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Morphology of *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae), an Endemic Fiddler Crab from Taiwan, with Notes on its Ecology

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Hsi-Te Shih, Hin-Kiu Mok, Hsueh-Wen Chang and Sin-Che Lee (1999) Morphology of *Uca formosensis* Rathbun, 1921 (Crustacea: Decapoda: Ocypodidae), an endemic fiddler crab from Taiwan, with notes on its ecology. *Zoological Studies* **38**(2): 164-177. *Uca formosensis* Rathbun, 1921, is an endemic fiddler crab species from Taiwan. The taxonomy of this species has long been constrained by the paucity of study material. Crane (1975) placed *U. formosensis* as a member of the subgenus *Thalassuca*, but important characters, like its handedness, presence of enlarged teeth on the fingers of the female's minor chela, structures of the anterolateral margin, suborbital margin, orbital floor, degree of arching of the carapace, and habitat preference, suggest that this classification is incorrect. It is suggested that *U. formosensis* should be excluded from the subgenus *Thalassuca*. In this study, a historic review is provided of the species and notes on its distribution, variation of morphology (chela types), live coloration, and taxonomy are included.

Key words: Handedness, Chela type, Coloration, Distribution, Study history.

The fiddler crab *Uca formosensis* Rathbun, 1921, is one of the few endemic species of marine crabs known from Taiwan and Penghu Island (the Pescadores). However, the species is not well known, despite many reports about it. Previous reports of this species are almost wholly taxonomic, and in those which include ecological and/or distributional information, data are either too brief or incorrect, for example, studies on its handedness (Barnwell 1982), the structure of the minor cheliped of the female (Crane 1975), and the construction of its burrow and habitat (Crane 1975). Morphological variation in this species is also not well reported. Considering the endemicity of *U. formosensis*, there is a need to better understand the taxonomy of this species as well as to ascertain its ecological habitats and distribution.

In the present paper, the distribution and morphological characters of *U. formosensis* are revised. Related ecological and behavioral studies on *U. formosensis* will be published elsewhere.

HISTORIC REVIEW

Uca formosensis was first found in 1918 at Lukang (as Rokko) by Moichiro Maki. Subsequently Masamitsu Oshima of the Institute of Science, Government of Formosa, sent specimens collected in 1919 at Lukang by students of Taihoku Normal School to Mary J. Rathbun of the US National Museum for identification. This information was published as a new species *Uca formosensis* in 1921. An important monograph on the crustacean fauna of Taiwan was published in 1923 by M. Maki and Kwan Tsuchiya. In this monograph, *U. formosensis* was recorded in Ilan, Yungan (as Hsinchuangtzu), and Lukang. Photographs of *U. formosensis* and its ma-

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jor cheliped were also provided (Maki and Tsuchiya 1923: pl. 23 (4), Shih 1997: fig. 2). The early naturalist, Sadae Takahasi, who had extensively studied the behavior and ecology of estuarine crabs of Taiwan, surveyed the littoral animals near the estuary of Tanshui (as Tamsui) and studied the behavior and ecology, including the burrow characteristic, of the fiddler crabs there (Takahasi 1934a,b 1935). He noted that *U. formosensis* lived in muddy beaches with clayey mud and "vegetation", and that the aggressiveness of *U. formosensis* was pronounced. He also reported *U. formosensis* from Keelung (Takahasi 1934c). Another naturalist, Hayao Sato, also found *U. formosensis* at Anping (Sato 1936a,b). Tune Sakai (1939) recorded *U. formosensis* at Tanshui on the basis of specimens collected by S. Takahasi. Yasuiti Horikawa (1940) listed all the crab species previously reported from Taiwan and also collected *U. formosensis* specimens at Lukang.

Chao-Chi Lin (1949) also listed the crab fauna of Taiwan and recorded specimens of *U. formosensis* from Lukang and Penghu (as the Pescadores). Wu et al. (1962) reported a female specimen of "*U. formosensis*" from Tanshui. According to the text, however, it was apparently actually a female *U. arcuata*!

Jocelyn Crane came to Taiwan once from late April to May 1963 (Crane 1975: 47, 295, 297, 474, 500, 662). She stayed at Tanshui to observe and collect fiddler crabs, including *U. lactea lactea* (de Haan, 1835), *U. arcuata* (de Haan, 1835), and *U. vocans borealis* Crane, 1975, but failed to find *U. formosensis* there (Crane 1975: 83). The *U. formosensis* that Crane examined in her monograph (1975) were the specimens collected at Lukang (as Rokko) (2 males and 1 female) and Ilan (as Giran) (1 male) by students of Taihoku Normal School and which were originally sent to M. J. Rathbun, as well as specimens collected at Tanshui (as Tamsui) (2 males and 1 female) by S. Takahasi which were sent to Crane as a gift by T. Sakai after she went to Japan (Sakai 1939: 620, Crane 1975: 597, Sakai 1981). As field data accumulated about *U. formosensis* were very scarce, Crane could not provide details about the biology of this species in her monograph (1975: 83, 84).

Sakai (1976) included *U. formosensis* in his monograph using his previous material (Sakai 1939). Barnwell (1982) compared the handedness of 3 *Uca* species of the subgenus *Thalassuca* Crane, 1975: *U. tetragonon* (Herbst, 1790), *U. vocans*, and *U. formosensis*. The subject material of *U. formosensis* studied was from the Smithsonian Institution, National Museum of Natural History, Washington, D.C. which had been examined by Crane (1975). Hung-Jen Su and Kuang-Yang Lue (1984) listed crab species found in the mangrove swamp of Chuwei on the northern bank of the Tanshui River and reported that *U. formosensis* was rare in the area. Pao-Lien Chang (1984) recorded *U. formosensis* at Tanshui, Sanhsingchiao (near Haishanku), Fangyuan, and Tungshih. Ai-Yun Dai, Si-Liang Yang, Yu-Zhi Song, and Guo-Xiao Chen (1986), and A-Y Dai and S-L Yang (1991) examined specimens of *U. formosensis* in the Smithsonian Institution. Hsi-Te Shih (1988) found that *U. formosensis* was very abundant at Shenkang in the southern area of the estuary of the Tatu Creek. Jung-Fu Huang, Hsiang-Ping Yu, and Masatsune Takeda (1989) described the fiddler crabs collected from Taiwan, with their collection localities for *U. formosensis* including the Lanyang Creek, Wuchi, and Chiku. Yasuo Fukui, Keiji Wada, and Chia-Hsiang Wang (1989) collected specimens of *U. formosensis* at Shenkang and Peimen. Syau-Yi Li (1991) studied the behavior and ecology of *U. formosensis* at Shenkang. Jin-Taur Shih, K.-Y. Lue, and C.-H. Wang (1991) studied the crab fauna at Chuwei, the same place examined by Su and Lue (1984), and found that *U. formosensis* was rare there. Jong-Shin Wu (1992) studied the fauna at Haishanku and recorded *U. formosensis* there. H.-T. Shih (1994) reviewed the history of fiddler crab studies in Taiwan and provided many color photographs of *U. formosensis*. Hung-Chang Liu and Chia-Wei Li (1994) studied the crab fauna at Hsiangshan (including Haishanku), Hsinchu City and found that *U. formosensis* was patchily distributed in this area. H.-T. Shih (1997) provided a preliminary report about the natural history of *U. formosensis* and found that most habitats of *U. formosensis* were facing developmental pressures and overgrowing mangroves.

