 13818, 13823, coll. H.-T. Shih, 15 July 1996; 1 ♂ (24.3 mm), NCHUZOO 13817, coll. H.-T. Shih, 16 July 1996; 1 ♂ (28.1 mm), 1 ♀ (21.5 mm), NCHUZOO 13815, 1 ♂ (26.6 mm), NCHUZOO 13822, 1 ♂ (28.1 mm), 1 ♀ (20.5 mm), NCHUZOO 13824, coll. H.-T. Shih, 21 July 1996; 1 ♂ (30.3 mm), NCHUZOO 13799, coll. H.-T. Shih, 22 July 1996; 30 ♂♂ (22.4–34.9 mm), NCHUZOO 13788, 13789, 13790, 13791, 13792, 13793, 13794, 13795, 13796, 13797, 13800, 13801, 13802, 13803, 13804, 13805, 13810, 13811, 13812, 13813, 13814, 13826, 13827, 13828, 13831, 13833, 13834, 13835, 13836, 13837, 1 ♂ (damaged), NCHUZOO 13843, 1 ♀ (25.4 mm), NCHUZOO 13798, 3 ♂♂ (24.3–28.3 mm), NCHUZOO 13844, coll. H.-T. Shih, 19 Aug. 1996; 1 ♀ (28.4 mm), NCHUZOO 13787, coll. H.-T. Shih, 24 Oct. 1996; 1 ♂ (31.1 mm), NCHUZOO 13825, coll. H.-T. Shih, 30 Nov. 1996; 1 ♂ (20.8 mm), NCHUZOO 13841, coll. H.-T. Shih, 14 Sep. 2005; 2 ♂♂ (21.0–22.1 mm), NCHUZOO 13838, 13842, coll. by students, 15 Sep. 2005; 1 ♂ (25.5 mm), NCHUZOO 13839, coll. by students, 20 Sep. 2005; 1 ♂ (23.9 mm), NCHUZOO 13840, coll. by students, 7 Oct. 2005; 1 ♂ (26.5 mm), NCHUZOO 13889, coll. by students, 13 May 2006; 1 ♂ (26.6 mm), NCHUZOO 13893, coll. by students, 21 Apr. 2007. **Lugang.** 6 ♂♂ (12.4–32.4 mm), TMCD, coll. H.-C. Liu, 24 May 1994. **Fangyuan.** 2 ♂♂ (20.2–24.4 mm), NCHUZOO 13747, coll. H.-T. Shih, 24 Oct. 1996. **Yunlin County: Mailiao.** 1 ♂ (31.3 mm), NCHUZOO 13866, coll. by students, Apr. 2008; 1 ♀ (23.0 mm), 1 ♀ (21.6 mm), NCHUZOO 13888, 13894, coll. by students, 27 Apr. 2008; 1 ♀ (21.9 mm), NCHUZOO 13890, coll. by students, 12 May 2008; 1 ♀ (25.8 mm), NCHUZOO 13751, coll. by students, 26 May 2008; 2 ♂♂ (24.2–28.7 mm), NCHUZOO 13875, 13904, 2 ♀♀ (18.3–24.8 mm), NCHUZOO 13903, 13906, coll. by students, 10 June 2008; 1 ♂ (22.6 mm), NCHUZOO 13863, 2 ♀♀ (17.5–18.1 mm), NCHUZOO 13881, 13897, coll. by students, 9 July 2008; 4 ♀♀ (18.5–26.9 mm), NCHUZOO 13879, 13898, 13900, 13905, coll. by students, 7 Aug. 2008; 1 ♂ (17.3 mm), NCHUZOO 13751, coll. by students, 1 Sep. 2008; 1 ♂ (30.2 mm), NCHUZOO 13873, coll. by students, 6 Sep. 2008; 1 ♀ (27.9 mm), NCHUZOO 13887, coll. by students, 22 Sep. 2008; 1 ♀ (22.9 mm), NCHUZOO 13882, coll. by students, 20 Oct. 2008; 2 ♀♀ (19.1–27.3 mm), NCHUZOO 13884, 13891, coll. by students, 21 Apr. 2010; 1 ♂ (29.0 mm), NCHUZOO 13883, coll. by students, 30 May 2010; 2 ♂♂ (29.7 mm, 1 damaged), NCHUZOO 13749, 13750, 1 ♀ (26.2 mm), NCHUZOO 13670, coll. by students, 2 June 2011. **Chiayi County: Dongshih.** 2 ♂♂ (21.0–21.7 mm), 3 ♀♀ (15.8–21.4 mm), NCHUZOO 13778, coll. H.-T. Shih, 17 Mar. 1996; 1 ovig. ♀ (21.3 mm), NCHUZOO 13910, coll. H.-T. Shih, 30 Mar. 1996; 3 ♂♂ (22.8–31.2 mm, 1 damaged), NCHUZOO 13774, 13776, 13779, 2 ♂♂ (13.2–18.2 mm), 1 ♀ (18.9 mm), NCHUZOO 13777, coll. H.-T. Shih, 30 May 1996; 4 ♂♂ (20.0–27.2 mm), NCHUZOO 13773, 4 ♂♂ (12.8–19.5 mm), NCHUZOO 13775, 5 ♂♂ (21.6–23.4 mm), NCHUZOO 13780, 13781, 13782, 13783, 13785, 3 ♀♀ (13.2–20.2 mm), NCHUZOO

13775, 1 ♀ (18.6 mm), NCHUZOOOL 13784, 2 ♂♂ (12.8–20.8 mm), 5 ♀♀ (12.1–18.0 mm), NCHUZOOOL 13899, coll. H.-T. Shih, 6 Aug. 1996; 2 ♂♂ (24.9–25.4 mm), NCHUZOOOL 13871, coll. by students, 28 July 2006; 2 ♂♂ (21.6–23.6 mm), 1 ♀ (damaged), NCHUZOOOL 13885, coll. by students, 6 Nov. 2006. **Budai.** 7 ♂♂ (20.5–28.8 mm), 6 ♀♀ (18.9–23.2 mm), NCHUZOOOL 13741, 13741, 13742, 13743, 13744, 13745, 13746, 13869, 13872, 13878, 13886, 13895, coll. H.-T. Shih, 30 Mar. 1996. **Chiayi tidal land.** 1 ♂ (29.1 mm), NCHUZOOOL 13786, 30 Aug. 1965. **Tainan City: Cigu.** 1 ♂ (28.1 mm), NCHUZOOOL 13674, 1 ♀ (21.5 mm), NCHUZOOOL 13675, coll. H.-T. Shih, 23 Jan. 1996; 1 ♂ (21.5 mm), NCHUZOOOL 13676, 1 ♂ (damaged), NCHUZOOOL 13677, coll. H.-T. Shih, 31 May 1996; 4 ♂♂ (19.3–29.7 mm), NCHUZOOOL 13680, 16 ♀♀ (15.7–25.5 mm, 1 damaged), NCHUZOOOL 13678, 2 ♀♀ (23.2–27.9 mm), NCHUZOOOL 13679, coll. H.-T. Shih, 29 June 1996; 9 ♂♂ (22.8–31.5 mm), NCHUZOOOL 13681, 13684, 13685, 13687, 13691, 13692, 13693, 13694, 13695, 5 ♀♀ (21.3–24.9 mm), NCHUZOOOL 13682, 13683, 13688, 13689, 13690, 1 ovig. ♀ (18.4 mm), NCHUZOOOL 13686, coll. H.-T. Shih, 05 Aug. 1996; 1 ♂ (21.0 mm), NCHUZOOOL 13696, coll. H.-T. Shih, 25 Aug. 1996; 3 ♂♂ (17.3–23.6 mm), NCHUZOOOL 13697, 13698, 13699, coll. H.-T. Shih, 17 Sep. 1996; 7 ♂♂ (19.7–31.8 mm), NCHUZOOOL 13907, 5 ♀♀ (20.1–29.5 mm), 3 ♀♀ (18.6–19.4 mm), NCHUZOOOL 13701, coll. H.-T. Shih, 21 Oct. 1996; 1 ♂ (30.3 mm), 1 ♀ (25.1 mm), NCHUZOOOL 13702, 1 ♀ (23.6 mm), NCHUZOOOL 13703, 3 ♂♂ (30.9–31.6 mm), NCHUZOOOL 13857, coll. H.