MATERIALS AND METHODS

All recorded localities of *U. formosensis*, and other possible habitats around the islands of Taiwan, Penghu and Lanyu (Orchid Island) were surveyed by the 1st author during September 1994 to April 1997. *U. formosensis* is active on mudflats during low tide of the spring tide period, but remains hidden in burrows during the neap tide. Localities of *U. formosensis* can also be identified by the typical large chimneys built by males (sometimes females) during neap tide periods in the reproductive season (Shih 1997). Most specimens were obtained by digging, while others were captured by use of traps (Wolfrath

1993). The Chinese location names with English names are shown in the Appendix.

Carapace width (CW), propodus length (PL), color pattern, handedness, and chela type (brachy- or lepto-chelous chela) of these specimens were recorded. The brachychelous chela is a short chela with teeth on the cutting margin, while a leptochelous one has a long chela without teeth on the cutting margin. Individuals whose chela has 1 leptochelous finger and 1 brachychelous finger are considered as leptochelous. In addition, individuals whose finger tip is broken are considered as brachychelous, if the finger has a tooth. Specimens were illustrated with the help of a drawing tube attached to a Carl Zeiss Jena stereo microscope. The morphological terminology follows Crane (1975) and Jones and Morton (1994). Some (n = 226) specimens were dissected to obtain tissues for allozyme analysis, and the remains were preserved in a −70 °C freezer. Chelipeds, gonopods, and gonopores were kept intact. Other specimens (n = 201) were preserved in 70% ethyl alcohol, catalogued, and deposited at the Institute of Marine Biology, National Sun Yat-sen University (NSYSU). Materials deposited at the Taiwan Museum (TMCD), Taipei, Taiwan, were also examined for comparison.

The procedures of Felgenhauer (1987) using scanning electron microscopy (SEM) to observe the gonopod and gonopore were used as modified. The right gonopod of males and the right gonopore of females were dissected, cleaned in an ultrasonic bath, and dehydrated in an ascending ethanol series. They were dried with liquid carbon dioxide in a critical point drier (Hitachi Model HCP-2) and coated with gold in an ion sputter (Hitachi Model E101). Observations were made with a scanning electron microscope (Hitachi Model S-2400) at accelerating voltages of 10-15 kV.

RESULTS

Family Ocypodidae Ortmann, 1894
Genus *Uca* Leach, 1814
Uca formosensis Rathbun, 1921
(Figs. 1, 2, 3, 4)

Uca formosensis Rathbun, 1921: 155 (type locality: Lukang, Changhua County, Taiwan); – Maki and Tsuchiya 1923: 205, pl. 23 (4); Barnwell 1982: 79; Shih 1988: 105, fig. 9, pls. 11-12; Huang et al. 1989: 199, fig. 8, pl. 4D-F; Fukui et al. 1989: 227, fig. 3; Wang and Liu 1996a: 54; 1996b: 73, figs. 66-70; Shih 1997: 68, figs. 5, 17-22, 41; Ho and Hung 1997: 54.

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 and Lue 1984: 64, fig. 5; Dai et al. 1986: 425, fig. 235, pl. 59 (1); Dai and Yang 1991: 465, fig. 235, pl. 59 (1); Shih 1994: 82, figs. 15, 16, 56-59.

Materials examined: Chuwei, Taipei County, 5 ♂♂ (CW 22.6-27.4 mm), May 17, 1996, NSYSU 960517; 1 ovig. ♀ (CW 25.9 mm), Aug. 20, 1996, NSYSU 960820; Chinshui, Hsinchu City, 3 ♂♂ (CW 26.8-30.0 mm), Nov. 4, 1995, NSYSU 951104; Haishanku, Hsinchu City, 1 ovig. ♀ (CW 27.9 mm), Apr. 8, 1996, NSYSU 960408; 5 ♂♂ (CW 17.3-31.2 mm), 4 ♀♀ (CW 18.9-28.6 mm), June 20, 1996; 1 ♂ (CW 26.0 mm), 9 ovig. ♀♀ (CW 19.4-31.6 mm), Aug. 19, 1996, NSYSU 960819B; 3 ♂♂ (CW 21.4-30.8 mm), 2 ♀♀ (CW 13.8, 15.8 mm), Oct. 28, 1996, 961028A; 4 ♂♂ (CW 16.0-24.0 mm), 3 ♀♀ (CW 16.1-22.0 mm), Nov. 28, 1996, NSYSU 961128; 2 ♂♂ (CW 23.4, 25.2 mm), Jan. 1, 1997, NSYSU 970101; 1 ♂ (CW 25.8 mm), 2 ♀♀ (CW 25.3, 28.3 mm), Mar. 1, 1997, NSYSU 970301; Kaomei, Taichung County, 1 ♀ (CW 19.0 mm), Oct. 28, 1996, 961028B; Shenkang, Changhua County, 1 ♂ (CW 27.4 mm), 1 ♀ (CW 19.7 mm), Oct. 24, 1995, NSYSU 951024; 1 ♂ (CW 21.4 mm), Dec. 28, 1995, NSYSU 951228; 1 ♂ (CW 23.0 mm), June 21, 1996, NSYSU 960621; 1 ♂ (CW 29.6 mm), 1 ♀ (CW 23.8 mm), June 22, 1996, NSYSU 960622; 2 ♂♂ (CW 26.8-30.7 mm), July 7, 1996, NSYSU 960707; 6 ♂♂ (CW 26.5-29.4 mm), 7 ♀♀ (CW 20.1-24.5 mm), July 9, 1996, NSYSU 960709; 5 ♂♂ (CW 28.3-33.3 mm), 6 ♀♀ (CW 14.0-24.3 mm), July 10, 1996, NSYSU 960710; 4 ♂♂ (CW 26.7-32.5 mm), 1 ovig. ♀ (CW 24.0 mm), July 15, 1996, NSYSU 960715; 1 ♂ (CW 13.2 mm), 1 ♀ (CW 21.0), July 16, 1996; NSYSU 960716; 4 ♂♂ (CW 26.4-30.3 mm), 2 ♀♀ (CW 20.5, 21.5 mm) (incl. 1 ovig. ♀), July 21, 1996, NSYSU 960721; 2 ♂♂ (CW 34.4, 34.6 mm), 2 ovig. ♀♀ (CW 25.4, 26.8 mm), Aug. 19, 1996, NSYSU 960819A; 2 ♂♂ (CW 25.0-27.7 mm), 3 ♀♀ (CW 24.2-28.5 mm), Oct. 24, 1996, NSYSU 961024A; 1 ♂ (CW 31.1 mm), Nov. 30, 1996, NSYSU 961130; Lukang, Changhua County, 2 ♂♂ (CW 24.7, 28.4 mm), date lost (see ***Remarks***), TMCD 28; 3 ♂♂ (CW 27.0, 28.8, 32.4 mm), May 24, 1994, TMCD 2841. Fangyuan, Changhua County, 2 ♂♂ (CW 20.0-24.4 mm), Oct. 24, 1996, NSYSU 961024B; Tungshih, Chiayi County, 2 ♂♂ (CW 21.1, 21.5 mm), 3 ♀♀ (CW 15.8-21.5 mm), Mar. 17, 1996, NSYSU 960317; 8 ♀♀ (CW 17.0-23.6 mm), 2 ♀♀ (CW 17.0, 18.9) (incl. 1 ovig. ♀), May 30, 1996; 3 ♂♂ (CW 18.8-19.5 mm), 4 ♀♀ (CW 13.5-20.3 mm) (incl. 1 ovig. ♀), Aug. 6, 1996, NSYSU 960806; Putai, Chiayi County, 7 ♂♂ (CW 20.5-29.0 mm), 7

Fig. 1. *Uca formosensis*. A, E, ♂, CW 31.1 mm, NSYSU 940926; B, ♀, CW 21.7 mm, NSYSU 960531; C, ♀, CW 26.5 mm, NSYSU 960805; D, ♀, CW 20.9 mm, NSYSU 960629; F, ♀, CW 21.4 mm, NSYSU 960428; G, ♂, CW 28.2 mm, NSYSU 951104; H, ♂, CW 26.8 mm, NSYSU 951104. A, dorsal view of male; B, C, D, dorsal view and color variation of female; E, F, front view of male and female; G, brachychelous chela; H, leptochelous chela.

♀♀ (CW 19.0-23.2 mm) (incl. 1 ovig. ♀), Mar. 30, 1996, NSYSU 960330; Chiku, Tainan County, 4 ♂♂ (CW 20.5-23.4 mm), 2 ♀♀ (CW 17.0, 21.7 mm), May 31, 1996, NSYSU 960531; 4 ♂♂ (CW 19.2-29.6 mm), 18 ♀♀ (CW 15.5-27.9 mm), June 29, 1996, NSYSU 960629; 5 ♂♂ (CW 17.9-28.0 mm), 6 ♀♀ (CW 18.0-26.5 mm) (incl. 2 ovig. ♀♀), Aug. 5, 1996, NSYSU 960805; 7 ♂♂ (CW 19.6-31.9 mm), 8 ♀♀ (CW 18.6-29.6 mm), Oct. 21, 1996, NSYSU 961021; 1 ♀ (CW 20.8 mm), Dec. 29, 1996, NSYSU 961229; Chingtsaolun, Tainan City, 1 ♂ (CW 31.1 mm), Sept. 26, 1994, NSYSU 940926; 2 ♂♂ (CW 24.2, 28.5 mm), Aug. 8, 1995, NSYSU 950808; 2 ♂♂ (CW 21.1, 21.9 mm), Mar. 29, 1996, NSYSU 960329; Chinglo, Penghu County, 2 ♂♂ (CW 30.8, 31.9 mm), Aug. 15, 1996, NSYSU 960815.

Diagnosis**:** *Male*: Front narrow; tip expanded; groove with anterior margin narrowly U-shaped; base moderately constricted (Fig. 2B). Anterolateral angles acute, produced forward. Anterolateral margins long, strongly developed, almost straight in most individuals, but some individuals showing variable degree of convergence (see ***Remarks***); turning at an angle into convergent, well-marked, dorsolateral margins (Fig. 2A).

Fronto-orbital margin almost straight. Carapace highly arched, branchial chambers strongly tumid.

Eyebrow broad internally, narrow externally. Suborbital crenellations rolled out in male, crenellations minute or absent except near outer angle. Orbital floor without mound and pile in male; suborbital region and upper pterygostomian regions naked in male (Figs. 1E, 2B).

Major cheliped with fingers flattened, smooth, pollex's lower margin and dactyl's upper one almost straight, not arched; cutting margins with distal 1/2 almost straight, without depression or enlarged teeth; proximal 1/2 with a shallow elliptic space; fingers with furrows very faint or absent. Outer manus with low, well-separated tubercles (Figs. 1G-H, 2E).

Minor cheliped with fingers longer than manus. Gape narrow, with very small blunt serrations and fine setae, dorsal margin of dactyl with brush of short setae, ventral margin of pollex with sparse setae; male without enlarged teeth in middle of gape (Fig. 2D) (see ***Remarks***).

Meri of 2nd and 3rd ambulatory legs wide, dorsal margin of 1st and 4th meri almost straight (Fig. 1A) (see ***Remarks***).

Gonopod with pore moderately large; anterior flange very narrow, distal tip tapering, beyond the tip of inner process; posterior flange broad, little curved, much wider than pore; inner process long, broad, thick, bent forwards at right angles; thumb of moderate length, not reaching base of flange (Fig. 3A-D).

Female: Most characters similar to those of male, except the following:

Anterolateral and dorsolateral margins strongly beaded. A definite boss, sometimes tuberculate, on carapace behind dorsolateral margin. Suborbital crenellations erect in female, crenellations strong, truncate, separate, increasing in size towards antero-external angle. Orbital floor with mound and pile; suborbital region and upper pterygostomian regions setose (Fig. 1F).

Minor cheliped of female with pair of enlarged teeth in middle of gape (Fig. 2C) (see ***Remarks***). Dorsal margin of meri of ambulatory legs slightly convex in female (Fig. 1B-D) (see ***Remarks***).