-T. Shih, 27 Apr. 2006; 4 ♂♂ (28.1–30.9 mm), NCHUZOOOL 13858, coll. H.-T. Shih, 03 June 2007. **Cingcaolun.** 1 ♂ (31.0 mm), NCHUZOOOL 13704, coll. H.-T. Shih, 26 Sep. 1994; 7 ♂♂ (18.9–27.5 mm), 2 ♀♀ (21.4–22.2 mm), NCHUZOOOL 13705, coll. H.-T. Shih, 23 Jan. 1996; 2 ♂♂ (21.0–21.9 mm), NCHUZOOOL 13706, coll. H.-T. Shih, 29 Mar. 1996; **Penghu: Cingluo.** 7 ♂♂ (22.3–28.6 mm, 1 damaged), NCHUZOOOL 13762, 13763, 13765, 13767, 13768, 13770, 13771, coll. H.-T. Shih, 14 Aug. 1996; 6 ♂♂ (26.6–32.0 mm), NCHUZOOOL 13761, 13764, 13766, 13769, 13772, coll. H.-T. Shih, 15 Aug. 1996. (*students from the author's laboratory)

APPENDIX 2. Comparative material examined.

Uca acuta: 1 ♂ (19.0 mm), NCHUZOOOL 13665, Amoy, Fujian, China, coll. H.-T. Shih & J.-H. Lee, 1 July 2004; 1 ♂ (18.8 mm), NCHUZOOOL 13650, estuary of Wujiang R., Kinmen, Taiwan, coll. J.-H. Lee, 21 May 2005. *Uca annulipes*: 1 ♀ (12.3 mm), NCHUZOOOL 13258, Phuket, Thailand, coll. H.-T. Shih, 5 Apr. 1995. *Uca arcuata*: 1 ♂ (38.2 mm), NCHUZOOOL 13660, Shengang, Changhua, Taiwan, coll. H.-T. Hung, 5 Aug. 2002; 1 ♀ (36.8 mm), NCHUZOOOL 13363, Dongzhai, Hainan, China, coll. H.-T. Shih & J.-H. Lee, 23 June 2004; 1 ♀ (25.2 mm), NCHUZOOOL 13651, Ganghwa I., Incheon, South Korea, coll. K. Kim, July 2005. *Uca bellator*: 1 ♂ (18.7 mm), NCHUZOOOL 13653, 1 ♂ (16.2 mm), NCHUZOOOL 13649, Labuan, Malaysia, coll. H.-T. Shih, 24 July 2010. *Uca bengali*: 1 ♂ (8.0 mm), NCHUZOOOL 13575, Selangor, Malaysia, coll. H.-T. Shih, 10 Feb. 2009. *Uca borealis*: 1 ♂ (22.4 mm), NCHUZOOOL 13207, Hong Kong, coll. B.K.K. Chan, July 2004. *Uca coarctata*: 1 ♀ (1.0 mm), NCHUZOOOL 13231, Citou, Penghu, Taiwan, coll. H.-T. Shih & Y.-H. Wang, 19 May 2007. *Uca crassipes*: 1 ♂ (damaged), NCHUZOOOL 13467, Okinawa, Ryukyus, Japan, Feb. 2002. *Uca elegans*: 1 ♂ (19.5 mm), QM W21038, Lacrosse I., West Australia, Australia, coll. J. Short, 20 Nov. 1995. *Uca forcipata*: 1 ♂ (30.9 mm), NTOU, Johor, Malaysia, coll. P.-H. Ho, 19 July 2001. *Uca inversa*: 1 ♂ (18.2 mm), NCHUZOOOL 13255, Dar es Salaam, Tanzania, 20 Sep. 2006; MZUF 1024 (specimen not examined, only for DNA study), Gazi, Kenya. *Uca jocelynae*: holotype, 1 ♂ (21.7 mm), NMNS 6177-001, Cingluo, Penghu, Taiwan, coll. H.