Gonopore in shallow sternal depression, rimmed postero-external quarter but not tubercular (Fig. 3E, F).

Measurements**:** See table 1.

Color in life**:** The color pattern of the carapace

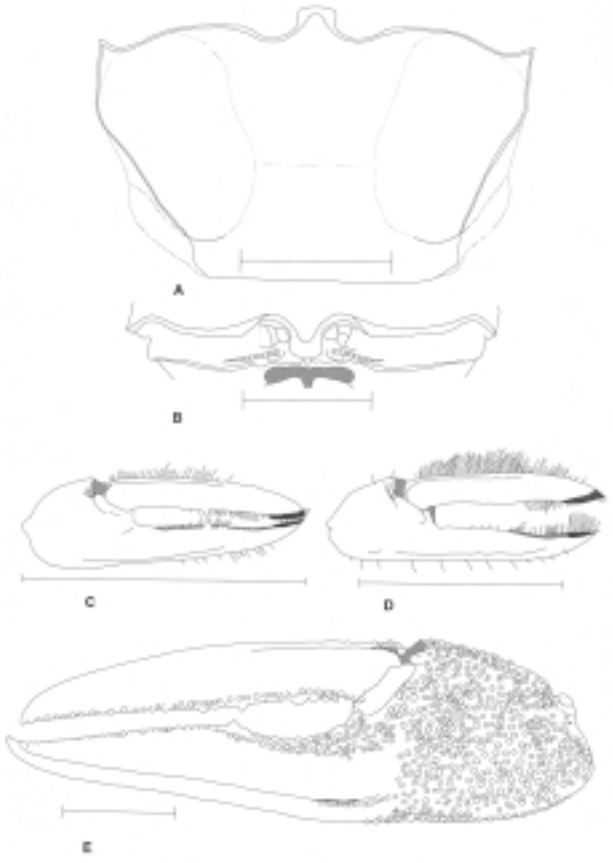

Fig. 2. *Uca formosensis*, carapace, front, major chela, and minor chela. A, B, D, E, ♂, CW 29.6 mm, NSYSU 960622; C, ♀, CW 23.8 mm, NSYSU 960622; A, carapace of left-handed male; B, anterior aspect of carapace of male; C, right minor chela of female; D, right minor chela of male; E, left major chela of male. Scale = 10 mm.

of most individuals of *U. formosensis* is dark brown with a white (or lighter) transverse band at the end of the carapace (Fig. 4A). Some individuals have many lighter patches on the carapace. Sometimes there are several darker patches on the white band (Fig. 4B-C). It was also found that some female individuals with different degrees of yellowish-white patches on the anterior carapace (Fig. 4D-G) at Chiku were also socially active (see ***Remarks***).

Fingers of major cheliped white; upper manus and carpus light brown, lower manus white to yellow, interface between upper and lower manus yellow, but reddish in young individuals; merus dark brown. Minor cheliped with fingers white or yellow. Ambulatory legs dark brown. White patches always present behind meri of 1st and 2nd (sometimes 3rd) ambulatory legs (Fig. 4H-I).

The white patches on the 3rd ambulatory legs

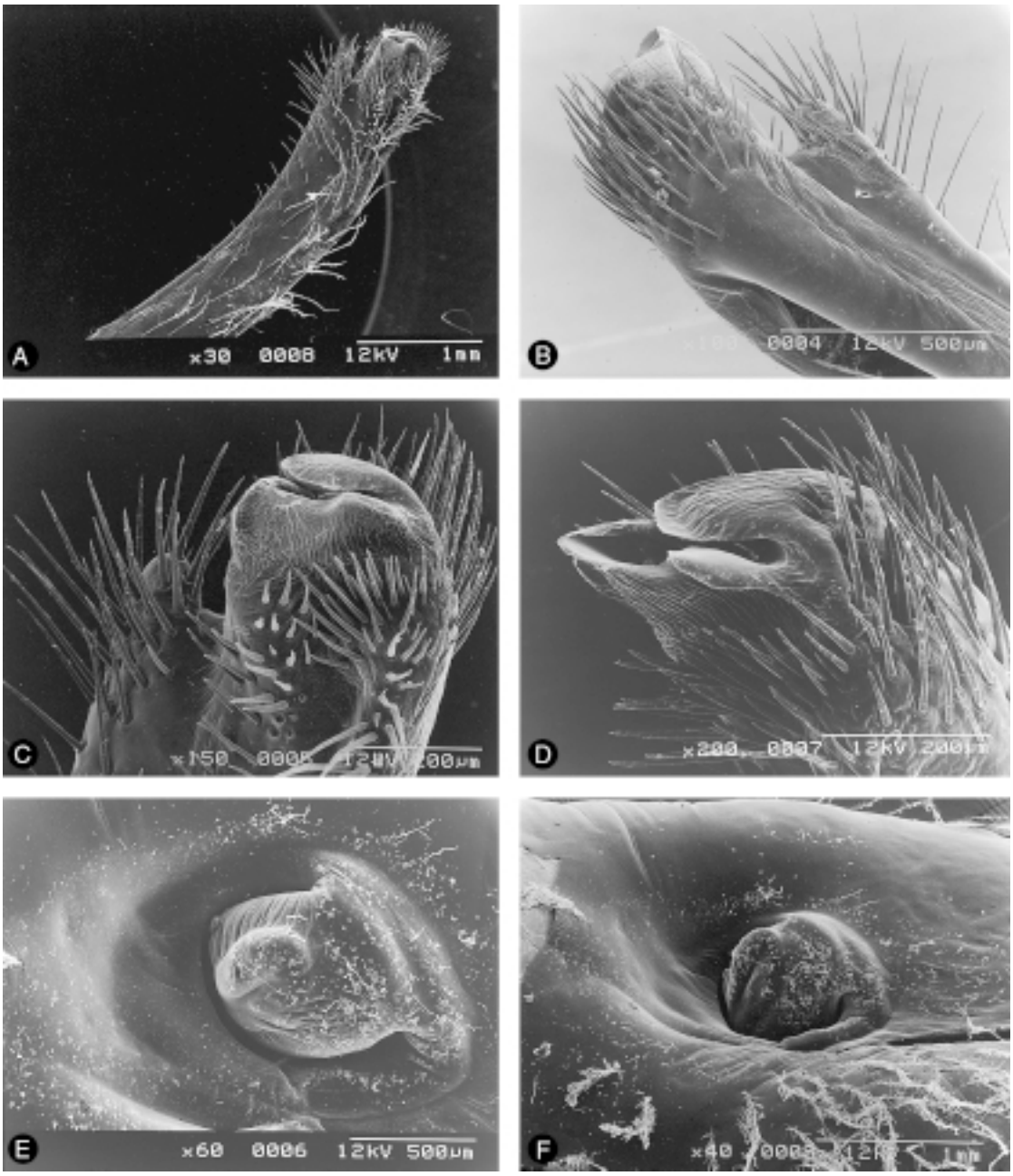

Fig. 3. *Uca formosensis*, gonopod and gonopore. A, ♂, CW 25.0 mm, NSYSU 961024; B, C, D, ♂, CW 17.2 mm, NSYSU 960620; E, F, ♀, CW 29.4 mm, NSYSU 961021. A, B, C, D, right gonopod; E, F, right gonopore.

were observed in 16 males and 2 females (one was ovigerous). The white patches of the ambulatory legs are very conspicuous when the male waves at the female with his back to her (see ***Remarks***).

***Distribution*:** Localities inhabited by *U. formosensis* in the present study are shown in Fig. 5, but habitats in some localities with previous records of *U. formosensis* have been destroyed, and the species can no longer be found there. The present distribution of *U. formosensis* is more restricted than before with the type locality damaged (see **DISCUSSION**).

***Habitat*:** *Uca formosensis* lives in diverse habitats. However, habitats with large populations are characterized by open and clean high intertidal mudflats with very clayey-muddy substrate and without mangroves. Small populations can sometimes be found on sheltered mudflats with some mangroves, mainly *Kandelia candel* or *Avicennia marina*. The typical habitat is covered by tides at least during the spring tide period. Consequently, temperatures of higher areas on the substrate can be as high as 40 °C. Nevertheless, there were many large chimneys built by *U. formosensis* on the hard hot surface (Shih 1997).

***Sympatric associates*:** *Uca formosensis* can generally be found sympatric with other ocypodids and grapsids, viz. *U. lactea lactea*, *Helice formosensis* Rathbun, 1931, *H. wuana* Rathbun, 1931, *U. arcuata*, and sometimes *U. vocans borealis*. However, it is sympatric with a different species assemblage, viz. *U. chlorophthalmus crassipes* (Adams and White, 1848), *U. lactea perplexa* (H. Milne-Edwards, 1837), *U. vocans borealis*, *U. dussumieri dussumieri* (H. Milne-Edwards, 1852), *U. arcuata, Helice* spp., *Scopimera* sp., and *Tmethypocoelis ceratophora* (Koelbel, 1897) at Chinglo, Penghu, probably because the habitat is different, with coarse sand and mud, which is atypical for *U. formosensis*.

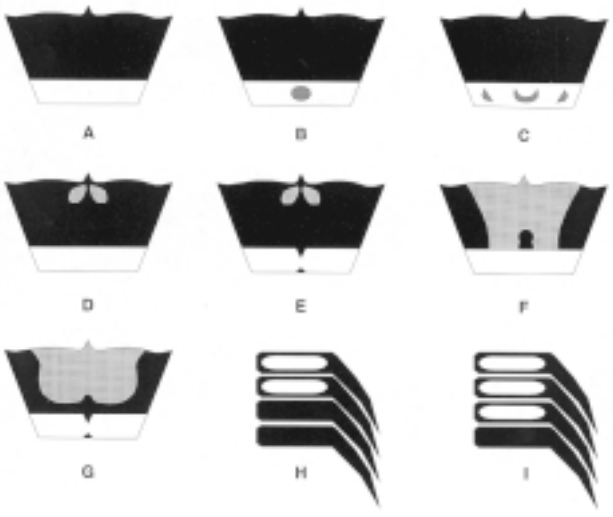

Fig. 4. *Uca formosensis*, color pattern variations of carapace and ambulatory legs. See text.

***Social behavior*:** Male *U. formosensis* shows a typical vertical waving behavior toward the female. Both surface and underground mating systems were found, even in the same population at the same time. In the underground mating system, after the male has successfully attracted a female into his burrow, he begins to build the chimney (Shih 1997, Shih et al. in preparation).

***Remarks*:** Two male specimens of *Uca formosensis* (TMCD 28) were deposited with other crab specimens of Maki and Tsuchiya (1923) in the Taiwan Museum. Only the locality "Lukang" and serial number "70" were found on the label. Unfortunately, the detailed information associated with the serial number was lost. However, it seems they were the specimens reported by Maki and Tsuchiya (1923) with a collection date in the 1920s.

Crane (1975: 83) stated, "It seems likely that *formosensis* is the northern, allopatric representative of *tetragonon*, a species that has not been recorded in this latitude." This supposition is no longer valid as *U. tetragonon* has since been recorded from coral reefs of southern (Nanwan, Wanglitung, and Houwan), eastern (Tulanwan), and northern Taiwan (Homei) (Ho et al. 1993) as well as from the Ryukyus (Sakai 1976) further north.

The anterolateral margins show variation in the degree of convergence, from gradually converging, almost straight, to diverging. This variation is evident in each of the populations surveyed. The degree of convergence of most individuals is restricted to between slightly converging and slightly diverging. Larger males generally have diverging anterolateral margins, being slightly more so on the side of the major cheliped (Fig. 2A).

There is generally an enlarged tooth on each fin-

Table 1. Measurements (in mm) of carapace width (CW) and propodus length (PL) of some special specimens

	CW	PL	Catalog number
Largest (brachychelous) male	34.9	78.4	NSYSU 960819A
Largest (leptochelous) male	31.9	80.6	NSYSU 960819A
Largest (ovigerous) female	31.6		NSYSU 960819B
Smallest (ovigerous) female	17.7		NSYSU 960806

ger of the female cheliped. However, some individuals show slight variations in this aspect. Some individuals have an enlarged tooth only on 1 finger; some have an enlarged tooth on 1 finger, a small tooth on the other; or are without a tooth on both fingers (2 females in Chiku specimens, NSYSU 960629). The female fingers without an enlarged tooth might be the result of regeneration (see **DISCUSSION**). In contrast, males always lack teeth on both fingers of the minor cheliped. However, 1 male (Chiku specimen, NSYSU 961021) has an enlarged tooth on the immovable finger of the minor cheliped.

The dorsal margin of the 1st and 4th ambulatory meri is straight, although it is slightly convex in females. However, it is different from Crane's description who stated that all ambulatory meri of females are broad.