-T. Shih, 26 June 2006; 1 ♂ (20.2 mm), NTOU, Dulanwan, Taitung, Taiwan, coll. P.-H. Ho, 7 Apr. 2001. *Uca lactea*: 1 ♂ (15.4 mm), NCHUZOOOL 13213, Shengang, Changhua, Taiwan, coll. H.-T. Hung, 23 July 2003; 1 ♂ (12.0 mm), NCHUZOOOL 13250, Hong Kong, coll. B.K.K. Chan, July 2004. *Uca longidigitum*: 1 ♂ (16.1 mm), QM W19274, Hervey Bay, Queensland, Australia, coll. P. Davie *et al.*, 25 Oct. 1993; 1 ♂ (16.7 mm), NCHUZOOOL 13656, Serpentine Creek, Queensland, Australia, coll. B. Campbell *et al.*, Oct. 1972. *Uca major*: 1 ♀ (16.8 mm), NCHUZOOOL 13652, Pigeon Creek, Bahamas, coll. A. Curran *et al.*, Feb. 2011. *Uca paradussumieri*: 1 ♂ (33.7 mm), NCHUZOOOL 13381, Dongzhai, Hainan, China, coll. H.-T. Shih & J.-H. Lee, 23 June 2004. *Uca princeps*, 1 ♂ (35.5 mm), SMF 13164, Puerto Pizarro, Tumbes, Peru, coll. M. Clüsener-Godt, 17 May 1984. *Uca rosea*: 1 ♂ (26.3 mm), NTOU, Johor, Malaysia, coll. P.-H. Ho, 19 July 2001. *Uca seismella*: ZRC 2000.2059 (specimen not examined, only for DNA study), West Papua, Indonesia. *Uca signata*: 1 ♂ (17.5 mm), QM W19211, Hucks Landing, Queensland, Australia, coll. P. Davie *et al.*, 28 Oct. 1993. *Uca stylifera*: 1 ♂ (21.9 mm), NCHUZOOOL 13578, Rodman, Panama, coll. J. Christy, 2008. *Uca tangeri*: 1 ♂ (26.9 mm), NCHUZOOOL 13655, 1 ♀ (31.3 mm), NCHUZOOOL 13585, Puerto de Santa María, Cádiz, Spain, coll. P. Fernández, 23 May 2007; 1 ♂ (17.8 mm), NCHUZOOOL 13654, Elmina, Ghana, coll. C.D. Schubart & K. Duffner, 4 July 2007. *Uca tetragonon*: 1 ♀ (17.0 mm), NCHUZOOOL 13666, Shanyuan, Taitung, Taiwan, coll. by students, 29 May 2004; 1 ♂ (12.8 mm), TMCD CHCD 526, Kenting, Pingtung, Taiwan, coll. H.-C. Liu & C.-H. Wang, 23 Sep. 1994; 1 ♂ (18.3 mm), NCHUZOOOL 13664, Dongsha I., Kaohsiung, Taiwan, coll. H.-T. Shih, 22 Mar. 2012; 1 ♂ (23.7 mm), ZRC THH04-17, Sarodrano, Madagascar, coll. H.H. Tan, 31 Jan.–9 Feb. 2004. *Uca triangularis*: 1 ♂ (12.4 mm), NCHUZOOOL 13574, Cebu, Philippines, coll. L. Liao *et al.*, 2 Sep. 2003. *Uca urvillei*: 1 ♂ (30.1 mm), NCHUZOOOL 13661, Ranong, Thailand, coll. H.-T. Shih, 27 May 2012; 1 ♂ (29.7 mm), ZRC 1999.1107, Poroani, Mayotte, 23 July 1998. *Uca vocans*: 1 ♂ (20.2 mm), NCHUZOOOL 13667, 1 ♂ (23.1 mm), NCHUZOOOL 13205, Bohol, Philippines, coll. H.-T. Shih, 2 Sep. 2003.