Coloration of *U. formosensis* was not included in Crane's monograph, because living specimens were not examined (Crane 1975: 83, 467). Different coloration of ambulatory legs (Fig. 4H-I) is present in each population of *U. formosensis*. The white patches on the ambulatory legs of males are believed to help attract the female when he displays by vertically waving at her and with his back to her.

Some females collected at Chiku show a variety of the color patterns on the carapace (Fig. 4D-G). This population of *U. formosensis* inhabits an abandoned fish farm which is connected to the open estuary of the Tsengwen Creek by a large artificial tidal creek. Males and females were always found immersed in the wide shallow tidal creek inside the fish farm and were active. This is a peculiar habitat and an unusual habit not found in other populations of *U. formosensis*. In addition, no other species of fiddler crabs was found in this isolated habitat during the study period. Many crustaceans change their color by acquiring pigments from their diet (e.g., Kent 1901, Wilson 1987, Guarino et al. 1993, Woods and McLay 1996). Therefore, it is possible that the color pattern variation in the carapace observed at Chiku is caused by the composition of the local diet in the substrate. Further study is necessary to clarify this. After capture, the color patterns remained, but tended to become darker. This is consistent with Crane's observation (1975: 467).

Handedness and chela type

Totally 272 males were collected; 152 are right-handed (Fig. 1H) and 120 are left-handed (Fig. 1G). The number of right-handed and left-handed individuals is not significantly different ($p > 0.05$, binomial test with correction for continuity; Siegel and Castellan 1988: 43). A total of 206 individuals with brachychelous chela (Fig. 1G) and only 61 individuals with leptochelous chela (Fig. 1H) were found. Some "atypical" chelae among the male individuals were collected: 1 individual with a leptochelous dactyl and a brachychelous pollex; and 2 individuals with brachychelous chelae, but with the tip of the dactyl broken.

The leptochelous chela is a regenerated one in fiddler crabs (von Hagen 1962, Crane 1975, Yamaguchi 1994). The number of brachychelous individuals is about 3 times that of leptochelous ones (206: 61) in *U. formosensis*. However, whether this is caused by fighting between males (intra- or interspecifically) or by predation (other crabs or birds) is not known. *U. formosensis* is frequently observed to participate in an "interlace" fight (Crane 1975: 489) between 2 males, although chelae being lost was not observed. In 1 observation, when a specimen of *Helice wuana* rushed towards a young *U. formosensis*, the small fiddler crab plunged its

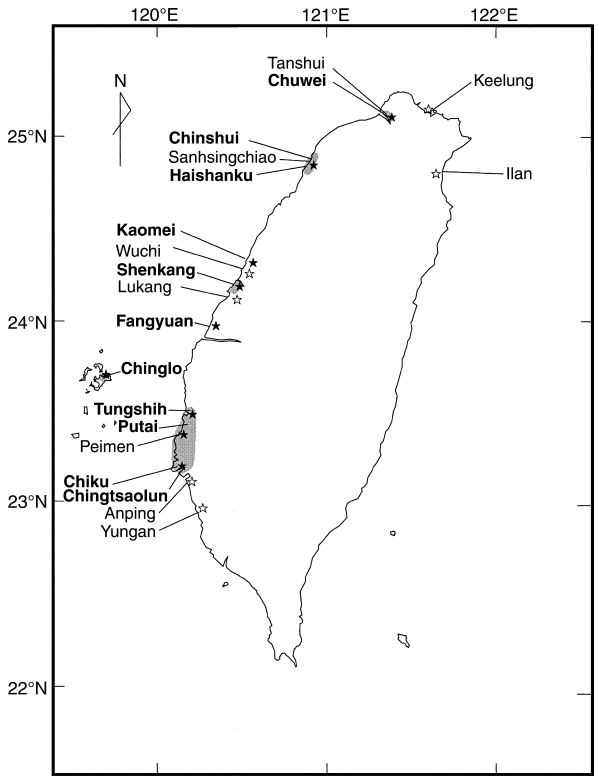

Fig. 5. Distributional records of *Uca formosensis*. Black stars (★) and place names in boldface represent habitats with active populations of *U. formosensis*; empty stars (☆) and place names in normal font represent habitats with no active *U. formosensis* populations found, although the species was formerly recorded at these locations.

major chela onto the leg of the *Helice* and then autotomized its chela.

DISCUSSION

The validity of *U. formosensis* belonging in the subgenus *Thalassuca* Crane, 1975

In Crane's monograph (1975), she proposed 9 subgenera under the genus *Uca*. However, Bott (1973) split the fiddler crabs into 10 genera in a preliminary revision that predated Crane's publication. Although Crane's scheme is well-defined and comprehensive, Bott's generic names have priority over Crane's subgeneric names (von Hagen 1976, Manning and Holthuis 1981, George and Jones 1982). However, some authors have followed Crane's subgeneric and/or subspecific names regardless (Barnwell 1982, Barnwell and Thurman 1984, Levinton et al. 1996, Sturmbauer et al. 1996). Here we temporarily retain Crane's scheme, because this problem cannot be resolved by the present study which treats just 1 species.

The subgenus *Thalassuca* Crane, 1975, has 3 members: *U. tetragonon*, *U. formosensis*, and *U. vocans*. According to Crane (1975), *U. vocans* consists of 6 subspecies: *U. vocans borealis* Crane, 1975; *U. vocans pacificensis* Crane, 1975 (= *U. neocultrimana* Bott, 1973); *U. vocans dampieri* Crane, 1975; *U. vocans vomeris* McNeill, 1920; *U. vocans hesperiae* Crane, 1975; and *U. vocans vocans* (Linnaeus, 1758). If priority is applied, *Thalassuca* Crane, 1975 must be replaced by *Gelasimus* Latreille, 1817 not *Mesuca* Bott, 1973 because the type species of *Gelasimus*, *Cancer vocans* Linnaeus, 1758 belongs in Crane's *Thalassuca* (Manning and Holthuis 1981).

The subgenus *Thalassuca* was defined by Crane (1975: 75) as "*Uca* with front narrow, antero-lateral margins short to absent; eyestalks slender; postero-lateral striae absent; no tubercles or other irregularities on orbital floor; suborbital margin erect, not rolled out, its crenellations always distinct and usually strong. Major manus outside rough with moderate to large tubercles; oblique ridge on palm never continued upward around carpal cavity; a long, lateral furrow sometimes present outside pollex, never on major dactyl. Serrations of minor cheliped absent or few and weak. Gonopod always with at least one flange well developed, without a projecting, distal tube; entire terminal portion often twisted. Gill on 3rd maxilliped with up to about 11 books in some individuals of each species. Female never with an enlarged tooth in cheliped gape".

Because only a few specimens of *U. formosensis* were preserved in museums worldwide (Crane 1975, Barnwell 1982), some taxonomic judgments had to be made before more material became available. After more specimens were examined, the placement of *U. formosensis* in *Thalassuca* now seems questionable (T. Yamaguchi and S.-L. Yang pers. comm.). Here we point out some important characters of *U. formosensis* that are inconsistent with the other 2 members of *Thalassuca*, *U. tetragonon* and *U. vocans* (Table 2).

***Handedness*:** The handedness of most species of male fiddler crabs is in about a 50: 50 ratio (Crane 1975, Yamaguchi 1994). This is also the case for *U. formosensis* (right: left = 152:120). Barnwell (1982), however, had concluded that *U. formosensis* is right-handed on the basis of only 5

Table 2. Comparison of some characters between species of the subgenus *Thalassuca* and *Uca arcuata* of the subgenus *Deltuca*

	U. tetragonon	*U. vocans*	*U. formosensis*	*U. arcuata*
Handedness	right-handed	right-handed	the same ratio	the same ratio
Minor cheliped gape of female	without an enlarged tooth	without an enlarged tooth	with an enlarged tooth on each finger	with an enlarged tooth on each finger
Carapace	little arched	little arched	highly arched	highly arched
Suborbital margin	erect	erect	rolled out in male, erect in female	rolled out
Oribital floor	naked	naked	naked in male, with mound and setose in female	with mound or ridge, sometimes setose in female
Habitat	low intertidal, sandy and/or rubble flat	low intertidal, sandy or muddy flat	high intertidal, muddy flat	middle to high intertidal, muddy flat

specimens preserved in the Smithsonian Institution (see **HISTORIC REVIEW**). Right-handedness is prevalent in the other 2 members of *Thalassuca*. Almost all males of *U. tetragonon* (see Barnwell 1982, Jones and George 1982, Ho et al. 1993, Yamaguchi 1994) and the 6 subspecies of *U. vocans* (see Green and Schochet 1972, Takeda and Yamaguchi 1973, Altevogt and Davis 1979, Williams and Heng 1981, Barnwell 1982, Jones and George 1982, Yamaguchi 1994) are right-handed. Some authors have suggested that handedness might help group fiddler crabs (Jones and George 1982, Yamaguchi 1994), so it is reasonable to question on the basis of handedness if *U. formosensis* is really a member of the subgenus *Thalassuca*. If *U. formosensis* is excluded from this subgenus, all members in the subgenus *Thalassuca* would be right-handed.

***Minor cheliped gape of female*:** One of the characters of Crane's *Thalassuca* was that the "... female [is] never with an enlarged tooth in cheliped gape" (1975: 75). This is not true of *U. formosensis* as it has an enlarged tooth on each finger of the minor cheliped (Fig. 2C).

Because the teeth of the fingers in the male's major cheliped always disappear when the cheliped regenerates (leptochelous chela) (Crane 1975, George and Jones 1982), it is possible that the absence of teeth on some toothed fingers of the minor cheliped is due to regeneration. In this study, some female individuals had lost a tooth on at least 1 finger and 1 individual had even lost both teeth (see ***Remarks***). Because only 2 female specimens were examined by Crane (1975: 597), it is possible that both these specimens had regenerated minor chelipeds.

***Anterolateral margin*:** The anterolateral margins of *U. formosensis* are relatively long compared with those of the other 2 members of *Thalassuca*. Although the anterolateral margins of the subgenus *Deltuca* are absent or short (Crane 1975: 21), the sole exception is *U. arcuata*, in which the anterolateral margins are long.

***Suborbital margin and orbital floor*:** The important characters of the subgenus *Thalassuca* are: erect suborbital margin, distinct and strong crenellations, and orbital floor without tubercles or any elevations (Crane 1975: 75, 619). The male and female of *U. vocans* and *U. tetragonon* are the same in the above characters. However, *U. formosensis* differs in that the suborbital crenellations are rolled out in males but are erect in females, with crenellations minute or absent in males but strong in females; and the orbital floor is without any elevations in males but with mound and pile in females.

***Carapace and habitat*:** From the degree of arching of the carapace, one can comment on the habitat of the species (Crane 1975: 451, 452). It is true that Crane predicted that the habits of *U. formosensis*, with its tumid branchial regions, was similar to that of *U. arcuata* and other species subjected to periodic desiccation (p. 84). *U. formosensis* lives on the high intertidal flat which is always not flooded by tides for 4 or 5 days during the neap tide period and with the substrate of its habitat very clayey-muddy (Shih 1997). In contrast, the habitat of the other 2 members of the subgenus *Thalassuca*, *U. tetragonon* and *U. vocans*, is muddy sand or shell-encrusted rocks and dead coral in the middle or low intertidal region (Table 2) (Crane 1975: 76, 79, 88, 532, Hartnoll 1975, Nakasone 1977, Icely and Jones 1978, Frith and Brunenmeister 1980, Ho et al. 1993, Takeda et al. 1996).

For the above reasons, it is unsatisfactory to retain *U. formosensis* in the subgenus *Thalassuca* Crane, 1975. Due consideration of all the characters listed above suggests that it is actually more similar to members of the subgenus *Deltuca* Crane, 1975.

In Taiwan, the subgenus *Deltuca* Crane, 1975, contains 3 species, *U. dussumieri dussumieri*, *U. arcuata*, and *U. coarctata coarctata* (H. Milne-Edwards, 1852). If priority is applied, *Deltuca* Crane, 1975, must be replaced by *Tubuca* Bott, 1973, because its type species, *Gelasimus urvillei* H. Milne-Edwards, 1837, belongs in Crane's *Deltuca* (von Hagen 1976).

The subgenus *Deltuca* was defined by Crane (1975: 21) as "*Uca* with front narrow, antero-lateral margins short to absent, eyestalks slender, postero-lateral striae absent at least in males. Major manus outside rough with tubercles that are usually largest near pollex base; oblique ridge on palm never continued upward around carpal cavity; longitudinal grooves along outside of both pollex and major dactyl. Postero-dorsal surface of ambulatory meri with simple tubercles, not with tuberculate striae vertically arranged. Gill on 3rd maxilliped small, without books. Females with rare exceptions have a pair of enlarged teeth in gape of at least one chela".

To decide the taxonomic status of *U. formosensis*, i.e., whether it belongs in the subgenus *Deltuca* or a new subgenus (S.-L. Yang pers. comm.), more information on its morphology, behavior, ecology, and biochemistry and that of related species are required.

Updating Crane (1975)

Some additional errors regarding *Uca formo-*

sensis in Crane's monograph (1975) are corrected as follows.

(1) Crane (1975: 83) stated that, "I was unable to find it in northwest Taiwan at the type-locality in its only known habitat". The type locality, Lukang (Rokko), is located in central Taiwan, not in northwest Taiwan.

(2) Crane (1975: 83) stated that, "According to Takahasi (1935), it lives on muddy shores near low tide level in the neighborhood of a river". The statement that *U. formosensis* lives near the low tide level was not found in Takahasi's report. In fact, *U. formosensis* lives near the high tide level.

(3) Crane (1975: 84) stated that, "According to Takahasi (1935), *formosensis* occurs on muddy beaches near the mouth of the Tamsui River, both in clayey mud with *arcuata* and in the "vegetation" zone, associating with *vocans* and *arcuata*". The original statement in Takahasi's paper, however, was "... in clayey mud with *arcuata* and *vocans* and in the vegetation zone with *arcuata*" (Takahasi 1935: 79, Table 1).

Distribution and conservation of *Uca formosensis*

In Taiwan, *U. formosensis* is patchily distributed along the western coast. The northern limit of its distribution is restricted from Ilan and Keelung to Tanshui. Its population in Tanshui is small, which may be caused by overgrowth of mangroves (see below). The southern limit is restricted from Yungan and Anping to Chingtsaolun. It is under pressure by the overgrowth of mangroves and development (Shih 1997).

Its generally diminishing population is caused by construction of illegal fish farms (e.g., in Shenkang and Chingtsaolun). In addition, the type locality, Lukang, was damaged by the building of an industrial park, and no specimens have been found there since May 24, 1994 (see ***Material examined***). Localities with large populations, Haishanku, Shenkang, and Chiku, however, are under pressure through the building of industrial parks or landfills (Shih 1997).

Some habitats of *U. formosensis* are under pressure by the overgrowth of mangroves, e.g., *Kandelia candel*. Mangroves change the substrate of the habitat and, as a result, *U. arcuata* ends up competing with *U. formosensis*. It is possible that Crane was unable to find *U. formosensis* in Tanshui in 1963 because *K. candel* was thriving there (Shih 1997).

As an endemic and endangered species, *Uca formosensis* must be protected immediately. Four approaches are suggested for its conservation. First, development (construction of illegal fish farms, highways, industrial parks, and landfills, etc.) on the mudflat habitats of *U. formosensis* must be avoided. Second, the replanting of mangroves by government officials or the public should be prohibited. This action is generally glorified in the media, but in fact, it destroys many vulnerable species living on the mudflat. Third, we suggest that *Uca formosensis* be included in the list of protected species of the Wildlife Conservation Law, R.O.C. Finally, more research funding for *U. formosensis* should be provided, especially since its larval morphology, genetics, behavior, and ecology remain mostly unknown.

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Appendix:

The Chinese names of localities used in the context in contrast to Wade-Giles Romanization are listed as follows:

Romanization	Chinese name
Anping	安平 (in Tainan City)
Changhua County	彰化縣
Chiayi County	嘉義縣
Chiku	七股 (in Tainan County)
Chinglo	青螺 (in Penghu County)
Chingtsaolun	青草崙
Chinshui	浸水
Chuwei	竹圍 (in Taipei County)
Fangyuan	芳苑 (in Changhua County)
Giran	宜蘭 (= Ilan)
Haishanku	海山罟
Homei	和美 (in Taipei County)
Houwan	後灣 (in Pingtung County)
Hsiangshan	香山 (in Hsinchu City)
Hsinchu City	新竹市
Hsinchuangtzu	新庄仔 (= Yungan)
Ilan County	宜蘭縣
Kaohsiung County	高雄縣
Kaomei	高美 (in Taichung County)
Keelung City	基隆市
Keelung River	基隆河
Lanyang Creek	蘭陽溪 (in Ilan County)
Lanyu (Orchid Island)	蘭嶼 (in Taitung County)
Lukang	鹿港 (in Changhua County)

Romanization	Chinese name
Nanwan	南灣 (in Pingtung County)
Peimen	北門 (in Tainan County)
Penghu County	澎湖縣
Pescadores	澎湖 (= Penghu)
Pingtung County	屏東縣
Putai	布袋 (in Chiayi County)
Rokko	鹿港 (= Lukang)
Sanhsingchiao	三姓橋 (in Hsinchu City)
Shenkang	伸港 (in Changhua County)
Taichung County	臺中縣
Taihoku	臺北 (= Taipei)
Tainan City	臺南市
Tainan County	臺南縣
Taipei County	臺北縣
Tamsui	淡水 (= Tanshui)
Tanshui	淡水 (in Taipei County)
Tansui	淡水 (= Tanshui)
Tatu Creek	大肚溪
Tsengwen Creek	曾文溪
Tulanwan	都蘭灣 (in Taitung County)
Tungshih	東石 (in Chiayi County)
Wanglitung	萬里桐 (in Pingtung County)
Wuchi	梧棲 (in Taichung County)
Yungan	永安 (in Kaohsiung County)

臺灣特有種招潮蟹—臺灣招潮（甲殼綱：十足目：沙蟹科）之形態修訂與生態觀察

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臺灣招潮是臺灣之特有種招潮蟹，過去由於保存於國外博物館的標本很少，造成許多分類上的錯誤，因此有必要針對歷來文獻中的誤解之處加以訂正。 Crane 在 1975 年把臺灣招潮歸類於海招潮亞屬 (subgenus *Thalassuca*) 之中，然而，許多臺灣招潮的重要特徵—雄蟹螯足左右性的比例、雌蟹小螯兩指間的大齒、前側緣、眼下緣、眼窩底部、背甲的隆起程度、棲所位置、基質成份—均與海招潮亞屬的另兩個成員 (四角招潮 *U. tetragonon* 和呼喚招潮 *U. vocans*) 很大的差異, 因此提議臺灣招潮應該排除在海招潮亞屬之外。本報告除針對臺灣招潮的分類地位做修訂之外，並整理歷年來對臺灣招潮的研究情形、在臺灣本島和澎湖地區的分布狀況、種內形態的變異（短細螯的比例）、活體的顏色、以及其他對臺灣招潮誤解之處的訂正。

關鍵詞：螯足左右性，螯型，體色，分布，研究歷史。

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